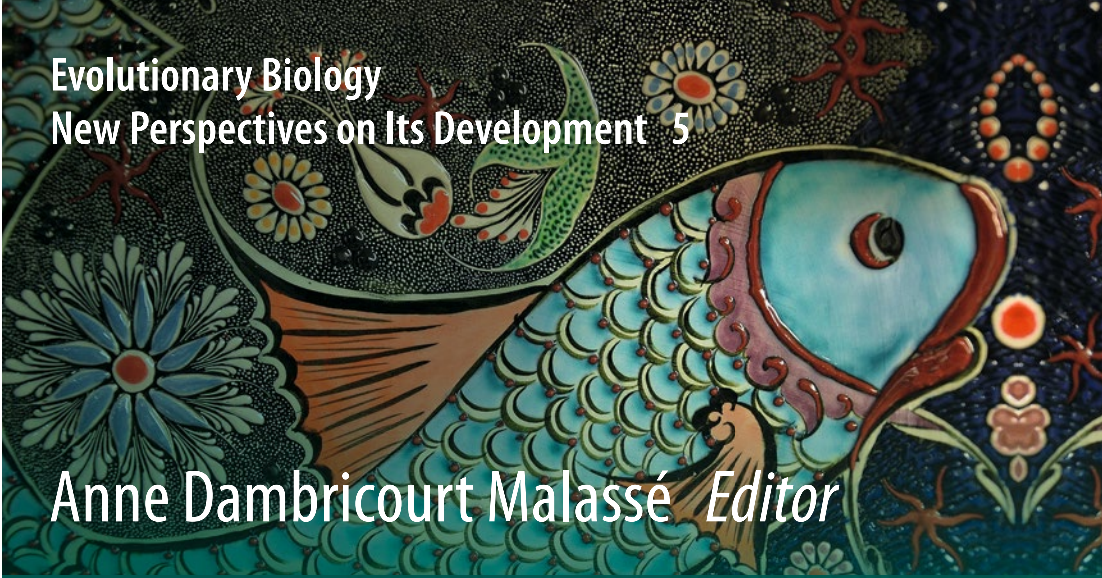

Evolutionary Biology
New Perspectives on Its Development 5

Anne Dambricourt Malassé *Editor*

Self-Organization as a New Paradigm in Evolutionary Biology

From Theory to Applied Cases in the Tree of Life

Springer

Evolutionary Biology – New Perspectives on Its Development

Volume 5

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* * *

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Editor

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ISSN 2524-7751 ISSN 2524-776X (electronic)
Evolutionary Biology – New Perspectives on Its Development
ISBN 978-3-031-04782-4 ISBN 978-3-031-04783-1 (eBook)
https://doi.org/10.1007/978-3-031-04783-1

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The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

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Part II Modernity of Self-Organization and Emerging Paradigms

1

Introduction: Understanding the Origins and Evolution of Living Organisms—The Necessity of Convergence Between Old and New Paradigms

Anne Dambricourt Malassé

> For several decades now, the field of evolutionary biology has been envisioned as organized around a profound and fundamental divide: theories relying on strong selective factors and those appealing to weak ones only [...]. This Introduction calls for a new and more consistent paradigm that would make sense of the overall development of evolutionary biology, one based on a realignment of the alliance between all partners pursuing research in this area.
> —*Richard Delisle (2021).*

Abstract

Global warming, the Anthropocene concept (Hamilton C, Nat News 536(7616): 251, 2016), the sixth mass extinction (Ceballos et al., PNAS 114(30):E6089–E6096, 2017), and the rapid progress in astrobiology looking for primitive life forms are raising the awareness of the actors of society toward evolution as the prime reality without which neither the biodiversity nor our species would exist, and our civilizations survive. This discernment leads us to a better understanding of the processes at the origin of the organization of dynamic structures and their reproductive properties, from the smallest cellular unit to the most complex interactions within the organism and then between organisms for the same unit

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_1

of time and space. This awareness also encourages us to discern, over very long geological and cosmic time scales, principles of self-organization of complex systems and generic laws of adaptation and complexification.

Keywords

Life · Evolution · Self-organization · Complexity · Emergence · Memory · Transdisciplinarity · Paradigms · Modeling · Epistemology · Basic and applied research

1.1 Introduction

The transformism formulated by Jean-Baptiste Lamarck in 1801 at the National Museum of Natural History, Paris, and the "natural selection" formulated by Charles Darwin in 1859 were the premises of a general systems theory (Bertalanffy 1968), necessary to understand the self-organized processes with the transmission of acquired characters, but they did not master the physical explanations for abiogenesis or the emergence of the cellular cycle, the beginning of life. Since then, the development of technics and methods of knowledge acquisition, as well as critical thinking, have made it possible to develop numerous models for the distinct levels of organization, thanks to physical, chemical, thermodynamics, and mathematics formulations, each one questioning the analytical processes creating order and stability, but also instabilities with innovative emergences, up to the level of reflexive consciousness and its creative abilities.

The sciences concerned with time (instant, duration, memory), energy (conservation, dissipation), form (mathematics, physical laws), and signals (information) had their precursors with Ernst Haeckel (1834–1919), Henri Bergson (1859–1941), D'Arcy Wentworth Thompson (1860–1948), Alexandre Oparin (1894–1980), John Haldane (1892–1964), Claude Shannon (1916–2001), René Thom (1923–2002), and Ilya Prigogine (1917–2003), among other remarkable theorists of the nineteenth and twentieth centuries. Their research has contributed to the development of new theories and paradigms, such as the deterministic Chaos theory with nonlinear dynamic systems, near or far from equilibrium in living phenomena: dissipative structures and geometric and dynamic fractals. Cybernetics in systems theory developed during the twentieth century and applied to robotics or nonliving natural phenomena help to distinguish the living properties from the artificial intelligence (AI) created by the human mind. AI is cut off from the irreversible processes of biological evolution, which have been going on for 4 billion years. Human biology and cognitive abilities emerge from this, with the trace of this evolution in each cell, that a robot even hybridized with a human cell will never have. A robot is the artificial product of mathematical knowledge and not an innovation of biological evolution. For this reason, a fundamental reflection is necessary to discuss self-organization not only in biological ontogeny, well-accepted, but also in evolutionary gametogenesis, which is much rarer and that raises difficulties at a conceptual level upstream of biological processes. Such difficulties are the processes of emergence, which become explicit with the origins of life.

Those scientific developments have been slowly integrated into the life sciences, to model the morphogenesis, the regulation of homeotic genes in the control of embryogenesis, the phylogenetic stability of ontogenetic geometric trajectories, the emergence processes, etc. The transdisciplinarity developed by Edgar Morin (Rigolot 2020) for half a century is a forthcoming method of the twenty-first century, allowing for the juxtaposition of such different fields of knowledge, in the acceptance of their differences and without mutual exclusion. The origins of life created the evolutionary properties of gametogenesis, and ontogeny and phylogeny are thus associated in recursive loops since phylogeny of gametes has created a great variety of ontogeny.

The volume divided into two parts does not claim to be exhaustive as the diversity of models varies according to the scales studied. Rather, it is meant to be representative of the immense scope of theoretical knowledge in need of attention, requiring a combination of open-mindedness, rigor, reflection, and the search for complementarity between explanatory models. These advances concern all scales of time and space in living systems, from complex molecular interactions and productions (memorized by transmission or innovative) to instinct, intuition, and memory until the self-reflexive consciousness.

The first part brings together chapters devoted to the modern relevance of nineteenth- and twentieth-century theories. The origins of life are analyzed since the abiotic phase with Georgy Levit and Uwe Hossfeld revisiting Ernst Haeckel (1834–1919) (Chap. 2). The authors recall that Charles Darwin never proposed a theory to understand the transition between an abiotic molecular environment and the formation of unicellulars necessary for the credibility of transformism. Ernst Haeckel postulated the spontaneous generations of monera, the precursor of Haldane-Oparin hypothesis, "we reconstruct Haeckel's theory of abiogenesis as a self-organization theory and demonstrate its importance as an early attempt to discuss the origin of life in the post-Darwinian era." In Chap. 3, Adam Scarfe develops the current influence of D'Arcy Thompson (1860–1948) calling in mind his Aristotelian and Kantian thinking patterns and his "physico-mathematical" approach of morphogenesis. The author refers to the Cambrian explosion under the angle of self-organized complex systems, referring to autopoiesis, teleology, and the hypothetical scenario of paleontologist Simon Conway Morris (1988) that "serves as a concrete example of how physico-geometrical factors entrain and/or present constraints that may canalize the behavioral selections of organisms."

Ilya Prigogine (1917–2003) has demonstrated the compatibility between the production of entropy and the spontaneous organization of a dynamical system. These are the dissipative structures far from thermodynamic equilibrium. Since then, the Brussels school of thermodynamics has multiplied the examples of physicochemical mechanisms whose behaviors resemble those of a living being engaged in an irreversible growth, the time arrow of life fighting against disorganization and death. Nonliving dissipative structures show that physicochemical components can generate complex dynamic organizations ordered in their own space and according to their environment. In Chap. 4, Dilip Kondepudi, James Dixon, and Benjamin De Bari describe the remarkable formation of a worm-like structure capable of displacement. "We will see how some fundamental traits such as end-directed behavior, self-healing, and mutations, can be described in thermodynamic terms, as phenomena in self-organized non-equilibrium systems, called dissipative structures."

The step of life requires properties missing in crystals that of self-memorization. A self-organization could not reproduce itself without its own memorization and the level of energy allowing the emergence of both its complexity and stability. The conditions are at least that of concentration thresholds of "islets" of complexities and energetical and informative interactions in permanent search of equilibrium. Those "islets" were composed of molecules whose properties allowed them to be recognized by other molecules to reproduce their information content, such as RNA and DNA, able to form membranes, produce energy, and synthesize proteins. Abiogenesis is a growing interest thanks to the search for exoplanets and studies of ancient Martian lake deposits with analysis of algal-like biota. "Our morphological and morphometrical investigations (. . .) suggest the presence of remnants of complex algal-like biota, similar to terrestrial procaryotes and/or eukaryotes; possible microorganisms that, based on absolute dating criteria used by other scholars, lived on Mars about 2.12 ± 0.3 Ga ago" (Rizzo et al. 2021).

Understanding the dynamics of self-memorizations still has a long way to go, with the models of dissipative structures and basins of attraction and their attractors. The diversity of unicellulars and their chemical–energetic environments have favored the Cambrian explosion with the emergence of multicellular organisms. Chapter 5 addresses this new threshold in the evolution of life with Valeria Isaeva. The author follows the arrow of negentropic time by comparing the current cyanobacteria (colonial and filamentous prokaryotes) and the metazoans such as sea urchins and analyzes the physical properties (forces) that constrain the morphogenesis of an embryonic body plan (or archetype). The aim is a discussion to identify the correlations between genome and phenotype that determine the body plan, from the molecular scale to the organs, thanks to a multidisciplinary approach introducing forms, energy, and topology according to René Thom (1923–2002). Indeed "the central problem of topology is that of reconstructing the global from the local" (Papadopoulos 2020), Thom's mathematics allows a more precise explanation of self-constrained dynamical systems and the emergence of new body planes coherent on the different spatial and temporal scales of ontogeny.

The first part ends with Chap. 6 on questions raised by Henri Bergson (1859–1941) still relevant: Stephen Robbins comes back to *Creative Evolution* (1907–1911) and "a pivotal discussion, the extreme complexity of instinctual behavior" such as Hymenoptera, which "'knows' precisely the three locations of motor–neuron complexes at which to sting a cricket such that it is paralyzed." These observations require mechanisms of analysis and recognition of signals, therefore previous memories before finding innovative solutions: "Any theory of evolution, be it selection, self-assembly, or self-organization, is equally bound to address not only the origin problem of an organism's structure but the correlated functional problem of instinct." The problem extends to intuition and memory and requires a consensus on the nature of consciousness, understood as a network of exchanges of signals, correctly identified, and therefore previously learned, memorized, and transmitted. Such complex processes have recently been described in the unicellular *Physarum polycephalum* (Broussard et al. 2019).

The second part of the volume presents contemporary models dealing with self-organization. Werner Arber describes harmless intestinal bacteria showing that "biological evolution occurs in microorganisms by consecutive steps of genetic variation [which] can be attributed to a process of self-organization that contributes to the permanent creation of appropriate biological capacities" (Chap. 7). Understanding the evolution of organogenesis under conditions of instability requires the distinction between cybernetics and living organisms affected by unpredictable fluctuations of global equilibrium and the ability of self-reorganization since fertilization. In Chap. 8, Stuart Newman discusses the concept of self-organization since the teleological formulation by Immanuel Kant in "*Critic of Judgement*" (1790) making the distinction between self-organization of non-living systems, living beings (embryogenesis), and the evolutionary processes that changed embryonic development. The concept has progressively replaced the metaphor of genetic program encoded in the DNA inspired by cybernetics in the 1950s. The emergence of new embryogenesis is not the one of a genetic program that assumes knowledge of the end (the final stage).

Life and the evolution of living organisms are not programmed robots, and fluctuations are innovative parameters that cannot predict bifurcations, but the complexity of gametes still misunderstood allows the reorganization of the ontogenetic memory and its hereditary transmission. Andrei Granovitch is engaged in a critical analysis of the synthetic theory (Neo-Darwinian doctrine) in which the notion of a highly integrated metastable system is missing, underlying that concept varies according to the scale of observation and regarding different evolutionary problems, adaptation, or transformation. In this Chap. 9, the author proposes to remove the doubt by unifying the distinct levels in a dynamical and dissipative system or morphoprocess and "a change of the evolutionary paradigm" to an "extended evolutionary synthesis."

Chapter 10 addresses self-organization in the plant kingdom with the concept *of* biosemiotics, or exchanges of signals between animals and their environment, elaborated in the 1930s by the ethologist Jakob von *Uexküll (1864–1944) and his concept of Umwelt* (Uexküll 1982). Marc-Williams Debono confronts the paradigm with his work based on pioneering phytoelectrography experiments. The results demonstrate the essential role of the electrome within the dynamic coupling between the plant and its singular milieu. These new interfaces open a new field of investigation by revisiting the concepts of plant cognition and more generally of bio- or eco-semiotics.

The quantum world is in permanent agitation, but the long durations of cosmogenesis and biogenesis show universal principles of order or of structural stability (Bois 2002), which allow distinguishing a chronology, a continuity between two different instants and not a stochastic dispersion without reference or information stabilized and reproducible. This information refers to nuclear forces and implies exchanges with the electronic orbital as developed in the nuclear–electronic orbital (NEO) approach (Hammer-Schiffer 2021).

Diogo Queiros-Condé, Jean Chaline, and Ivan Brissaud analyze in Chap. 11 a log-periodic law by showing its meaning and its relationship with fractality described by quantifying its length, time, and mass. Relying further on the work of Louis de Broglie's "hidden thermodynamics of the particle," they introduced kinetic–thermal chaining of lineage evolution that allows a fractal and quantum thermodynamic description of log-periodicity, which leads to what could be called a "*quantum thermo-fractality" of the evolution of systems, especially species, astronomical, economic, historical, artistic, and social.*

Chapter 12 presents the embryonic and phylogenetic origins of the vertical organization of our species, of which permanent bipedal locomotion is one of the many postnatal consequences (Anne Dambricourt Malassé). This discovery is replaced in its historical context that of the classification of species with Georges Buffon and Jean-Baptiste de Lamarck with the theory of evolution, two characters who have profoundly marked the naturalist tradition of the National Museum of Natural History (Paris). The discovery highlighted a dynamic architectural and morphogenetic unity between dental occlusion and the orientation of the axial endoskeleton that supports and protects the central nervous system from the brain stem. The process was demonstrated as early as 1987. The phylogeny matches with the curve of the increasing complexity of the brain, but the strengthening occurred according to a succession of long stable periods followed by increasing angulation thresholds. The first stage of the verticality was the *Hominidae* (vs semi-erect *Panidae* and *Pongidae*), the last one being ours (sapiens). The stability of the evolutionary trajectory does not conform to divergent representations of chaotic bifurcations and allowed us to infer memorization properties specific to gametes. The emergence of the operating chains at the threshold of verticality called here the *cerebro-cerebellar Rubicon*, and the symbolic thought would result in the integration of the cerebellum in the loops of cognitive reflection of the brain, necessary for the control of its balance, the stability of the organism, and to anticipate the fall.

Chapter 13 closes the volume with Edgar Morin who has devoted his life looking into human nature and its singularity in the evolution of life, namely the highest evolutionary degree of the reflexive consciousness of the world and oneself. His method is the most extensive transdisciplinary approach that can be conceived, from quantum mechanics to cybernetics, and human societies to ecosystems and reflexive consciousness. His approach is unified by a definition of the complexity that recognizes through the antagonisms, the manifestations of a single reality that assimilates these conflicts by self-organizing recursive loops, and from which new properties emerge. Fundamental research attempts to grasp these properties at the basis of emergence, and the mind, then, notes the ever-widening extent of the unknown of which it is itself a stakeholder, emerging from universal evolutionary creativity. Reflexive self-consciousness cannot objectively abstract from it. Confronted with all scales of its complexity, the awareness of the limits of the consciousness is a recognition of its mystery that returns this last to its links with the evolution of the living complexity and those processes of emergence.

These 13 chapters illustrate the diversity of evolutionary processes according to the space-time scales considered, as well as the relevance of the avant-garde schools of thought during the nineteenth and twentieth centuries in explaining the processes of self-organization. Open to the physics of chemistry, to the thermodynamics, mathematics, then cybernetics, and quantum mechanics, their common denominators are the interactions between particles, atoms, and molecules, ordered into their form according to energy levels, capable of association, source of biochemical innovations with the natural creation of autonomous systems, and consequently a complexification of their environment and interactions. The concept of natural selection has paved the way to their discovery for an even finer approach to the threshold of the emergence of life and the modalities of the self-reproduction of unicellular that imply preexisting self-memorization properties. Those modalities have allowed adaptation to their environmental diversifications, fluctuations, and complexified interactions, and then emergences of complexified organizations into multicellular organisms. The concept of natural selection nevertheless is devoid of these looping processes of integration and self-amplification and does not match the natural logic of the creative complexity with memorization properties. Such living properties may react to the risks of Anthropocene extinction, thanks to innovative creativities, but also to the memory of processes proper to the different lineages, which were useful for their survival in the past.

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Part I

The Modernity of Old Paradigms

2 Self-Organization Meets Evolution: Ernst Haeckel and Abiogenesis

Georgy S. Levit and Uwe A. Hossfeld

Abstract

Although Darwin proposed a logically coherent theory of evolution, which presupposed the natural occurrence of initial life forms, he never offered a theory of the origin of life. This task was instead taken up by his German pupil Ernst Haeckel. In contrast to Darwin, Haeckel paid lots of attention to abiogenesis. Already in his first major Darwinian book, *Generelle Morphologie* (General Morphology), he postulated the origin of life on Earth by way of *archigonia*, i.e., spontaneous generations of *monera* (the most primitive structureless microorganisms) directly from inert matter. For Haeckel, all living organisms on earth evolved from monera, and until his very last publication, he admitted the initial occurrence of monera was a repetitive event; i.e., the very initial evolution was polyphyletic. This created a tension between his monistic and pro-Darwinian tendency toward strictly monophyletic explanations on the one hand and his theory of abiogenesis on the other hand. Essentially, Haeckel's concept was a self-organization hypothesis built into the framework of Darwinian theory, and it fits into the more comprehensive doctrine of Haeckelian philosophical monism as well. Although it appears archaic from the modern viewpoint, Haeckel's theory of abiogenesis contributed to the growth of experimental studies of abiogenesis in the early 1920s—for example, in the development of the Oparin–Haldane hypothesis. In his book, *The Origin of Life*, Aleksandr Oparin explicitly mentions Haeckel and discusses Haeckel's concept of abiogenesis in some detail. In this chapter, we reconstruct Haeckel's theory of abiogenesis as a self-organization theory and demonstrate its importance as an early attempt to discuss the origin of life in the post-Darwinian era.

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_2

Keywords

Abiogenesis · Ernst Haeckel · Self-organization · Evolution

2.1 Introduction

Ernst Haeckel is known, first of all, as a crucial figure in the growth of Darwinian biology in the nineteenth century—as the "German Darwin" (Fig. 2.1). He was undoubtedly the major figure of the first Darwinian revolution in German lands and, arguably, on the continent as a whole. In his time, more people worldwide learned evolutionary theory from his publications than from any other sources, including Darwin's own writings (Richards 2018). Haeckel's popular scientific *Natural History of Creation* went through 12 editions, and *The Riddles of the Universe* sold more than 650,000 copies, "making it the most successful work of popular science in German history" (Finkelstein 2019). He defended and developed the Darwinian theory with unmatched passion and energy and created a conceptual framework within which the majority of Darwinians worldwide worked over subsequent decades. Contemporary biology and related sciences are unthinkable without terms

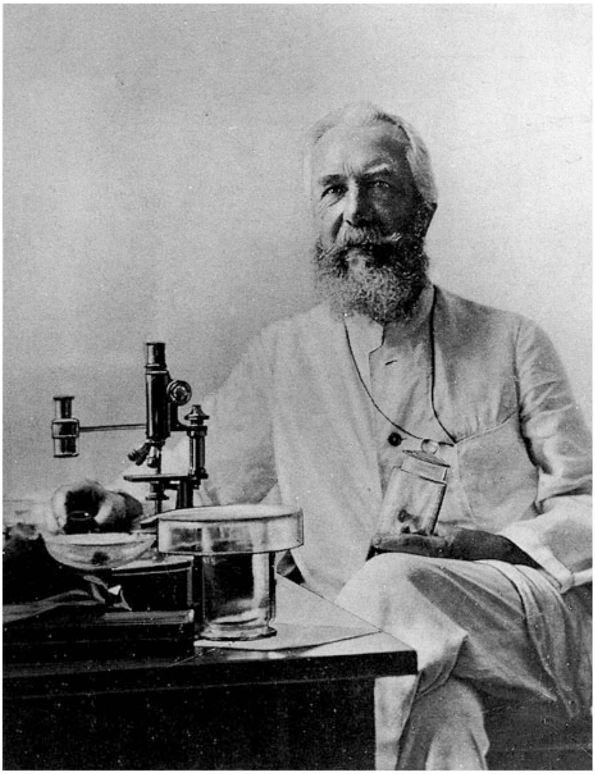

Fig. 2.1 Ernst Haeckel in his laboratory in the Buitenzorg Botanical Gardens on the Island of Java, 1901 (Courtesy: archive U. H.)

and concepts introduced by Haeckel, such as “phylogeny,” “monophyletic,” “polyphyletic,” “ontogeny,” “biogenetic law,” or “ecology.” Moreover, his novel theories were encouraged and admired by Darwin himself (Levit and Hossfeld 2019). It was Haeckel who crucially contributed to the visualization of the Darwinian theory by designing multiple “phylogenetic trees” reflecting evolutionary pathways of various organismic groups, including humans.

In addition to being Darwin’s most influential and faithful disciple on the continent, Haeckel also significantly broadened Darwin’s scientific agenda. While Darwin largely constrained himself to the establishment of the theory of biological evolution, Haeckel aimed at the creation of a universal evolutionary theory explaining the evolution of the entire universe—a theory mobilizing all natural sciences and philosophy. Given these grand ambitions, Haeckel was compelled to offer a theory of life’s origins, whereas Darwin bracketed the issue in favor of his immediate theoretical interests: “Charles Darwin’s self-imposed task was the understanding of the evolutionary processes that underlie biological diversity, a task that epistemologically can be undertaken even if it provides no explanation of the origin of life itself” (Peretó et al. 2009). Although Darwin never came up with a proper theory of abiogenesis, his correspondence proves that he was speculating about it.[1] In the published works, Darwin was very cautious though; for example, he did not even mention microorganisms in the *Origin of Species* (Darwin 1859; Davies 2009), and it was Haeckel who first brought the Darwinian agenda to bear on the fields of microbiology and the origin of life (Kutschera 2016). Never afraid of brave speculation, Haeckel developed an idiosyncratic theory of the origin and early evolution of life which he regarded as a further extension of the Darwinian paradigm.

Haeckel’s theory of abiogenesis is not simply a matter of historical curiosity. There is a causal chain connecting Haeckel’s work with modern theories of life’s origins. Until very recently, it has seldom been recognized that Haeckel played a significant or even key role in shaping Alexander I. Oparin’s (1894–1980) theory of the origin of life from lifeless matter (Lazcano 2016). As argued by Kolchinsky and Levit (2019), Haeckel’s hypothesis contributed to the growth of experimental studies of abiogenesis in the early 1920s, the best known of which became the works of Oparin. In his path-breaking book, *The Origin of Life* (the earliest version was published in 1924 in Russian: Oparin 1924), Oparin acknowledges Haeckel’s view that spontaneous generation is a “logical postulate of philosophical natural science” (i.e., this concept follows logically from everything we know from natural science), although it is not yet proven by immediate experience, and discusses his concept of abiogenesis in some detail (Oparin 1941, pp. 48–49). At the same time, Oparin criticized Haeckel for making no principal difference between the occurrence of crystals and “anucleate monera.” He classified Haeckel’s views therefore as naïve and “mechanistic” and took issue specifically with the immediate emergence of living matter from inorganic substances: “This was Haeckel’s essential error” (Ibid., p. 49).

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[1] E.g., Letter no. DCP-LETT-7471, Darwin to J. D. Hooker (01.01.1871).

In the present chapter, we outline Haeckel's views on the origin of life and early evolution and explain his motivation for developing these ideas. We come to the conclusion that in developing his theory of abiogenesis Haeckel followed his monistic creed and established several speculative hypotheses in the absence of sufficient experimental and observational data.

2.2 The Philosophical Background to Haeckel's Theory of Abiogenesis

Haeckel played a central role in the history of monism, which in his interpretation was simultaneously an ethical worldview and a research program in the natural sciences, ontology, and epistemology (Stewart et al. 2019). In contrast to Darwin himself, Haeckel tried to turn Darwinism into a universal worldview, a "philosophy." His universalism did not merely connect academic philosophy with science; it made philosophy and natural science into an inseparable whole. For Haeckel, "all true natural science is philosophy, and all true philosophy is natural science. All true science (*Wissenschaft*), however, is natural philosophy" (Haeckel 1866, Bd. II, p. 447; Hossfeld and Levit 2020).

At the core of Haeckel's doctrine was the concept of evolution as a universal phenomenon affecting everything from inert matter to man. He believed in the unity of body and soul and of spirit and matter:

> We adhere firmly to the pure, unequivocal monism of Spinoza: Matter, or infinitely-extended substance, and Spirit (or Energy), or sensitive and thinking substance, are the two fundamental attributes, or principal properties, of the all-embracing divine essence of the world, the universal substance (Haeckel 1900, p. 21).

Monism guided Haeckel's work from his first major Darwinian book, the *Generelle Morphologie* (1866), to his last book, the *Kristallseelen* (Crystal Souls 1917). The adoption of *substance monism* as a scientific meta-methodology and basis for a new worldview (*Weltanschauung*) was Haeckel's major philosophical acquisition. *Substance monism*, such as materialist, idealist, or neutral monism, supposes that all concrete objects fall under one highest type (namely, matter, ideas, or neutral substance, respectively). Haeckel combined matter, energy, and psychoma (the world's soul) into the trinity of substance, thus embracing all basic physical and psychological phenomena within one doctrine. All three elements of the trinity had corresponding conservation laws: the conservation of matter, of energy, and of psychoma (or *Empfindung*: perception). In his last philosophical manifesto, *Gott-Natur* (*Theophysis)* (God-Nature [Theophysis] 1914: Haeckel 2008), Haeckel claimed that his universal concept of substance served to reconcile old and still continuing controversies between materialism, energetics, and panpsychism. From the epistemological viewpoint, Haeckel saw cognition as a "natural physiological process whose anatomic organ is our human brain" (Haeckel 2008, p. 48). For Haeckel, the only secure foundation for science was empirical knowledge [Erfahrung, Empirie], and the ultimate objective of modern science was to cognize the "unconscious laws" governing the universe, as "everything happens with absolute necessity in accord with mechanical 'causal' laws" (Haeckel 2008, pp. 74–75).

Although Haeckel considered himself a part of the Spinozian movement, his own teachings centered first and foremost around the doctrine of the omnipresence of evolution (Hossfeld and Levit 2020). He proposed an all-embracing but organism-centered evolutionism, which took energetic, life-possessing matter to be its substantial, causal foundation. This proposal led him to adopt a kind of anthropocentrism rooted in pan-psychism, which expressed itself in a vectored, apparently teleological evolutionary development. Haeckel explicitly denied genuine teleology in biological evolution (and even introduced the term "dysteleology" as a doctrine of "goallessness" in evolution) (Haeckel 1866, Vol. II, p. 266ff), but the whole logic of his doctrine suggests inevitable progress toward "more perfect" organic creatures [Vervollkommnung]: "The notion of progress is the key of Haeckel's evolutionary theory" (Dayrat 2003). Haeckel's progressivism is not about the intrinsic tendency toward perfection, but follows from natural laws governing cosmic and organic evolution and the ontological structure of the universe. For Haeckel, "there was no teleological providence in the universe, only a naturalistic law of progress" (Di Gregorio 2005, p. 189), but the progress toward perfection followed from these laws such that gradual perfecting in biological evolution (*teleosis*, in Haeckel's terms) is the *inevitable* result of natural selection (Haeckel 1900, p. 272). The transition from inert to living matter is a necessary logical link in this worldview.

Monism and evolutionary theory were, for Haeckel, parts of the same research program, labeled the "monistischen Entwickelungslehre" (the monistic doctrine of evolution). At the core of the monistic worldview was the idea of the fundamental unity and cognizability of the world. The strong connection between the concepts of evolution and monism can be seen in Haeckel's work, *The Monism and the Link between Religion and Science. The Creed of a Natural Scientist* (1892). In a printed lecture known as the "Altenburg speech," Haeckel asserted that the monistic idea of God is compatible with the natural sciences, and he recognized the spirit of God in all things. God cannot be seen as a personalized being anymore, namely an individual with a constrained spatial and temporal extension; instead, "God is nature itself" (Haeckel 1914 in: Haeckel 2008, p. 71). Furthermore, he claimed that the Truth, the Good, and the Beautiful are the three noble divinities before which we kneel. There will be new altars built in the twentieth century, Haeckel argued, to celebrate the "trinity of monism" (Levit and Hossfeld 2017).

Haeckel distinguished theoretical and practical monism. Theoretical monism was a worldview grounded in experience, "pure reason," and science, with the latter based on evolutionism and proceeding from the unity of the universe. The theory of abiogenesis was part of theoretical monism (Krause 1984). Practical monism, on the other hand, was a set of ethical rules for a "reasonable lifestyle" in accord with theoretical monism.

Haeckel's monistic creed, which brought him into open conflict with traditional religions, determined the internal dynamics of his theoretical system including issues concerning the origin of life. In his popular treatise, *The Riddle of the Universe,* Haeckel introduced abiogenesis in the chapter on "The Unity of Nature," summarizing its logical steps in the chapter's abstract: "The monism of the cosmos. Essential unity of organic and inorganic nature. Carbon-theory. The hypothesis of abiogenesis" (Haeckel 1900, p. 260). He called the first spontaneously generated living bodies on earth, "monera," and he claimed: "But as these remarkable Monera are from one point of view of the greatest interest, so from another they deserve general attention from the inestimable importance which they possess of affording a mechanical explanation of vital phenomena, and *especially for a Monistic explanation of entire organic nature* [our italics]" (Haeckel 1869, p. 223). There were three elements of this monistic creed that were crucial for Haeckel in this respect: (1) the universe is a united whole evolving in a certain direction; (2) the direction of the world's evolution is of dysteleological (as opposed to teleological) nature and is determined exclusively by natural laws; (3) natural laws embrace not only "mechanical" (material) processes, but also psychoma that makes Haeckel's understanding of "natural laws" much broader than in contemporary science. Proving abiogenesis was therefore absolutely essential for Haeckel. If there is no abiogenesis, the world is not a united whole and the monist creed fails. If there is no abiogenesis, life is a product of supranatural forces and evolution is a teleological process.

2.3 Spontaneous Generation and Early Evolution in Haeckel's Writings

Haeckel began speculating about the origin of life and looking for the most primitive organismic forms before he published his magnum opus, *Generelle Morphologie der Organismen* (Haeckel 1866). In a letter to Darwin from November 11, 1865,[2] Haeckel described *Protogenes primordialis*[3] as one of the most primitive types of Rhizopoda [eines der allereinfachsten Geschöpfe], the "organism without organs." Haeckel emphasized that *generatio aequivoca* (spontaneous generation)[4] of such a "protein clump" [Eiweiss-Klumpen] is clearly intelligible, and if true, this would contribute to solving the difficult problem of the beginnings of the evolutionary theory.

In the *Generelle Morphologie,* Haeckel already presented a coherent theory linking planetary and organismic evolution. The metaphysical foundation for his theory was the notion of the unity of organic and inorganic nature, which, Haeckel believed, was "empirically proven" (Haeckel 1866, Vol. II, p. 447). Combined with

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[2] "Letter no. 4934," accessed on June 10, 2021, https://www.darwinproject.ac.uk/letter/DCP-LETT-4934.xml

[3] *Protogenes primordialis* is a moneron Haeckel believed to have observed in 1864 in the Mediterranean by Nice (Nizza) (Haeckel 1865).

[4] Haeckel deployed the terms "generatio aequivoca" and "generatio spontanea" interchangeably; see, e.g., Haeckel (1866, Bd. II, p. 34).

Haeckel's belief in the "almighty" causal law governing all of nature "without exceptions," the idea of the "absolute unity of nature" rendered abiogenesis a logical necessity. As he believed in building his theory on the ground of empirical observations, Haeckel was forced to establish a theory compatible with available biological data.

Haeckel published his theory in the mid of the controversy between Louis Pasteur and Felix Pouchet generated by Pasteur's experiments on spontaneous generation (Farley and Geison 1974). Haeckel was critical of both sides in the controversy and claimed that *plasmogonia* (spontaneous generation) was not yet proven, although it was theoretically impossible that Pasteur would ever be able to prove its nonexistence (Haeckel 1866, Vol. II, p. 34). In clear support of Pouchet, Haeckel proposed the existence of a group of very primitive microorganisms, which he called monera (plural): "A *Moneron* was defined as a primitive form of life consisting of undifferentiated protoplasm and lacking a nucleus" (Rupke 1976). Nothing is as important as the discovery of monera for explaining the origin of life, Haeckel argued (Haeckel 1870, p. 178). Being a "missing link" between macroorganisms and lifeless matter, monera became the crucial element of Haeckel's concept of abiogenesis. Monera, Haeckel claimed, were absolutely homogeneous, structureless organisms, which served as the stem forms (i.e., parent forms) [Stammform] from which all other organisms evolved by way of differentiation (Haeckel 1866, Vol. I, p. 179). Monera spawned directly from inorganic liquid in the same way that crystals appear in their mother liquor [Mutterlauge]. In 1866, Haeckel was uncertain whether spontaneous generation of monera and their subsequent evolution into higher organismic forms was an ongoing process or whether it happened only in the remote past (Haeckel 1866, Vol. II, p. 33, Vol. XXIII, p. 367).

In the *Generelle Morphologie,* Haeckel introduced several terms he would continue to employ when discussing the origin of life. The term *autogonia* was used as a synonym for spontaneous generation [Urzeugung] (Haeckel 1866, Vol. I, p. 179). Specifically, the autogonia hypothesis suggested that structureless monera spawned immediately from the interaction of inorganic substances in a primordial liquid. Another important notion Haeckel introduced was *plasmogonia* (Haeckel 1866, Vol. II, p. 34), which is another kind of parentless procreation of organisms. The difference between autogonia and plasmogonia is that, in the latter case, monera spawn not directly from inorganic matter, but from an organic liquid [organische Bildungsflüssigkeit]. An umbrella notion embracing both kinds of spontaneous generation was *archigonia* (Haeckel 1866, Vol. II, p. 33), which explains why Haeckel called the first monera, "archigonian parent forms." This sophisticated terminological hierarchy was important for Haeckel, because he did not exclude that monera would be spontaneously generated from lifeless matter even today. If this is the case, they would occur in liquids saturated by organic substances, via plasmogonia. In the late publications, Haeckel tended to see the occurrence of monera as a double-step process (first appear organic substances and then monera out of this organic substances) even in the ancient times.

Haeckel presented a mature classification of various monera and a description of their morphology in a lengthy journal paper entitled, *The Monograph of Monera*

[Monographie der Moneren], published 2 years after *Generelle Morphologie* (Haeckel 1868). In 1869, an English version of the *Monograph* appeared in the *Quarterly Journal of Microscopical Science* (Haeckel 1869) (Figs. 2.2 and 2.3). In the *Monograph*, Haeckel emphasized that monera were the most simple and primitive [unvollkommenere] of all imaginable life forms (Haeckel 1868, p. 64); even purely theoretically, there could be no organisms simpler than monera. He even hesitated to label monera *as* organisms as they are not constituted by smaller parts. A most primitive moneron is not a cell (as it is not yet separated into the nucleus and the plasma), but a homogenous protein body in a solid–liquid aggregate state having no rigid geometric characteristics, but becoming spherical when resting and experiencing no external influences. Monera, as structureless plasma globules, are, for Haeckel, proof that an ultimate separation between the two kingdoms of plants and animals is impossible, as they (monera) are so indefinite that they can equally serve as the origin of both plants and animals. Accordingly, Haeckel placed them into the kingdom of Protista along with Rhizopoda, amoeba, diatoms, etc. (Ibid., p. 65).

It is important to emphasize that monera, for Haeckel, were not a matter of mere theoretical speculation. The first moneron was discovered by Haeckel in 1864, "and the number has gone on steadily increasing ever since," as one of Haeckel's contemporaries, the French protozoologist Aimé Schneider noticed (Schneider 1873). The immediate impulse to write the *Monograph* came from "new observations" Haeckel made in the winter of 1866/1867 on the coasts of the Canary Island Lanzarote, already after completing *Generelle Morphologie*. From a contemporary scientific perspective, Haeckel's monera were relatively macroscopic organisms; for example, *Protogenes primordialis* (one of the first monera he described) was between 0.1 and 1.0 millimeters in diameter. As Schneider commented: "This little creature, hardly visible to the naked eye, and, at most, as big as a small pin-head, is of a fine orange-red color, consists of a perfectly homogeneous and transparent mass of jelly, and offers the paradox of *an organism without organs*" (Schneider 1873). As monera live in water, they are able to move by means of protoplasm contractions and building of pseudopodia. They propagate by fission, in an asexual mode (Ibid., p. 130).

Already in the *Monograph of Monera*, Haeckel claimed the extraordinary importance of his monera theory for the hypothesis of spontaneous generation: "If the natural history of the Monera is already, on these grounds, of the highest interest as well for morphology as for physiology, this interest will be still more increased by the extraordinary importance which these very simple organisms possess for the important doctrine of spontaneous generation, or archigony" (Haeckel 1869, p. 30). In the follow-up to the *Monograph* published 2 years later and entitled *Nachträge zur Monographie der Moneren* (Supplement to the Monograph of Monera), Haeckel added a special chapter, "Die Moneren und die Urzeugung" (Monera and the Spontaneous Generation), where he summarized his theory of abiogenesis and early evolution (Haeckel 1870, pp. 177–182). Haeckel begins by establishing a theoretical connection between his hypothesis and Darwin's theory of descent and emphasizes that "every thinking reader" of Darwin's book should have been asking

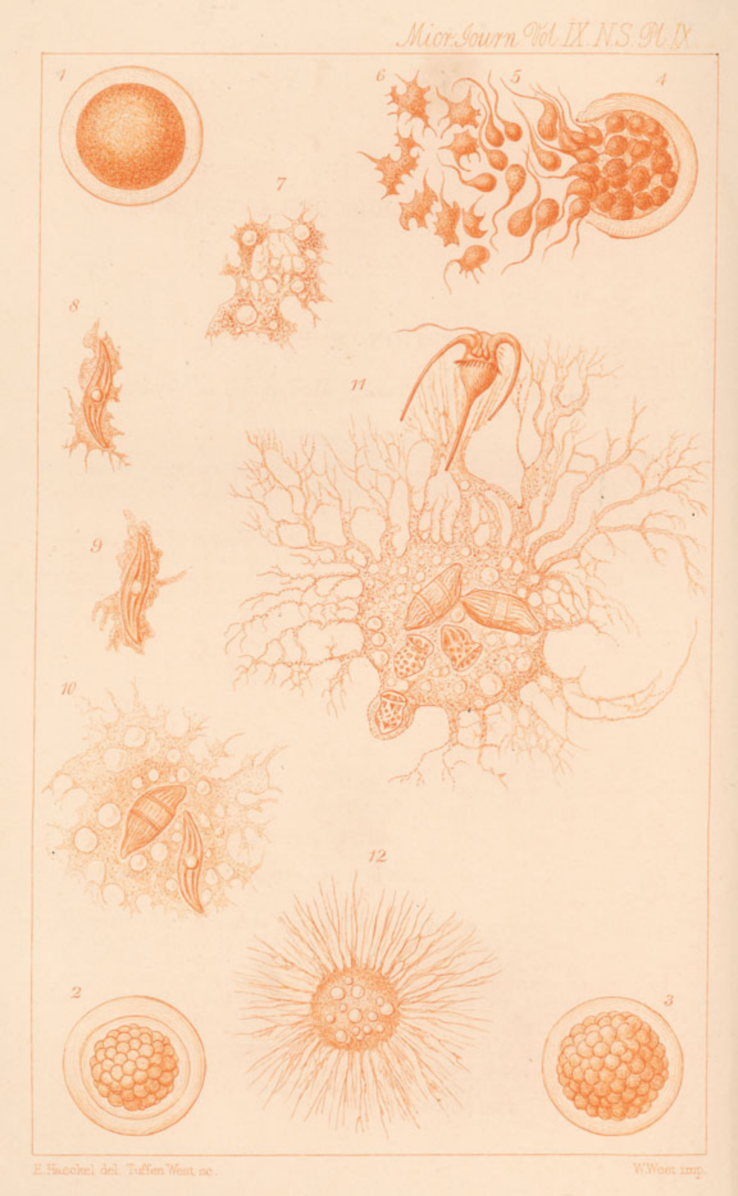
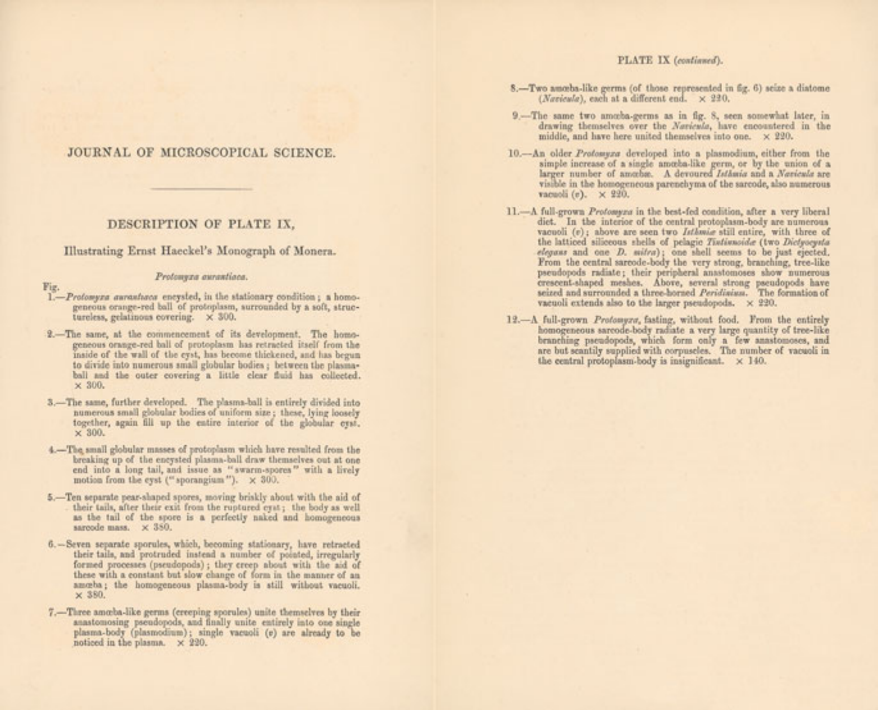


Fig. 2.2 Plate IX from Haeckel's "Monograph of Monera": (Quarterly Journal of Microscopical Science, Vol. IX, 1869). The plate depicts one of the new monera Haeckel found on the coastline of the Canary Island Lanzarote. The orange-colored "Rhizopod-like" organism was found on empty shells of *Spirula peronii*



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DESCRIPTION OF PLATE IX,

Illustrating Ernst Haeckel's Monograph of Monera.

Protomyxa aurantiaca.

Fig.

1.—*Protomyxa aurantiaca* encysted, in the stationary condition; a homogeneous orange-red ball of protoplasm, surrounded by a soft, structureless, gelatinous covering. × 300.

2.—The same, at the commencement of its development. The homogeneous orange-red ball of protoplasm has retracted itself from the inside of the wall of the cyst, has become thickened, and has begun to divide into numerous small globular bodies; between the plasma-ball and the outer covering a little clear fluid has collected. × 300.

3.—The same, further developed. The plasma-ball is entirely divided into numerous small globular bodies of uniform size; these, lying loosely together, again fill up the entire interior of the globular cyst. × 300.

4.—The small globular masses of protoplasm which have resulted from the breaking up of the encysted plasma-ball draw themselves out at one end into a long tail, and issue as "swarm-spores" with a lively motion from the cyst ("sporangium"). × 300.

5.—Ten separate pear-shaped spores, moving briskly about with the aid of their tails, after their exit from the ruptured cyst; the body as well as the tail of the spore is a perfectly naked and homogeneous sarcode mass. × 380.

6.—Seven separate sporules, which, becoming stationary, have retracted their tails, and protruded instead a number of pointed, irregularly formed processes (pseudopods); they creep about with the aid of these with a constant but slow change of form in the manner of an amœba; the homogeneous plasma-body is still without vacuoli. × 380.

7.—Three amœba-like germs (creeping sporules) unite themselves by their anastomosing pseudopods, and finally unite entirely into one single plasma-body (plasmodium); single vacuoli (*v*) are already to be noticed in the plasma. × 220.

PLATE IX (*continued*).

8.—Two amœba-like germs (of those represented in fig. 6) seize a diatome (*Navicula*), each at a different end. × 220.

9.—The same two amœba-germs as in fig. 8, seen somewhat later, in drawing themselves over the *Navicula*, have encountered in the middle, and have here united themselves into one. × 220.

10.—An older *Protomyxa* developed into a plasmodium, either from the simple increase of a single amœba-like germ, or by the union of a larger number of amœbæ. A devoured *Isthmia* and a *Navicula* are visible in the homogeneous parenchyma of the sarcode, also numerous vacuoli (*v*). × 220.

11.—A full-grown *Protomyxa* in the best-fed condition, after a very liberal diet. In the interior of the central protoplasm-body are numerous vacuoli (*v*); above are seen two *Isthmiæ* still entire, with three of the latticed siliceous shells of pelagic *Tintinnoidæ* (two *Dictyocysta elegans* and one *D. mitra*); one shell seems to be just ejected. From the central sarcode-body the very strong, branching, tree-like pseudopods radiate; their peripheral anastomoses show numerous crescent-shaped meshes. Above, several strong pseudopods have seized and surrounded a three-horned *Peridinium*. The formation of vacuoli extends also to the larger pseudopods. × 220.

12.—A full-grown *Protomyxa*, fasting, without food. From the entirely homogeneous sarcode-body radiate a very large quantity of tree-like branching pseudopods, which form only a few anastomoses, and are but scantily supplied with corpuscles. The number of vacuoli in the central protoplasm-body is insignificant. × 140.

Fig. 2.3 Detailed description of the Plate IX from Haeckel's "Monograph of Monera" illustrating the development of spores by *Protomyxa aurantiaca*. Haeckel characterized the generic character of *Protomyxa* as follows: "A simple shapeless protoplasm-body (with the formation of vacuoles), which protrude ramifying and anastomosing pseudopods. Reproduction by zoospores, which combine together into plasmodia" (Haeckel 1869, p. 340)

himself "where the first simplest proto-form [Urform]" is coming from (Ibid., p. 177). It is this proto-form, Haeckel argued, that gave rise "to all other organic forms" by means of Darwin's natural selection. Haeckel emphasized that the theory of the origin of life is a "necessary and integral constituting part of the universal evolutionary theory" (Ibid., p. 177). It is a "natural bridge" between the Kantian–Laplacian theory, which provides causal explanations of cosmic evolution, and evolutionary biology, which provides causal explanations of the origin of plant and animal species. The essence of the hypothesis is that a moneron consists of structureless protein binding, which appears directly from the lifeless substances of the primordial liquid by adapting to its immediate environment (Ibid., 178). We have observed the occurrence of various carbon compounds in our laboratories so many times, Haeckel argued that it is easy to imagine protein compounds occurring under natural conditions as nature is more powerful than any laboratory. He even hoped that 1-day monera could be produced synthetically (Krause 1984, p. 62).

Haeckel summarized the specific character of carbon compounds in a so-called carbon theory, which, he emphasized, was monistic:

> The peculiar, chemico-physical properties of carbon—especially the fluidity and the facility of decomposition of the most elaborate albuminoid compounds of carbon—are the sole and the mechanical causes of the specific phenomena of movement, which distinguish organic from inorganic substances, and which are called life, in the usual sense of the word. (Haeckel 1900, pp. 262–263).

Abiogenesis for him was the occurrence of the living protoplasm out of inorganic carbonates in the form of monera. Monera are held together by purely mechanical forces. Furthermore, the concept of ontogeny is not applicable to the simplest monera (such as *protamoeba* and *protogenes*),[5] as they do not develop, but simply grow larger, analogous to inorganic crystals. When a moneron achieves a certain body size, it splits into two parts simply due to the weakening of the molecular cohesion forces; i.e., it is a purely mechanical process far less sophisticated than cell division.

Haeckel developed a detailed systematics of monera. In 1870, he counted 16 different species of monera arranged into eight genera (Haeckel 1870) of which the most important from the viewpoint of the origin of life became the genus *Bathybius*, consisting of one species, *B. haeckelii*. In 1870, Haeckel believed that this marine benthic amoeboid organism, discovered by Thomas Huxley in the Atlantic Ocean and defined as a new moner,[6] was the nearest living relative of the ancestral monera (Haeckel 1870, p. 181; McGraw 1974; Rupke 1976). As *Bathybius* was not just a single organism swimming in the ocean, but a thick biomat-like layer covering the "deepest parts of the sea bottom," Haeckel regarded *Bathybius* as very strong evidence in favor of continuous spontaneous generation, a Lamarckian view that the spontaneous generation of life from lifeless matter is a repetitive event. Otherwise, Haeckel argued, it would be very difficult to explain the origin of this "protoplasma blanket" (Haeckel 1870, p. 181). Yet, to the end of the 1870s, Haeckel abandoned this belief. His rejection of the *Bathybius* hypothesis in his 1880s publications may be seen as one of the factors, which biased him toward the view that the occurrence of life is not an ongoing process. His late masterpiece *Systematische Phylogenie* (1894–1896) does not mention *Bathybius* anymore (Di Gregorio 2005, p. 437). As Haeckel never explicitly explained his decision to eliminate any mentionings of this fictitious discovery from the late publications, Rupke labeled the end of the Bathybius story a "silent exit" (Rupke 1976).

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[5] Protamoeba and Protogenes are two genera belonging to the most primitive kind of monera. The genus Protamoeba consisted of five species, three of which were found in the freshwaters near Jena. The genus Protogenes consisted of only one species discovered in the Mediterranean, which Haeckel labeled *P. primordialis*.

[6] "I propose to confer upon this new 'Moner' the generic name of Bathybius and to call it after the eminent Professor of Zoology in the University of Jena, *B. haeckelii*" (Huxley 1868).

2.4 Trees and Bushes: Polyphyletic vs. Monophyletic Evolution

Haeckel's hypothesis, clearly expressed in early writings, that monera are continuing to spontaneously generate and evolve to higher forms even today (Haeckel 1866, 1868, 1869, 1870), was at odds with the Darwinian notion of strictly monophyletic evolution. Besides, strict monophyletism was better compatible with Haeckel's very own monism as the perfect unity of the world required perfect unity of life and of its origin. From the other side, if monera are simple homogenous aggregates of organic matter held together by purely mechanical forces—if they are, in fact, something between proper organisms and inert matter—it is difficult to explain why they should not arise repetitively in both the past and present. This contradiction created a tension which Haeckel never fully overcame, although his bias toward perfectly monophyletic evolution is well known (e.g., Haeckel 1887, p. 46; see also Levit et al. 2022). As Olivier Rieppel emphasizes, Haeckel "never rejected the polyphyletic origin of life through multiple spontaneous generation events" (Rieppel 2011). Benoît Dayrat even claims that Haeckel coined the very terms "monophyletic" and "polyphyletic" to discuss this question of whether the whole organic world owes its origin to a single instance of spontaneous generation or to several (Dayrat 2003).

In *Generelle Morphologie,* Haeckel formulated three hypotheses describing possible relations between the spontaneous generation of monera and living organisms (Fig. 2.4). His first hypothesis suggested that one single species of monera arose through autogonia. All other organisms, without exception, are descendants of this one monera species and compose a single phylum [Phylon] (1866, Vol. I, p. 199). His second hypothesis supposed that autogonia resulted in the creation of two different monera species, one of which was vegetative [vegetabilische] and the other of which was animal [animalische]. According to this hypothesis, all plants are descendants of the vegetative monera, and all animals have their origin in the animal monera (1866 Vol. I, p. 200). The third hypothesis suggested that there were "more than two different monera-species," which gave rise to "more than two independent stems [Stämme] of organisms" (1866 Vol. I, p. 200). Haeckel considered this "the most probable of all three hypotheses" [bei weitem wahrscheinlichste von allen drei] and never completely abandoned it. Although in 1866, Haeckel "did not yet introduce the technical term polyphyly," the third hypothesis clearly expressed the concept of polyphyly, which is the idea that "a variable number of independent phyla" originated from separate events of spontaneous generation (Rieppel 2011). In this case, each of the three kingdoms would be defined as "one single natural stem (phylum)" [ein einziger natürlicher Stamm (Phylum)] originating from an "independent spontaneously generated stem-form" [selbstständige autogone Stammform] (1866, Vol. II, XXXI). Haeckel was even open to the thought that there may be more than three monera and that a certain monera species could be, for example, a common stem form (common ancestor) [gemeinsame Stammform] of all vertebrates or of all coelenterates: "In our view it is most probable that each of the major stems [Hauptstämme] or phyla of animal and plant kingdoms evolved [entwickelte sich] from a separate monera stem-form" (Haeckel 1866, Vol. I, p. 185). According to this view, all major stems are descendants of "autogone" (independently generated)

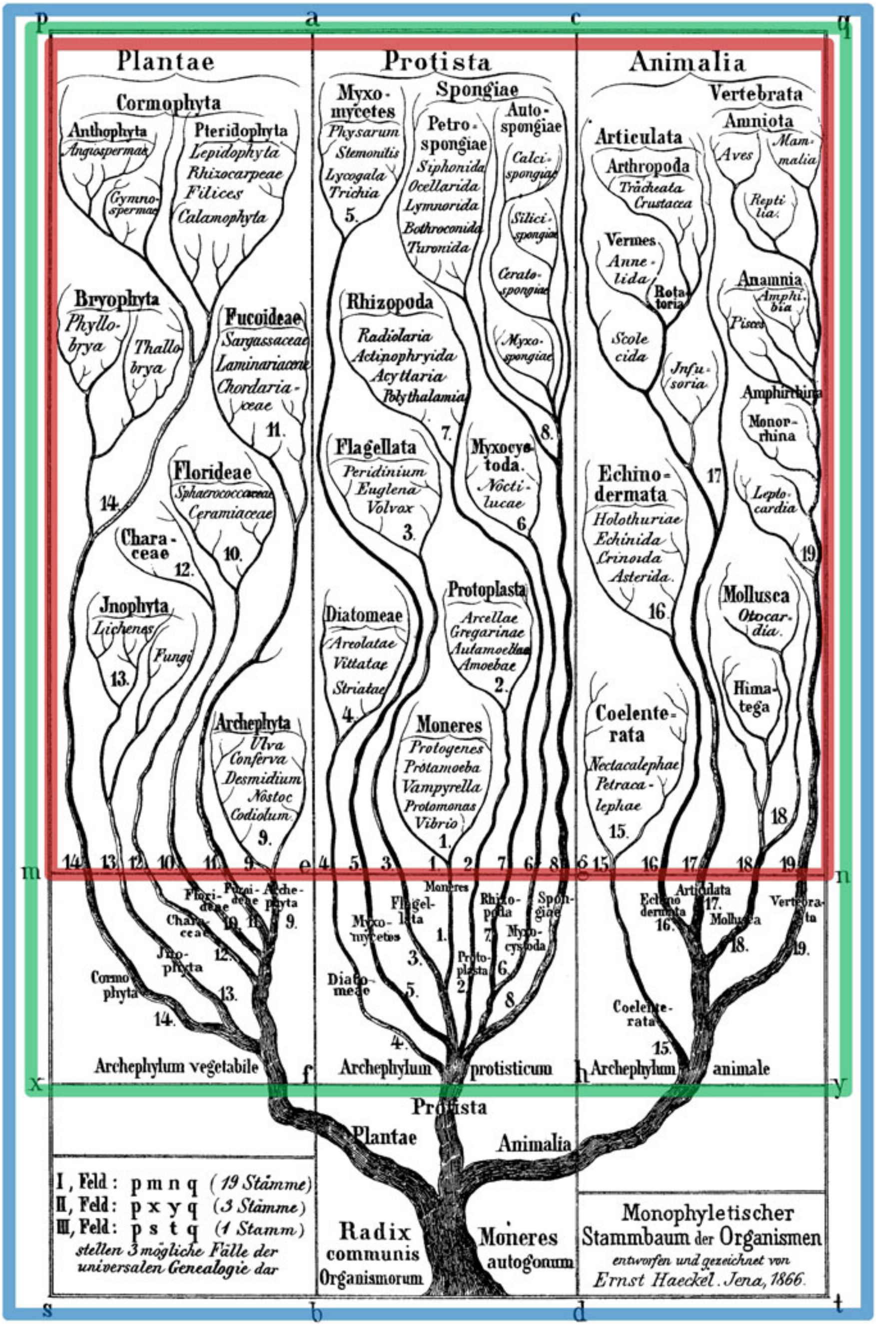

Fig. 2.4 Monophyletic stem tree from *General Morphology* [Generelle Morphologie] (Haeckel 1866, Vol. II, Table I). Color lines are added by us. Although entitled by Haeckel "Monophyletic Stem-Tree of Organisms," this stem tree, in fact, includes three different diagrams illustrating three hypothetical "universal genealogies." I. Rectangle "pmnq" represents 19-stem model (red line). II. Rectangle "pxyq" represents 3-stem model (green line). III. Rectangle "pstq" represents 1-stem

monera, which evolved by means of divergence of characters and natural selection (Vol. II, 419). Elsewhere in the *Generelle Morphologie,* Haeckel writes: “The protoforms themselves, which form roots of the single stems, arose completely independently of each other via spontaneous generations [. . .]” (1866, Vol. II, p. 394).[7]

Neither Haeckel nor Darwin considered the polyphyletic origin of life as a danger for evolutionary theory. The British master himself did not exclude the possibility that animals and plants could have descended from distinct progenitors (Richards 2008, p. 137). Haeckel followed in Darwin’s footsteps: “Whether we finally assume a single common parent-form (the monophyletic hypothesis), or several (the polyphyletic hypothesis), is wholly immaterial to the essence of the theory of descent”), and it is equally immaterial to its fundamental idea what mechanical causes are assumed for the transformation of the varieties” (Haeckel 1879b, p. 3). Even Haeckel’s successor in Jena, Ludwig Plate (1862–1937), the leading Darwinist of his time (Levit and Hossfeld 2006), wrote in 1925 in a paragraph devoted to the origin of life that “polyphyly [Vielstämmigkeit] does not arise any serious objections against evolutionary theory” (Plate 1925, p. 144).

In the first and several subsequent editions of the *Natürliche Schöpfungsgeschichte* (*The Natural History of Creation*), Haeckel argued along the same lines (e.g., Haeckel 1868, 1879a, 1880). In the first German edition of the text, Haeckel repeated the idea that monera, which we observe today, could have existed since the “primordial time,” or alternatively, that spontaneous generation could be a repetitive process, and if so, it would be hard to deny that they could well be generated even today (Haeckel 1868, pp. 345–346). He illustrated the hypothesis of repeated spontaneous generation with a polyphyletic stem tree diagram (Fig. 2.5).

In the English edition of the book, titled *The Evolution of Man* (Haeckel 1879c), Haeckel emphasized again that the issue of the origin of life corresponded to the issue of the spontaneous generation of monera: “In the definite, limited sense in which I maintain spontaneous generation (*generatio spontanea*) and assume it as a necessary hypothesis in explanation of the first beginning of life upon the earth, it merely implies the origin of Monera from inorganic carbon compounds” (Haeckel 1879c, Vol. II, pp. 30–31). As in the *Generelle Morphologie* and *Monograph der Moneren*, he again admits that it is “very possible” that Monera will be “produced daily by spontaneous generation” (Haeckel 1879c, p. 32). In the seventh German edition of the *History of Creation*, Haeckel still employed the terms phytomonera [Phytomoneren], neutral monera [neutrale Moneren], and zoomonera [Zoomoneren] while admitting that distinct kinds of monera could be responsible for the origin of plants and animals. Haeckel also presented a modified diagram illustrating the

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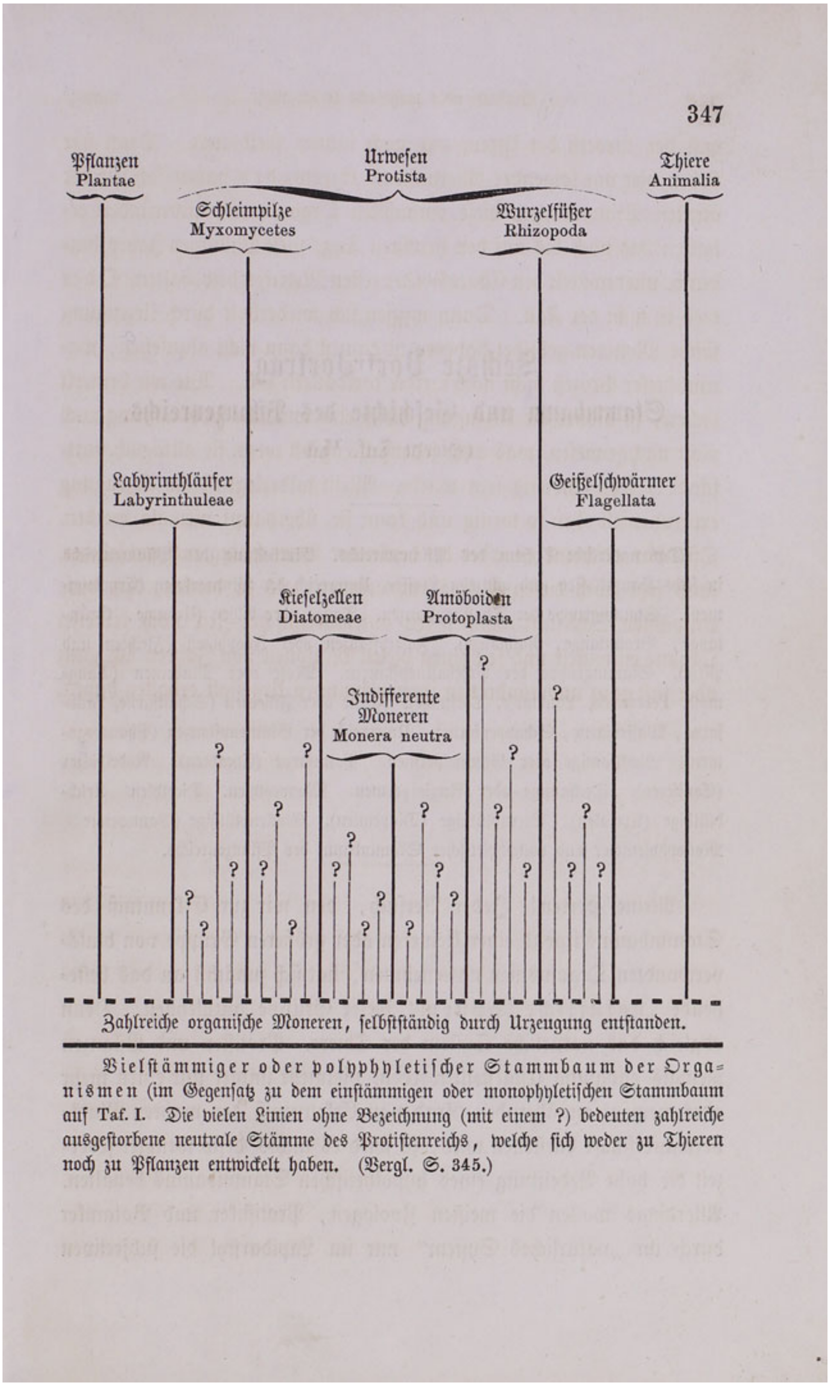
[7] German original: “Urformen selbst aber, welche die Wurzel der einzelnen Stämme bilden, sind gänzlich unabhängig von einander durch Geueratio spontanea entstanden, wie wir bereits im sechsten und siebeuten Capitel erläutert naben.”

Fig. 2.4 (continued) model (blue line), i.e., all living organisms origin from a single-kind moneron (single common parent form). In 1866, Haeckel considered the model I (multi-monera model) as the most probable (Krause 1984, p. 64)



Vielſtämmiger oder polyphyletiſcher Stammbaum der Organismen (im Gegenſatz zu dem einſtämmigen oder monophyletiſchen Stammbaum auf Taf. I. Die vielen Linien ohne Bezeichnung (mit einem ?) bedeuten zahlreiche ausgeſtorbene neutrale Stämme des Protiſtenreichs, welche ſich weder zu Thieren noch zu Pflanzen entwickelt haben. (Vergl. S. 345.)

Fig. 2.5 Polyphyletic stem tree from the first German edition of the *History of Creation*; it illustrates the idea of multiple independent spontaneous generation of monera and their evolution polyphyletic origin of life (Haeckel 1879a, p. 401; Reynolds and Hülsmann 2008) (Fig. 2.6). At the same time, he introduced the concept of "archigone monera," which could have been giving rise to all other kinds of monera (Haeckel 1879a, p. 400) and presented a diagram illustrating the hypothesis of the monophyletic origin of life (Fig. 2.7). In a comment on these diagrams, Haeckel explained that a "well-founded decision between monophyletic and polyphyletic hypotheses is completely impossible [ganz unmöglich] considering our present imperfect phylogenetic knowledge" (Ibid. 1879a, p. 399). The same idea was repeated in the English edition of the *History of Creation* published in 1887, where he stated that a safe means of deciding between the monophyletic and polyphyletic hypotheses is "as yet quite impossible" (Haeckel 1887, p. 73). At the same time, Haeckel, again, clearly expressed his bias toward the concept of spontaneous generation as a repetitive process and toward the independent origin of the three kingdoms:

> But the more deeply we penetrate into the genealogical secrets of this obscure domain of inquiry, the more probable appears the idea that the *vegetable kingdom and the animal kingdom are each of independent origin*, and that midway between these two great pedigrees a number of other independent small groups of organisms have arisen, *by repeated acts of spontaneous generation*, which on account of their indifferent neutral character, and in consequence of their mixture of animal and vegetable properties, may lay claim to the designation of independent Protista" [our italics—*auth.*] (Haeckel 1887, p. 73).

Of these two issues—repetitive spontaneous generations and the polyphyly controversy—Haeckel considered the latter as a minor issue as the whole body of a moneron consists anyway only of a formless mass "made up of a single albuminous combination of carbon," and therefore, primary monera were quite uniform, morphologically identical, differing only by their "chemical nature" (Haeckel 1887, p. 45). In other words, in Haeckel's typological approach to phylogeny, even major organismic groups originating from different acts of spontaneous generation (kingdoms) could be depicted as elements of the same monophyletic stem tree.

In the first volume of his very last technical (i.e., strictly scientific, as opposed to popular) work, the three-volume *Systematische Phylogenie* (Systematic Phylogeny), Haeckel devoted several paragraphs to the discussion of polyphyly vs. monophyly (Haeckel 1894, pp. 31–32; pp. 88–89) and formulated a general principle determining the relations between these two concepts. In §69 of the chapter "The Unity of the Organic World" (vol. I), Haeckel, again, explained that monism, "the doctrine of the perfect unity of the organic world," is the true foundation of his understanding of evolution. This unity can be observed everywhere; for example, he observes that "the same protein-like substance, called plasma, is the common material foundation of the organic life" (Haeckel 1894, p. 88). He posed the question of how the "perfect morphological and physiological unity of the world" relates to the concept of phylogeny: "May we conclude from this that all different organic forms originally

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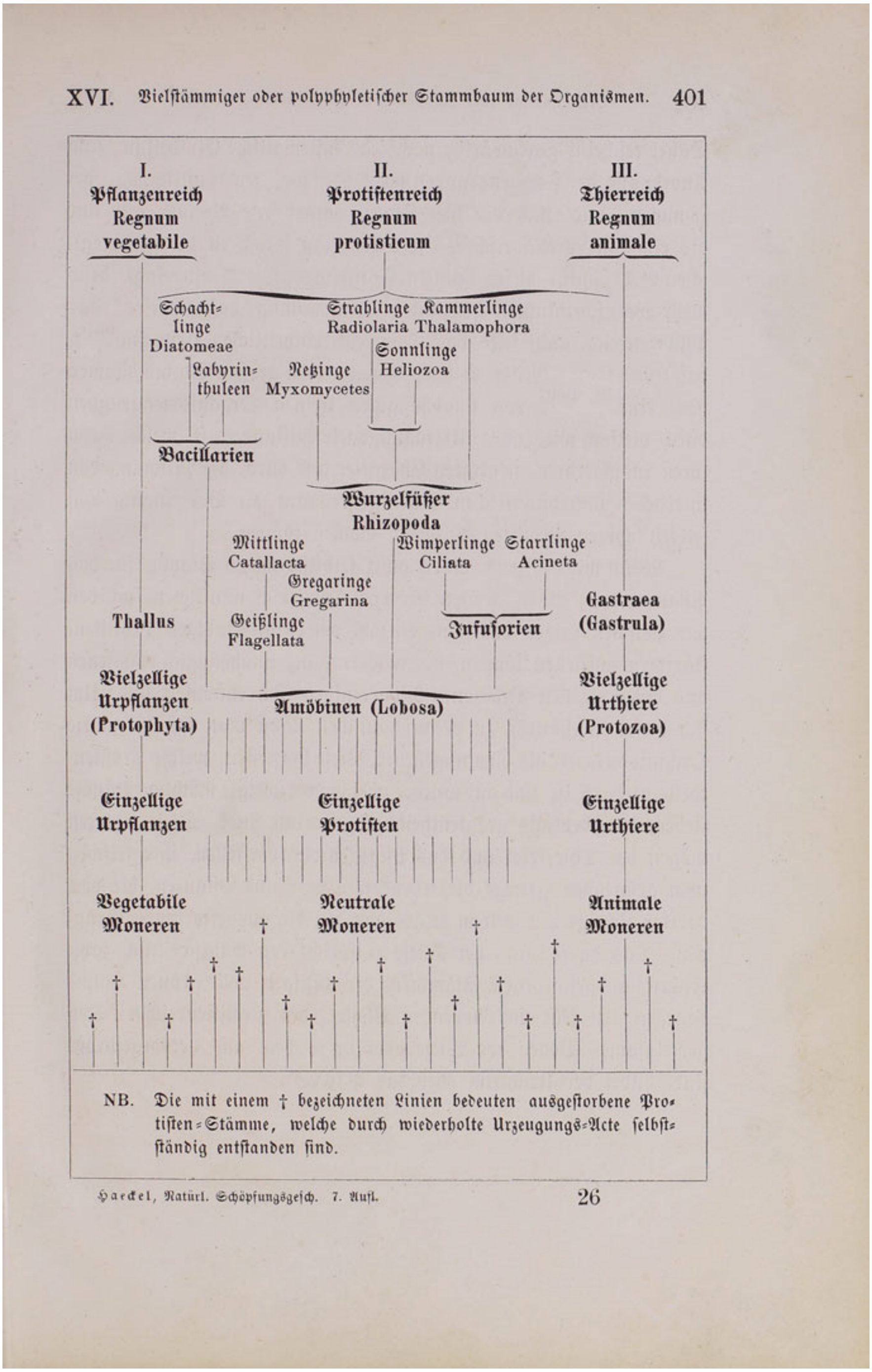
Fig. 2.5 (continued) to higher organisms by means of natural selection (Haeckel 1868, Nat. Schöpfungsgeschichte, 1. Auflage, S. 347)


XVI. Vielſtämmiger oder polyphyletiſcher Stammbaum der Organismen. 401

NB. Die mit einem † bezeichneten Linien bedeuten ausgeſtorbene Protiſten-Stämme, welche durch wiederholte Urzeugungs-Acte ſelbſtſtändig entſtanden ſind.

Haeckel, Natürl. Schöpfungsgeſch. 7. Aufl. 26

Fig. 2.6 Polyphyletic stem tree published in the 7th German edition of the *History of Creation* (Haeckel 1879a, Nat. Schöpfungsgeschichte, 7. Auflage, S. 401). †† symbolizes extinct independent stems

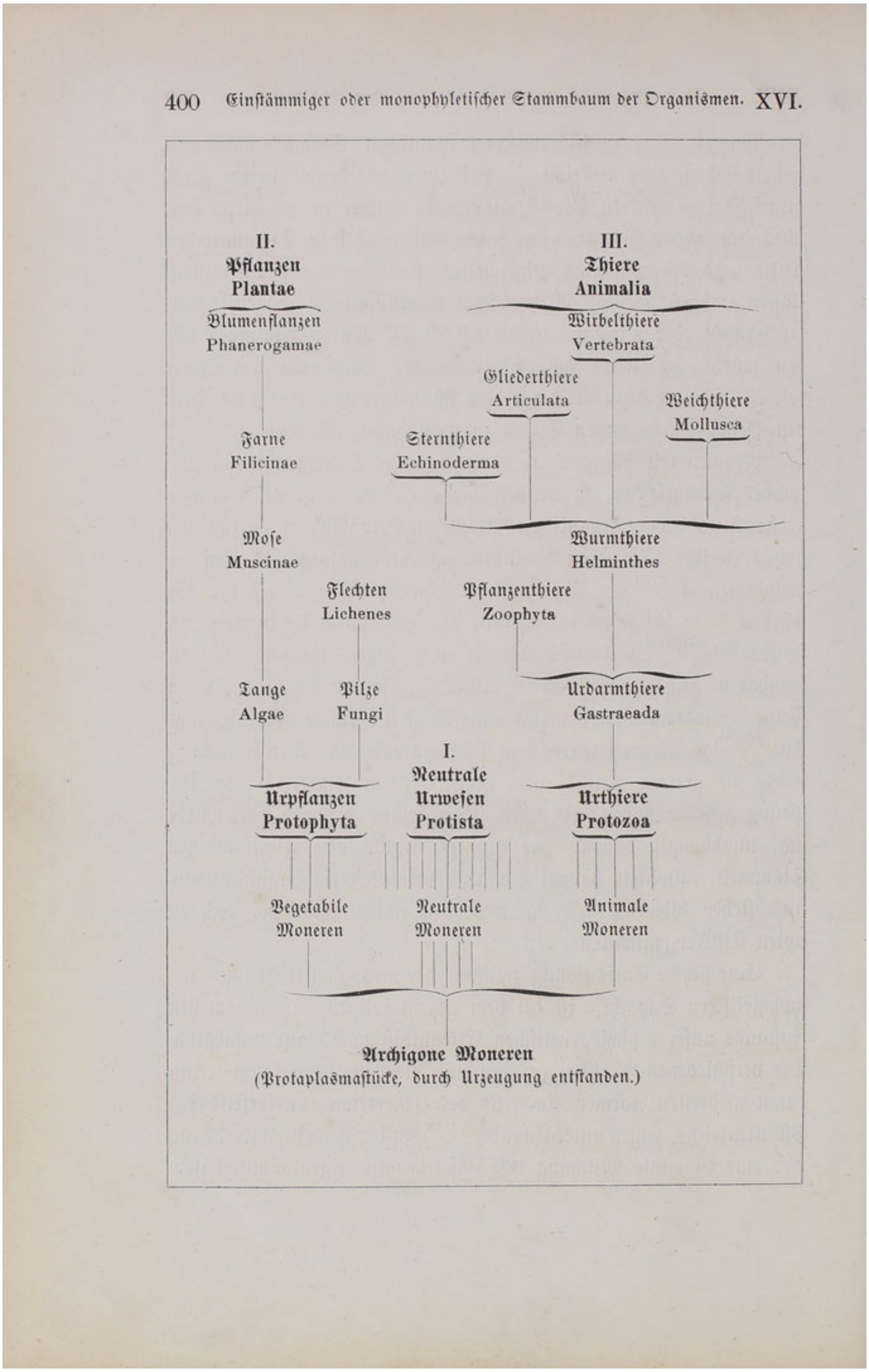


Fig. 2.7 Monophyletic stem tree from the 7th German edition of the *History of Creation* and published next to the polyphyletic tree (Haeckel 1879a, S. 400). The single lines at the very bottom of the tree symbolize multiple monera produced by spontaneous generation

evolved [historisch entwickelt] from one and the same common proto-form [Urform]?" (Ibid., p. 89). The answer to this question, Haeckel comments, is simultaneously "yes" and "no." One can apply the polyphyletic hypothesis to the origin of "organic stems" (phyla) as in the initial period of "biogenesis" (Haeckel meant abiogenesis, in modern terms), whereby monera spawned from lifeless matter by means of *archigonia* multiple times. However, this process can *also* be described as monophyletic, whereby *archigonia* took place everywhere in the same manner. Haeckel illustrated this typological vision of early phylogeny with a monophyletic-looking diagram (Fig. 2.8).

Elsewhere in the same volume, Haeckel argued that the application of the polyphyletic or monophyletic hypotheses to a certain evolutionary episode must be decided individually for each case (Haeckel 1894, Vol. I, pp. 31–32), although in general monophyly becomes more plausible the higher one climbs in a given phylogenic tree. For example, it is indubitable that all vertebrates evolved in a strictly monophyletic mode, but the polyphyletic hypothesis may be applicable to the low protists.

Haeckel tended to narrow the scope of the polyphyletic hypothesis to early evolution in the latest writings. Yet, he still maintained that abiogenesis was not a unique event, but took place multiple times giving rise to various organismic kingdoms—and in that sense, early evolution was polyphyletic. At the same time, he believed that various kingdoms could have their ultimate roots in monera of the same kind—and in that sense, early evolution was monophyletic.

2.5 Conclusions

Haeckel's theory of abiogenesis, consisting of the hypothesis of spontaneous generation "and the allied carbon theory," was central to his monistic worldview as it allowed him to overcome both ontological dualism and teleology in favor of a purely causal (mechanistic, in his terms) interpretation of natural phenomena (Haeckel 1900, p. 264). For Haeckel, abiogenesis was a necessary logical consequence of his monistic "substance theory," which asserted the fundamental unity of organic and inorganic matter. Being a universal evolutionist, he also saw abiogenesis as a concept linking the Kant–Laplace nebular hypothesis with Darwin's theory of evolution. All events leading from inorganic to organic evolution are law-governed, proceed without external or supranatural influences, and can therefore be thought of as self-organizing (although Haeckel himself did not employ this term, his concept of *autogonia* [linguistically consisting of two parts, *auto* = self and *gonia* (gonos) = creation] suggests he was thinking along these lines). The immediate product of *autogonia* was the simplest living creatures, monera, which gave rise to all other forms of life on earth. In his very late works, Haeckel tended to describe the occurrence of monera as a two-step process: first, the rise of the simplest organic substances, and second, the appearance of monera out of these substances (Haeckel 1900, p. 263).

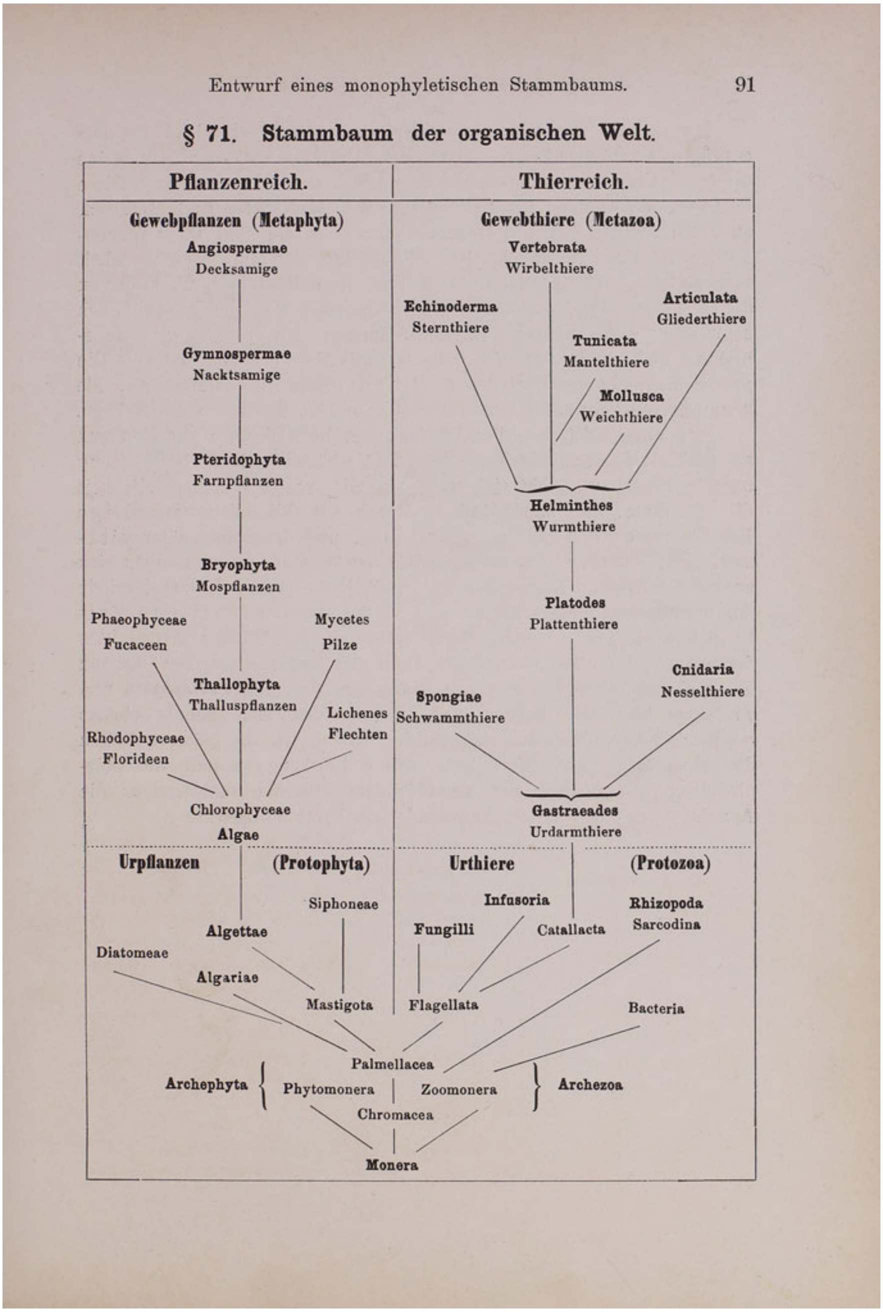


Fig. 2.8 Monophyletic stem tree of the entire organic world published in the *Phylogenetic Systematics* (Haeckel 1894, S. 91). Note that the three lines at the very bottom of the scheme, symbolizing the early evolution of monera, remain separated and do not unite to a single line as on the monophyletic stem tree from the *History of Creation* (1879)

He distinguished three organismic kingdoms (Animalia, Plantae, and Protista) and speculated about their polyphyletic origin—about the possibility that different kinds of monera brought about each kingdom. He even admitted that there could be many (more than three) primitive parent forms, as was reflected in his diagrams of extremely polyphyletic early evolution (Figs. 2.5 and 2.6). Although his monism and the Darwinian paradigm he championed urged him to accept strict monophyly, Haeckel remained biased toward the polyphyletic model of life's origins throughout his life. In his latest works, he narrowed down his application of polyphyly to the early evolution and abandoned the hypothesis of extreme polyphyly he admitted for a long period of time. He elaborated a general principle unifying both concepts (polyphyly and monophyly), which declared that the higher one climbs the phylogenetic trees the more strictly monophyletic they appear. On a purely empirical level, Haeckel's theory was lacking experimental data or direct observations proving the hypothesis of continuing spontaneous generations in fresh or ocean waters. At the same time, Haeckel's monera hypothesis was hardly compatible with strict monophyly, because it favored the idea that multiple and continuing spontaneous generations of various kinds of monera occur repetitively throughout the early history or even throughout the whole history of earth. In accord with the "carbon theory," monera were so easy to generate that it would be difficult to explain why they should not spawn multiple times after the early earth cooled down. In other words, the theory of the origin of life was the terrain, where Haeckel's monistic epistemology came into conflict with his monistic ontology as the former required secure empirical foundation for the abiogenesis theory—which was absent—while the latter required abiogenesis as a necessary logical link in his theoretical system.

Acknowledgments The authors would like to thank Cameron Yetman (Canada) for valuable suggestions.

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3

D’Arcy Wentworth Thompson’s “Physico-Mathematical” Approach to the Investigation of Morphogenesis and Its Pertinence to Cognitive-Behavioral and/or Learning-Based Explanations of Evolution

Adam C. Scarfe

Abstract

This chapter highlights the influence of the Aristotelian and Kantian thought patterns on D’Arcy Wentworth Thompson’s (1860–1948) elucidation, in *On Growth and Form* (1917, 1942) and elsewhere, of his “physico-mathematical” approach to the investigation of morphogenesis. Writing and working prior to the modern synthesis, for Thompson, the explanations of organismic form that had been provided by selectionists, geneticists, and vitalists seemed to him to be implicitly teleological in nature. As a response, Thompson held that proper scientific focus on the physical forces that underlie, entrain, and constrain organismic growth patterns was being neglected. Following Kant, for Thompson, it was the duty of the natural sciences to orient themselves via a “physico-mathematical” approach and to carry such an approach as far as possible in research. That said, although emphasizing a mechanistic perspective as regard formal scientific inquiry, in a manner consistent with Aristotle and Kant, Thompson also did justice to teleology as a heuristic for inquiry. The latter sections of this chapter express the pertinence of Thompson’s “physico-mathematical” orientation, as exemplified by his notion of “mechanical efficiency,” to explanations of how the behavioral selections made by organisms can be a trigger of physiological evolution, potentially channeling its direction (as in the Baldwin effect/the theory of organic selection). Specifically, Thompson’s theses are brought to bear on Simona Ginsburg and Eva Jablonka’s notion of “(unlimited) associative learning” in their exploration, in *The Evolution of the Sensitive Soul* (2019) and elsewhere, of the cognitive-behavioral and/or learning-based causes of the

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_3

Cambrian explosion, namely, the "morphological big bang" out of which most of the generalized organismic forms that are found in our present evolutionary epoch are alleged to have emerged. Conway Morris' (The crucible of creation: the burgess shale and the rise of animals. Oxford University Press, New York, 1998) hypothetical scenario involving the Cambrian, priapulid worm, *Ottoia prolifica*'s (alleged) habitualized mode of seizing certain prey (i.e., the hyolith, *Haplophrentis*) given the latter's obstructive "helens," serves as a concrete example of how physico-geometrical factors entrain and/or present constraints that may canalize the behavioral selections of organisms.

Keywords

Morphology · Morphogenesis · Epigenesis · Autopoiesis · Teleology · Mechanism · Mechanical efficiency · The Baldwin effect (i.e., the theory of organic selection) · (Unlimited) associative learning · The Cambrian explosion · *Ottoia prolifica* · *Haplophrentis carinatus*

3.1 Introduction: D'Arcy Wentworth Thompson and the Aristotelian Foundations of Morphology

Morphology (Gr. *morphe*: "form" and *logos*: "study") designates scientific investigation into the causes of the physiological shape, form, pattern, "ground-," or "body plans" (Ger. *Baupläne* or *Bauplan*) (Woodger 1945)[1] of organisms *qua* phenotypes. As a diverse discipline of inquiry that is interrelated with most others in biology, among other things, morphology involves (1) the tracing of sequences of transformation and deformation as regards the physiological structures of individual organisms, and of groups of organisms over time, with reference to the fossil record; (2) the comparison of the physiological forms of organisms and of groups for the sake of identifying genealogical kinship, homological, and/or phylogenetic relations (e.g., species), the sorting or classification of organisms with explicit reference to commonalities and differences as regards physiological form, and/or for understanding the relationships between stem and crown lineages of groups or varieties; (3) the investigation of the connections between the structures of organisms and their functioning relative to the environment over time; (4) inquiry into the conformation and de-conformation of the physiologies of organisms to stereotypical, isomorphic,

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[1] Joseph Henry Woodger, "On Biological Transformations," in *Essays on Growth and Form Presented to D'Arcy Wentworth Thompson*, eds. W. E. Le Gros Clark and P. B. Medawar (Cambridge, MA: Cambridge University Press, 1945, p. 104). Speaking to the importance of the term *Bauplan* in biology, Woodger states that "by a taxonomic group . . . we shall mean any set of lives which is determined by a *Bauplan*)" (104–105). For Katherine E. Willmore, in "The Body Plan Concept and Its Centrality in Evo-Devo," *Evolution: Education and Outreach* 5 (2012), "a body plan is a suite of characters shared by a group of phylogenetically related animals at some point during their development. The concept of *bauplane*, or body plans, has played and continues to play a central role in the study of evolutionary developmental biology (evo-devo)" (219).

or generalized body plans; and (5) the explanation of morphogenesis, namely, the processes, mechanisms, influences, constraints, and/or causal factors (e.g., physical, geological, environmental, genetic, epigenetic, biochemical, molecular, hormonal, homeostatic, chronobiological, autopoietic, intellectual, behavioral, and symbolical, etc.. . ., and/or interrelations thereof), through which organismic structures issue forth (i.e., in the course of growth, differentiation, and development), are maintained (e.g., with reference to the relations between organismic wholes and their members), and/or are deformed. As the German zoologist Ernst Haeckel (1834–1919) defined it in his *General Morphology of Organisms* (1866):

> morphology, or the theory of form in organisms, is the comprehensive science of the internal and external relations of form among [and within] living natural bodies, animals, and plants," its task being "to identify and explain these relations of form, i.e., to trace their occurrence back to precise natural laws (Haeckel 1866).[2]

The modern scientific discipline of morphology is generally held to have originated with Johann Wolfgang von Goethe's (1749–1832) *The Metamorphosis of Plants*[3] in 1790 and his investigation of variations in form among vertebrates. Yet, the concept of "form" is a metaphysical one that has foundations within Ancient Greek Philosopher Aristotle's (384–322 BCE) substance-ontological philosophy of nature,[4] something that was recognized explicitly by D'Arcy Wentworth Thompson

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[2] Ernst Haeckel, *Generelle Morphologie der Organismen. Allgemeine Gründzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie, Volume 1 of 2* (Berlin, Germany: Reimer, 1866), 3, as translated and cited in Nolan Hele, "Ernst Haeckel and the Morphology of Ethics," *Journal of the Canadian Historical Association* 15.1 (2004), 8, emphasis in original, my addition.

[3] See a translation of Goethe's *The Metamorphosis of Plants* and Adolph Portmann's interpretation of it, in *Essays in Philosophical Zoology by Adolf Portmann: The Living Form and the Seeing Eye*, trans. Richard Carter (Lewiston, ME: Edwin Mellen Press, 1990, pp. 161–276.

[4] Pointing to the importance of the Aristotelian substance-metaphysical notion of physiological "form" to modern biology, the whole meaning of evolution in general is typically construed to involve the charting of the sequence-in-flux of the physiological forms of organisms over time. Of course, among laypersons, the standard yet naïve and anthropocentric and anthropomorphic "march of progress" and "tree of life" views of evolution (see Stephen Jay Gould's characterization of these typical habits of thought in relation to biological evolution in the first chapter, "The Iconography of an Expectation," in *Wonderful Life: The Burgess Shale and the Nature of History* [New York: W. W. Norton & Company, 1989], 23–52) tend to measure it nearly exclusively in terms of a linear "teleological progression" of physiological forms toward the human and/or the superhuman. Also, while the fossil record does provide an empirical and reliable record of organismic form, this form requires interpretation, not only in terms of the appearance of the physiological structures of the organisms in question but the manners of functionality of those structures, as well as their modes of life, their behaviors, and their mentalities, for example. Furthermore, an overemphasis on physiological form in terms of the meaning of evolution can often overlook other dimensions, such as mental, behavioral, and chronobiological patterns. A case can be made, for example, that modification of the thought patterns and the behavioral habits of organisms over time, considered not only as causal factors as regards physiological transformations (as emphasized in the standard formulation of the Baldwin effect), but taken of themselves, should also be taken seriously as constituting a part of the meaning of evolution. So, there are very good reasons to question modern biology's fixation

(1860–1948), the renowned Scottish classicist and naturalist who was knighted in 1937. In his celebrated volume *On Growth and Form* (1917, 1942) and elsewhere, Thompson emphasized the focusing of inquiry on the physical forces involved in morphogenesis and he embraced mathematical methods as a key to explaining it. It is the purpose of the first portion of this chapter to unpack Thompson's "physico-mathematical" approach to the study of morphology with reference to the Aristotelian and Kantian thought patterns that influenced it.

Thompson had a wide knowledge of Aristotle's corpus, having translated Aristotle's *The History of Animals*.[5] On the subject of Aristotle's biological inquiries, his philosophy of nature and metaphysics, as well as the influence of his thinking on biology and its importance to contemporary morphology and our understanding of morphogenesis, Thompson wrote and delivered papers such as "*Magnalia Naturae* (the Wonderful Nature) or the Greater Problems of Biology" (Thompson 1911) and "On Aristotle as Biologist (with a Prooemion on Herbert Spencer)" (Thompson 1913), wherein he accoladed the Ancient Greek Philosopher as a "morphologist and embryologist" who had "the keenest insight into physiological problems,"[6] and whose thought is "of the highest possible interest to us."[7] Furthermore, Thompson credited Aristotle's comprehensive philosophical understanding of the world and the practical wisdom that he kindled largely to the latter's original biological researches and experiments (Thompson 1913, p. 15). After all, for example, Aristotle had looked upon the political state as an organism (Thompson 1913, p. 25). And in his ethics, Aristotle employed the concepts of excess, deficiency, and moderation (of which Thompson made very good use in exploring the geometry of organismic forms[8]), which undoubtedly stem from a keen understanding of organismic processes akin to what is today understood as homeostasis, which serves to maintain their physiological functioning. Thompson noted that more than

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on physiological transformation as the core meaning of evolution, to the neglect of other factors. Nevertheless, physiological form remains crucial. Relating explicitly to evolutionary developmental biology, embryogenesis is, in some sense, early-stage morphogenesis pertaining to organisms that reproduce sexually. It reveals morphogenetic processes that are concealed in later stages of organismic development. It should be highlighted that when referring to organismic form it is really dynamic form-in-process, of course, with some degree of stability.

[5] See Aristotle's "The History of Animals," translated by D'Arcy Wentworth Thompson, comprising Volume IV of Smith JA and Ross WD (eds.), *The Works of Aristotle* (Oxford, UK: Clarendon Press, 1910). Thompson's translation remains a definitive English version of this Aristotelian work even today.

[6] D'Arcy Wentworth Thompson, "*Magnalia Naturae* (the Wonderful Nature), or the Greater Problems of Biology," *Science (Proceedings of the British Association for the Advancement of Science)* 34.875, October sixth, 1911, 417.

[7] D'Arcy Wentworth Thompson, *On Aristotle as a Biologist with a Prooemion on Herbert Spencer* (Clarendon Press: Oxford, UK, 1913, reprinted BiblioLife, LLC, 2019), 17.

[8] For example, see D'Arcy Wentworth Thompson, "Morphology and Mathematics," *Transactions of the Royal Society of Edinburgh* (Volume 50, Part IV, Number 27, London, UK: Williams and Norgate, 1915), 861, and see D'Arcy Wentworth Thompson, "Excess and Defect: Or the Little More and the Little Less," *Mind* 38.149 (January 1929), pp. 43–55.

just whispers of the "greater problems of [modern] biology" were present in Aristotle's work, the philosopher being knowledgeable of most topics studied therein (Thompson 1911, p. 418).

While Aristotle's philosophy of nature is seemingly archaic to modern neo-Darwinian sensibilities, some understanding of Aristotle's conceptual framework, as Thompson emphasized, remains essential to the examination of some of the presuppositions underlying modern evolutionary theory, to the understanding of the metaphysical foundations and the basic problems of the science of morphology (which he aimed to renew), as well as to the effort of deciphering the causes of morphogenesis. Hence, in order to gain a proper understanding of Thompson's approach to the study of morphogenesis, it will be first necessary to examine some aspects of Aristotle's philosophy of nature and his overall metaphysical framework.

3.2 Aristotle's Philosophy of Nature and Metaphysics

As contrasted with the modern understanding of nature as an environmental backdrop and external to human civilization, as expressed in his *Physics*, *Metaphysics*, and elsewhere,[9] for Aristotle, the word nature (*physis*) meant several interconnected things. Nature (*physis*) designated a teleological process involving the "coming-to-be," emergence, genesis, growth, formation, production, and/or bringing forth (*poiesis*) of substances, for example, whether they involve crystallization in the case of inorganic molecules, the blooming forth of leaves and flowers in the cases of various plants, the growth of fur and horns in the cases of some animals, or the development of a human embryo. A key notion within Aristotle's metaphysics is that of substance (*ousia*), representing the core ontological unit out of which the world is composed, and correlatively, the basic unit of predication in rational and scientific discourse. A substance, for Aristotle, is *hylomorphic*, namely, it is defined as a unity of matter and *form*. Whether they are animate or inanimate, substances are said to have their essences immanent within themselves, so as to be able to persist and/or to remain one and the same through alterations to their accidental properties. Contrary to modern postulations of the notion of a substance as merely static and self-contained, as in Descartes' definition of them as "a thing which exists in such a way as to depend on no other thing for its existence" (Descartes 1988, pp. 197–198), Aristotle's concept of a substance emphasized their dynamism. While considered separate, self-subsistent, and individual, at the same time, Aristotle's substances are marked by their movement as well as their causal capacity and/or their ability to act on another entity from without, as in external relations. Pointing to their self-organizing character, for Aristotle, the production of substances is partly due to their own autonomous power (*dunamis*) and/or their teleological movement from potentiality to actuality according to their intrinsic capacities. As contrasted with the

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[9] See *The Complete Works of Aristotle (Vols. 1–2)*, ed. Jonathan Barnes (Princeton, NJ: Princeton University Press, 1984).

process of emergence explicitly inherent in nature (*physis*), the process of production involved in *techne*, whereby human artisans and engineers participate in the process of bringing forth (*poiesis*), directing it so as to craft objects according to their own designs supposedly "perfected" that of nature. Although the two modes of bringing forth are to be viewed as interconnected rather than separate, the notion that (technological) production somehow "perfects" nature puts on display Aristotle's tendency toward anthropocentrism (although there are many other elements of his philosophy of nature that may be considered "biocentric" in character).

From an Aristotelian standpoint, the developmental process an organism undergoes is purposive, given that its mature form is greatly predictable on the basis of inductive reasoning from its immature form. For instance, providing that they have what they require in terms of nutriment, water acidity, oxygen, sunlight, etc.. . . in their marine environment, and are not thwarted in this regard, tadpoles mature into frogs through their specific process of growth, differentiation, and development. While each individual organism varies slightly, the fact that their mature form is that of a frog only, rather than say, a water buffalo, is evidence of such causal, goal-directed, or teleological unfolding. According to Aristotle, the physiological structures (e.g., a fish's scales, gills, and fins) or organisms are suited to an environment (e.g., a fish's "proper" environment is in a river or a lake) and a particular mode of life, carrying out inherent functions (e.g., swimming, foraging for food), and it is a bad state of affairs for them when they cannot do so (e.g., a fish that is out of water suffocates).

Based on these notions, for Aristotle, the concept of nature (*physis*) first names the teleological process by which matter enters into shape or form (*morphe* or *eidos*), relating to the processes by which substances, be they animate or inanimate, emerge. Second, the term nature (*physis*) points to the aforementioned essence of the thing in question (i.e., what it is in itself) through which it determines itself and maintains an identity, even though its attributes may be changed. Third, for Aristotle, nature (*physis*) designates the primal material ground out of which the process of emergence takes place, regardless of whether or not the substance in question is animate or inanimate. On this note, however, the etymological meaning of the later Latin term for nature (i.e., *natura*) was "the uterine orifice of a female quadruped" (Schadewaldt 2014, pp. 25 and 31),[10] relating specifically to a physiological part of an *organism* that is responsible for the generation of offspring rather than to an inanimate entity or member thereof.

Aristotle's threefold conception of nature (*physis*) and his notion of substance (*ousia*), defined as a dynamic unity of matter and form, relates directly to his doctrine of fourfold causality (*aition*). From an Aristotelian orientation, the process of emergence/the teleological movement is explicitly a causal one. When inquirers seek to understand what is responsible for any given emergence, be they animate, teleological centers of life or inanimate objects, they may point to four interrelated

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[10] As regards this Latin meaning of the term, nature (*natura*), Schadewaldt indicates that "for this important fact I am indebted to the erudition of my friend Ernst Zinn."

causes. First, the material cause (i.e., "what is it made out of?") is said to comprise the material component(s) that underlie and/or make up the substance in question, these entering into form in the process of production. Second, the formal cause (i.e., "what is it?") entails both the shape or form that the matter enters into and its nature, as in its essential identity. The biological discipline of morphology can be said to have straddled both of the elements involved in formal causality in that the shape or form of an organism is a core criterion for how it is to be classified. Parallel with the move, on the part of the neo-Darwinism of the twentieth century, to consider the unit of selection the genotype in contrast to the phenotype, genes or genomes have been assumed to represent the organism's "essential biological identity," although more recently, with the advance of epigenetics, the genome has been decentered somewhat in this regard.

Aristotle's metaphysical notion of the "unmoved mover," representing his speculation as to what is responsible for subtly moving or "luring" the organism toward the actualization of its teleological potentiality but which is not of itself subject to this process or reciprocally moved or affected, resonates with the Weismannian conception of the relation between the germplasm and the somatoplasm that was, by and large, accepted by modern biology through the modern synthesis.[11] The "hard inheritance" view adopted therein supplanted Lamarckism and "soft inheritance." Under it, the germplasm was deemed to be the hard basis of heredity and the linear cause of the somatoplasm, the former providing the "program" for the growth, differentiation, and development of the phenotype (i.e., coding for proteins) and acting on it, without any reciprocal response or causal action by the latter on the former. This gene-centered orientation, which considered the relation between genotype and phenotype as one of external relations only rather than also of internal relations, has been eclipsed somewhat in the twenty-first century with the rise of epigenetics, which points to alterations in gene expression, prompted by environmental, somatic, and behavioral factors, which may produce inheritable effects. Today, genes (e.g., homeotic genes) are still considered to be highly important causal factors in an organism's unfolding and in the formation of its physiological structures, but they are but one highly important factor among many and are considered more along the lines of a "mover" that is, to some extent, "moved," for somatic factors, such as morphogens, also contribute in this regard.

Third, the efficient cause (i.e., "how is it produced?") is the activity through which an emergence comes to be. For neo-Darwinian biology, natural selection operating on genes or genomes is the chief efficient cause of evolution. Curiously,

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[11] While in *Evolution: The Modern Synthesis* (Cambridge, MA: MIT Press, 2010), Julian Huxley admitted that "the distinction between soma and germplasm is not always so sharp as Weismann supposed," he commended him for this differentiation, since it had contributed "a great clarification" (17–18) in preparing the way for the modern synthesis, specifically, its emphasis on "hard inheritance" over "soft inheritance." The assumption of a "hard" separation between germplasm and somatoplasm in modern biology, the former directing the development of the latter without any reciprocal response, is evidenced by Francis Crick's recognition of "The Central Dogma of Molecular Biology," *Nature* 227 (1970), pp. 561–563.

modern scientific inquiry into the causes of morphogenesis largely comprises a search for the efficient causes of organismic form, in a curious intermingling of formal causality with efficient causality. Fourth, the final cause (i.e., "why?" or "for what purpose?") is the function, goal, or *telos* that the substance fulfills or is meant to accomplish. Traditionally, organisms have been viewed chiefly as unfolding teleologically from potentiality to actuality. However, given, for example, (1) the Darwinian notion that in the course of evolution, organismic structures can be adapted to the performance of new functions, such that there is really no ultimate "purpose" to attribute to them; (2) that organisms evolve in terms of their form (in both of the senses outlined above), such that there is no immutable essence or a priori identity; and (3) that Darwinian natural selection has been characterized as mechanical and algorithmic, rather than as purposive or intentional,[12] modern neo-Darwinian biology has typically eschewed final causality and has concentrated instead on efficient causality, namely, on explaining phenomena by way of discovering "the mechanisms" underlying them. The mechanistic lens through which modern neo-Darwinian biology typically investigates organisms, which emphasizes efficient causality largely to the exclusion of teleology and/or final causality, has recently come into question. "Mechanism" is an a priori metaphysical concept just as much as "teleology" is, yet it underpins much scientific research, while the natural sciences are supposed to have an empirical foundation. While the concept of mechanism, or, alternatively, the machine metaphor, stemming originally from Descartes' emphasis of its indispensability in the study of nature, has generally been "selected for" in the life sciences, some philosophers of biology have aimed to show that organisms are not machines, given that they are autonomously self-organizing entities which are bearers of intrinsic purposiveness, whereas machines are not.[13] Whereas, on the one hand, organisms implicitly maintain the integrity of their interior milieu in the face of entropy, for example, by way of homeostatic, chronobiological, homeorhetic, and autopoietic processes, it is held that machines, on the other hand, are only extrinsically purposive, in that they are bearers only of the programming issuing from the intrinsically purposive agents operating outside of them. However, this distinction has led to further questioning about the bifurcation of animate entities and inanimate ones (this bifurcation being something that D'Arcy Thompson actively seeks to prevent). An interesting remark pertaining to the tension within the history of the life sciences regarding Aristotelian efficient and final causality stems from mathematician and process-relational philosopher, Alfred North Whitehead (1861–1947), who was D'Arcy Thompson's undergraduate colleague at Cambridge and who corresponded with him intermittently from 1906 to 1945. Whitehead wrote that:

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[12] For example, see Daniel Dennett, *Darwin's Dangerous Idea: Evolution and the Meanings of Life* (New York: Simon & Schuster, 1995), pp. 48–60.

[13] For example, see Hans Jonas, "Cybernetics and Purpose: A Critique," in *The Phenomenon of Life: Toward a Philosophical Biology* (Evanston, IL: Northwestern University Press), 1966, reprinted 2001, 108–134; and Daniel Nicholson, "Organisms ≠ Machines," *Studies in the History and Philosophy of Biological and Biomedical Sciences* 44 (2013), pp. 669–678.

> Aristotle's . . . philosophy led to a wild overstressing of the notion of "final causes" during the Christian middle ages; and thence, by a reaction, to the correlative overstressing of the notion of "efficient causes" during the scientific period. One task of a sound metaphysics is to exhibit final and efficient causes in their proper relation to each other. (Whitehead 1978).[14]

Another important aspect of Aristotle's philosophy of nature was his classification of life forms into groups, in a manner that is somewhat akin to modern taxonomy. He divided up organisms that had blood from those that did not, as well as those that reproduced sexually and those that did not. But perhaps his most notable philosophical division was his classification of organisms on the basis of the kind of "soul" (Gr. *psyche*, as in "psychology") that they appeared to have. By the term "soul" Aristotle can be said to have meant not only the underlying principle of life (as Thompson says, "the ruling force of the body" (1913, p. 23), but also representing the organism's particular kind of "mental" and/or "behavioral" disposition, which related to the particular manner of their teleological unfolding. In short, the soul played a key role in "enforming" the emergent body. Aristotle proposed that there were three types of organism in nature: (1) those with "vegetative" souls (i.e., plants which move and grow); (2) those with "sentient" or "sensitive" souls (i.e., animals [with subjective feelings, and that can experience pain and pleasure and can learn]); and (3) those with "rational" souls (i.e., human beings), whose teleological process is not only physiological, as in the previous two categories, but intellectual as well.

The relevance of this division of "souls" for investigations of the causes of morphogenesis has been articulated recently by Ginsburg and Jablonka in their landmark volume, *The Evolution of the Sensitive Soul: Learning and the Origin of Consciousness* (2019). As they state, they employ the term ("soul") as a tribute to Aristotle, whom they consider to be the greatest philosopher of life and the very founder of the life sciences. For Ginsburg and Jabonka, in *De Anima (On the Soul)*,

> Aristotle carved the living world at its teleological joints. He considered the soul as the principle of life, the cause and source of the living body: "It [the soul] is the source of movement, it is the end, it is the essence of the whole living body." The Aristotelian soul is

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[14] Alfred North Whitehead, *Process and Reality: Corrected Edition*, eds. David Ray Griffin and Donald W. Sherburne (New York: The Free Press, 1978), 84. As for the relationship between Thompson and Whitehead, see Thompson's 1918 letter to Whitehead on the importance of forces of gravity for organismic existence and the question of whether there are "three dimensions of space." The letter is published online by Suzan Mazur under the title "'Three Dimensions of Space'?—D'Arcy Thompson Letter to Whitehead," *Huffington Post*, November 10th, 2017 (accessed June 23rd, 2021) at: https://www.huffpost.com/entry/three-dimensions-of-space-darcy-thompson-letter_b_59f040a0e4b00a4ce5a222cd. See also the references to letters to Whitehead in A. G. Mackenzie (Librarian), *Index to the Correspondence and Papers of Sir D'Arcy Wentworth Thompson* (St. Andrews, UK: St. Andrews University Library, 1987), 194. Furthermore, in "'Problematic Idiosyncrasies': Rediscovering the Historical Context of D'Arcy Wentworth Thompson's Science of Form," *Science in Context* 27.1 (2014), Maurizio Esposito suggests that Whitehead belonged to a close group of Thompson's friends (100), with whom he was in correspondence and that Thompson was (later) "attracted by the [holistic] organicist metaphysics of Whitehead" (99).

> the dynamic embodied form (organization) that makes an entity teleological in the intrinsic sense—having internal goals that are not externally designed for it but that are dynamically constructed by it. (Ginsburg and Jablonka 2019, pp. 8–9)

Ginsburg and Jablonka employ Aristotle's threefold division of organisms based on their type of soul as a heuristic that frames their investigation of the evolutionary emergence of consciousness (i.e., of organismic "subjective feeling"), and of the causal factors contributing to the Cambrian Explosion, which they characterize as "the morphological big bang" (ib, p. 410) on this planet. Later in this chapter, after taking up some of the main contours of Thompson's approach to the study of morphogenesis, I shall unpack and extend Ginsburg and Jablonka's theses, along Thompsonian lines. However, in the next section of this chapter, I will briefly take up the Kantian construal of the metaphysical notions of "form" and "substance," as well as the analogy to the theories of embryonic development of his day (i.e., preformation and epigenesis) that he supplies in relation to the question of the origin of the a priori concepts of the understanding. In so doing, I shall display Kant as a major forbearer of contemporary theories of autopoietic self-organization, his thinking having informed Thompson's physico-mathematical approach to the scientific study of morphogenesis and the latter's stance in relation to the dichotomy of teleology and mechanism.

3.3 Kant on Substance, Teleology, and Mechanism

Immanuel Kant (1724–1804) construed the metaphysical notions of "form," "matter," and "substance" in a different way than Aristotle had done. "Substance," for Kant, was considered an a priori concept of the understanding, alongside other metaphysical notions such as time, space, causality, necessity, self, mechanism, teleology, the principle of sufficient reason, etc.. . . . While Aristotle assumed that "form," with its dual sense, was inextricably linked to "matter" and that both belonged intrinsically to emergent substances themselves, Kant emphasized the notion that rational beings give "form" to perceived "matter" in constituting objects of experience. It is not simply that "form" and "matter" were sub-components of the a priori concept of substance, and to be considered a priori categories unto themselves, but as Kant defines in *Critique of Pure Reason* (1781, 1787), matter and form were inseparable in terms of providing the ground for the possibility of the experience of rational beings in general. For him, matter "signifies the determinable in general," whereas form provides matter with its "determination." (Kant 1984, pp. 369–370). While impressions of sensation may lend themselves to particular modes of determination, ultimately, rational beings order and give form to objects of experience, their experience being mediated by their a priori conceptual framework. To be sure, Kant writes:

> the impressions of the senses provide the first occasion for opening the entire power of cognition to them and for bringing about experience, which contains two very heterogenous

> elements, namely, a matter for cognition from the senses and a certain form for ordering it from the inner source of the pure intuiting and thinking... (Kant 1984, pp. 220–221)

Pointing to the influence of metaphysical categories in science, morphologists not only study and categorize the empirically apparent forms belonging to diverse organisms, but, at the same time, as Kant suggests, in the process of cognition, they give form to the objects of their inquiries. From a Kantian orientation, like any rational being, morphologists necessarily view the unstructured manifold that is present to their senses through the mediating lens of an a priori conceptual framework (e.g., be it implicitly mechanistic or teleological). In the same manner, and hinting at a basis of contemporary thinking relating to self-organization, such as *autopoietic* and enactivist theories, from a Kantian outlook, cognition even gives form to itself and to the body that houses it in the process of self-constitution.

As for the epistemological question as to the "origin" of this a priori conceptual framework, which includes the notions of substance, causality, necessity, etc.... and which is inherent to rational beings, Kant sought to carve out a position that went beyond Descartes' rationalism, on the one hand, which held that such prized ideas were innate (i.e., implanted into the minds of rational beings by God at birth), and Hume's empirical realism, on the other hand, which maintained that all meaningful ideas are a posteriori, or derived from impressions of sensation/experience. In defining his own transcendental idealist position, Kant described the a priori categories as "self-thought" (ib p. 265) and as "arising from the understanding," (Kant 1997, p. 10) the understanding being "their birthplace" (Kant 1984, p. 202). Of course, much later, in the twentieth century, renowned ethologist Konrad Lorenz (1903–1989) postulated the "evolutionary neo-Kantian" thesis that something like the framework of a priori categories of reason, which Kant had posited, existed, but that it owed its origin to the same forces of Darwinian natural selection that preserved individuals with adaptive phenotypic traits that gave them an advantage in the struggle for existence and weeded out individuals with maladaptive traits.[15] For Lorenz, human beings are in possession of such categories [e.g., substance (including the associated concepts of matter and form), causality, necessity, mechanism, teleology, the principle of sufficient reason] as part of their rational natures because they provide a great survival advantage in the struggle for existence. Lorenz paints the picture that, over eons of evolutionary time, such core ideas have consistently demonstrated their indispensability, not only to the particular mode by which human beings constitute the world in the context of their experience, but also in guiding their actions, such that they have been profusely assimilated into the human

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[15] Konrad Lorenz, "Kant's Doctrine of the A Priori in Light of Contemporary Biology" in *Philosophy After Darwin: Classic and Contemporary Readings*, ed. Michael Ruse (New Jersey: Princeton University Press, 2009), pp. 231–247. Lorenz' outlook positively connects Kant to modern biology, but his position is perhaps incomplete, for it does not provide insight into the questions of whether there are objective foundations as regards such categories (as in a putative evolutionary neo-Hegelianism) and whether such prized, "naturally selected," categories can be refined or altered.

genome. Lorenz theorizes that experiential releasing events in the course of the organism's development may be requisite in order for them to be made fully manifest.

Returning to Kant, other than locating the origin of this metaphysical framework in the intellectual faculties of rational beings (i.e., it being "grounded in the nature of human reason" (Kant 1984, p. 400), in the *Critique of Pure Reason*, Kant suggested an analogy to the theories of embryonic development of his day, most notably, preformationism, spontaneous generation (*generatio aequivoca*), and epigenesis.[16] First, Kant implied an association of Descartes' rationalist belief in "innate" ideas with preformationism. Preformationism is the traditional view (asserted, for example, by William Harvey [1578–1657] and Charles Bonnet [1720–1793]) that, following conception, which stimulated the egg to grow, an embryo already has the form of the mature organism that it will become within it (e.g., miniature organs are already present at conception); for humanoids, the embryo is a homunculus that simply grows into its mature form without differentiation. Here, form is already present and emerges purely by way of growth, namely, without development and/or differentiation. While the maternal environment may provide nourishment for the embryo, which enables growth, it otherwise does not alter the vital, intrinsic essence (in some instantiations of the theory instilled directly by God at the creation of the world, members of the same species sharing somewhat in the same form) that provides the embryo's growth or unfolding with its purposive potentiality. Second, Kant associated unmitigated Humean empiricism with the theory of spontaneous generation, wherein especially the so-called lowliest of organisms issue forth from material nature, for example, flies and maggots from the presence of a carcass or of rotting meat, and worms and slugs from the presence of moist soil. While this theory was present in Aristotle's works, Kant meant to compare Hume's skeptical tracing of all of our ideas, including the concepts of the understanding, back to prior impressions of sensation, having all content in them, insinuating that their lowly status is ultimately conditioned by sensation and/or that they result from "the mere confluence of aggregated concepts" (Kant 1984, p. 692), something he would never accept.

Third, Kant associated mitigated (in terms of the level of skepticism) Humean empiricism, which left room for certain prized metaphysical concepts (lest the human species should perish), with the theory of epigenesis. Epigenesis is the traditional view that, following fertilization, the embryo starts off as cells that divide: the embryo's development toward its mature form involving successive differentiation in stages. The embryo is said to contain certain elements that, during development, react together to bring forth others that were not originally present in it (Van Speybroeck 2002, p. 67). Here, organs and limbs are not present in the embryo.

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[16] Of course, as Hein van den Berg reminds us in *Kant on Proper Science: Biology in the Critical Philosophy and the Opus Posthumum* (New York: Springer, 2014), these theories are also "frameworks for understanding what we might call various types of organic generation, including regeneration, and growth" (193).

Rather they develop as a by-product of (cellular) differentiation. In the theory of epigenesis, the maternal environment is said to play a greater role in the development of the embryo, not only providing what is needed for its growth (i.e., nourishment) but also helping to trigger appropriate processes of (cellular) differentiation. It should be noted that the traditional notion of epigenesis is a root of today's key term, epigenetics,[17] being the study of the layer of biological connections that "sits atop the genome" regulating gene expression, but that can be affected by behavior and environment in ways that can be inherited.[18] But the meanings of these terms are not merely synonymous.

Based on Kant's characterizations of competing epistemological standpoints by way of his analogies to the theories of embryonic development of his time, Kant sought to characterize his own transcendental idealist position—which involved the notions that rational beings "cannot think any object except through categories" (e.g., substance, mechanism, and teleology) and that they "cannot cognize any object that is thought except through intuitions that correspond to [the *a priori*] concepts" (Kant 1984, p. 265)—apart from Descartes' rationalism (which was implicitly compared with preformationism) and the unmitigated and mitigated versions of Hume's empirical realism (as implicitly associated with the theories of spontaneous generation and epigenesis, respectively). While the yardsticks and contours of his formulation of his position seem to "move" somewhat in his presentation of the analogy, and for a great deal of his prior career, Kant had emphasized "preformationism," in the revised 1787 version of the *Critique of Pure Reason*, Kant moved closer to associate his own epistemological position with that of a considerably tempered "epigenesis" as compared to the one he had implicitly associated with the Humean empirical realism of the mitigated variety.[19] While the

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[17] As Jonathan B. L. Bard, in "Waddington's Legacy to Developmental Theoretical Biology," *Biological Theory* 3.3 (2008), suggests "epigenetics is actually a portmanteau term and a conflation of epigenesis—the belief that development is the gradual process of taking a simple egg and allowing complexity to develop (contrasting with preformationism, the idea that development is just the expansion of structures already present in the fertilized egg)—and genetics, the study of the laws of heredity" (p. 191).

[18] Conrad Hal Waddington's coining of the term "epigenetics" takes aspects of both "preformationism" and "epigenesis" into account, synthesizing them together. To be sure, in *Principles and Problems of Development and Differentiation* (New York, Collier Macmillan Ltd., 1966), Waddington wrote, "we know that a fertilized egg contains some preformed elements, namely, the genes and a certain number of different regions of cytoplasm, and we know that during development these interact in epigenetic processes to produce final adult characters and features that are not individually represented in the egg. We see, therefore, that both preformation and epigenesis are involved in embryological development" (p. 15).

[19] While for most of his career, Kant had been a preformationist, following from the work of Caspar Friedrich Wolff's (1733–1794) *Theoria Generationis* (1759) and Johan Friedrich Blumenbach's (1752–1840) *Institutiones Physiologicae* (1787), Kant only gradually came to assert that the theory of epigenesis was superior to that of preformation. In the *Critique of the Power of Judgment*, Kant attempts to provide evidence that supports the former, but it must be noted that Kant's defense of epigenesis was of a considerably weak form, when compared with Herder's, and later Schelling's versions of the theory. Kant was uncomfortable with the idea of epigenesis up until 1787, which

proper word connecting his synthetic position to a designated theory of embryonic development remained unnamed in the first Critique, what is clear is that Kant aimed to present the contrast between the possibilities of "a system of the epigenesis of pure reason" and a "preformation system of pure reason" (Kant 1984, pp. 264–265).

It was not until the *Critique of the Power of Judgment* (1790) that things become somewhat clearer. There, Kant more fully recognized the interrelationship between preformationism and epigenesis, by asserting that:

> the system of epigenesis . . . can also be called the system of generic preformationism, since the productive capacity of the progenitor is still preformed in accordance with the internally purposive predispositions that were imparted to its stock, and thus the specific form was preformed *virtualiter*. (Kant 2000, p. 291)

In other words, Kant displayed a mitigated "adherence to epigenesis, with the relevant qualification being that the causality responsible for the epigenetic capacities of organic bodies be conceived in preformationist terms" (Fisher 2014, pp. 25–26). Writing well prior to the onset of modern genetics, with its concrete understanding of "genetic instructions" directing embryonic development, Kant recognized that an element of preformationism lay regnant in the context of epigenesis. Nevertheless, had the contemporary keyword "autopoiesis" (Gr. self-creation, self-production, self-maintenance) been coined at that time, Kant might very well have employed it (i.e., as in an "autopoiesis of reason") in representing his more synthetic epistemological position beyond the competing notions that "form precedes development" and "development precedes form." For elsewhere in the *Critique of the Power of Judgment*, Kant displays himself explicitly as a chief forbearer of contemporary autopoiesis theory.

For Kant, the nature of an organism revolves around being a "natural end" (i.e., a bearer of intrinsic purposiveness), a whole in which its members constitute a reciprocally active, mutually productive, causal network that supports the persistence of that whole. He writes that:

> for a thing to be a natural end it is requisite, first, that its parts (as far as their existence and their form are concerned) are possible only through their relation to the whole . . . [but] second, that its parts/members be combined into a whole by being reciprocally the cause and effect of their form. For in this way alone is it possible in turn for the idea of the whole conversely (reciprocally) to determine the form and combination of all of the parts . . . For a body, therefore, which is to be judged as a natural end in itself and in accordance with its internal possibility, it is required that its parts reciprocally produce each other, as far as both their form and their combination is concerned, and thus produce a whole out of their own causality. . . . consequently, the connection of efficient causes could at the same time be judged as an effect through final causes.

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makes his analogies here confusing for interpreters. To make things even more puzzling, Kant had sought initially to make the connection between his transcendental philosophy and preformationism, rather than with epigenesis, in order to make the case that the a priori categories were pre-given in the understanding, but revised this analogy in the 1787 version of the first *Critique*.

> In such a product of nature each part is conceived as if it exists only through all the others, thus as if existing for the sake of the others and on account of the whole, i.e., as an instrument (organ), . . . [but also] it must be thought of as an organ that produces the other parts (consequently each produces the others reciprocally) . . . only then and on that account can such a product, as an organized and self-organizing being, be called a natural end [my addition]. (Kant 2000, p. 245, my additions in square brackets).

So, from a Kantian perspective, judgments of entities as bearers of intrinsic purposiveness entail that the members internal to them are reciprocally means and ends for themselves. In other words, the members internal to the entity in question are reciprocally causes of, and effects for, one another, operating conjointly for the sake of the cumulative production of, and the maintenance of the integrity of, the supervenient whole. In such a manner, living systems are intrinsically purposive, autonomously self-organizing, self-creating, self-producing, self-forming, self-maintaining, self-repairing entities, their members working in a causally reciprocal manner for the sake of maintaining the whole, and the integrity of the whole also being a condition for the possibility for the particular functioning of the parts. Kant goes on to assert that:

> an organized being is thus not a mere machine, for that has only a motive power, while the organized being possesses in itself . . . a self-propagating formative power, which cannot be explained through the capacity for movement alone (that is, mechanism). . . . As natural ends . . . organized beings . . . provide natural science with the basis for a teleology. (Kant 2000, pp. 246–247).

As Weber and Varela assert in "Life After Kant: Natural Purposes and the Autopoietic Foundations of Biological Individuality" (2002), in these passages, Kant gave "a visionary account of self-organization that anticipates the definition of autopoiesis almost literally, but within the bounds of a transcendental analysis."[20] However, Kant did not simply give "free rein" to teleology. Rather, he painstakingly examined the contours of the antinomy between the logically contradictory claims that "all generation of material things is possible in accordance with merely mechanical laws," and that "some generation of things is not possible in accordance with merely mechanical laws."[21] On the whole, Kant attempted to cultivate a synthetic position between teleology and mechanism, giving both sides their due, although treating the former as a "regulative" and the latter as "constitutive." He sought to

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[20] Andreas Weber and Francisco J. Varela, "Life After Kant: Natural Purposes and the Autopoietic Foundations of Biological Individuality," *Phenomenology and the Cognitive Sciences* 1 (2002), 120. For Weber and Varela, some of the new developments and research programs in the life sciences of the late twentieth and early twentieth century necessitated revisiting and reframing of Kant's ideas. They question the use of Kant's stance on teleology to support the relegation of it in contemporary neo-Darwinian biology to the status of an "appearance only," as in the notion of "teleonomy" (in which the specter of goal directness is present, but held ultimately reducible to mechanical explanation). That said, Maturana and Varela's original formulation of autopoiesis in the 1970s was explicitly mechanistic in nature.

[21] Kant, *Critique of the Power of Judgment*, 259.

avoid a chaotic situation in which the teleological and mechanical notion were simply “jumbled together” (Kant 2000, p. 249) haphazardly in the context of scientific inquiry. For Kant, both were necessary for understanding organized beings, and the study of organized forms must operate in the space of (dialectical) tension between them, even though he strongly believed that it was the duty of the natural sciences, as far as possible, to strive to carry out a mechanistic explanation of natural phenomena.

In the third Critique, the rationale Kant provides for his position is basically as follows. On the one hand, there is the claim quoted above, that, given their teleological, circular structure of the process of self-organization, the natures of living creatures cannot be fully grasped in purely mechanistic terms, even though mechanistic analysis could serve to illuminate many of the important causal underpinnings belonging to this teleological process. Also, for Kant, mechanistic principles were limited in that they could not serve to explain the underpinnings of the universe or the system of nature which included organismic teleology within it. In these regards, Kant thought that it was a “necessary maxim of reason not to bypass the principle of ends in the products of nature” (ib, p. 280). On the other hand, he held that to emphasize the teleological to the neglect of the efforts of mechanistic explanation came too close to an attempt to penetrate into entities as they are in themselves (e.g., reason somehow being able to know the exact conceptual content that was communicated in the firing of a neuron comes to mind), which is precisely what Kant had sought to criticize. It was simply beyond the capacities of reason, in general, to arrive at a determinate cognition of nature’s noumenal substratum. Furthermore, Kant saw the wisdom of not bifurcating nature (as Descartes had done) into entirely separate categories (i.e., inanimate versus animate entities), which would suggest that a separate set of non-mechanistic laws, beyond Newton’s laws of nature, would have to be derived for the latter in order to account for their unfolding. This would thereby place organisms into the category of non-natural entities and would inevitably lead to the justification of theological speculation into what could not be known by human reason, doing so in the context of scientific discourse. So, for Kant, while mechanistic principles could be used to help explain teleological phenomena with certainty, teleological principles were hard-pressed to be able to unpack material nature without resorting to a different level of metaphysical abstraction, involving discourses about the intentions of nature, the supersensible, theological speculation, which would require the assertion of truth claims based on that which is inaccessible to human reason.

It was Kant’s stance that teleology was indeed a positive heuristic for guiding scientific inquiry (such that, for example, offhand functionalist language could productively be employed by inquirers as long as was treated as an “as if”), but he stood firm in asserting that it ought not be constitutive in terms of the methods of the natural sciences or their concrete explanations. For Kant, the over-extension of the teleological principle into that which goes beyond what reason can know would ultimately end up in tautological assertions, and rational beings would not be able to achieve a “proper cognition of nature” (ib, p. 259). As he states, “it is of infinite importance to reason that it not allow the mechanism of nature in its productions to drop out of sight and be bypassed in its explanations; for without this no insight into the nature of things can be attained" (ib, p. 279). From a Kantian point of view, the over-extension of the teleological principle into the methodology of the natural sciences would end up "snuffing out" the need to inquire that the "principle of sufficient reason" promoted. Teleology could thereby "stand in" for explanation where explanation was not forthcoming, but it could not ultimately of itself provide proper explanation. It is for these reasons that Kant (2000, pp. 292–293) commended the work of Johann Friedrich Blumenbach (1752–1840), who, in "On the Formative Drive" (1781, 1789), had elucidated an epigenetic theory of embryonic development, showing how it was consistent with preformationism. At the same time, whereas Blumenbach had posited the existence of a "vital force" that directs organismic formation and regeneration, Kant did not go so far as to embrace it (van den Berg 2014, pp. 190–198 and pp. 204–220). For it committed Blumenbach to the bifurcation of nature, and as a case in point regarding teleology, other than acknowledging its existence, this "vital force" introduced a concept that was without an objective correlate into the material world, and was said to have causal capacities that stood against the established laws of nature. Taken "as is" this "vital force" could not be pointed to empirically, its origins could not be illuminated, it could not be explained, and from a scientific point of view, the question of how, in fact, it caused organismic form could not be inquired into, without at least deploying some measure of mechanistic analysis. But also, its own purpose (as in final causality) could not be unpacked. Really, other than being able to refer to it conceptually, nothing further could be said objectively about this "vital force," at least not easily. Kant also criticized Johann Gottfried von Herder's (1744–1803) concepts of "genetic force" and "organic force," deemed to represent the cause of epigenesis *period*, in that, without sufficient elucidation of their mechanistic underpinnings and their own origins (i.e., how it is that they came to exist), these and other concepts pointing to the supersensible, for Kant, did "not belong to natural science but merely to speculative philosophy" (ib pp. 206–208). In short, Kant thought that it was necessary to employ the concept of teleology in the context of describing the nature of organisms, but he objected to teleological principles being invoked as causal explanations for organismic phenomena in a manner that portrayed them as "black boxes" containing "occult" qualities, or that simply came with a "period" of finality after them, namely, in a dogmatic way that neglected precise mechanistic analysis and/or that went beyond nature and its laws.

On the whole, Kant certainly gave the teleological perspective its due in the context of outlining the contours of what greatly approximates today's conception of autopoietic self-organization. Nevertheless, for Kant, it was the "meritorious" duty of natural scientists "to pursue the mechanism of nature, for the sake of an explanation of the products of nature, as far as can plausibly be done, and indeed not to give up this effort" (Kant 2000, p. 286). While Kant admitted that it was "impossible in itself to find the purposiveness of nature by [way of] this route," (ib) this was not a defect of mechanistic explanation, but part of the wider limitations to the capacities of reason that he had emphasized throughout his philosophical system. Kant staunchly maintained that a proper natural science should be systematic, have an objective grounding, and be apodictically certain. And of course, in light of these conditions, it should be mathematical, as in his famous dictum that:

> in any special doctrine of nature there can be only as much *proper* science as there is *mathematics* therein . . . a pure doctrine of nature concerning determinate natural things . . . is only possible by means of mathematics. . . . a doctrine of nature will contain only as much proper science as there is mathematics capable of application (Kant 2004, p. 6).[22]

For Kant, the science that modeled these principles the best, of course, was physics, whose chief tool was mathematics. Accordingly, while it was welcome for scientific inquiries into the unfolding of organisms to direct themselves with the help of the regulative principles of teleology, ultimately, they ought to restrict themselves to the pursuit of mathematically precise, mechanistic explanation.

While evidently, Aristotle and Kant, as grand figures of the history of Western philosophy, have been interpreted in innumerable, different ways, it is in the light of the above understanding of Aristotle's and Kant's thought that I turn now to the thinking of D'Arcy Wentworth Thompson surrounding morphogenesis. Thompson was a scholar-naturalist whose contributions were original in their own right. He was undoubtedly inspired in his work by a vast number of past figures (e.g., Galileo, Newton, Descartes), and he had a wide international network of colleagues whom he interacted with in the context of his own research program.[23] Clearly, Thompson was not simply an Aristotelian or a Kantian, or both. But the influence of Aristotle's and Kant's respective doctrines (e.g., as outlined above) concerning substance, matter, and form, as well as teleology and mechanism in science, on Thompson's overall "physico-mathematical" approach to the study of morphogenesis, including his stance as regards the proper scientific outlook, the methods for investigating it, and his respective criticisms of vitalism, Darwinian natural selection, and genetics, cannot be overlooked. After all, Thompson wrote in his introduction to *On Growth and Form* that:

> physical science and philosophy stand side by side, and one upholds the other. Without something of the strength of physics, philosophy would be weak; and without something of philosophy's wealth physical science would be poor. (Thompson 1942, p. 14).

Thompson was not alone in his "Kantian," or alternatively, "neo-Kantian" interests. As for the explicit historical connection of Thompson to Kantian biophilosophy, Thompson can be said to have belonged to a diverse, multi-generational group of scholars and naturalists on the British intellectual scene that "all had bequeathed, through diverse routes and ways, Kant's bio-philosophical tradition" (Esposito 2013, p. 49) although each may have expressed it differently (e.g., neo-Kantian, post-Kantian). This group included figures such as Adam

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[22] Also see van den Berg, *Kant on Proper Science*, 15–51.

[23] For an elucidation of the scope of Thompson's network of intellectual contacts and research colleagues, see Maurizio Esposito, "Problematic 'Idiosyncrasies,'" 79–107.

Sedgwick (1854–1913), John Scott Haldane (1860–1936), Joseph Henry Woodger (1894–1981), and many others. The closest to Thompson was his personal friend and colleague, Haldane, who had pursued training in philosophy and biology in Germany, and had attended some of Ernst Haeckel's and August Weismann's lectures (afterward being critical of the latter). Haldane had a deep interest in both Kant's and Hegel's respective philosophies, Hegel having attempted to point to the objective aspect of the category of teleology as found in organisms.[24] Early on in his career, Haldane had co-written material relating to Kantian biophilosophy, pointing to the Kantian notion that organisms are "self-conserving systems," and that Darwinian natural selection and adaptation say nothing about such a notion.[25] Thompson had numerous scholarly and scientific interchanges with Haldane (Esposito 2013, p. 54), as for instance, their 1918 Symposium on the question: "Are Physical, Biological and Psychological Categories Irreducible?" and their mutual participation in a 1929 conference on "The Nature of Life."[26] Haldane had

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[24] Although disagreeing with Kant's self-imposed limitation of reason, Georg Wilhelm Friedrich Hegel (1771–1830) followed the latter's theses concerning the nature of life, suggesting that "one of Kant's great services to philosophy consist in the distinction he has made between relative or external, and *internal purposiveness*; in the latter he has opened up the notion of life" (*Science of Logic*, trans. A. V. Miller [New Jersey, NJ: Humanities Press, 1969], 737). Another of Kant's "great services to philosophy," according to Hegel, is his exhibition of the general dialectical "opposition between teleology and mechanism" (*Science of Logic*, 737). Consistent with Kant, elsewhere, Hegel states that "all of the body's members are reciprocally both means and ends for each other from moment to moment" (*Encyclopaedia Logic*, trans. T. Geraets, H.S. Harris, and W. A. Suchting, Indianapolis, IN: Hackett Publishing Company, 1991], §216, 291) and the organism "maintains itself by self-production. . . . This activity of the members is just the One [activity] of the subject into which its productions return—so that in all this only the subject is produced; i.e., it simply reproduces itself" (Hegel, *Encyclopaedia Logic*, §218, 292). In the *Logic*, Hegel goes on to discuss the categories of Chemism, Mechanism, and Organism, and their dialectical relationships, the latter category involving the notion of intrinsic purposiveness which has actuality. As regards the Kantian notion of "appearance" (as in the notion that reason is limited to appearances only and cannot penetrate to the noumenal), in the *Encyclopedia Logic*, Hegel argues that when something "appears" (*scheinen*) to be such and such (e.g., living organisms appear to be teleological), there is an objective element that can be inquired into (see "The Doctrine of Essence," sections 112–141). In relation to Hegel and dialectics, in "Organism: A Meshwork of Selfless Selves," in *Organism and the Origins of Self* (Boston Studies in the Philosophy of Science 129), ed. Alfred I. Tauber (Dordrecht, Germany: Springer, 1991, my additions), Francisco Varela suggests that "the concept of an organism connotes a knotty dialectic: a living system makes itself into an entity distinct from its environment through a process that brings forth," autopoiesis entailing a "dialectic between the local component levels [i.e., the organism's members: organelles, cells, tissues, organs, systems, etc.] and the global whole [i.e., the organism as a whole], linked together [in interpenetrating and] reciprocal [causal] relation" (84).

[25] For example, see chapter three of Maurizio Esposito's *Romantic Biology, 1890–1945* (New York: Routledge, 2013), pp. 53–82, and his "Between Holism and Reductionism: Organismic Inheritance and the Neo-Kantian Biological Tradition in Britain and the USA, 1890–1940" (PhD Thesis) (University of Leeds, UK, October 2011), 61–64, also see 87–89 and 103–106.

[26] See J. S. Haldane, D'Arcy W. Thompson, P. Chalmers Mitchell, and L. T. Hobhouse, "Symposium: Are Physical, Biological and Psychological Categories Irreducible?," *Proceedings of the Aristotelian Society*, Supplementary Volumes, Volume 1: Life and Finite Individuality

taken to the more holistic, organicist, teleological line of Kantian–Hegelian biophilosophy, whereas Thompson (non-reductively) took to Kant's more materialistic and mechanistic side in the context of scientific inquiry while still doing justice to teleology. Arguably, of the two, Thompson's approach was more accurate to the overall stance taken by Kant himself.

3.4 Thompson's "Physico-Mathematical" Approach to the Study of Morphogenesis and His Criticisms of Vitalism, Natural Selection, and Genetics

Thompson defined "morphology" (the science he wished to reinstate) broadly as "the study of Organic Form," this study being "but a portion of that wider Science of Form which deals with the forms [and patterns] assumed by matter under all aspects and conditions, and in a still wider sense, with Forms which are theoretically imaginable" (Thompson 1915, p. 856). In *On Growth and Form*, Thompson characterizes that:

> we are dealing with Form in a very concrete way. To Aristotle it was a metaphysical concept; to us it is a quasi-mechanical effect on Matter of the operation of chemico-physical forces. To Aristotle its Form was the essence, the archetype, the very "nature" of a thing, and Matter and Form were an inseparable duality. Even now, when we divide our science into Physiology and Morphology, we are harking back to the old Aristotelian antithesis. (Thompson 1942, p. 82).

For Thompson, inquiry into the causes of the physiological forms of organisms was to be viewed largely as an extension of the study the causes of physical form of entities in general, thereby counteracting the bifurcation of entities into the domains of the living and the non-living. To be sure, there was "no essential difference between phenomena of organic form and those which are manifested [more generally] in portions of inanimate matter" (Thompson 1915, p. 858),[27] recognizing that the interiority of the body and its vast, interconnected tapestry of organs and cellular fields are by no means places of deviance from the laws of physics and chemistry, the organism not only being a part of energetic nature, but helping to compose it. For Thompson, living substances embodied emergent manifestations of those same laws, differing only in terms of the levels of order and complexity involved in their confluence. While he played up the importance of the "old" laws of Newtonian physics in this regard, he was open to having inquiry also be guided by the principles

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(Oxford, UK: Oxford University Press, 1918), pp. 11–74. The second conference that Haldane and Thompson participated in was the *British Association for the Advancement of Science Meeting* in Cape Town, South Africa, July 22–August 3, 1929.

[27] Thompson reiterates this statement in *On Growth and Form* 1942, 1029.

of the "newer" physics (e.g., relativity physics, and we might add in quantum mechanics).[28]

From a scientific standpoint, for Thompson, organisms should not be treated as though they were simply (supernaturalistic) exceptions to the established laws of physics and chemistry, as, for example, he felt vitalism had been apt to promote. He emphasized that morphology ought to focus its investigations of every manner of physical force acting on and "sculpting" the physiologies of organisms (e.g., "gravity, pressure, cohesion, friction, viscosity, elasticity, diffusion, ... [and] surface tension" (Thompson 1911, p. 424) over time. One might also include factors such as temperature, humidity, stress, stretching, twisting, fracturing, adhesiveness, chemical interactions, velocity, density, electromagnetism, nuclear force, entropy, geological rhythms, (approximate) fractal symmetry and symmetry breaking, illumination, and color. For Thompson, "stress and strain are concerned in the fabric and in the physiology, of the organism" and it was his intent to investigate "how physical and mechanical relations ... and incident forces of gravity, growth, and pressure control or determine the shape of the leaf and bone and single cell" (Thompson 1913, p. 6).

One might consider the physical pressures that cause the elongated, conical shape of a newborn baby's skull after it has passed through the birth canal.[29] One of Thompson's own examples involved the tying of a rag tightly around a "little round gourd," which applies a pressure that instead of producing one round or oval form grows into one resembling a weightlifter's barbell, with two spherical masses joined together (Thompson 1942, p. 1049). Still another pointed to the effect on the human body of gravity over time, leading to the sagging and droopiness of various parts in old age after having been initially adroit in youth (ib, p. 1050). Although such an observation may seem at first to entail scientific platitudes, upon further reflection, today, we are certainly learning about the drastic effects on the body stemming from protracted periods of relative weightlessness in space (e.g., deterioration of bone and muscle, loss of fluid volume, intracranial pressure). If humanity is to pursue space exploration, more research will have to be carried out in order to deal with the question of how to minimize the dire physiological effects that will stem from prolonged periods spent on other planetary environments (e.g., Mars' gravitational acceleration [3.72 m/s^2] is only 38% that of the Earth's [9.81 m/s^2]). While the evolution of the life forms of which we have knowledge has been terrestrial, extrapolations might be made about evolution within other planetary environments.

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[28] See D'Arcy Wentworth Thompson 1942, pp. 15–21.

[29] With this example, there is a risk of interpreting Thompson as being onside with Lamarckian reasoning in that a giraffe's stretching of its neck causes the evolution of neck length. Of course, Baldwinian reasoning, following Darwin, is that the giraffes with longer necks which assisted them to carry out the "good trick" of reaching food on high branches, a behavior that had become important for survival, were cumulatively selected for. Yet, a Thompsonian could respond by saying that physical causes still play the key role and not just the novel behavior, as it is the mechanical efficiency that is afforded by the shape or form of the necks that bestows onto giraffes the ability to exploit the new niche in the environment.

In terms borrowed from chronobiology, from a Thompsonian perspective, organismic form is, at once, (1) generated by the endogenous physical forces, energies, oscillations, and rhythms underpinning organismic growth and (2) *entrained* exogenously to a great extent by way of physiological immersion over time in the confluence of physical forces, energies, and rhythms belonging (in specific magnitudes) to its particular geological environment and more widely the general regularities holding (as far as we expect) throughout the cosmos; the endogenous and the exogenous physical forces in play ultimately are manifestations of the self-same cosmic constants.

Thompson felt that morphology ought not just compare organismic forms and patterns with other organismic forms and patterns, but also organismic forms and patterns with those belonging to inanimate entities. The more or less similar and repeated forms and patterns that belong to the general six-sidedness of crystals of snow, soap suds, the hexagonal structure of honeycomb, and even "the waves of the sea, the little ripples on the shore, the sweeping curve of the sandy bay between the headlands, the outline of the hills, the shape of the clouds" (ib, p. 10)[30] had demonstrably been chiseled out by the interplay of various physical forces over time. Although each snowflake, bubble of ocean foam, or living cell may be different, each has a general, characteristic shape, emerging and stemming from the confluence of physical forces acting within, and on, them according to the laws of nature (which determined what was possible for them in terms of physical form). From a Thompsonian position, fields of living cells in organisms in terms of their replication and adhesion would have commonalities with, say, crystalline sheets, in terms of their development, as they would be subject to similar physical forces acting on, and inherent in, them. Or, studying the physical dynamics of mixing oil and water could be edifying in terms of similar physical dynamics within living organisms. However, for Thompson, not only did inanimate entities present clues as to the nature and causes of organismic form (e.g., spherical, radially symmetrical, bilaterally symmetrical), but similar patterns could be seen in the very constitutions of those organismic forms. For instance, from a biophysical point of view, rounded bodily structures preserve warmth the best, of any shape, a sphere having the least surface-area-to-volume ratio, meaning the least area for warmth to escape. Or, for aquatic organisms to live "successfully" in an underwater environment their bodies must be neutrally buoyant (i.e., they must offset the gravitational force, which, of course, is constant, but also not float on the surface). This requires a morphology (e.g., having a swim bladder) that is suited to its environment in that it counteracts the forces underlying both negative buoyancy and positive buoyancy. Among other factors, the average density of their bodies cannot either be denser or significantly less dense than the water (warmer saltwater being less dense than colder freshwater) in which they are immersed.

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[30] Thompson also made comparisons between organisms and structures built by humans such as houses and bridges.

For Thompson, the growth of organisms was not only constrained by physical forces but was a confluent manifestation of physical and chemical forces and transferences of energy. Organisms were emergent, dynamic products, arising out of this complex confluence of forces. And ecosystems could themselves be interpreted as transferences of mass and energy. As such, Thompson characterized the living organism as representing or occupying "a field of force . . . of immense complexity" (ib, p. 1030) and their forms as "diagrams of forces" (ib, p. 16). They and their members (including the germplasm) constituted dynamic "seat[s] of energy and center[s] of force," (ib, p. 20) internally speaking, manifesting themselves in the context of a tension with the offsetting constraints posed on them by other physical forces acting on them. Thompson endeavored to show how alterations of geometric form, or transformations, could occur greatly as a result of the interpenetrating and reciprocal causal interaction occurring between the forces underpinning organismic growth and the external physical forces over time, aspects of which in many cases could be measured in precise mathematical terms.

In charting the geometrical changes pertaining to the physiological forms of organisms over time, Thompson drew on Aristotle's notion of the "golden ratio" and/or the virtuous "golden mean" (ib, p. 923 and p. 932, as well as Thompson 1929, pp. 43–55) between excess and deficiency (or "defect" as Thompson writes), as outlined in *Nicomachean Ethics*. Thompson relates that his own physico-mathematical inquiries into the forms of organisms were based on the principles that Aristotle had established. Precisely, Aristotle had demonstrated that generally, "the essential differences between one 'species' and another are merely differences of proportion, of relative magnitude, or of 'excess and defect,'" and it was this insight upon which Thompson based his signature "co-ordinate method" (Thompson 1942, pp. 1034–1035). By placing diagrams of various organisms and organismic structures on a "Cartesian grid," Thompson aimed to disclose the systematic deformation of an initial physiological structure as a result of physical forces. Formation could in many respects equally be construed as deformation. As he writes,

> in a very large part of morphology, our essential task lies in the comparison of related forms . . . and the *deformation* of a complicated figure may be a phenomenon easy of comprehension . . . This process of comparison, of recognising in one form a definite permutation or *deformation* of another . . . lies within the immediate province of mathematics, and finds its solution in the elementary use of a certain method of the mathematician. This method is the Method of Co-ordinates, on which is based the Theory of Transformations (Thompson 1942, p. 1032).

As a crude representation of his coordinate method, at holiday events, Thompson "used to entertain children by drawing pictures of dogs on rubber sheets and stretching them from poodles to daschunds" (Wolfram 2021; Ruth D'Arcy Thompson 1958, p. 230). This is nearly the exact metaphor that Richard Dawkins employed in elucidating the nature of his own "biomorph algorithm" (of course, Dawkins adds that it is genes that "mathematically control the stretching" of the evolving rubber) (Dawkins 2015, pp. 191–195). Illuminating the Thompsonian point here, Newman et al. (2006) insist that non-living viscoelastic materials such as clay, rubber, lava, and jelly, for example, are subject to being molded, formed, and deformed by the external physical environment. Recognizing that such materials have been called "soft matter" by the physicist de Gennes (1992), they state:

> Most living tissue are soft matter and all of them are also what physicists term "excitable media" . . . materials that respond in active and predictable ways to their physical environment. It is clear that some, if not much of organismal plasticity results from such material properties. (Newman et al. 2006, p. 90).

Ultimately, according to Thompson, living organisms are made of malleable materials (e.g., the human body is made up of about sixty percent water, and some organs are of a higher percentage), not only impressed upon, and molded, by external physical forces, but their internal milieu is composed and maintained by way of physicochemical forces. Its integrity also depends on those from outside. Physicochemical forces also pervade the interior-exterior divide. Further, organisms are also active in mustering up the physical forces necessary to impress upon, and mold, what is outside of them (including objects and other organisms in the natural environment). Thompson also refers briefly to the father of homeostasis research Claude Bernard's stance that, without remainder, "mechanical, physical, and chemical forces [adequately] summed up all with which the physiologist has to deal" (Thompson 1911, p. 421), regardless of the implicit goal directedness that seems to be involved with homeostatic processes. Some key issues here involve the questions of how exactly the physical elements and forces that pervade the body are organized ongoingly in a self-productive fashion and whether there is some potentially teleological element transcending them that was responsible for the phenomenon of self-organization. Following from Kant, Thompson did not deny the apparently teleological aspect(s) of the organism, but he was content to focus on what could be demonstrably known and measured mathematically. Taking the "road of observation and of experiment," (ib, p. 422) he was largely critical of overt claims and conjectures as regards the former (e.g., as in the vitalisms of his day).

In chapter seventeen of *On Growth and Form*, "On the Theory of Transformations or the Comparison of Related Forms," Thompson most prominently exhibits his "co-ordinate method" of placing his two-dimensional drawings of the forms of various organisms onto rectilinear grids, the outlines of their bodies being at fixed coordinates. He then carried out a geometrically uniform "angular stretching" of the underlying axes on grid, mimicking various physiological forces and patterns of organismic growth in their tension with the exigencies of the physical forces acting on it in its particular environment, thereby displaying potentially interspecific "transformations." By the sheer manipulation of the grid, namely, by way of simple mathematical equation, the shape or body plan of one arthropod, fish, or crab species could be "stretched" excessively, pressed into deficiency, or deformed into that which was held to belong to another species. In comparing the initial form with the resultant one, while the species in question were deemed in the context of the norms of Linnaean taxonomy to be entirely separate species (largely on the basis of their "form"), in actuality, their forms were different only due to

Thompson's manipulation of the underlying grid (representing the impact of physical forces on organismic growth). He concluded that the resulting forms could be construed as variants of the former forms (i.e., topologically related to them in morphospace) and that a change in quantity pertaining to a physical force operating on organisms could cause a change in quality as regards their forms.

Thompson cites Aristotle to the effect that while some organisms have parts that do not resemble those of others, "as a general rule, most parts and those that go to make up the bulk of the body are either identical with one another, or differ from one another in the way of contrast and of excess and defect. For 'the more' and 'the less' may be represented as 'excess' or 'defect'" (ib, p. 1035). For instance, for Thompson, the morphologies of a puffer fish and a sunfish were basically the same, the differences being mostly representable mathematically through the Aristotelian notions of excess and deficiency. A sunfish's morphology was generally representable as an excess of that of a puffer fish, and, in turn, that of a puffer fish was representable as a deficiency of the sunfish's. The Aristotelian notions of excess, deficiency, and the golden mean may be said additionally to be aligned with the notion of homeostasis through which the far-from-equilibrium mean, set point, or stable state (which serves to maintain the internal milieu of the organism in the face of external perturbations and/or the forces of entropy) is "attained" in a dynamic, vibratory, oscillatory, and processive fashion by way of positive and negative feedback, rather than statically. Connecting the theme of homeostasis with the Thompsonian perspective on morphogenesis, it may be said that physical forces provide feedback and negative feedback which entrain and canalize the relatively stable, far-from-equilibrium, morphological states, which are characteristic of the limited number of forms belonging to the "tree," or "cone," of life on this planet. Thompson's emphasis on the mathematical aspect of Aristotle's notions of excess, deficiency, and the golden mean also reverberate with the wondrously uncanny Fibonacci sequences that are found throughout physical and organismic nature (e.g., in the adaptive patterning of the petals of various flowers [as in phyllotaxis], or in the complex logarithmic spiral belonging to snail shells). Later, inspired by Thompson, in the light of producing his reaction-diffusion theory of morphogenesis, Turing attempted to decipher the meaning of the apparently widespread phenomenon of Fibonacci sequences implicit in the forms of plants (ib, pp. 923–924; Okabe et al. 2019, pp. 1–7; Swinton 2004, pp. 477–495).

One key aspect of the rationale Thompson gave for his overall "physico-mathematical" (Thompson 1958, p. 233) approach to the study of morphogenesis (i.e., grounded in the hypothesis that "the forms of living things, and . . . the parts of living things, can be explained by physical considerations, and . . . that in general no organic forms exist save such as are in conformity with physical and mathematical laws" (Thompson 1942, p. 15)) leaned toward Kantian thought patterns concerning natural science. Thompson cites the Kantian maxim that scientific inquiry should, as far as possible, attempt to explain organismic phenomena in mechanistic terms, indicating that his evidence specifically supports the possibility of basing the interpretation of "the observed facts of organic form on mathematical principles, [so] as to bring morphology within or very near to Kant's demand that a true natural science should be justified by its relation to mathematics" (Thompson 1911, p. 426). This point also frames the beginning of the introduction to *On Growth and Form*.

In the context of arguing that the investigation of organismic form should take place using the same descriptive, mechanistic, and mathematical language as that belonging to physics in studying inorganic forms, Thompson writes that it is an elementary scientific duty to take explanation by way of the properties of matter and energy as far as possible. He asserts that:

> It is of the essence of physiological science to investigate the manifestations of energy in the body, and to refer them, for instance, to the domains of heat, electricity, or chemical activity. By this means a vast number of phenomena, of chemical and other actions of the body, have been relegated to the domain of physical science and withdrawn from the mystery that still attends on life. (ib, p. 422).

And he suggests that physics should be seen as morphology's proper "guide and teacher in many matters regarding organic form" (ib, p. 423). For Thompson, morphology should not be deterred from "attempting to explain organic forms by mathematical or physical law," namely, by reference to forces and to "simple laws of spatial arrangement where molecule fits into molecule" (ib, p. 422). Even though absolute geometrical perfection is not present in either organismic or inanimate forms, he felt that this "unduly neglected" (ib, p. 427) approach, which "related to mechanical considerations, to mathematical laws, or to physical and chemical processes" (ib, p. 426), would prove to be the most productive, fertile soil for the scientific explanation of organismic form. This was largely because "the form of an object is defined when we know its magnitude, actual or relative, in various directions; and Growth involves the same concepts of magnitude and direction, related to . . . the 'dimension' of Time" (Thompson 1942, p. 22).

Organismic form was a (non-perfect) geometrical determination of "spatial magnitude" pertaining to the extension of the volume and surface area of the body. At the end of the introduction to *On Growth and Form*, while Thompson admitted that physical science also changes in terms of orientation, causality, which he cites as being one of the key Kantian a priori concept of the understanding, would always still be an important guide for inquiry (ib, pp. 20–21). Thompson believed that, even though it had some limitations, the physico-mathematical approach, which would be based on the well-trodden and established principles of physics, would see to the type of rigorous investigation that was best suited to finding out the causes of organismic form.

Thompson's Kantian leanings (e.g., his emphasis on mechanistic principles, rather than teleological ones, in formal scientific inquiry as a means to explain phenomena) are not only evidenced in his emphasis on a physico-mathematical approach in the study of organismic form, but they also pervade his criticisms of natural selection, genetics, and mutationism, as well as the vitalism of his day. Here, we must remember the historical context behind in his criticisms. Thompson was writing prior to the neo-Darwinian Modern Synthesis that took shape from the 1930s–1940s, a time in which biology had not settled upon its foundations and a plethora of differing perspectives were being articulated. Darwinian natural selection and Mendelian Genetics (together with mutationism) had not yet been deemed to be commensurate and there was a tension between selectionists and geneticists. The modern synthesis eventually heralded them as the core pillars of modern biology going forward, but Thompson expressed profound criticisms of both (although he was not simply dismissive of them). *On Growth and Form* (originally published in 1917) deviated from them in terms of orientation, and its publication in its full, revised form in 1942, namely, in the same year as Huxley's *Evolution: The Modern Synthesis*, was perhaps uncomfortably discordant with the consensus that had emerged.

On the one hand, Thompson considered that natural selection, being an eliminative principle, did not provide insight into the positive origination of organismic form (at least not in the way that it was being construed by the selectionists of his day).[31] Anticipating Stephen Jay Gould's and Richard Lewontin's "spandrels" (Gould and Lewontin 1979) from a Thompsonian perspective, natural selection did not account for the existence of so-called ornamental features and structures of organisms that did not exhibit themselves as having an identifiable "adaptive value" in the struggle for existence. For Thompson, the selectionist emphasis on the teleological notion of "adaptive functions" did not present an adequate focus on the mechanical efficiencies of the physiological structures that were deemed to be "advantageous" in terms of the performance of various functions. He thought that the selectionist focus on the attainment by organisms on advantageous adaptations (i.e., adaptation being the efficient cause) in the struggle for existence (i.e., survival being the final cause) was implicitly teleological, and "adaptation" tended to rely on the concoction of non-empirical "just-so" stories from the evolutionary past in order to explain organismic form. Thompson further felt that selectionists tended to emphasize a progressive, teleological, or "upward" direction to evolution. And, in contrast to them, he was open to the notion that saltational changes, stemming from physical forces, could occur as regard organismic form. Also, one might add that from a Thompsonian perspective, natural selection might be seen largely to be contextualized as an extension of kinetic selection (Pross 2012, pp. 138–139), and/or constitutes a special aspect of the law of entropy. With this possibility in mind, given that living organisms are part of the natural world and help to compose it, entropic and other forces not only act on them, but belong intrinsically to them. Furthermore, beyond the typical selectionist focus on natural selection acting on phenotypes, genomes, or genes, from outside of them, one can point to the (Baldwinian) notion that organisms are not only objects upon which natural selection acts, but can be valuative-selective-appropriative agents of selection (their own behavioral selections playing a role in the eliminations of other organisms and organismic capacities).

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[31] For a synopsis of some of Thompson's criticisms of natural selection, see the editor's introduction in the abridged version of Thompson's *On Growth and Form: Abridged Edition*, ed. John Tyler Bonner (New York: Cambridge University Press, 1961, reprinted 1992), pp. xiv–xxii.

On the other hand, genetics seemed to Thompson to point to unexplained, non-physical, mysterious, preformed origins of heredity that presumably could produce organismic form in a teleological manner without limits. After all, the physicochemical nature of genes was not clear at that time, and it was not evident how genes themselves had come into existence and evolved, much less how they transmitted "instructions" or "information" that would produce organismic form. "Gene action" seemed too much to smack of an unexplainable quality. Thompson felt that Mendelian genetics (together with Morgan's and De Vries' mutationism) and conceptions of heredity (e.g., Weismann's separation of germplasm from somatoplasm and consideration of their external relations, the former acting on the latter in a one-way fashion) were being used as vehicles for the introduction of teleological principles that breached the continuity of nature and its regularities, in order to explain the unfolding of the living organism and evolution. To be sure, for a natural science to explain that some substances, in this case, genes, are deemed not to be affected by the causal action of the forces emerging from the material swaddling them certainly sounds like pointing to the supernatural. While Thompson's own emphasis on organismic growth and on physical forces constraining it could be interpreted to ally itself with preformationism, at the very least, for Thompson, the germplasm should have to be considered a site of a confluence of energies and forces, some from without, which is a point that he thought warranted his emphasis on physical forces. In contrast to genetic determinism, it may be interpreted in a contemporary light that Thompson was pointing to the contribution of developmental processes to gene expression, including to the notion that epigenetic forces act reciprocally on genes, constituting a causal factor in the emergence of organismic form. He was also skeptical of what may be crudely termed the "beanbag" nature of the genetics of his time, wherein each gene is seen as the cause of each phenotypic trait. Thompson opposed the artificial separation of genes and traits, respectively, when, in truth, the organism comprises "one integral and indivisible whole" (Thompson 1942, pp. 1036–1037) gene working interactively, often in a cascading fashion. For Thompson, there was no "strict dividing line" between the organism's seemingly disparate characters and members which operated correlatively for the sake of that whole. The process of growth was a phenomenon to be analyzed at the level of the whole organism, not just its parts, and the genetics of his time seemed to be based too much on an abstract, intellectual carving up of the characters and members of the organs and their placement into separate compartments, rather than looking at the whole.

As for his criticism of the vitalisms that were still regnant in his day (e.g., of Roux's theory of "auto-determination," Driesch's "entelechy," and Bergson's "élan vital"), Thompson relegated them to the status of merely being re-discoveries of Aristotelian teleology or Aristotelian teleology "dressed in new garments" (Thompson 1913, p. 29). Relating back to Kant's critique of Blumenbach's positing of the existence of a "vital essence," the dubious admittance of "invisible" vital principles "alien to the province of the physicist" (Thompson 1911, p. 419) for Thompson, there was no clear rule or guidance as to what was "vital" and what was not. For him,

> the whole assemblage of so-called vital phenomena . . . cannot be clearly classified into those that are physical in origin and those that are *sui generis* and peculiar to living things. All we can do meanwhile is to analyze, bit by bit, those parts of the whole to which the ordinary laws of the physical forces more or less obviously and clearly and indubitably apply (Thompson 1942, p. 19).

While Thompson admitted that there may be processes going on in cells that do not readily admit to any known physical force, for him, it is incumbent on the scientist to diligently inquire in order to find out whether they yield to physico-mathematical investigation. From a Thompsonian standpoint, the fact that living organisms persist in the face of entropy, for instance, by way of homeostatic, chronobiological, homeorhetic, and autopoietic processes of self-organization, does not mean that a separate "vitalistic" law either antithetical to or beyond the second law of thermodynamics, somehow belonging specifically to their unfolding, needed to be created. Rather, much like the persistence displayed in oscillating chemical reactions, the living organism is a site where its own concrescent forces, in their interaction, offset the forces of entropy but in a progressively decremental manner over time toward a more stable state.[32]

All of that said, Thompson did pay homage to "the teleological side" of Aristotle, which was focused on final causation and/or intrinsic purposiveness. Thompson wrote that living things "have also, doubtless, their immanent teleological significance" even if it is on "another plane of thought from the physicists" (Thomson 1961, p. 7) that such determinations are made. He also stated that:

> like warp and woof, mechanism and teleology are interwoven together, and we must not cleave to the one nor despise the other; for their union is rooted in the very nature of totality. We may grow shy or weary of looking to a final cause for an explanation of our phenomena; but after we have accounted for these on the plainest principles of mechanical causation it may be useful and appropriate to see how the final cause would tally with the other, and lead towards the same conclusion (Thompson 1942, p. 7).

Elsewhere, Thompson eloquently put the matter as follows:

> and if wonderment springs, as again Aristotle tells us, from ignorance of the causes of things, it does not cease when we have traced and discovered the proximate causes, the physical

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[32] In "*Magnalia Naturae*," Thompson criticizes "others, like Felix Auerbach, still holding to a physical or quasi-physical theory of life, believe that in the living body the dissipation of energy is controlled by a guiding principle, as though through Clerk Maxwell's demons; that for the living the law of entropy is thereby reversed; and that life itself is that which has been evolved to counteract and battle with the dissipation of energy" (427–428). On the subject of the constraints posed to self-organizing systems in relation to the law of entropy, and anticipating the theses of Erwin Schrödinger in "What is Life: The Physical Aspect of the Living Cell" (1944), in *On Growth and Form* (1942), Thompson also writes that "organic evolution has its physical analogue in the universal law that the world tends, in all its parts and particles, to pass from certain less probable to certain more probable configurations or states. This is the second law of thermodynamics. It has been called the *law of evolution of the world*; and we call it, after Clausius, the Principle of *Entropy*, which is a literal translation of *Evolution* into Greek" (11).

> causes, the efficient causes of our phenomena. For beyond and remote from the physical causation lies the end, the final cause of the philosopher, the reason why, in which are hidden the problems of organic harmony and autonomy and the mysteries of apparent purpose, adaptation, fitness and design. Here, in the region of teleology, the plain rationalism that guided us through the physical facts and causes begins to disappoint us, and intuition, which is of close kin to faith, begins to make itself heard. (Thompson 1911, p. 428).

Arguably, Thompson may be here construed to be suggesting that the mechanistic approach should not merely proceed to explain what was apparently teleological on its own terms (as in the notion of "teleonomy"), such as to suggest that there was nothing concrete or objective in the teleological interpretation at all. Rather, the mechanistic approach should treat teleology *as if* it was only an appearance, namely, to carry out its reductive analysis amidst the backdrop of a persistent intuition that the living is intrinsically purposive. Given the mechanistic neo-Darwinian interpretation that most anyone referencing intrinsic purposiveness in the same breath as nature or the living is suggesting a theological discourse,[33] on the note of Thompson and the subjects of faith and religion, Dobell (1949) qualifies in his Thompson's obituary that "D'Arcy Thompson was deeply religious, but he had no 'religion', in a sectarian sense; indeed, from the depths of his Hellenism he sometimes even called himself a 'Pagan': yet he had the noblest ideals, and ever strove to attain them with all of his heart and soul" (Dobell 1949, p. 614). Nevertheless, Michael Ruse has asserted that while Thompson "may not have been an explicit vitalist, . . . there is certainly the odor of spirit forces about what he claims."[34]

In contrast to Ruse's perspective, however, in understanding Thompson's payment of tribute to Aristotelian teleology while overall emphasizing physical forces and mathematics in the study of organismic form, one might consider the vast diversity of Aristotle's inquiries, which also encompassed physics and mathematics, and that Paley's Teleological Argument for the existence of God is based in a mechanistic conception of nature to which neo-Darwinians (e.g., like Dawkins) tend to subscribe. Also, regardless of the justice he did to teleology in several sections of his work, Thompson argued staunchly that it was only by proceeding through a comprehensive examination of the physical causes of morphogenesis, namely, by carrying a physico-mathematical approach as far as possible (following Kantian sensibilities) and by being dutifully "unprejudiced by vitalistic hypothesis,

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[33] Here, we may recall Stephen Jay Gould's statement in "D'Arcy Thompson and the Science of Form," *New Literary History* 2.2 (Winter 1971), that "it is still unfashionable, in biological circles, to use such words as 'design', 'purpose', or 'teleology'. Since final cause is so indispensable a concept in the elucidation of adaptation, and since natural selection can produce a well-designed structure without any conscious intervention of God's super-human wisdom or the sub-human intelligence of the animal in question, one would think that these terms would again be admitted into orthodoxy. Evidently, however, in our choice of words, we are still fighting the battle with theologians that we won in deeds almost a century ago" (258, note 59).

[34] Michael Ruse, "From Organicism to Mechanism—and Halfway Back?" in *Beyond Mechanism: Putting Life Back Into Biology*, eds. Brian G. Henning and Adam C. Scarfe (Lanham, MD: Lexington Books/Rowman and Littlefield, 2013), 416.

along the road of observation and experiment" (Thompson 1911, p. 422), that something ultimately might be gathered about a putative teleological aspect pertaining to self-organization. That said, there is no indication in Thompson's writings that he was ever implying that the arrival at the teleological was to be directly the instrumental purpose of his own diligent, physico-mathematical investigations. On the contrary, the direction of one's inquiries with, and focusing solely on, the teleological aspect first and foremost, as he thought the vitalists of his time were doing, could only result in the contribution of an empty dogmatism to the understanding of life. To prejudge, prior to mechanistic scientific investigation, the results of such an investigation (i.e., that teleological conceptions could never play a role in terms of the findings of such an analysis) could also not be said to represent proper scientific objectivity. After all, by way of logical elimination, a thorough physico-mathematical approach to the study of morphogenesis could disclose what, if anything (teleological or otherwise) was left, to be explained (e.g., the specific informational "content" that is expressed in neural, electrochemical, cellular, morphogenetic, and/or genetic signaling), and the understanding garnered from concrete physico-mathematical explanation of living organisms might one day point to self-organization as an emergent product, with supervenient teleological properties, based on the confluence of physical or mechanistic conditions for its possibility.

In the light of his adherence to the (aforementioned) Kantian maxims concerning the constitution of proper scientific inquiry, and making his case against the selectionists, the geneticists, and the vitalists in terms not unlike Dennett's (1995) distinction between "explanatory cranes" and "skyhooks" (Dennett 1995, pp. 74–76) for Thompson, it was a matter of the duty of life scientists, as far as possible, to carry out precise examinations of the life processes of organisms as compositional manifestations of physical laws, keeping to the so-called mundane, rather than to jump hastily and impatiently into the "lazy arguments" (Thompson 1942, p. 960) and grandiose "teleologistic" generalizations. However, for Thompson, wonder book-ended such precise scientific inquiry. Wonder was to be found both at the outset of scientific inquiry, motivating it, and at the end of such inquiry, enabling reflective generalization, as Plato and Aristotle had postulated. But it would take care of itself. While wonder is representable in scientific discourse (e.g., see Waddington 1961, pp. 15–17) and, for Thompson, the Aristotelian notion of teleology had heuristic value (as it had for Kant), it was not to be the primary focus of bioscientific inquiry in terms of its precise methods or goals.

It is interesting to note the diversity, and, on occasion, the clash of scholarly interpretations of Thompson. On the one hand, Ruse has smelled an "odor of spirit forces" in Thompson's work, and on the other hand, in a short correspondence piece, entitled, "Follow Thompson's Map to Turn Biology From a 'science' Into a 'Science,'" Enquist and Stark (2007) have characterized Thompson as a staunch mechanist in order to argue against Evelyn Fox Keller's article "A Clash of Two Cultures" (2007) (which questions whether biologists should focus so heavily on the search for all-encompassing laws governing animate entities, given the complexity of what is being studied [i.e., life]). Previously, Keller (2002) has presented a sober look at Thompson's contributions, suggesting that the accolades that have been bestowed onto some prominent figures in the history of biology (including Thompson) have been somewhat arbitrary, when compared to how other researchers doing similar things have been treated (e.g., Stéphane Leduc).[35] In any case, according to Enquist and Stark, Thompson provided a staunch mechanistic and mathematical "roadmap" for biology going forward, one that stood parallel to the one that chemistry has embraced. And, for them, arguing against Keller, Thompson's mechanistic and mathematical "roadmap" needs to be embraced today, given the urgency of "the need to understand and predict the response of the biosphere to climate change, the spread of emerging diseases, the collapse of biological diversity and the need to improve the human condition through medicine and agriculture," all of which "demand the development of a quantitative, mechanistic and predictive biology" (Enquist and Stark ib., p. 611).

While the embracing of a thorough mechanistic and mathematical reduction may enable the study of such issues precisely, one problem with Enquist and Stark's argument is that, alone, such reductionism does not enable humanity to act on such problems in order to resolve them. For if, from a materialist, mechanistic perspective, living organisms are considered a priori as "bits of matter . . . hurrying about" (Whitehead 1978, p. 50) then there is no reason to truly care for their plight. However, a more holistic approach that focuses on the intrinsic purposiveness of self-organizing agents (i.e., as autopoietic loci of valuative-selective-appropriative activity) thereby providing a basis for their having intrinsic worth (e.g., as "teleological centers of life" (Taylor 1981, pp. 210–211, pp. 217–218) or as "subjects of a life" (Regan 1983, pp. 235–236), and which emphasizes the cultivation of what Waddington called "biological wisdom," is able to generate profound reasons for why humanity must deal with the ecological crisis. The point is to make sure that the teleological conceptions of the living that are expressed in the domain of evolutionary-environmental ethics are demonstrably consistent with the findings of the biological sciences.

Thompson cannot be considered a mechanistic reductionist. While placing emphasis on physical and chemical laws in understanding physiological form, trying to carry these principles as far as possible in understanding the phenomenon of morphogenesis (along Kantian lines) Thompson certainly recognized the limits of that approach by suggesting that "though we push such [physicalist and mathematical] explanation to the uttermost, and learn much in the so doing," for example, about "what is implied in the organization of the living organism," we shall "be left wondering still" (Thompson 1911, p. 427). In so doing, Thompson did recognize the (Aristotelian) teleological, self-organizing character of the organism's processes of growth, development, and differentiation, which took place in the context of, and within the constraints posed by, those laws. The phenomena behind the appearance

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[35] For Keller's synopsis and discussion of Thompson's work, see her *Making Sense of Life: Explaining Biological Development With Models, Metaphors, and Machines* (Cambridge, MA: Harvard University Press, 2002), especially 15–82. Also see Keller's "Physics in Biology—Has D'Arcy Thompson Been Vindicated?" in *D'Arcy Wentworth Thompson's Generative Influences in Art, Design, and Architecture: From Forces to Forms*, 35–46.

of teleological, autonomous self-organization in living organisms are indeed a wonder, but they are not, for Thompson, to be considered a priori as transcendent of nature's physical regularities. Rather, they are, most likely, subject to them, and more strongly, emergent compositional manifestations of them. As in the more recent depiction of the notion of autopoiesis as involving the notion that organisms are distinct from inanimate entities in that they "organize the production of their own components" (Luisi 2006, p. 158) so as to maintain their interior milieu in the face of the forces of entropy, whereas the latter do not, for Thompson, the special organization of the organismic whole itself is also not a deviance from the laws of nature.

As regards Thompson's critiques of natural selection, genetics, and vitalism, for some contemporary scholars and scientists who are aligned with calls for a novel extended synthesis in biology (i.e., one that does more justice to a multiplicity of areas of study [e.g., systems biology, emergence theory, homeostasis, chronobiology, autopoiesis, the Baldwin effect, niche construction, evolutionary developmental biology, epigenetics, biosemiotics, morphic fields, etc.] that in many ways go against the grain of the neo-Darwinian modern synthesis), Thompson's central contribution is that his approach constitutes a "holistic" stance that explores effects other than, or complementing, natural selection and genetic inheritance (or seeing these in the light of physics and chemistry). Specifically, Thompson's work represents a "demonstration of how the mechanics of physical force are central to generating living forms present[s] an alternative to purely selectionist, Neo-Darwini [an] formulations of evolution that resonate today" (Levy and Terranova 2021, p. 1). Some may see Thompson as articulating an epigenetic orientation that is not explicitly concerned with processes such as DNA methylation or histone acetylation. Such proponents tend to value Thompson's emphasis on the notion that "evolutionary diversification [is] not due to stochastic gene mutation and selection but to specific changes of growth and form happening during individual development" (Esposito 2013, p. 51). It is not the case that Thompson simply dispensed with natural selection and genetics, for as can be seen in *On Growth and Form*, he is still talking about adaptation and heredity. Rather, he saw them as merely two of many important factors in biological explanation—just not the only ones—and questioned the particular "tunnel vision" of some selectionists and geneticists of his day who were emphasizing adaptation and heredity in ways that simply bypassed physical considerations. It is this partially non-selectionist and non-gene-centric take on morphogenesis that some proponents of an extended evolutionary synthesis find so appealing today (Levy and Terranova 2021, pp. xxiii, 1). For Thompson, what was problematic was the narrow way that they were being portrayed in the face of the sheer complexity of the living being, a manner that excluded consideration of physical forces. In his view, selection and genetics simply could not provide the whole story on their own.

Overall, in investigating the phenomenon of morphogenesis, Thompson placed his emphasis on physical forces as a fundamental part of the overall crucible within which organismic form emerges. To a significant degree, one can place Thompson's criticisms of Darwinian natural selection, genetics, and vitalism and his own emphasis on the physical and the mathematical in scientific inquiry in the context of the connection of Aristotle's philosophy of nature and Kant's biophilosophy, both of which had contributed significantly to the shaping of his own mindset. In this light, Thompson should not be seen as "eclectic," "intellectually lonely," "out of step with his time," "idiosyncratic," "anachronistic," "unorthodox," which are terms that various interpreters have used to characterize his overall position (Esposito 2013, pp. 79–81) and which serve to label Thompson as someone who was doing something that was completely disconnected from long-established thinking patterns, from modern biology, and/or from its concrete interests. We must recall that Thompson was working prior to the modern synthesis when there was not yet a consensus concerning biology's foundations going forward and there was great divergence among biologists at that time as to the proper path forward. Furthermore, Thompson was a critical thinker who did not follow the developing mainstream consensus that would amount to the modern synthesis, which Huxley had outlined so eloquently in *Evolution: The Modern Synthesis* (1942). In hindsight, the modern synthesis has been deemed by many scholars and biologists today as "incomplete," something which has only increased interest in the work of Thompson and other non-mainstream figures like Waddington.

With his eleven-hundred-page treatise, Thompson aimed to show that an emphasis on the physical and the mathematical had been "unduly neglected" with the widespread move on the part of biologists to focus their researches on adaptation, natural selection, genetics, and mutation, and he had some very good reasons for his position. Furthermore, from a Thompsonian perspective, as regards "origin of life" research, given that organisms, including their genes, emerged out of chemical matter and evolved, and many truths of chemistry are found in physics, the nature of the living should certainly be explored with a focus on the physical forces underlying such processes. The term *Phusitic* evolution has been employed to point to the earliest phase of evolution in which primarily "physical forces that directed the formation of organic compounds" which enabled the transition to the *Zoetic* phase involving the "chemical coding of instructions" (Silverstein 2021, p. 3) and the efficient causal action of natural selection on the emergent entities in question. Even so, some research into the origination of multicellular organisms has focused on physical causes (e.g., Newman et al. 2006), given that other factors (Darwinian, genetic, epigenetic, behavioral, mental) are deemed not as significant or applicable to early life in comparison with the complex forms we see today.

More strongly, Newman and Linde-Medina (2013) state that "rather than being encoded in genes, form emerges when cells and certain of their molecules mobilize physical forces, effects, and processes in a multicellular context" (Newman and Linde-Medina 2013, p. 274). Even though, admittedly, Thompson's work has been on the "scientific margins throughout the twentieth century" (Newman and Linde-Medina ib., p. 275) Newman (2018) identifies Thompson's "physicalist concepts of growth and form" as one important source for the contemporary notion of "inherency" (Newman 2018, p. 129). "Inherency" suggests that "aspects of the phenotype are latent in the organism's material identity and that these features will spontaneously emerge if the conditions are right" (Newman ib., p. 121). For Newman, "inherency" breaks with the main tenets of both the modern synthesis and the proposed extended evolutionary synthesis by assuming that "generation of form [is] ontologically prior to its uses" and that "the major factor in the establishment of new lineages is not competitive struggle in pre-existing niches but ingenuity of organisms in using the means at their disposal" (Newman ib., p. 122). At any rate, Thompson's stance effectively represents the constraints of what is physically possible in terms of organismic form, and suggests that beyond what is biologically, logically, and historically possible (Dennett 1995, pp. 104–107) there needs first to be a consideration of the category of what is physically possible. Consequently, while Thompson's "back-to-basics," physico-mathematical approach cannot be seen as all comprehensive in terms of investigating the causes of morphogenesis, it will perhaps always have a complementary "card in the game" of biological explanation in the context of a multi-level, multi-perspectival, and multi-dimensional orientation.

3.5 Thompson's Notion of "Mechanical Efficiency" and the Baldwin Effect

Exemplifying the importance of Thompson's physico-mathematical approach to the study of morphogenesis, in the present section I demonstrate that his notion of "mechanical efficiency" ought not to be overlooked when it comes to scientific explanations which cite the Baldwin effect (i.e., the theory of organic selection) as a cause of evolutionary phenomena.[36] In the latter sections of this chapter, I point specifically to the pertinence of Thompson's emphasis on physical forces, especially through his notion of "mechanical efficiency," in the context of Ginsburg's and Jablonka's cognitive-behavioral account of the causes of the Cambrian explosion, as articulated in *The Evolution of the Sensitive Soul* (2019).

In the chapter of *On Growth and Form* entitled "On Form and Mechanical Efficiency," Thompson begins by stating outright that in elucidating the importance of the notion of "mechanical efficiency" his focus is specifically on physiological adaptations, namely, those that are "in the clearly demonstrable form of mechanical fitness for the exercise of some particular function or action which has become inseparable from the life and well-being of the organism" (Thompson 1942, p. 958). This is to the exclusion of types of adaptations that he feels have been nebulously ascribed to organisms without sufficient justification by Darwinians under a teleological rubric. In emphasizing the notion of "mechanical efficiency," Thompson is suggesting that it is the material structure and/or the physiological form of the organism that provides the mechanical conditions for the possibility of gainful adaptations. Here, function is not set in stone, as there is no one singular purpose for any physiological structure. Physical structures can be coopted or "exapted" to

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[36] John Bonner, in his abridged version of *On Growth and Form* (1961/1992), has in his short introduction to the chapter on "Form and Mechanical Efficiency" (221–222) briefly mentioned the possibility of bringing together this Thompson's notion with themes pertaining to the Baldwin effect and to Waddingtonian genetic assimilation.

new modes of getting on in the natural world. While instinct and innateness exist, their function is not something a priori or absolute. But, for Thompson, the degree to which such physical structures can serve to support the organism's performance of gainful actions by manifesting forces is something that can be inquired into and largely quantifiable. The physical capacities and limits of the mechanical structures in producing the minimal forces requisite to the successful performance of the function are also largely measurable. As such, Thompson says that "the biological interest" that is connected with the principle of mechanical efficiency "lies chiefly in the mechanical construction" (ib, p. 972), specifically in "the mechanical properties of the material of which [the physiological structures of the organism] are built," for instance "in relation to the strength [they] ha[ve] to manifest or the forces [they] has to resist" (ib, p. 967).

Organismic structures that are of adaptive significance to the organism are, for Thompson, feats of tremendous complexity as regards their "engineering" via (rhythmic) processes of growth and development. And in his view, rather than focusing on select parts, inquirers should take into account the whole interconnected fabric of physiological structures that permit gainful actions, including adjoining tissues, given that bone and muscle "are inseparably associated and connected; they are moulded one with another; they come into being together and act and react together" (ib, p. 135). As he says:

> ligament and membrane, muscle and tendon, run between bone and bone . . . the beauty and strength of the mechanical construction lie not in one part or in another, but in the harmonious concatenation which all the parts, soft and hard, rigid and flexible, tension-bearing and pressure-bearing, make up together." (ib, p. 969)

But further, for Thompson, along the lines of his criticisms of selectionism and genetics, elucidated above, in identifying the adaptive features of an organism and in thinking about mechanical efficiency, the organism as a whole must not simply be reduced to its parts. According to him, "as we analyse a thing into its parts or into its properties, we tend to magnify these, to exaggerate their apparent independence, and to hide ourselves (at least for a time) the essential integrity and individuality of the composite whole" (ib, p. 1018). It is the whole organism that flies or swims, not just its parts or members, and mechanical efficiency is ultimately efficiency of the whole. As he says, an organism "is not a bundle of parts but an organization of parts, of parts in their mutual arrangement, fitting one with another, in what Aristotle calls 'a single and indivisible principle of unity'" (ib, p. 1019).

From these Thompsonian considerations, the notion of mechanical efficiency can be said to involve the degree to which an organism's whole integral set of physiological structures, in all of their complex unity representing a "field of force" (ib, p. 1025), can effectively and sustainably produce physical forces requisite to the successful performance of actions that have survival value for the organism and that may become habitualized. Such efficiency may come in degrees, and the organism's physiological structures may not be sufficient to produce physical forces necessary to carry out various movements, pointing to a Thompsonian interpretation of adaptation in the face of natural selection. Thompson concludes that his reflections on the topic of mechanical efficiency "are of no small importance to the morphologist" (ib, p. 1002), given his view that, on the one hand, "similarities of form endure in the absence of conflicting forces," but on the other hand, "new system(s) of forces, introduced by altered environment and habits, impinging on those parts of the fabric which lie within this particular field of force, will assuredly not be long of manifesting itself in notable and inevitable modifications of form" (ib, p. 1025). This last quotation, in emphasizing that changes of environment and habit, which introduce "new systems" of physical force which may operate on, over against, or in conjunction with those manifested by the organism, are major efficient causes responsible for morphological change, asserts what basically amounts to the Baldwin effect. The key Thompsonian addition here is his placement of it upon a foundation of emphasis on physical forces. To reiterate, Thompson's emphasis is on the notion that changes of physiological form arise largely due to changes to the regime of confluent physical forces that are at play in the organism's development (including those forces which issue from the organism and those forces that issue from the environment): on the one hand, the mechanical efficiency of the organism's (growing) physiological structures as regards its carrying out of novel movements that are requisite for survival, and, on the other hand, the physical forces in its given environment acting on it.

The Baldwin effect, or the theory of organic selection, was co-developed by evolutionary psychologist James Mark Baldwin (1861–1934) in "A New Factor in Evolution" (1896), although his most mature expression of it is to be found in *Development and Evolution* (1902). It is a theory that has undergone a resurgence in terms of interest over the last thirty years. Although a multiplicity of interpretations or versions of the theory of organic selection have been presented by various sources, in a nutshell, what the theory involves is the notion that organisms have a degree of developmental plasticity and that novel behavior can effect morphological change, this being explained from within a Darwinian framework and without resorting to Lamarckian principles. In short, the Baldwin effect shows how behavioral change can be an efficient cause of morphological change. The theory of organic selection entails the postulation that, especially in times where organisms find themselves in a new or changing environment, where the resources they previously exploited are scarce or no longer available in sufficient quantities to keep them alive, they may take it upon themselves to adapt by developing new ways to survive, modifying their established behavioral habits. The organism's development or discovery of behavioral novelties may take place in a multitude of various ways, for example: (1) by targeting new resources that may be profitably exploited; (2) by randomly discovering new "behavioral novelties" or "good tricks," as Dennett (1995) calls them, in the process of performing habitualized actions when procuring resources; (3) by way of imitating, appropriating, or learning from other organisms that have themselves discovered new good tricks; (4) by engaging in exploratory learning activities; or (5) by way of activities such as animal play by which new movements are attempted and tested through bite, roll, and tumble. The learning of effective movements that positively procure needed resources is selected for future use and potentially refined or imitated by other organisms, while the ineffective ones are, in general, left inoperative. If a species or group faces selection pressures, and the selected behavioral good trick becomes requisite for survival, unless they are able to perform it, they will be eliminated in the struggle for existence via natural selection. Everything else being considered equal, in subsequent generations of the variety, natural selection will generally ensure that the phenotypic or morphological characteristics of such organisms will evolve in a manner that is channeled by the behavioral good trick. In other words, *natural selection will favor phenotypic or physiological traits that serve to amplify the ability for the organism to perform the requisite good trick and/or that assist in honing their ability to perform it*. In this way, according to Baldwin, behavior and mentality have an important role to play in evolution, and along these lines they may provide "a directive determination" in terms of the course of physiological evolution (Baldwin 1902, p. 142).

When the Baldwin effect is cited as an explanation of some emergent phenomenon the attention tends to be centrally on the novel behaviors in question as a cause of physiological evolution. But D'Arcy Thompson's emphasis on "mechanical efficiency" can be said to help us place proper attention on the physico-mechanical aspects of the theory, specifically, on the interplay of physical forces which are introduced by the organism entering into new environment, by the environment changing, or by the new behavioral habit. Thompson's orientation can refocus some of the attention on the physiological structures and physical forces that serve to amplify the organism's ability to perform and/or to perfect the novel good trick. After all, the good trick is only of survival value to the organism to begin with if it has the physical capacity to be able to perform it with minimal efficiency, based on their physiological features. The physiological form of the organism must fit the particular environmental niche that contains the resources it needs to "unlock" in order to survive.

As a hypothetical example, the land-based predecessor of the marine iguana (*Amblyrhynchus cristatus*) the only sea-going iguana species in the world), originating presumably from the jungles of South America, did not just embrace the novel behavioral habit of diving into the ocean for short periods of time to procure food resources when it first appeared as a castaway on the barren islands of the Galapagos (Dawkins 2005). Rather, along with other physical features, *its tail needed to have a shape, size, strength, curvature, and a muscularity that made it mechanically efficient enough in terms of being able to provide the organism with some of the means to produce the physical forces necessary to perform the behavioral good trick of propelling itself through the (resistance of the) water, with some velocity, for short periods of time and to avoid drowning*. The novel behavior of swimming in rough oceans enabled the predecessor of the marine iguana to survive, as the organism became successful in procuring macrophytic algae on the ocean floor when few other resources were available. Further, in association with the organism's physiological features, the novel behavior allowed it to reproduce and to pass on the advantageous traits that it had (i.e., those enabling it to perform the good trick), which were "captured" by the Baldwin effect, thereby channeling out the course of physiological evolution of the species (e.g., toward longer, flatter, more muscular tails in comparison with other iguana varieties). But of course, there are also constraints on tail and body size that relate to foraging efficiency in deep, rough, cold oceans (including thermoregulation and energy requirements) where there are strong currents. In drawing attention to the physical aspect of Baldwinian adaptations, Thompson would not allow us merely to focus on one or a few advantageous traits (e.g., the long, flattened, eel-like tail of the marine iguana) enhancing the abilities of organisms to perform requisite good tricks. Rather, he would draw attention to the whole network of organic fibers, rigid, gristly, and spongy tissues, ligaments, bones, cartilage, membranes, muscles, tendons, and other joining parts and anatomical structures that support its capacity for such hydrodynamic movement (e.g., those that bear load, tension, and pressure; that flex, thrust, bend, and stretch elastically; that buoy and balance the organism in water, etc.. . .) through which the iguana’s anguilliform swimming is made possible. After all, it is the whole organism (its physical bulk appearing near its elongate front) that swims, not just the tail exerting a physical force on the water. The marine iguana’s swimming involves “strong lateral undulations of *the entire body* and tail,” they “sometimes use the[ir] front legs for balance,” and, for example, “in deeper water, . . . their buoyancy becomes neutral as a result of compression of the air in their lungs” (Bartholomew et al. 1976, p. 712, my emphasis; p. 716), reflecting the non-reductionist, Thompsonian point that the organism is not just to be viewed as a “bundle of parts” (Thompson 1942, p. 1019). Pointing to the whole organism, the marine iguana species has evolved a host of other traits that “suit” its whole physiology toward the performance, amplification, and refinement of the behavior of swimming in an ocean environment. In comparison with other iguana varieties, marine iguanas have evolved a blunter snout with which to effectively scrape algae off of rocks and they have larger hooked claws which enable them to cling to rocks when exiting the water. They mediate the timing of their ocean foraging ventures by way of chronobiological synchronization with the tides. The good trick of swimming in the rough ocean is strenuous for marine iguanas in terms of the physical forces required, given the build-up of blood lactate levels, their muscles eventually seizing up. Marine iguanas may forage several times a day, but after engaging in burst swimming it may take hours of rest in order to moderate their blood lactate levels in order to be able to return to the water.

The Thompsonian point here as regards this hypothetical example of the Baldwin effect is that the typical focus on the behavioral change that allowed the marine iguana to survive is only a fraction of the whole story. Thompson’s notion of “mechanical efficiency” may point to the notion that physical forces constrain what good tricks (e.g., swimming underwater and locating algae) are operative and which are not, as well as provides positive or negative feedback on the behaviors being entertained and performed by the organism. It is the novel behavior, together with the degree of mechanical efficiency belonging to the physiological structures of the organism in terms of mustering up the physical forces necessary to performing it, that is, as a whole, tested by natural selection and potentially amplified by subsequent morphological changes over subsequent generations, as in the Baldwin effect.

3.6 Ginsburg and Jablonka's Cognitive-Behavioral and/or Learning-Based Account of the Causal Fuses Leading to the Cambrian Explosion

In Chap. 9, "The Cambrian Explosion and Its Soulful Ramifications" (pp. 405–450) of their landmark volume, *The Evolution of the Sensitive Soul* (2019), Ginsburg and Jablonka argue that the evolutionary emergence of consciousness during the Cambrian period, together with all of the "Baldwinian" ramifications of this development (e.g., in terms of learning and behavior), was one of the main drivers of the Cambrian explosion—the "morphological big bang" (Ginsburg and Jablonka 2019, p. 410) on this planet that allegedly took place some 542–485 million years ago, out of which a majority of the generalized organismic forms (e.g., arthropods, mollusks, and chordates) that are found in our present evolutionary epoch emerged. The wondrous creatures immortalized in the Burgess Shale (near Field, British Columbia, Canada) and other fossil discoveries (e.g., the Qingjiang biota in Hubei, China) around the world have given us a glimpse into this key period in the evolutionary past, in which metazoan bodies, "characterized by axial symmetries and asymmetries, multiple tissue layers, interior cavities, segmentation, and various combinations of these properties" (Newman et al. 2006, p. 293), emerged. Although their focus is on the evolutionary emergence of consciousness (or mentality) in life forms as one efficient cause of the Cambrian explosion, Ginsburg and Jablonka take a multi-dimensional view, citing the plethora of major theses that have been advanced in attempting to explain this seminal evolutionary event (Ginsburg and Jablonka ib., pp. 411–417). While Thompsonian physical forces or mechanical efficiency are not directly named among them, Ginsburg and Jablonka do briefly cite the research of Stuart Newman and his colleagues (2006, 2009, 2010) pointing to "the constraints imposed by the physical nature of multicellular animals"[37] in inquiring into the morphological diversification of the Cambrian explosion. Nevertheless, Ginsburg and Jablonka might be more attentive to the aspect of the physical forces that constrain what good tricks are entertainable, operative, and performable by the organism.

It must be qualified that paleontologists and evolutionary biologists generally hold that deep in the evolutionary past "there was a [morphological] explosion of some sort," as Levinton (2008, p. 863) suggests, but there is still substantive disagreement about some of the details, including its time frame (based on the study and interpretation of fossil data), molecular clock estimates, and genetic evidence, with some suggesting that "bilaterian animal groups seem to appear in the fossil record at or just before the beginning of the Cambrian" (ib, p. 858) geological era. For Levinton, the Cambrian explosion hypothesis holds that a

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[37] See Ginsburg and Jablonka, *The Evolution of the Sensitive Soul*, 421, citing Newman, Forgacs, and Müller (2006); Stuart A. Newman and Ramray Bhat, "Dynamical Patterning Modules: A 'Pattern Language' For Development and Evolution of Multicellular Form," *International Journal of Developmental Biology* 53 (2009), pp. 693–705; and Stuart A. Newman and Gerd B. Müller, "Morphological Evolution: Epigenetic Mechanisms," in *Encyclopedia of Life Sciences* (Chichester, UK: John Wiley and Sons, Ltd., 2010), pp. 1–9.

menagerie of life forms diverged from a common ancestor, establishing a spectacular diversity of body plans in the relatively short time frame, evolutionarily speaking, of about 20 million years. An alternative version of this hypothesis allows for a divergence a few million years before the Cambrian, with an explosion of larger-bodied organisms in the Early Cambrian (ib, p. 855). Levinton questions the estimates that are typically assumed in the hypothesis as to the pace of body plan evolution, suggesting that the fossil record tells us that evolution is dominated by radiations of form and genetic structure that are discontinuous in time.

On a similar note, Briggs and Fortey (2005) have taken issue with several assumptions that are present in Stephen Jay Gould's account of the Cambrian explosion in *Wonderful Life* (1989). They suggest that "new sources of data have arisen" and some of the claims in this work "have not stood the test of time," although they note that the challenges it posed "have served to move the science forward" (Briggs and Fortey 2005, p. 109). Gould had claimed that the Cambrian explosion produced more morphological diversity than is found on the Earth presently, meaning that, whereas the Burgess Shale fossils point to the predecessors of mollusks, arthropods, and vertebrates existing today, because of the mass extinction of groups like trilobites there are fewer body plans today. Briggs and Fortey take issue with Gould's "all-too-narrow focus" on phyla or body plans in interpreting the morphological differentiations of the Cambrian radiation, given that the science had since moved toward recognizing morphological relations using molecular data. They suggest that Gould's "claims about a maximum of morphological disparity in the Cambrian [have not] stood up to analysis," suggesting that "at most, disparity of design was equal to that at the Recent" (ib, p. 209). After all, Gould had claimed that instead of views of the course of evolution of life on the planet being represented as a linear cone of increasing diversity, it was more like an upside-down tree with maximum diversity occurring during the Cambrian explosion, followed by a period mass extinction (e.g., eliminating the trilobites) and a lessening of diversity occurring during the Cambrian decimations, leaving basically three main branches of phyla (i.e., arthropods, mollusks, and chordates). Briggs and Fortey state that cladistic analyses have shown "morphological disparity ... to be similar in Cambrian times as now" (ib, p. 94) and they suggest that the history of life might better be represented as "a 'tube' with a diameter that remained roughly constant following its establishment in the early Cambrian."[38] Briggs and Fortey further remark that the more that new Cambrian arthropods are discovered, "the more (morphologic) evolution seems to have happened already by the Cambrian." They also cite Budd and Jensen (2000) to the effect that "a great amount of body-plan reorganization must have taken place post-Cambrian."[39] For them, there is not enough evidence for

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[38] Briggs and Fortey, "Wonderful Strife," 97, citing Matthew A. Wills and Richard A. Fortey, "The Shape of Life: How Much Is Written In Stone?," *BioEssays* 22 (2000), pp. 1142–1152.

[39] Briggs and Fortey, "Wonderful Strife," 100, citing Graham E. Budd and Sören Jensen, "A Critical Reappraisal of the Fossil Record of the Bilaterian Phyla," *Biological Reviews* 75.2 (May 2000), 259.

Gould's thesis that there was greater morphological disparity in the Cambrian. Nevertheless, they say, "the rapid evolution of form still remains to be explained" (Briggs and Fortey 2005, p. 98).

Ginsburg and Jablonka explicitly recognize the discordant scientific perspectives surrounding the Cambrian explosion hypothesis and its details. However, they maintain that molecular evolution and morphological evolution "are often decoupled" in terms of their pace, that "an increased rate of molecular evolution is correlated with periods of speciation," that with many new fossil discoveries and analysis "the fossil evidence still stubbornly suggests that in a geologically very short period, most extant metazoan phyla made their first appearance in the fossil record and diversified," and that there is still a scientific consensus that "a remarkable ecological and morphological diversification occurred during the Cambrian" (Ginsburg and Jablonka 2019, p. 410). As such, they proceed in providing their rationale for why a confluence of cognitive and behavioral factors is to be viewed as an important efficient cause, among many, that fused this "morphological big bang," establishing in a brief, geologically speaking, burst the thirty-five or so categories of generalized body plans (with some exceptions, e.g., complex plants) that we see in the world today.

Indeed, in *The Crucible of Creation* (1998), Simon Conway Morris asserted that "on balance the evidence suggests that the Cambrian explosion is indeed genuine," subject of course "to some important qualifications" (Conway Morris 1998, p. 141) pertaining to the level of diversification. For him, "the diversity of trace fossils emerging in the Cambrian," as evidenced, for example, by the Burgess Shale, "is a clear indication *of a dramatic increase in behavioral repertoires and, by implication, of neurological sophistication*" (ib, my emphasis) as compared, for example, with what fossils tell us about prior Ediacaran fauna (about 600 million years ago, generally involving "simpler sheetlike, or budded, segmented tube-like multicellular biota" (Newman and Bhat 2009, p. 693)), a point which coincides directly with Ginsburg and Jablonka's arguments. Conway Morris concludes that "the Cambrian explosion does … appear to be a genuine evolutionary event, and thus one that demands an explanation" (Conway Morris 1998, p. 141).

As mentioned earlier, Ginsburg and Jablonka employ Aristotle's notion of "sensitive-souled" organisms as a symbol, metaphor, and heuristic for what they seek to explain: the emergence of the first minimally "conscious" and/or "sentient" organisms, and how the emergence of consciousness, in turn, propelled the Cambrian explosion. They associate Aristotle's "sensitive-souled" organisms with two phases of mental development that Dennett identifies in his multiple drafts theory of consciousness: those he calls "Skinnerian creatures" and those he calls "Popperian creatures," in contrast to the more limited capacities of "Darwinian creatures" (Ginsburg and Jablonka 2019, p. 406). As a "Baldwin booster,"[40] Dennett's "multiple drafts theory" (Dennett ib., pp. 370–383) is a hypothetical sketch characterizing,

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[40] See, for example, *Evolution and Learning: The Baldwin Effect Reconsidered*, eds. Bruce H. Weber and David J. Depew (Cambridge, MA: MIT Press, 2003), x, 53, 69–80.

first, how natural selection may favor organisms that have some degree of behavioral plasticity over those that do not. For Dennett, there are gradations in terms of the ability of organisms to select, habitualize, or dehabitualize their behaviors. Second, Dennett's theory highlights how greater degrees of mentality can emerge by way of adaptation and natural selection. Dennett tracks the evolution of mentality in incremental stages from what he calls "Darwinian creatures" (i.e., organisms without central nervous systems, with little going on in the way of mentality, learning, or "neural buzz" (Ginsburg and Jablonka ib., p. 406), as in Aristotle's "vegetative-souled" creatures, e.g., single-celled microorganisms, plants, fungi, sponges) to "Skinnerian creatures" (i.e., organisms with central nervous systems beholden to entrenched behavioral habit, but also of conditioned behavior, being capable of learning by way of trial and error, pain and pleasure, e.g., worms, crabs, insects, fish, frog) to "Popperian creatures" (i.e., organisms that have, to some degree, have a capacity to pre-select behaviors from among recalled alternatives, potentially eliminating at the outset those that will cause the creature harm/death, e.g., mammals, birds, but also some cephalopods) to "Gregorian creatures" (i.e., organisms with "mental tools" [i.e., the Lorenzian, evolutionary neo-Kantian a priori concepts of the understanding; symbolic language; e.g., human beings], and a mature degree of "look ahead" (i.e., the ability to "see beyond the present" and to anticipate future events on the basis of the uniformity of the past). While "Gregorian creatures" are "sensitive-souled" from an Aristotelian point of view, they are not merely that, as they may proceed toward and/or constitute "rational-souled creatures." It is to be noted that Dennett's divisions between the different types of creatures are not to be viewed rigidly. Rather, in applying them to the vast diversity of biota on the planet over the course of evolutionary history, there will be gradations and overlappings of the categories.

Drawing from a plethora of understandings of consciousness,[41] including Dennett's, what Ginsburg and Jablonka understand by consciousness is "subjective experiencing" (Ginsburg and Jablonka 2019, pp. ix–12), namely, having an awareness of self, body, and environment and a capacity for what they call "unlimited associative learning" (ib, pp. 347–403). For them, the notion of "open-ended" or "unlimited associative learning" represents a minimal, evolutionary, transition marker for designating the emergence in organisms of "consciousness." The notion of "unlimited associative learning" is said to adequately represent what capacity is logically sufficient and necessary for accepting the presence of the overlapping hallmarks that most theorists would associate with basic "conscious experience" in feeling animals (e.g., subjective awareness, discriminative awareness of objects,

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[41] Given that there is a vast plethora of different conceptions of consciousness that have been advanced and at least on first consideration it would seem preposterous to attribute "consciousness" to the creatures of the Burgess Shale (e.g., *Opabinia*, *Anomalocaris*, *Wiwaxia*, *Pikaia gracilens*), it might better be qualified that there are various gradations of mentality, ranging from physical feelings to consciousness, of which consciousness involves a "high level" of mentality (given the intensity of operations of selectivity, division, and negation, with reference to "mind tools," which characterizes the cognitive awareness of human beings).

mental differentiation of body from other objects, integration of information given by perception, selective attention, awareness of the "internal-external situation," agency).[42] For Ginsburg and Jablonka, consciousness *qua* "unlimited associative learning" is "open-ended learning that enables an organism to ascribe motivational value to a compound stimulus or action and use it as a basis for future learning" (Ginsburg and Jablonka 2019, p. 35; p. 191). It is a capacity which allows for the possibility of "open-ended behavioral adjustments" (ib, p. 225). Through it, they maintain that both the range and "the number of associations among stimuli and the number of possible reinforced actions that can be generated are practically limitless" (ib, p. 347). A crucial point for them is that "inherent in the notion of associative learning is the assumption that the reinforcement of new behavior depends on internal evaluation" (Ginsburg and Jablonka 2007, p. 232), whether this involves "Skinnerian" habit formation through conditioning or more sophisticated "Popperian" pre-selection of behavior from among alternatives.

Ginsburg and Jablonka suggest that unlimited associative learning is present today "in most vertebrates, some cephalopod molluscs (. . . octopods, squids, and cuttlefish) and some arthropods (including honey bees and fruit flies)," although they recognize that with more research it may be found that "the distribution of unlimited associative learning may be broader than currently assumed" (Birch et al. 2020, p. 11). However, they point to the evolutionary transition from "Darwinian creatures" with limited experience to those with "limited" and "unlimited associative learning" (e.g., of "Skinnerian" and "Popperian creatures," respectively), the latter especially in arthropods and vertebrates, as a key driver of the Cambrian explosion. One assumption here is that if "unlimited associative learning" is present in these animal groups today, and this is partly responsible for their forms, then it should have been present (at least more rudimentarily) at the time of the emergence of their stem groups and earliest ancestors (i.e., in the Cambrian period), for example, with the creatures of the Burgess Shale which included ancestors of today's mollusks, arthropods, and vertebrates. For Ginsburg and Jablonka, "associative learning, both limited and unlimited did not just originate in the Cambrian explosion, but was one of the major *driving forces* behind that explosion" (ib, p. 12), their theses further suggesting that the Cambrian explosion was not just one of organismic form but, at the same time, an explosion in terms of the cognitive and behavioral capacities of organisms.

Ginsburg and Jablonka hypothesize that the evolution of the Cambrian bilaterians may initially have been spurred on by an open range of ecological niches that was made possible by the co-existence of sessile Ediacaran organisms living on the ocean floor. These organisms are purported to have provided "organic carbon resource heterogeneity that rendered increased motility and burrowing beneficial" (Ginsburg and Jablonka 2019, p. 415), leading to an increase in body sizes, larger muscle fields, and larger sensory organs. The (mostly) benthic existence of pre-Cambrian

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[42] Simona Ginsburg and Eva Jablonka, "The Transition to Experiencing: II. The Evolution of Associative Learning Based on Feelings," *Biological Theory* 2.3 (2007), 242, their qualification.

organisms gave way to a "world of burrowing and swimming creatures," (ib) in which numerous ecological opportunities opened up. This transition required the evolution of "a throughput gut, muscles, an internal or external skeleton, and a central nervous system that could coordinate internal movements and locomotion" (ib), as well as regulating development, maintaining the constancy of the internal milieu, connecting neural circuitry, providing a condition for the possibility of experiential feeling (of pain and pleasure), and directing adaptive behavior. But, for them, it was the emergence of various heightening gradations of learning from prior ones (i.e., from non-associative learning, to limited associative learning, to unlimited associative learning) that chiefly promoted the Cambrian morphological explosion. As they describe, in the Cambrian world, "a whole orchestra of neural circuits started the great symphony of intensely active, highly interactive, and competitive animal life" (ib, p. 407), and led to a transition in the living between merely "reproductive teleological system(s)" to "new teleological systems" that had "consciousness," "subjectively felt experiences," and which could develop novel behavioral strategies with which to fulfill their biological "needs" (Ginsburg and Jablonka 2015, p. 59), including the agential ability to select among potentialities for action.

Citing the Baldwin effect as well as West-Eberhard's (2003) notions of "morphological, physiological, and behavioral plasticity" and "genetic accommodation" (Ginsburg and Jablonka 2019, pp. 417–421), in the context of describing the competition that must have transpired between predators and predators, predators and prey, and prey and prey, Ginsburg and Jablonka suggest that organisms that animals with capacities for associative learning had a selective advantage over those that did not: being able to adapt to a host of environments and to use new resources, and being more successful in predation and/or in escape. They state:

> organisms that could learn flexibly by association had an enormous selective advantage. They could associate many *new* stimuli with old ones and many new acts with outcomes. They therefore had an increased capacity to discriminate and could anticipate the effects of environmental change and their own actions. Their ability to adapt ontogenetically to a variety of environments and to use new resources increased dramatically. These onto-genetic adaptations determined where animals looked for food and protection, how they sought mates and handled food, how they reacted to predation, and so on. They were fundamental to the construction of the niches that animals and their off-spring inhabited . . . . For example, an animal that learned that food sources are available in a particular area tended to stay and reproduce there; an animal that learned that a hole in a rock affords protection against predators tended to hide in holes, and was likely to reproduce in or near them. Such behaviors introduce the offspring to the same learning environment and learning opportunities, and may lead to the genetic accommodation of any physiological, neurological, or morphological feature that enables more effective adaptation to this learning environment (including more sophisticated or more efficient learning ability). The explosion of new behaviors was therefore accompanied by an explosion of new congruent morphologies, which were probably based on regulatory modifications of genes in the existing developmental networks. (Ginsburg and Eva Jablonka 2007, p. 240).

The results were organisms with "new body plans" as well as "various types of rigid skeletons, protective shells, armored plates and spines, claws, and striking and efficient mouthparts" (Ginsburg and Jablonka 2019, p. 407), including in such wondrous organismic forms like those appearing to belong to Burgess Shale creatures such as *Anomalocaris*, *Opabinia*, *Sanctacaris*, and *Sidneyia*, among predators, whereas other creatures like the small filter-feeder, fish-like vertebrates, *Haikouichthys* and *Metaspriggina,* "swam hurriedly in the Cambrian seas to escape the arthropod predators, and the members of other phyla evolved ways of camouflaging and protecting themselves" (ib, p. 408). Ginsburg and Jablonka claim that the sensory apparatuses of organisms (e.g., eyes, mouths, touch sensitivity) were also enhanced by way of the novel modes of interaction among organisms (e.g., predators and prey) that were promoted by associative learning. The morphological arms race was also a competition in terms of cognitive ability, learning, and behavioral plasticity. They state:

> in addition to directing the morphological and behavioral evolution of the lineage in which it evolved, learning had effects on other species' evolution, because learning in one animal can exert strong selection pressure on the organisms with which it interacts. For example, as the learning ability of a predator species improves, there is strong selection for morphological and physiological adaptations (such as protective hard parts and escape reactions) in its prey species, and also for the prey's ability to learn. Consequently, not only did associative learning lead to the radiation of the group in which it emerged, it also probably led to learning-guided morphological co-evolution and a learning arms race in interacting species (Ginsburg and Jablonka 2007, p. 240).

In this sense, the ability to learn is also an adaptive trait, which, of course, requires memory stemming from sophisticated neural functioning and/or brain structures, and some interpretations of the Baldwin effect focus almost exclusively on the amplification of the organism's capacity to learn. Ginsburg and Jablonka go on to argue that the competitive race of learning leads to overlearning and stress which necessitated the adaptation of a homeostatic stress response.[43]

Overall, for Ginburg and Jablonka, the presence of associative learning, by which organisms may exploit new resources in the environment, settle into new ecological niches, and become more effective predators, more evasive prey, and/or more selective mates, is a mark of behavioral and developmental plasticity which can potentially generate adaptive and phenotypic novelty. In their view, the emergence of associative learning and especially of unlimited associated learning in some organisms promoted an intensification of selection pressures on other organisms. The competition that was spurred on by the emergence of associative learning and its refinement is, for them, what primarily drove the dramatic diversification of organisms during the Cambrian period (Birch et al. 2020, p. 12).

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[43] This claim has been criticized by John Mallatt in "Unlimited Associative Learning and Consciousness: Further Support and Some Caveats About a Link to Stress," *Biology and Philosophy* 36.22 (2021), 3–4.

3.7 Embodying the Baldwin Effect: Complementing Ginsburg and Jablonka's Cognitive-Behavioral and/or Learning-Based Account of the Cambrian Explosion with the Thompsonian Approach—A Hypothetical Scenario Involving *Ottoia prolifica* and the Hyolith, *Haplophrentis*)

In this section, I shall show how Thompson's emphasis on physical forces and mechanical efficiency can help to complement Ginsburg and Jablonka's account of the production of novel physiological structures and morphologies in the Cambrian explosion by way of the emergence of consciousness, including learning new behaviors. From a Thompsonian perspective, there is a need to "embody the Baldwin effect," so to speak, by placing more emphasis on the physical side of things within cognitive and behavioral accounts of morphogenesis. After all, "Skinnerian," "Popperian," and "Gregorian" creatures are also physical creatures, the so-called more sophisticated ones still retaining basic properties of the former categories (e.g., "Darwinian creatures"), and in a parallel fashion, for example, to some extent, the creatures of the Burgess Shale would have shared with their earlier Ediacaran counterparts the element of being molded by physical factors (where highly integrated genetic programming and developmental processes as well as selectionist explanation do not apply to the same degree) (see Newman et al. 2006). Learned behaviors and strategies like scavenging, seizing prey without being reciprocally harmed by their defenses, detecting and fleeing from predators, burrowing in marine sediment, hiding in holes, and swimming (as "consequences of the evolution of associative learning" (Ginsburg and Jablonka 2007, p. 240) require morphologies that "fit," at least minimally, with the environment, and that produce the physical forces that are requisite to perform them in the particular context. For instance, in order to burrow into muddy sediment so as to avoid epibenthic predators in a minimal fashion, an organism's appendages must have sufficient and coordinated digging or thrust power to carry this out and its bodily form as a whole must not present undue physical obstruction. Otherwise, the possibility of even minimal burrowing activity is closed or inoperative. Furthermore, there are limits as to the range of ecological niches that may be efficiently exploited as well as limits to the physiological energies of organisms as they attempt to take advantage of them.

As in the Baldwin effect, over evolutionary time, morphologies that provide the conditions for the possibility of the organism performing a requisite novel good trick will be selected for, and the evolution of the species will be canalized toward those which amplify the ability of the organism to perform them. Habitualized good tricks may only go so far in dealing with the exigencies of changing environments. And it is the overall phenotypic plasticity of the organism, its physicality included, that will help to determine its fitness. At the same time, evolutionary trade-offs must be made: an aquatic organism that has developed a morphology like a "Swiss army knife" may be limited in terms of its hydrodynamism, or one that must constantly exapt its existing appendages to new required functions will impede spontaneity in its performance of requisite behaviors. On the one hand, as is aptly shown by the Baldwin effect generally as well as by Ginsburg and Jablonka, the organism's degree of mentality *qua* associative learning and the generation of novel behavioral selections both promote and constrain what physiological and/or morphological novelties will emerge. However, on the other (Thompsonian) hand, *behavioral innovation by way of associative learning is both enabled and constrained by the intrinsic and extrinsic physical forces in play in the performance of the behavior as well as by the organism's overall morphology, its physiological structures, and their mechanical "fitting" with the environment, including the objects and other organisms interacted with therein*. In other terms, although behavioral innovation can canalize morphological change in evolution, behavioral innovation is enabled, largely determined, limited, and canalized by what is physically possible, in the interaction of the organism with a specific morphology and the given environment. As such, from a Thompsonian orientation, Ginsburg and Jablonka's use of the term "unlimited associative learning" as a marker for consciousness can be said to be nebulous in this regard, and the "open-endedness" of what is meant requires further qualification.

Indeed, other commentators[44] have for more clarification about the meaning of this term (although not explicitly on these Thompsonian lines). While Ginsburg and Jablonka do admit that while the behavioral possibilities in relation to exploratory activities involving "unlimited associative learning" are "sufficiently open-ended that there is no serious prospect of all the possible associative links" being exhausted by an organism over the course of its realistic lifespan, unlimited associative learning is "not . . . entirely free of constraint" (Birch et al. 2020, p. 8).[45] That said, they do not specify what factors present constraints on the organism's generation and performance of good tricks as well as on the range of behavioral novelties that may be entertained. Surely, what they call "unlimited" associative learning is, to some extent, limited to what is physically possible for the organism, which canalizes behavioral innovation. Again, Thompson's notion of "mechanical efficiency" can be said to point to the notion that physical forces constrain what good tricks are operative and which are not, providing positive or negative feedback on the behaviors (burrowing, attacking prey, swimming) being entertained and/or performed by the organism. So, from a Thompsonian perspective, what Ginsburg and Jablonka putatively call "unlimited associative learning" is not truly "unlimited." Rather, the actionable content of so-called unlimited associative learning and behavioral selection is enabled, entrained, and constrained by way of physical forces and the requirements of mechanical efficiency as regards the organism's physiological structures. Hence, synthesizing the Baldwin effect and Ginsburg and Jablonka's emphasis on behavioral innovation together with Thompson's physico-mathematical

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[44] For example, see Mallatt, "Unlimited Associative Learning and Consciousness," 21–22.

[45] Also see Ginsburg and Jablonka, "The Teleological Transitions in Evolution," where they state "there are, of course, many constraints on unlimited associative learning in any learning animal (including humans), but nevertheless, the number of possible learned associations is vast, and learning-based plasticity is never fully exhausted" (59).

orientation, it can be said that both physical forces and behavioral innovation are to be viewed as cooperating efficient causes of morphogenesis.

While providing a wealth of insight and detail, Ginsburg and Jablonka do not provide many concrete examples of detailed, plausible scenarios of behavioral innovation in Cambrian times generated by (unlimited) associated learning leading to morphogenesis. However hypothetical such scenarios would be (given that the actual behavior of the Cambrian organisms in question can only be interpreted and reconstructed on the basis of physical fossil evidence with reference to the behavior of similar modern organisms), such examples would go a long way to demonstrate the soundness of their theories. In carrying out such "speculative ethological" interpretations of cognitive- and/or behaviorally induced evolution in Cambrian fauna, special care would be required not to interpret such examples as fixed, representative "stand-ins," eliminating all difference, for the behaviors of the organisms in question. And it would be best that such examples be based on the analytical and interpretive study of Cambrian fossils by paleontologists.

Consistent with the theses advanced by Ginsburg and Jablonka concerning the causes of the Cambrian explosion, Vannier and Chen (2005) have provided evidence for the notion that "the burst of anatomical innovations (new body plans) . . . was accompanied by the rapid development of new feeding strategies and by an unprecedented expansion of ecological interactions (prey–predator relationships) (Vannier and Chen 2005, p. 3). Specifically, they chart out a range of predator–prey interactions among diverse Cambrian fauna at various levels of the water column, ranging from endobenthic predators (e.g., *Ottoia prolifica*), through meiobenthic prey (e.g., *Ercaia*) and epibenthic predators (e.g., *Naraoia*) and prey (e.g., hyoliths, trilobites), to midwater predators (e.g., *Anomalocaris*) and prey.

One (at least partly) endobenthic middle-to-upper Cambrian Burgess Shale creature was the tube-shaped, bilateral, radially symmetrical, non-segmented, "cycloneuralian" worm, *Ottoia prolifica*. *Ottoia prolifica* represents one of the more widespread of Cambrian fossils, and it resembles some priapulids of today (e.g., *Priapulus caudatus*). *Ottoia* was on average eight centimeters in length, with an eversible and retractable proboscis at one end, and a trunk "marked by cuticular annulations" (Banta and Rice 1976, p. 84) encasing a long digestive tract of around two-to-five millimeters in diameter. *Ottoia*'s particular morphology appears "suitable for a large metazoan moving through a uniform environment like mud than crawling over the substrate" (ib, p. 84). *Ottoia* had about twenty-five rows of hooks on its proboscis, a battery of teeth around its mouth (at the end of the proboscis). And lining its "pharynx"[46] (which could be "outside" or "inside" depending on whether the proboscis was everted or introverted) there was another forty or so more rings of teeth, each ring containing as many as twenty teeth. These presumably assisted in scraping soft material in the process of feeding. *Ottoia* had bands of teeth of various

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[46] Banta and Rice suggest that "there is no agreement as to the proper term for this organ; we shall refer to it as a "pharynx" ("A Restudy of the Middle Cambrian Burgess Shale Fossil Worm, *Ottoia Prolifica*," 88).

distinct types, progressively decreasing in size. These ranged from "conical spines fringed with accessory denticles," to "quincunxially" patterned, widely-based, broad spines, to "edentate cones" (Smith et al. 2015, pp. 14–16). A number of *Ottoia*'s teeth "project[ed] inwards and downwards" (assuming an introverted proboscis) such that "if the prey were to struggle free when it was swallowed, it [would] impale itself against these teeth" (Conway Morris 1998, p. 69).[47]

Ottoia had up to half a dozen sickle-shaped spines on its tail, which may have provided an anchor for its body in its burrow and a means of defense for its anterior. For part of its time, *Ottoia* burrowed powerfully into the muddy sea-floor by way of its proboscis and the "peristaltic" movement of the muscles of its body wall. *Ottoia*'s burrowing would have involved the eversion of its proboscis, pushing its trunk backward, and requiring it to have to wedge itself into the sediment (with the use of its proboscis hooks), followed by retracting the proboscis. Feeding would also have involved the partial eversion of its proboscis. *Ottoia* was "basically a large sac, filled with bodily fluid [that was] … effectively incompressible," its proboscis everting "by way of hydrostatic pressure" (Conway Morris ib., p. 69). Anchored in a curved U-like position in a similarly shaped burrow, its proboscis at one end of the burrow would be "ready to shoot out and capture" (Foster 2014, p. 272) epibenthic prey. Its anus at the other end would presumably enable the ejection of fecal elements safely outside of the burrow while awaiting prey. *Ottoia* had a 0.3-millimeter-wide longitudinal nerve cord running ventrally down the inside of its bellied trunk, with regular ganglia (Conway Morris 1977, p. 27). However, *Ottoia* lacked complex sensory organs and awareness of prey was probably based on chemoreceptors that are found in modern priapulids (Vannier 2012, p. 12). *Ottoia* was probably "a generalist," namely, a scavenger-predator flexible in its behavioral strategies, which displays "a high level of trophic complexity" that has no precedent in prior geological eras, and "foreshadows modern-style ecosystems" (ib, p. 16).

Of the specimens of *Ottoia prolifica* collected, approximately twenty percent of these fossils were found to have preserved gut contents, and of these, almost half of the identifiable contents were found to be one or several hyoliths, such as *Haplophrentis carinatus*, (ib pp. 6–7) a small, semi-sessile, epibenthic organism. *Haplophrentis*' body was encased in a ten-millimeter-long (on average), bilaterally symmetrical, conelike, aragonite shell (or conch), which owed its production to the biomineral secretion of calcium carbonate (in a similar fashion to a clam or a snail). The shell was pointed at its tip, flat on the bottom, with a small aperture lid or operculum at its front. Similar to the shape of a crossbow, two curved, "oarlike" (Briggs et al. 1994, p. 113), "stiltlike," or "strutlike," appendages, named "helens" (by Charles Walcott after his daughter), protruded laterally from the aperture on the hyolith's shell. Other hyoliths did not have these appendages (Liu et al. 2020, p. 453). As for *Haplophrentis*, these rigid, bent, skeletal, biomineralized appendages, perhaps three-to-four millimeters in length, could be rotated ventrally

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[47] Banta and Rice report that "the teeth are directed posteriorly" (88). They appear to be assuming a retracted proboscis. See their Figure 30 on page 88.

about one-hundred-and-eighty degrees. It is thought that these helped the organism to move itself ("inefficiently" (Briggs et al. 1994, p. 113)) along the top of soft, muddy, ocean floor as it searched for small organic matter. *Haplophrentis* also had a small tentaculate band protruding out of the bottom of its operculum and a protrusible "pharyngeal" organ (Moysiuk et al. 2007, p. 394). Hyoliths were a major food resource for *Ottoia*, but only one of many (e.g., other brachiopods, small trilobites, and decaying wiwaxiids and sidneyians being some of the others), it being able to adapt its diet to circumstance. However, neither *Ottoia*'s "pharyngeal" teeth could macerate the conch shells of the hyoliths, nor could *Ottoia* digest them chemically along with the soft matter. Along with sediment, the conches passed through *Ottoia*. And presumably, the helens could be disarticulated, but also not digested by *Ottoia*.

Of the hundreds of *Ottoia* fossil specimens found with one or more hyolith impressed in their guts, almost eighty percent of them were oriented such that the apertures of their shells were pointed toward the posterior end of the *Ottoia*'s gut, in a "head down" fashion (Vannier 2012, p. 7). This orientation allegedly pervaded the entire digestion process. The nearly "unidirectional orientation" of the hyoliths in *Ottoia*'s gut indicates that they were "caught *preferentially* by one side,"[48] namely, "grasped and drawn into the gut by their anterior side, where they probably offered a stronger grip point to the pharyngeal teeth of *Ottoia*" (Vannier 2012, p. 7, my emphasis). It was only on rare occasion that the helens of the digested hyoliths were found intact, such that most "became partly disarticulated as they entered the digestive tract of the worm (e.g., by the muscular contractions of the pharynx)" (ib).

With these descriptions of *Ottoia* and *Haplophrentis* in mind, Conway Morris (1998) has provided a dramatic, hypothetical re-enactment of the predator–prey interaction between *Ottoia* and *Haplophrentis*, which asserts an explanation for the nearly uniform orientation of the hyoliths in the *Ottoia*'s narrow, muscular gut, as follows:

> the hyoliths browse peacefully on the surface of the sediment, seeking out organic detritus. But now close to a group of these hyoliths the sediment has begun to move slightly. What happens next is very fast. Suddenly the snout of an *Ottoia* rears out of the sediment, a hyolith is seized and quickly swallowed. … Three times the group is attacked before *Ottoia* sinks back into the mud. Each time a hyolith is swallowed in the same fashion, the priapulid grabbing the front end first. Why does *Ottoia choose* to attack this way round? Consider the curved struts (or "helens") sticking out of the hyolith. … *These struts point backwards, and if the Ottoia swallowed the hyolith from the other direction there would be a danger of the prey becoming jammed in the gut of the priapulid*. (Conway Morris, 1998, p. 72, my italics for emphasis, my addition for clarity in brackets)[49]

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[48] Vannier and Chen, "Early Cambrian Food Chain," p. 22, my emphasis. Also see Conway Morris, who states (in "Fossil Priapulid Worms") that the hyoliths "were eaten alive for food rather than ingested by chance; whilst the *preferred* orientation indicates that *O. prolifica chose* the method of ingestion, i.e., the hyolithids were hunted" (26, my emphases).

[49] Vannier (2012) indicates incomplete agreement with some elements of Morris' claims, and the manner of "swallowing" the hyoliths may just be a function of their own direction of movement, while Conway Morris asserts that "*Ottoia* is a voracious predator. Sometimes it will emerge out of the sediment to seize shellfish known as brachiopods. But *Ottoia* also hunts for food as it burrows

It should be noted that Conway Morris' (1998) hypothetical scenario predates some important revelations that were made about *Ottoia* [e.g., see Smith, Harvey, and Butterfield (2015) in relation to its teeth] and *Haplophrentis* (e.g., about the nature of the possibilities as regards the orientation of its "helens" and of its tentaculate band), and it should definitely be taken with a "grain of salt." That said, taken "as is," in it, *Ottoia* is alleged to have some degree of valuative-selective agency in that it is said to have "preferences," "choices" (as per the language employed by researchers), and/or to make behavioral selections that it applies in a "downward causal" fashion (coinciding with Ginsburg and Jablonka's theses concerning associative learning). However, Morris' scenario points explicitly to the importance of the physical context, as in Thompson's physico-mathematical approach to the study of morphogenesis. For the putative behavioral strategy of *Ottoia* to tend to seize hyoliths from the front was, from Morris' account, predicated on the *physico-geometrical form* of the hyolith's conch and "oarlike helens," in relation to *Ottoia*'s morphology (i.e., with its tubular, digestive tract, and also the inward and downward facing teeth [when the proboscis is introverted]). *Ottoia*'s pre-selection of this behavior was, in all likelihood, based on (associative) learning from "problematic" episodes in its past experience of feeding specifically on *Haplophrentis* (i.e., the hyolith getting caught in the *Ottoia*'s narrow gut or on its teeth [in a fashion much like putting a crossbow on the hooked prongs of a wall storage rack] due to its obstructive helens). Presumably, it would not matter which way prey—other than *Haplophrentis* (and/or those which did not have such obstructive "helens" as part of their anatomy)—were to be seized by *Ottoia*. Admittedly, Conway Morris' scenario depends on an unconfirmed hypothesis that the *Haplophrentis*' helens could pose a physical obstruction to the digestive apparatus of the *Ottoia*, and there could be other explanations for why the hyoliths were seized, swallowed, and digested in "head-first" fashion. Nevertheless, pointing to the importance of the Thompsonian outlook in cognitive, behavioral, and/or learning-based accounts of morphogenesis and evolution, based on it, *Ottoia*'s *behavioral innovation and/or selection was entrained and/or canalized by the physico-geometrical constraints posed by the Haplophrentis' obstructive helens and conch in relation to the morphology of its digestive tract and the pointing direction of its "pharyngeal" teeth.*

Finally, following the logic of the Baldwin effect, one might speculate that had diverse food sources not been available to the *Ottoia* population, such that, for example, its diet was substantially narrowed down to *Haplophrentis* (with its obstructive helens) then in light of *Ottoia*'s habitualization of the good trick of

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through the mud. It readily consumes soft-bodied prey, and will even attack weaker individuals of its own species. *Ottoia* the predator is also a cannibal." Vannier (2012) has not verified that *Ottoia* was a cannibal, suggesting that this conclusion can only be drawn from a single poorly preserved specimen ("Gut Contents as Direct Indicators," 10). Briggs et al. (1994) had suggested that one specimen involved the proboscis of another *Ottoia* in its gut (*The Fossils of the Burgess Shale*, 122), but Vannier asserts that it is not known whether *Ottoia* was more of a scavenger than a predator ("Gut Contents as Direct Indicators," 14).

seizing its prey from the front, natural selection would have favored a morphology, including any physiological features, that would assist in this task. For example, adaptive features (e.g., proboscis, mouth, and/or gut shapes) that were more mechanically efficient, namely, more able to muster up the physical forces required to seize and to swallow such prey in such a manner, or muscles, tooth shapes, and teeth pointing in directions that could help *Ottoia* to reorient the hyolith in the "pharynx" after being swallowed, if necessary, would be selected for, thereby channeling the physiological transformation of *Ottoia* in the direction of the good trick over evolutionary time.[50]

3.8 Conclusion: The Importance of D'Arcy Thompson's Physico-Mathematical Approach to the Study of Morphogenesis—Teleology and Mechanism

The preceding analysis has unpacked some of the Aristotelian and Kantian undercurrents of D'Arcy Wentworth Thompson's "physico-mathematical" approach to morphogenesis and evolution as well as his critiques of the vitalism, selectionism, and geneticism of his time, which may serve to place into question various prominent characterizations of his biological thought as "eclectic," "unorthodox," etc.. . . . And it has attempted to show the continuing importance of Thompson's approach today, as representing a key conceptual "lens" for researchers to look through in the context of a holistic, multi-level, multi-perspectival, and multi-dimensional orientation as regard the study of life. Pointing to its application in the context of supplementing cognitive-behavioral and/or learning-based explanations of morphogenesis and evolution (with all of their "apparently" teleological implications), such as that represented by the Baldwinian theory of organic selection and/or that of Ginsburg and Jablonka (2019), the Thompsonian approach positively assists us to "keep one eye on" the physical dimension within the physical-behavioral nexus that is involved in organismic agency. Furthermore, by way of its emphasis on the entrainment and/or the canalizing constraints posed by physical forces in relation to the cognitive-behavioral selections of organisms ("the *teloi* of which" according to Ginsburg and Jablonka "are the fulfillments of feelings, needs, and desires" (Ginsburg and Jablonka 2015, p. 59)), Thompson's "physico-mathematical" approach may be seen, in turn, to assist in resolving the tension between "the teleological" and "the mechanistic" as regards what concepts are most proper to the study of self-organization and of life, as we move (ongoingly) toward an extended evolutionary synthesis and beyond.

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[50] Additional clues as to the evolution of *Ottoia* may come from comparisons of *Ottoia prolifica* and *Ottoia tricuspida* (such as in Smith et al. 2015) who compare the teeth of specimens and suggest that these varieties may be reliably distinguished on this basis) as well as *Ottoia* with the morphologies of various Cambrian priapulids (e.g., *Fieldia*, *Louisella*, *Ancalagon*, and *Selkirkia*). Further insights may issue from further comparisons of the morphologies of *Ottoia*, fossils of earlier priapulids, or the anatomies of modern priapulids.

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From Dissipative Structures to Biological Evolution: A Thermodynamic Perspective

4

Dilip Kondepudi, James Dixon, and Benjamin De Bari

Abstract

In the second half of the twentieth century, it was recognized that systems far from thermodynamic equilibrium can spontaneously self-organize into structures that exhibit chemical oscillations, propagating and stationary chemical patterns. These nonequilibrium structures are called *dissipative structures*. Rapid development of research in this field came from the seminal work by the Brussels School of Thermodynamics under the leadership of Ilya Prigogine. Developments in the last decade have given us a new perspective on the emergence of organism-like behavior in non-living systems. It was found that highly complex, organism-like behavior can spontaneously emerge in dissipative structures. An example is the formation of a worm-like structure which moves to locations that provide more of the energy needed to sustain it. General characterization of such complex behavior in terms of rates of entropy production has been formulated. In this chapter, these recent advances will be reviewed and the relationship between dissipative structures and biological evolution is discussed.

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_4

> We shall come closest to understanding the principles of life if we can discover the principles according to which life *could* begin. This is a challenge addressed to the physicist, even if he calls himself a biophysicist, a biochemist or a molecular biologist. How *did* life begin, however, can probably only be understood by appeal to historical evidence (Eigen and Winkler-Oswatitsch 1992).

Keywords

Self-organization · Dissipative structures · End-directed evolution · Entropy production · Self-healing · Symmetry-breaking transitions · Biological chiral asymmetry · Bio-analog systems · Maximum entropy production

4.1 Self-Organization in Non-equilibrium Systems

In physics and chemistry, self-organization is a phenomenon that occurs in systems that are far from thermodynamic equilibrium. In the 1960s and 1970s, it was realized that irreversible processes that increase entropy, and thus *destroy* order, when a system is at or near thermodynamic equilibrium, can do just the opposite and spontaneously *create* order when a system is far from thermodynamic equilibrium. These findings generated a flurry of research on self-organizing nonequilibrium systems (Nicolis and Prigogine 1977; Haken 1977; Vidal and Pacault 1981; Field and Burger 1985; Epstein and Pojman 1998). This research laid a new path to address a challenging question in physics: as material process, how *could* life originate?

In this chapter, we describe how our current understanding of self-organization in nonequilibrium systems provides a foundation on which we can begin to extend physics to address the challenging question: how could life originate and evolve? We will build a bridge between the language of biology and language of thermodynamics. We will see how some fundamental traits, such as end-directed behavior, self-healing, and mutations, can be described in thermodynamic terms, as phenomena in self-organized nonequilibrium systems, called *dissipative structures*.

4.1.1 Classical and Modern Thermodynamics

Though the reader may be familiar with the basic concepts of thermodynamics and self-organization, for the sake of completeness, we will begin with a brief review of modern thermodynamics, which was formulated in the twentieth century.

In its inception, thermodynamics was formulated as a *theory of equilibrium states*, with the introduction of the two fundamental laws of thermodynamics, one governing energy and the other entropy. Transformations in the state of a system were described and the limitations nature imposed on the possible changes were clarified: every change in the system can only happen in such a way that the energy is conserved, a change in the energy of a system compensated exactly by an opposite

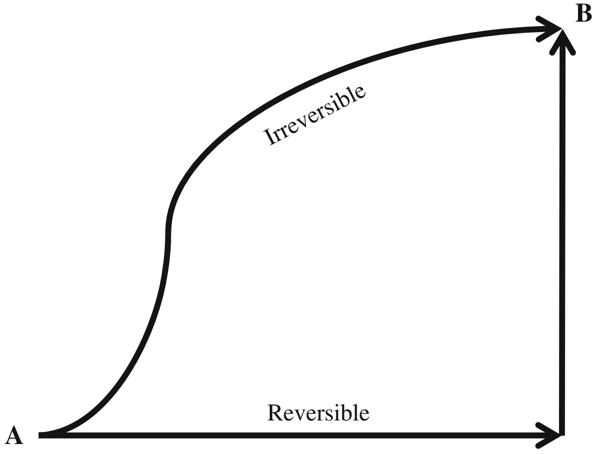

Fig. 4.1 In classical thermodynamics, change in entropy between equilibrium states A and B is calculated using an imaginary, reversible path along which $dS = dQ/T$. The actual change takes place along an irreversible path

change in the world exterior to it. And every change can only increase the total entropy of the system and its exterior. Every process in nature only increased the entropy of the universe. Energy and Entropy are state functions; they are dependent only on the current state of the systems, and not on the path that brought it to the current state. However, in this nineteenth-century classical formulation, changes in entropy are calculable only for "infinitely slow" *reversible* processes (also called quasi-static processes), a concept introduced in the foundational work of Sadi Carnot (Carnot 1824; Mendoza 1977). For this idealized process, changes in entropy, dS, are calculable using the equality $dS = dQ/T$, in which dQ is the heat exchanged with the system and T its absolute temperature. In reality, transformations in the state of a system occurred in finite time due to *irreversible* processes, for which the classical formulation could only provide the inequality $dS > dQ/T$. There was no direct relationship between irreversible processes and entropy in the classical thermodynamics. Still, changes in entropy between equilibrium states could be calculated using the concept of the reversible process: when a system underwent a change from a state A to state B, in a finite time due to irreversible processes, the same change could be realized using a reversible process[1] and the change in entropy calculated using $dS = dQ/T$ (Fig. 4.1). Classical theory did not have a way to make a connection between irreversible processes and the entropy they generated (Kondepudi and Prigogine 2015).

Twentieth-century formulation of thermodynamics that originated in the work of Onsager, De Donder, Prigogine, and others (Onsager 1931; De Donder and Van Rysselberghe 1936; Prigogine 1947, 1967) relates entropy directly to irreversible processes that produce entropy. In this formulation, changes in entropy of a system are expressed as:

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[1] It was tacitly assumed this was always possible.

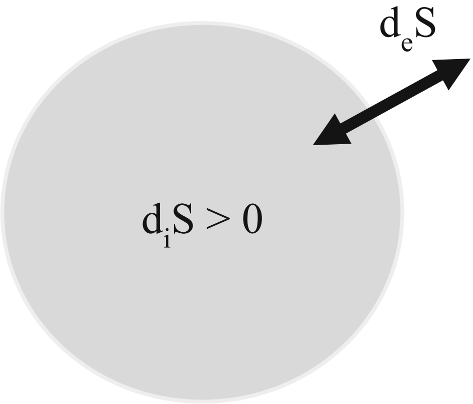

Fig. 4.2 Changes in entropy of a system consist of entropy produced in the system by irreversible processes, d_iS, and entropy exchanges with the system's exterior, d_eS

$$dS = d_iS + d_eS. \tag{4.1}$$

In this expression, d_iS is the entropy produced by irreversible processes within the system, which according to the second law is always positive, and d_eS is the exchange of entropy with the system's exterior (Fig. 4.2).

d_iS is directly related to the thermodynamic processes occurring within the system which are describable in terms of thermodynamic forces and flows. Thermodynamic forces are gradients of intensive variables X (e.g., temperature and chemical affinity) divided by temperature, and flows are time derivatives of the corresponding extensive variable J (heat flow and reaction rate, respectively). The entropy production per unit volume is calculated as the sum of the product of all thermodynamic forces and flows in the system (Prigogine 1967; De Groot and Mazur 1969; Kondepudi and Prigogine 2015):

$$\frac{d_is}{dt} = \sigma = \sum_i X_i J_i. \tag{4.2}$$

Here, s is the entropy density, S/V. Flows are driven by forces. Flow of heat driven by a temperature gradient is an example. Flows are not functions of the forces alone; flows may depend on other variables. For a given thermodynamic force, flows can vary due to system properties; the presence or absence of a catalyst in chemical reactions is an example. Critically, Eq. (4.2) establishes that the entropy is a direct function of the processes driving changes in a thermodynamic system. The rate at which entropy is generated can be calculated if the thermodynamic forces and flows are known.

The second law of thermodynamics is distinctly different from Newtonian mechanics in two aspects. First, it states that that nature is fundamentally irreversible with an arrow of time, in stark contrast to Newtonian mechanics which is time reversible.[2] Second, it predicts the final state of a system (the equilibrium state), not the path the system will take to reach this state; in this way, it portrays nature as "end directed." Depending on the nature of the constraints, the second law predicts that the system will eventually reach a state of maximum entropy, or minimum Helmholtz or Gibbs energy, but its path to this state or how long it will take to reach the ultimate state of equilibrium is not specified. This is in contrast to Newtonian mechanics which, given the initial conditions and the forces, predicts the entire path in the future and the past. The second aspect will become significant when we discuss end-directed behavior in non-living dissipative structures that is analogous to the behavior we see in living organisms.

4.1.2 Self-Organization in Systems Far from Thermodynamic Equilibrium

When a system is near equilibrium, flows are linear functions of the forces that drive them. These conditions are termed "the linear regime." When a system is driven farther away from equilibrium by flows of matter and/or energy, the relationship between thermodynamic flows and forces is no longer linear and the system is said to be in the nonlinear regime. It is in the nonlinear regime that the phenomenon of self-organization appears. When a system is moved away from equilibrium through a flow, for instance, beyond a critical value of the flow or a concentration, the system can make a transition to a self-organized state with an identifiable structure, either spatial, temporal, or spatio-temporal. (For an extensive discussion of such systems, see Nicolis and Prigogine 1977; Haken 1977; Epstein and Pojman 1998). Chemical oscillations and spiral waves in the well-studied Belousov–Zhabotinsky (BZ) reaction are examples. Such periodic dissipative structures appear in living organisms as biochemical oscillation and rhythms (Goldbeter 1996, 2017). In addition, as predicted by Alan Turing, spatial patterns of varying concentrations can form (De Kepper et al. 1994) – Turing suggested it as a model for morphogenesis. Such structures are generated and maintained by entropy generating irreversible processes that dissipate free energy. For this reason, they are called *dissipative structures*. From the time dissipative structures were discovered it became clear that living organisms, whose creation and survival depends on flow of matter and energy, are dissipative structures (Prigogine et al. 1972). As described below, dissipative structures have general characteristics and properties that can be recognized as traits that we see in living organisms. In our recent studies, we discovered that dissipative structures also exhibit end-directed behavior, such as seeking energy that sustains the structure, thus giving us a firm foundation for the notion that living organisms are a class of dissipative structures.

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[2] This distinction is important when we consider the fundamental difference between machines and organisms (Kondepudi et al. 2017).

4.1.3 Dissipative Structures

In general terms, evolution is a result of mutation, adaptation, and survival of the fittest. If organisms are a class of dissipative structures, we need to understand living organisms on an individual level, as well as their evolution on the species level, in terms of general features of dissipative structures. Let us note a few general characteristics of dissipative structures that are significant for a discussion of self-organization as a paradigm for biological evolution.

4.1.3.1 Instability, Amplification of Fluctuations, and Establishment of a New Structure

According to the second law, entropy generating irreversible processes drive the system to the state of maximum entropy, the equilibrium state. In the equilibrium state, all thermodynamic forces and flows vanish and there is no entropy production. The equilibrium state is stable to random fluctuations. All thermodynamic systems have intrinsic thermal fluctuations in its state variables, such as temperature, pressure, and concentrations of chemical components. Since the equilibrium state has the maximum entropy, thermal fluctuations can only decrease the system's entropy; irreversible processes that increase entropy then come into effect and restore the state of equilibrium.[3] Thus, the equilibrium state is stable in the face of random thermal fluctuations.

In contrast, nonequilibrium states may become unstable to specific types of fluctuations (Nicolis and Prigogine 1977; Haken 1977; Kondepudi and Prigogine 2015). As a system is forced away from equilibrium through a flow of energy and/or matter, initially, the states that are close to the equilibrium state remain stable, but this stability is not guaranteed. Under far-from-equilibrium conditions, a state can become unstable to a particular type of fluctuations depending on the boundary conditions. This fluctuation is then amplified by irreversible processes and the system undergoes a transition to an organized state, a dissipative structure. The new organized state is stable, but its stability is not assured by any general maximum or minimum principle, such as the second law. A principle in terms of the rate of entropy production, the so-called maximum entropy production principle (MEP), has been suggested. In Sect. 4.3, we shall discuss this principle and its validity in one of the systems we have studied extensively.

If the boundary conditions (environmental factors) are changed, a dissipative structure may become unstable to another type of fluctuation and be driven to a different dissipative structure. This phenomenon is similar to random changes in the genetic code (which are analogous to fluctuation in dissipative structure) and the consequent response of an organism. We shall discuss the analogy further in a later section.

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[3] The probability of a fluctuation in the equilibrium state is given by Einstein's formula: $\mathrm{Exp}(-\Delta S/k)$, in which ΔS is the change in entropy due to the fluctuation, and k is the Boltzmann constant.

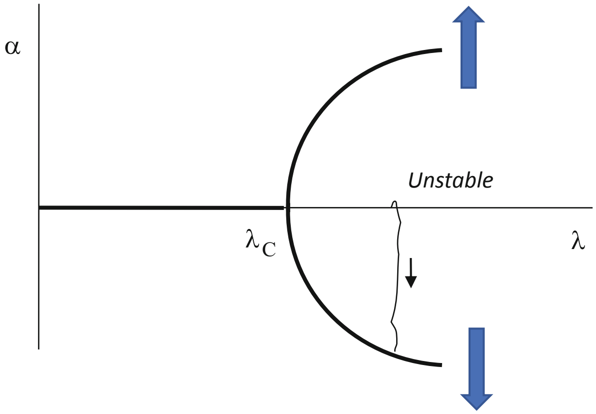


Fig. 4.3 Bifurcation of symmetry-breaking states to possible states with opposing polarity. α is a measure of the polarity and λ is a parameter that quantifies the system's nonequilibrium state

Nonequilibrium instability and transition to a dissipative structure occurs at a particular *critical value* of a parameter, such as a flow rate or a concentration or voltage. Mathematically, this appears as bifurcation of new solutions to nonlinear differential equations at the critical value of a parameter. Each of the new solutions corresponds to a possible organized state/dissipative structure; driven by fluctuations, as described above, the system makes transition to one of the available stable states. Often, there are multiple new solutions that are related to the symmetries of the system. To which one of the possible states the transition takes place may depend on environmental factors.

4.1.3.2 Spontaneous Symmetry Breaking, States Selection, and Sensitivity

More often than not, dissipative structures arise out of a *symmetry-breaking transition (Prigogine and Nicolis* 1967). In such a transition, the state to which the system evolves does not have the symmetry of the processes that generate it. In mathematical terms, it means the solution to a differential equation does have the symmetry of the differential equations; hence it is called *spontaneous symmetry breaking*. For example, even if there is no intrinsic bias in a system to one direction or its opposite, still, the solutions to the equations that describe the system may have a polarity, pointing to one or the other direction; however, there will be two new solutions with opposing polarities (Fig. 4.3).

The symmetry is reflected in the multiplicity of solutions. It means, beyond the critical value, there are two possible dissipative structures, with opposing polarity, to which the system can transition. Such a transition occurs in the Rayleigh–Bénard convection. Above a critical temperature gradient, convection rolls emerge. An individual roll could emerge with clockwise or Counter clockwise rotation (from a given perspective). These new states are equiprobable, emerging due to the amplification of microscopic random fluctuations during the critical transition. A similar situation arises in the formation of chemical spatial structures in which a concentration gradient forms in one direction or its opposite. This amplification of fluctuations into self-organized states is what Prigogine and Stengers (1984) called "order through fluctuations." In such situations, which of the two possible structures the system will transition to depends very sensitively on environmental or external influence, such as a gravitational field or a temperature gradient, which biases the system toward one of the two possible polarities. Though the field only exerts a very weak influence on the system, the self-organizing processes intrinsic to the system will amplify the fluctuations induced by the embedding field. This induced symmetry breaking or nonequilibrium sensitivity is one of the ways a nonequilibrium system becomes highly sensitive to their environment (Kondepudi and Prigogine 1981; Kondepudi 1982). This is in contrast to equilibrium systems whose stable state is only perturbed a little due to an environmental factor such as gravity.

The selection of states through environmental factors makes the system very sensitive to its environment. Through such a mechanism, internal structure and dynamics of a dissipative structure become correlated with external factors. It was noted that through such a mechanism, internal states of small living cells can become aligned with the direction of gravitational field, thus providing a gravity detection mechanism for living cells (Kondepudi 1991; Bizzarri et al. 2014). It could be said that in symmetry-breaking transitions, the environment imprints on the structure.

Higher order symmetries result in a larger number of states to which the system can make a transition. In the case of a breaking of a spherical symmetry along an axis, the multiplicity of solutions is infinite, each corresponding to an axis of the sphere. Development of a sea urchin is an example. In the early stages of the development, the sea urchin's embryo is spherically symmetric in the sense that the animal–vegetal axis can be induced along any axis of the spherical embryo. Which axis will actually become the animal–vegetal axis depends generally on an external factor such as the point at which the embryo is in contact with another object. Once the animal–vegetal axis is fixed, spherical symmetry is completely lost due to complex morphogenetic processes.

In systems that have multiple self-organized states, a large enough perturbation may drive it from one stabe state to another. If a system has a very large number of states, the system's interactions with the environment may cause it to make transitions between these states. It is a mechanism through which a system's internal states become correlated with the world around it in complex ways making the system "aware" of various factors in its environment. In the Sect. 4.3, we will present an example of such environmental sensitivity in an electrically driven dissipative structure with a large number of internal states.

4.1.3.3 Self-Healing

Dissipative structures are stable to perturbations. If a spatial or a temporal structure is perturbed, in due course the structure is reestablished (Nicolis and Prigogine 1977; Kondepudi et al. 2017). This occurs due to the intrinsic dynamical stability of these structures. As discussed above, the emergence of structured states corresponds with the emergence of new solutions to the dynamical equations. When a dynamical system exhibits a stable state (e.g., a fixed point or limit cycle), the system demonstrates a resilience to perturbations, relaxing back to the stable state after being pushed out of it. This implies "self-healing," a characteristic property of living organisms. When there is damage to the structure, the structure is restored due to stability of the structure. Since the irreversible processes that created a dissipative structure are within the structure, the system has the ability to restore the structure and "heal" damages. This aspect is an important characteristic of biological organisms, and, as we discuss below, is clearly visible in some non-living dissipative structures. It is in contrast to machines and computers whose structure originates from a process outside the system (Kondepudi et al. 2017).

In living organisms, self-healing is not strictly structural or morphological. It also has a functional component. A damaged organ or limb might heal but not to the exact structure that it was before the damage; the healing also needs to maintain the function of the organ. This feature is also exhibited in dissipative structures in which a function could be clearly identified. An example of this feature can be seen in an electrically driven dissipative structure which is discussed in Sect. 4.3. Thus, we see that selfhealing is a consequence of the stability of dissipative structures.

We conclude this section with the following observation. In physics, there is no clear definition of a complex system, but for a dissipative structure there is. And, complexity is an integral part of a dissipative structure; we do not need to define our system as a "complex system," which has no clear definition. We only need to clearly define a dissipative structure and observe or describe its behavior in various conditions; its behavior can become quite complex. By identifying living organisms as dissipative structures, we are able to clearly identify the class of systems they belong to. If they are defined as complex systems, though it is an apt descriptive term, it is not a well-defined classification.

4.2 Universal Chiral Asymmetry in Biological Realm

In the words of Francis Crick, "The first great unifying principle of biochemistry is that the key molecules have the same hand in all organisms" (Crick 1981).

Life, as we know it, is a dissipative structure with a broken chiral symmetry. When an object is not identical to its mirror image, it is said to be chiral. The key biomolecules, amino acids, the building blocks of proteins, and nucleotides, the building blocks of DNA, are chiral molecules: they have two possible forms, like the left and right hand, called the L- and the D-form. Two mirror image forms of a chiral molecule are called enantiomers. When synthesized in a lab from smaller non-chiral molecules, both enantiomers are produced in equal amounts. In fact, since basic laws of chemistry have no preference for one hand or the other, this is the expected result. So it is with every chiral molecule synthesized from smaller non-chiral molecules. In view of this, it is quite remarkable that we find only L-amino acids in proteins and D-nucleotides (due to the D-sugar component of these molecules) in all of life, from the smallest to the largest living organism. Life is a clear example of a dissipative structure with a broken symmetry.

From the viewpoint of dissipative structures, biochemical asymmetry is a case of spontaneous breaking of chiral symmetry. The chemical reactions that synthesize chiral molecules from non-chiral molecules have no preference for any of the two enantiomers. Consequently, the chemical rate equations for these reactions are symmetric, or invariant, under the interchange of the two enantiomers. Nevertheless, when a certain reaction mechanism is present, the system can break the chiral symmetry of the underlying reactions and generate unequal amounts of the two enantiomers. In mathematical terms, the solutions to the chemical rate equations do not have the symmetry of the rate equations. How this can happen can be demonstrated using the following set of chemical reactions:

$$S + T \leftrightarrow X_L \text{ or } X_D. \tag{4.3}$$

$$X_L + S + T \leftrightarrow 2X_L. \tag{4.4}$$

$$X_D + S + T \leftrightarrow 2X_D. \tag{4.5}$$

$$X_L + X_D \leftrightarrow P. \tag{4.6}$$

Here, S and T are non-chiral molecules that react to form a chiral molecule X in the two enantiomeric forms, X_L and X_D as shown in reaction (4.3). Each of these enantiomers can catalyze their production, as indicated in reactions (4.4) and (4.5). Finally, the two enantiomers can combine to form an inactive product P. This model chemical reaction is a modification of a model proposed by Frank (1953).

The chiral symmetry of the reaction is clear: the two enantiomers have identical reactions. Yet, under appropriate nonequilibrium conditions, this system can make a transition to a state in which the concentrations of the enantiomers are unequal. This can happen when the reaction system is subject to an inflow of reactants S and T, such that the concentrations of S and T are maintained at a constant value, and an outflow of the product P (Fig. 4.4). By defining a parameter $\lambda = [S][T]$, as the product of the concentrations of S and T, the transition to an asymmetric state with unequal concentration can be described as a bifurcation of asymmetric states from a symmetric state (Fig. 4.4). Many models, such as the one above one, have been proposed (see Plasson et al. 2007 for a review). Such models show how biochemical asymmetry could arise as a dissipative structure. There have been many suggestions for the origin of chiral asymmetry in amino acid and DNA in particular, but there is no consensus on a plausible answer. It is a historical question, as Eigen noted.

Handedness in biology extends to morphology and behavior as well. The placement of liver or heart and dominance of righthandedness in humans are examples. Naturally, the question arises as to the possible connection between molecular asymmetry and morphological asymmetry; in more general terms, the effect of chiral asymmetry at one level on chiral asymmetry on a higher level. In fact, the theory of spontaneous symmetry breaking provides a general framework to understand how asymmetries at various levels may be linked. For the breaking of a twofold symmetry such as chirality, one can derive an equation whose general form is based on the symmetry, and not on the details of a particular system. In the vicinity of the transition point, all systems that break chiral symmetry are described by the following equation:

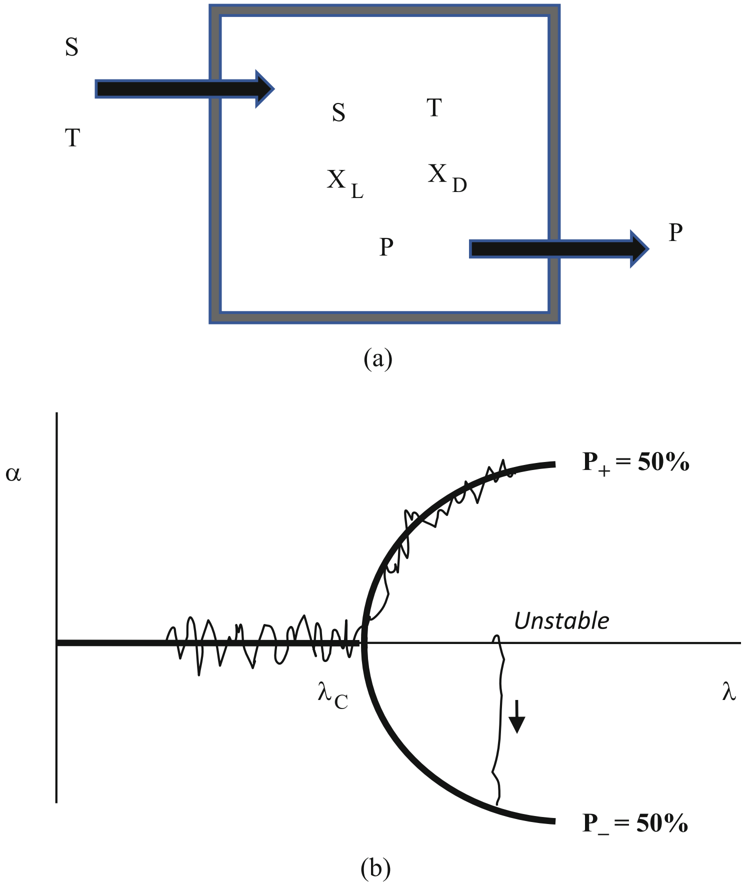
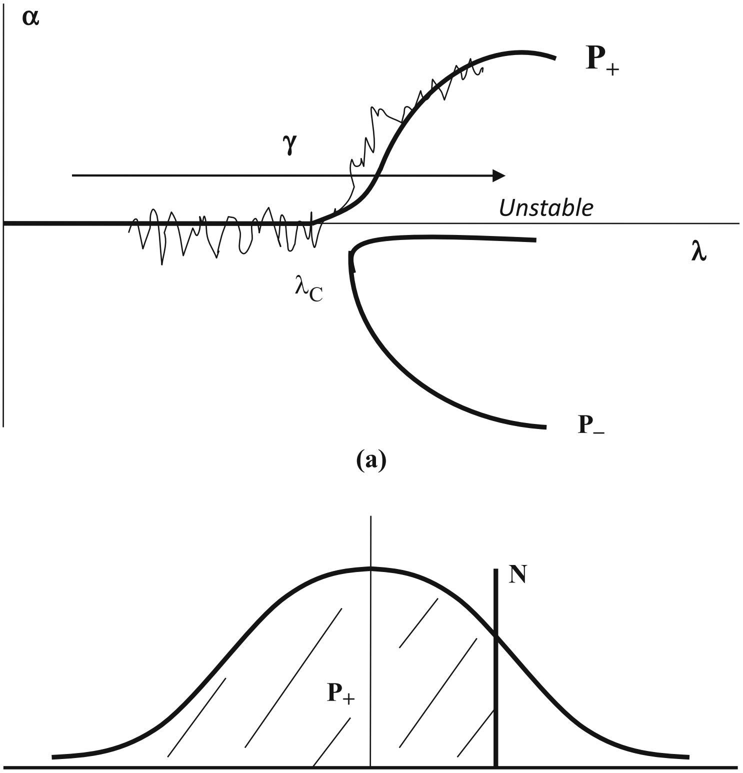


Fig. 4.4 Spontaneous chiral symmetry breaking in a model chemical system, summarized as a bifurcation of asymmetric states from an unstable symmetric state. (**a**) Non-chiral S and T flow into the reactor where they from chiral X in the two enantiomeric forms, X_L and X_D. The product P is removed from the system. (**b**) $\lambda = [S][T]$ and $a = [X_L] - [X_D]$. When $l > l_C$, the symmetric state, $a = 0$, becomes unstable and two new asymmetric states, $a > 0$, and $a < 0$, bifurcate. Random fluctuations drive the systems to one of the two branches. P_+ and P_- are probabilities of reaching the two branches. In the absence of any chiral bias, both branches are equally probable

$$d\alpha/dt = -A\alpha^3 + B(\lambda - \lambda_C)\alpha + \varepsilon(t). \tag{4.7}$$

In this equation, α is a measure of the asymmetry such that it is zero when there is no asymmetry, and positive or negative when there is an asymmetry. For example, in the above model chemical system $\alpha = [X_L] - [X_D]$. Coefficients A and B depend on the detailed symmetry-breaking mechanism, but the general form depends only on the symmetry that is broken. $\varepsilon(t)$ represents random fluctuations that drive the system to one of the two asymmetric states. Steady-state solutions of this equation give the bifurcation diagram shown in Fig. 4.4b.



(a)

(b)

Fig. 4.5 Bifurcation of asymmetric states in the presence of a small bias that favors one of the asymmetric state. P_+ and P_- are the probabilities of transition to the shown branches as the parameter λ sweeps through the critical value, λ_C, at rate γ. P_+ can be graphically represented as an integral of a Gaussian in which N is given by Eq. (4.9)

Using this general approach, we can also formulate a theory of how a small bias, g, which favors one branch over the other, can influence the transition. This theory enables us to study the sensitivity of the systems to a small bias (Kondepudi and Nelson, 1984). With the bias, Eq. (4.7) has an additional factor g:

$$d\alpha/dt = -A\alpha^3 \ + \ B(\lambda - \lambda_C)\alpha \ + g \ + \ \varepsilon(t). \tag{4.8}$$

The corresponding bifurcation diagram is shown in Fig. 4.5. There is a small separation of the two branches at the critical value λ_C. The probabilities of transition to the two branches, P_+ and P_-, are no longer equal. The sensitivity of the system is relative to the strength of fluctuation $\varepsilon(t)$. At first, it might appear that the bias g will not have a noticeable effect on the probabilities, P_+, P_-, if its magnitude is smaller than the root-mean-square value of $\varepsilon(t)$. However, closer analysis revealed that the system's sensitivity depends not only on the relative values of g and $\varepsilon(t)$, but also on the rate at which the parameter λ crosses the critical point, λ_C, sweeping from a value, λ_0, below the critical point λ_C (Kondepudi and Nelson 1985). Let us assume that $\lambda = \lambda_0 + \gamma t$ so that λ moves through the critical value at a rate γ. Detailed analysis shows that, when g is positive, the probability P_+ is given by the following Gaussian integral (Fig. 4.5):

$$P_+ = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{N} \mathrm{Exp}\left(-\frac{x^2}{2}\right) dx \quad N = \frac{g}{\varepsilon}\left(\frac{\pi/B}{\gamma}\right)^{1/4}. \tag{4.9}$$

This result shows that the probability depends not only on the relative values of g and ε but also inversely $\gamma^{1/4}$, making the system more sensitive when it moves slowly through the critical point. This general theory shows how asymmetry at one level can influence asymmetry at another level. It is remarkable that chiral asymmetry is at all levels, from elementary particles to morphology of mammals (Hegstrom and Kondepudi 1990), and there are indications that it might extend to the universe (Longo 2011). So, in addition to the questions relating the possible connection between biomolecular asymmetry and morphological asymmetry, one might wonder if biomolecular asymmetry is itself a consequence of a more fundamental asymmetry at the level of elementary particles and fundamental forces of nature. The electroweak interaction between the electron and the atomic nucleus creates a small energy difference between enantiomers of a chiral molecule (Hegstrom et al. 1980; Mason and Tranter 1984; Quack 2002). These energy differences, called parity-violating energy differences (PVED), are extremely small when compared with thermal energy fluctuation of a molecule. Using the theoretical calculations of these energy differences, one can estimate that the rates of reaction of enantiomers may differ in one part in 10^{17} making it impossible to detect under laboratory conditions. PVED could be several orders of magnitude larger, depending on the molecules. However, in prebiotic times, in large volumes of water of the order of several cubic kilometers, and slow increase of concentrations of compounds on a time scale of 10^4 years, PVED could indeed influence the outcome of molecular chirality in model reaction systems such as the one discussed above (Kondepudi and Nelson 1985). Calculations by Mason and Tranter (1984) have shown that the biologically dominant L-amino acids have a lower energy and hence are favored. Later calculations have confirmed this result. Thus, we see that the asymmetry at the level of fundamental electro-weak forces *could* influence biochemical evolution to favor the observed L-amino acid dominance. Whether this indeed happened is a historical question that cannot be answered at this time.

The theory of sensitivity of chiral symmetry-breaking systems to small influences also points to a possible mechanism through which molecular chiral asymmetry, progressing hierarchically through macro-molecular assembly and fibers, could propagate upward to a level of morphological chirality. Helical plants wind consistently as left or right helices, and this trait is inherited. The helical winding is due to the helicity of growth fibers which can be traced down to a molecular level. At each level, if a system can break chiral symmetry, it would be influenced by asymmetry at lower level. In some cases, as in the case of the right-handed double helix of DNA, the influence of D-sugars is strong as it is probably the case with many molecular assemblies in biomolecules. But there might be a situation in which the relationship is not so clear; in such situations, the above theory provides a framework for investigation. Nonequilibrium self-organization and theory of dissipative structures thus provides a basis for the asymmetries of life at all levels in an evolutionary context.

4.3 Bio-Analog Dissipative Structures

We have offered that, rather than investigate the particular historical circumstances that precipitated Terran life, the physics of self-organization and dissipative structures provides a framework for understanding the generic emergence of life-like systems. In other words, our work prioritizes understanding *processes and functions* that support biology rather than the particular *structures* that compose living organisms. In line with this, we have developed and studied two non-living dissipative structures—called *bio-analogs*—that demonstrate compellingly life-like phenomena. Though their instantiation (described below) is in stark contrast to the unique architecture of Terran life, the thermodynamic processes and self-organizing capabilities share some fundamental characteristics of biology. The evidence summarized below serves to support the plausibility of dissipative structure theory as a suitable basis for explaining the emergence and evolution of life-like systems.

One such system is an electrically driven dissipative structure that self-organizes into a tree-like morphology and demonstrates foraging and even complex coordinated dynamics (Davis et al. 2016; De Bari et al. 2020; Dixon et al. 2016; Kondepudi et al. 2015). The system consists of metal beads in a dish with a shallow bath of oil. The dish also includes a circular metal ring along the interior edge of the dish that is attached to a grounding electrode. A source electrode is positioned above the dish, separated by an air gap (typically 5 cm), and a voltage in the range of 20–30 kV is applied. Charges are sprayed out over the dish, collecting on the beads and the surface of the oil. The charged beads become dipoles, are attracted to each other and the grounding electrode, and ultimately aggregate into branching strings of beads (Fig. 4.6). These tree structures serve as pathways for the conduction of charges to ground, and this flow of charges through the trees maintains their stability. This system demonstrates a rich host of bio-analog behaviors, including an intrinsic end-directedness, self-healing, foraging dynamics, and even coordinative capabilities. Due to the primacy of the foraging behavior (detailed below), the system is referred to as the Electrical Self-Organized Foraging Implementation (E-SOFI).

A key feature of the E-SOFI is that it appears to abide by a variational principle to maximize the rate of entropy production (REP). Several empirical (De Bari et al. 2019, 2021; Davis et al. 2016; Kondepudi et al. 2015) and simulation-based results (De Bari et al. 2019, 2020) have supported this assertion by demonstrating that the

Fig. 4.6 The E-SOFI. Electrically charged beads aggregate into a branching "tree" that serves as a pathway for conducting charges to ground

system tends to exhibit changes that facilitate *increasing* the REP. That is, when the system has access to several states (morphological or dynamical) it will tend to occupy the state with higher REP. The adherence to a variational principle means that the system's future state constrains the present dynamics, in concert with circumstantial boundary conditions. This intrinsic state-selection principle is effectively an intrinsic *end-directedness*, like that fundamental to biological behavior. It manifests in several types of bio-analog behavior. The REP per unit volume σ is a function of the applied voltage V, the current through the system I, and the temperature T. The current is a complex function of the bead structures' morphology and dynamics (i.e., position x and time t).

$$\sigma = \frac{VI(x,t)}{T} \tag{4.10}$$

The total entropy production, $\Sigma = VI/T$, is the integral of σ over the system volume. The formation of structures demonstrates an immediate and dramatic increase in the REP (Kondepudi et al. 2015; Fig. 4.7). The REP is proportional to the length and number of trees, consistent with the hypothesis that trees form to facilitate entropy production. When a tree's structure is perturbed by breaking up the beads, due to the stability of this structure is spontaneously and quickly restored. This phenomenon is analogous to the self-healing and self-repair exhibited by organisms when subject to injuries. For small perturbations the original morphology may return, while larger perturbations can result in novel architectures. When the tree is broken, its entropy production decreases. Critically, when structure is restored, the REP is restored to nearly the exact level as before the perturbation,

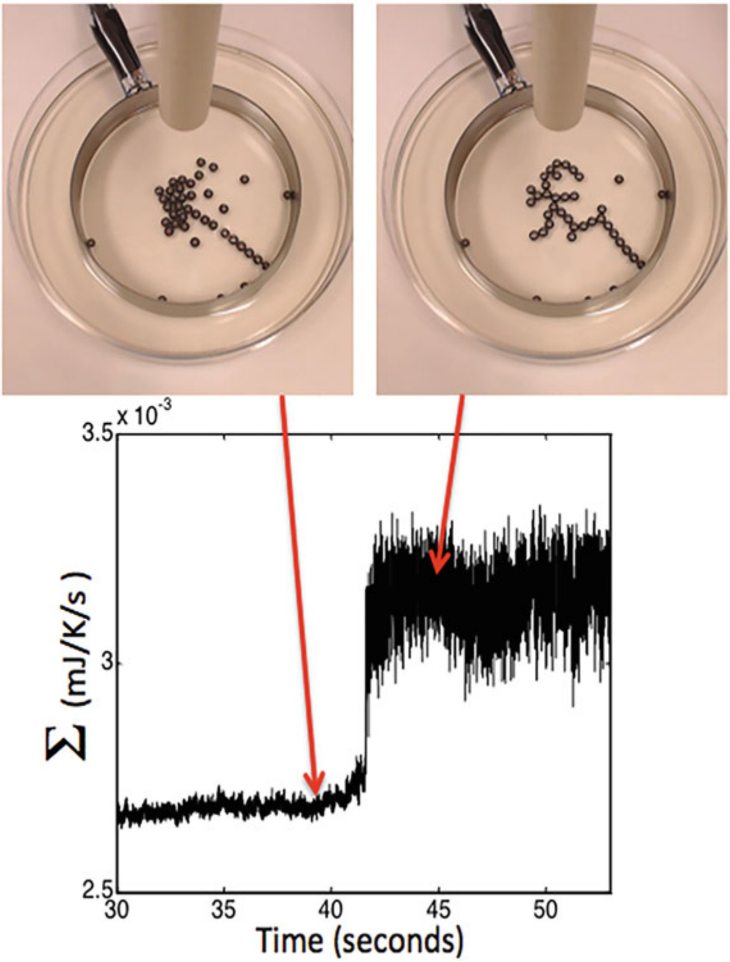


Fig. 4.7 The rate of entropy production by the E-SOFI increases dramatically with the emergence of structured trees

independent of a change in morphology (Kondepudi et al. 2015). This kind of *process equifinality* supports the hypothesis that the structures' dynamics and morphology emerge to maximize the REP. Moreover, much like in biological self-repair, the changes favor *functional* organization over *structural/morphological* organization. A remarkable example in biology is in nervous tissue, such as when the localization of functional brain regions changes due to developmental events (Johnson et al. 2015) or after traumatic injury (Levin 2003). The function of the nervous tissue persists, while the specific morphological organization may not. Various tree morphologies are displayed in Fig. 4.8. The current conducted by these differently shaped trees is nevertheless remarkably similar.

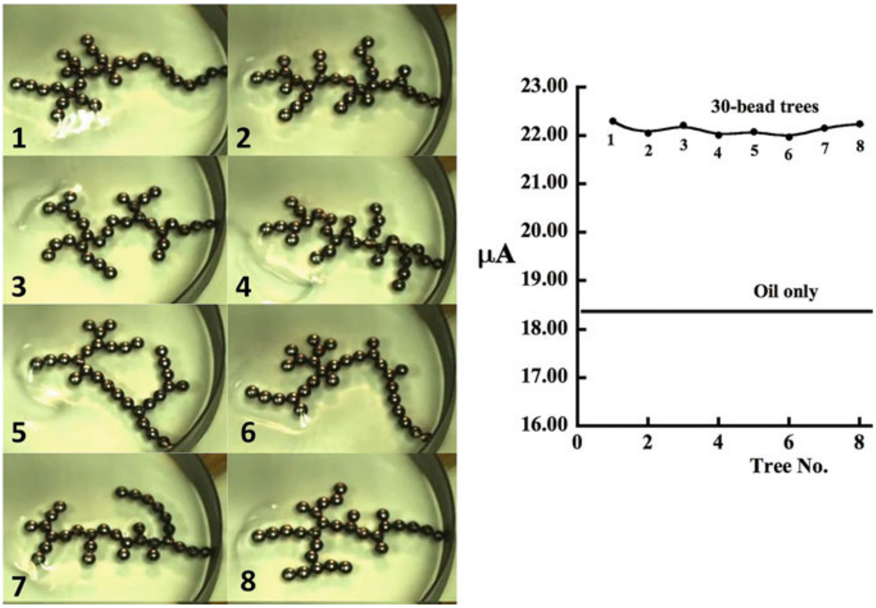


Fig. 4.8 (Left) Several different tree configurations in the E-SOFI. (Right) the various morphologies conduct very similar levels of current. Tree structure appears to favor functional organization in the conductivity over structural organization

The E-SOFI's morphology also exhibits some context sensitivity during development. Organisms can exhibit developmental differences due to many small environmental deviations; for example, a species of alligator, *Alligator mississippiensis*, exhibits differential sexual development due to small differences in ambient temperature during egg incubation (Ferguson and Joanen 1982). The E-SOFI can similarly exhibit morphological differences in the presence or absence of a weak magnetic field (Kondepudi et al. 2020). The system is prepared with a mix of both magnetic chrome beads and nonmagnetic aluminum beads, all initially concentrated in the center of the dish under the source electrode. Two experimental conditions were investigated, (i) with a magnet below the dish and (ii) no magnet below the dish. In condition (i) the magnet was set to a distance from the bottom of the dish that was just below the threshold at which lateral motion of the magnet would move chrome beads (when the beads were in the oil bath, but without any applied voltage). Experiments were conducted simply by turning the electrical flow on and waiting for tree structures to form. A statistical analysis of the distribution of beads within the trees revealed morphological differences between trees in conditions (i) and (ii). Thus, the self-organizing developmental processes of the E-SOFI are sensitive to very small changes in environmental condition.

In addition to structural evidence, the dynamics and behavior of tree structures also demonstrate a tendency for the system to maximize the REP which manifests as energy-foraging behavior. Consider the following experimental setup: Initially, a

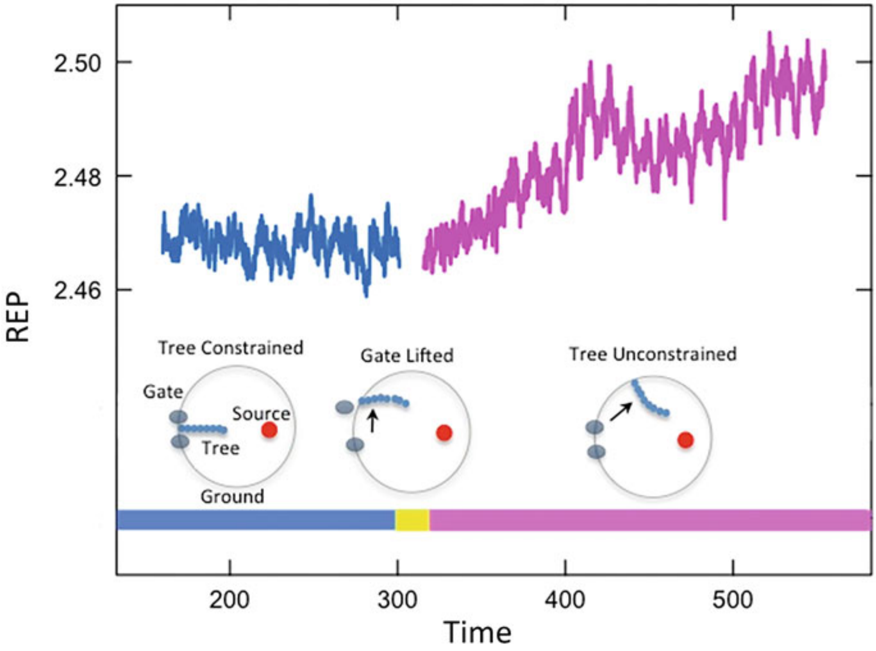


Fig. 4.9 Experimental setup to demonstrate foraging. After removing the plastic constraints, the tree will move along the edge of the ring over to the right region of the dish. It will remain in this charge-rich region once it arrives there

tree is formed maximizing REP with the source electrode at the center. Then plastic constraints around its base bead that prevents translation along the grounding ring are imposed, limiting its motion to oscillatory swaying. Then the source electrode is moved to the right side of the dish, off-center (Fig. 4.9). With the source electrode off center, the tree is no longer drawing the maximum current it could. This asymmetry makes it such that charges build up in greater concentration in regions of oil nearer the electrode than those further (i.e., in the steady state there are more charges on the right side of the dish than the left) creating a gradient of charge concentration that increases from left to right. The tree is positioned in the left side of the dish, maximally displaced from the source electrode. When a plastic constraint is removed, the tree continues to sway, but additionally begins to traverse the grounding ring, moving into the region of greater charge density.

Over time, the tree settles into the region under the source electrode, where it will remain. During the relaxation process to this new steady state the REP increases, until it saturates when the tree reaches the region of minimum displacement from the source electrode. Thus, the tree appears to *forage* for electrical charges and for circumstances that maximize the current and in turn its own stability. Other results have indicated that the oscillatory swaying (De Bari et al. 2019) and even inter-tree interactions (Davis et al. 2016; De Bari et al. 2020, 2021) facilitate maximizing the

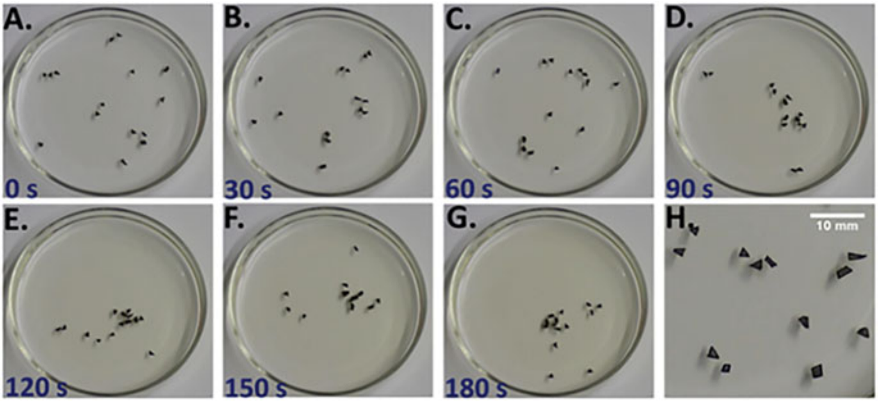


Fig. 4.10 Benzoquinone pellets float at the air–water interface, aggregating into a dynamic flock. Sub-figures show time samples of the flock at (**a**) 0 s elapsed, (**b**) 30 s elapsed, (**c**) 60 s elapsed, (**d**) 90 s elapsed, (**e**) 120 s elapsed, (**f**) 150 s elapsed, (**g**) 180 s elapsed, and (**h**) a close-up of the flock. Reprinted with permission from Satterwhite-Warden J. E., Kondepudi D. K., Dixon J. A., Rusling J. F., (2019) Thermal- and magnetic-sensitive particle flocking motion at the air-water interface. The Journal of Physical Chemistry B, 123, 3832–3840. Copyright 2019, American Chemical Society

REP. The intrinsic end-directedness thus endows the system with a host of bio-analog properties. We have studied a sister system of the E-SOFI, a chemical bio-analog known as the C-SOFI. This system is composed of solid pellets of benzoquinone (BQ) floating on the surface of water that exhibit self-motion due to surface-tension gradients caused by the dissolution processes. Solid BQ dissolves into the liquid phase, generating local concentration and surface-tension gradients. Individual pellets are propelled along increasing gradients of surface tension. When several particles (e.g., 10–16) are present in the same dish, they will tend to aggregate into a dynamic collective of particles that moves through the dish as a largely cohesive unit (Fig. 4.10). This emergent collective is referred to as a *flock* and constitutes the *structure* that is maintained by the dissipative flow of BQ into the aqueous phase.

These flocks have interesting properties and capabilities. One such property is the emergent sensitivity to weak magnetic fields. This occurs when one of the 15 pellets is prepared with a small amount of ferrous material embedded in it, making it magnetic, while all other members of the flock are nonmagnetic. To establish the experimental setup, the single ferrous pellet is placed in the dish. This *sensor* pellet—as it will be called—exhibits self-motion qualitatively indistinct from its nonmagnetic counterparts. A magnet is positioned above the dish, raised to a height that has minimal interaction with the sensor pellet—the sensor continues to swim through the entire dish and is not confined to a small region by the magnetic field. After setting the magnet height, the remaining non-magnetic particles are added to the dish. Over time, the pellets create a flock that includes the sensor particle.

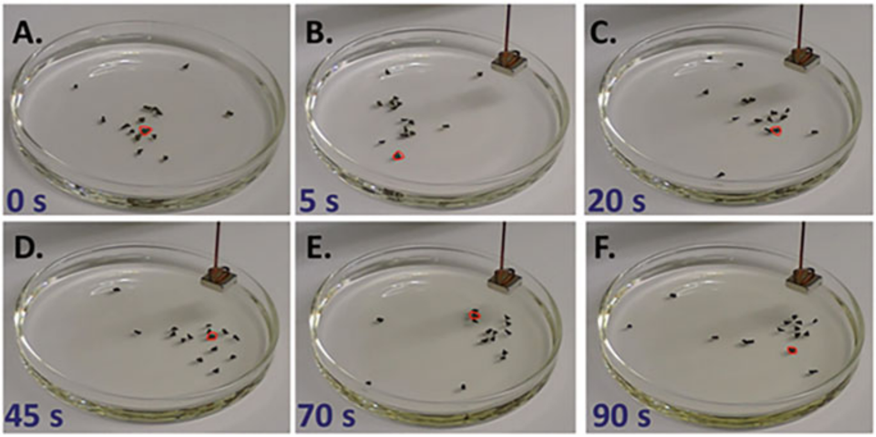


Fig. 4.11 Benzoquinone pellets form a flock, incorporating a single ferrous pellet. After a weak magnet is introduced above the system, the flock tends to swim in the region below the magnet. Reprinted with permission from Satterwhite-Warden J. E., Kondepudi D. K., Dixon J. A., Rusling J. F., (2019) Thermal- and magnetic-sensitive particle flocking motion at the air-water interface. The Journal of Physical Chemistry B, 123, 3832–3840. Copyright 2019, American Chemical Society

Critically, the *entire flock* is observed to move under the magnet and remain close to the magnet (Fig. 4.11).

This is despite the fact that the force is too weak to capture the single sensor particle. Nevertheless, the nonlinear interactions between particles appear to amplify the sensitivity of the flock to the magnetic field; in other words, the flock with the magnetic pellet is more sensitive to the magnetic field than the single magnetic pellet. This phenomenon is analogous to the perceptual sensitivity exhibited by organisms, wherein sensitivity is maintained by virtue of a self-organized state. Further, the perceptual fields (e.g., light arrays, chemical gradients) that organisms are sensitive to only exhibit very weak (Newtonian) interactions with organisms (Kugler and Turvey 1987), like the very weak magnetic forces in the case of the C-SOFI. Much like the E-SOFI, C-SOFI flocks have shown evidence of foraging, in this case foraging for regions of the dish with higher surface tension and which facilitate dissolution (Chen et al. 2019). Interestingly, this foraging even results in the flocks' capability to cross through barriers, as was observed in the following experiment. A dish is prepared with a hydrophobic sheet in the middle that effectively divides the water into two compartments, joined by a small opening in the middle of the sheet (Fig. 4.12).

After pellets are placed on the surface of the water, they will take some time to aggregate into a flock, ultimately aggregating on one side of the dish. After some time, the flock will make a transition to the other side of the dish, moving through the gap as a whole unit. This transition process is correlated with a switch in the relative surface tension on either side, such that the flock moves after the second side develops higher surface tension. The flock is apparently foraging for higher surface tension, and even navigates rudimentary obstacles as a collective unit to do so.

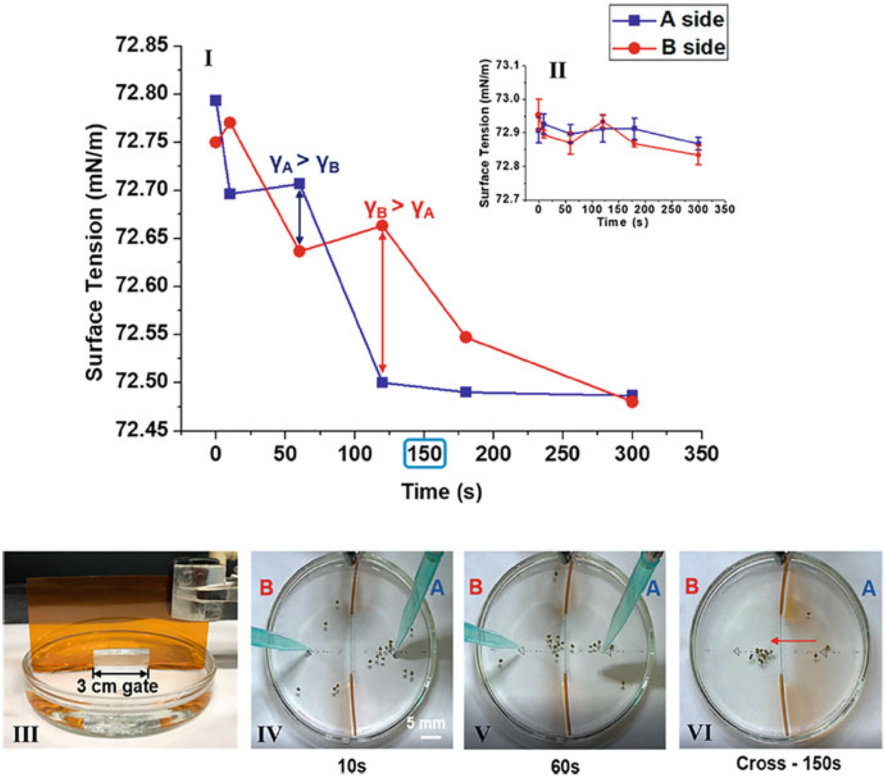


Fig. 4.12 The surface tension on either side of the dish was measured at discrete time points (top). The flock tended to make a transition to the high-surface tension side of the gate (bottom). Reprinted with permission from Chen T. Kondepudi D. K., Dixon J. A., Rusling J. F. (2019) Particle flock motion at air-water interface driven by interfacial free energy foraging. Langmuir, 35 (34), 11066–11070. Copyright 2019, American Chemical Society

Many other remarkable and interesting dissipative structures have been developed, especially in the field of autonomous chemical swimmers. These include oil droplets with embedded hydrolysis reactions that exhibit self-motion and chemotaxis (Hanczyc et al. 2007). Aqueous droplets of Belousov–Zhabotinsky reactants have been shown to swim through oil baths, demonstrating nonlinear dynamics by virtue of the embedded oscillatory reaction (Suematsu et al. 2016). Systems such as these demonstrate a host of interesting life-like behaviors and further support the notion that dissipative structures are a foundational feature of living systems.

It is possible that proto-life systems, which we assert were very likely dissipative structures, capitalized on this intrinsic self-stabilizing behavior present in these bio-analogs. The processes of evolution could play out on such proto-organisms, selecting for increasing self-stabilizing processes and morphologies, ultimately leading to increasing complexification. As we discuss in the following section, key aspects of nonequilibrium thermodynamics have direct analogs to processes in biology and evolution.

4.4 Thermodynamics, Self-Organization, Dissipative Structures, and Evolution

A thermodynamic theory of biological evolution must bridge the gap between the concepts in thermodynamics and biology. In the thermodynamic theory of dissipative structures, we have concepts such as energy, fluctuations, instability, self-organization, entropy production, and end-directed evolution. In biology, at the level of an individual organism, we have basic properties such as self-replication, ability to respond to environment, ability to heal and retain function, and goal-oriented behavior; at the species level, we have mutations, evolution, and survival of the fittest. Bridging the gap between the two subjects involves description of the biological processes in thermodynamic terms. This needs to be done at both the biochemical and the organism levels. In this section, we discuss to what extent the key properties and concepts of dissipative structures provide a thermodynamic language for biological processes.

4.4.1 Self-Replication and End-Directed Behavior

Self-replication occurs in nature at all levels. The simplest of particles, the photon, can self-replicate by stimulating an atom in an excited state to emit a photon identical to itself. On a molecular level, autocatalysis in general and chiral autocatalysis in particular are known (Asakura et al. 1995; Soai et al. 1995). Self-replication at the level of crystals is known to result in interesting competition between enantiomeric crystals with one type dominating over the other (Kondepudi et al. 1990). Self-replication was also observed in the formation and growth of vesicles (Albertsen et al. 2017, Lin et al. 2021). These systems are not dissipative structures that are maintained through continuous entropy production.

Self-replication in dissipative structures has also been studied both theoretically (Pearson 1993; Reynolds et al. 1997, Lesmes et al. 2003) and experimentally (Lee et al. 1994). In these systems, chemical patterns of dots form and these dots self-replicate. Such self-replicating dots form complex patterns resembling organism development (Munteanu and Sole 2006). Thus, we can say self-replication of organisms is within the domain of dissipative structures, though in organism the process is much more complex.

End-directed behavior we see in organisms has analogs in non-living dissipative structures as we have noted in the previous section while discussing E-SOFI. In this system, the tree structure moves toward its energy source. This and other observed behavior could be explained as the system's movement toward states of higher entropy production. For organisms, we do not yet have a thermodynamic explanation but perhaps some of the behavior of an organism could be explained as process that optimizes a thermodynamic quantity. Here, again we see that a characteristic property of organisms is in the realm of dissipative structures.

4.4.2 Nonequilibrium Sensitivity

Organisms rely on a variety of physical media to guide behavior, including chemical, mechanical, and electromagnetic fields. An organism has only weak interactions with these fields, and yet those fields constrain the dynamics of the organism, as in an ambient light distribution guiding locomotion. This is directly analogous to the nonequilibrium sensitivity in dissipative structures: a weak embedding field biases endogenous self-organizing processes (here, bio-mechanical motor processes broadly) to constrain more macroscopic dynamics.

Dissipative structures can demonstrate emergent sensitivity to weak energy fields by virtue of endogenous self-organizing processes. How this can come about in chemical systems embedded in gravitational or electrical fields was noted (Kondepudi and Prigogine 1981; Kondepudi 1982; Kondepudi 1989). Such sensitivity could be a suitable mechanism to explain gravity detection in microorganisms (Bizzarri et al. 2014; Kondepudi 1991). The sensitivity of E-SOFI and thermotaxis and sensitivity of C-SOFI when embedded in weak magnetic field was described in the previous section.

Such mechanisms point to the many ways in which dissipative structures can become sensitive to their environment. In these processes, internal structures and their behavior are correlated with the environment, providing a physical basis for understanding the sensitivity of life to its environment. When there are a large

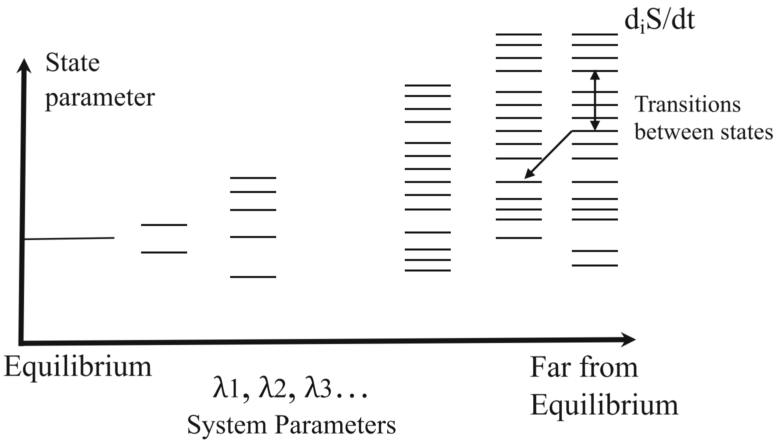


Fig. 4.13 Transitions between internal states due to interaction with environmental factors. λ_1, λ_2, λ_3 … are system parameters that indicate the nonequilibrium conditions. In dissipative structures that have a large number of internal states, interaction with the environment may cause transitions between these states. Through such mechanism, perceptual sensitivity of organisms can emerge

number of internal states between which a dissipative structure can undergo transitions due to its interaction with its environment, complex behavior can emerge (Fig. 4.13). We propose that it is also a good explanation for the perceptual sensitivity of organisms in general (De Bari et al. 2020). It should be noted that maintenance of an organized state and transitions between organized states is at the expense of entropy production. Where appropriate and possible, it is worthwhile looking at the behavior of the rate of entropy production in organisms.

4.4.3 Self-Healing

Self-healing is an intrinsic feature of biology, and one of the most remarkable capabilities of organisms. We identified self-healing capabilities in our bio-analog system the E-SOFI. When the bead structures are mechanically perturbed or broken, they will tend to reform into *functionally* identical systems, though morphology may vary. The same can be said of biological self-healing. Moreover, this intrinsic self-stabilization is foundational to a theory of evolution, which must account for survivability as a fundamental feature; natural selection must *select for* something, namely adaptation to the environment. Some interpretations of natural selection treat survivability as a matter of happenstance; insofar as an organism happens to survive and reproduce, it is demonstrating adaptation and survivability. Thus, if traits are passed on by natural selection, then they are adaptive traits, but they are supposed to be selected for on the basis of their adaptability. Rather than this kind of circularity, the self-healing and self-stabilizing properties of dissipative structures (living and non-living) provide a firmer foundation for natural selection to operate on. Stability, survivability, or normativity (e.g., that stability is “better than” or “preferred” to instability) is intrinsic to dissipative structures (Bickhard 2009).

4.4.4 Mutations and Appearance of New Traits

This process can be understood in terms of self-organizing amplification or “order through fluctuations” (Prigogine and Stengers 1984) which was described earlier in detail. It is the observation that all physicochemical systems have thermal and other form of fluctuations of the state variables such as concentrations of chemical species, temperature, and pressure. In a system at or close to thermodynamic equilibrium, these fluctuations are damped by irreversible processes and equilibrium values of these state variables are restored. But if a system is far from thermodynamic equilibrium, instability leads to the growth of certain type of fluctuations and a transition to a new organized state occurs. Which fluctuations will grow and establish a new structure depends on the “boundary conditions” or “the system’s environment.”

Genetic mutations are essentially this same process, but taking place in the complex dissipative structure that is a living organism. Each mutation is a fluctuation; some mutations can be “amplified” or find expression through the intrinsic self-organizing processes and alter some aspects of the complex organism's structures and produce new traits. Mutations in the genetic code can occur due to thermal as well as non-thermal processes such as radiation. The genetic code is imbedded in a system that can amplify certain changes, depending on various factors. This non-equilibrium process of amplification of fluctuations generates an astounding diversity of organisms. There is not yet a non-living dissipative structure that reflects, even in a primitive way, the production of diverse forms of organisms. Nevertheless, the processes of amplification of mutations (fluctuation) and evolution of new forms are a general feature of dissipative structures.

4.4.5 Competition and Survival of the Fittest

Dissipative structures rely on flows of energy and matter to maintain organization and stability, and organisms are no exception to this. While some microorganisms and the vast majority of plants rely primarily on the energy delivered through solar radiation, the rest of the biosphere is a complex web of predator–prey relations, with organisms serving as a source of energetic material for other organisms. From the thermodynamic point of view, this aspect of life is transformation of energy and matter, or the transformations from one structure to another. When an osprey catches a fish, in some sense we are witnessing a fish transforming into an osprey, as its biomass is incorporated into that of the osprey and used to power subsequent fishing expeditions. The entire struggle for survival is the transformation of one organism (complex dissipative structure) into another, or complex transformations of energy and matter. We do not yet have a laboratory example of non-living dissipative structures that predate and convert from one from to another, but we can conceive of such systems.

4.4.6 Complexity and Complexification Through Evolution

As we have noted above, in physics there is no clear definition of a complex system, but there is a clear definition for a dissipative structure. And, in dissipative structures, complexity is an integral part.

This complexity in dissipative structures appears in terms of the composing network of thermodynamic forces and flows (Kondepudi 2012). Emergent force–flow couplings can provide novel organizational states for a dissipative structure. If these novel processes and configurations affect the stability of the system, they can be selected for. A schematic of natural selection can thus be inferred as a process of fluctuation-induced emergence of dynamics (i.e., mutation) leading to differential self-maintenance dynamics (i.e., phenotypic differentiation) that are selected for by the embedding circumstances (i.e., adaptability). The complexification of organic life by evolution need not appeal to statistical or morphological measures of complexity, but rather can be indexed by the network of thermodynamic force–flow couplings and the related multiplicity of organizational states.

In discussing complexity, we would like to note the non-algorithmic nature of organisms. Being a product of human planning and design, a machine is algorithmic; in other words a machine can be simulated by a computer code and its behavior reproduced as the output of this computer code. An algorithm simulating a machine is a logical structure representing each component of the machine and their interrelationships. It is a map between the machine's design and a computer language. Organisms are complex dissipative structures, and living organisms, in particular, are fundamentally different from a machine (Kondepudi et al. 2017). Their structure and function do not originate from a logical design. Though organisms have components with functions, they operate with a self-reference: the parts make the whole and the whole supports the parts. For these reasons, we do not think organisms can be described by an algorithm. Algorithms can capture some aspects but not the entire behavior of an organism.

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5

Self-Organization at Different Levels of Metazoan Complexity in Comparative Genomic–Phenomic Context

Valeria V. Isaeva

Abstract

The chapter presents an analytic description of evolutionary and developmental morphogenetic events in Metazoa using concepts of self-organization, morphological and molecular–genetic data, and the topological approach to the analysis. Biological objects are complex systems capable of dynamic self-organization at all levels of biological complexity. Some examples of self-organization in cyanobacteria, metazoan cells in vitro (chick embryo myogenic cells, molluscan hemocytes, sea urchin embryo cells), and animal communities of some vertebrates are shown. Following René Thom, a topological interpretation of some evolutionary and developmental transformations is presented using well-known mathematical concepts. Toroidal forms are considered as examples of functionally optimized biological design and attractors in metazoan morphogenesis. Molecular–genetic evidence of genomic–phenomic correlations determining the body plan and evolutionary trajectories in Metazoa is discussed. Gene regulatory networks and whole metazoan genomes are interpreted as self-organizing network systems dynamically transforming in development and evolution. Symmetry breaking, topological discontinuities and catastrophes, and body plan transformations are fundamental phenomena in metazoan development and evolution.

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_5

Keywords

Cyanobacteria · Metazoa · Cell interactions · Social behavior · Topological transformations · Gene regulatory networks · Genome–phenome correlations

5.1 Introduction

The concept of self-organization originated within cybernetics (Ashby 1947; Gershenson 2012). Alan Turing (1952) and N. Rashevsky (1958) theoretically predicted spontaneous pattern formation as the emergence of inhomogeneities in some chemical reactions. Later, Ilya Prigogine proved the possibility of dissipative structure formation as spatial inhomogeneities in open nonequilibrium systems by the flux of energy and matter (Nicolis and Prigogine 1977, 1989; Prigogine and Stengers 1984; McCusker 2020). The conception of self-organization resulting in the emergence of spatial and/or temporal order (Haken 1977) was propagated into an extended interdisciplinary field of scientific research from physics to biology and engineering, in nonliving, living, and artificial systems (Camazine et al. 2001; Gershenson 2012; Johnson and Lam 2010; Feistel and Ebeling 2011; Lane 2015; Wedlich-Söldner and Betz 2018; McCusker 2020; Gershenson et al. 2020).

Living systems are open, far-from-equilibrium complex network systems, maintained by continuous flows of matter, energy, and information. Almost any network system can be described as self-organizing one (Ashby 1956; Gershenson 2012; Gershenson et al. 2020), so self-organization is inevitable in complex biological network systems with nonlinear dynamics, characterized by feedback, robustness, flexibility, hierarchy. If a complex network system has a set of attractors as organized “preferred” states, the system will self-organize toward these attractors (Gershenson 2012). The great French mathematician René Thom (1923–2002) had shown that biological objects and events might be described in terms of vector fields, attractors, and catastrophes (Thom 1969, 1996, 1997). Since topology operates with the most general properties of spaces, an adequate description of biological morphology can be obtained by using topological concepts and terminology. The topological approach to the description and interpretation of some morphogenetic events in onto- and phylogenesis is presented here.

Biological systems provide countless examples of self-organization at all levels, from molecular one to ecosystems (Kauffman 1993; Babloyantz 1986; Misteli 2001; Kirschner and Gerhart 2005; Karsenti 2008; Gershenson 2012; Gloag et al. 2015; Balaban et al. 2018; Saha and Galic 2018; Wedlich-Söldner and Betz 2018; Dong and Fisher 2019; McCusker 2020; de Astacio et al. 2020). For example, at the cellular level, cells in vitro reveal remarkable capabilities for self-organization without controlling the influences of a whole body; in different animal communities (flocks, schools, and herds), vertebrates coordinate their collective behavior and reach “collective decisions.” In this chapter, examples of self-organization of the cyanobacterial cells and different metazoan cells in vitro (chick embryo myoblasts, molluscan hemocytes, sea urchin embryo cells) as the transition from chaos into order are presented, as well as self-organization phenomena in communities of vertebrates.

For contemporary theorists, biological self-organization in the living world is directed and fixed genetically by natural selection (Kauffman 1993; Parrish and Edelstein-Keshet, 1999; Camazine et al. 2001; Blazis 2002; Parrish et al. 2002; Gershenson 2012; Kirschner and Gerhart 2005; Johnson and Lam 2010; Goldenfeld and Woese 2011; Glancy et al. 2016). The selection of self-organizing systems leads to an increase in robustness, flexibility, plasticity, adaptability, and evolvability. During self-organization, the global pattern of a system emerges as epiphenomenon generated by numerous local interactions between the elements of the lower levels (Kauffman 1993; Parrish and Edelstein-Keshet 1999; Camazine et al. 2001; Parrish et al. 2002; Gershenson 2012; Wedlich-Söldner and Betz 2018). In an effort to understand some genomic-phenomic correlations as a genotype-phenotype mapping (Minelli 2015; Ogura and Busch 2016; Isaeva and Rozhnov 2021), the Molecular genetic background of metazoan axial body plan is considered in this chapter.

5.2 Self-Organization in Cyanobacteria Cell Communities

Three major domains of the living world, Archaea, Bacteria, and Eukarya (Eukaryota), are distinguished, and the first two domains often are named Prokaryota (Woese 2002; Muller et al. 2010; Wassenaar 2012). It is known that life arose around half a billion years after the earth's formation, but Bacteria and Archaea have remained simple in their morphology up till now (throughout about 4 billion years). Bacteria had invented most forms of metabolism, including multiple forms of respiration and photosynthesis (Lane 2010). It is widely accepted that photosynthesizing cyanobacteria played a crucial role in the evolution of the biosphere and were responsible for the accumulation of atmospheric oxygen during the Great Oxidation Event starting 2.45 billion years ago, hence dramatically changing life on the planet (Lane 2010; Little et al. 2012; Wassenaar 2012; Schirrmeister et al. 2013). Cyanobacteria are morphologically diverse prokaryotic organisms, with morphotypes ranging from unicellular to multicellular filamentous forms; phylogenetic evidence indicates that multicellularity evolved very early in the history of cyanobacteria and coincided with the onset of the Great Oxidation Event (Schirrmeister et al. 2013). In the evolution of both Prokaryota and Eukaryota, multicellularity has apparently evolved many times (Rainey and Kerr 2012; Strassmann and Queller 2012; Olsen et al. 2012). Among other recent cyanobacteria, *Oscillatoria terebriformis* and *Microcoleus chthonoplastes* used in our investigations of self-organization (Isaeva et al. 2013) are multicellular filamentous species. Oscillatoriales have long multicellular, usually straight filamentous trichomes consisting of uniform cylindrical cells. The trichomes are flexible, motile, and capable of the formation of bundles, multiradial aggregates, biofilms, and three-dimensional mats in laboratory cultures (Castenholz 1968; Richardson and Castenholtz 1987, 1989; Petroff et al. 2008; Shepard and Sumner 2010; Sumina and Sumin 2013; Isaeva et al. 2013).

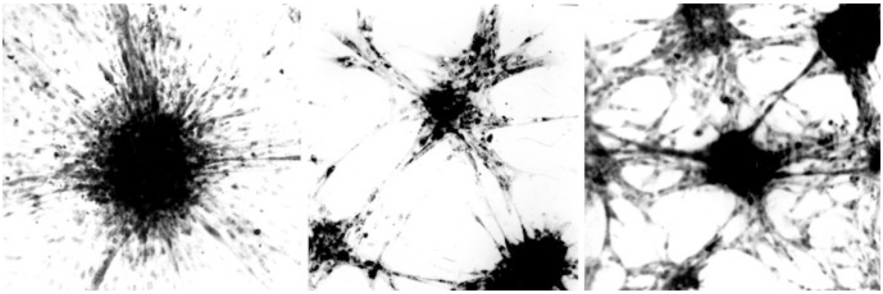

Fig. 5.3 Microscopic patterns in myogenic cell in vitro (from left to right): radial migration pattern from single-cell aggregate; triangular connection between tree neighboring aggregates; hexagonal pattern forming myoblasts migrating from several cell aggregates (from Isaeva 1994)

It is usually assumed that stromatolites, the petrified reefs of prokaryotic communities having regularly layered macroscopic inner structure, are early fossils formed by cyanobacterial communities (see Lane 2010; Sumina and Sumin 2013; Seilacher and Gishlick 2015). Seilacher and Gishlick (2015) supposed that the regular layered morphology of stromatolites was controlled by self-organizational principles and environmental conditions. Nick Lane in his book "Life ascending" gave a photograph of the "living stromatolites"—natural cyanobacterial colonies, about 1 m in high, in Western Australia (Hamlin Pool, Shark Bay) (Lane 2010, Fig. 3.3, p. 75); outer layers of these formations were filled with living cyanobacteria (Lane 2010). Earlier A.W.D. Larkum (1999) described the "stromatolites" at Hamlin Pool, Shark Bay (Fig. 5.3, p. 151), as a cyanobacterial symbiosis with coral reefs. Needless to say, cyanobacteria predate coral reefs by billions of years as stromatolite formers and their role in the modern reef formation is a different one (Larkum 1999). Petroff et al. (2008) considered living cyanobacterial aggregates (without any corals) as analogs of ancient stromatolites.

Similar "living stromatolites" (up to 10 cm in high) were spontaneously self-organized by communities of two cyanobacterial species, *O. terebriformis* and *M. chthonoplastes,* cultured by Eugenia Sumina in the laboratory of Moscow State University. The coordinated behavior of bacterial communities led to the perception of bacterial mats as "cities" of microorganisms (Li and Tian 2012), so the underwater landscape created by *O. terebriformis* and *M. chthonoplastes* I venture to name "Cyanopolis" (Fig. 5.1).

Evidently, the multicellular filamentous cyanobacteria *O. terebriformis* and *M. chthonoplastes* are capable of forming various macroscopic structures of large-scale order by self-organization.

In this culture, *O. terebriformis* was the main, prevalent component of the bacterial community (Sumina and Sumin 2013). At the microscopic level, three-dimensional polygonal networks with hexagonal tessellation formed by filamentous cyanobacteria, in particular *O. terebriformis,* were found (Petroff et al. 2008; Shepard and Sumner 2010; Sumina and Sumin 2013; Isaeva et al. 2013). Exploratory activity and complex movements of trichomes including contact inhibition and

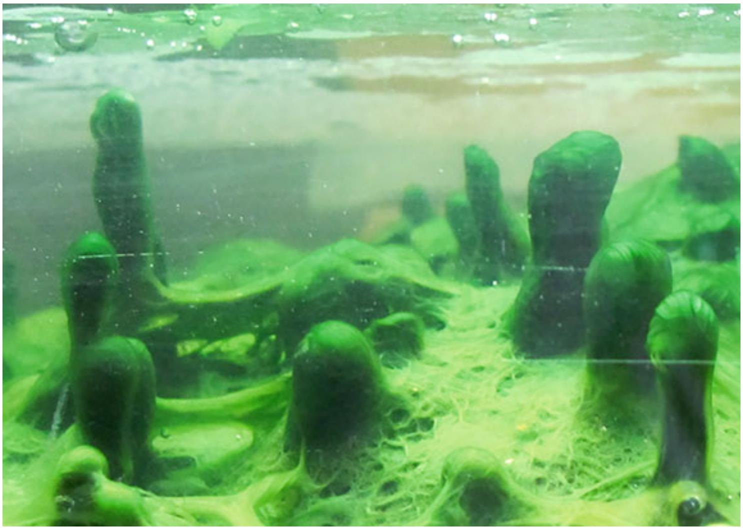

Fig. 5.1 "Cyanopolis" formed by cyanobacteria (cultured by E. Sumina; photo by V.V. Isaeva)

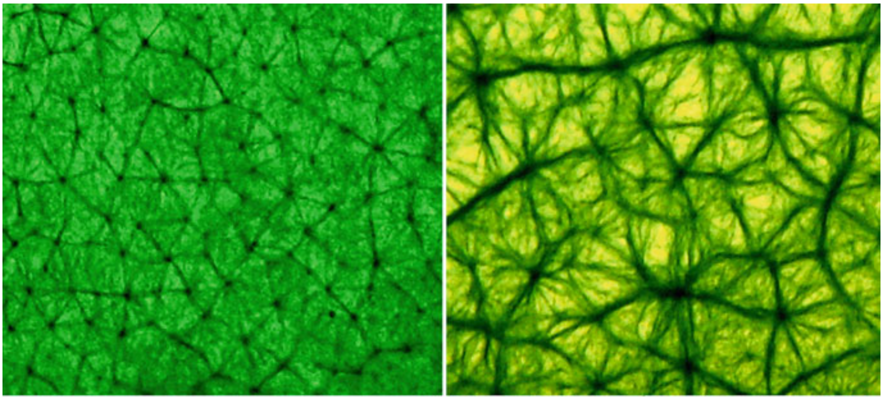

Fig. 5.2 Microscopic view of three-dimensional polygonal networks formed by the cyanobacteria *O. terebriformis*; right—higher magnification; modified from Isaeva et al. (2013)

contact guidance (see Sect. 5.3) and the sequential transformation of multi-array radial aggregates into three-dimensional networks were revealed in *O. terebriformis* (Sumina and Sumin 2013; Isaeva 2014a). The formation of these network patterns is due to the mobility of multicellular filaments (trichomes); dynamic collective behavior of trichome bundles led to the formation of three-dimensional polygonal networks (Sumina and Sumin 2013; Isaeva et al. 2013) (Fig. 5.2).

Thus, coordinated social behavior and self-organization of complex cell assemblies including polygonal networks of large-scale order were demonstrated in cyanobacterial communities, which are phenomenologically comparable with behavior of metazoan cells in vitro (Isaeva et al. 2013; see Sect. 5.3). The dynamic and reversible rearrangement of random trichome patterns into highly ordered polygonal networks is analogous to physical phase transition depending on external conditions. Since cyanobacteria are photosynthetic organisms, the most important and prominent morphogenetic reactions of their communities are the reactions to changes in illumination (Sumina and Sumin 2013; Isaeva 2014a). Structures formed by cyanobacteria *O. terebriformis*, in particular the multi-arrayed aggregates, have also mechanosensitivity (Sumina and Sumin 2013).

Coordinated cell movements resulting in ordered spatial patterns of bacterial colonies were observed repeatedly (Ingham 2012; Mastropaolo et al. 2012; Olsen et al. 2012). For example, *Escherichia coli*, *Bacillus subtilis*, *Pseudomonas aeruginosa*, and *Staphylococcus aureus* form radial, spiral, and fractal patterns of colonies (Ben-Jacob et al. 2004, 2012; López et al. 2010). In *Paenibacillus vortex* and some members of the genera *Pseudomonas* and *Proteus*, "swarming" as coordinated movement provided by the flagellar activity is found (Ingham 2012; Mastropaolo et al. 2012).

Microbiologists have discovered an unexpectedly high degree of coordinated social behavior in cell communities of Bacteria and also Archaea (Crespi 2001; Ben-Jacob et al. 2004, 2012; Brodsky 2009; Foster 2011; Chandler and Greenberg 2012; Olsen et al. 2012; Isaeva 2014a; Balaban et al. 2018). Among Archaea, for example, two species of the genus *Giganthauma* may form long filaments, in which *G. karukerense* are associated with bacterial cells (Muller et al. 2010; Olsen et al. 2012). A new field of research, sociomicrobiology, emerged, considering bacteria as social beings, capable of complex activity including social interactions, "quorum sensing," dynamic adaptation to environmental changes, and even "altruism" (Chandler and Greenberg 2012; Olsen et al. 2012; Strassmann and Queller 2012). For example, evidence for altruism in *E. coli* responding to the attack of lytic phage by committing suicide to prevent parasite transmission to nearby relatives was demonstrated (Refardt et al. 2013). Many microorganisms and cells within eukaryotic multicellular organisms secrete small signaling molecules and sense their concentration in the environment; different types of bacterial cell-to-cell signaling systems are considered quorum-sensing systems. The term "quorum sensing" was introduced to specifically refer to the cell density-linked coordinated gene expression in populations that experience threshold signal concentrations to induce a synchronized population response (Fuqua et al. 1994; De Monte et al. 2007; Atkinson and Williams 2009; Li and Tian 2012; Olsen et al. 2012; Balaban et al. 2018). So, bacterial communications include cell–cell chemical signaling that provides a bacterial "quorum" involving coordinated transcription (Waters and Bassler 2005; Atkinson and Williams 2009; Chandler and Greenberg 2012; Olsen et al. 2012). Quorum sensing confuses the distinction between prokaryotes and eukaryotes because it enables bacteria to act as multicellular organisms (Bodman von et al. 2008; Brodsky 2009). Quorum-sensing signaling is not restricted to bacterial cell-to-cell communication, but also includes interkingdom signaling as communication between microorganisms and their hosts, i.e., prokaryote–eukaryote cross-communication (Bodman von et al. 2008; Anetzberger and Jung 2010; Hughes and Sperandio 2012).

Adaptive interactions of “smart” cooperating bacterial cells permit to treat their behavior as a “bacterial wisdom,” “social intelligence,” and “collective intelligence” (Ben-Jacob et al. 2004, 2012; Balaban et al. 2018) of a bacterial community able to take collective decisions (Ben-Jacob et al. 2004, 2012; Balázsi et al. 2011; Ingham 2012). The collective cell behavior such as information generation, collective memory, and efficient cell-to-cell communication is an emergent property of the group and not of the individual cells (Balaban et al. 2018). Collective behavior refers to complex macroscopic dynamics of microbial communities exhibiting emergence and self-organization properties without a global controller (Balaban et al. 2018). The self-organization of collective behaviors often manifests as dramatic patterns of emergent large-scale order (Gloag et al. 2015). Bacterial stigmergy is a self-organization principle that explained how random and independent movements of individual cell (or trichomes) could result, by the transfer of local information (chemical, for example), coordinated behavior at a global level (Gloag et al. 2015). Many other researchers of bacterial aggregations and collective rearrangement of the cells in colonies and metabolic dynamics also considered the coordinated social behavior in bacterial communities as self-organization (Caratozzolo et al. 2008; Brodsky 2009; Hengge and Sourjik 2013; Ebrahimi et al. 2019; de Astacio et al. 2020; You et al. 2021).

Thus, the studied community of cyanobacteria, as well as other bacteria and archaea, is capable of complex social interactions and transition to large-scale orders with dynamic and reversible adaptation to environmental changes.

5.3 Cell Social Behavior and Self-Organization in Metazoan Cell Assemblies In Vitro

It is assumed that Bacteria and Archaea gave rise to Eukaryota: The mitochondria and chloroplasts were derived by endosymbiosis of proteobacteria and archaea (Margulis 1981; Woese 2002; Wassenaar 2012; Strassmann and Queller, 2012; Lane 2015). In addition, horizontal gene transfer has increased the complexity of the recipient cell design (Woese 2002; Lane 2015). Complex life arose through a singular endosymbiosis between an archaeon and a bacterium; there are no surviving evolutionary intermediates between the bacterial morphological simplicity and the complexity of eukaryotic cell (Lane 2015). Nick Lane (2015) believes that energy is central to evolution, and the endosymbiosis broke those constraints, enabling the evolution of vastly more complex cells; the clue to the eukaryotic cell complexity lies in the energy generation by mitochondria. Mitochondria and complex internal membrane structures ensure an essential intensification of the flux of energy and matter in comparison with prokaryotic cells (Lane 2015).

Besides nucleus and mitochondria (in plant cells also plastids), eukaryotic cells contain complex membrane system and cytoskeleton capable of self-organization. At the subcellular level, self-organization can be defined as the ability of cell organelles or macromolecular complexes to determine their own structure based on the functional relations of the components (Misteli 2001). Macromolecular complex formation during the construction of cytoskeletal structures (including actin, tubulin, motor proteins, and other molecular components) is traditionally considered as self-organization (Kirschner and Gerhart 2005; Karsenti 2008; Johnson and Lam 2010; Sasai 2013; Tee et al. 2015; Dasbiswas et al. 2018; Wedlich-Söldner and Betz 2018; Kadzik et al. 2020; McCusker 2020). The polymerization of actin and tubulin forms cytoskeletal actin filaments and microtubules that define the shape of a cell, its migration and polarity, intracellular transport, and mitotic division. The data on the assembly of actomyosin favor the interpretation that intracellular waves of actin polymerization and contractility are indeed self-organized by biomechanical feedback mechanisms (Wedlich-Söldner and Betz 2018; Kadzik et al. 2020). Self-organization was repeatedly demonstrated for the cytoskeleton microtubule system with the formation of various structural patterns. For example, dynamic and complex patterns of microtubule self-organization were observed in the very simple system that included solely tubulin and GTP (Tabony 2006). Microtubules and their associated motor proteins can be self-organized into various large-scale patterns: asters, vortices, and a network of aster poles connected by aligned microtubules. It was also shown the formation of structurally diverse microtubule patterns depending on the concentration of tubulin and the motor proteins (Misteli 2001).

A polarized cellular architecture is fundamental to the establishment of the anterior–posterior polarity of animal egg and zygote. Both the actin and microtubule cytoskeletal elements work together to convert an initial asymmetry into a global cell polarity. The cytoskeletal system transmits and integrates information across cellular dimensions; a polarized cellular architecture is fundamental to the formation of embryonic axes (Li and Bowerman 2010; Isaeva 2012, 2014b). Egg cytoskeleton functions as a global morphogenetic determinant, which directs and maintains the anisotropy of molecular information distributed in the ooplasm so determining axis polarity of a future adult organism (Isaeva et al. 2008, 2012).

The investigation of the interlink between membrane tension and signaling events that are triggered by rapid tension variations has led to the conclusion on biomechanical, feedback-driven self-organization (Wedlich-Söldner and Betz 2018). It was shown that mechanical tension influenced cell proliferation, differentiation, and morphogenesis (Stamenovic and Ingber 2009; Beloussov 2012, 2015; Isaeva et al. 2012; Eroshkin and Zaraisky 2017). The cytoskeleton is the generator of morphogenesis at the cellular and supracellular levels, and cytoskeletal reorganization is the basis of metazoan morphogenesis (Vasiliev 2007; Stamenovic and Ingber 2009; Wedlich-Söldner and Betz 2018). Cell cytoskeleton is responsible for the control of the shape and mechanical properties of cells, orients most of the cell's metabolic machinery, and mediates mechanotransduction, i.e., the process by which cells sense and respond to mechanical cues by altering intracellular biochemistry and gene expression (Stamenovic and Ingber 2009; Eroshkin and Zaraisky 2017). Cells control their shape and mechanics through the use of an architectural mechanism known as "tensegrity" (tension + integrity) to structurally integrate thousands of different molecular components; tensegrity may facilitate mechanochemical transduction and convert mechanical forces into changes in molecular biochemistry (Stamenovic and Ingber 2009). In multicellular Metazoa, cytoskeletal tensional forces are transferred to the extracellular matrix via integrin receptor-containing focal adhesions and to cytoskeletons of neighboring cells through cadherin-containing cell–cell adhesion complexes, so external mechanical signals can propagate a long distance (Stamenovic and Ingber 2009). The mechanical tension is able to activate gene expression; the molecular mechanisms translating mechanical forces into the expression of some genes including mechanotransduction across cell and cytoskeleton were shown (Farge 2003; Desprat et al. 2008; Brunet et al. 2013; Beloussov 2015; Eroshkin and Zaraisky 2017; Wedlich-Söldner and Betz 2018).

It is evident that collective behavior and social networking such as quorum sensing are not limited to the bacterial kingdom (Atkinson and Williams 2009; Brodsky 2009). Eukaryotic cells inherited from Prokaryota some features of unicellular organisms and enhanced their abilities for explorative and adaptive "intelligent" social behavior and self-organization (Brodsky 2009; Isaeva 2014a). In 1985, Albrecht-Buehler in his remarkable article entitled "Is cytoplasm intelligent too?" wrote on an ability of metazoan cells to perceive information from other cells, process it, and realize an adaptive answer. It is well known also that the aggregation of the *Dictyostelium* amoebae (directed by the chemotactic mechanism in response to the concentration of the chemoattractant cAMP) forming concentric or spiral waves of cells movement is recognized as a classic example of self-organization.

Metazoan cells are involved in the organization of multicellular organisms at all levels. A metazoan organism, a "state of cells," strictly controls the self-renewal, differentiation, apoptosis (morphogenetic cell death), and behavior of own cells, promoting their "altruism" and suppressing cell individuality; a "tyranny of the organism" (Gould 2002) is inevitable. Nevertheless, a cell in a multicellular eukaryotic organism retains some features of an individual being capable of exploration, collective behavior, and collective self-organization, as evidenced by experiments with dissociated cells cultured outside the organism, in vitro (Kirschner and Gerhart 2005; Vasiliev and Gelfand 2006; Isaeva et al. 2008, 2012, 2013). Experiments with dissociated metazoan cells in vitro clearly reveal their remarkable possibilities of self-organization in the absence of controlling influences of the whole organism, organs, and tissues. Dissociated cells in vitro are able to explore and coordinate social behavior and the spontaneous generation of some ordered morphological patterns (Kirschner and Gerhart 2005; Deisboeck and Couzin 2009; Isaeva 2012, 2014a). The coordinated social behavior of metazoan cells in the monolayer cultures in vitro involves the contact guidance resulting in parallel cell orientation and the contact inhibition of cell movement and cell reproduction resulting in the self-organization of ordered spatial patterns (Weiss and Garber 1952; Weiss 1961, 1968; Abercrombie 1980; Turner et al. 1983; Trinkaus 1984; Lackie 1986; Isaeva et al. 2008, 2012, 2013).

5.3.1 Myogenic Cells In Vitro

Dissociated chick embryo skeletal myoblasts (myogenic cells from the femoral muscle of 11-day-old chick embryo) in monolayer cell culture are supplied with nutritive medium and able to proliferate, move, and differentiate into multinuclear myotubes. The myoblasts usually maintain their typical elongated, spindle-like shape. Spatial patterns in a monolayer myogenic culture are determined by intercellular interactions: the contact inhibition of cell movement and contact cell-to-cell orientation. The contact inhibition of cell movement preventing cell crossing over in vitro (Abercrombie 1980; Heaysman 1980) results in radial patterns of cell migration from aggregates, which are common in monolayer cultures of different cell types (Isaeva et al. 2008, 2012, 2013). Chick embryo myoblasts migrating from aggregates in vitro are also radially arranged around each aggregate due to the contact inhibition of cell movement (Fig. 5.3).

These migrating myoblasts form cell bridges between the aggregates (Fig. 5.3); the following myoblast migration along these cell bridges is due to cell–cell contact guidance (one cell along the other). Thus, cell bridges connecting the aggregates direct subsequent cell movements along these bridges reinforcingthe emerging reticular pattern of polygonal tesselation. Some myoblasts in cell bridges differentiated with the formation of multinuclear myotubes; the cell bridges evidently are stretched and disposed above the artificial solid substrate (Fig. 5.3).

This reticular pattern that emerged in myogenic culture is similar to the integrated polygonal networks of the cyanobacteria *O. terebriformis* (Fig. 5.2) and in cell cultures derived from different tissues and species of metazoan animals (Isaeva et al. 2008, 2012). For example, P. Weiss (1961) described how neurons and nerve fibers formed the bridges between two chick embryo spinal ganglia in vitro; later, Weiss (1968) found also a triangular pattern connecting three explants and directing cell traffic.

These reticular patterns and structural patterns of topological singularities (see Sect. 5.4) emerged by self-organization of myogenic cells only in vitro; such myogenic patterns are absent in vivo, during normal myogenesis in the whole embryo. The skeletal myogenesis in vivo is tension-dependent, and in vivo, it is also necessary for the mechanical tension for myotube differentiation. Myoblast attachment to an artificial solid substrate in vitro ensured the possibility for mechanical stress as a prerequisite for the completion of skeletal myogenesis (Isaeva et al. 2008, 2012). It was shown that myogenesis is essentially modified in the rotating suspension culture: myoblasts in three-dimensional aggregates fused with the formation of atypical massive myosymplasts with dozens of randomly clustered nuclei (Isaeva 1980, 1994). After replating in monolayer culture and attachment to a solid substrate, these myosymplasts undergo gradual elongation and differentiation into typical cross-striated myotubes (Isaeva et al. 2012). The morphogenetic role of mechanical stress in myogenesis was demonstrated experimentally (Vandenburgh 1982), as well as in tension-dependent developmental cytomechanics (see above).

The influence of physical relief of the substrate in vitro on the orientation of myoblasts and myotubes in the myogenic monolayer culture was also demonstrated as the contact guidance of myoblasts and myotubes along grooves of artificial substrate (Isaeva 1980, 1994; Isaeva et al. 2008, 2012). The ordered arrangement of cells determined by physical properties of the substrate is maintained and transmitted by intercellular contact cell orientation side by side. The parallel orientation of myotubes on the substrate with ordered microrelief imitates the parallel arrangement of muscle fibers in the skeletal muscle in vivo; topological singularities are absent (Isaeva et al. 2008, 2012). So, in monolayer culture, bipolar myogenic cells, becoming free from controlling influences of tissue and organism, spontaneously, by self-organization formed two-dimensional cell direction fields, with or without topological singularities depending on physical microrelief of artificial solid substrate.

Thus, the spatial patterns in myogenic and fibroblast cultures are the result of cell interaction games: contact guidance and contact inhibition of cell movement. The cell–cell and cell–substrate interactions (short-range order) generate cell direction fields (long-range order). Cell contact guidance is the cellular basis of myogenic morphogenesis both in vivo and in vitro as a transition of the local order of cell interactions into the global order of cell fields. While at the cellular level the biological mechanisms of self-organization in monolayer culture are contact inhibition and contact guidance of cell movement, at the molecular level it is the fibrillar actin function necessary for actin–myosin interaction (Isaeva et al. 2008, 2012). The treatment with cytochalasin B or D (a specific inhibitor of the fibrillar actin system) prevented cell migrations, cell differentiation, and all cell–cell and cell–substrate interactions so completely inhibiting the formation of structural patterns and morphogenesis in vitro (Isaeva et al. 2008, 2012). Therefore, myoblast migration and pattern formation are due to the F-actin-dependent mechanism including the actomyosin interaction.

5.3.2 Hemocyte Aggregation In Vitro

Early stages of cell aggregation in suspension at high cell density are similar in diverse cell systems: Cells of different organisms and different tissue origins form cell clusters of varying size and shape. The early aggregation phase proceeds in the same fashion as it was described initially for sponge cells (Wilson 1907) and later for sea urchin embryo cells (Spiegel and Spiegel 1975, 1986). The same aggregation pattern is observed in cell suspensions of other cell types from different animals at high cell density. Free circulating cells, for example, molluscan hemocytes and echinoderm coelomocytes, are the emergency systems of rapid response characterized by chaotic dynamics and rapid transition from one state to another. These systems consisting initially of isolated cells are suitable to study phenomena of self-organization. The contact of the hemolymph, coelomic fluid, or blood with the external environment causes immediate cell aggregation.

The earliest cell aggregations having the fractal dimension with values of 1.6 to 1.7 are similar to fractal “monsters” (Mandelbrot 1983) and to chaotic fractal clusters arising during diffusion-limited aggregation (DLA) (Witten and Sander 1981). After

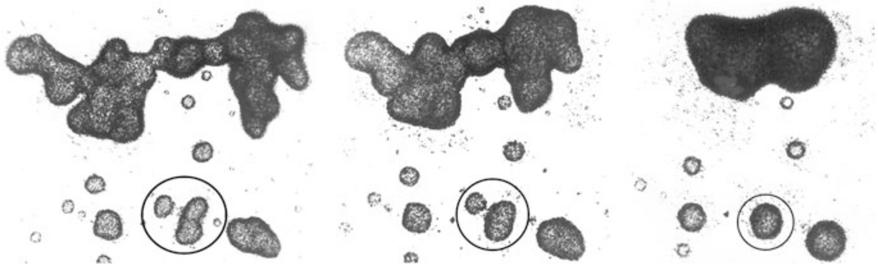

Fig. 5.4 Contraction dynamics of cell aggregate formed by hemocytes of the scallop *M. yessoensis*; the sequence of aggregate fusion is shown within circles; modified from Isaeva et al. (2008)

completion of the chaotic aggregation phase (within a few minutes), the hemocyte aggregates became spherical ones and for several hours transform into ordered spherical bodies, formed by several layers of elongated flattened cells and similar to encapsulation bodies (Isaeva 2012). Thus, a cell aggregate is an integrated whole showing emerging properties due to coordinated "social" cell behavior.

When the hemolymph of the scallop *Mizuhopecten yessoensis* was transferred into a Petri dish, we observed very rapid aggregation of hemocytes followed by contraction of the hemocyte aggregates (Isaeva et al. 2008) (Fig. 5.4).

Thus, contact of the *M. yessoensis* hemolymph with an external medium causes an immediate aggregation of hemocytes as a modified in vitro protective clotting reaction. During the phase of compactization and contraction, the fusion of neighboring aggregates originally connected with a narrow bridge of few cells is observed (Fig. 5.4). Freshly isolated molluscan hemolymph or echinoderm coelomic fluid contains numerous aggregates of various shapes and sizes. During aggregate contraction, the linear size of the aggregates was essentially reduced (Fig. 5.4). Cytochalasin B or D (2–5 μg/ml) completely inhibits both the contraction and the fusion of aggregates—so revealing the dependence of these processes on an intact system of actin filaments. Therefore, aggregate compaction is a fibrillar actin-dependent process, comparable to muscle contraction.

Molluscan hemocytes and echinoderm coelomocytes fulfill in vivo such cell-protective functions as clotting, encapsulation, phagocytosis, and primary wound reparation. In vitro, reactions of phagocytosis and encapsulation are expressed as the attachment to an artificial substrate, while clotting reaction appears as cell aggregation (Isaeva 1994, Isaeva et al. 2008; Kotolupov and Isaeva 2013) (Fig. 5.5).

Thus, coordinated, social behavior metazoan cells lead to the formation of ordered morphological patterns of cell assemblies (Abercrombie and Heaysman 1954; Vasiliev and Gelfand 2006; Deisboeck and Couzin 2009; Isaeva 2012, 2014a; Isaeva et al. 2008, 2012, 2013). It was revealed a change in cell behavior in vitro as a sudden spontaneous transition from chaos (irregular movement of individual cells) to order (collective cell behavior resulting in the self-organization of 3D cellular aggregates or 2D ordered patterns) similar to a phase transition in physical systems (Bird 2003; Deisboeck and Couzin 2009; Isaeva et al. 2008, 2012,

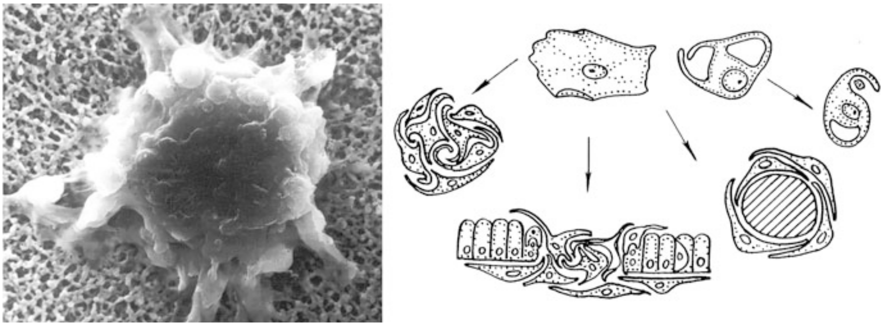

Fig. 5.5 Hemocyte protective reactions: left—an aggregate of hemocytes from *M. yessoensis* on microporous substrate in vitro; cell–cell and cell–substrate adhesion is evident (scanning electron microscopy); right—a scheme of defensive–morphogenetic reactions of hemocytes and coelomocytes (clotting, wound reparation, encapsulation, phagocytosis); modified from Isaeva and Korenbaum (1989), Demenok et al. (1997)

2013). By the contact guidance cell–cell and cell–substrate, translation of the local order of cell interactions into the global order of cell fields is realized in vitro.

5.3.3 Metazoan Embryonic Cells

Experiments with dissociation embryonic cells of some animals provided evidence of tremendous self-organization and regulatory properties of these cells capable of spontaneous reaggregation and development into the whole organism. Recent data demonstrated striking regulatory capacities of dissociated and reaggregated embryonic cells of the cnidarian *Nematostella vectensis* (Kirilliva et al. 2018). The reaggregated cells of dissociated gastrulae showed enormous plasticity including the capacity of the ectodermal cells to convert into endodermal ones and using various pathways of the gastrulation process as alternative developmental trajectories. The data suggest that the spectrum of developmental trajectories accessible for a species might be far broader than can be concluded from the observation of normal development, which might involve only a subset of available morphogenetic capacities (Kirilliva et al. 2018).

It has been shown earlier that the reaggregates of dissociated sea urchin embryonic cells formed swimming “embryoids,” or “embryoid bodies,” which were capable to develop into more or less normal larvae, to undergo metamorphosis, and finally become fertile sea urchins (Giudice 1962; Hinegardner 1975; Spiegel and Spiegel 1986). During the development of the echinoderm embryoids from dissociated blastomeres, blastulation, gastrulation, and mesoderm formation occurred in another way in comparison with normal embryogenesis, however, can lead to the development of normal organisms (Tamura et al. 1998; Isaeva et al. 2008; Presnov et al. 2010). For example, in the period corresponding to the stage of blastula epithelialization (mid-blastula transition), dissociated blastomeres of echinoderm embryos, lying on the bottom of a Petri dish as a loose layer of cells, formed the local plates of tightly joined epithelial cells. Later, edges of each local monolayer plate became bent, risen above the substrate and finally closed with the formation of a three-dimensional embryoid; such unusual embryogenesis in vitro was called "blastulation" (Dan-Sohkawa and Fujisawa 1980; Dan-Sohkawa et al. 1986; Kadokawa et al. 1986). We observed the similar blastulation process in experiments with dissociated blastomeres from embryos of the sea urchin *Strongylocentrotus nudus*) (Isaeva 1994; Isaeva et al. 2008; Presnov et al. 2010; Kotolupov and Isaeva 2013). In starfish embryoids developing from reaggregates of dissociated embryonic cells, mesoderm formation occurred by the normal enterocoely (evaginations of the gut wall) or by schizocoelic-like pathway (cell immigration following aggregation and cavitation), which is unusual for echinoderms and all Deuterostomes (Tamura et al. 1998). In embryoids separated from large chimeric aggregates, which were formed after the dissociation of many urchin embryos, we observed similar alternative developmental trajectories, including also gastrulation by the cavitation process instead of the normal invagination (Isaeva 1994).

Recently, it was shown also that small aggregates of mouse embryonic stem cells (ESCs) in vitro, with appropriate stimulation, can undergo gastrulation-like self-organizing resulting in "gastruloids" containing neural, mesodermal, and endodermal derivatives that mimic embryonic spatial–temporal Hox gene expression (Beccari et al. 2018). Cloning intestinal stem cells is also self-organized forming mini-guts (Sato and Clevers 2013).

Thus, many experimental data indicate that the experimentally revealing spectrum of potencies of embryonic cells is broader than the possibilities realized in normal development (Kirilliva et al. 2018). These regulatory events in vitro considered as self-organization (Isaeva et al. 2008, 2012; Beccari et al. 2018; Kirilliva et al. 2018; Sato and Clevers 2013) represent the scenario of transition from chaos into order by means of cell social interactions. Self-organizing systems of embryonic cells are able to achieve a normal finite state using various developmental trajectories and demonstrating the equifinality of development morphogenetic equifinality presumedly due to the streaming of the trajectories to a final attractor.

5.4 Topological Approach: Transformations in Metazoan Development and Evolution

The spatial organization of living systems has a dynamical character; these are forms sustained in a metabolic flow. V.N. Beklemishev (1890–1962), an outstanding Russian zoologist and comparative morphologist, considered an organism as a morphoprocess (Beklemishev 1964). Since topology operates with the most general properties of spaces as mathematical subjects, an adequate description of biological morphogenesis can be obtained through the use of the topological approach. Topology enables us to analyze a transition from local parameters to global ones, so the topological models would be adequate models of real biological objects. However, the traditional description of biological forms does not contain topological concepts and terminology. Living organisms inhabit and develop in the real physical space and are organized according to the global topology of this space (Presnov et al. 2010, 2014). General principles in physics, geometry, and topology are applicable to many situations in biology (Bouligand 1996). Nicolas Rashevsky (1958) initiated a topological approach to biological research, which he named "biological topology" or "biotopology"; later, G. Edelman (1988) proposed a similar name, "topobiology."

René Thom, a brilliant mathematician, who devised catastrophe theory, was the first to show that biological concepts can be formulated in terms of vector fields, attractors, and bifurcations (catastrophes) (Thom 1969, 1996, 1997). For example, René Thom (1969, 1996) considered gastrulation as a topological catastrophe and cell movements during gastrulation as a topological spatial mapping. R. Thom put forward the topological description and modeling of embryogenesis in his paper "Topological models in biology" (Thom 1969). Thom argued that quality is not reduced to quantity, and the discrete character of biological morphogenesis involves qualitative discontinuities such as topological bifurcations (catastrophes) and qualitative evolutionary innovations (Thom 1969, 1996, 1997). R. Thom considered a continuous spatial–temporal configuration that relates the parent individually with the offspring as the major object of biological investigation; according to Thom, the hen and the egg are only the temporal sections of the global configuration of trajectories (Thom 1997). The topological approach to the description of biological morphogenesis and using the elementary topological language for the formalization of biological forms and processes and for modeling of form dynamics in ontogeny and evolution have become a more common practice (Maresin and Presnov 1985; Presnov et al. 1988, 2010, 2014; Jockusch and Dress 2003; Isaeva et al. 2006, 2008, 2012; Cherdantsev 2006; Honda 2012).

Following R. Thom, we introduced the topological language in descriptions and analysis of biological morphogenesis using some well-known theorems to reveal a topological inevitability of some events in early embryogenesis (Presnov et al. 1988, 2010, 2014; Isaeva et al. 2006, 2008, 2012, 2014). Forms of a developing organism such as cell sets and closed surfaces are topological objects; maps as mathematical functions are additional topological constructions in these objects including polarization, singularities, and curvature. We applied elementary topological concepts to describe and interpret structural dynamics of biological forms and morphogenetic processes in ontogeny and evolution since developmental and evolutionary modifications of topological patterns are discrete events. For example, the spatial organization of the biological fields is analyzable in topological terms; topological singularities inevitably emerge in biological morphogenesis and are retained and transformed during pattern formation. T. Elsdale pioneered in applying a topological theorem (the theorem on the sum of the indices of the singularities in a vector field) to experimental biology and revealing singularities in fibroblast confluent layer in vitro (Elsdale 1972, 1973; Elsdale and Wasoff 1976). In a monolayer myogenic culture, self-organization of planar directional fields with a certain set of topological singularities was observed (Isaeva et al. 2008, 2012; Presnov et al. 2010). The limited number of topological singularities of directional planar fields (Penrose

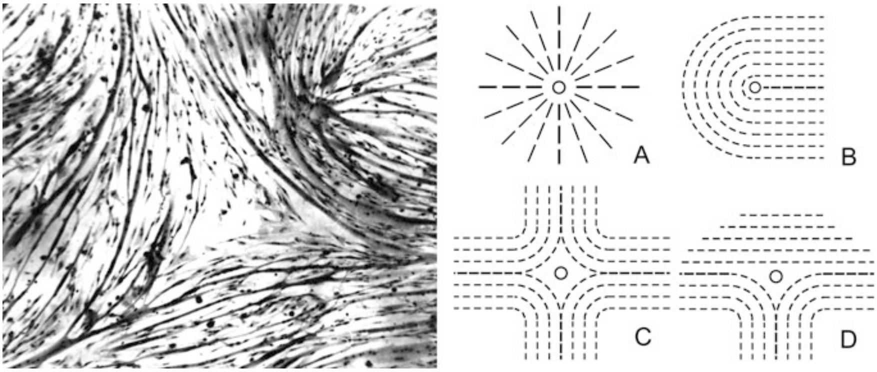

Fig. 5.6 Topological singularities in planar fields: left—two singularities (the triradius and the loop) in monolayer myogenic culture; right—schematic representation of possible singularities in planar direction fields: (**a**) the radial pattern; (**b**) the loop; (**c**) the saddle; and (**d**) the triradius; the central circle is the point zero (from Isaeva 1994)

1979) determines the corresponding topological constraints of planar morphogenesis in monolayer cell cultures (Elsdale 1973; Isaeva et al. 2008).

In confluent monolayer cultures, human epidermal cells form patterns resembling dermatoglyphics (Green and Thomas 1978); human fibroblasts pack side by side due to contact guidance (Weiss 1961) and contact inhibition (Abercrombie 1980) aligning parallel to one another and forming a “patchwork” of many local cell flows, with discontinuities between cell arrays (Elsdale 1972, 1973; Elsdale and Wasoff 1976). These cell fields and dermatoglyphic patterns are considered in topology as planar, nonoriented vector fields, or direction fields (Elsdale 1973; Elsdale and Wasoff 1976; Penrose 1979). The direction fields include points where the field directions are not defined becoming zero, and each point was referred to as a discontinuity or a topological singularity of the field; it is possible only a limited set of topological singularities (discontinuities) of planar direction fields (Elsdale and Wasoff 1976; Penrose 1979). In the monolayer culture of completely dissociated chick embryo myogenic cells, the moving myoblasts were self-organized into parallel arrays by the contact guidance; later, myotubes were also aligned one along another forming cell flows, resulting in the emergence of topological singularities in this planar cell field (Isaeva 1994; Isaeva et al. 2008, 2012, 2013). For example, two singularities, which are usual in myogenic monolayers, the triradius and the loop, are shown here, as well as a schematical image of all possible planar singularities (Fig. 5.6).

Thus, in the myogenic monolayer culture, we observed spontaneous patterning as self-assembly in direction cell fields with the emergence of topological singularities (discontinuities of the direction field). In the monolayer myogenic culture, all the possible singularities of the planar direction field were observed (Isaeva et al. 2008, 2012). A radial pattern of cell migration from aggregates in monolayer culture (Fig. 5.3) is the common typical phenomenon of self-organization in monolayer cell cultures. The limited set of topological singularities of planar directional fields determines the topological basis and topological constraints of the biological two-dimensional pattern formation (Penrose 1979; Elsdale 1973; Elsdale and Wasoff 1976; Isaeva et al. 2008, 2012).

We used well-known mathematical axiomatics for an extended topological description of biological development. For example, a topological interpretation of some events of early morphogenesis was given based on the known concepts of mathematics, for example, Poincaré–Hopf and Gauss–Bonnet theorems (see Isaeva et al. 2008, 2012, 2014a, b; Presnov et al. 2010, 2014). We proposed that the inevitability of oocyte/egg polarization follows from Poincaré–Hopf theorem. According to this theorem, a vector field on a sphere has inevitably at least one singularity (the point where the value of the field becomes zero). This singular point may be either vegetal or animal pole. The singular point on the cortical sphere of an egg coincides with actin concentration and/or localization of the microtubule aster, and the cytoskeleton polarization determines the axial polarization of an egg, zygote, and developing embryo. In chordates, a new singularity besides preexisting animal/vegetal egg pole emerges following sperm penetration. After fertilization, zygote cleavage creates a pattern of cell contacts on the embryo surface, a discrete morphogenetic field with inevitable topological singularities. The positional information of a discrete morphogenetic field is described by the Gauss–Bonnet theorems as the relationship between the local and integral orders. At least in some animals, the localization of invagination (or immigration, ingression) during gastrulation coincides with the location of the singularities of negative curvature, i.e., with the highest value of the cell field on the vegetal surface of embryos (Presnov et al. 2010, 2014).

In metazoan evolution, the appearance of the epithelial tissue was one of the most significant innovations. Epithelial cells form cohesive cell sheets; the structural and functional connectivity of an epithelial layer during epithelial morphogenesis is ensured by the system of specialized intercellular contacts that integrate cells into a united morphological and functional entity, integrating cytoskeletons in "histoskeleton" and creating "an envelope" of an organism (Presnov et al. 2010, 2014; Isaeva et al. 2006, 2008, 2012, 2014; Honda 2012). Epithelial cell layers are characterized by connectivity, the closeness of an intact surface, and apical–basal polarity. To translate traditional morphological descriptions of a metazoan morphogenesis into topological language, the external shape of an organism is modeled as a set of smooth, closed, orientable surfaces formed by epithelial layers, which thickness is neglected. According to the theorem of elementary topology, any closed surface in three-dimensional space is homeomorphic (topologically equivalent) to the sphere with a certain number (p) of handles. If there are no topological surgeries (cutting and gluing of epithelial sheets as "cut and paste" operations), the genus of the surface (p) is a topological invariant, and any geometrical deformations such as surface curvature and linear and angle values are not essential. The closed surfaces of the genus $p = 0$ (sphere), $p = 1$ (torus), $p = 2$ (double torus, or "pretzel"), and $p = 3$ (triple torus) are discrete forms, separated by discrete topological transformations producing reorganization of whole-body plan. The topological approach makes it possible to consider the succession of spherical surgeries changing the topological genus of a metazoan body surface. In some animal taxa, topologically complicated fractal-like systems increase the genus of the surface, so that the body surface becomes homeomorphic to a high-order torus. The topological differences between these surfaces are qualitative and fundamental. Topological handles in biological objects are usually realized as channels (canals), for example, the digestive tube, and we consider only epithelized through hollow channels as topological handles. There are various evolutionary modifications of the archetypical body plan in many phyla due to additional topological surgeries; for example, in Spongia, some Cnidaria and Ctenophora, an increase in genus p up to very high values and the shaping of topologically complicated fractal systems are evident. We considered only basic archetypical body plans for each metazoan taxon, i.e., a plesiomorphic topological design neglecting variations and modifications inside the taxon.

The first important topological surgery in the evolution of Bilateria (Triploblastica) is the appearance of a hollow, through the intestinal tube instead of a blind gut. Among Bilateria, animals of many phyla have the stable topological pattern, with the through the digestive tube only, without any other through channels, and their external surface is topologically homeomorphic to the torus, $p = 1$. Topologically, the digestive tube is outer surface of an organism and the ectodermal surface of the organism; both ecto- and entodermal epithelia form united continuous surface, the outer surface of an organism. An analysis of topological organization of the closed epithelial layer that covers the outer body surface as a continuous envelope is applicable also to the topological organization of the body surface in metazoan development (Maresin and Presnov 1985; Presnov et al. 1988, 2010, 2014; Isaeva et al. 2006, 2008, 2012, 2014).

Gastrulation is a topological catastrophe, transition from the sphere with an inevitable singularity (singularities) of its vector field to the topologically stable torus (a toroid embryo or a larva) with a homogeneous field (Fig. 5.7).

The evolutionary invention of a through gut probably involved duplication of an ancestral homeobox gene cluster (ProtoHox) to yield two paralogous gene clusters, Hox and ParaHox; it was proposed that Para-Hox genes were components of an ancient system for patterning the bilaterian gut (Holland 2015; Ferrier 2019; Zhong et al. 2020). ParaHox genes are notable for their roles in patterning the development of the gut and the central nervous system in Bilateria. The origin of a through gut, with the mouth, digestive regions, and anus, may have facilitated the evolution of predation and active burrowing as key drivers of animal diversification in the Cambrian (Holland 2015; Ferrier 2019; Zhong et al. 2020). The emergence of a through gut is a topological innovation of a high evolutionary value, which provided vectorized functioning and regional differentiation of the gut tube (Isaeva 2014b). The epithelial body surface is the boundary layer, the interface between the internal medium of a metazoan organism and its environment. Therefore, adaptive topological transformations of the body surface during metazoan evolution result in an enlargement of this interface ensuring the better distribution of external medium flows within an organism, better utilization of necessary nutrients with directed, more complete excretion. This functional advancement (P. Holland 2015) is named "ecological engineering." A transition of blind archenteron to through intestine tube

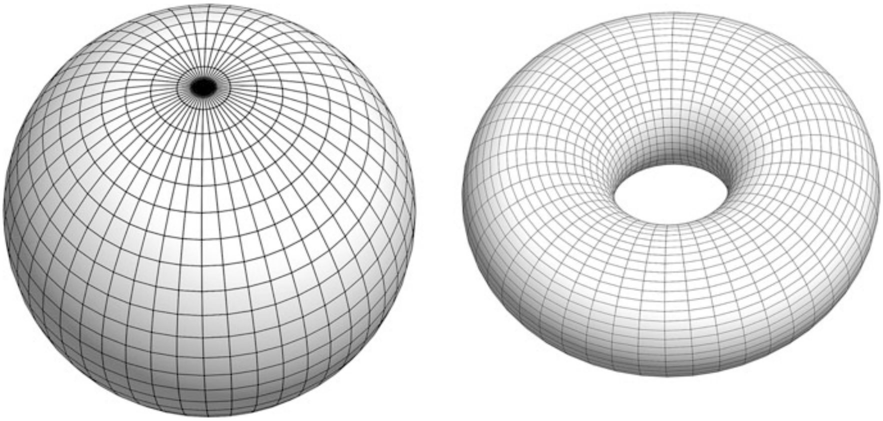

Fig. 5.7 Topological transformation during gastrulation: left—the singularity of the vector field of a fertilized egg; right—a postgastrulation embryo topologically homeomorphic to a torus with the homogeneous vector field; modified from Isaeva et al. (2014)

is realized during gastrulation by the formation of another opening besides the blastopore (a primary mouth), which becomes the definitive oral opening in Protostomia or anal opening in Deuterostomia.

Subsequent evolution has led to the formation through channels of the coelomic and respiratory systems; the emergence of additional through epithelial channels transformed the body surface of animals in different taxa into a double, triple, and sometimes multiple tori (Isaeva et al. 2006, 2008, 2012). For example, mollusks and echinoderms exhibit, besides the digestive tube, the second through a channel formed by the coelomic system ($p = 2$). The next evolutionary level of topological organization in animals is attained through the development of the respiratory system: the system of paired tracheal tubules (of ectodermal origin) with lateral connections in higher terrestrial arthropods or paired gill slits (of endodermal origin) in a chordate archetype. This evolutionary transition from the torus to the surface of the genus $p = 1 + 2n$ occurred by adding an even number of channels (gill slits) of the respiratory system in Chordata; among chordates, the ascidian body surface is a high-order torus due to the presence of numerous pharyngeal openings (gill slits) (Fig. 5.8).

Thus, in evolution and embryonic development, the body surface of an organism (its epithelial “envelope”) in most Metazoa undergoes spherical surgery(ies), which changes the topological genus of the surface, the value of which is determined by the number of through hollow channels. In embryogenesis, the topological surgeries occur locally and involve such complex cell events as epithelial sheet disintegration followed by cell adhesion and cytoskeletal and intercellular rearrangements giving rise to a newly formed cell layer. Therefore, local topological surgeries inevitably lead to global topological transformation (topological catastrophe) of an organism.

Topological rearrangement by cutting and pasting can be found at all levels of biological organization. “Evolutionary cut and paste” (Shubin 1998), as well as

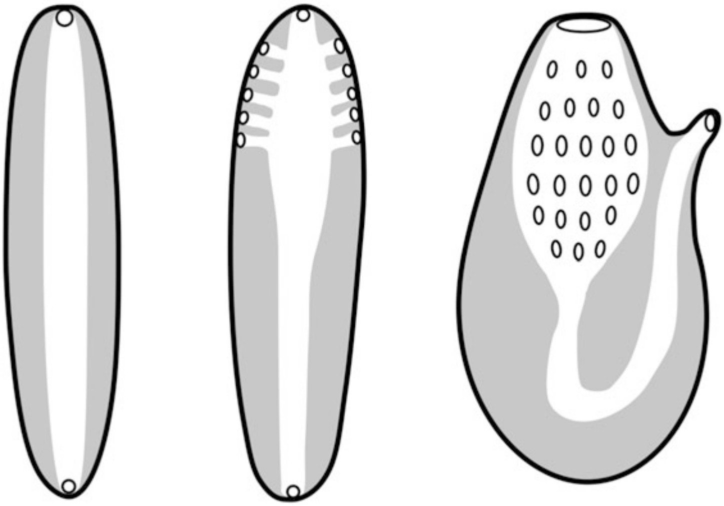

Fig. 5.8 Topological organization in some metazoans (left to right): digestive tube only (most worms); digestive tube with several pairs of gill slits (Hemichordata and chordate archetype); digestive tract with numerous pharyngeal openings (Ascidia); modified from Isaeva et al. (2012)

rearrangements of gene regulatory networks, are the topological operations; Hox/ParaHox collinearity phenomenon is the topological mapping (see Sect. 5.5).

5.5 Metazoan Body Plan in Molecular–Genetic and Macroevolutionary Context

5.5.1 Gene Regulatory Networks: The Inevitability of Self-Organization

Metazoan genome is not a "bag of beans," but a complex hierarchical network system, including many intragenomic connections and many feedbacks, capable of self-organization and dynamic transformations in developmental processes (Koonin 2012; Ryan 2015; Srivastava 2015; Simakov and Kawashima 2017). Gene regulatory networks are modeled by the abstract topological random Boolean network (RBN) (Kauffman 1993; Gershenson 2012; Erwin 2020; Gershenson et al. 2020). RBNs can be described as self-organizing systems simply because they have attractors, a set of "preferred" states because any such system is able to self-organize toward the attractors (Gershenson 2012). It was studied how changes in the nodes and connections affect the global network dynamics and critical regimes of RBNs; the phase transition is characterized by its criticality as the "edge of chaos" (Kauffman 1993; Gershenson 2012). The critical regime is advantageous for adaptability, evolvability, and robustness; probably, natural selection can guide the self-organization of genetic regulatory networks toward the critical regime (Gershenson

2012). Investigations concerning the molecular mechanisms of development reveal the modular hierarchical architecture of developing systems and networks of their gene regulation (Davidson 2006; Peter and Davidson 2011), and the modular architecture of gene regulatory networks has emerging properties (Davidson 2010). The modularity, a ubiquitous topological feature of most biological networks, is crucial for the self-organization of the global network dynamics (Siebert et al. 2020). Thus, self-organization is inevitable in complex biological networks.

Gene regulatory networks include a large number of genes that code for transcription factors, ligands and receptors of intercellular signaling, and the sequences that control the expression of each of these genes. These elements of coding and noncoding sequences of DNA altogether comprise the regulatory genome; interacting regulatory genes form the regulatory network, i.e., the gene program of development (Erwin and Davidson 2009; Peter and Davidson 2011). The program of development is encoded in the form of a huge network of functionally interrelated *cis*-regulatory DNA modules; various subcircuits are active in various embryo domains and in various periods (Davidson 2006; Erwin and Davidson 2009; Peter and Davidson 2011; Erwin 2020). Evolutionary change in animal morphology results from alteration of the functional organization of the gene regulatory networks (Peter and Davidson 2011). Only about two percent of the human genome is protein coding; it is leading to a reevaluation of the potential complexity in the regulatory circuits embedded in the DNA, at least for vertebrates (Tschopp and Duboule 2011). The "dark matter" of the animal genome, DNA that does not encode proteins, which has recently been considered as "junk," is now being studied. A significant part of such DNA encodes various RNA, including long and short noncoding RNA, transposons, and microRNA; the very important regulatory functions of some of these RNAs have been identified (Koonin 2012; Carey 2015; Ryan 2015; Srivastava 2015; Shapiro 2016; Simakov and Kawashima 2017). Changes in "noncoding" sequences can result in important phenotypic alterations (Shapiro 2016). Possibly, cells possess "read–write genomes" and can rearrange DNA molecules (Shapiro 2016). It is well known that the relation between the genotype and phenotype can include polyphenism when the same genotype can ensure alternative developmental trajectories resulting in various phenotypes (see Kirschner and Gerhart 2005; Gilbert 2010). Thus, the simple unambiguous interconnection between genotype and phenotype is absent; the genotype–phenotype mapping turns out to be very complex. Thus, a bilaterian genome is a "hypertext," a dynamic hypercode.

5.5.2 Genome–Phenome Mapping/Correlations

In an effort to integrate body plan and genomic levels, let us try to consider a genome–phenome mapping, at least some genome–phenome correlations. Evolutionary genomics made it possible to link the diversity of genomes to the phenotypic diversity of Metazoa and other Eukaryota, in particular, revealing genomic correlates of morphological complexity and diversity in animal body plans (Erwin 2009; Dunn and Ryan 2015; Srivastava 2015). A significant, clearly pronounced correlation between the regulatory complexity of a genome (determined by the total number of transcription factors and other transcription regulators) and morphological complexity (measured by the number of cell types) in Metazoa was identified as a causal evolutionary relationship between genomic regulatory complexity and morphophysiological complexity of a metazoan body (Lang and Rensing 2015; Srivastava 2015). Expansion of transcription factors as a result of genomic duplication and the subsequent neofunctionalization of paralogs are assumed to be the source of evolutionary innovation with the acquisition of new cell types and an increase in morphological complexity (Lang and Rensing 2015; Srivastava 2015).

Generally, the relationship between genotype and phenotype, genome, and phenome of a metazoan organism is a complex network of interactions at all levels of biological complexity. Understanding the relationship between the genotype and the dynamic phenotype or, according to topological terminology, mapping genotype → phenotype is a central challenge of current biological research. In evolutionary developmental biology, the correlation between genes and phenotype, or a genotype–phenotype mapping is considered as a complex nonlinear web of the signaling systems and transcription regulators; the following events involve pleiotropy, extensive feedback loops, self-organization processes, physical forces, and environmental cues, all contributing to the final morphology of the organism (Wilkins 2002; Davidson 2006; Gilbert 2010; Minelli 2015, Dunn and Ryan 2015; Ogura and Busch 2016; see also Isaeva 2018; Isaeva and Rozhnov 2021). In short, genome-to-phenotype mapping is an extremely complex network, the many-to-many mapping (Koonin 2012).

However, it is a unique unambiguous example of the topological mapping as the transfer of the linear vector of the spatial gene arrangement through the spatial and temporal sequence of the gene expression along the axis of an embryo into the axial morphological pattern of a future organism—the Hox/ParaHox gene collinearity in their clusters in Bilateria. It is known that genetic mechanisms, which determine the anteroposterior patterning of a bilaterian body, are related to the order of the Hox genes in the cluster: Genes located closer to the 3′ end of the cluster (and the chromosome) are expressed closer to the anterior end of an embryo and earlier than their 5′-associated neighbors, so showing spatial and temporal collinearity (see Duboule 1994, 2007; Holland 2015; Darbelay and Duboule 2016; Ferrier 2019; Deschamps and Duboule 2017). Thus, clustered Hox genes perform the fundamental function of coding positional information along the bilaterian anteroposterior axis so determining the global phenotypic architecture of organisms. The ability of Hox cluster to the coordinate functioning of the entire complex of Hox genes with the performance of the integral function of coding the axial body pattern allows considering the Hox cluster as a metagene (Duboule 1994; Darbelay and Duboule 2016). Therefore, collinearity of Hox genes is the example of topological mapping, projection of the gene spatial order into the spatial–temporal order of their expression, and global axial pattern of developing organisms (Minelli 2003, 2015; Isaeva et al. 2008, 2012; Isaeva 2018). Besides Hox genes, three ParaHox genes (*Gsx, Xlox/Pdx, and Cdx*), the evolutionary sisters to the Hox genes, also exhibit collinearity: The order of the genes along the chromosome corresponds to their order of expression (Duboule

2007; Deschamps and Duboule 2017; Ferrier 2019; Zhong et al. 2020). The genes of the Hox/ParaHox clusters, which play a central role in the determination of the anteroposterior axis and the entire complex of the main features of the bilaterian body plan, are present only in Metazoa. Thus, Bilateria "invented" additional coding of global axial body plan by clusters of coordinately operating Hox/ParaHox genes and new mechanisms of metagenic, supragenic regulation of higher level.

Hox genes are known as genes–architects determining the body plan in Bilateria (see Gilbert 2010). The Hox genes encoding transcription factors, like the related genes of the ParaHox and NK groups, belong to the homeobox-containing genes of the ANTP class. The emergence and evolutionary expansion of Hox genes and their cluster (in vertebrate—clusters), accompanied by the loss of some genes, served as the genetic basis for the evolutionary transformation of the bilaterian body plan and its diversification (Holland 2015; Srivastava 2015; Halanych 2016; Ferrier 2019). There is a correlation between the increase in the number of Hox genes (as well as the total number of genes of the ANTP class) with the increasing complexity of the body plan (Garcia-Fernández 2005; Holland 2015; Halanych 2016; Ferrier 2019). In the evolution of Metazoa, the number of Hox genes increased from a small set to a diversified toolkit, presumably as a result of duplications of the ancestral cluster, the entire genome, and individual Hox cluster genes. Although the occurrence of Hox genes preceded the Bilateria radiation, the Hox system as a coordinated assemblage of Hox genes is specific to the bilaterian animals. Probably, the Cambrian explosion with the advent of most bilaterian types was ensured by "Hox gene explosion" (Davidson 2006; Erwin and Valentine 2013; Holland 2015; Peterson and Eernisse 2016). The topological rearrangement of the gene order in the Hox cluster, as well as the loss of one or several Hox gene(s), can cause large-scale macroevolutionary transformation in body morphology associated with various developmental and evolutionary strategies (Duboule 2007; Tschopp and Duboule 2011; Srivastava 2015; Isaeva 2018; Isaeva and Rozhnov 2021). Hox cluster is an important node in the vertebrate patterning network (Peter and Davidson 2011). Studies of Hox gene reveal several dozens of direct target genes including other regulatory genes and a plethora of downstream genes encoding proteins active in apoptosis, cell-cycle control, cell adhesion, cell polarity, signaling, and cytoskeletal functions (Carroll 2008; Peter and Davidson 2011). It is known that cluster Hox genes determine the development and axial patterning of mammalian limbs (Peter and Davidson 2011; Deschamps and Duboule 2017), considered as evolutionary duplicates of the main body axis (Minelli 2000, 2003, 2015). At the early stages of mammalian limb bud development, *Hoxd* genes are transcribed in the same spatiotemporal order as during trunk extension, and the underlying mechanism is likely identical to that at work during body axis extension (Deschamps and Duboule 2017).

Thus, the Hox gene system is a very important regulatory node of the genome–phenome relationships that determine a wide range of developmental processes and global body architecture. Paraphrasing the well-known statement of George Orwell, one can say that "All genes are equal but some genes are more equal than others" (Isaeva 2018).

5.5.3 Developmental Molecular–Genetic Machinery in Vertebrates

Recent data obtained on mammals demonstrate remarkable molecular–genetic machinery of highly coordinated patterning of the primary body axis in the early development of both axial and limb patterns: the embryonic timing, directional Hox clock, dynamics of the chromatin structure, and the axial progenitor generation, all functioning as “a time machine” (Deschamps and Duboule 2017). In other words, mammals achieve the appropriate Hox-mediated spatial patterning through the initial timed-sequenced activation of their Hox clusters in response to early embryonic signals (Neijts et al. 2016). Hox genes are initially switched as a response to Wnt signaling, which usually predates zygotic Hox activity; thus, the trigger for Hox activation is a canonical Wnt signal activating Hox in a temporally collinear way (Neijts et al. 2016, 2017; Deschamps and Duboule 2017). Both Hox and Cdx (ParaHox) genes encoding transcription factors are pivotal regulators of axial patterning and tissue generation along the vertebrate body axis (Neijts et al. 2016, 2017; Deschamps and Duboule 2017). Cdx genes are crucial for the timing mechanism driving collinear Hox activation and key regulators of Hox genes, as their inactivation affects central Hox gene expression (Neijts et al. 2016, 2017; Zhong et al. 2020). Cdx genes are implicated in a range of taxa in the posterior growth of the body (axial elongation); mutations in Cdx genes lead to arrest of axial extension as a result of the exhaustion of axial progenitor cells in the posterior growth zone (Neijts et al. 2016, 2017; Zhong et al. 2020). Thus, central Hox genes and their Cdx activators ensure posterior growth by maintaining axial progenitor cells active in the growth zone and defining a trunk segment in the Hox cluster topology (Zhong et al. 2020), so translating a temporal genetic system into spatial coordinates via the fate of these progenitors (Deschamps and Duboule 2017). During axial elongation, the early timing mechanism synchronizes Hox gene expression with the progressive generation of the trunk and tail from the posterior embryonic growth zone (Neijts et al. 2016, 2017). The stepwise activation of the clustered Hox genes appears as at least one of the molecular–genetic fundaments of the temporal collinearity of Hox gene expression; chromatin opening around trunk Hox genes is Cdx-dependent (Neijts et al. 2017; Zhong et al. 2020). Finally, the *Hoxa13* gene and the Hoxa13 protein constitute the most posterior module ending central Hox gene temporally collinear activation, possibly by direct competition with the trunk effector Cdx: Hox13 proteins antagonize Cdx by binding to the same targets, and so doing arrests axial elongation (Neijts et al. 2017).

During the development of vertebrate animals, Hox genes provide positional information to the emerging embryonic axial tissues, thereby instructing them on how to undergo appropriate morphogenesis; i.e., axial progenitors translate the Hox clock into spatial coordinates (Deschamps and Duboule 2017). The pluripotency factor Oct4 is a crucial player in determining progenitor activity. The translation of sequential Hox gene activation into spatial cues in axial tissue anlagen occurs in all vertebrates examined, including amphibians (Deschamps and Duboule 2017).

5.5.4 Molecular–Genetic Background of Metazoan Axial Body Plan

The body plan (Bauplan) as a characteristic of the morphological organization of Metazoa is one of the basic concepts of comparative and evolutionary biology (Beklemishev 1964; Gould 2002; Isaeva and Rozhnov 2021). Body axes form the basis of animal body plans. Because a metazoan body is formed from a spherically symmetrical egg, symmetry breakdown is one of the fundamental processes of development (Hirokawa et al. 2009). Symmetry breaking inevitably arising during early development plays a key role in biological morphogenesis. Topological bifurcations are tightly coupled with symmetry breaking, as developmental and evolutionary transformations of symmetry are discrete steps in biological morphogenesis inevitably disrupting a preexisting pattern of symmetry. Data on genetic mechanisms of axial pattern establishment, creating a coordinate system of the metazoan body plan, bilaterian segmentation, and left–right symmetry/asymmetry are necessary to an understanding of the evolutionary diversification and phenotypic expression of various body plans. Besides the crucial role of the axial Hox/ParaHox code as the mapping of the Hox/ParaHox cluster metagenes into the anteroposterior axis (see above), the broad variety in metazoan forms appears to be founded on a few signaling pathways—Wnt, BMP, Notch, and Hedgehog cascades, which determine metazoan body axes (De Robertis 2008; Manuel 2009; Petersen and Reddien 2009; Niehrs 2010; Neijts et al. 2014, 2016; Dunn et al. 2017; Simakov and Kawashima 2017; Erwin 2020; Fields and Levin 2020; Isaeva and Kasyanov 2021). Molecular components of the signaling systems are diffusible morphogens, which carry positional information, determining axial coordinates in morphogenetic fields of a developing embryo by means of instructive clues for genes to be expressed differently in cells located in different spatial areas (see Isaeva and Kasyanov 2021). Developmental gene transcriptional regulatory cascades and the signaling pathway responsible for the patterning of the metazoan body plan are remarkably similar throughout Metazoa. So, molecular positional information determines metazoan body plan.

The Wnt signaling pathway is the ancestral and most important program for animal development in the crosstalk with other gene regulatory cascades—not only patterning the primary axis, but also regulating morphogenetic cell movements and axial differences in cell fate, including the specification of cell lineages, cell proliferation, and posterior growth elongation (Petersen and Reddien 2009; Holstein 2012; Hogvall et al. 2019; Erwin 2020; Fields and Levin 2020; Isaeva and Kasyanov 2021). The growth of the metazoan body by the terminal addition of progenitor cells localized at the posterior growth zone was a cardinal evolutionary innovation. The formation of a localized Wnt signaling center at the site of gastrulation determines the orientation of the primary body axis in both bilaterians and non-bilaterians, in deuterostomes and protostomes, indicating that the conserved Wnt signaling pathway is at the base of polarized development in all metazoans. Data revealed by comparative genomics have shown that members of the Wnt signaling pathway are specific for metazoans as important regulators of embryogenesis and cell differentiation (Dunn et al. 2017; Hogvall et al. 2019; Erwin 2020).

In the canonical Wnt pathway, binding of Wnt(s) to their receptors induces intracellular gene cascades that lead to the release of β-catenin, which then regulates the transcription of Wnt target genes; β-catenin is the key intracellular effector of the canonical Wnt signaling pathway and plays an important role in the early polarization of the animal–vegetal axis of the embryo (Petersen and Reddien 2009; Holstein 2012; Hogvall et al. 2019; Erwin 2020). In planarians with their extraordinary morphological plasticity, the Wnt/β-catenin pathway provides positional information pivotal for proper head regeneration (Iglesias et al. 2008). Iglesias et al. (2008) studied the role of the β-catenin homologues from the asexual freshwater planarian *Schmidtea mediterranea*, mainly the gene *Smed b-catenin-1*. In *S. mediterranea*, experimental amputation of both head and tail produces trunk fragments usually regenerating both anterior and posterior structures, but if β-catenin is depleted by RNA interference, a head is generated instead of a tail, resulting in two-headed or multi-headed planarians (Iglesias et al. 2008; Petersen and Reddien 2009; Fields and Levin 2020). Thus, silencing of the gene *Smed β-catenin-1* in regenerating and intact planarians induces a gradual anteriorization of the animals that finally leads to a radial-like hypercephalized phenotype, demonstrating the requirement for *Smed β-catenin-1* in anterior–posterior axis reestablishment and maintenance (Iglesias et al. 2008; Fields and Levin 2020). Thus, the anterior–posterior axis can be symmetrized and duplicated to such an extent that it effectively disappears and is annihilated, leaving a radially symmetric, fully anteriorized form (Fields and Levin 2020). Unique examples of striking body symmetry transformation were observed in the most extreme cases, when planarians not only lose their tail, but ectopic heads with eyespots begin sprouting around the periphery of the body, eventually forming almost a radially transformed organism whose perimeter essentially consists of multiple heads (Fields and Levin 2020; Petersen and Reddien 2009; Fields and Levin 2020) (Fig. 5.9).

In normal planarians, the central nervous system is composed of two anterior cephalic ganglia located at the anterior end of two ventral nerve cords, while in radial-like hypercephalized planarians, the cephalic ganglia and ventral nerve cords are transformed into a thick ring from which cephalic branches ectopically differentiate all around the body, and all photoreceptor cells appeared to be connected through their visual axonal projections to the circular brain (Fields and Levin 2020). Thus, in the asexual freshwater planaria, specific experimental manipulations can symmetrize the anterior–posterior axis producing a radially symmetric, anteriorized form around the remaining dorsal–ventral axis (Fields and Levin 2020).

It was suggested that radial and bilateral body plans could have been generated with the same or similar genetic toolkit but with different regulatory networks (see Isaeva and Kasyanov 2021). Possibly, the silencing and knockdown of the gene *Smed β-catenin-1* expression cause a dramatic rearrangement, a topological catastrophe of the gene regulatory network (a contour including *Smed β-catenin-1*), which results in the radical symmetry transformation—bilaterality into radiality.

It is well known that embryonic morphogenetic fields, in which molecular positional information determines metazoan body plan, have the remarkable ability of self-organization, self-regulation, and self-regenerating after experimental

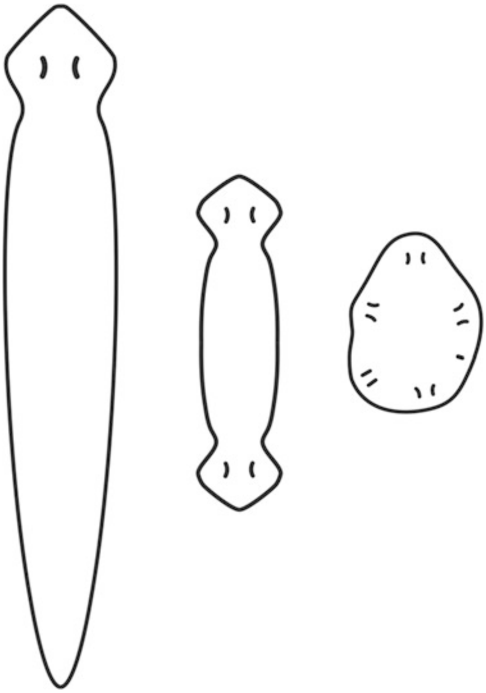

Fig. 5.9 A scheme of body symmetry transformation in planarians (left to right): an intact planaria; two-headed bipolar form; “hypercephalized,” radialized form (β-catenin knockdown with RNAi); modified from Isaeva and Kasyanov (2021)

manipulations (De Robertis 2008; Niehrs 2010; Seilacher and Gishlick 2015; Loh et al. 2016). The “self-organizing” morphogenetic mechanisms were important in evolutionary processes; of course, they are genetically controlled, but not in a simple one-to-one relationship; the relationship between the self-organizing processors and their genetic control has been referred to as “genomic assimilation” (Seilacher and Gishlick 2015).

5.6 Social Behavior in Vertebrate Communities

Social behavior is found at every level of biological complexity, ranging from quorum sensing in bacteria to human altruism (Parrish et al. 2002; De Monte et al. 2007; Ballerini et al. 2008; Balázsi et al. 2011; Leu et al. 2013; Attanasi et al. 2014; Gloag et al. 2015). Sociobiology is an attractive interdisciplinary field. The synchronized collective behavior of animals with the appearance of various ordered spatial patterns, which has been investigated for eusocial insect colonies, fish shoals, and bird flocks, is considered as the usual example of self-organization (Camazine et al. 2001; Parrish et al. 2002; Ballerini et al. 2008; Gershenson 2012; Attanasi et al. 2014; Gloag et al. 2015; Wedlich-Söldner and Betz 2018). The most commonly recognized social factors and benefits of being in a group include dilution of predation risk, increased vigilance and early predator detection, thermoregulation, and enhanced feeding through the use of social information (see Leu et al. 2013).

Nevertheless, there are also costs to group formation, which are often proportional to group size and include increased competition within the group, travel distances, and susceptibility to parasites and pathogens (Leu et al. 2013). The collective behavior of animal associations is not always adaptive; however, during evolution, the features of organism assemblies or cell associations inevitably become an object of natural selection (Camazine et al. 2001; Parrish et al. 2002; Kirschner and Gerhart 2005; Johnson and Lam 2010; Glancy et al. 2016).

The growing field of sociogenomics is revealing how complex social behavior can be dissected at the molecular level (Foster 2011). Multilevel selection theory (including kin selection) provides a theoretical foundation for sociobiology (Hamilton 1964; Gould 2002; Wilson and Wilson 2007). Evolutionary theory interprets social behavior in terms of fitness: cooperation among relatives can thus extend to altruism, in which an individual sacrifices its chance of reproducing to advance those of a relative (Olsen et al. 2012).

The self-organization of collective behaviors often manifests as dramatic patterns of emergent large-scale order; this is true from relatively "simple" entities such as microbial communities and robot "swarms," to more complex self-organized systems such as those displayed by social insects, migrating herds, and many human activities (Gloag et al. 2015).

Here are two examples of self-organization among vertebrate animals: tadpoles of the toad *Bufo gargarizans* and well-known flocks of the starlings, *Sturnus vulgaris*. In anurans, tadpole aggregations have been reported in many species (Leu et al. 2013), but among anurans of the south Russian Far East, only tadpoles of the toad *Bufo gargarizans* reveal collective self-organized behavior forming aggregates with coordinated movement (Far Eastern *Bufo gargarizans* http://www.ecosystema.ru/) (Fig. 5.10).

The factors driving this behavior remain unclear, as well as the aggregation of tadpoles of the frog *Litoria aurea* (Leu et al. 2013). Leu et al. (2013) suggested that small tadpoles are more vulnerable to predation and therefore more likely to form aggregations as an antipredator behavior; the observed inverse relationship between tadpole size and aggregation preference supports the notion of adaptive antipredator behavior (Leu et al. 2013). Another social route to tadpole schooling is the benefit of social foraging and the transfer of social information to obtain food (Leu et al. 2013). Tadpole schooling has evolved multiple times in distantly related anuran taxa and occurs in at least ten families (Leu et al. 2013).

Bird flocking is a striking example of collective animal behavior, and a vivid illustration of this phenomenon is provided by the aerial display of vast flocks of starlings as a paradigmatic case of collective behavior in animal aggregations with extraordinary spatial coherence (Ballerini et al. 2008). Starling flocks show strong spatial coherence and capability of fast, highly synchronized maneuvers, either spontaneously, or as a response to predator attacks (Ballerini et al. 2008). Individual birds kept a minimum distance from each other (comparable to their wingspan); during a turn, orientation changed with respect to the direction of movement (Ballerini et al. 2008). A. Attanasi et al. (2014) studied the orientational order in

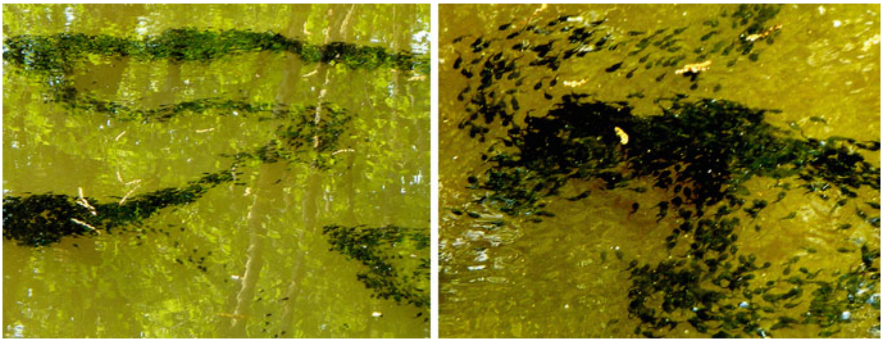

Fig. 5.10 Self-organization of coordinated movement and aggregation by tadpoles of the toad *Bufo gargarizans* in a natural forest pond near Vladivostok (wright—higher magnification). (Photo by V.V. Isaeva)

Fig. 5.11 A flock of the starlings, *Sturnus vulgaris* performing collective turn at 90° (Photo by V.V. Isaeva)

starling flocks performing collective turns; fast and robust transfer of information between birds, with the inclusion of behavioral inertia, was found.

Here is an example of the social collective behavior illustrated by the turning flock of the starlings *Sturnus vulgaris*, trying to escape a hawk attack, over Moscow (Fig. 5.11).

Fish schools, mammal herds, and insect swarms represent other examples of collective animal behavior that have fascinated biologists for many years; in all these examples, collective behavior emerges as the result of the local interactions between the individual units, without the need for centralized coordination (Ballerini et al. 2008).

5.7 Conclusions

Self-organization and social behavior are observed at all the levels of biological complexity ranging from quorum sensing in bacteria to human altruism (De Monte et al. 2007; Balázsi et al. 2011; Balaban et al. 2018), from cyanobacteria to Metazoa. The communities of both cyanobacterial (Prokaryota) and metazoan (Eukaryota) cells, with their essential differences in biological mechanisms of cell motility and cell–cell interactions, are capable of exploratory and coordinated social cell activity resulting in the formation of ordered patterns. Metazoan cells retain some features of individual beings as evidenced by experiments in vitro with dissociated cells, which display a coordinated social behavior and self-organization into ordered patterns without a global control of whole body (Isaeva et al. 2008, 2012, 2013; Isaeva 2012, 2014a, b). Eukaryotic cells have evolved from prokaryotic cells, inheriting and enhancing their exploratory ability, intercellular communication, collective behavior, “social intelligence,” and adaptability.

Earlier, many developmental biologists proposed holistic solutions of the problem of integrating factors in metazoan morphogenesis: the concepts of morphogenetic fields (Gurwitsch 1922; Weiss 1968), organizers (Spemann and Mangold 1924), gradients (Child 1941), and positional information (Wolpert 1969, 1989; Stern et al. 2006). Diffusion of the interacting morphogens (activators and inhibitors of cell differentiation) and self-organizing morphogenetic fields was the traditional assumption in modeling (Turing 1952; Wolpert 1969, 1989; Meinhardt 2006; Newman 2012). Wolpert (1969, 1989) introduced the term “positional information,” provided by gradients of diffusible morphogens and determining cell fate in relation to the position in a developing system. Now, this abstract language is translated into the molecular–genetic one: the coordinate system of the metazoan body plan, bilaterian segmentation, and left–right symmetry/asymmetry is created by the signaling pathways Wnt, BMP, Nodal, and Hedgehog as the major morphogenesis and by the mapping of the Hox/ParaHox metagenes into the anteroposterior axis (Duboule 1994, 2007; see Isaeva and Kasyanov 2021). Modern phylogenomics reveal genomic–morphogenetic correlations determining the body plan complexity and evolutionary trajectories in Metazoa. A correlation between genomic regulatory complexity and morphological complexity of a metazoan body was found (Dunn and Ryan 2015; Lang and Rensing 2015; Srivastava 2015). The Hox gene system is an important regulatory node of the genomic–phenotypic relationships, which determines a wide range of developmental processes, global body architecture, and alternative evolutionary trajectories of different bilaterian taxa (Duboule 1994, 2007; Tschopp and Duboule 2011; Srivastava 2015; Isaeva 2018; Isaeva and Rozhnov 2021). The genome-to-phenotype mapping is an extremely complex network (Koonin 2012). The relationship between genes and phenotypes is seen as a nonlinear web of events, involving pleiotropy, self-organization processes, physical forces, and environmental cues, all contributing to the final morphology of the organism (Wilkins 2002). Developmental and evolutionary transformations can involve phase transitions in gene networks (Solé et al. 2002). Gene regulatory networks and a whole metazoan genome are a unified, hierarchical network system, including many feedbacks, capable of self-organization and dynamic transformations in development and evolution.

The complexity of the living world is constrained by the simplicity of the basic laws of physics (Mandelbrot 1983; Goldenfeld and Kadanoff 1999); general principles in physics, geometry, and topology are applicable to many situations in biology (Bouligand 1996; Isaeva et al. 2008, 2012). Like all aspects of biology, self-organizing morphogenetic processes are subjected to natural selection and evolution. Evidently, biological self-organized systems are both the products of and subject to natural selection (Blazis 2002). Natural selection directed and fixed genetically biological systems capable of self-organization (Camazine et al. 2001; Kirschner and Gerhart 2005; Johnson and Lam 2010; Isaeva 2012; Isaeva et al. 2012). The living organisms inhabit and develop in the real physical space, and biological morphogenesis cannot be independent of the physical and topological properties of our space. Self-organization is a fundamental force that shapes our world and should be placed alongside natural selection as a complementary mechanism of evolution (Nicolis and Prigogine 1977; Kauffman 1993; Camazine et al. 2001; Karsenti 2008; Glancy et al. 2016). Moreover, self-organization can guide natural selection (Glancy et al. 2016). Evolution is a collective phenomenon (Goldenfeld and Woese 2011). The selection of self-organizing systems and self-constructing modules of development can increase flexibility, adaptability, and evolvability. Evolution itself is a self-developing, self-organizing process. The course and outcome of biological evolution are strongly influenced by constraints. The inevitable topological dependence and constraints of the symmetry transformations are integrated and fitted into genetically determined processes of biological morphogenesis; the physical and topological imperative restricts and directs the biological morphogenesis (Isaeva et al. 2012, 2014).

Biological morphogenesis is under strict genetic control, but shape evolution itself is a physical process; genes do not produce forms and shapes, and physical mechanisms do it (Neagu et al. 2005). Embryonic tissues are chemically "excitable media," the physical properties of which can explain some enigmatic developmental phenomena; physico-genetic determinants are essential in the evolution of development (Newman 2012). For developmental and evolutionary biology, the important physical constraint is mechanodependence (Ingber 2005; Nelson 2009; Stamenovic and Ingber 2009; Gilbert 2010; Beloussov 2012, 2015; Ambrosi et al. 2013). It is necessary to incorporate and integrate the physics into system biology (Stamenovic and Ingber 2009; Johnson and Lam 2010; Beloussov 2012, 2015). It was shown that mechanical tension is essential for the organization of the cytoskeleton and influences cell viability, proliferation, differentiation, and morphogenesis in cell systems (Vasiliev 2007; Isaeva et al. 2008; Beloussov 2012, 2015). Mechanodependent modulation of gene expression was experimentally shown, for example, for the *twist* gene expression under mechanical deformation during gastrulation in Drosophila (Farge 2003; Desprat et al. 2008). The mechanical tension that is able to activate gene expression is inherent to the morphogenetic fields of an embryo. It was found that a key link between exogenous mechanical forces and gene expression stimulation is the same in the fly and vertebrate embryos: This is phosphorylation of β-catenin and its interaction with E- cadherins of cell–cell junctions (Brunet et al. 2013). It has been demonstrated that an important regulator of the embryonic differentiation mesoderm, the gene *Brachyury*, is mechanosensitive (Brunet et al. 2013; Eroshkin and Zaraisky 2017). Thus, the mechanosensitivity of gene expression, the mechanotransduction across the cell, the cytoskeleton, and regulatory pathways involved in the expression of some genes, i.e., the molecular mechanisms that translate mechanical forces into gene expression, were demonstrated (Eroshkin and Zaraisky 2017). It was also shown that mechanical force alters morphogenetic movements and the patterns of segmental gene *engrailed* expression during *Drosophila* embryogenesis; the chromatin conformation change due to mechanical strain and mechanodependence of the gene expression during development was observed (Kumar and Shivashankar 2012). The authors concluded that the developing embryos are highly sensitive mechanical systems and suggest a link between physical modulation of cell morphogenetic movements, actomyosin reorganization, and pattern of the gene *engrailed* expression (Kumar and Shivashankar, 2012). It was shown that intracellular waves of actin polymerization and actomyosin contractility are self-organized by biomechanical feedback mechanisms (Dasbiswas et al. 2018; Wedlich-Söldner and Betz 2018). Cell migration and morphogenesis emerge from the interaction between biochemical signaling and physical forces orchestrating self-organized cortical actomyosin rearrangements, and membrane tension is an important player in the actin polymerization and actomyosin contractility (Saha and Galic 2018). Taken together, the data give evidence on mechanodependent regulation of biological morphogenesis and suggest that developing embryos comprise a collective dynamic mechanical network linking physical modulation of cellular morphogenetic movements, actomyosin reorganization, and gene expression (Kumar and Shivashankar 2012; Saha and Galic 2018; Wedlich-Söldner and Betz 2018). Thus, the morphogenetic and developmental role of mechanical stresses is recognized; tissue geometry and mechanical stress as inductive cues are entangled within the causal web of structural and functional relationships that drive developmental processes (Nelson 2009).

Topological methodology reveals a topological imperative as a certain set of topological rules, which constrains and directs biological morphogenesis (Isaeva et al. 2006, 2008, 2012, 2014; Presnov et al. 2010, 2014). The topological structure of phenotypic space gives the topological clarification of evolutionary transitions as "the topology of the possible" (Stadler et al. 2001). The inevitable topological dependence and constraints are integrated into biological morphogenesis depending on the topological organization of our space. It was supposed that some biological forms, such as branching structures, are the most functional biological design; these forms are topological attractors that evolution cannot avoid (Thomas and Reif 1993). Toroid forms also can be considered functionally optimized biological designs and attractors in metazoan morphogenesis. For example, topological methodology interpreted spherical surgeries of the metazoan body surface in development and evolution as adaptable transformations (Presnov et al. 2010, 2014). In evolution and embryonic development, the body surface of an organism (its epithelial "envelope") in most Metazoa undergoes spherical surgery(ies), which changes the topological genus of the surface, the value of which is determined by the number of through hollow channels. In the evolution of Metazoa, there was a transition from organisms lacking any through epithelial channels, in which body surface is topologically homeomorphic to a sphere, to organisms with a through the intestinal tube and the body surface homeomorphic to a torus. The epithelial body surface is the boundary layer, an interface between the internal medium of a metazoan organism and its environment. Topological and fractal transformations increase this interface resulting in better distribution of flows to and from the external medium used as the source of nutrients, oxygen, and the sink of excreta, so increasing intensity and efficiency of metabolic processes and ensuring better adaptation of the organism to the environment.

All living organisms are sustained by far-from-equilibrium conditions in their environment in the flux of energy and matter, in a "stream of order" (Schrödinger 1944; Lane 2015). Energy is central to evolution promoting the self-organization of matter, and some sort of physical channeling would also seem to be necessary to extract order from the environment (Lane 2015). The channeling similar to water mills maximized energy input (Lane 2015). It is the channeling provided through canals in metazoan organisms that ensured evolutionary energetic gains. Evolutionary topological transformations of the metazoan body surface led to the enlargement of the interface between an organism and its environment; benefits include better utilization of energy and matter from the external medium flowing through the animal organism and radical metabolic intensification.

Acknowledgments This work was supported by the Russian Scientific Foundation, the grant 19-14-00346.

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Instinct as Form: The Challenge of Bergson

6

Stephen E. Robbins

Abstract

In *Creative Evolution* (1907/1911), a pivotal discussion is the extreme complexity of instinctual behavior. As one of many examples, a member of the Hymenoptera "knows" precisely the three locations of motor-neuron complexes at which to sting a cricket such that it is paralyzed, yet remains fully alive for the wasp's larvae. Two points: (a) This behavior is as much an "irreducible" complex of *acts* as the structural organization of the wasp's body, and just as inexplicably formed by natural selection, and (b) the instinctual behavior is actually at the same level as the vital processes of the organism. This is to say that any theory of evolution, be it selection, self-assembly, or self-organization, is equally bound to address not only the origin problem of an organism's structure, but the correlated functional problem of instinct.

Instinct, however, was Bergson's prime source for holding, firstly, that we must see Consciousness as the impetus behind evolution and secondly that it is only by utilizing the essence of instinct, conjoined with intellect—his "intuition"—that mind and science can penetrate these mysterious evolutionary processes. This double thesis of the role of Consciousness and the role of intuition likely helped to cause Bergson's neglect in the biological world, but subsequently there has emerged the current sharp awareness of the "Hard Problem" of Consciousness (Chalmers, J Conscious Stud 2:200–219, 1995). The ongoing failure on a solution to this problem—its very, very unresolved status—should give us pause. In fact, integral to the argument of *Creative Evolution*, though always only obliquely referenced, was *Matter and Memory* (1896/1912), and in this work was a remarkable solution to the Hard Problem—when understood, an amazing feat of "intuition." This, we will see, casts Bergson's view of the role of Consciousness

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_6

in evolution, and the nature of instinct as one of evolution's lines of development, in a new light.

Keywords

Bergson · Instinct · Intuition · Time · Consciousness · Gibson · Affordances

6.1 Introduction

Intuition. Bergson is perhaps most famous for his emphasis on this. Intuition—this is something everyone has a feel for, understands somewhat, experiences, but as usual with Bergson it is highly doubtful this concept is understood with its radical implications for our Science. Bergson's vision of it was developed in the context of evolution, i.e., how is evolution explained, what is the "mechanism" behind it, and thus in analysis of Darwin and Neo-Darwinism. It is the salient feature of *Creative Evolution* (1907/1911; henceforth, CE). In Bergson, intuition merges with the problem of instinct, with instinct itself being seen as an inescapable problem for any theory of evolution. One cannot separate a theory of the evolution of *forms*—birds, bees, butterflies—from a theory of the instinct these forms display. These are inseparable problems.

We are going to go immediately to a pivotal point in CE. Bergson begins here on the problem of the Hymenoptera—the wasps (and sawflies, bees, ants). Per Wiki, females "typically insert their eggs in hosts." Fine, one would think this is not a problem for evolution theory. Here's Bergson:

> We know that the different species of Hymenoptera that have this paralyzing instinct lay their eggs in spiders, beetles or caterpillars, which, having first been subjected by the wasp to a skillful surgical operation, will go on living motionless a certain number of days, and thus provide the larvae with fresh meat. (Bergson 1907/1911, p. 172)

Yes, a bit gruesome, and:

> In the sting which they give to the nerve-centres of their victims, in order to destroy its power of moving without killing it, these different species of Hymenoptera take into account, so to speak, the different species of prey they respectively attack. (ib)

Continuing:

> The Scolia, which attacks the larvae of a rose-beetle, stings it in one point only, but in this point the motor ganglia are concentrated, and those ganglia alone—the stinging of other ganglia might cause death and putrefaction, which it must avoid. (ib)

And:

> The yellow-winged Sphex, which has chosen the cricket for its victim, knows that the cricket has three different nerve-centres which serve its three pairs of legs—or at least acts as if it

> knew this. It stings the insect first under the neck, then behind the prothorax, and then where the thorax joins the abdomen. (ib)

Finally:

> The Ammophila Hirsuta gives nine successive strokes of its sting upon the nine nerve-centres of its caterpillar, and then seizes the head and squeezes it in its mandibles, enough to cause paralysis without death. (ib)

How can we account for this knowledge by evolutionary "steps"? Neo-Darwinism gives us:

- Random mutations
- Carried by DNA…
- …IF the mutation has *survival value*.

We ask: an Ammophila once learned all the necessary nine strokes plus the head squeeze—all at once? And transmitted this in its DNA? Less than this, say, transmitting just one of the nine strokes—this is a NO, by definition—no survival value! How were these wasps providing for their offspring before this, how were the larvae staying alive—before this knowledge? And how is such a complex knowledge/action "encoded" in DNA?

There is, of course, the *new synthesis* position. This adds self-organization to Darwinism, where self-organization implies the self-creation of structures employing constant energy input (i.e., dissipative structures). But how does a system—an organism—"self-organize" into this *knowledge:*

- The exact three points to sting a cricket???
- The exact nine points to sting a caterpillar (plus head squeeze)???
- The precise location of the critical knot of motor neurons?

And note, *this knowledge implies the structures* (stinger, ovipositor, muscular support…) with their functionality required to support the actions implementing this knowledge.

So, the problem is inverted—function (the *concept* of the *action*) precedes structure. We are not simply "self-organizing" (or mutating) new structures which beings (like wasps) then discover are useful, say, for stinging caterpillars at precise points! We already have to account for the concept of the function, or as Bergson will term it, the *impetus* driving the birth of this function. This is to say that we need consider whether we are dealing with a problem of Consciousness, i.e., a Consciousness behind evolution. For Bergson, Consciousness is the impetus of evolution. It is for this reason that our intellect, by itself, cannot penetrate the wasp, the origin of its instinct, the origin of its structure. Why? This is what we're about to see. A bit paradoxically, we will be mixing an analysis of the problem of instinct and form with

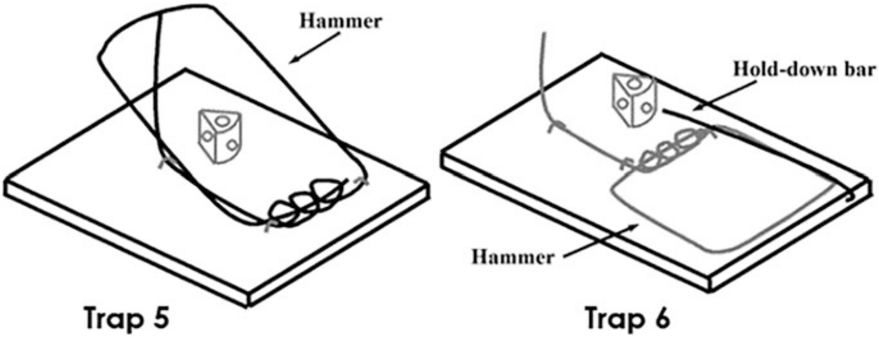

Fig. 6.1 McDonald's Traps #5 and #6

a methodological prescription to its solution based in the very nature of instinct. But firstly a couple of correlated things.

6.2 The Problem of Commonsense Knowledge

The nine stings necessary for paralyzing the caterpillar, the three stings at precise points for the cricket: Of what does this remind us? "Irreducible complexity" and Behe's (1996, 2000, 2007) mousetrap—the mousetrap being only a metaphor for the complexity of the organization of parts in an organism. The force of Behe's argument was not that one cannot imagine simpler mousetraps than say, our standard mousetrap. McDonald (2000, 2002), in fact took on the mental exercise of constructing a series of such, starting from an extremely simple trap, yet functional, to increasingly more complex versions. The force of Behe's argument was that, to evolve to a new and different form of trap, one cannot evolve (or mutate) just one part of an already functional mousetrap for the resultant new trap, given just this one change, is useless—non-functional—the one change then itself having no survival value. Or if transitioning from trap A to trap B, make one change to trap A which leaves it non-functional (until we get to B)—we need the entirety of the function changes or transformations at once. We need an interrelated set of parts/changes that create a functional whole. Consider (Fig. 6.1) the transformations required to move from one of McDonald's "fully functional" mousetraps to a next, more advanced, functional stage:

Transformation steps (partial list), from Trap 5 to 6:

- Expand platform
- Reposition spring
- Rotate hammer down
- Create slot for hold down bar
- Position hold down bar
- Create fancy release for hold down bar

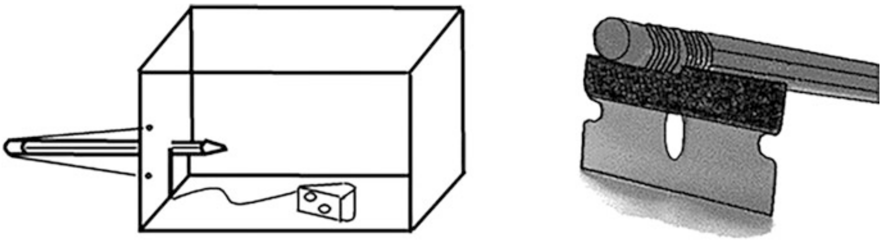

Fig. 6.2 Crossbow trap, axe for a beheading trap

Elsewhere (Robbins 2002, 2012), I argued that evolutionists, in treating this problem, have simply bumbled, with apparently no awareness, into the massively unsolved problem of AI—*commonsense knowledge*. AI oscillates from ignoring the problem to renewed enthusiasm as new developments come along. For example, LeCun (2016) expresses explicitly a new determination to solve the problem (per him, “a very old, classic problem in AI”) via deep learning networks with their many variants. In truth, the commonsense problem is simply a restatement of the “frame problem” (McCarthy and Hayes 1969) already deeply recognized in the 1960s. One can state the frame problem as such: How does a robot, watching coffee being stirred (a very commonsense piece of our knowledge of things), recognize an anomaly? Anomaly examples might be: The coffee surface erupts in geysers, or the spoon collapses and melts, or the coffee liquid periodically rises one inch above the cup and falls back. The problem is that the robot is (constantly) checking his very, very long list of “frame axioms”—things that *do not change* while this event (a “frame”) occurs—the cup stays in a stable position, the cup does not collapse, the table holds steady under the cup, the president stays the same, the sun stays up, etc. How to perform this axiom-check against this very, very long list in real time against the ongoing event? As Wheeler (2008) notes, this problem was attacked enthusiastically for 30 years, then simply “faded,” i.e., despite occasional claims that the problem was solved (which LeCun is obviously disregarding), never actually solved.

The exercise considered in the 2012 paper was creating a mousetrap out of a pile of components, say, for a partial list: a small box, rubber bands, paper clips, tooth picks, string, staples, a razor blade, a pencil, a piece of cheese. This was actually a little creativity test for engineers, and the paper was sourced originally in contemplating an AI paper by Freeman and Newell (1971) we will discuss further in a later section. The paper purported, by implication, to do this kind of thing, i.e., to *design* a device. So, back to the component list: One could construct a type of “crossbow trap” with pencil as arrow, rubber bands pulling the arrow back, paperclip locking the pencil in position, string attached to the cheese and clip. Or (Fig. 6.2) one could construct a form of “beheader,” with the razorblade and pencil forming an “axe,” rubber band providing the downward force, pencil propped up by a toothpick, string/cheese attached to toothpick, the pencil’s (non-axe) sharp end lodged in the box corner, etc.

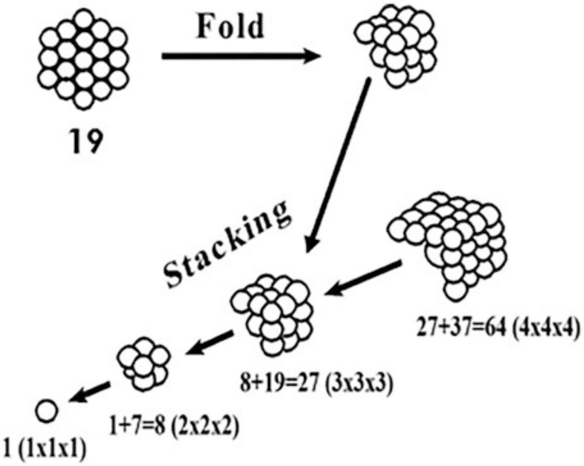

Fig. 6.3 Penrose's visual proof of a computation that does not stop: Adding two successive hexagonal numbers always results in a cubical number. A hexagonal number (like 7, 19, 37) is *folded* into a three-sided cube, then *stacked* over the previous cube, the resultant always being a cubical number

These are dynamic transformations of (visual, kinesthetic) imagery in thought. They must occur in an indivisible flow of time. This cannot be within the discrete state "time" of the computer model of mind, where, as each state arrives, the previous disappears. In this framework, there is only one (abstract) state at a time. There is no *transformation* per se, i.e., there is no basis for continuity in this abstract framework, but continuity is intrinsic to "transformations." (I'll expand these statements in a later section on the *classic metaphysic* of space and time this framework reflects.)

This point is precisely that of Penrose (1994) in his examples of "non-computational thought," a process he argued required *consciousness*, though unfortunately neither Penrose nor his many angry critics were aware of this implication of his argument. One example he gives (Fig. 6.3) is a *visual* proof of "a computation that does not stop" (i.e., the halting problem). In this, he takes a hexagonal number, folds it into a three-sided cube, then stacks this three-sided structure over the previous cube, the result being again a cube (thus a cubical number, with each successive stacking also being a cubical number). It is obvious that this process and its cubical result will never end, and it is obvious that this is a *continuous* visual event-transformation—folding, stacking—each transformation preserving certain *invariance*—cubicalness, three-sided structure, rigidity, stability, spatial fit.

The problem of consciousness and the nature of time are inseparable. Consciousness itself, as we shall explore, is an indivisible, continuous flow. This underlies the perception, shall we term it, of the *globality* of the transformation, with the various invariants being preserved. This is not possible via a discrete state machine. This is not grasped nor understood as a need by AI, consciousness being yet an epiphenomenon in its "cognitive" framework; consciousness exists, yes, but its function is mysterious, apparently unneeded. In fact, this is why *consciousness is required for true cognition* (Robbins 2009), not only for transformations upon forms in proofs, but even for the transformations of pencils while creating lowly mousetraps.

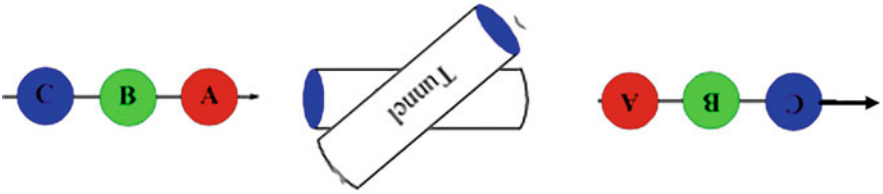

Fig. 6.4 Piaget's Tunnel-Bead Experiment. The beads (on a wire) are pushed into the tunnel, the tunnel given N half-turns, and the child is asked in which order will the beads emerge

"Continuous transformations" is a bit insufficient to cover what is intended here. We are talking continuous transformations in a perceptual (or cognitive-perceptual) *modality*—the visual, the auditory, the kinesthetic. The great theorist of child cognitive development, Jean Piaget, studied these extensively. In one example (1946), the children, ranging from ages 3–7, are shown a tunnel into which three beads, ABC, on a wire are moved (Fig. 6.4). The tunnel is semi-rotated (180°) and the children asked in which order the beads will come out (inverted: CBA). The questions are ultimately generalized: What is the order after 3 semi-rotations, after 7 semi-rotations, after 8? The abstract generalization—the invariance—is the "odd-even" rule: The order remains the same after an even number of rotations and the order changes (inverts) with an odd number (yes, again, a computation that does not stop). But the children struggle until roughly the age of seven to reach this generalization—to perceive the invariance. In the meanwhile, over the years of their developmental trajectory (i.e., over the changes of their neural organization), they are working on improving the visualizing of the semi-rotations. They will come to a point for example where they can predict the result of 3 or 4 semi-turns, but are yet lost when asked to jump to, say, 7 or 8—they cannot visualize this many half-turns. For Piaget, the eventual achievement of the odd-even rule or invariance (his "concrete operations" stage) is the result of *schematizing* these visual transformations, until they become like a little schematic experiment that does not actually have to be fully performed.

This is what is required: a "device" that supports, in multiple modalities, continuous transformations over which invariance is preserved. This is a "device" far beyond a standard computer, its intrinsic discrete time framework and its homogeneous substrate for memory (e.g., magnetic cores). Indeed, if the universe is capable of creating such contraptions as beetles (variant after variant), butterflies, or brontosaurs, it must be a far different "device" from a Turing form of "cosmic computer" employing AI-like processes for design. Yet it is not difficult to show that *the evolutionists and AI are allies,* with evolutionists implicitly, covertly appealing to AI-like processes, for the concept is apparently that these transformations of parts into new functionality, i.e., commonsense knowledge, is easily solved, in fact algorithmic. Noting Miller's (2003, 2004) concept of pools of available biological parts, Dawkins (2006) held that evolution is simply "commandeering" from these pools of biological parts and modifying them into new "devices" or forms. The concept is already there in Darwin's "exaptation":

> On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for that purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms. (Darwin, quoted by Shermer 2006, p. 68).

Though Darwin is clearly going to be no better off than Miller in coaching AI on creating programs for the design of mousetraps, in lieu of "commandeer," Shermer confidently employs the term "co-opt," as in evolution "co-opts" features to use for another purpose. For "commandeer," Scott (2004) uses "borrowing and swapping." For "commandeer," Dennett (1996) substitutes the term "generate and test," holding, with no explication, that evolution simply "generates" new devices such as flagellar motors (or mousetrap #6) to test them out. Finally, Kevin Miller (2004) himself simply uses "mix and matching" saying, ". . .it's to be expected that the opportunism of evolutionary processes would mix and match proteins to produce new and novel functions" (2004, p. 88). It is difficult to resist stating that if Dennett, Shermer or the evolutionary biologists know secretly how to program these things, if they have solved the problem of commonsense knowledge, they should be transmitting this to the folks in AI.

6.2.1 DNA and Coding "Commonsense"

There is the problem then of the transformations of forms, say, from beetle variant 1 to beetle variant 2—the implicit force of Behe's argument. But this is equivalent to *employing* these forms, using these in behavior—a human making the mousetrap out of handy materials, or, if one is a spider, constructing webs. This is the "commonsense" of spiders. One could spend much time, for an example, on the incredible complexity of spider web construction. Gunther (2012) takes us through a thought exercise, scaling up the web problem to human size. We would face stringing a web between two 90-foot-high trees separated by 300 feet. We end up employing nearly one mile of rope, casting the first line across from one tree to the other, somehow, and then creating the radial spokes, constantly adjusting the spokes for tension, and always tailoring the web, contextually, to the conditions of wind, to the precise configuration of branches from which it will be hung. Each web is thus slightly to even largely different. As a spider, we can do this from Day 1, and since the spider can do this on Day 1, all this knowledge, this ability to make contextually dependent, complex engineering feats called webs—this *instinct*—is supposedly encoded, yes, like an AI program, in DNA.

Just like the wasp, the question becomes: How can DNA possibly "code" such knowledge? One could explore the possibility of morphic fields (Sheldrake 2012), but even were these fields to explain the memory (passed from spider generation to generation), they could not explain the *initial creation* of the ability. There was Spider #1, and Wasp #1. We are forced to the beginning—to Consciousness.

6.3 Consciousness, the Hard Problem, and Evolution

If there is a deepest theme in CE, it is: Consciousness is the impetus behind the explosion of forms in evolution. My suspicion is that the role of Consciousness in CE is considered "interesting" at best. It does not carry close to the weight it should. Why? Because *Matter & Memory* (1896) is the foundation of CE, and the difficulty is that M&M and its significance was little understood. Even by its admirers, its concept of perception was considered "obscure." This is because it was a holographic theory, fifty plus years before Gabor's 1947 discovery. It was elegant, yet abstruse, well beyond Pribram's (1971) attempt to use the holographic concept, and anticipating but well beyond Bohm's approach (1980). It was, as well, a solution to the Hard Problem—before the Hard Problem was (somewhat) understood or "announced" (e.g., Chalmers 1995). In CE, it is amazing how minimal is Bergson's explication of his M&M model of consciousness and perception, barely a, "I said things on this in another work…".

The Hard Problem is still not understood. But this problem is key, the salient problem of our times, hovering over physics with QM's measurement problem and over the whole endeavor of AI! It is interesting to ask: Suppose this problem and Bergson's solution were really grasped and accepted? Would CE then be weighed far more seriously? *This* is the problem: If consciousness is merely an epiphenomenon, a mere "phosphorescence from the brain" (as Bergson described this materialist position), all is just *matter*, and Consciousness cannot be the impetus of evolution, rather, it is just a result. But if not an epiphenomenon, then, particularly in Bergson's framework, we have something else entirely.

The Hard Problem, as stated by Chalmers (1995), is generally this: Given some neural or computer architecture, i.e., given chemical-neural flows or changing bit patterns, how does this architecture account for the qualia of the perceived world? Here "qualia" is generally construed as "the redness of a sunset," the taste of cauliflower, the feel of sandpaper, the brown and cream color of a coffee surface. These are somewhat "static" qualities, but this is typical: Time is not considered a problem in this literature. Though the term qualia was not used by Chalmers in 1995, this was the import. The emphasis since Chalmers has been on explaining qualia or qualities, or "why things 'feel like' something."

This has been a misdirection: The problem is more generally stated as that of explaining *the origin of the image of the external world*. There is nothing in our image of the world that is not qualia, to include its dynamically changing forms—rotating cubes, buzzing flies, swirling coffee liquid and stirring spoon. Witness Hardcastle's description of qualia: "…the conductor waving her hands, the musicians concentrating, patrons shifting in their seats, and the curtains gently and ever-so-slightly waving…" (Hardcastle 1995, p. 1). Here, we see form as qualia too, in fact, dynamically changing form, for all qualia exist only over time; all qualia is *dynamic*. The experiential image of the orchestra Hardcastle is describing is entirely qualia, to include, and especially include, its dynamically changing, qualitatively changing forms—as equally non-computable as the colors and sounds. It is the image of the external world that must be explained—that coffee cup, "out there,"

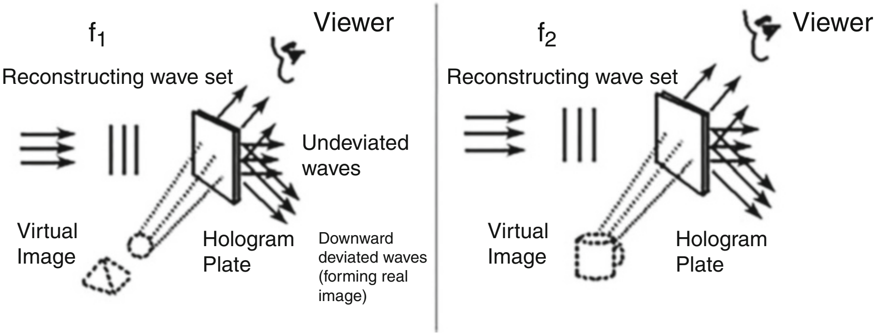

Fig. 6.5 Modulating the reconstructive wave. Modulating the reconstructive wave to frequency 1: The original wave front (object wave) from the pyramid-ball is specified. Frequency 2: The object wave from the cup (the original source) is specified. The holographic plate becomes the universal field; the brain is the wave passing through this "plate."

on the table, liquid surface swirling. This has been the dilemma: Neuroscience certainly has found nothing like the image of the coffee cup with its swirling surface and circling spoon in the brain, nor does such a thing exist in a computer with its changing bit patterns (save by pure conceptual *attribution*, e.g., "this bit pattern must be, or correspond to, a coffee cup").

Bergson addressed this exact question, in 1896, in *Matter and Memory*. Surely, he noted, there is no "photograph" of the external world in the brain. The neuroscience of the day was already sufficient to know this—no image of the coffee cup was anywhere to be found in neural structures. But he noted, if one examines the implications of Leibniz and his monads, or better, Faraday and his atoms, each atom being the nexus, the intersection of lines of force in every direction from all other atoms in the universe, one must be led to this conclusion, ". . .the photograph, if photograph there be, is already developed in the very heart of things and at every point of space." (Bergson 1896/1912, p. 31) This was his declaration, years before Bohm (1980), that the universal field is a *holographic field*. When one draws out the implications of M&M's subsequent theoretical development, upgrading it into current terms/concepts that have been birthed subsequent to holography's discovery, this describes his vision of the role of the brain: In essence, the brain is *a modulated reconstructive wave*, passing through this holographic field, specifying or "specific" to a source within the field (Fig. 6.5)—the coffee cup and stirring spoon (Robbins 2000, 2002, 2004, 2006, 2013, 2017, 2020). There is no image being developed or being represented in the brain; the coffee cup is being specified right where "it says it is," external to the body, on the table top, within the holographic field.[1]

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[1] The brain's modulation pattern is driven by the external event, specifically by the dynamic structure of invariants defining the event. For stirring coffee, a partial list of such: (1) a radial velocity flow field over the swirling liquid surface, (2) an adiabatic invariant—the ratio of energy of oscillation to frequency of oscillation for the spoon, (3) an inertial tensor defining the momenta of

A fly "buzzing by" the coffee cup, his wings beating at 200 cycles/s, is perceived with its wings as a *blur*—this being an index of our "normal" *scale of time*. This scale of time is determined by the brain's dynamics, its underlying chemical velocities, themselves underlying the brain as a very concrete, resonant wave form. Other scales can be specified: increase the chemical velocities: the fly becomes heron-like, barely flapping his wings. Note too: This specification is to the *past*, to past portions of field's transformation, for any light reflected from the fly, striking the retina and transduced through the perceptual system is now "long ago," long in the past when taken relative to the presently specified fly. How is this possible?

This is where Bergson's conception of time must be factored into the picture. Briefly, for we must return to this, he argued that motion, say, an object's motion from point A to B, cannot be treated as a series of static, discrete states, as though we are simply carving up a space—a line or trajectory we visualize from A to B—into points, each point corresponding to an "instant" of time. This is an infinite regress. Between each pair of static points on this line, to account for the motion, we must re-introduce yet another line of points—ad infinitum. In other words, we are applying *a principle of infinite divisibility*. This is the source of Zeno's paradoxes. Rather, motion must be seen as *indivisible*. Thus, the transformation (motion) of the ever-changing holographic field is indivisible. There are no discrete instants, where each "past" instant is falling into the past (non-existence). Rather the field is inherently 4-D.

And this is the kicker, where we meet that larger, that Cosmic scale Consciousness. For, taken at the "null scale" of time (the most minute scale imaginable), the transforming holographic field inherently carries elementary attributes of consciousness. Firstly, there an elementary awareness defined throughout the field via its holographic property, for the state of each "point" in the field reflects that of every other point; thus, there is an elementary awareness at each point of the Whole of the field. Secondly, there is an elementary memory via the field's indivisible transformation, for state of each moment or "instant" is reflecting the entire history of the Whole.

Thus, the specification (by the brain as a reconstructive wave) is to *a time-scaled form of the elementary awareness defined over the field*. As Bergson stated, "*…questions of subject and object, in their distinction and the union, must be treated in terms of time, not space*" (Bergson ib., p. 77). At the null scale of time—the smallest scale, the "tiniest instant" imaginable—one can see that our body has no sharp differentiation, spatially, from the field or, for that matter, from a fly within the field. But specify increasingly larger scales: The fly changes from, say, a cloud of electrons to a motionless vibrating, crystalline being, then to a heron-like fly barely flapping his wings, to the "buzzing" being of normal scale. Subject is differentiating from object, in terms of time. The homunculus (or the observer's eye, the viewer, in Fig. 6.5) is removed.

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the spoon, (4) a ratio of cup height to position on the surface texture gradient, etc. This is where Bergson merges with J. J. Gibson (1966).

So, yes, this is a panpsychic theory, but a theory that has no "aggregation problem," i.e., no need for answering this: How do tiny "proto-conscious" particles aggregate or combine to become an experienced coffee cup and spoon, and (though no one notes this piece of the problem) at some particular scale of time? As well, it is a theory, as opposed to standard panpsychism, that actually has the wherewithal—a dynamical mechanism—to explain the origin of the image of the external world. Standard panpsychism has nothing such.

Our individual consciousness, then, is a flowing aspect of/within that larger, flowing Consciousness, the Consciousness defined over the ever-transforming field. The individual aspect is specifying from a unique spatial perspective and specifying a scale of time placed upon this larger whole. So, this is a significance of which to take note: already in M&M, *in the context of the one solution to the Hard Problem that exists when the problem is actually understood*, *we see the Consciousness—Cosmic scale—that Bergson sees as the impetus behind evolution* and which is the force behind both the knowledge (instinct) of the wasp, and the formation of the wasp as an organic structure.

For Bergson, our intellect is incapable, in and of itself, of understanding this process, this knowledge (instinct), the organic formation of structure. What is the nature and origin of intellect? Why must it be augmented, augmented in fact nearly paradoxically, by something equivalent to, if not itself sharing in instinct? It already starts in the nature of perception.

6.4 The Intellect, the *Classic Metaphysic*

The holographic field is a vast field of information. Bergson visualized this field as a vast sea of motions or "real actions," all forming a vast (holographic) interference pattern. Any given object acts upon all other objects in the field and is in turn acted upon by all other objects. It is in fact obliged:

> . . . .to transmit the whole of what it receives, to oppose every action with an equal and contrary reaction, to be, in short, merely the road by which pass, in every direction the modifications, or what can be termed real actions propagated throughout the immensity of the entire universe. (Bergson 1896/1912, p. 38).

What is the principle for the selection of a subset of this and its specification as an image, say, as a coffee cup? From this information or real actions, our body selects only that (the subset of real actions) related to its action capabilities. Highly correlated to J. J. Gibson's (1966, 1979) "affordances," what is specified and selected from the real actions is now "virtual action"—how the body can act, and at a specific scale of time. A fly specified as barely flapping his wings is indicative of different action possibilities relative to the normal "buzzing fly." Speaking of organisms as centers of action in this field, Bergson would state, ". . .the real action passes through, the virtual action remains." Thus, per Bergson, perception is *virtual action*.

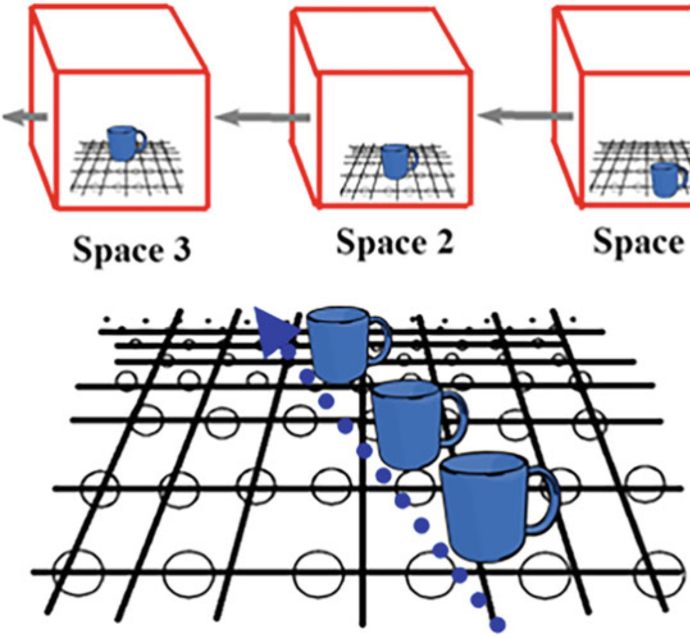

Fig. 6.6 Successive positions of the moving cup across the continuum of points/positions. Each point/position of the cup corresponds to instant of the all of Space

From this undifferentiated, ever-transforming field, our body's first order of business is to carve out "objects" on which it can act—to hold a baby bottle, to shake a rattle. Thus begins the partition of the field into "objects" and their "motions."

This partition gets ever more rarified. Beneath and through the surrounding field we place a (mental) mesh as it were (M&M). The meshes are made ever smaller; we end with *the continuum of points or positions.* As noted, the "motion" of an object from point A to point B is now treated as a series of points comprising a line or trajectory though this static continuum. And as noted already, this is an infinite regress. Between each pair of static points on the line, to account for the actual motion, we must re-introduce a new line with its points, ad infinitum. Each point, further, corresponds to an "instant" of time. "Time" is simply the fourth dimension of this abstract space, the series of static instants.

If we take one these instants/positions of the moving object, we can take it as a point in the "all of Space" at an instant, where this "all of Space" can be visualized as a huge Cube (Fig. 6.6). As the limit of the division operation is a mathematical point, each Cube of Space, corresponding to a point on the object's trajectory, has the time-extent of a mathematical point. Each Cube is thus utterly stripped of quality—homogeneous. This aspect of this overall conceptual framework on space and time is the *start* the "whence qualia?" problem (Robbins 2013). In fact, we could note, as did Lynds (2003), each Cube is frozen, never to change again—unless some extra agent or "force" is envisioned to create the next Cube and then the next, etc. (To Descartes, seeing this implication, this had to be where God was needed.) This is the *classic metaphysic*. This is the playground of our intellect. All our science, our mathematics, our calculus—based upon it.

But this conception is further rarified. The motions are *relative*. One can move the object across the continuum of points/positions, or one can move the continuum (or coordinate system) beneath the object. Motion becomes *rest*, merely upon perspective. Thus, all *real*, concrete motion is lost. But there must be *real* motion. Stars explode, trees grow, roses bloom. Thus, Bergson would argue, we must see the Whole is changing, like a kaleidoscope. In this, the "motions" of "objects" become, rather, *changes or transferences of state*, like waves in the ocean, within this global transformation.

In such a global transformation, there is clearly simultaneity. Biologists should take note: *It is in organic motion that the classic metaphysic, with its intrinsic relativity, most clearly fails and falls*. The blooming expansion of a rose cannot be relativized. The branching growth of a tree cannot be relativized. If for a "stationary" observer, two opposite petals of the blooming rose strike equidistant points simultaneously, the fact that a physicist, in motion, passing the rose, taking an instantaneous cross section of this motion (an abstract "instant"), says "not simultaneous"—this is totally irrelevant, an artifice of the abstraction; it cannot possibly be so without destroying the simultaneous flows of the organic growth, the integral blooming process of the rose. Einstein's famous lightning bolts, simultaneous to a stationary observer, supposedly non-simultaneous to a moving observer, when both bolts are generated simultaneously from a massive, organic storm system with all its complex forces—the "non-simultaneity" (supposed per one observer) is equally an abstract artifice, without reality (Robbins 2010, 2014a, b). In this, we see an example of Bergson's (in CE) critique of Kant and Kant's vision of a unified structure of science, where the classic metaphysic, in essence, is applied to physics, to biology and to psychology—*uniformly, across all subjects*. But the essence of CE (we shall visit the why of this in closing) is that the classic metaphysic, as it describes and is applied to the extended world of matter, is only an *ideal limit—never actually reached*. This metaphysic works for physics—practically, to a large extent, though not entirely. Applying it to the biological and psychological takes it increasingly beyond its applicability.

With the classic metaphysic, it all started with solids—with our perception parsing those "objects" upon which we can act.

> Let us start then from action, and lay down that intellect aims, first of all, at constructing. This fabrication is exercised exclusively on inert matter. . .And of inert matter itself, fabrication deals only with the solid. The rest escapes by its very fluidity. (Bergson 1907/1911, p. 153).

He adds:

> If therefore the tendency of the intellect is to fabricate, we may expect to find that whatever is fluid in the real will escape it in part, and whatever is life in the living will escape it

> altogether. Our intelligence, as it leaves the hands of nature, has for its chief object the unorganized solid. (Bergson 1907/1911, p. 153).

To the intellect, we are surrounded by a material field—extended—objects (absolutely distinct) external to other objects, parts external to parts. Each part infinitely divisible—all treated as units. The "objects" (solids) are certainly mobile. But from the motion itself the intellect turns away.

> But the intellect is meant for something altogether different. Unless it does violence to itself, it takes the opposite course. It always starts with immobility, as if this were the ultimate reality. When it tries to form an idea of movement, it does so by constructing movement out of immobilities put together…Of immobility alone does the intellect form a clear idea. (Bergson 1907/1911, pp. 154–155).

Of course, he notes, "Motion as a series of immobilities is an absurdity."

This homogeneous, empty medium, infinitely divisible, lends itself to any mode of decomposition:

> This space is therefore, preeminently, the plan of our possible action upon things… the intellect is characterized by the unlimited power of decomposing according to any law and it does so by constructing movement out of immobilities put together. (Bergson 1907/1911, p. 155).

The "symbols" we use in language, logic, are themselves derived from solids.

> As these symbols are derived from the consideration of solids, as the rules for combining these symbols hardly do more than express the most general relations among solids, our logic triumphs in that science which takes the solidity of bodies for its object [geometry]. (Bergson 1907/1911, p. 160).

Intellect behaves as if fascinated by inert matter. "Hence its bewilderment when it turns to the living and is confronted with organization." (Bergson 1907/1911, p. 161) And just as it fixes in things in space, it fixes in time. It cannot deal with pure mobility. Again, the series of static "instants"—the actual motion is lost.

This framework rejects *creativity*. All is the *re-composition of static elements*—of the already old. "The intellect is characterized by a natural inability to comprehend life." (Bergson 1907/1911, p. 163) The intellect is only an aspect, a cutout, of the larger, flowing Whole; therefore, it cannot be that which comprehends this Whole.

6.4.1 Instinct

So, he states: "Instinct, on the contrary, is molded on the very form of life. While intelligence treats everything mechanically, instinct proceeds, so to speak, organically." (Bergson 1907/1911, p. 165). He adds:

> For [the consciousness driving it] only carries out further the work by which life organizes matter—so that we cannot say. . .*where organization ends and instinct begins*. (Bergson 1907/1911, p. 165, emphasis added)

Again, I repeat the starting question: How is the organic structure of the wasp separate from the "concept" of the action [instinct] it will be performing? So he says, "The most essential of the primary instincts are really, therefore, vital processes." (Bergson 1907/1911, p. 166).

The cells of our body, all working for a common end, yet each living for itself, preserving itself, reproducing itself, like so many instincts, each cell instinctual. The bees and their hive—each bee a "cell" united by an invisible bond. A bee separated, even given food/water, dies. The "instinct" that animates the bee is indistinguishable from the force that animates a cell. Here, instinct coincides with "organization"—organizing matter.

> Thus the instinctive knowledge that one species possesses of another on a particular point has it root in the very unity of life. . .a 'whole sympathetic unto itself'.(Bergson 1907/1911, p. 167).

Instinct and intellect are two divergent lines of evolution:

- Intelligence = > fluid composition/decomposition of inert matter.
- Instinct = > Within itself, totally embedded in the concrete.

Perception is an example: The intellect asks, "How is it we see the coffee cup 'out there', on the kitchen table?" We understand touching the cup. The light hitting the retina—like a touch! But seeing the cup "out there," at a distance, is literally *action at a distance*. Yes, it is the same problem Newton had with his own theory of gravitation: It relies upon an abhorrent (to him) unexplained effect of one object upon another a distance away—action a distance—through no medium of transmission. So, starting with the light touching the retina, our intellect begins constructing mechanisms, logic, computer programs, neural nets—to effect all this *inside* the brain (or computer). Witness AI and self-(seeing)/driving cars, Elon Musk, etc., etc. But the "image" of the coffee cup is now "inside" the computer (i.e., the bits being attributed to be such), while the coffee cup is seen as "out there," on the table. Action at a distance still reigns—and unsolved.

Bergson simply says here, in CE, "But we have shown elsewhere that. . .the philosophical explanation of perception. . .must be of another kind." (Bergson 1907/1911, p. 168). But we have seen what he is so vaguely referring to, namely, the holographic/reconstructive wave model of M&M, where the coffee cup is *specified* right where it says it is—"out there," within the external holographic field. So we know what this massively "of another kind" means.

> Thus the instinctive knowledge that one species possesses of another on a particular point has it root in the very unity of life. . .a '*whole sympathetic unto itself*'. (Bergson 1907/1911, p. 167)

So how does the wasp solve the “construction” of this instinctive behavior? It does so by sympathy. It is a sympathy between the wasp and its victim, a sympathy which teaches the wasp from within the caterpillar’s vulnerability.

> This feeling of vulnerability might owe nothing to outward perception, but result from the mere presence together of the Ammophila and the caterpillar, considered no longer as two organisms, *but as two activities*. (Bergson 1907/1911, p. 173, emphasis added)

“Objects” in “motions” (the wasp, the caterpillar) are changes or transferences of state within the global motion of the Whole. Each—the wasp, the caterpillar—are two flows, or two *activities*, in the larger, global flow. This is the basis for the operation of instinct. This instinct is not resolvable in terms of intelligent elements, or even in terms necessarily intelligible. But it is not beyond the limits of *mind*.

6.4.2 Intuition

Instinct is sympathy. It is oneness with life, union with other beings, w/all Being. Intelligence dwells on the surface of life with its “objects,” with the infinity and composability of their relations.

> But it is to the very inwardness of life that intuition leads us—by intuition *I mean instinct that becomes disinterested*, self-conscious, capable of reflecting on its object and enlarging it indefinitely (Bergson 1907/1911, pp. 175–176, emphasis added).

This simple sympathy is possible to mind, for there are no true spatial separations in the ever-transforming holographic field. The wasp is one with the caterpillar—as two activities, two flows within this single Flow. This is the basis; it extends to all beings, even to scientific theorists. What Bergson is saying: To take our Science to another stage, to penetrate the instinct (the mysterious intelligence) of the wasp, to penetrate evolution’s formation of the organic structure of the wasp, humanity itself must move to a new evolutionary stage. Pure intellect alone is a dead-end stage of one evolutionary line. Humanity and Science must move to intellect guided by intuition. How science solves the origin of instinct and form (and their inescapable and intrinsic correlation)—this in essence will merge with the very form of sympathy (intuition) by which instinct itself solves problems.

Intuition, let us simply note here, is not all that mystical or mysterious when put into practice. Yes, it can be exemplified in meditation practices, where, as an example, for many a session, one intently contemplates a tree as the object of meditation, to the point where—as meditators have reported—one experiences oneself *as the tree*, sap literally flowing through one’s being, branches growing, leaves budding. But Bergson describes the process more mundanely: It can be absolute immersion in a subject—for years—reading, absorbing everything within it, contemplating a problem within the subject constantly. In other words, merging with the subject.

If there is an example, it certainly would be Bergson's own model of perception. Once one understands it, one can only stand back in complete awe. In his brief descriptions of how Life might form a being, or an eye, one says, "Wow, to go further, deeper, more detailed…this will take one heck of an intuitive absorption." To give a very brief idea of what I mean…

6.4.3 The Eye

The eye is massively complex—"an infinity of mechanisms." *Mechanism* attempts to explain the putting of all these "parts" together, gradually, by chance, with no ability to explain their correlation. *Finalism* sees all the parts brought together by a pre-conceived plan. Like a workman constructing a watch. (Finalism would correspond to the Intelligent Design position.) Beyond both: "Life does not proceed by the association and addition of elements, but by dissociation and division." (Bergson 1907/1911, p. 89) Note the extreme contrast—the simplicity of vision, the complexity of the eye. "…[this complexity] may be only the simple act of vision, divided for us into a mosaic of cells, whose order seems marvelous to us because we have conceived the whole as an assemblage" [of those so-loved "parts"]. (Bergson 1907/1911, p. 90)

> Nature has had no more trouble in making an eye than I have lifting my hand. Nature's simple act has divided itself automatically into an infinity of elements which are then found to be coordinated to one idea…just as the [in fact, indivisible] movement of my hand [from point A to point B across the continuum of points/positions] has dropped an infinity of points which are then found to satisfy one equation. (Bergson 1907/1911, p. 91).

This is what our intuition must penetrate.

6.4.4 To Return: Creating Mousetraps and Wasps

In the literature of the new (or extended) synthesis, Stuart Kauffman appears in some ways very Bergsonian. Kaufmann (2013) states: "No law entails the evolution of the biosphere."

One key to this, he argues:

> We cannot name all the causal consequences or uses of any object, say a screwdriver, alone or with other objects. The set of uses appears to be both unbounded or "indefinite", and on-orderable. But this means we cannot know that we have ever "listed" all the uses of a screw driver alone or with other objects or process. (Kaufmann 2013, p. 519)

So, this looks very much like the commonsense knowledge problem I described that afflicts AI, to include the creation of mousetraps from components. My own thought on this began years ago in contemplating the implications of a program for "design" by Freeman and Newell (1971). Here, a database, so to speak, was contemplated listing *objects* and their *functions*, specifically, for each object, the object's functional *requirements* and functional *provisions*. To design a KNIFE, the program discovered (in its database) that a BLADE provided "cutting" (a functional provision) and it has a functional requirement, namely, "being held." Matching to the functional requirement, a database search found HANDLE (which has a functional provision of "holding"); a "match" was made, a KNIFE was "designed."

The difficulty (of many), again, is that these functional provisions/requirements emerge only over transformations. The "provision" of the box corner for "holding" (or "lodging") the pencil when it is employed as an "axe-handle" would hardly have been prelisted as a functional provision in a database, assuming a "box corner" was even a database entry, nor that the box-side has a functional provision for anchoring the rubber bands for the pencil-arrow. Again, trying to generalize this, from functions to "features" brings the same problem. A sock may be "floppy," but under a forceful swatting transformation, displays the needed "rigidity" to squash a fly. "Features" emerge over transformations. Needless to say, one cannot imagine a database with all possible transformations on objects. These cannot be pre-set, pre-defined.

But worse, these transformations must occur in that time that is an *indivisible flow*, and this again brings us back to Bergson's model of individual conscious perception—the brain, as a modulated reconstructive wave, intrinsically embedded within the indivisible transformation of the holographic field, specifying a past transformation of the field—coffee being stirred. This *individual* model is telling us the basis on which we must scale to the universal problem of evolution, and the creation, not of mousetraps, but of biological devices—birds, butterflies, bees.

Kaufmann adds:

> Now consider an evolving cell in which one or more objects or processes, each with myriad causal consequences, finds a novel use that we cannot prestate, but which enhances the fitness of the cell, and so is grafted by natural selection into the evolving biosphere. This "finding of a novel use that we cannot prestate" occurs *all* the time. The famous flagellar motor of some bacteria made use, via Darwinian *preadaptations or exaptations*. . .of fragments of its flagellar proteins that were serving entirely different functions in other bacteria. (Kaufmann 2013, p. 519, emphasis added).

"Exaptation." This (and other names) was precisely what we saw the evolutionists (Kevin Miller, Dennett, Shermer, Dawkins. . .) all use to implicitly appeal to a form of (cosmic) AI program, as though they've solved the problem of commonsense knowledge. Kauffman would have to be saying that exaptation is nothing like AI, and requires an entirely different form of cosmic "device." But, unfortunately, he says all this is effected by natural selection. Not possible. We are back to the problem of irreducible complexity: The mouse trap must have all the parts to be functional, to be selected. And—the wasp must know *all* the places to sting the cricket.[2]

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[2] Since this writing, Kauffman and Roli (2021) have argued in terms of affordances not being computable, or "UTMs [Universal Turing Machines], at least those not embodied, cannot find new

When we created the “crossbow mousetrap,” it was done so on the basis of a *knowledge about a desired function* (to kill, disable, or trap a mouse) and on *knowledge of the mouse*—how it can be killed (cut off head, pierce it) or be trapped given its action capabilities (we must make a “prison cell” trap). This knowledge about both mice and the intended function was integral in creating some form of trap. Equally so, even were Dr. Kauffman to create a wasp from components, there is still that knowledge (manifesting as “instinct”) that was guiding the design, e.g., the vulnerability of the caterpillar (for the stinger), nest creation, nectar slurping, what the young need. This still must be addressed and accounted for; it is still part of the problem of creating mousetraps, wasps or beetles.

So, Kauffman holds:

(a) Natural selection still works, is operative.
(b) Irreducible complexity is not a problem.

Why b? Intelligent Design proponents argue via the massive improbability of natural selection selecting all the changes simultaneously. But Kaufmann argues, given there is “no law of evolution” and the unforeseen uses of parts, probabilities can no longer be computed; we don’t know the “space.” This is an easy escape route. Too easy. Examples abound where things are just mathematically fixed. In the case of proteins, we know the space. There are 20 amino acids, they can only be joined in, say, 2035 ways that will get a string that is 35 amino acids long—a peptide. There is not any question as to what the space is.

The difficulty is the same for the pencil. There is an enormous number of possible functions:

- Pungi stake
- Spear
- Axe handle
- Pillar/support
- Fuel/fire
- Fork
- Stirrer
- Prison cell bar

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affordances,” though elsewhere they state, “. . .we are not merely embodied UTMS.” “Affordances” have tended to carry a precise meaning in ecological psychology discussion as a relation (mathematical) between bodily action capabilities and the environment, e.g., “climability” as the ratio of stair riser height to knee height. Extending this usage to a pencil poking a mouse or a box corner securely lodging the pencil seemed a bit too much of an extension, and in 2002/2012, I stayed in the standard framework of functional provisions, properties, etc. Further, the affordance term tends to obscure the structure of invariance laws at their core. Kauffman and Roli, I might note, in their analysis, still think finding affordances is possible by natural selection, and more critically, are unaware of the classic metaphysic of space and time at the core of these problems.

- Baton
- Etc.

You cannot state *all* the uses of a part, but you can make a huge finite list for each, and assign probabilities of use. Then you quickly get the massive joint improbability of selecting the correct uses for the combination of all the different parts required for the total transformation. But we have seen already that this is only the beginning of the problem: One cannot pre-define all the possible transformations under which functions or features emerge.

Kauffman is trying to save natural selection [per (a)] as the mechanism—a virtual algorithm—for evolution. A lost cause. The unforeseen uses of "parts" by evolution—yes, exactly, but the universe must be a far different form of creative device—nothing like a Turing computer. The transformations on these parts—transformations that must occur over an indivisible time are a fatal enough problem for any mechanistic [abstract space-based] conception of this, but notice, the "parts" themselves are no longer simply the "same part." The pencil is no longer truly a pencil, the box corner is far from a simple "corner." Thus part of this difficulty is the very focus of science on "parts"—on *reusing* parts, on *rearranging* parts—to create new devices. This is to say, in this framework, there is no room for *true creation*. Bergson would note:

> . . .if after the fact *we could know these causes in detail*, we could explain them by the form that has been produced; *foreseeing the form* is out of the question. (Bergson 1907/1911, p. 27, emphasis added)

But "causality" is a creature of the classic metaphysic:

> Such is the case with astronomical, physical and chemical facts, with facts which form part of a system in which elements supposed to be unchanging and merely put together, in which the only changes *are changes of position*, in which there is no theoretical absurdity in imagining that things are restored to their place, in which, consequently the same elementary phenomena can be repeated. (Bergson 1907/1911, p. 27).

The billiard ball model is the standard paradigm here: We apply the "same" forces, the "same" vectors, to the "same" billiard ball: We get the same path for the ball, over and over, and this is deemed a "law." But NONE of these things are actually the same from instant to instant. The billiard ball is not the same, the cue is not the same, the force is not the same—only *practically* the same. It is a practicality that largely works for physics, astronomy, chemistry, but increasingly less so as we move toward the biological. Nothing is actually the "same" in a universal field that is constantly changing, no matter how small the interval of time examined. Thus:

> But against this idea of the absolute originality and unforeseeability of forms our whole intellect rises in revolt (Bergson 1907/1911, p. 27). . .[for to our science]. . . "*What you call an unforeseeable form is only a new arrangement of old elements"* (ib, p. 30)

For Science, the epitome of intellect. . . .

> . . .in dealing with things, science is only concerned with the aspect of repetition. Though the whole be original, science will always manage to analyze it into elements or aspects that are absolutely a reproduction of the past. (ib, p. 27).

But this is only possible in the abstract space and the abstract time (again, a dimension of the abstract space) of the classic metaphysic—an absolutely homogeneous, perfectly repeatable continuum. And this metaphysic is the child of the intellect. And this intellect is only a *cut out*, an *aspect* within the ever-transforming Whole of the universal field. This is why intellect *must* be augmented by intuition. But this should be placed in the context of Bergson's larger vision of this evolving Whole.

6.4.5 Bergson's Larger Vision of the Transforming Field

This transforming Whole is both physical and psychical. In Bergson's framework, it has two aspects: the *extended* (matter) and the *in-extensive* (the psychical). The in-extensive pushes forth, so to speak, *continually*, both as the emerging forms of evolution and more mundanely, as the everyday (and at every instant) extended world of matter. This is to say this impetus, this creation, is *continuous*. As noted, the refined, logical extension of the extended world—the abstract space expressed in the classic metaphysic—is but the *ideal limit* of this thrust; it is never truly reached, but extended matter comes close enough for the geometric method of physics to, by and large, work very well, but ever less so as we move back upwards so to speak, away from this ideal limit, toward the original impetus or source, first into the biological and further upwards, to the psychological.

Bergson noted that this "impetus" driving evolution is but a metaphor/image. It is the essence of the psychical to enfold a confused plurality of interpenetrating terms. The psychical elements within a dream are not truly separable—these do not exist in an abstract space. The complex psychical state of a Beethoven while he imagined the fifth symphony is not something describable using independent "elements." It appears to be so only afterward, as this intermingled complex of interpenetrating "elements" is expressed with a quill pen in the extended world of matter as separate "notes" on a manuscript. Only in [abstract] space is distinct multiplicity possible. "But what is psychical cannot entirely correspond with space, nor enter perfectly into categories of understanding." (Bergson 1907/1911, p. 257).

Certainly, this is not the framework of materialism. Biology can wait, fruitlessly I would predict (Robbins 2014a, b), for the quintessential expression of the materialist framework and its spatial metaphysic—AI, neural networks, deep learning networks—to solve the commonsense knowledge problem and effect true creativity, or one can accept that we are dealing with, indeed, *creative evolution*, and that to deal with this reality we need a new framework, a new metaphysic, namely, the temporal metaphysic of Bergson, yes, even a model of consciousness incorporating a solution to the hard problem. When this larger framework on the universe is grasped, one can see that for comprehending and penetrating evolutionary development, it becomes a fundamental necessity to meet this requirement: the achievement of a higher union of the two evolutionary lines—of instinct, of intellect. This takes the form of intuition—to which intellect becomes the scribe and expositor.

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Part II

Modernity of Self-Organization and Emerging Paradigms

Biological Evolution of Microorganisms

7

Werner Arber

Abstract

Life on our planet earth must have started with quite simple unicellular organisms. Nowadays we have a large number of their evolutionary descendants in the world of microorganisms. We report here on scientific investigations with harmless intestinal bacteria which serve the scientists to explore molecular genetic processes of biological evolution. This research leads to the conclusion that biological evolution occurs in microorganisms by consecutive steps of genetic variation. This historical advance can be attributed to a process of self-organization that contributes to the permanent creation of appropriate biological capacities.

Keywords

Bacteria · Molecular genetic processes · Biological evolution · Self-organization

7.1 Introduction

Astrophysical evidence leads to the notion that our solar system with its planets must have an age of approximately 4000 million years. Traces of living organisms indicate the presence of single-cellular microorganisms already about 3500 million years ago. So far, we do not know how the existence of such primitive organisms came to be on our planet earth.

Bacteria are a large group of single-cellular microorganisms. We generally assume that in the course of 3500 million years consecutive steps of biological

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evolution led on the one hand to the rich variety of bacteria with different biological functions and, on the other hand, to all kinds of other living organisms including plants and animals. Many different kinds of bacteria exist on our planet mainly at and near its surface and in the depth of the oceans. Of importance for the human health conditions are, on the one hand, cohabiting bacteria carrying out in microbiomes (Blaser et al. 2013) essential functions for our life processes and on the other hand, pathogenous microorganisms (some bacteria and viruses). Experimental and theoretical studies carried out in the twentieth century with microorganisms provided to us essential insights into the chemical nature of the genetic information (DNA) and its molecular functions and evolution processes. Some details on the thereby acquired knowledge will be presented in the following sections.

7.2 Molecular Genetics of *Escherichia coli* Bacteria and Their Phages

Intensive research has been carried out with a few related strains of nonpathogenic intestinal *E. coli* bacteria and their viruses (bacteriophages or shortly phages). Almost all genes of *E. coli* bacteria are carried on a single circular DNA molecule, i.e., on the bacterial genome. Some strains may, in addition and for some time, also carry one or a few plasmids. These are in general also circular DNA molecules and they carry just relatively few genes. An example is the genome of phage P1 in P1-lysogenic bacteria (Sengstag and Arber 1983). Some other phage genomes (e.g., phage lambda) can, upon infection, become incorporated into the host genome which renders the host cell also lysogenic (Arber 1960). Lysogenic bacteria can spontaneously, or by experimental induction with UV irradiation, produce progeny phage particles with the genome of their carried prophage. A prophage is the phage genome carried in lysogenic bacteria.

For many kinds of experimental investigations, *E. coli* bacteria can become efficiently propagated in different kinds of liquid media at about 37 °C. Under good growth conditions, the bacteria replicate their genome and undergo cell division where each cell receives a newly replicated genome. These conditions, with rapid growth facilitate experimental investigations on occasional genetic variations in single cells of the growing population.

7.3 Mechanisms of Genetic Variation in Bacterial Genomes

Series of experimental investigations revealed a number of specific molecular processes to produce a novel genetic variant. Genetic variation is the driving force of biological evolution by occasionally enabling a bacterial strain to adapt to an alternative growth medium which is not accessible to the parental strain of bacteria. In this context, the direction of biological evolution taken by a novel genetic variant is dependent on the kind of new growing condition used by the variant cell. This situation is called “natural selection”, a term introduced by Charles Darwin.

A multitude of so far known mechanisms of genetic variation can be attributed to three natural strategies of genetic variation (Arber 2007):

(a) Occasionally occurring alterations of one or a few adjacent nucleotides of the genome can be brought about upon the DNA replication at sites of a short-living tautomeric form of a nucleotide that has another pairing specificity than its stable form (Watson and Crick 1953). Tautomeric adenine pairs with cytosine and tautomeric guanine pairs with thymine. A point mutation results if this replication error escapes a repair process shortly after its production.

(b) The second strategy of genetic variation is the occasional transposition of a mobile genetic element within the genome (Arber 2007). Depending on its new insertion site, transposition can contribute to the formation of a new functional fusion product. Different kinds of mobile genetic elements are widespread in bacterial strains and they can also exist in other living organisms. Their transposition is under the control of the enzyme transposase, which is their own gene product. In favor of a high genetic stability, the expression of the gene for transposase may become under serious control. This became obvious in experimental investigations with the mobile genetic element IS30 (Arini et al. 1997). In front of its reading frame for the transposase we found, to our surprise, a normally active transcription promoter segment and it starts actively the production of messenger RNA. But with a probability of 50%, a terminator segment stops the messenger synthesis early. The other half of synthesis complexes stop regularly at the end of the expressed gene. But a majority of the full length messenger RNA becomes quickly inactivated by the production of antisense RNA that can block the functional expression of the transposase. Therefore, when IS30 is present, it has a relatively high genetic stability and IS30 transposition is a rare event.

(c) The third natural strategy of genetic variation is the horizontal gene transfer. This process is widespread in bacterial populations and it also occurs in other living organisms. Horizontal gene transfer between bacteria can be brought about by several different processes. In transformation (Avery et al. 1944), free DNA molecules liberated from a donor cell can become taken up into a genetically different receptor cell, which sometimes integrates the transferred genetic information into its own genome. Horizontal gene transfer occurs also by bacterial conjugation (Lederberg 1947), when a donor cell associates by cell contact with a receptor cell and actively transfers a copy of its genome to its partner cell. In this process, the receptor cell can often profit from the use of a hitherto lacking genetic capacity having been developed and functionally used in another organism. Still another process of horizontal gene transfer occurs by transduction (Morse et al. 1956). Transducing bacteriophage particles carry along DNA segments from a former host bacterium. After infection of a new host bacterium, the latter can sometimes maintain and use the received genetic information.

Still other genetic variants can originate under the activities of environmental mutagens such as some chemicals or by irradiation.

7.4 Bacterial Restriction and Modification Systems

In the context of horizontal gene transfer by bacteria, it is good to know that many bacterial strains are genetically equipped with a strain-specific restriction-modification system. This phenomenon had originally been encountered when a phage grown in a bacterial host was used to infect another bacterial host strain. In this case, only very few progeny phages became produced and liberated upon cell lysis. These few progeny phages now grew normally upon reinfection of their second host, but they became strongly restricted in their previous host. This phenomenon was tentatively attributed to properties of the phage, but it remained unexplained.

In the early 1960s we could show that upon infection of an alternative host strain, the DNA of the infecting phage becomes relatively rapidly degraded (Arber and Dussoix 1962; Dussoix and Arber 1962). This degradation is not limited to phage DNA. The responsible restriction endonuclease cuts any invading foreign DNA into fragments which then become acid solubilized by the host enzyme DNA exonuclease. Restriction thus also acts upon conjugation (Arber and Morse 1965), transformation, and phage-mediated transduction (Arber 1965).

In the meantime, restriction endonucleases became isolated from many different bacterial strains (Roberts et al. 2015) and their restriction activities revealed a few principle mechanisms. In general, foreign DNA becomes recognized at short-specific sequences of nucleotides. Many restriction enzymes cut the foreign DNA at its recognition sites, whereas other restriction enzymes become activated at the recognition sequences and cut the foreign DNA more randomly elsewhere.

Restriction enzymes make no harm to the DNA of their own bacterial host thanks to methylating (Kühnlein and Arber 1972) all of its recognition sites. This explains also the rare survival of infecting restricted phages and of occasionally acquired DNA markers originating in another bacterial strain. We can interpret this natural phenomenon as follows: In the wide population of bacterial strains, great care is being taken not to mix up DNA from various different genomes. However, by a fast methylation of some recognition sequences on invading foreign DNA, the restricting bacterium can occasionally take up a short properly modified foreign DNA segment in its own genome. Such an acquisition of a foreign gene that had already proved its functional capacities in the donor strain can, in some cases, be welcome for the life activities of the restricting host.

Bacteria can sometimes possess and express more than one restriction/modification system. Relevant genes for a specific restriction/modification system have become known to be located on the genome of the transducing phage P1. As we have already discussed, in P1-lysogenic bacteria, the prophage is propagated as a plasmid. Interestingly, in the P1-lysogenic situation, bacterial host strains express besides their own restriction/modification activities, also the restriction/modification activity expressed by the P1 prophage (Lark and Arber 1970). Similarly, it has become known that occasionally another bacterial plasmid can carry and express another specific restriction/modification system.

7.5 Role of Restriction Enzymes in Structural and Functional Genome Analysis and Genetic Engineering

As we have already discussed, upon infection of restricting bacteria with foreign DNA, the latter becomes fast cut into fragments. Restriction endonucleases of type II cut the invading foreign DNA at all of its short DNA sites recognized by the restricting host. In in vitro experiments with purified restriction enzymes, the resulting fragments of foreign DNA can be separated according to their size by gel electrophoresis. This methodic approach has become a welcome help in structural and functional studies of DNA molecules in order to reveal their functional specificities. In genetic engineering, specific knowledge on transferred functions is of importance for the safety of in vitro horizontal gene transfer (Berg et al. 1975).

7.6 Evolution Genes and the Duality of the Bacterial Genome

Referring to the bacterial capacities to occasionally produce a genetic variant, specific gene products are involved either as variation generators or as modulators of the frequency of genetic variation. Their activities ensure on the one hand that various rare genetic variants become present in bacterial populations and, on the other hand, that a relatively high genetic stability is characteristic for bacterial populations. This situation ensures that a growing bacterial population has the capacity, thanks to the occasional presence of appropriate genetic variants, to adapt to alternative nutritional environments without losing its inherited essential growth capacities.

When it became obvious that at least some of the genes acting as variation generators or as modulators of the frequency of genetic variation could lose by mutagenesis their evolutionary characteristics without affecting the normal propagation of the concerned host bacteria (Wood 1966), we decided to call the genes contributing to the evolutionary development “evolution genes” (Arber 2005). This situation indicates that the bacterial genome has a duality: A majority of the genes are essential for the daily life activities of the bacterial cell, whereas a minority of the genes serve for the biological evolution by ~~paying attention~~ not ~~to~~ seriously affecting the genetical stability of the concerned bacterial population. It is obvious that only a few gene activities can exert their biological functions both in favor of the cellular life activities and for the bacterial evolution.

7.7 Self-Organization of the Biological Evolution of Microorganisms by Permanent Creation

As we have already discussed before, extensive molecular genetic studies carried out with bacteria and phages have revealed their capacities to adapt their functional activities stepwise to newly encountered environmental conditions. However, there is no indication that these primitive organisms could identify a specific functional need and actively fulfill it upon their contact with a novel alternative living condition. Rather, any growing population acquires in the course of time a number of different genetic variants not causing any functional harm to the relevant cells. One or a few of these mutants may by chance fulfill a novel functional requirement and propagate under the novel growth conditions. We are aware that this procedure corresponds to single steps of biological evolution of the concerned microorganism. On the other hand, an occasionally produced genetic variant may sometimes by chance improve an already existing biological function.

Different kinds of microorganisms that exist today must have a very long history of many million years undergoing occasionally steps of their biological evolution to reach their different specific functional capacities. This process can go on in future times. As we have already discussed it, a number of specific processes can contribute by genetically determined activities to such historical advances. This is a permanent process of self-organization (Arber 2019) of the biological evolution of these haploid and thus relatively simple living organisms. Their actual presence is not to explain by a single step of creation. Rather, we can explain their present functions by a natural process of permanent creation during many million years.

7.8 Conclusions

Research investigations with *Escherichia coli* bacteria revealed genetically exerted capacities to occasionally adapt to alternative living conditions. The latter can either be another kind of growth medium- or longer-term functional cooperations by cohabitation with other types of living organisms in so-called microbiomes. Bacteria are able by self-organization not only to occasionally adapt to novel functional capacities, but also to insure maintenance of the inherited functions in a large majority of the cells of the given bacterial strain. On the short-term, bacteria are able to stepwise adapt and to exert new functions by maintaining a majority of the parental genome in a stable condition. This generalized conclusion from the data available today should merit additional systematic investigations involving many bacterial strains and many living conditions including various growth media and cohabitations with various other living organisms.

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Self-Organization in Embryonic Development: Myth and Reality

8

Stuart A. Newman

Abstract

"Self-organization" has become a watchword in developmental biology, characterizing observations in which embryonic or induced stem cells derived from animals replicate morphological steps and outcomes seen in intact embryos. While the term was introduced in the eighteenth century by the philosopher Immanuel Kant to describe the goal-directed properties of living systems, it came into modern use for non-living materials in which complex forms and patterns emerge through dynamical, energy-expending physical processes. What is the relationship among these uses of the term? While multicellular forms arose dozens of times from single-celled organisms, only some of these undergo development, and not all developmental processes are self-organizing. The evolution of the animals (metazoans) from unicellular holozoans was accompanied by the addition of novel gene products which mediated the constitution of the resulting cell clusters as liquid-, liquid crystal-, and solid-like materials with protean morphogenetic propensities. Such materials variously exhibited multilayering, lumen formation and elongation, echoing the self-organizing properties of nonliving matter, "generic" based on such parallels, though with biologically based subunit properties and modes of interaction. These effects provided evolutionary starting points of and templates for embryonic forms and morphological motifs of diverse metazoan lineages. Embryos and organ primordia of present-day animal species continue to generate forms that resemble the outcomes of these physical effects. Their development, however, employs overdetermined, highly evolved mechanisms that are often disconnected from their originating processes. Using the examples of gastrulation,

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somitogenesis, and limb skeletal development, this chapter provides instances of, and a conceptual framework for understanding, the relationships between transparently physical and evolved types of developmental self-organization.

Keywords

Gastrulation · Somitogenesis · Limb development · differential interfacial tension · Clock-and-wavefront · Turing-type process · Evolution · Homomorphy

8.1 Introduction

A series of findings beginning in the 1980s, including ones arising from improved cell culture methods, comparative phylogenomics, cellular and genetic manipulation of embryos, and progress in understanding the dynamical and other physical properties of multicellular materials, led to the mostly unacknowledged disappearance of the notion of a "genetic program" from the theoretical discourse in developmental biology. This idea, inspired by the rise of the digital computer in the 1950s and the associated hardware–software distinction, attempted to locate the information acquired during phylogeny in each organism's nuclear DNA, where it was deployed in a hierarchical fashion during ontogeny (Istrail et al. 2007; Peluffo 2015; Sarkar 1998). What increasingly replaced the computer program model was the concept of "self-organization," whereby complexity of form and pattern (usually, but also potentially of function) emerges from apparent simplicity due to interactions of unorganized components. This term had already been in use in the physics of materials of the meso-, or middle-scale, "soft matter" (de Gennes 1992) such as viscoelastic fluids, and "excitable media" such as complex chemical and mechanochemical systems (Elphick et al. 1990). In a sense, the conceptual change echoed the centuries-old transition from preformationism to epigeneticism that had been played out in the pre-genetic, pre-evolution era of biology (Van Speybroeck et al. 2002).

Some findings from the fields mentioned above which led to changes in how development and its evolution were conceptualized included:

(i) The capacity to generate and maintain stably differentiated cell types, as well as early embryo- and organ-like structures, in culture. These depended on identification of soluble growth factors such as Wnt, TGF-βs, and FGFs and extracellular matrix (ECM) molecules such as collagens, fibronectin, and laminin (Gospodarowicz 1984; Gospodarowicz et al. 1986; Hay 1991; Massagué 1987). Later it was shown that members of the same set of factors could elicit differentiated cell types and early embryonic structures ("gastruloids") from both embryonic stem (ES) cells and induced pluripotent stem (iPS) cells (Beccari et al. 2018; Hanna et al. 2008; Hoffman and Carpenter 2005).

(ii) Advances in sequencing techniques and comparative phylogenomics, which led to the recognition that these same growth and ECM molecules were among a few dozen conserved members of a phylogenetically conserved "developmental genetic toolkit." The products of these genes were found to induce changes in form and pattern in embryos across the full range of animal phyla (Carroll et al. 2004).

(iii) Visualization of gene expression in whole embryos, which showed that given toolkit gene products could be involved in the formation of morphological characters that were both homologous (e.g., the legs of different vertebrates) and analogous (e.g., the legs of mice and of flies) across phyla. This "homology-analogy paradox" (i.e., anatomical analogs are not homologs, but the molecules that mediated both could be homologous) was difficult to reconcile with the widely accepted notion of the evolutionary continuity of purported genetic programs (Newman 2006).

(iv) Mathematical and computational models of cell movement and differentiation in response to toolkit gene products, which consistently found that physical determinants such as differential adhesion, reaction–diffusion ("Turing-type") processes, and oscillations in gene expression provided the most coherent and convincing explanations of the relationships between gene action and morphological phenotype (reviewed in Forgacs and Newman 2005).

(v) Genetic manipulation, including full and conditional knockouts and overexpression, which indicated that gene function could be decoupled from morphological outcome in ways difficult to reconcile with the program notion. The discovery of "constructional unit autonomy" and "developmental system drift" pointed to a similar phenomenon of gene-morphology decoupling over evolution (Müller and Newman 1999; True and Haag 2001).

(vi) The formation of chimeras from mammalian species as evolutionary distant as sheep and goats, which diverged 14–16 Mya by some estimates. Blastomeres of these species could be mixed together to produce healthy full-term animals of intermediate phenotype (Fehilly et al. 1984). This was exceedingly difficult to reconcile with a genetic program notion since chimeras are cellular mosaics of the two originating species. The cells (unlike those of hybrid organisms) retain their species-specific genomes along with whatever additional cytoplasmic information is used for development and read each other's signals in constructing an evolutionarily unprecedented animal. No conventional definition of computational programs would admit of this kind cooperation among fortuitously associated entities.

Despite this evidence against the genetic program notion, the concept of "self-organization" as applied to embryogenesis or organogenesis is nonetheless ambiguous. It is not identical to the claim that physical processes underlie morphogenesis, which is an uncontested assumption of modern biology. Something more is implied by using the term "self-organization" instead of simply "development." Machines are physical entities contrived to produce specific outcomes. While organisms and their constituent processes are not machine-like (Nicholson 2019), their structure–function relationships are often difficult to discern, not least because their protein constituents are often intrinsically disordered and alter their roles based on conditional interactions with other components (Uversky and Giuliani 2021; Niklas et al. 2015). Machine analogies are often a recourse of convenience.

Complex materials can undergo morphological changes over time and arrive at a reproducible endpoint that might not resemble anything else in nature. This is true of certain minerals, as well as the developing tissues of plants and fungi. The morphogenetic mechanisms that produce flowers, pinecones, and gilled mushrooms are poorly understood, but there is no reason to doubt that are physical processes. Under certain conditions they produce patterns of exquisite mathematical regularity that have plausible physical interpretations (Douady and Couder 1992; Azpeitia et al. 2021). It is possible that these systems are "self-organizing" in the sense of being mesoscale, excitable materials with physically explicable, reliable outcomes. But the enigmatic physical nature of plant and fungal tissues as growing, deformable solids makes this difficult to establish.

Physical organizing processes and effects, and corresponding morphological outcomes, have been termed "generic" if they are common to both living and nonliving materials (Newman and Comper 1990). While even non-generic physical processes can be self-organizing, it is only for systems with generic properties that self-organization can feasibly be confirmed to be an important mode of development. This is because generic processes are governed by known physical principles with predictable outcomes. The possibility that generic processes were active during the periods when a lineage's morphology first arose in evolution can also provide insight into why they look the way they do.

In this chapter, I define "physical self-organization" (or "self-organization" for short) in conformity with the classical usage in physics: the generation of geometric structures or chemical patterns by dynamical interactions of unorganized components. The outcomes of such processes, also referred to as "dissipative structures" (Goldbeter 2018), only occur in thermodynamically open systems, in which there are fluxes of matter or energy across the boundaries. Physical self-organization is distinguished from "self-assembly," the fitting together of a system's components (as in protein quaternary structures) that does not involve such system-environment exchange (Halley and Winkler 2008). Since, as noted, generic processes pertain to living as well as nonliving systems, in the former cases, where the generic physical mechanism (e.g., the random motion of subunits in a liquid-like material; see below) depends on a biological, rather than a nonbiological, function (undirected cell motility vs. Brownian motion in this example), the term "biogeneric" is used (Newman 2016a).

In contrast to multicellular plants and fungi, aggregative microorganisms such as the cellular slime mold *Dictyostelium discoideum* and the bacterium *Myxobacteria xanthus* present uncontroversial examples of physical self-organization, employing generic processes (Fujimori et al. 2019; Fukujin et al. 2016; Wu et al. 2011). But even in these seemingly simple systems, interpretation of morphogenetic processes is confounded by the capacity of individual cells to act as autonomous agents, with apparent goals of their own, a feature not seen in nonliving matter (Arias Del Angel et al. 2020).

Regarding the animals, the subject of this chapter, the liquid-like nature of their embryonic tissues imposes coherency and collective behaviors on their cells. This affords possibilities of generic-type self-organization, as does the ability of such tissues to serve as excitable chemical and electrical media. In the discussion here, processes internal to individual cells, including those driving their random motion or regulating the expression of genes, and the bases of fluidity and excitability, will be "bracketed" with no attempt to explain them. Development will only count as self-organized in this framing if it is attributable to physical processes that act on the multicellular, rather than the subcellular level.

Newer in vitro culture techniques which permit isolated embryos or aggregates of embryonic or induced pluripotent stem cells to develop along normal pathways have permitted detailed investigations of developmental capabilities and subsystem interactions. Development of "embryoids" or "gastruloids" initiated from stem cells under these conditions is often taken as evidence of self-organization (Bedzhov and Zernicka-Goetz 2014; Beccari et al. 2018; Etoc et al. 2016). But simply because an embryo can be removed from its normal gestational setting and in the presence of appropriate nutrients execute the same set of steps it does in vivo, does not mean it is exhibiting physical self-organization. It could be behaving as a more complicated (because highly evolved) or causally obscure (see below) physical assemblage.

This is true even if the starting point of in vitro embryogenesis is a collection of embryonic ES or iPS cells. After all, such cells are derived from organisms that emerged as distinct mammalian species millions of years ago and retain their respective species-specific genomes when reverted to the stem-state. It would be surprising if they had not evolved the means to recover the morphogenetic routines characteristic of their type. The kind of self-organization exhibited, however, is not the physical variety, for which complexity is a truly emergent effect. It is rather the restorative behavior of a highly evolved, complex "self."

While the fact of evolution thus complicates the ascertainment of self-organization, the possibility of such effects, particularly if they have generic properties, can provide insights into the processes of evolutionary innovation. In the older "genetic program" picture, an organism's developmental mechanisms were presumed to have evolved gradually by random mutation and selection, with no role for the material properties of the forming tissues. Although organisms with programmed development could potentially result from such a random search, they might resemble the self-constructing contrivances theorized by the mathematician John von Neumann (Von Neumann and Burks 1966). Such machines would be vanishingly likely to arise and could only operate to produce the requisite forms if all their parts assumed their precisely evolved relationships. In contrast, if self-organization of tissue masses plays a part in embryogenesis, or once did in a lineage's phylogenetic history, pathways of morphological evolution would have had preferred directions and predictably achievable outcomes, contrary to the logic of undirected Darwinian natural selection.

In the next section, I show how physical self-organization in fact helped to kick-start the evolution of developmental systems. I describe how animals and their tissues arose from ancestral holozoan cells that were recruited into multicellular entities by the products of a specific, evolutionarily assembled genetic toolkit. These masses of cells constituted parcels of novel fluid-like living matter with unique morphogenetic propensities. In the subsequent section, I discuss three examples from vertebrate embryogenesis: gastrulation, somitogenesis, and limb skeletogenesis, which have been proposed, with experimental evidence, to employ various generic physical processes to realize their morphological outcomes: differential adhesion, a biochemical oscillation in conjunction with a molecular gradient, and a Turing-type reaction–diffusion standing wave-generating system.

My goal is to show that whereas generic physical processes typically continue to be involved in the developmental events, they are not always, or in all relevant species, equally, the decisive factors in morphogenesis. In consequence, they are not generally explanatory of the observed developmental phenomena. If this is correct, descriptions of purported self-organization of stem cell embryoids and gastruloids, which are increasingly prominent in the developmental biology literature, are misleading regarding mechanistic understanding. In the concluding section, I suggest that only with an analysis incorporating an evolutionary dimension, i.e., a recognition of how development in an extant species reflects the originating processes of its lineage followed by their reconfigurations and transformations, can we hope to comprehend in causal terms how the morphological phenotype is realized.

8.2 Metazoan Matter: Physical Bases of Self-Organization

For the concept of "self-organization" to be nontrivially different from "development," the forming structures should emerge de novo from unstructured precursor materials by known effects with generally predicable outcomes. The non-self-organizational alternative would be the playing out of the morphogenetic potential of a complex, composite material that has evolved to unfold in certain ways. Animal embryos generally fit the second description. Do they partly conform to the first?

The animals are members of Holozoa, a phyletic group which also includes unicellular and transiently colonial organisms. Premetazoan holozoans are inferred to have contained cadherin-like cell surface proteins (Nichols et al. 2012). In the transition to the metazoan form of life some of these proteins acquired a cytoplasmic domain that mediates attachment to the cytoskeleton. The resulting "classical" cadherins are exclusive to the animals, and some of the cytoplasmic adaptor proteins of the linkage are also animal-specific (Abedin and King 2008).

Materials composed of subunits (e.g., atoms, simple molecules, polymers, or cells) that have strong affinity for one another while readily changing their neighbors are defined as liquids (Widom 1967). The homophilic adhesive function of classical cadherins, with their unique transmembrane–cytoskeletal connection that permits the cells of metazoan embryos and organ primordia to move relative to one another while remaining attached to their changing neighbors, causes the cell clusters to behave like liquids (Foty et al. 1994; Steinberg 2007; Miller et al. 2013). Unlike nonliving liquids, however, where nanoscale subunits change position by Brownian motion (which is independent of their internal structure), for liquid tissues, the active mechanochemical processes of the (macroscopic) cells' interiors are essential to drive their random movement.

In determining whether embryos and organs develop by self-organization rather than by some alternative, complex, mechanistically obscure set of physical processes, we can ask whether the morphological features that appear during ontogenesis are among the inherent modes of this liquid-tissue "ground state." For example, in nonbiological liquids, mixtures of subunits which are sufficiently different in composition (e.g., adhesivity) can undergo phase separation, forming immiscible layers (e.g., oil and water) (Flory 1973). If the subunits have nonuniformly distributed interactive properties ("binding polarity") lumens or interior spaces can form. Further, liquids whose subunits have asymmetric shapes can form liquid crystals, droplets of which become oblate or elongated rather than (as in more typical liquids) spherical (Yang et al. 2005).

All these liquid phenomena—multilayering, cavity formation, reshaping of masses, and some additional behaviors of this state of matter—spreading on (or "wetting") solid substrata, and "jamming," a liquid-to-solid phase transformation in which the subunits move closer to one another (Bi et al. 2011), halting their relative movement—are features of embryonic development, though not all of them in every phylum. As noted, the subunits of liquid-like tissues are motile cells, and the gene products responsible for the strength of their mutual adhesion and their binding and shape polarity are well known. These gene products did not appear all at once during evolution, but sequentially, with the present-day descendants of earliest emerging animals, marine sponges, placozoans, cnidarians, and ctenophores having some, but not all of them. Organisms in these groups are correspondingly morphologically simpler than ones such as arthropods, mollusks, and chordates (including humans) that have fuller genetic toolkits (reviewed in Newman (2019b)).

With demonstrable liquid-like properties and structural motifs that resemble those seen in liquids, it is reasonable to expect that animal embryos and organ primordia would generate their forms by known physical means. However, as mentioned above, this supposition is often incorrect. For example, development can deviate from generic physics owing to the capacity of the cellular subunits to actively participate in morphogenetic processes. Rather than simply moving in random directions (the prerequisite for their aggregates behaving as liquid-like materials) they act as signaling and reactive centers (Forgacs and Newman 2005) and differentiate into specialized types (Newman 2020).

The capacity of cells to differentiate is a feature of animal development that previously had been thought to be based on generic physical effects. Specifically, the panoply of specialized cell types—a few in sponges and placozoans and more than 200 in mammals—was proposed to be the mathematically determined dynamical modes of behavior of the respective genomes. Genes regulate other genes in all forms of life and are thus organized into gene regulatory networks, or GRNs. These systems can be modeled as Boolean switching networks (BSNs) in which genes turn one another on or off at successive discrete time steps based on the states of their input genes at the previous time step, or as ordinary differential equations (ODEs), where both the time progression and concentration of gene products are continuous variables. Formally, both kinds of networks exhibit multiple stationary modes of activity or dynamical "attractors," in which the concentrations of the system's components (e.g., gene products or on-off states) are unchanging over time, or cycle among a small subset of the possible states of the system. Since transitions are possible between such attractor states, these generic mathematical representations were proposed to reflect the properties of genomic organization, with the dynamical attractors providing the explanation of the existence of cell types (Kauffman 1993).

More recent work, however, has led to the recognition that the physical basis of cell differentiation in animals is not generic in the sense defined here. Specifically, the system of expression hubs in which functionally related genes are partitioned into insulated nuclear regions (topologically associated domains: TADs) by a combination of the mechanics of chromatin fibers and phase transformations of associated transcription factors and scaffolding proteins (Furlong and Levine 2018; Newman 2020) has no nonbiological counterparts. Some of the proteins involved, and the distant gene regulatory sequences known as enhancers, which congregate in TADs in up to the thousands in differentiated cells, are specific to metazoans, not even being present in other holozoans. The lack of stoichiometric and mass action relationships among cell-type-specific genes and their molecular regulators, as well as the transience of the causal nexuses in which they are involved, make BSN or ODE representations applicable to these GRNs at most on in a local (lineage-adjacent) sense, but not on the level of the global "regulatory genome" (Peter and Davidson 2015). Moreover, it is highly implausible that a system of physiologically coordinated cell and tissue types could be produced as a purely mathematical consequence of the balance of effects leading to dynamical attractors (Newman 2020).

But even if generated by processes that by most definitions are not self-organizing, differentiated cell types can be induced and spatially patterned by self-organizing processes acting on a multicellular scale. The resulting arrangements, in turn, can trigger additional self-organizing processes. Some of these effects resemble ones seen in nonbiological systems. A simple case is the appearance in some embryos or developing organs of a specialized group of cells that secrete a "morphogen," a molecule that causes other cells to change their states depending on concentration or duration of exposure. The transport of the morphogen away from its source can be by diffusion (Yu et al. 2009), a generic process, or by something more complicated and cell dependent (Ben-Zvi et al. 2011). A more complex case involves the coupling of molecular transport (however it may be mediated) across spatial domains with the biochemical responsivity (excitability) of cells of those domains. This can produce nonuniform patterns such as standing waves (i.e., spots or stripes) of molecular concentration, followed by periodic distributions of an induced cell type (Kondo and Miura 2010).

Processes of this sort (often referred to as "Turing-type" owing to a paper in which the mathematician A.M. Turing proposed them as "the chemical basis of morphogenesis"; Turing 1952), a paradigmatic example of self-organizing pattern formation in nonliving systems (Castets et al. 1990; Boissonade et al. 1994; Ouyang and Swinney 1991), have been proposed to underlie patterning of digits in the vertebrate limb (Newman and Frisch 1979; Zhu et al. 2010), pigment stripes and spots of animal skins (Kondo and Asai 1995), and hair follicles (Sick et al. 2006). As we will see below, however, actual developmental patterning mechanisms, while they may have originated in the form of these generic ones, are typically evolutionary transformations of these mechanisms into more elaborate, mostly non-generic ones.

Other seemingly generic physical effects, e.g., phase separation of tissue layers by differential adhesion, and segment formation by the interaction of synchronized biochemical oscillations and tissue gradients ("clock-and-wavefront" mechanisms), have also been transformed over evolution, and are differently realized in different lineages, sometimes being supplanted by very different mechanisms (Newman 2019a; Haag and True 2018). A theoretical rationale for such divergences is that if a layered or a segmented morphology becomes intrinsic to the organism's identity, conserving the forms will impose constraints on retained genetic changes, leaving the structural motif (layers, segments, or endoskeletal elements such as digits) in place as the developmental process evolves into something more complicated or entirely different (Müller and Newman 1999; Newman et al. 2006).

Finally, as mentioned, the living cells of developing embryos and organs, though participating in the reorganization of liquid-like materials, are not physically passive like the subunits of nonliving liquids. The reactive and agent-like natures of these entities will therefore complicate attribution of generic self-organization to morphogenesis (Arias Del Angel et al. 2020). This agential behavior has many intersecting determinants and an obscure evolutionary history. As noted above, autonomous cell behavior is important in the development of organisms, both non-metazoan eukaryotes and prokaryotes, in which multicellularity is achieved by aggregation. In more complex forms in which multicellularity is achieved zygotically, individual cell agency is more restricted. In plants, although extensive cell–cell communication is employed via plasmodesmata during development and growth, the presence of encapsulating walls curtails cell autonomy and thus agency. In animal embryos, directed cell movement and other autonomous behaviors are also less prominent than in aggregative forms, but always remain a possibility, and are sometimes employed, in the generation of animal form and pattern.

8.3 Evidence for and Against Developmental Self-Organization

In this section, I discuss three embryonic processes in animals: gastrulation, segmentation, and endoskeletal patterning, for which there is good evidence from in vitro studies for self-organization of the generic type. I will also describe evidence from in vivo, or other in vitro studies that challenge these attributions. Apart from these contrasts, I make no attempt to provide a detailed account of these developmental events. Each of these embryological phenomena occurs in invertebrate as well as vertebrate organisms, but the examples I explore are all taken from the latter group.

8.3.1 Gastrulation

Gastrulation is the formation and arrangement of distinct tissue layers during the establishment of the body plan in early animal development. About half a dozen distinct kinds of cell behavior are employed, depending on the species (see Fig. 8.1, top panel, for the zebrafish case), and each requires a differentiation step that

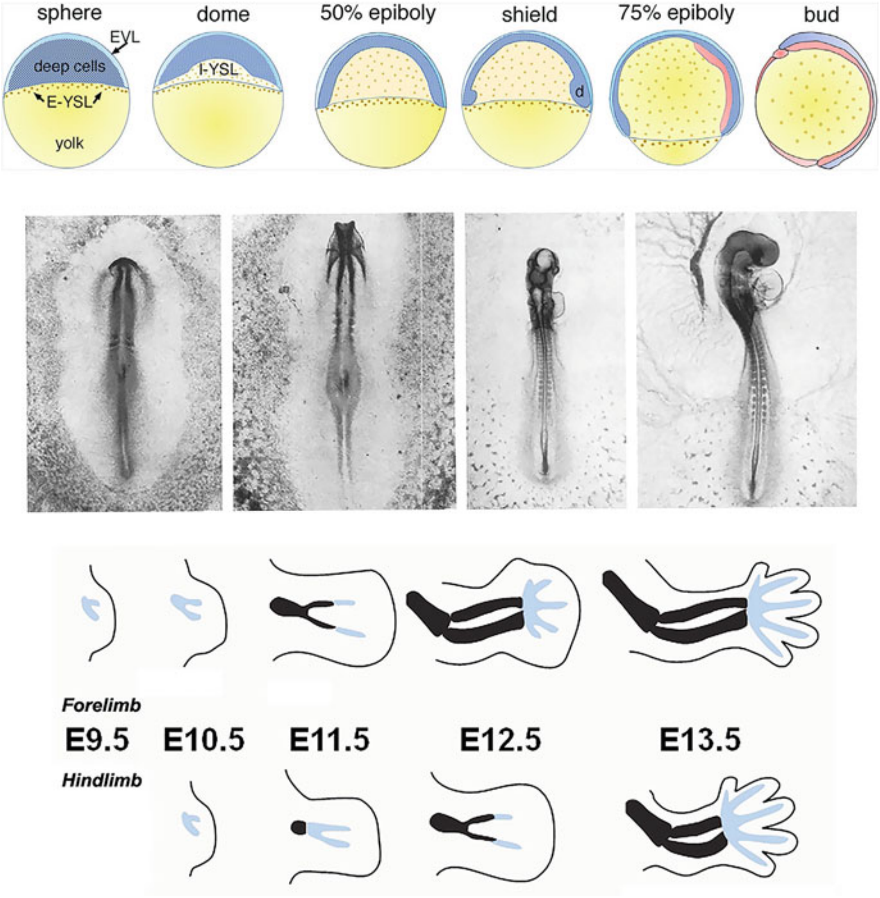

Fig. 8.1 The three embryonic systems discussed in this chapter. Top panel, drawings of successive stages (left to right) of gastrulation in a zebrafish embryo, beginning from the formation of the interface between the germ layers at 4 h postfertilization to the envelopment of the yolk cell layer by the blastoderm at 10 h postfertilization. (Reprinted from Bruce and Heisenberg (2020) Mechanisms of zebrafish epiboly: A current view. *Curr Top Dev Biol* 136: 319–341, used by permission of Elsevier.) Middle panel, photographs of chicken embryos during the period of somitogenesis (26–53 h; 8–22 somites). (Adapted from Hamburger and Hamilton (1951).) Bottom panel, drawing of cross-sections of upper and lower embryonic mouse limbs between 9.5 and 13.5 days of development. Gray shading represents precartilage mesenchymal condensations, and black shading cartilage. (Adapted from Taher et al. (2011).)

designates a subpopulation of the original clump of cells derived from the zygote (variously, blastula, morula, inner cell mass) as distinctive. Often the defining character is an adhesive differential that causes the subpopulation to be more, or less, cohesive than the other cells of the mass (reviewed in Newman (2016b) and Forgacs and Newman (2005)).

How the different cell populations are established during gastrulation may depend on maternal determinants stored in the egg, or external cues during oogenesis or gestation. Self-organization may also be involved in the early stages of cell allocation: some evidence points to one or more Turing-type reaction–diffusion mechanisms (Muller et al. 2012).

Steinberg and his colleagues, referring to the physics of phase separation, attributed the layering of germ layers in gastrulating frog embryos to measured cohesivity differences of the tissues. The interfacial tensions between the layers, which were the relevant determinants for this putative thermodynamically driven effect, could not be directly measured, but were inferred indirectly by comparing the surface tensions (measured by a compression tensiometer) of rounded-up parcels of isolated tissues (Foty et al. 1994). The values confirmed the predictions of the Differential Adhesion Hypothesis (DAH), which, under the assumption that the tissues were liquid-like (which is generally correct, see previous section), asserted that surface and, by inference, interfacial tensions, were due exclusively to quantitative or qualitative differences between the tissues' cell types in adhesive proteins, such as classical cadherins (Steinberg 2007).

Experiments on sorting-out of mixtures embryonic cells from later-stage embryonic primordia (liver, limb bud, retina, etc.) were also consistent with the DAH. Here, the equilibrium configuration of the tissues resulting from demixed cells from given sources was always identical to the morphological results obtained by direct confrontation of the intact tissue fragments. This was true with respect to which mass was engulfing and which engulfed, or (where full engulfment did not occur) to the direction of convexity of the interface (Duguay et al. 2003). These experiments confirmed the liquid nature of the tissues and their phase separation-like behavior (a generic physical effect). They did not prove the attribution of the tissue configurations to differential adhesion per se, however. This aspect of the hypothesis appeared to be pinned down, however, when Steinberg and Takeichi genetically engineered mouse L-cells, a cell type with no adhesive proteins of their own, to express different amounts of P-cadherin (Steinberg and Takeichi 1994). Here, sorting out occurred when the levels of expression were sufficiently different, and the resulting artificially produced tissue-like masses exhibited engulfment behaviors and interfacial contours exactly as predicted by the DAH.

Cells, however, are different from subunits of nonbiological liquids in that they have mechanically complex, responsive interiors. Interfacial tension, the driving force for cell sorting and tissue engulfment in liquid tissues was postulated by the DAH to result simply from cell surface-based adhesive differentials between the cells. But Brodland countered this by observing that the compression tests used by the Steinberg group measured not only the surface tension between the aggregate and the surrounding medium, but (indirectly) also the effective viscosity and contractility of the cells' cytoplasm, which affect the cohesivity of the aggregates. This led him to propose an alternative differential interfacial tension hypothesis (DITH) for cell sorting and tissue engulfment in vitro and in vivo (Brodland 2002).

While adhesive differentials alone can be the determining factor for cell sorting or phase separation of tissue fragments if internal cell states are equivalent, as in the genetically engineered L-cells in the Steinberg–Takeichi experiments, the more general DITH was ultimately recognized (even by advocates of the DAH) as more relevant to embryonic systems (Manning et al. 2010). In vitro experiments on tissues of gastrulating embryos appeared to confirm the idea that the boundaries of immiscibility between germ layers and the relative spatial arrangements of the layers were the result of differential tissue surface tension (TST)-based self-organization. Thus, progenitor cells from the ectodermal and mesendodermal germ layers of zebrafish embryos sort out from mixtures in vitro, and fragments of these layers adopt configurations that correspond to TSTs predicted from direct measurement of cell adhesivities and cortical tensions by atomic force microscopy (Krieg et al. 2008). Moreover, the configuration of the leading edge of the spreading epiblast during epiboly (envelopment of the yolk cell mass) in zebrafish was consistent with the physics of surface wetting, i.e. TST-driven rearrangement (Wallmeyer et al. 2018).

But what holds in vitro does not necessarily reflect the in vivo process, as Winklbauer and coworkers noted when they reported "[c]adherin-dependent differential cell adhesion in *Xenopus* causes cell sorting in vitro but not in the embryo" (Ninomiya et al. 2012). Further, the group that had previously obtained in vitro evidence for TST-driven rearrangement of germ layers (Krieg et al. 2008) used optical methods to directly measure differences in germ layer TST when the germ layers are first established. They found, surprisingly, that the magnitude of this difference was insufficient to drive progenitor cell sorting and tissue rearrangement under physiological conditions (Krens et al. 2017). The disparity between the in vitro and in vivo results was attributed to differences between the fluids bathing the cells under the two conditions. The low osmolarity of the interstitial fluid between the intact embryo's epiblast cells caused a reduction in the interfacial tension between the tissue layers compared to that in the tissue cultures. These results suggest that the self-organized germ layer phase separation seen in vitro was artifactual. If so, a different explanation is required for this phenomenon.

The study's authors provided evidence that the germ layer interface was formed by directed cell movement, possibly under the guidance of a gradient of interstitial fluid (Krens et al. 2017). Though biologically plausible, this explanation, which appeals to the agent-like properties of the embryo's constituent cells, challenges the postulate of physical self-organization. It implies, instead, that the cells have an evolved capacity to assume their proper positions in the embryo based on something akin to a predetermined program.

But even if directed cell migration is involved in germ layer formation in zebrafish, it is not necessarily the mechanism for this developmental process in other species: there is extensive phylogenetic variability of gastrulation-related molecules and cell behaviors even among the vertebrates (Schauer and Heisenberg 2021). Moreover, the liquid-like properties of animal tissues are deeply entrenched in metazoan origins and the observed germ layer boundaries conform to the predictions of the physics of wetting (Wallmeyer et al. 2018). One possibility is that the inferred program of directed migration may have been templated by, and over time supplanted, the formation of germ layers by the generic physical mechanism of tissue phase separation in a vertebrate ancestor (Newman 2019a). What is clear, though, is that for extant animals any genuine physical self-organizing processes that may act during gastrulation are integrated into more complex multidetermined developmental routines of these organisms, notwithstanding claims to have observed "self-organization" of gastrulation in vitro (Beccari et al. 2018; Etoc et al. 2016; Rosado-Olivieri and Brivanlou 2021).

8.3.2 Somitogenesis

In vertebrates, the mesoderm directly to either side of the notochord in the early embryo becomes organized into parallel blocks of tissue called "somites." The first somite forms as a tight aggregate or condensation of cells at the anterior region of the trunk. Each new somite forms immediately posterior to the previous one, budding off from the more anterior portion of the unsegmented presomitic mesoderm (PSM) (see Fig. 8 1, middle panel, for the chicken case). The somites mature into the vertebrae and the ribs, and the associated muscles. They also send muscle progenitors into the limb buds (in species that have them) which extend from the body wall (Chevallier et al. 1977). Eventually, 30 (zebrafish), 65 (mouse), or as many as 500 (certain snakes) somites will form (Maroto et al. 2012).

Cooke and Zeeman presented a mathematical model for somitogenesis in 1976, before any of the involved molecular components had been identified (Cooke and Zeeman 1976). It drew on two physical processes, intracellular biochemical oscillations and a traveling morphogenesis-permissive signal sweeping across the length of the embryo. In this "clock-and-wavefront" mechanism, the unsegmented tissue at any position along the axis was postulated to be in a "phase-linked" (i.e., synchronized) state. When a cohort of cells that were at a certain phase of the cycle experienced the wavefront signal, they would coalesce into a somite. A spatial gradient of phase values, the slow unidirectional passage of the wave, or both, could ensure that somite pairs formed in the observed anteroposterior order.

While both the oscillatory and spatially progressive aspects of the Cooke–Zeeman model were speculative, periodic cell regulatory processes, most prominently the cell cycle, were long known. Sustained oscillations in energy metabolites had been observed a few years previously in yeast cells (Ghosh et al. 1971) and their biochemical mechanism established in cell-free reactors (Pye and Chance 1966). The connection between such intracellular oscillations and the hypothesized synchronous oscillations that the somitogenesis model posited was obscure, but the authors were drawing on new theoretical initiatives on the dynamics of periodic phenomena in biological systems taking place during the same period (Winfree 1970; Goldbeter and Lefever 1972).

In the late 1990s, Pourquié and coworkers appeared to establish the validity of the clock-and-wavefront model by identifying molecular components that played the predicted roles. In chicken embryos the product of the Hes1 gene is expressed in the paraxial mesoderm in cyclic waves whose period corresponded to the formation time of one somite (Palmeirim et al. 1997; Pourquié 2003). This protein and its homolog Her7, another member of the Hes/Her family of transcriptional coregulators were found to be similarly expressed in zebrafish and mouse, and dynamical bases of the intracellular oscillation were inferred (Lewis 2003; Monk 2003). As noted above, however, self-organizing biochemical processes in individual cells do not constitute developmental self-organization, unless they come to act on the multicellular level. Lewis and Kageyama and their respective coworkers independently demonstrated that the Hes/Her oscillations become entrained so that, as predicted by Cooke and Zeeman and suggested by the experiments of Palmeirim et al., the PSM at each tissue domain about to undergo somite formation is a synchronized multicellular oscillator (Giudicelli et al. 2007; Özbudak and Lewis 2008; Masamizu et al. 2006). This collective behavior is uncontroversially the result of self-organization, but the way synchrony is brought about appears to differ in different species and remains in dispute even in well-studied organisms.

There are two possibilities. The first is that the cells are individually clock-like: they can keep time (i.e., undergo cyclic changes in Hes/Her concentration) even if isolated from one another, that is, autonomously, and can come into phase synchrony by interacting with each other in weak, non-specific ways. This so-called Kuramoto effect is a mathematically confirmed consequence of the physics of oscillations, and is observed, for example, in the behavior of fireflies in the wild and initially asynchronous arrays of metronomes that have been lined up on a flexible board (Strogatz 2003).

The second possibility is that the cells, though potentially oscillatory, are excitable entities that mainly enter this dynamical mode by interacting with each other. In this case, the establishment of clock-like behavior at the individual cell-level coincides with synchronization of the collective (Baibolatov et al. 2009). It is this second phenomenon which is commonly referred to as dynamical self-organization, because it mediates an emergent synchronized state. But the Kuramoto mechanism, which brings coherence to a set of phase incoherent oscillations is also a form of physical self-organization by the definition used in this chapter. Recent experiments suggest that synchronization of PSM cells in some somite-forming species is due to the non-Kuramoto emergent type of self-organization (Hubaud et al. 2017).

In intact embryos, somite boundaries form when cells which have left the posterior growth zone move sufficiently far from a source of FGF8 (and in some species additional, or different factors) in the posterior tip of the embryo (Dubrulle et al. 2001; Mallo 2016). But when PSM is dissociated and placed in culture, somite-like structures form whose size and shape are controlled solely by local cell–cell interactions, involving neither a clock nor a wavefront (Dias et al. 2014). This indicates that important aspects of somitogenesis result from inherent mechanical instabilities of the PSM.

Electron microscopic studies by Meier from the late 1970s suggested that, at least in chicken embryos, the relevant tissue is already arranged into somite-like cell clusters (termed "somitomeres") before the cells would have moved outside any posterior zone of morphogenetic inhibition (i.e., the wavefront of the Cooke–Zeman model) (Meier 1979, 1984). Furthermore, experimental application of mechanical strain to living embryos was shown to induce supernumerary well-formed somites between existing ones, by a mechanism involving somite splitting and reorganization (Nelemans et al. 2020). This provided evidence that mechanical organizational effects are operative in situ, even under normal stress conditions. Finally, newer electron microscopic observations revealed a posteriorly progressing front of adhesive changes in the presomitic mesoderm, accompanied by signs of tissue segmentation, developmentally much earlier than overt intersomite boundary formation (consistent with Meier's findings). The investigators have advanced a model of mechanical instability of the PSM incorporating this work, challenging the fundamentality of the clock-and-wavefront mechanism (Adhyapok et al. 2021).

As with gastrulation, developmental processes in the embryo are much more complex than in isolated tissues, and it seems plausible that the clock-and-wavefront (with somewhat different molecular-genetic bases in different vertebrate species) evolved to reinforce a more primitive segmentation scheme that evolved in an ancestral form (Stern and Piatkowska 2015; Mallo 2016). (Strikingly, short germband insects like beetles and grasshoppers, though not directly ancestral to vertebrates, also employ clocks and wavefront-like activity gradients, using some of the same genes as the latter in their segmentation processes (Clark et al. 2019).) Nonetheless, the cell aggregate-forming process that occurs in vitro, and which is essential to somite formation in the intact embryo, appears to be an authentic self-organizing process (Dias et al. 2014).

Oscillator synchrony, by whichever means it is brought about (e.g., via the Kuramoto or emergent modes) also appears to be a category of generic self-organizing process. Its effect is to coordinate cell states across multicellular tissues in a variety of developing systems (see below). The generation of such "morphogenetic fields" (Levin 2012; Gilbert et al. 1996) enables the reliable and coherent operation across broad tissue domains of system-specific spatiotemporal signals.

8.3.3 Limb Skeletogenesis

The jawed vertebrates (gnathostomes) typically have two sets of paired appendages, either fins or limbs. These structures are characterized by species-specific arrangements of bony or cartilaginous endoskeletal elements that arise from focal condensations of "mesenchyme," i.e., loose embryonic connective tissue, similar to those observed in early somite formation. The mesenchymal cells are initially dispersed in a dilute extracellular matrix (ECM), but this material is lost or greatly reduced at the sites of condensation, and the cells come to directly adhere to one another. Mesenchymal condensation is a transient effect. The skeletal primordia progress to cartilage tissue in cartilaginous fish such as sharks where it forms the definitive skeleton, as well as in lobe-finned fish, such as coelacanths, and tetrapods, where it is mostly replaced by bone later in development. Replacement bone (e.g., that formed with the intermediary of cartilage) also occurs to a limited extent in ray-finned fish, but the bony endoskeleton in these species mostly develops by direct differentiation of mesenchymal condensations into bone in the so-called dermal rays of the fins (Clack 2012; Hinchliffe and Johnson 1980).

There were indications as early as the 1960s that self-organizing processes contribute to vertebrae limb skeletogenesis. Zwilling performed a series of experiments in which he disrupted the mesoblast from isolated chicken limb buds and packed the fragments or reaggregated cells into a jacket of ectoderm (i.e., embryonic skin) from a different limb bud. When the composite was grown as a graft, recognizable limb structures, consisting of nodules or small rods of cartilage, developed (Zwilling 1964). These experiments were repeated by Fallon and coworkers, with the addition that expression of Hox genes was monitored in the "recombinant" limbs (Ros et al. 1994). According to the theory of "positional information," a developmental program-type model that was popular in limb research at the time, the distribution of various Hox gene products in the normal limb was what specified the locations of the skeletal elements (Tickle 1994). But the investigators found that discrete, parallel rod-like elements reminiscent of digits could appear without the reestablishment of normal Hox protein gradients. This provided further evidence that the Zwilling result was indeed due to some form of self-organization.

In tetrapod limbs and lobe-finned fish fins, the skeleton is arranged so that there is generally one element attached to the body, with increasingly distal rows containing more of them (see Fig. 8.1, bottom panel, for the mouse case). In the human arm, for example, the proximal humerus is followed by the radius and ulna, two tiers of wrist bones, and then five digits. In birds and mammals these elements are generated proximodistally during development, so that rows containing successively larger numbers of elements (initially parallel rods of cartilage) emerge sequentially over time (Hinchliffe and Johnson 1980).

There are generic physical mechanisms of self-organization that permit well-spaced spots or stripes of chemical concentration or states of mechanical compression to form, with different numbers appearing as a result of fine-tuning of system parameters or changes in domain shape (Alber et al. 2005). The Turing mechanism is one of these, and was proposed to underlie limb skeletal patterning beginning in the 1970s (Newman and Frisch 1979; Hentschel et al. 2004). We can ask if any of these generic mechanisms underlie the patterning of the mesenchymal tissue of the limb mesoblast. The proximodistal generation of the different tiers of the skeleton does appear to draw on such physical processes. But since the spatiotemporal ordering depends on regulated tissue elongation and the regulated decreasing suppression of pattern formation in the distal regions of the limb bud by proteins (mainly fibroblast growth factors; FGFs) secreted by the apical ectoderm, there are aspects of the process that while mechanistically comprehensible, are not themselves physically self-organizing (Glimm et al. 2020; Zhang et al. 2013).

Like somitogenesis, fin and limb skeletogenesis depends on patterns of mesenchymal condensation in which cells form focal aggregates that come to be distributed in a regular fashion across the developing tissue. There is, in fact, evidence for one or more Turing-type reaction–diffusion processes occurring in fin and limb development and in avian and mammalian limb bud cells in vitro (Christley et al. 2007; Kiskowski et al. 2004; Raspopovic et al. 2014; Sheth et al. 2012). But simulations show that fairly regular spot and stripe patterns can also result from local cell–cell and cell–ECM interactions in the absence of diffusible activators and inhibitors (Zeng et al. 2003). Unlike Turing processes, which require such factors, the simpler cell–cell and cell–ECM-based mechanism of Zeng and coworkers has no intrinsic wavelength. Its capacity to generate regular patterns is conditional, dependent on the density of the cells and the strength of their local interactions (Zeng et al. 2003). As in the case of somite formation, superimposed dynamical processes, some with self-organizing properties, which may differ in divergent lineages (e.g., cartilaginous fishes, birds, mammals) could serve to regularize the patterns formed by the simpler, likely more ancestral, mechanism.

In attempting to determine whether there is a self-organizing condensation-generating process common to all fin and limb development, it is helpful to compare experimental studies that have traced the development of condensations in vivo and in vitro. Although fibronectin, an ECM molecule that is abundant in avian and mammalian limb precartilage condensation is important in the consolidation of these foci as they mature (Frenz et al. 1989; Downie and Newman 1994), and it is part of an elaborate reaction–diffusion system involving various growth factors and their receptors (Hentschel et al. 2004), it is not the developmentally earliest molecule to mark these structures. A receptor for bone morphogenetic protein (BMP), a diffusible morphogen produced by the mesenchymal cells is present earlier, when cell “compactions” or “protocondensations” appear in anticipation of the condensations (Barna and Niswander 2007). There is also evidence for a Turing-type network incorporating BMP in conjunction with another morphogen, Wnt, and Sox9, a master transcription factor for the differentiation of cartilage in the formation of digits in the developing mouse limb (Raspopovic et al. 2014). However, this “BSW” network falls short as a candidate for the ancestral self-organizing system for fin and limb skeletogenesis.

In the first place, protocondensations form in the absence of Sox9, i.e., when it is knocked down genetically (Barna and Niswander 2007). This makes sense for the dermal endoskeleton of ray-finned fishes, where the bones form without a cartilage intermediate. While recent evidence suggests the dermal rays are organized in part by the same pattern-forming system as tetrapod limb endoskeletons (Gehrke et al. 2015), here the master transcription factor of bone, Runx2, is involved rather than Sox9.

Second, there is no evidence that skeletal elements other than the digits are patterned by the BSW mechanism. A primordial self-organizing process that has been recruited across all fins and limb would be expected to function not only in the digital plate (which is a novelty of tetrapods) and its counterpart in the distal region of the developing fins of cartilaginous fish (Onimaru et al. 2016), but at all proximodistal levels of the limb, particularly those with deeper evolutionary roots than the digits (Stewart et al. 2017).

Third, none of the components of the BSW network are cell–cell adhesive or ECM molecules. Factors that mediate changes in the arrangement of cells are prerequisites for the kind of ancestral condensation self-organizing system postulated above.

The one experimentally confirmed molecular mechanism that promotes condensations in limb mesenchyme consists of galectin-1 (Gal-1) and galectin-8 (Gal-8), two members of the galectin family of sugar-binding proteins (Bhat et al. 2011). Galectins are matricellular proteins (i.e., ECM components that are rapidly turned over and play both adhesive and signaling roles; Gabius (2009)). In the avian limb bud tissues where the role of galectins has been studied, Gal-1 localizes to prospective sites of condensation where it promotes aggregation of limb mesenchymal cells, while Gal-8 blocks the ability of Gal-1 to perform this function. Though antagonistic at the protein level, the two galectins mutually induce each other's expression at the gene regulatory level. This combination of antagonistic and reinforcing interactions, along with the effects that each galectin has on the production (or mobilization at the cell surface) of its specific and shared ligands, constitutes a multiscale network capable of forming regular patterns (Glimm et al. 2014).

Although the galectin-based mechanism can be described as a Turing-type system, it depends on local cell–adhesive cell–ECM interactions similarly to the mechanism proposed by Zeng et al. (2003) rather than on a balance of diffusible morphogens and their effects, as in classical Turing mechanisms. Because Gal-8 interferes with cell–cell adhesion mediated by Gal-1, it is superficially analogous to the inhibitory morphogen in a reaction–diffusion mechanism. But it acts entirely locally. In a model based on its experimentally determined action, changing its expression rate and binding affinity to a postulated shared receptor with Gal-1 changes the pattern wavelength, but altering its diffusion rate does not (Bhat et al. 2016; Glimm et al. 2014). Further, the simulated galectin mechanism only forms patterns if the cells it acts on move up gradients of Gal-1, another feature not part of Turing mechanisms. This has led it to being termed a "reaction-diffusion-adhesion" mechanism (Glimm et al. 2014).

Cell movement in response to an adhesive gradient is a generic effect since it does not require the cells to be anything other than randomly motile. The galectin-based protocondensation-forming mechanism can thus be considered an example of tissue self-organization.

Although little is yet known about the role, if any, of the galectin network in non-avian species, homologs of Gal-1 and Gal-8 are present in all tetrapods and ray-finned and cartilaginous fishes for which genomic data are available. The sequence and conformation of Gal-8s in these groups provide a basis (insofar as computational models permit) for understanding the different numbers of limb skeletal elements in these species. Moreover, the acquisition of putative cis-acting regulatory sequences by the Gal-8 genes of tetrapods provides an explanation (by simulations) of the proximodistal increase in element number in this group

(Bhat et al. 2016). Thus, the two-galectin network, which may have recruited the lineage-determining transcription factors of cartilage (Sox9) or bone (Runx2) during the evolution of various fishes and tetrapods, is the best current candidate for a primordial self-organizing basis of skeletogenesis (Newman et al. 2018).

A second self-organizing process active during skeletogenesis resembles the synchronization of cellular oscillations employed in somitogenesis. As in the PSM, Hes1 oscillates in limb bud mesenchyme, and when these oscillations were suppressed in vitro, condensation patterning was perturbed (Bhat et al. 2019). Depending on the time in culture when this was done there was either an increase in the number of protocondensations with less regular spacing between them, or a decrease and fusion of neighboring condensations. Suppression of Hes1 oscillations in the limb buds in intact embryos similarly led to pattern irregularities, including fused and misshapen skeletal elements (Bhat et al. 2019).

A functional connection between Hes1 and the core two-galectin network motivated computational studies of the effects of perturbing variables representing the concentration of each protein on the dynamics of the others. When Hes1 was made not to oscillate, the simulations showed that the galectin system formed regularly spaced condensations with sharp boundaries, and when Hes1 oscillated in a synchronous fashion the result was the same. However, if Hes1 was allowed to oscillate asynchronously, or its concentration was assigned randomly across the field of cells, the precision of the pattern was degraded (Bhat et al. 2019).

The implication is that synchronization of oscillators, rather than being a pattern-forming mechanism itself, is a dynamical means to place all the cells in a developing field on the "same page." That is, if the levels of the multifunctional transcription coregulator Hes1 are uniform across the tissue, patterning signals such as nonuniform concentrations of galectins (in limb skeletogenesis) or the release from posterior suppression of aggregation (as in somitogenesis) can act in a spatiotemporally coherent fashion over distances greater than the range of the diffusible signals that typically coordinate development (Bhat et al. 2019).

8.4 Conclusions

Animal embryos and developing organs, being parcels of excitable soft matter, will inevitably exhibit physical self-organizing effects. Does that mean that embryos, or embryo- and organ-like structures derived from stem cells, are physically self-organizing? The studies described here suggest that they are not, and the most suitable description for what they do in cultures (as in their normal gestational environments) is just "development." As the examples have indicated, physical processes of self-organization are clearly employed in the embryos and organ primordia of extant animals: envelopment of the yolk by the blastoderm in the zebrafish embryo by tissue surface tension according to the differential interfacial tension mechanism, PSM condensation, and limb/fin mesenchymal protocondensation compaction by mechanical instabilities. The multicellular synchronization of oscillations of transcriptional regulators is another self-organizing effect employed in embryogenesis and evidenced in vitro. But the constitution of the interface between the reorganizing germ layers in the fish embryo, the organization of PSM condensations into tandem somites and the limb/fin condensations into patterned endoskeletons, occur by agent-type and growth-dependent processes that are “biological” in ways not readily explicable by physical mechanisms.

Like the reorganization of tissue layers during gastrulation, the recruitment of simple nodule-generating self-organizing effects into patterned blocks of tissue along the body axis, or cartilaginous and bony fin or limb endoskeletons, evolved away from their presumed ancestral states. Somitogenesis required integration of tissue condensation into the elongating body in a way that suppressed it until it moved beyond the influence of an inhibitor emanating from the embryo’s posterior tip. In all vertebrate species, the condensation process is under the control of Hes/Her family transcriptional regulators. These oscillate in concentration, so the resulting blocks of tissue are tandemly repetitive. But the posterior inhibitory factor is taxon-specific and varies in molecular mechanisms and timing, indicating phylogenetic divergence (Stern and Piatkowska 2015).

In the case of fins and limbs, the presumed ancestral protocondensation-initiating molecule Gal-1 may have generated randomly distributed supportive nodules in the appendages of ancient gnathostomes. But it then acquired embellishments that made the nodules more regular (coregulation with Gal-8), more stable (linkage to a reaction–diffusion network for fibronectin production), more solid (linkage to reaction–diffusion control of Sox9 or Runx2 for cartilage and bone, respectively). Finally, with acquisition by Gal-8 of cis-acting gene regulatory modules, the skeletogenic system acquired position-dependent differentiation capabilities. This “evolving complex of self-organizing systems” generated, in a stepwise but divergent progression, the fins of cartilaginous and ray-finned fishes and the limbs of tetrapods (Newman et al. 2018).

The described scenario posits major roles for physical processes of self-organization, not in the development of present-day embryos and organs, but in the origination of the forms and patterns of these forms. Since we cannot experiment on the ancestral forms to determine how they arose, the best evidence for this hypothesis is the “generic” look of some morphological features of the modern forms, that is, the appearance of having been formed by physical processes that are well understood via nonliving counterparts (Newman and Comper 1990). The configuration of embryonic germ layers, the segments of the vertebrate embryo, and the repeated endoskeletal elements of gnathostome appendages are examples of this. But as we have seen, however they first arose, evolution can also draw established morphological traits away from their original genetic and even physical foundations by the processes of “developmental system drift” (True and Haag 2001) and “homomorphy” (Newman 2019a).

The eighteenth century philosopher Immanuel Kant coined the term “self-organization” to describe certain enigmatic properties of organisms. He described them as “natural purposes,” entities that not only maintain coherent identities, but produce the ingredients and embody the means to perpetuate themselves (Kant 1790; trans. 1966). Kant wrote in the context of Newtonian physics, unaware of the thermodynamic and dynamical phenomena that later scientists would term self-organizational. Since many of these self-organizing processes operate in living systems, Kant's usage was highly prescient.

But Kant was also only vaguely aware of organic evolution, and it is this, as we have seen, that transforms organisms into something different from the self-organizing systems of physics. Indeed, the complex, overdetermined entities that have resulted from evolutionary processes occurring over the more than 650 million years since the origin of the animals are, despite Kant's lack of appreciation of this dimension, aptly described by his term "natural purposes" (Moss and Newman 2015).

Finally, to return to the recent flush of allusions to self-organization, mentioned at the beginning of this chapter, in reference to formation of gastruloids and organoids produced by stem cells in culture (Beccari et al. 2018; Etoc et al. 2016; Rosado-Olivieri and Brivanlou 2021; Shahbazi et al. 2019), it is difficult not to consider it problematic, both scientifically and regarding social uses of the associated technologies. One recent paper, for example, describes what occurs when stem cells generate embryo-like structures in culture as akin to coalescence in a supersaturated vapor, phase separation of immiscible liquids, Turing processes, and so forth (Shahbazi et al. 2019). Public lectures by principals of the field contain confidently asserted, but similarly oversimplified or misleading treatments (Brivanlou 2016). These analogies (understandable in the past, but less so now that the physics of some developmental systems have been investigated in depth, with documented complicating effects) give the false impression that there has been more progress in understanding embryonic development than there truly has been. Based in part on such "hand-waving" explanations, investigators are drawing inferences about human development and its genetic and environmental vulnerabilities from in vitro models, seeking to mobilize medically targeted funding to this end (Clark et al. 2021). Notwithstanding the hazards of genetically modifying systems whose principles of organization are poorly understood (Newman 2017), some are forthright in their intention to eventually perform such alterations in human embryos based on data and purported conceptual advances acquired from stem cell development in vitro (Turocy et al. 2021).

As we have seen, however, development of the embryo in its in vivo setting does not generally occur by the action of physically straightforward processes. Further, development of reconstituted embryo cells in vitro does not always occur in the same way it does in vivo. It would be unfortunate if we find ourselves having emerged from a period of misconceived genetic program metaphors only to land in a brave new world captivated by equally misguided ones about self-organization.

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The Morphoprocess and the Diversity of Evolutionary Mechanisms of Metastable Structures

9

Andrei I. Granovitch

Abstract

This study is a long-overdue attempt to tackle the complexity of evolutionary problems by mutually complementary conceptual approaches rather than from the standpoint of a single dominating evolutionary hypothesis. As a first step, I identify the major problems preventing a clear understanding of evolutionary mechanisms. They are associated with three "uncertainties" accompanying the analysis of evolutionary phenomena: (1) Terminological ambiguity, bordering on a logical inconsistency, in the construction of evolutionary concepts, (2) The uncertainty of direct observation, associated with the difficulties of documenting the evolutionary process and (3) The uncertainty of applicability, arising from the complex multilevel nature of the living matter. Then I outline a fairly substantial approach to the consideration of living systems. The analysis of the uncertainty of applicability suggests that the most productive approach is to apply the notion of an "evolving system" to systems of the organismic rank, understood as an object–process or a morphoprocess. Such systems (highly integrated metastable structures–processes) are dissipative structures with a cyclic character of implementation. Once we have identified the evolving system, we can determine three different conceptual models of transformism of these structures. Importantly, the delimitation is based on a unique set of their characters rather than an affiliation with a particular historic scientific tradition. These models of microevolution are indirect adaptogenesis, direct adaptogenesis and constructional transformism. The logic of each of them has often been used in various evolutionary concepts in the course of the last two centuries. Finally, I present a general outlook on the diversity of mechanisms of transformism. They fall into two groups: combinatory

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_9

mechanisms (transformation through combinations) and transformational mechanisms as such (transformation without combination). It is the transformational mechanisms that are encompassed by the three conceptual models mentioned above. It is becoming evident that the evolutionary process is based on mechanisms described by different models. A time has come for a careful examination of various transformistic possibilities and the identification of prevailing and accessory mechanisms. Different groups of organisms/types of morphoprocesses may be characterized by different leading mechanisms of transformism, which may belong to both "combinational" and "transformational" phenomena. We have to consider a broad kit of potential evolutionary tools and try to comprehend evolutionary phenomena at a new level of conceptual synthesis.

Keywords

Evolutionary concepts · Morphoprocess · Natural selection · Adaptogenesis · Self-organization · Models of microevolution

9.1 Introduction

Pluralism has been making a comeback to evolutionary discussions in the last decades. The single-mindedness of the Modern Synthesis is giving way to the contemplation of the diversity of potential mechanisms of the evolutionary process. One of the reasons is the failure of the Modern Synthesis, with its supremacy of population genetics, to explain many important features of evolution (Lewontin 1974; Gilbert et al. 1996). Another is the pressure of the enormous bulk of information that has recently been obtained in five major directions. Our knowledge of (1) the molecular framework of the living cell has increased dramatically. It is becoming clear that the processes of self-regulation and regular self-assembly of complex intracellular structures prevail over stochastic mechanisms of functioning and morphogenesis. We have looked inside the cell and found not *The Blind Watchmaker* (Dawkins 1996) "but [...] a genetic engineer [...], and she has an impressive toolbox full of sophisticated molecular devices for reorganizing DNA molecules" (Shapiro 1995). Self-organization in the cell is expressed not only in reparation and replication of DNA. This principle pervades the entire cell, from molecules and their complexes to organoids (Misteli 2001; Denton et al. 2003; Kurakin 2005; Carazo-Salas and Nurse 2006; Cortès et al. 2006; Glick 2007; Misteli 2007; Karsenti 2008; Loose et al. 2008; Johnson and Lam 2010 and others).

Our understanding of (2) phenotypic plasticity of multicellular body and transgeneration inheritance (West-Eberhard 2003; Pigliucci 2010; Jablonka and Lamb 2010; Danchin et al. 2011; Kull 2014; Laland et al. 2014) has also expanded. The new information calls for a revision of the relationships between the mechanisms of phenotypic plasticity and those of genotypic adaptations and, potentially, for a change of the evolutionary paradigm to an “extended evolutionary synthesis”.

A new outlook emerges from the data on (3) a routine exchange of genetic information between organisms from different taxonomic groups, the diversity of non-canonical means of horizontal transfer of hereditary material in different organisms and non-genetic vertical inheritance within a strain of organisms (Ochman et al. 2000; Gladyshev et al. 2008; Gladyshev and Arkhipova 2010; Boschetti et al. 2011; Haegeman et al. 2011; Koonin 2011; Husnik et al. 2013). At the same time, we are beginning to realize the importance and depth of (4) symbiotic relationships in the functioning of biological systems (Kooijman et al. 2003; Gilbert et al. 2015). Finally, (5) paleontological description of the biota’s historical development is now relying on much more complete data (Benton and Pearson 2001; Smith and Ortega-Hernández 2014; Aria et al. 2015; Darroch et al. 2018; Kaufman 2018).

These advances pave the way for a rethink of the relative importance of evolutionary mechanisms: which of them are master mechanisms and which play a subordinate role. Approaches expanding the orthodox Modern Synthesis and laying the ground for a new evolutionary synthesis have already been developed (Kirschner and Gerhart 2010; Müller 2010; Newman 2010; Pigliucci 2010; Jablonka and Lamb 2010; Koonin 2011). Let us not forget that while the Modern Synthesis claimed to possess the gospel-truth about evolution, several dozen comprehensive concepts suggested in the last two hundred years have interpreted the evolutionary process from other vantage points (see for review, Berg 1969; Bowler 1975; Lyubishchev 1982; Gould 2002; Vorontsov 2004; Nazarov 2005; Esposito 2017; Levit and Hoßfeld 2017; Loison and Herring 2017; Kutschera 2017; Popov 2018). These concepts, often branded as “dead ends” or considered as a marginal part of the scientific knowledge, might well turn out, once the rethink has been achieved, to be its solid ground, while their diversity may emphasize the plurality of mechanisms ensuring the general process of evolution of the organic world.

In such a situation, an overview of various concepts and possibly their classification by the key features is long overdue. The need for such an overview is associated not with a historical ordering of the existing knowledge but, crucially, with the development of a heuristic approach to the analysis of the diversity of evolutionary mechanisms. It was exactly such a prudent analysis of the diversity that was advocated by A.A. Lyubishchev in his paper *On the classification of evolutionary theories* (Lyubishchev 1982).

In this work I will give an example of a possible approach to the classification of conceptual approaches to the explanation of evolutionary phenomena. Its substantial part consists of three successive steps or sections. First I will consider the major difficulties arising during interpretation of evolutionary phenomena (Sect. 9.2). Then I will outline a fairly substantial approach to the consideration of living systems (Sect. 9.3), which I will then apply in the third section (Sect. 9.4) dealing with key concepts modelling the mechanisms of the evolutionary process (*Three principal models of the evolutionary process of highly integrated metastable structures*). In

Conclusion, I will compare the available models of evolution by their key characteristics.

9.2 Major Problems in Understanding Evolutionary Mechanisms

Two centuries have elapsed since the first holistic evolutionary concept was suggested (Lamarck 1955) but the question about major mechanisms of the evolution of the organic world remains debatable. The reason is associated with three "uncertainties" accompanying the analysis of evolutionary phenomena. To begin with, (1) the subject matter of the notion "evolution" is not formalized strictly enough. This entails a *terminological ambiguity* and even a *logical inconsistency* in the construction of evolutionary concepts. Besides, the evolutionary process is difficult to document experimentally, which may be referred to as (2) an *uncertainty of direct observation*. Finally, a complex multilevel nature of the living matter, represented by a hierarchical series of mutually involved systems of various levels of organization, complicates the choice of the key system, with which the mechanisms of evolutionary process are associated. The latter uncertainty may be referred to as (3) the *uncertainty of applicability*. It is easy to see that the first uncertainty refers predominantly to epistemological problems while the second and the third uncertainties are mostly ontological.

I will deal with these three uncertainties one by one in the three subsequent sections.

9.2.1 Epistemological Problem of the Ambiguity of the Notion of Evolution and the Associated Problem of Uncertainty of the Term "Evolution"

The ubiquity of the term "evolution" is in stark contrast with the singularity of attempts at its clear definition. The most profound analysis of the contextual basis of this term can be found in the works of P.J. Bowler and A.A. Lyubishchev (Bowler 1975; Lyubishchev 1982). The former study considered the changes of the meaning of the term "evolution" in historical retrospective, from the denotation of embryological preformism to the denotation of changes of the living systems (transmutation of species) (Ch. Lyell, Principles of geology 1832, cited in Bowler 1975) and even nature in general (Spencer 1864). The latter study analysed various semantic meanings of the term "evolution" (Lyubishchev 1982) using the principle of contrapositions.

The most frequent meaning of the term "evolution" is the possibility of transformation of some species into others as opposed to the immutability of species. For a terminological specification of this semantic context—changes of species in time—the term "transformism" was suggested (Berg 1969). Other meanings of the term "evolution" (evolution as preformation; evolution as gradual development;

evolution as ascent, progress; evolution as irrevocable development (Lyubishchev 1982) as well as evolution as the emergence of the new as opposed to combinations) are very important for the definition of the key features of any hypothesis characterizing the evolution of the organic world. Their analysis calls for a special study. Here let us take note that the semantic ambiguity of this term should necessarily be taken into account in studies of evolutionary phenomena.

The choice of parameters is paramount for the comparison of various evolutionary hypotheses by their key characters. Any hypothesis describing the mechanism of evolution answers, directly or by implication, several major questions. Following A.A. Lyubishchev (1982), I will present these questions as contrapositions. Some of them were suggested by Lyubishchev himself in his paper *On the classification of evolutionary theories* (Lyubishchev 1982). Each of the contrapositions presents an evolutionary hypothesis in the continuum of the key semantic character.

A. An assessment of the degree of finality of evolution in general: TELEOGENESIS (the development of the biota moves towards a certain result, the movement is directed, conforming to laws) VS ATELEOGENESIS (evolution is not directed, there is no movement towards any goal).
B. An assessment of the formation of correspondence between organisms and their environment: ADAPTOGENESIS (the process of adaptation to the environment [evolutionary adaptation] is directly associated with the impact of evolutionary mechanisms) VS ANADAPTOGENESIS (adaptation of an organism is a side effect of evolution; it is secondary and is not directly associated with the impact of evolutionary mechanisms).
C. An assessment of predominance of external or internal factors in evolution: ECTOGENESIS (the main driving forces of evolution are entirely associated with the effect of the environment, which forms corresponding evolutionary changes; functionalism sensu Kellogg 1907; Gould 2002) VS AUTOGENESIS (the entire morphogenetic potential is associated with the structural features of organisms; the environment merely triggers internal evolutionary processes of self-assembly and eliminates the organisms that fail to adapt; structuralism sensu Kellogg 1907; Gould 2002).
D. The assessment of the degree to which evolutionary mechanisms and the processes of formation of taxa are gradual: GRADUALISM (slow and gradual modifications of species; a relative uniformity of the rate of evolution, including the cases of origin of new large taxonomic groups) VS PUNCTUALISM (an abrupt alternation of periods of evolutionary stasis and evolutionary changes; the possibility of fast formation of organisms with new complexes of characters, including those of a high taxonomic rank).
E. The assessment of the uniqueness and the directionality of evolutionary changes: IRREVERSIBILITY (impossibility to reverse evolution following from Dollo's law (Louis 1893) as well as the uniqueness of the evolutionary emergence of species and taxa of a higher rank) VS REVERSIBILITY and REPEATABILITY (possibility of reversal to the ancestral state in the process of evolution; the possibility of multiple formations of species and higher taxa).

F. The assessment of the integrity of evolutionary changes: MEROGENESIS (a transforming organism is a set of useful and harmful characters; some characters may change while others may remain intact) VS HOLOGENESIS (the organism is a holistic system; no character can transform by itself; a transformation is always a reconstruction of the entire system).

It goes without saying that this list is not exhaustive and may be extended by additional criteria for comparison. However, even those given above make it possible to compare evolutionary concepts on the basis of their key features rather than their affiliation with vaguely defined directions such as Darwinism or Lamarckism. On closer examination, it turns out that these directions combine several conceptual and logical approaches and are united under one and the same name merely owing to inertia and tradition (see, e.g., Delisle 2017).

9.2.2 The Problem of Uncertainty of Direct Observation

The prolonged nature of the evolutionary process means that it is difficult to study experimentally. Our knowledge about its course is mainly derived from the fossil record. Paleontological data, being the only source of information about the direction and features of the macroevolutionary process, are insufficient for any reliable conclusions about potential microevolutionary mechanisms. Attempting an interpretation of the available temporal series of non-ontological data, one encounters a problem of distinguishing evolutionary events as such in the series of dynamic regulatory populational phenomena (Altukhov 2003).

Numerous post hoc conclusions about the mechanisms of microevolution, based on the assessment of the frequencies of alleles/haplotypes in populational groups of the same species or in the distribution of populations of closely related species, actually allow different interpretations of the formation of these changes. Thus, they are also ill-suited for making sound conclusions about the realization of this or that microevolutionary mechanism.

Studies on "experimental evolution" of prokaryotes are probably the closest we can get to direct experimental observation of evolutionary processes (see for review Lenski (2017a, b)). These studies, based on whole-genome sequencing of the same-strain microorganisms separated by thousands of generations, made it possible to identify the key features of the mutation process and to establish the connection between the changes in the genome and the adaptive abilities of the strain. However, even for this remarkable evidence, the question about the prevailing mechanisms of microevolution largely remains open to interpretation.

9.2.3 The Problem of Uncertainty of Applicability

The analysis of evolutionary phenomena, similar to any other study of biological objects, requires a clear definition of the biological systems in question. The structure of living matter is hierarchical. Studies of various levels of its organization in the context of transformism broadly operate such notions as molecular evolution, the evolution of genomes and other functional systems of organisms, cell evolution, the evolution of tissues and organs of multicellular organisms, the evolution of behaviour, the evolution of populations, communities, etc. All these viewpoints (the angles from which evolution is considered) undoubtedly provide important data characterizing various features of the evolutionary process. All of them are a reflection of the general evolutionary change of the organic world at some level of organization. However, if we are to understand the driving mechanisms of the evolutionary process, we have to identify the level of the living matter organization which makes the decisive contribution into the formation of the evolutionary trajectory. On the other hand, we also have to identify the systems at the levels of which changes are largely a reflection of the operation of the main evolutionary mechanisms.

In the hierarchy of systems, the best integrated and the most individualized (holistic) ones are unitary organisms, which exhibit a high physiological autonomy and complex behaviour as well as a high degree of morphogenetic closedness (Beklemishev 1970; McShea 2001; Levit and Scholz 2002; Granovitch et al. 2010).[1]

The organismic level of individuality may be expressed both at the poly- and at the mono-cellular level. This is the reason why there are two "peaks" of the degree of integration of living systems, characterized by a very different complexity of organization. One of the peaks corresponds to cellular organisms (protists and prokaryotes), while the other corresponds to the meta-cellular level of organization and, correspondingly, to multicellular or, rather, meta-cellular organisms (Metazoa, Metaphyta) (Beklemishev 1970; Granovitch et al. 2010).

Formation and existence of the systems that constitute the elements of a multicellular organism (organelles and their systems, cells, organs, and their systems) are mostly regulated by the organism itself (a highly integrated whole regulates its parts). Systems of the supraorganismic level such as populations and communities are, in their turn, distributive (Serzhantov 1972). Their elements (organisms) have a much greater systemic integrity than the system on the whole. Both biocenoses and populations are characterized by a low degree of physiological and morphogenetic closedness (Beklemishev 1970).

This means that the most significant evolutionary mechanisms should be looked for at the level of systems of the organismic rank: cells-organisms and multicellular organisms. However, even this understanding does not fully clarify the issue of the key objects of the evolutionary process because one needs to account for other essential features of the living matter such as its dynamic nature and temporal changes of the system's characteristics. For organisms, these features are represented by ontogenetic aspects of their existence. In addition, the life of an organism is

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[1] Not to be confused with a more abstract term "closure" (Mossio and Bich 2017; Kauffman 2019) denoting mutual dependence of flows of energy and matter (causal regime according to the authors) ensuring the existence of biological structures far from thermodynamic equilibrium.

confined to a narrow time frame, while the issues of transformism can only be solved if we consider time frames comparable with a sequence of a series of generations (see Sect. 9.2.1): the required systems should be defined transgenerationally (see Mossio and Bich 2017). All these features of the chosen systems should be taken into account when constructing models of the evolutionary process.

In order to clarify the features of the systems with which evolutionary changes are associated most directly, let us consider a certain outlook on the living systems of the organismic rank. This outlook, which has a long and venerable history, is also promising for the solution of the current problems.

9.3 Conceptualization of the Morphoprocess

The dynamic character of organization of living systems of the organismic rank was understood at the earliest stages of the development of comparative anatomy. Georges Cuvier made an exhaustive characterization of stability of form due to the dynamic nature of its components when he wrote:

> [...] the essence of life [...] consists in the ability that certain corporeal combinations have of enduring for a time and in a definite form, incessantly attracting into their composition a part of environmental substances and rendering to the elements portions of their own substance. (Cuvier 1817, 12–13).

V. N. Beklemishev developed this view on the organism and formalized it in the concept of an "object-process" or an "organic morphoprocess" (see Beklemishev 1994; Levit and Scholz 2002; Granovitch et al. 2010; Granovitch 2021). This concept is rooted in the idea that an organism is simultaneously an object and a process (a morphoprocess)—a form enduring in a metabolic flow. The dynamics of the system's components ensures relatively stable maintenance of its specific features (Beklemishev 1994). However, the form of an organism (as an epiphenomenon of the processes ensuring its existence) is not constant. It undergoes changes in the process of ontogenesis. Thus, the morphoprocess implies an inherent change of the form, which reflects dynamic changes in the functional characters of an object (an individual) in the course of its ontogenesis.

In the late twentieth century, the ideas about organisms as objects–processes found unexpected support in studies of physical and chemical properties of matter. Open systems, which absorb and give up matter and energy into the environment, may exist far from the point of energy equilibrium (that is, the maximum entropy point) for a long time. Under these non-equilibrium conditions the so-called dissipative structures are formed. These are well-ordered complexes, whose dynamic morphofunctional integrity and stability are ensured by their passage through the system of energy flow (Prigogine 1978; Cramer and Prigogine 1993). The concept of dissipative structures describes perfectly the behaviour of certain chemical reactions and physical processes and is also applicable to biological objects and probably even to social phenomena (Artigiani 1987; Cramer and Prigogine 1993; Karsenti 2008).

In fact, it is a universal characteristic of behaviour of non-linear open systems under non-equilibrium conditions. At the same time, the formation of order and a regular dynamics of such systems–processes emphatically pose the question about the laws and regularities of self-assembly and self-organization of the living systems (Johnson and Lam 2010; de Paoli et al. 2017; Simunovic and Brivanlou 2017; Werner et al. 2017; Bizzarri et al. 2018; Sazer and Schiessel 2018).

The term "metastable pattern", broadly applied to physical and chemical systems–processes, denotes the phenomenon when a system, situated in a certain area of the phase space, may undergo an abrupt transition into another area following a change of the external conditions (Kivelson and Reiss 1999; Alexandrov and Nizovtseva 2014). This pattern is also used to describe the properties of "biological" molecules, e.g., the molecular dynamics of DNA oligomers (Horenko et al. 2008), as well as the organization of chromosomes (Sazer and Schiessel 2018), the organization of cellular systems into tissue constructions (Jakab et al. 2004) and molecular dynamics of cellular processes ("metastable network" processing) (Kurakin 2005, 2007). In general, a more exact term for dissipative structures existing stably far from the maximum entropy point is "metastable processes" (Johnson and Lam 2010). This term emphasizes both their dynamic exchange (absorption/expulsion) of elements with the environment (process) and their ability to maintain form under certain conditions and to shift to an entirely different form of the process under other conditions (metastable).

The application of the term "metastable process" to complex living systems highlights the fact that such dissipative structures are not structures sensu stricto. They are a process, that is, a form enduring in the flow of matter and energy exchange with the surrounding world (Johnson and Lam 2010). To note, the term "metastable process" fully conforms to the definition of the morphoprocess given by Beklemishev (1994) when applied to systems of the organismic rank. At the same time, it has a broader scope and may be extended to living systems of any level of organization such as enzymatic reactions, glycolytic cycle, formation of multicellular aggregates in *Dictyostelium discoideum* and self-organization in insect populations (Prigogine and Stengers 1984) as well as to complex non-living systems such as dynamic and stable atmospheric phenomena (Johnson and Lam 2010). Bearing in mind this terminological difference, I will apply the term "morphoprocess" only to organisms.

Developing the ideas about the morphoprocess in an earlier study, we have pointed out the need to specify this term in accordance with the ontogenetic features of organisms and the scheme of the life cycle (Granovitch et al. 2010; Granovitch 2021). As a result, we gave several definitions reflecting various aspects of the morphoprocess (Fig. 9.1).

Instant morphoprocess (Fig. 9.1, IM) is an organism in a given time moment. This notion emphasizes the mode of existence of a dynamic form; a living organism exists only in the present; an epiphenomenon of its existence in a vanishing lapse of time is an "instant form". This notion illustrates the uniqueness of the form reflecting the interaction of structural elements and the flows of energy and information (Granovitch et al. 2010; Granovitch 2021).

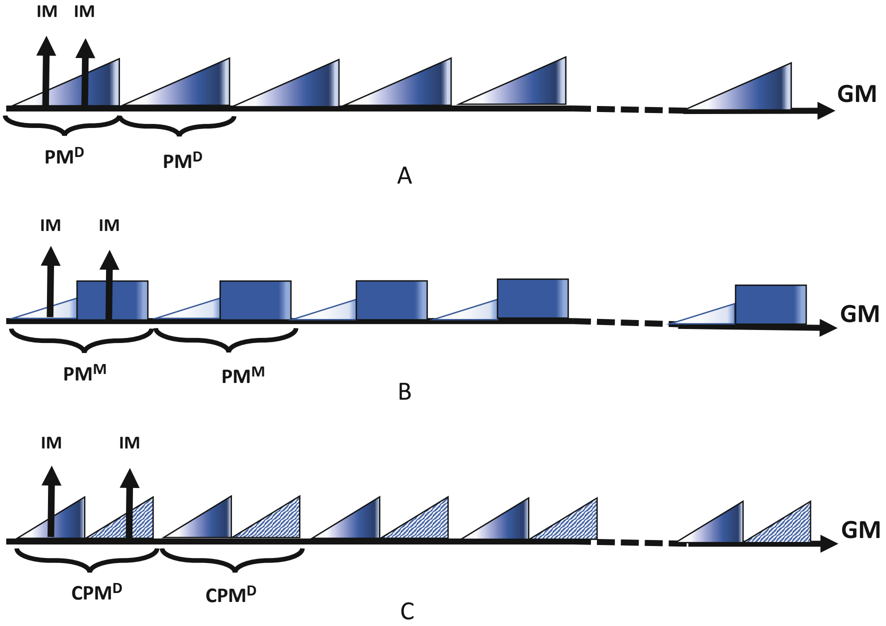

Fig. 9.1 A scheme of the structure of General Morphoprocesses (GM) with arbitrary assessments of Instant Morphoprocesses (IM), Partial Morphoprocesses (PM) and Compound Partial Morphoprocesses (CPM). Partial morphoprocesses: (**a**) Of organisms with direct development (PM^D); (**b**) Of organisms with metamorphosis in the development (PM^M); (**c**) Of organisms with direct development and a complex life cycle involving two different generations (CPM^D)

Partial morphoprocess (Fig. 9.1, PM), the "first derivative" of the instant morphoprocess, is the existence of an organism enduring from its origin (the merging of gametes or cell division) to its death or the next division. A partial morphoprocess is the entire sequence of morphofunctional changes of an organism throughout its lifetime, ending with the disintegration of the system due to its death or the division of the cell-organism. Morphofunctional characteristics of a partial morphoprocess are not constant. They are dynamically stable at certain stages (propagation of the form) and change in a regular manner at other stages (Granovitch et al. 2010; Granovitch 2021).

Compound partial morphoprocess (Fig. 9.1, CPM) is a sequence of several different partial morphoprocesses in case of a complex life cycle (Granovitch et al. 2010; Granovitch 2021) such as the sequence of medusoid and polypoid generations in Cnidaria, the alternation of parthenogenetic and amphimictic forms in Aphididae, Cynipoidea and Rotifera Monogononta, the alternation of generations in Trematoda, etc.

General morphoprocess (Fig. 9.1, GM), the "second derivative" of the instant morphoprocess, is a rhythmic repetition of partial morphoprocess/compound partial morphoprocess at a sufficiently large time scale. General morphoprocess is characterized by a dynamic stability of the form, as is partial morphoprocess, but, in contrast to the partial and the compound partial morphoprocess, it is also characterized by repeatability (reproducibility, cyclic nature) in a series of ancestor–progeny generations. A cycle of general morphoprocess may consist of a partial (simple) morphoprocess or a regular sequence of two or several partial morphoprocesses (a compound partial morphoprocess) (Granovitch et al. 2010; Granovitch 2021).

In the conceptual field under consideration a partial morphoprocess is an integral of instant morphoprocesses. It is characterized by considerable temporal changes of its morphofunctional characteristics even in the case of the direct development of the organism (Fig. 9.1, PM^D). Using a multicellular organism as an example, we can describe the succession of these types of changes of a partial morphoprocess. First come changes associated with the dynamics of embryonic and postembryonic development. They are followed by changes associated with the formation of propagative elements (formation of reproductive structures). After that, “necrotic” changes, associated with the organism’s senescence, set in. A partial morphoprocess often consists of two or several “stable” morphofunctional states connected by fast transitions (metastability of a partial morphoprocess). A clear illustration is formed with successive stages of the larva and the imago. The most dramatic reconstructions of a morphoprocess—those that involve fast and vast changes—are called metamorphosis (Fig. 9.1, PM^M). Vivid examples of such phase transitions of the partial morphoprocess may be found among annelids, molluscs, arthropods, cestodes, acanthocephalans, etc.

General morphoprocess (Fig. 9.1, GM) is a rhythmic repetition of the partial morphoprocess in a series of generations. This means that the characteristics of the partial morphoprocess set the rhythmic basis of the general morphoprocess.

The typology of morphoprocesses is such that these systems can usually be considered within similar groups called species (to be more precise, species morphoprocesses). Organisms with amphimictic reproduction are characterized by an incomplete morphogenetic closedness (Beklemishev 1970) (secludedness sensu Levit and Scholz 2002) in relation to each other within these groups. In contrast, species morphoprocesses of agamic species are fully characterized by a morphogenetic closedness. Such species exist as sets of parallel clonally reproducing ancestor–progeny lines. At the same time, however, these morphoprocesses, similarly to those of amphimictic species, are typologically separated from those of other species.

Intraspecific variability of the morphoprocesses is set by the plasticity of the morphoprocess and by the multiple genetic variants of species morphoprocess (genetic heterogeneity). Despite its intraspecific variability, a group of species partial morphoprocesses is characterized by a stable manifestation of a complex of the species characters. In this way, modality—the most stably reproducing complex of characters of the partial morphoprocess of a species—manifests itself. Thus, general morphoprocesses of species, as series of partial morphoprocesses constituting them, rhythmically reproduce the modal characters of a given species.

The above conceptual scheme allows a more concrete discussion of evolutionary phenomena because, overcoming the “uncertainty of applicability” (see above, Sect. 9.3), it points to the category of living systems promising for the evolutionary analysis. It becomes clear that *the object of evolution is a concrete general morphoprocess*, in other words, the ancestor–progeny line, considered as an object–process. From this viewpoint, an evolutionary phenomenon is a stable modification of a general morphoprocess in the process of its cyclic realization.

Having identified a potential evolving system and having defined an elementary evolutionary phenomenon, we should turn to mechanisms ensuring the modification of the general morphoprocesses, in other words, the mechanisms of evolutionary changes. It is clear that they should operate at the level of the partial/compound partial morphoprocess. There are many diverse ideas on this topic, and the leading role may be attributed to different mechanisms depending on the preferred scheme of the evolutionary process. Nevertheless, all the schemes may be boiled down to three conceptual models of microevolution. They will be discussed in the next section.

9.4 Three Conceptual Models of Microevolution of Highly Integrated Metastable Structures–Processes

9.4.1 The Model of Indirect Adaptogenesis (Granovitch 2018, 2021)

Indirect adaptogenesis is currently the most popular model within the framework of transformistic interpretations of evolution. It includes selection-based notions and postulates natural selection as the main evolutionary force. Its correspondence to empirical facts is frequently taken for granted, and other models are ignored. Indirect adaptogenesis is based on the assumption that information about changes in the environment is reflected in the general morphoprocess not through a specific direct impact but through a generalized "signal" of the magnitude corresponding to the degree of reproduction of the partial morphoprocess. At the same time, the external signal causing the transformation does not result in adequate changes of the partial morphoprocess transferred to the general morphoprocess but regulates the arrangement of partial morphoprocesses in the population. This, rather than anything else, consistently results in the change of the modality of morphofunctional characteristics of the general morphoprocesses of a given population. Hence, the name of the model—indirect adaptogenesis or indirect impact of the environment on the modality of the general morphoprocess. The model in general is logically based on *tychogenetic* and *selectogenetic* ideas. It assumes that the mechanism of evolutionary change is selectogenesis (*selectogenesis*, term—Berg 1922, cit. ex (Berg 1969; Lyubishchev 1982)), from the Latin selectio—choice, selection), that is, a differential contribution of partial morphoprocesses into the modality of the totality of general ones. The material making the selection possible is, it would seem, a random distribution of minute hereditary deviations of the species morphoprocess (*tychogenesis*). *Tychogenesis* (term—Osborn (1929); from the Greek týche—chance) assumes that small hereditary deviations are the basis of further evolutionary changes. The key aspect of the tychogenetic approach is the assumption that initial hereditary deviations are random, that is, (a) variation, accumulation of small mutations is unlimited and non-directional and (b) the primary act of variation is independent of the need for it and the character of the need for it.

The acknowledgement of tangible differences in the effectiveness of reproduction of the carriers of such deviations introduces into play the action of the environment (*ectogenesis*). Its effect on the morphoprocess, however, is not direct but mediated by selection. On the one hand, it is postulated that organisms are different in respect of their reproductive characters and that these differences are random, independent of the environment (whose impact may only be reflected in a non-specific increase of the frequency of deviations). On the other hand, it is postulated that the input of individuals into the next generations is, correspondingly, different. These two postulates are crucial for the choice of the major mechanism of transformation within the model of indirect adaptogenesis—it is the selection of "the fittest", or natural selection.

In general, indirect adaptogenesis is a change of the modality of the general morphoprocess *without a corresponding change* of the partial morphoprocess. The change of the modality is based on the choice of the totality of partial morphoprocesses available in the variation set of a population. Transformism is modelled as *ectogenesis* meaning that the environment is its initiating and directing force. The model is a variant of *adaptogenesis* since its mechanism is associated with the multiplication of the most successful partial morphoprocesses in the general morphoprocess and the maintenance of a "correspondence" between the modality of the general morphoprocess and the environment.

Consistently applying the model of indirect adaptogenesis, one has to assume that evolution is gradual and divergent, that the evolutionary process is undirected and that every act of speciation is unique, creating a new species, which is unique genetically, ecologically and physiologically. The stochasticity of the model's mechanisms betrays its idiographic character: each transformation phenomenon is the result of a unique combination of the impact of factors and the work of essentially stochastic mechanisms of tychogenesis and selectogenesis. This means that the evolutionary process, in general, is also thought of as undirected—a superimposing succession of unique events. The only system in which the mechanisms of indirect adaptogenesis may operate is the totality of partial morphoprocesses. Hence, the assumption that *the population is the smallest unit of evolutionary transformations* and the promotion of the so-called populational thinking.

9.4.2 The Model of Direct Adaptogenesis (Granovitch 2018, 2021)

The model of direct adaptogenesis presents other potential mechanisms of the transformation of the morphoprocess than those described in Sect. 9.4.1. It is based on the assumption that changes conforming to the external impact, which occur during the implementation of a partial morphoprocess, can be imparted to the general morphoprocess. Changes in the environment result in corresponding fine-tunings of the implementation of a partial morphoprocess, which are specifically (that is, in conformance with the impact of the environment and in accordance with the internal systemic organization of the object) reflected in the morphoprocess. It was this directed specific impact (as distinguished from the indirect input of differing individuals into the next generation or, in other words, of partial morphoprocesses into general ones, see Sect. 9.3) that gave the model of direct adaptogenesis its name. This logical scheme is characteristic of all the hypotheses implying the mechanism of inheritance of characters acquired by the organism during its lifetime. Direct adaptogenesis is the conceptual basis of various groups of "Lamarckian" evolutionary theories (see for review, Gould 2002; Vorontsov 2004; Nazarov 2005; Bowler 2017; Esposito 2017; Loison and Herring 2017).

In the light of this model, transformism is a constant modification of the partial morphoprocess, ongoing under the influence of the changing external conditions and accumulated, in the series of its cyclic implementation, in the general morphoprocess. Information about the changes in the environment is imparted to the general morphoprocess in a direct manner rather than as a generalized signal of the degree of reproduction. If so, it is the partial morphoprocess (not the population, which is the combination thereof!) that is the key object of potential evolutionary changes.

In the light of modern knowledge, the mechanisms of direct adaptogenesis seem to be quite diverse. They are united by one feature: a possible "trans-generational" transition of adaptive modification responses of the organism/partial morphoprocess. In other words, these responses can be reproduced in successive partial morphoprocesses. These are mechanisms of adaptive long-term modifications with subsequent genetic assimilation (Schmalhausen 1982; West-Eberhard 2003; Levis and Pfennig 2016; Levis et al. 2017), paramutation phenomena associated with epigenetic regulation of an allele under the influence of another allele (Chandler 2010; Suter and Martin 2010; Hollick 2017), various other instances of epigenetic and structural inheritance (Jablonka and Lamb 2010; Goldberg et al. 2007; Danchin et al. 2011; Rissman and Adli 2014; Tikhodeyev 2018), phenomena associated with the canalization of development and the genetic basis of phenotypic plasticity (Kirschner and Gerhart 2010; Newman 2010; Pigliucci 2010), mechanisms determining the resistance of bacteria to phages based on CRISPR-CAS system (Koonin and Wolf 2009; Deveau et al. 2010; Horvath and Barrangou 2010; Chylinski et al. 2014). An important contribution to our understanding of the potential importance of mechanisms of direct adaptogenesis is an immense bulk of data describing mechanisms of cell reparation and mechanisms of induced mutagenesis including site-specific mutagenesis under the impact of specific factors (Ponder et al. 2005; Galhardo et al. 2007; Lynch 2010) and ideas about structural limitations and dynamic nature of the genome, including those associated with environmental factors (Capy et al. 2000; Shapiro 2009, 2016; Koonin and Wolf 2010; Laos et al. 2014).

An important aspect of the model of direct adaptogenesis is its ectogenetic nature. It assumes the possibility of transformation under the impact of external factors, that is, ectogenesis. If we speak about understanding the course of evolution in general, the model is also idiographic: each act of transformation is considered unique, being determined by the impact of a unique combination of environmental conditions. In this regard, the model lacks the prerequisites for understanding evolution as a vector process with a regular character.[2]

9.4.3 The Model of Constructional Transformism (Granovitch 2018, 2021), syn. Orthogenesis (Term—Haacke 1893, cit. ex. Popov 2018), from the Greek ὀρθός—Straight)

Within the framework of this model, the driving force of transformation are internal regularities of morphofunctional organization of living systems. The logic of the model may be characterized as self-assembly (not selection!) of increasingly more complex systems. This means that it is the only model that consistently assumes *autogenesis*, the change based on internal structural–functional laws of the morphoprocess, rather than ectogenesis. Based on this feature, this model may be defined as "constructional transformism". It was used in numerous evolutionary concepts, from Galton's polyhedron to the nomogenesis of L. Berg (1922), the typostrophism of O. Schindewolf (1993) and the organicism of A. Vandel (1964) (cit. ex. Popov 2018). Variation of organisms is recognized to be not random but strictly directed. The model is *nomothetic*, being aimed at the search for strict laws of evolutionary transformations and implying the possibility of predictive interpretations. On the whole, the model recognizes the internal directivity of the evolutionary process, i.e. orthogenesis. The main problem of orthogenetic evolutionary interpretations is the seeming lack of a logical explanation of the formation of adaptations of organisms in the course of evolution, that is, their conformity to the environment (Lyubishchev 1982; Gould 2002).

The explanation of evolutionary changes with the help of constructional transformism is based on an enormous body of evidence from three major subject domains: (1) Evidence of a limited character of variation, its non-homogenous character, (2) Evidence of a regular and correlated character of morphogenetic processes in multicellular organisms and (3) Evidence of self-assembly of molecular and cellular structures. It would be futile to try to analyse all this evidence within the framework of this paper. So I will simply list the main information units providing argumentation in these three domains.

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[2] Significantly, it is this feature (understood or intuited) of direct adaptogenesis that made scientists look for additional macroevolutionary mechanisms when constructing holistic concepts based on this logical scheme. These additional conditions were necessary to impart directivity to the evolutionary process, to represent it as a progressive advance. Such were the "gradation principle" of Lamarck (1955), the "principle of perfection" of morphological characters of C. Nägeli (1884, cit. ex. Nazarov 2005) and the "batmism" of E. Cope (1904).

9.4.3.1 Evidence of a Limited and "Non-homogenous" Character of Variation Has Been Analysed Before (Granovitch 2018, 2021), the Main Points Being as Follows

- Fossil record indicates that morphogenesis has a limited character and that there are numerous parallelisms in the evolution of large taxonomic groups (Rozanov 1973, 2005; Tatarinov 1976; Ponomarenko 2005, 2008; Markov 2010).
- "Non-homogenous" character of variation of extant and extinct species is confirmed by the methodology of construction of potentially possible (mathematically calculated) spaces of certain characters (D'Arcy Thompson 1961; Raup 1966, 1967; Raup and Stanley 1978; Thomas and Reif 1993; Ubukata 2005; McGhee 2007; Meyen 2007; Brakefield 2010).
- The manifestation of variability range and separate characters is rather conservative in species from the same genus and even family (Vavilov 1987).
- Broad occurrence of agamic, autogamic and parthenogenetic species among protists and multicellular organisms (Hausmann et al. 2003; Ruppert et al. 2004; Grebel'ny 2008).
- The existence of numerous cryptic species (see for review, Hausmann et al. 2003; Trontelj and Fišer 2009), that is, genetically distinct groups that have all the prerequisites for a morphofunctional divergence based on genetic isolation (Bickford et al. 2006) but remain within the same typological framework.
- Canalized nature and regular character of variation of characters early in the ontogenesis (Kovalenko 1996a, b; Kovalenko and Danilov 2006).
- Ideas about systemic organization of genomes, coordinated functioning of systems of reparation of matrix processes, regulation of the level of mutational variation, directed transposition of mobile genetic elements in the genome of different species (Radman 1974; Echols 1981; Khesin 1984; Gierl 1990; Fedoroff et al. 1995; Golubovskii 2000; Ponder et al. 2005; Shapiro and von Sternberg 2005; Galhardo et al. 2007; Karpen and Hawley 2007; Asis et al. 2008; Koonin and Wolf 2009; Koonin 2010).
- An essentially non-stochastic functioning of epigenetic systems reflecting interactions based on the feedback of the genome sensu stricto (a set of species-specific sequences of DNA nucleotides) and other molecular components of the cell associated with the regulation of functioning of protein-synthesizing apparatus, dynamic structure of chromatin, the laws of "protein" heredity, the functioning of the system of "small RNA" (see a series of reviews, Allis et al. 2007; Tikhodeyev 2018).

9.4.3.2 Evidence of a Regular and Correlated Character of the Morphogenetic Processes in Multicellular Organisms

Ideas about a regular and correlated character of morphogenetic processes in multicellular organisms were first developed by Waddington (1957) and Schmalhausen (1982). These authors, aiming at a better understanding of the nature of an organism (a morphoprocess), emphasize its representation as a system of dynamic correlations. The ontogenetic development of a multicellular organism follows a stable trajectory owing to the internal correlations and the regular character of the major processes, a phenomenon referred to as the canalization of development (Waddington 1957; Scharloo 1991). Evo-devo, currently a flourishing research direction, focuses on the following mechanisms of self-organization, autonomous development and regulation of morphogenesis.

- Self-organization of cellular aggregates into regular multicellular structures, including canalized development of embryos at the early stages of embryogenesis (van den Brink et al. 2014; Baillie-Johnson et al. 2015; Bedzhov et al. 2015; Ozone et al. 2016; Turner et al. 2016; Simunovic and Brivanlou 2017; Bizzarri et al. 2018).
- Formation of specific architectonics of organs using interaction of differentiating cells, including the formation of complex organ-like aggregates from pluripotent iPS cells (Taguchi et al. 2014; Dye et al. 2015; Sakaguchi et al. 2015; Takasato et al. 2015; Guye et al. 2016; Koehler et al. 2017; McCauley and Wells 2017).
- Autonomous patterning of repeated structures based on the physical–chemical reaction–diffusion model (Turing model, Turing 1952) (Cooke and Zeeman 1976; Sheth et al. 2012; Tsiairis and Aulehla 2016; Liao and Oates 2017).
- Processes of self-organization, autonomous coordination of different cell types during the formation of tissues and complex systems of organs of a multicellular organism (Sheth et al. 2012; Raspopovic et al. 2014; Onimaru et al. 2016; Walton et al. 2016).
- Systems switching the development to new stable trajectories based on dynamic modules (Newman 2010).
- Potential mechanisms responsible for the emergence of evolutionary novelties (West-Eberhard 2003; Müller 2010).

9.4.3.3 Evidence of Self-Assembly of Molecular and Cellular Structures

A plethora of data accumulated in the last decades indicates that self-assembly and self-organization of molecular and cellular structures are often due only to their constructional features and are not directly connected with the genetic apparatus of the cell. Both self-assembly and self-organization processes are of interest to us. The distinction between them is traditionally based on energy dependence (Gerhart and Kirschner 1997; Halley and Winkler 2008; Werner et al. 2017). Processes considered as self-assembly are characterized by the minimization of energy in the system, which has approached the state of thermodynamic equilibrium. Correspondingly, these processes do not need an energy supply. On the contrary, self-organization implies the formation of elaborate complexes in a system that is far from the zone of thermodynamic equilibrium. Stable existence and increasing complexity of such systems are possible only under conditions of constant energy flows through them (Prigogine and Stengers 1984). It is noteworthy that processes of both types also contribute to the canalized development of a multicellular organism (see above Sect. Sect. 9.4.3.2).

There is ample evidence of self-assembly and self-organization of molecular complexes and organoids of the cell. Leaving aside self-organization and replication of the genetic apparatus, which are quite well studied, I would like to note that almost all major structures and functions of the cell operate based on these physical and chemical principles. There are data about the self-assembly of membranes, locomotor systems ensuring motility of cellular elements, the self-assembly of organoids, the assembly of cell division apparatus, the formation of vacuoles and, finally, the spatial organization of chromosome material (Palade 1983; Attardi and Schatz 1988; Mitchison 1992; Warren and Wickner 1996; Nédélec et al. 2003; Denton et al. 2003; Carazo-Salas and Nurse 2006; Cortès et al. 2006; Misteli 2007; Papanikou and Glick 2009; Svetina 2009; Inagaki and Katsuno 2017; Sazer and Schiessel 2018). Considering these data, we begin to intuit that the entire morphofunctional organization of the cell is a totality of coordinated processes of self-organization (Misteli 2001; Kurakin 2005; Kholodenko 2006; Karsenti 2008; Johnson and Lam 2010). Hence, we may characterize the cell as a morphoprocess implemented regularly under given physical conditions.

Concluding the third section, I would like to remind the reader that the three models explaining the mechanisms of microevolutionary process (transformism) are far from being new. The first model had underlain the ideas about natural selection in the classical Darwinism and Modern Synthesis (but see Delisle 2017, 2021 to emphasize the differences of the concepts). It incorporated the ideas of Weismann about the continuity of germplasm, assimilated views on heredity, was reborn as Modern Evolutionary Synthesis and underwent numerous modifications under the pressure of new data (Gould 2002; West-Eberhard 2003; Newman 2010; Müller 2010; Pigliucci 2010; Jablonka and Lamb 2010). The second model is rooted in the ideas of Lamarck and Saint-Hilaire, which have been repeatedly reborn as Neo-Lamarckism. The third model also has a venerable history in its numerous guises of ortho-Lamarckian/orthogenetic evolutionary concepts. A comparative characteristic of the three logical schemes presenting potential evolutionary mechanisms transforming the morphoprocess is given in Table 9.1.

These three mechanisms, as well as a group of mechanisms based on a combination of different morphoprocesses (transformation through combinations), are presented in Fig. 9.2, which is discussed in more detail in Conclusion.

9.5 Conclusion

In the three main sections of this work, we specified what exactly we wanted to know about living systems by singling out transformism as the central meaning in the polysemantic notion of "evolution". Then we identified morphoprocesses as the systems to which this notion can be applied most productively. Finally, we concluded that most of the explanations of the mechanisms of transformism ever suggested can be arranged into three logical models describing the transformation of the modality of the general morphoprocess.

Let us now present the differences between the models (and, strangely enough, their similarities too) as a "cladogram of similarities and dissimilarities". In order not to mislead the reader, who might be used to phylogenetic constructions, I specifically state that this scheme bears no relation to the historical outlook on the development

Table 9.1 A comparative characteristics of the three major logical models of transformism

	Indirect adaptogenesis	Direct adaptogenesis	Constructional transformism
Degree of finalism of evolution in general	Ateleogenesis (micro- and macroevolution)	Ateleogenesis (microevolution) Teleogenesis (macroevolution)	Teleogenesis (micro- and macroevolution)
Relationship between the formation of adaptations and the mechanism of microevolution	Adaptogenesis	Adaptogenesis	Anadaptogenesis
Prevalence of internal or external evolutionary forces	Ectogenesis	Ectogenesis	Autogenesis
Degree of gradualness of microevolution	Gradualism	Gradualism	Punctualism
Degree of irreversibility of evolution	Irreversibility	Irreversibility	Reversibility and repeatability
Degree of autonomy of separate features of an organism	Merogenesis	Hologenesis or merogenesis	Hologenesis
Nomothetic or idiographic character	Idiographic	Idiographic (microevolution) nomothetic (macroevolution)	Nomothetic
The unit of microevolution	Population/set of several general morphoprocesses	Single general morphoprocess	Single general morphoprocess

of ideas. Its only purpose is to illustrate the differences in the logic of the models in the order of their similarities and dissimilarities (Fig. 9.2).[3]

Thus, evolutionary changes in the sense of a stable transformation of the modality of the general morphoprocess may occur in two essentially different ways. The first way is the possibility of a combination of characters of partial morphoprocesses of different modalities owing to their incomplete physiological and morphogenetic closedness of organization (see Beklemishev 1970). This category embraces hybridogenesis, symbiogenesis and horizontal transfer of hereditary material—phenomena whose importance for the evolutionary process, in general, have been actively discussed in recent years. Suffice it to say that the symbiogenetic hypothesis is currently considered as the best suited for explaining the origin of various structural types of the eukaryotic cells (Margulis and Fester 1991; Chapman and Margulis 1998; Antonelli et al. 2003; Kozo-Polyanskii and Raven 2010). Horizontal

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[3] Let us note, nevertheless, that all “phylogenetic schemes”, seemingly reconstructing evolutionary events and based on any character basis, are, strictly speaking, simply diagrams of “similarities and differences”. On the contrary, the means of their evolutionary interpretation (evolutionary hypothesis for a given group of organisms as such) would be radically different depending on the assumed model of transformism.

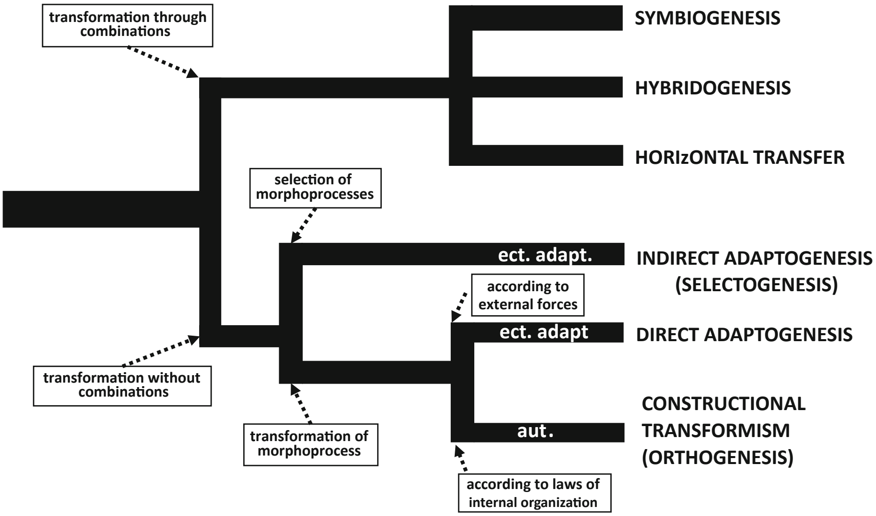

Fig. 9.2 A scheme showing relationships of different models of transformism in the form of a hierarchical tree. Brief comments on the semantic dichotomies of different concepts are given in brackets. *Ect.* ectogenesis; *adapt.* adaptogenesis; *aut.* authogenesis

transfer of genetic material is already assumed to be a leading evolutionary mechanism in prokaryotes (Koonin 2011), while the body of evidence indicating its importance for multicellular eukaryotic organisms is also growing (Gladyshev et al. 2008; Boschetti et al. 2011; Fussmann 2011; Haegeman et al. 2011; Husnik et al. 2013).

In this work, I focussed on other means of transformation, those that do not imply the above combinatory phenomena. The basis of their diversity is the principle of “transformation without combination”, that is, without the combination of partial morphoprocesses belonging to different “species” (see Fig. 9.1). In this case, we deal with a situation when the transformation of the general morphoprocess should be ensured only by its own properties under the influence of environmental factors.

The most important dichotomy associated with this idea results in two different interpretations of the leading mechanisms of the evolutionary process. The first interpretation assumes the leading role of two coupled phenomena, tychogenesis and selectogenesis. It is based on the idea that the modality of the general morphoprocess changes using a selection of partial ones (See Sect. 9.4.1; indirect adaptogenesis). The recognition of such a model as the only correct one necessarily leads to the recognition of the stochastic character of evolution in general and the idiographic nature of our ideas about it. The directivity of the evolutionary process is then a moot question.

Non-fulfilment of the conditions of tychogenesis entails the admission that the mechanism of indirect adaptogenesis is secondary. In this case, the leading role among the mechanisms of transformism should be given to non-selective phenomena, shown in the scheme in the second branch as “transformation of partial morphoprocesses". In this case, we assume a change of the modality of the general morphoprocess using transformation of partial morphoprocesses successively implemented within it. This interpretation, in turn, implies two different emphases on the prevailing mechanisms of transformation.

The first emphasis is on the recognition of the possibility and the leading role of the changes of the partial morphoprocess commensurate with the environment, which are imparted to the general morphoprocess (Sect. 9.4.2, direct adaptogenesis). To note, in this case, too, the ideas about microevolution are idiographic, being based on the direct fixation of stochastic fluctuations of the environmental impact in the general morphoprocess. The second possible emphasis is on the primacy of structural–functional features of the partial morphoprocess for its further modification and the recognition of the environmental impacts as a potential trigger of such modifications (Sect. 9.3.3, constructional transformism). Only these ideas can be the basis of an outlook representing evolution as a regular, directed process and promoting a nomothetic understanding of evolutionary phenomena.

In two out of the three concepts of "transformation without combinations" (indirect and direct adaptogenesis), the adaptation of the morphoprocess to the conditions of the environment and the formation of adaptations are a direct consequence of the operation of the mechanisms of transformism (selectogenesis in the former case and direct, hereditarily fixed reaction in the latter case; adapt. on the scheme). In the case of constructional transformism, an adaptive character of evolution is not evident and calls for additional explanations. I have suggested a possible explanation of the formation of multilevel adaptations within the framework of this model in earlier work (Granovitch 2018).

In the same two concepts (indirect and direct adaptogenesis) transformism appears as an ectogenetic process (ect. in the scheme). In both cases, evolution is triggered, directed and fully determined by the impact of the environment. In contrast, constructional transformism is an autogenetic process (aut.). The emphasis in the explanation of the transformation of the morphoprocess is shifted to internal constructional features of the living matter, the environmental impact being at best a trigger.

In one of the models (indirect adaptogenesis), the leading role in the transformation of the modality of the general morphoprocess is ascribed to natural selection (the mechanism of selectogenesis). In direct adaptogenesis and constructional transformism, the role of the selective principle and hence natural selection is downplayed to an accessory mechanism altogether lacking morphogenetic significance.

In conclusion, I would like to note that, on the one hand, each of the three conceptual models of transformism has its own internal logic. On the other hand, however, these concepts cannot and should not be considered mutually exclusive. The reign of a single concept—indirect adaptogenesis embodied by the Modern Synthesis—is over. A time has come for a careful examination of various transformistic possibilities and the identification of prevailing and accessory mechanisms. Different groups of organisms/types of morphoprocesses may be characterized by different leading mechanisms of transformism, which may belong to both "combinational" and "transformational" phenomena (Fig. 9.2). A vivid example is the recognition of the horizontal transfer of genetic material as one of the leading evolutionary mechanisms in prokaryotes (Koonin 2011). What we currently need most is a balanced assessment of the contribution of different mechanisms characteristic of a given group of organisms/types of the morphoprocesses and the identification of the leading ones. In the age of "postmodernism in the understanding of evolutionary phenomena" (Koonin 2011), we have to consider a broad kit of potential evolutionary tools and try to comprehend evolutionary phenomena at a new level of conceptual synthesis, "Transformism 2.0", based on the input from all conceptual approaches.

Acknowledgments I am eternally grateful to Natalia Lentsman for her creative, thoughtful, generally invaluable contribution to the English translation of the manuscript. This study was supported by a grant from the Russian Science Foundation (RSF) no. 19-14-00321-П.

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Mesological Plasticity as a New Model to Study Plant Cognition, Interactive Ecosystems, and Self-Organized Evolutionary Processes

10

Marc-Williams Debono

Abstract

The plasticity of living systems acts at several levels of evolutionary biology including self-organization, phenotypic, phylo-, onto-, and epigenetic processes, while mesology is an approach situated in between ecology and phenomenology. After a description of the specific objects of plasticity and mesology as non-dualist studies of the dynamical coupling between beings and their singular milieu, we will develop some arguments regarding the perception–action loop and the sensory flux of informations crossing the evolution of the living, before focusing on recent discoveries about plant electrome. Using for the first time mesological plasticity as a frame to reanalyze the Uexcküll's assertions about Umwelt and meaning-making theories of plants, this chapter shows the leading rule of electromic interfaces in the generation of spontaneous low-voltage variations continuously emitted by plants via electrophytographic or EPG recordings. Used as early markers, EPGs are considered in this framework as natural systems of monitoring and discrimination of environmental stimuli that allow the identification of the electromic signature of a plant–stimulus pair in a given milieu. More generally, we will develop the trajections associated with complex behaviors of plants: a bottom-up transdisciplinary view of co-evolutionary or ecosemiotic processes highlighting their specific sensitive fields and cognitive accesses to experience (their otherness) as well as new phenomenologies about interactive ecosystems and phytosemiotics.

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_10

Keywords

Plant electrome · Electrophytography · Plasticity concept · Interactive ecosystem · Mesological plasticity · Cognition · Phytosemiotics · Transdisciplinarity

10.1 Introduction

Plant "intelligent" behaviors (Trewavas 2003) upset today notions rooted in our evolutionary schemata, largely anthropocentric, questioning self-organized knowledge-accumulating and non-linear dynamic evolutionary systems including as main marker bioelectrical correlates of their extensive communication strategies and embodied or extended cognitive abilities compared to neuroplasticity and the rapid sensorimotor coordination of animals. We will show that plants are plastic interfaces that behave as self-organized entities with protoneural abilities leading to active perception systems close to those of animals and non-linear dynamic processes which have progressively conducted to the eclosion of complex brain networks during evolution. The sensory and bioelectrical (or electromic) abilities of plants constitute indeed a privileged field of study of the interface between living organisms and the environment (mesology) as well as their non-nervous ways of processing information (Debono 2013a, b; Debono and Souza 2019).

After describing the confluence between the two major approaches of plasticity as a "science of forms" and mesology as a "science of environments," we will detail the electrical dimension of plant life (de Toledo et al. 2019) and the primordial role that electromic pathways play in communication and rapid diffusion of information in plants. Among these electromic activities, we will focus on the little known and underestimated role of spontaneous extracellular variations or EPGs (electrophytograms)[1]emitted at the level of plant tissues, looking in particular in the mesological approach for the Uexcküllian flaws that led to this positioning. This will lead us to the modeling of a new approach to the relationship between the plant and its milieu (mesological plasticity) and the discovery of specific signatures of the electrome in relation to some stimuli or field experiments that have important implications and repercussions in experimental works in evolutionary biology or plant electrophysiology, but also in botany, agro-ecology, biosemiotics, ecophysiology, and cognitive sciences.

We will also explore throughout this chapter new worlds that intersect and co-signify each other and more generally re-interrogate around this new botanical front of science on the notions of form, intelligence, sensitivity, metamorphosis, cognition, or identity. A journey that, we hope, will allow us to take a new look at the otherness of plants and the primordial impact of epigenetic plasticity as well as the influence of the milieu differentiated from the environment during evolution. "What

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[1] See paragraph 10. Section 10.4.2 related to the epistemological context linked to the discovery of EPGs in plants.

a plant knows?" asked Chamovitz (2017) discussing about the sensory system of plants. It is clearly the question. We will see that plants can show complex behaviors, sensibility, and minimal cognition (Calvo and Keijzer 2011). At the level of evolutionary biology, the real question regards their specific relationships with the milieu and their interactive ecosystem, their otherness. In such an area, we will show that plants are: (1) *plastic interfaces* having as main motor the form/matter cople, acting mainly at the level of phenotypic (direct impact on their life cycle and fitness), morphogenetic, and epigenetic plasticity; (2) *electromic interfaces* using bioelectrical networks and non-linear dynamic systems as facilitator and discriminative processes to communicate and spread information; (3) *mesological interfaces* using phytosemiotics and the plant/milieu entity to grow optimally and fit in (Debono and Souza 2019; Debono 2020b). Starting from there, we can break out of the zoocentric or neurocentric mold done by many authors and affirm that, if plants use the same directory of cell signalization (ionic channels, bioelectric currents, chemical neurotransmitters...) without brain and neurons (contrarily to the enteric nervous system, for instance) and are eukaryotes as us, they do not have the same sensorial and subjective experience at the end. This is because or dynamical coupling with the milieu is singular, based on morphisms, meanings, topological situations, and *subjectivity* (Berque 2015).

10.2 The Epistemic Concept of Plasticity: Ontology and Complexion

Born from an observable—the brain plasticity—(which is of course not a metaphor), linked to my activities as a researcher in neurobiology, the scope of this universal property of matter that describes also a process, very early on imposed itself on me as fundamental to be explored, both on theoretical and experimental levels. Indeed, the progressive elaboration of the epistemological concept of plasticity was initiated by the publication of "L'ère des plasticiens" (Debono 1996) describing a new evolutionary logic (non-binary and transversal) taking plasticity out of its ruts (until then focalized on visual arts or biological functionality) and opening it up to transversal grids of lecture. At the experimental level, the implementation of transdisciplinary (TD) research groups working around evolutionary processes using mathematical modelization, biology, cognitive sciences, neuroplasticity, experimental medicine and posturology, biophysics, genetics, paleoanthropology, neurosemantics or art and science relationships, was effective during several years within the framework of the GDP[2] founded in 1994 in Paris. The success of this enterprise has allowed to gradually mark out the different plastic interfaces and to create a research background on the concept of plasticity and its evolutions, notably through the opening of a new research area on plastic processes and the regular publications of the

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[2] Groupe des Plasticiens: see the minutes of the GDP Conferences on the PSA website referenced in 4.

Transdisciplinary Review of Human Plasticity *Plastir*[3] founded in 2005 which gathers nearly 150 authors around TD themes having plasticity as a junction point, which you can follow on the official website of the PSA (Plasticities Sciences Arts) research group.[4]

As a matter of fact, the term of plasticity from the Greek *plassein* concerns form and matter in the first place. For a long time exclusively attached to esthetics, fine arts, and the humanities, now concerns all scientific fields (plasticity of materials, of the brain, human plasticity. . .) as well as philosophical ones. It has been sometimes misused due to its ubiquity (Aristotle), man's power of self-transformation (Plato's myth of epimetheus), universality and historicity (from Harvey with his *vis plastica* and Pic de la Mirandole with his "*De dignitate hominis oratio"*) (1486) to different scientific traditions (biology, embryology, genetics, morphogenesis, anthropology...) including the works of Wolffe (2000), Driesch (1892), Pigliucci (2001), Haeckel (1904), Woltereck (1909), Johannsen (1911), Thom (1966, 1977), D'Arcy Thomson (1917), the plastic nature of the neoplasticians Cudworth (1820) and the philosophical approaches of Leibniz (*Monads*, 1646–1716),[5] Goethe 1999, 2004 (*Plastizität,* 1749–1832), Heidegger (1961, 1982), Kant (1967, 1781) and specifically Hegel linking subjectivity, temporality, and plasticity in "The phenomenology of mind" (1939–1941).

At the contemporary level, only two concepts are operational today to my knowledge, presenting common points—about plastic dynamics—and divergence—about objects and methodology—: our epistemic and transdisciplinary approach to the concept of plasticity and the Malabou's philosophical positioning linking ontology, temporality, and the post-historical future of man. This approach takes us out of passivity by describing an active and sometimes negative (or explosive, plasticizing) plasticity following Deleuze and the deconstructivist post-Hegelian philosophical current (Malabou 1996). We share this dynamic conception of plasticity (plastids vs plasmas, ex. sculpture) taking into account the intelligibility of forms and the temporality of the plastic process, provided that we place it in the transdisciplinary context of the third included which allows us to exceed the active–passive or negative–positive antagonist terms (Contradiction logic, Lupasco 1970, 1986) and indicates that we are dealing with a ternary Lupascian process and/or an imprint-matrix mode (Berque 2014a) more than with an emerging property. This is true for developmental and functional plasticity and at the junction between the humanities and the fundamental sciences embodied by a plastic process in progress. The plasticity of the living includes indeed self-organized and dynamic non-linear systems that co-determine or co-signify themselves reciprocally, participating in the genesis of the forms from which they originate and not only undergoing it. The different interfaces and plastic complexes that we will describe

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[3] Plastir: the Transdisciplinary Review of Human Plasticity is available online on the PSA website (see summary and English abstracts): http://www.plasticites-sciences-arts.org/plastir/

[4] PSA Website: http://www.plasticites-sciences-arts.org

[5] Please also look at the more recent reference on Leibniz (2004) and More (1969, 1987).

Table 10.1 Plasticogenesis—from plastic interfaces to epistemic processes. The unformed–formed step symbolizes the primitive link prefiguring the formation of matter while the matter–form interface is the operational one, which may involve energetic processes. Both interfaces can generate plasma–plastid or structured–structuring relationships, fundamental in morphogenetics or developmental plasticity (Debono 2005, 2021b). The three main steps of the plasticogenetic process are: (1) the formation of plastic interfaces (PI), (2) of active bondings (AB), and (3) of irreversible plasticity complexes (PC) like BEP-BMP leading to ternary paths conducting to co-meaning metaplastic or epistemic processes (see Table 10.2). © MW Debono

Plastic Interfaces	Plasticity complexes	Co-meaning Processes	Epistemic Processes
Articulation *Unformed-Formed* (Plastid-Plasma) ▼ Matter-Form (Matter-Energy)	Active Bonding ▼ Complexion (Irreversibility)	Co-implication Co-construction ▼ Ontology Semiotics Recipro city	Metaplasticity *(plasticity of the plasticity)* ▼ Ternary Paths & Complexes Tierceity Tetralemna T State

more specifically in the plasticogenetic process allow plasticity to seal this movement and to inscribe it in a common ontology (Table 10.1).

The concept of plasticity is then not dualistic and seeks the principles of coherence and defragmentation of knowledge, following a transdisciplinary approach (Debono 2005, 2010, 2012). More generally, plasticity could be assimilated to the science of forms. It is not either purely descriptive but has a raised predictive value of the dynamic behavior of nonliving systems, being a founding property and not only a systemic or an emergent one. In this direction, regarding advances in systemic plasticity, biophysical science, cognitive neurosciences, or ecosystemics, it is necessary to speak of metaplasticity as a way to explore the genesis of natural processes. As explained in a recent paper summarizing the evolution of the epistemic concept of plasticity—from the concept to the complex of plasticity—and then a description of its mesological part (Debono 2021a, b), plasticity is a key notion in any evolutionary process that looks at form and matter in the first place. It concerns all inert or living systems and contrary to elasticity, flexibility, or malleability, leads to an irreversibility of the dynamic link established between two interfaces that cannot be reduced to each other (plastic interfaces) and then to the formation of plasticity complexes[6] of which plasticity is an included third.

As a matter of fact, the specificity of plasticity, apart from its primary function within the matter–form interface, is its irreversibility and ability to active processes of transformation in which the events evolve while co-signifying mutually, in other

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[6] From complexion or aggregation (not from complexity), look at the main plasticity complexes described in Table 10.2.

Table 10.2 Some of the main plasticity complexes. At the level of vegetal plasticity, the primacy of the form (implying phenotypic as well as epigenetic plasticity) is expressed mainly through plant morphogenesis and the mesological plasticity of the dynamical coupling between plants and their singular milieu (BEP). © MW Debono (2021a, b)

Main plasticity complexes
MFP (Matter–Form–Plasticity): Autopoietic Plasticity, Self-Organization, Materials Plasticity (Physics), Structured–Structuring Relationships, Morphogenesis, Cosmogonies...
IAP (Innate–Acquired–Plasticity): Evolutionary Biology, Ontogenesis, Phenotypic, Philo- and Epigenetic Plasticity
BMP (Brain–Mind–Plasticity): Neuroplasticity, Experience–Consciousness Relationships, Affect. . .
SOP (Subject–Object–Plasticity): Plasticity of the living (PL), Interobjectivity/subjectivity, Sociobiological Systems, Ontological Plasticity, Alterity, Identity, Human Plasticity. . .
BEP-BMP (Being–Environment–Plasticity, Body–Mind–Plasticity)

words are structured as much as structuring, including a reciprocity between ascending and downward systems inside the same system or of interacting systems (e.g., brain/mind or experience/consciousness). This behavior implies a universal capacity of articulating fundamental pairs such as form vs matter, form vs object or subject, etc. This active binding includes non-linear dynamic systems (like EPGs and electromic interfaces) and obeys a transverse logic by creating irreversible plastic complexes where plasticity is a catalyst. The important point is that plasticity is the third included of the complexes formed (see below) and acts directly at the anchorage point of dimensions or irreducible expressions by including the object or subject in the plasticity of the world. Ontology and complexion are thus two fundamental steps of the plastic process. The following tables summarize the four steps of plasticogenesis, showing the main plasticity complexes from matter–form–plasticity to brain–mind–world (Tables 10.1 and 10.2).

The plasticity of living systems is more specifically related to our field of study and to the subject we are addressing in this chapter. It is classically defined as a self-organizing and order-generating capacity of living systems and/or a durable deformability of structures. Systemic studies of functional trajectories and variability differentiate rigid systems like robots with functional invariance and flexible or homeostatic systems with structural invariance including systematic variability from plasticity including vicariance and further modifications (Paillard 1976; Debono 2017). Elasticity describes a systemic auto-adaptability to program changes while plasticity assumes the ability of a stable or autostabilized system to be deformed or to deform in a lasting and sensitive way its own structures or sub-structures (synaptic plasticity) and to exceed its own limits (transformation or fine equilibration of thermodynamic couplings or environmental pressures). The plasticity of the function is therefore described as an open system or a systemic unit (Weiss 1941, Jacob's integron) that is specified by its structure, functioning, and function (SFF). Only plastic systems can modify this trivalent system.

To summarize: plasticity is opposed to flexibility and systemic stability and an irreversible deformability, capable of surviving its initial causes, distinguishes plasticity from elasticity, flexibility, or malleability. It concerns the form as well as the function of living organisms, their sensitivity to the external environment, their structured–structuring relationships of which the phenotypic (Pigliucci 2001; West-Eberhard 2003) and epigenetic plasticity[7] are strong anchors. In other words, plasticity is a unique dynamic interface between two sensitive worlds, concerning as much the simplest self-organized systems as cortical representations of the human brain. It includes the capacity of the mature system to reshape its own structure and/or to create new entries in the system: typically motor and somatotopic cards or synaptic and cognitive plasticity leading to structural reshuffling of networks at the cerebral scale (Greenwood and Parasuraman 2010).

The recent rise of the evo-devo approach in laboratories around the world has led to a revaluation of the effective and dynamic role of plasticity in living organisms, whether it is phenotypic, ontogenetic, or phylogenetic, highlighting the major influence of interactions with the environment and the milieu during development. Plasticity has indeed become a major evolutionary concept because it is finally recognized for what it is, an efficient means at the scale of individuals as well as populations to develop innovative adaptive strategies (micro as well as macro-evolutionary) responding to or thwarting the heterogeneous spatiotemporal distribution maps of the environment by optimizing survival as well as the singular relationships between living beings and their environment. More generally, plasticity revolutionizes a part of the history of science by becoming a central concept in evolutionary and humanistic biology.[8]

10.3 The Concept of Mesology: Being, Environment, and Trajection

Before focusing on the plant electrome as a privileged interface for the study of this new concept of mesological plasticity, we will present the basis of the contemporary mesological approach and its interest in the study of living systems during evolution. We will adopt here the contemporary scientific approach of the orientalist geographer Berque as to the contemporary definition of mesology, which can be generically described as the science of environments (singular milieu, habitat, or immediate environments with which plants and animals directly interact) as opposed to classical environmental sciences. Indeed, this classification was based on the naturalistic foundations of the founder of ethology Jacob von Uexküll about the Umvelt and the quasi-contemporary discoveries of the Japanese philosopher Watsuji Tetsurô (1934–1935) who, listening to Heideggerian philosophy (1992), introduced the

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[7] Related to the historical works from Harvey (1651), Buffon (1749), Waddington (1942, 1957), Lamarck (1815–1822). See reference list.

[8] The biology of the twentieth century in PhasPhen (2017), CNRS Savoie Thematic School, GDR (University of Lyon 1 CNRS - LBBE/Biometry and Vegetal Biology Laboratory UMR5558-INRA).

concept of fûdosei 風土性 meaning "the structural moment of human existence" or the dynamic coupling of the being and its environment (Berque 2014b, 2016). This is one of the founding principles of mesology about human or ecoumenical environments (Berque 2000).

The Berquian school or ecologists like Tassin (2020) are more generally opposed to a scientific ecology that considers the environment and biodiversity as socio-economic variables to be adjusted and not the singular and sensible links established directly between living organisms (animals, plants, or humans with the notion of ecumene) and the milieu. This approach is not limited to niches or to Darwinian adaptation but takes into account the topological, biosemiotic, and ontological dimension of these specific links that are independent of the raw and universal data of the environment (Umgebung). The milieu is thus regarded as being relative to a subject and conversely, contrary to the dualist or mechanicist considerations of the West. It is what exists concretely for the subject (or a given species: famous example of the tick), whereas the environment is a universal object carried by the glance of an abstract observer. Between the environment and the being concerned expresses itself thus a "counterpoint" (Kontrapunkt) or a "counter-assemblage" (Gegengefüge), which makes that the two terms are inseparable (Berque 2014a,b, 2016).

Mesology can thus be compared to ecophysiology (Souza et al. 2018), a scientific discipline that integrates the behavioral and physiological responses of living organisms in a given environmental context and seeks to understand how populations of different species of living beings constantly face the constraints of their environment during evolution. However, it has an ecophenomenological, semiotic, and societal dimension that clearly distinguishes it from classical ecology, a term with which it has historically co-evolved.[9] Indeed, as already mentioned, the new contributions developed by Berque from the works of Watsuji and Uexküll introduce the concept of trajection resulting from the landscape trajection, then resituated as a ternary passage compared to the Chôra of Plato—at the same time imprint and matrix—and to the Indian tetralemma: Berque (2014a) and the state of mediance (translation of the dynamic coupling between the being and its environment or fudôsei). According to the author: "It is the seizure of the Umgebung as Umwelt"; in other words, it is the "as that" by which the Earth is seized (by the senses, the action, the thought, the word), as a world." This seizure is analogous to a predicate, in which the mesological reality (which is the reality at all for the being considered) can be represented by the formula: $r = S/P$, where r is the reality, S the logical subject (what it is about, i.e. the Earth or the nature), the oblique or diagonal, the "as that" and P the predicate (what is seized from S, i.e., the world). In other words, concrete reality is neither simply objective (S), nor simply subjective (P); it is trajective (S/P). Several trajective chains like the semiological chains of Barthes or Pierce can be involved (Berque 2019).

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[9] Haeckel published the term ökologie in 1866 (*Generelle Morphologie*, Berlin, Reimer Vol. 2, p. 286). See also the recent publication of Levit GS and Hossfeld (2019) on the subject.

10.4 Plant Electrome and Cognition

10.4.1 Behaviors and Signalization in Plants

The cellular communication of plants is as complex as that of animal cells with a directory of similar ion channels although with specific differences such as their intra- and extracellular compositions or the existence of proton pumps (H^+ transport against metabolic gradients and ATPases), several membranes (plasmatic, vacuolar, pectocellulosic wall) of which the plasmalemma is the most important autoregenerated electrome, transporters, and membrane proteins forming several dozens of sensory receptors. Among these, growth hormones like auxin, efficient photoreceptors, and the ability to distinguish certain wavelengths, chemoreceptors capable of synthesizing some 3000 molecules or chemical compounds emitted and processed by plants, including methyljasmonate, anti-stress substances, or BVOCs (Biogenic Volatile Organic Compounds) allowing remote exchange or defense against attacks from herbivores. In the same way, many sensitive sensors allow a direct interaction with the ecosystem or the environment (insect pollinator, soil moisture, gravitation, electromagnetism, exploration of the chemical composition of the soil, air or space—climbing plants—, mechanosensory receptors, phonotropism—effect on the direction of the roots—, emission and capture of clicks for the purpose of intra and interspecies communication, etc.). Behaviors involving mobility, memorization and certain forms of learning that are described in many species (*Mimosa pudica*, Venus flytrap, *Dionaea muscipula*, Nepenthes) and present adapted behaviors and learning capacities according to the danger of predators (insects, lizards, small mammals, worms) or the search for nitrogen in the soil essential to produce proteins (Wildon et al. 1992; Volkov et al. 2010; Volkov 2014; Cheung et al. 2020 for a recent review).

Among the many recent discoveries of plant neurobiology research launched by the school of Florence and Bohn and refocused today around the signaling and behaviors of plants (Baluška and Mancuso 2009; Brenner et al. 2006), we can quote the highlighting of the underground communication carried out by roots allied to mycelia and hyphae forming one of the densest symbiotic networks: the mycorrhiza or the “wood wide web” (Volkov et al. 2019). This signaling network considerably increases the volume of soil and the active surface of the roots (factor 700) by ensuring a dosed distribution of sugars and water to the plants and their neighbors according to their needs and to the changes of situations (drought, stress, priorities, obstacle circumvention, etc.). It can be thousands of years old in some trees and measure several tens of km^2. The question of individuality and quasi-immortality of the plant kingdom is also raised at this level, given the plurality of possible genomes of a single tree whose own individuality or its progressive colonization of close organisms is not known. In addition, the efficiency of this high-speed network allows trees to communicate with their congeners, or even with other species, that can present behaviors interpreted as solidary or social (intertwining, defense and prevention strategies; Simard et al. 2012).

These complex modes of plant communication relayed by the interconnected meristems and efficient aerial networks of plants through a body anchored to the ground and required to react permanently to environmental stimuli are one of the findings leading us to rethink the scale of plasticity of living systems. In particular, it raises the question of the divergence of the kingdoms; many works underlining the fact that it is not so clear-cut. This taxonomic re-evaluation of the evolution of plants compared to animals (Selosse 2012),[10] added to the classical observation of inter-species co-evolutionary processes between plants and animal pollinators, deserves to be developed. The crucial role of hormones and neurotransmitter analogs in growth, sensory responses (light, orientation, gravity, oxygen, moisture, inorganic nutrients for roots) or stress in plants, the emission of toxic substances or long-distance volatile gases like ethylene,[11,12] repair or vascularization of plants are also clear signs of high sensibility (different from the nervous system of animals) and access to immediate experience necessary to optimize their survival and growth.

New scientific approaches of plant behavior, signaling, and cognition clearly show since two decades that perception–action loops, cognitive abilities (Calvo and Keijzer 2011, 2016), or intelligent behaviors (Trewavas 2003, 2005; Mancuso and Viola 2013) are widely developed in plants. These extensive studies including the biomolecular, genetic, and epigenetic plan as well as the whole plant behavior show the benefit that plant evolution brings in terms of sensory coding, learning, directed individual variation, and adaptability (Calvo 2016). Plant complex behaviors and goal-directed changes are used to face adverse or competitive environments, giving them the best response to adapt and improve their survival. Several mechanisms including competition, regeneration, mutualism, cooperation, local memory, or learning are involved using common electrochemical communication and functions (perception, sensory inputs, hormonal system, growth, reproduction, development, cognition maps described here for niche construction) than animals. They legitimately raise questions about the nature of emerging behaviors in plants, including terms like intelligence, sentience, or cognition.

Perhaps the problem has been posed backwards from the start and we should have seen before the "radical otherness" advocated by Hallé (2014) concerning plants rather than trying to compare animal and plant kingdoms at all costs? Still, without entering into this semantic debate, which has ancient roots with the fundamental pioneering work of Bose on bioelectricity and the nervous mechanism of plants (1901, 1902, 1926)[13] or even earlier by von Sachs noting the analogies between the responses of plants and those of animal skeletal muscles (1874, 1862) or by Darwin

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[10] Common evolutionary tree until before the divergence of the kingdoms and introduction to a new classification of eukaryotes (Chlorobiont vs Zoobiont).

[11] Plants dose their responses according to the danger involved: from leaves rendered inappetent to some pests to poison like tannins for their predators.

[12] Wouter Van Hoven, Wildlife Management Centre, Pretoria, South Africa. Famous observation of emission of toxic substances and volatile gas by kudu-killing acacia trees (over-interpreted? as an ability to warn neighboring trees of danger).

[13] See Bose refs and Tandon (2019) for a recent review of Bose's pioneering work.

working on the movements of plants[14] and the self-recognition of Orchids (1864, 1881), the observation is that, apart from some overly anthropo- or neurocentric statements, it has given rise to a wealth of indisputable scientific results ranging from botany to epigenetics and interdisciplinary discoveries updating the remarkable capacities of the plant world in terms of communication or sensitivity (Baluška et al. 2006). Many philosophers, engineers, anthropologists, or ecologists have also taken up the issue with anthropocentric, metaphysical, or ethical overtones.[15]

10.4.2 Role of Low-Voltage Spontaneous Variations or Electrophytograms (EPGs) Recorded at the Whole Plant Level: Dynamics of the Plant Electrome

The electrome, term introduced by De Loof (2016) in analogy to the biome or the genome represents the totality of the ionic and electric dynamics present at different scales of organization of the plant or the electrical dimension of plant life (de Toledo et al. 2019). Knowing that cell signaling and bioelectricity are two major ways of processing information in plants, we have demonstrated by pioneering works (Debono and Bouteau 1992) that spontaneous microvolted extracellular variations or oscillations called electrophytograms contribute actively to the expression and signature of plant's electrome (Debono 2013a) considered as a self-organized complex with "multicolored" noise summing up all of the ionic repertory and bioelectrical activity of plant tissues (Souza et al. 2017). This non-random bioelectrical activity is analogous in terms of amplitude to EEGs conventionally recorded in animals (mathematical derivative representing the algebraic sum of biomolecular signals associated with polarization–depolarization of cell membranes), but present neither the same temporality, nor the same degree of correlation and complexity.

As a matter of fact, the spontaneous oscillations that I described and named electrophytograms or EPGs in a pioneering way (Debono and Bouteau 1992) due to their EEG-like chaotic characteristics were for a long time confused with background noise due to their weak voltage and amplitude but also obscured by the researchers themselves due to what has been called the "Backster effect."[16] Today

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[14] Current research on the root apex confirm Darwin's predictions and are described as synapse-like properties by Baluška and Mancuso (2013) Baluška et al. (2004, 2005).

[15] Philosophers such as Calvo and Keijzer (2011), Coccia (2016), Marder (2013a, b), Hall (2011), Hiernaux (2019), Morizot (2020); anthropologists like Kohn (2013) or Descola (2005, 2019), ecologists like Tassin (2020), ethicists like Pouteau (2014, 2018), forest engineers such as legal approaches about plant law, political status, human–plant relationship, or the planthropocene (Marder 2013a, b, Myers 2017, Haraway 2003, 2008, Tsing 2012) are widely published. See reference list for details.

[16] This side-effect was related to the pseudo-scientific experiments of a former CIA agent who interpreted the same kind of bioelectrical traces (weak oscillations recorded with a galvanometer) by lending intentions and feelings to plants, which in the context of the New Age had the echoes that one could expect (mediatized by the worldwide best seller of Tompkins and Bird "*The secret life of plants*"), but above all had the serious consequence of obscuring electrophysiological researches in

this debate is totally outdated and our results validated by several independent teams in the world. The aim is now to understand the exact role played by EPGs in the life of plants with various approaches (modeling, quantification, monitoring in natural environment with multisensors or EPG kits, filtering) searching for patterns or specific signatures of the electromic field related to certain stimuli (Parise et al. 2020, 2021; Debono and Souza 2019) We detail in this chapter several of these approaches and our up-to-date working hypothesis concerning the precise role of EPGs in the operability of the plant–environment relationship and its cognition modes (Debono 2013a, b, 2021a, b). Contextually, much long-muted plant electrophysiology work is now becoming audible and this new perception of two-way information flows and complex communication strategies in plants points to a radically different perspective on our anthropocentric view of life or otherness (Debono 2004, 2018) which goes hand in hand with the need to reconsider taxa as well as the notion of boundaries between living beings. One of the fundamental ways to measure these activities at the cellular and organic level is to proceed to a precise bioelectrical survey of the perception–action loop or of the physiological state of plants. Valuable information on the duration, amplitude, type of conduction, function, and localization of signals will provide us in the coming decades with essential clues on the communication capacities of plants. Two anatomical sites are particularly promising at this level: meristems, vascular tissues located at the ends of underground (root) and aerial branches that interconnect with each other, and the electrome representing the global electrical activity of the plant organism, which can be collected, in addition to the cellular level, in the form of spontaneous low-voltage (20–200 μV) variation potentials or EPGs permanently emitted at the level of sets of tissues that can propagate themselves in network at the whole plant level (Debono 2013a, Fig. 10.1). This synchronization of EPG activities between different tissues of the same plant has been validated by Masi et al. (2009) with a multi-electrode array recording technique (60 channel MEA) able of quantifying them and following their spatiotemporal course in high resolution in maize roots.

These spontaneous EPG variations were shown interspersed with isolated spikes or sharp oscillations lasting several seconds or minutes after a natural or evoked stimulation (Debono 2013a), evoking a marked reactivity to certain stimuli (Fig. 10.1). EPG activities are indeed added to the panoply of classical bioelectrical signals brought into play during the various scenarios physiologically soliciting the plants (Fromm and Lautner 2007; Chen et al. 2016). It is about action potentials or APs triggered by a depolarization of the membrane following ionic flows, variation potentials or VPs specific to plants produced in the xylem and mainly induced by biotic or abiotic mechanical stimuli, injuries or herbivore attacks, systemic potentials or SPs which are hyperpolarized signals (H^+ pump) gradual in nature propagating at long distance (5–10 cm/min) in the phloem and local potentials or LPs emitted directly at the stimulated area under the influence of environmental factors (light,

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this area, made outside of us by two or three other teams in the world like that of Pickard in the USA (1971), for almost three decades!

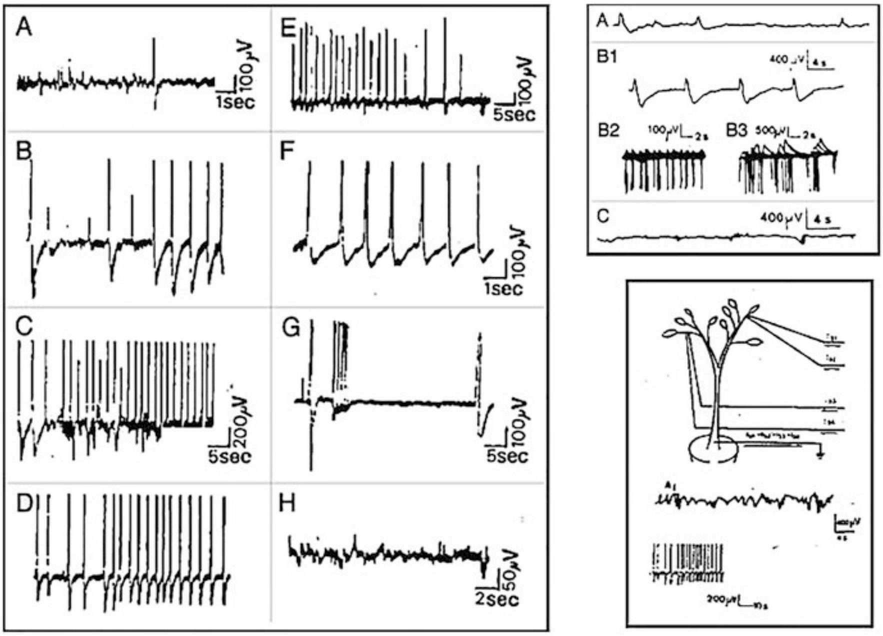

Fig. 10.1 Dynamic protoneural networks in plants: a new approach of spontaneous extracellular potential variations (From M-W Debono, Plant Signaling and Behavior, Vol 8, N°6, 2013a, © Landes Biosciences). Left plots: Spontaneous low-voltage oscillatory activity or electrophytograms (EPGs) and isolated “spikes” recorded in Kalanchoe Daigremontiana. (**a**) followed by a train of higher amplitude spikes evoked by a mechanical stimulus (**b–g**) and a recovery of the baseline (**h**). Right plots: **b1**, **c** Chemical activation (Fusicoccin 3.7 μM) inducing spike-wave discharge for 27 min interrupted by application of a metabolic inhibitor (FCCP 50 μM). Diagram on the bottom right: experimental setup including both spontaneous and evoked EPGs

temperature, air humidity, water, hormone, pathogen infection...) plus long-distance signals using glutamate like Ca^{2+} waves (spiking and oscillations) emitted for plant-defense signaling (Toyota et al. 2018) following herbivore attacks or mechanical wounding converting local signals to a systemic defense program in the whole plant (Tian et al. 2020).

10.4.3 Signature of the Electrome and Plant Cognition: A New Electromic Reading Grid

More generally, being preponderant in any process engaging perception, reaction, or non-linear behavior of plants, the electrome dynamics generates a constant electrical activity as a consequence of the movement of electrically charged particles and the emission of electric fields partly due to the electrochemical gradients formed. To this must be added the action of mobile and immobile charges involving polymers or macromolecules, electrogenic pumps or electronic flows in chloroplasts and mitochondria. Propagation of signals at short distance is done via plasmodesmata forming a symplasm and permitting cell to cell or intercellular communication. Propagation of signals at long distance concerning vascular and hydraulic systems like the transport of liquids or sugars (essential energy and photosynthesis) is made bottom-up (Xylem) or top-down (Phloem) with rapid conductivities implying hydric or hormonal signals (auxin), calcium oscillations, and chemical mediators (Hedrich et al. 2016).

The EPG chaotic activity was recently attributed by Souza et al. (2017) to a self-organized critical state (SOC) of the whole plant. According to a work to which I am currently contributing, it could correspond to a non-linear dynamic behavior able to manage the permanent influx of stimuli of all kinds that assail the plant (wind, rain, drought, mechanical shocks, predation, etc...) and have a central role in the relational life or cognitive ecology (Real 1993) of plants. The same team recently demonstrated that the EPGs show a distribution according to the power law which is defined by two constants: a (proportionality) and k (exponent) which characterize large systems presenting invariant scales. Under some conditions, they can push them toward a SOC conventionally observed in non-linear dynamic systems (Souza et al. 2017). Power density spectrum (PSD) and autocorrelation studies carried out by these authors, respectively show that SOCs and non-linear dynamic behaviors present different patterns and colored noises, depending on the kind of stimulus applied (Mannitol, cold, low light. . .), corresponding to the previous isolated spikes or evoked potentials in the form of regular oscillations that we had recorded outside spontaneous EPGs (Debono 2013a, b). As previously described, temporal correlations on large scales show also a long-distance treatment of complex information emerging from different temporospatial patterns propagating through all plant tissues (Masi et al. 2009). Other teams like that of Gimenez et al. (2021) have recorded different patterns of bioelectrical oscillatory signals in different Miconia species, using learning machine techniques and in non-invasive in loco recordings, several specific patterns and spectral densities were recorded depending on the species influenced by environmental factors. We therefore assume that EPGs are widely used for the detection and discrimination of the stimuli when dynamic coupling occurs via SOCs, allowing plants to prioritize warning or defense signals and optimize their survival and growth. A constant EPG monitoring of plants will permit to measure this discrimination rate and the management of the environmental stimuli done in real time by plants (water supply during drought, brutal climate changes, interspecies relations, osmotic shock, stress...) in order to ensure their optimal growth (Saraiva et al. 2017; Debono and Souza 2019; Debono 2021a, b).

Indeed, EPG like signals[17] having been recently validated by several teams in the world like those of Masi et al. (2009) or Cabral et al. (2011), I am now pursuing my

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[17] Our EPG technique (Debono 2013a, initially published in 1992) must not to be confused with a recent technique called electropenetrography or EPG measuring the electrical penetration graph to study plant–insect interactions. This technique is also used to study plant virus transmission, host plant selection by insects, and the feeding process of insects in plant tissues. Lucini and Panizzi (2018) describe, for instance, experiments with aphids (phytophagous stink bugs or pentatomids)

research since 2016 in collaboration with the laboratory of plant cognition and electrophysiology (Department of Botany, Institute of Biology, Federal University of Pelotas, Brazil directed by Pr. Souza). This research team has indeed validated and quantified EPG activities in plant tissues analyzing the chaotic dynamic of their time series (Pereira et al. 2018). The results obtained also highlighted spikes following a power law only when plants were subjected to specific stimuli such as osmotic stress (Saraiva et al. 2017; Souza et al. 2017). Next experiments will be done in natural environment, assuming that laboratory experiments do not allow having an exhaustive survey of the reactivity and interactivity of plants in their natural ecosystem.[18] As a matter of fact, recordings with EPG kits or multiple sensors in constant monitoring could allow to validate definitively our operational hypothesis and to show synchronization among bioelectrical signals and formation of specific patterns or signatures of the electrome following external stimuli. We hope especially that these in loco experiments will confirm our hypothesis about the watch (spontaneous variations) and discriminative role of plant's EPGs responding to environmental stimuli and downstream: (1) the Uexkül's functional circle as support of meaning-making theory, Umwelt and more generally the value of bio- or phytosemiotics; (2) the mesological plasticity and "subjectivity" of plants.

Indeed, our recent publications assimilate plants to plastic electromic interfaces displaying cognitive abilities[19] into interactive ecosystems (Debono and Souza 2019). Several specific signature of the plant electrome using synchronized bioelectric networks of different types of vegetal tissues (phloem, xylem, symplasm) distributed over the whole body of the plant which cells are not separated, were detected highlighting plastic ternary complexes [plant–environment–world] (Table 10.2) and an effective mesological plasticity (Debono, 2020b). This plastic process neither purely phenotypic nor epigenetic was for the first time reported about plants by Debono (2016, 2018) who adapted the concept of plasticity he developed to the trajective and medial behavior of plant's body anchored to the soil and dynamically coupled to their singular milieu.

As we will develop later, this position allows to attribute to plants a cognitive access to experience whose modes of action will have to be specified. It can be expressed as the capacity to co-construct and perceive an intelligible world or a sensitive reality activated by the sensory system of plants representing dynamic ecosensitive interfaces showing communicative, intelligent, or resilient strategies. The question of their intelligent behavior is here secondary, because related to all living systems (from bacteria to man) having absolute needs to evolve adequately and survive in their environment; the way to do it being very likely linked to phytosemiotics and plant mesological interfaces (see next sections).

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using a simple device for the extracellular recordings at the level of plant tissues (xylem and phloem) that are connected by inserting an electrode into the soil next to the plant. Such recordings are done as soon as the aphid starts plant penetration and allow the registration of EPG waveforms.

[18] Work in progress.

[19] According to the biological and post-cognitivist acception of this term.

Our experiments have indeed shown, far ahead of current discoveries, that if the nature of bioelectrical events linked to their cellular ionic directory or to local responses is well known, the permanent spontaneous oscillations collected at the level of the whole plant with electrophytographic techniques actually play a preponderant role in their sensitive relationship to the natural environment. As previously mentioned, long assimilated to noise due to the low amplitude and chaotic nature of their signals, EPGs constitute for us, with the whole electrome, a unique facilitating system of monitoring, management, and discrimination of stimuli allowing plants to make operational choices to survive and grow optimally, i.e. to have a form of sensitive access to experience or cognitive ability without representation or need for a brain. Collected chronically in their natural environment, it would allow us to draw up the electrical profile of a species, an organism, or an individual by reflecting the efficiency and the inseparable character of the direct dynamic coupling taking place between the plant and its milieu or Umwelt (mesological plasticity). Moreover, EPGs could constitute valuable early markers of activity in biology or agronomy (diagnostic or monitoring tools, multisensors, EPG kits). We are experimenting in this way. Simmi et al. (2020) also recently showed that infection by pathogens affected the dynamics of the electrome, even when it was located far from the infected site and before these effects were visually detectable.

The electrome signature of a given species or plant thus indicates a cohesive factor and/or unit of behavior observable in their singular environment despite the sessile, modular, and non-individualized nature of the plant system. The electrome signature or response patterns detected in our EPG experiments or in calcium oscillations are also specific signs of reactivity potentially indicating stress-responses, discriminative choices among stimuli, or complex behaviors of plants. At the population level, it could concern resilient or "empathic" strategies. Consequently, it is necessary to adopt a new ecoplastic (and electromic) reading grid of the levels of sensitivity, reactivity, and capacities of adaptation to new situations of plants in a constantly changing environment (Debono and Souza 2019; Debono 2021a, b).

10.5 Mesological Plasticity as a New Model to Study Plant Evolutionary Biology

If we consider now the path that led to the development of the epistemological concept of plasticity, it has totally different sources and objects at the beginning from the mesological one, namely it does not have as object the eco-phenomenological study of the world per se, but overlaps it on many points, mainly ontological, epistemic, and transdisciplinary. The plasticity of living systems is however one of its main field of research (see Sect. 10.2). It is indeed instructive in this context and for the rest of the discussion to describe how I came to make this connection with mesology. The tree of causes has two parallel branches indeed: (1) my discovery of this school of thought while attending the seminar of mesology at the School of Higher Studies in Social Sciences (EHESS Paris) directed by Berque where I was invited to give a lecture in 2016, and then during a Cerisy colloquium dedicated to the mesological paradigm at the time of the Anthropocene (Debono 2017, 2018); (2) my work in plant electrophysiology questioning the sensitivity of plants and their close link with the milieu while they are rooted in the soil and permanently subjected to environmental stimuli. However, it was the first time that these two concepts (plasticity and mesology) met, and it quickly became apparent that in Uexcküll's precursory work, the place of the plant world had not been studied at all. Only a few allusions to it are made in his great work. We will come back to this in the next sections because we can interpret these elements differently today.

In any case, there are two excellent reasons to study this question further, which is directly related to the subject of this book on the self-organization of living beings during evolution. Indeed, the body–medium–world ternarity is impacted at several scales during evolutionary processes whether they concern phylogenesis, ontogenesis, or epigenesis. This concerns as much the development of populations and/or acquired characters as the scale of the individual. However, the mesological part is situated between the micro and macro-evolutionary scale since it refers to a non-dual process of imprinting-matrix and being–environment totally linked to interactive ecosystems and biotopes common to species. It implies therefore, just like the fundamental plasticity of the matter–form, co-constructive mechanisms, and bijective Nature–Culture Relations. If we integrate the subject as a predicate and the "as that" as properly trajective, we end up with an operational conjunction: the mesological plasticity.

10.5.1 Plasticity as the "as that" or the Third Included of the Mesological Formulation

The principle raised by Berque in the form of a digression following my work highlighting the potential complementarity of the two concepts and the rule of perception–action loops in plants (Debono 2016) opened up perspectives at the global level on the study of beings–subjects immersed in a given environment, but also, and this is above all what I would like to explain for the first time in the context of this work, on the specific field of plant behavior and cognition. The aim was to describe a cognitive ethology that differs in form and function according to species, and not to confuse intelligent behaviors or post-cognitivist definitions that can apply to plants, particularly in the observation of mechanisms related to extended or embodied cognition (Debono 2021a) with the notions of animal sentience and cognitive representations or human introspective consciousness. At this level, the preponderant emotional part must lead us to question at another level the qualifiers or typologies proper to the universal intelligence of the living and the specificity of human or animal feelings (Damasio 2021). In any cases, an interaction prevails at this stage, whether it is represented or not in a brain, it is that of the immediate presence of the subject included in its singular milieu, the mediance of the dynamic pair formed at this level, and by that, of the operating forms of life which result from it: a meso-logic of the place and of the interaction with a third included or the ternarity common to all forms of life.

The concept of mesological plasticity (Debono 2016, 2018, 2020b, 2021a, b) is then a recent evolution resulting from the combination of my work about the epistemological concept of plasticity developed since the 1990st and that of Berque (EHESS, Paris France) concerning mesology (Berque 2014a, b, 2016). It starts from the observation that plasticity is indeed the meeting of two worlds: the world of forms and the world of meanings, which co-signifies the reality that we inhabit. By making a comparative analysis of these two approaches, it becomes clear that the plastic component of this new formulation combining the two concepts (mesology and plasticity) is efficient at the level of living systems, and in particular of the organisms fixed to the ground like plants. As previously evoked, Berque has largely developed and theorized the mesological approach deepening the notion of trajectivity and of the relationship between living beings and their singular milieu (instead of environment). Concerning plasticity, he has precisely located it in the "*as that*" (*en-tant-que*) or the slash of the major mesological formulation $r = S/P$ previously described and where trajection finds its full meaning (Berque 2017, see Fig. 10.2). Trajectivity is synonymous with crossing "beyond," with a close link between the milieu and the subject (*S/P*) through an existent (E) defining the ternary link SEP from the tetralemme of the Indian logicians "both A and not A" (contradictory terms then described by Aristotle and Plato still prisoners of the excluded third) and signifying for Berque "this movement by which there is "subjectivation of the environment and environmentalisation of the subject." This assertion from Imanishi Kinji implies more precisely for all plastic and trajective processes, the notion of subjecthood (or subjectivity) concerning any self-organized structures during evolution (Berque 2015).

10.5.2 Mesological Relationships Between Plants and Their Milieu: The Uexküll's Gap

In the context of an opposition to Darwinist, Tainian, and especially monistic theories of Haeckel, Uexcküll describes the correlate of the perceptive activity of animal perception and the irreducibility of the milieu to a given species by focusing on the perception–action loop and the relations between the environment and its living being. Canguilhem will analyze this relationship on an epistemological level later (1965), showing that the transition from the notion of milieu to that of Umvelt described by Ratzel (1899) shortly before Uexcküll[20] is not so clear-cut, at least on a linguistic and terminological level (Feuerhahn 2009). Uexküll, focused on animal ethology, will consider indeed very early on the living being as a subject in its own right. In this regard, he interprets the environmental data adopting a new vision of specific links between species and their milieu. Numerous examples of specific flora

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[20] Uexcküll replaces it with Merkwelt in certain writings: see following paragraphs and note 27.

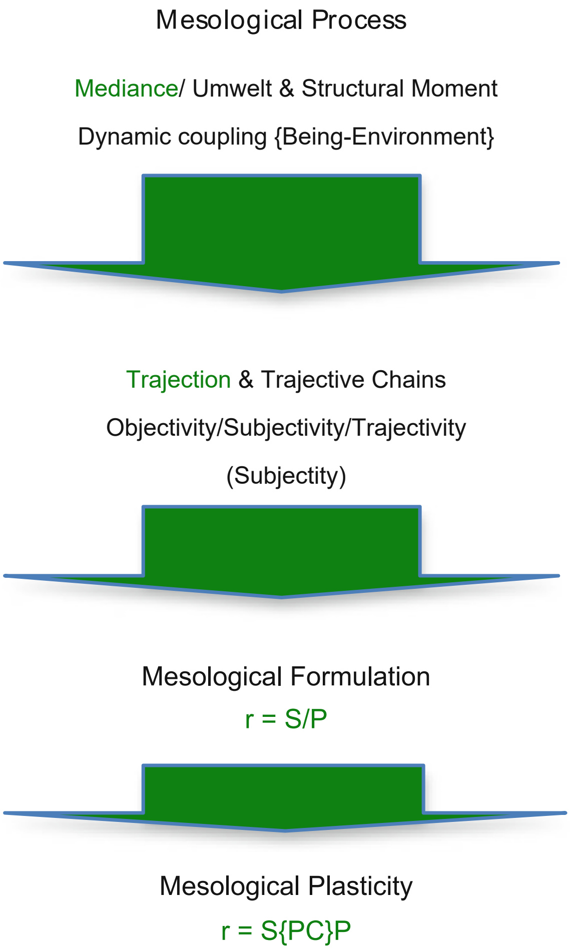

Fig. 10.2 The Mesological Process. Mesological Main steps. For mesological plasticity, the plasticity complex PC replaces the "*as that*" or the slash of the mesological formulation where *r* is the reality, *S* the subject, *P* the predicate. © Debono (2021a, b) following discussions with Berque (2016, 2017)

or fauna support these observations, which ensure the dynamic pair established between a living being and his singular milieu, an optimal growth and mutualistic links. The example of the tick is classic. More generally, what turns out to be a sign associated with the typical behavior of an animal or plant species (the stem for a bird or such a color associated with a specific wavelength for bees or the direct effects of a given human culture) leads to a specific biosemiotic (Kull 2020) or a globalizing semiosis if we refer to the anthropologist (Kohn 2013). This author reminds us indeed, that as far as our human societies are concerned, they are inscribed in the symbolic function of the language and the representation and that it is necessary to go out of it by taking into account a globalizing semiosis exceeding the human. According to this hypothesis, all forms of life or forest's signs would admit representations and symbolic functions that are expressed differently from us, i.e. according to an eco-bio-semiotic paradigm (a living thought) for anthropologists like Kohn taking into account a globalizing semiosis that goes *beyond the human* *being*. One can notice here that if the biosemiotic value of plant–environment relationships has a strong value in animism and Amazonian cultural approaches, it should be primarily interpreted here according to its subject status. We have seen that it would rather be for plants and all living systems a subjectivity (*shutaisei* 主体性) according to Imanishi, than a classical subjectivity that is limited to the individual organism. This subjectivity is extended to the whole biotic society (different from the biosphere) according to Imanishi or a speciety for Berque that translated him (2015), indicating in our context the unique otherness of plants rooted in a specific milieu compared to object–subject relationships of classical societies.

Indeed, the central object here is not the environment, but the dynamic coupling of the being with its milieu, which is always interpreted singularly and differs from the raw data of the environment interpreted similarly by all living species. This posture of subject inscribed in an environment and in strong interaction with the adjacent ecosystems is radically opposed to the dualistic or Cartesian positions separating body and brain or subject and object. What is important in our biologic, plastic, and mesological position is the relation and its significance in a lived reality. We will see that it has strong implications: (1) at the level of the individual and the species for what concerns the autonomy of the living being and (2) at the level of a possible access to experience (sensitive, sensible, cognitive, conscious or not).

Concerning plant plasticity, a point of importance is noted for the first time in this chapter: the almost total absence of reference to the mesological relationships between plants and their environment by Uexküll, the father of ethology and mesology. Indeed, he barely mentions them for the first time in 1940, when he had completed his pioneering work while Rowohlt published the original text of Uexküll related to the plant world in 1956.[21] We will quote here the extracts of the few pages of his major work "Animal Worlds and Human World" followed by the "Theory of Meaning" (Bedeutungslehre") and in its French translation by Denoel/Pockett (1934)[22] evoking the place of plants and their relation with the environment. A later translation was made in Semiotica in 1982 where Uexküll mentioned plants as part of his attempt to define the meaning theory.[23] "The question of meaning is, therefore, the crucial one to all living beings," he says, including plants considered as able to use or be immersed in habitats or "houses" despite their lack of brain, receptor–effector relations, mobility, and "meaning-carriers." However, they are considered as not autonomous, contrarily to animals, and totally dependent on the environment.[24]

Uexküll admits however that plants have in common with animals "to make selections among the environmental stimuli that constantly assail them" and unlike inert systems use meaning to evolve and grow optimally in their immediate

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[21] von Uexküll (1956, pp. 110–111).

[22] von Uexküll (1934, pp. 101–102).

[23] von Uexküll (1982, pp. 33–53).

[24] Like fungus-cells differentiating themselves from bacteria by interpreting their surroundings and signs like food in terms of meaning-carriers and minimal perception–action loops.

environment. If we consider these assertions in their historical context (early XIX^{e}, governed, biologically speaking, by mechanism at one end and vitalism at the other), and before discussing Uexcküll's arguments related to his positioning as a precursor of ethology and biosemiotics, this simple observation or hypothesis regarding the possible selective rule of plants vs environmental stimuli is fundamental regarding our discoveries on the function of EPGs and the signature of the electrome in the relational life of plants, whose discriminative role it would be precisely on the functional level via electromic mechanisms and mesological plasticity (Debono and Souza 2019; Debono 2021a, b). We hope that new in loco or in situ EPG monitoring experiments will confirm this hypothesis as soon as possible.

Uexküll uses indeed the term "Wohnhülle" (dwelling-integument) in place of Umwelt for plants, considering them to be sensitive through their lipid cell bilayer and use primary meaning-making where stimuli act as cofactors through the *wohnhülle*. Another important consideration that can be linked to the current knowledge of plant physiology in Uexcküll's hypotheses is the fact that plants capture and respond to environmental stimuli through their shape and all their organs (medial body), even though he associated it in its historical context to a "building plan" or bauplan. It means for the author that take often the example of the deformation of trees under the influence of the wind or of the form of tree foliage directing rainfall toward the root tips, a meaning-factor operating between the shape of plants and the environmental conditions (rain, wind, drought) which corresponds today to mechanosensitivity, proprioception, or thigmomorphogenesis commonly observed in plants (Moulia and Fournier 2009; Hamant and Moulia 2016).

Many other authors have addressed this issue in different contexts. Among these, Sharov's definition (2015) issued in the context of primary meaning-making modeling states that "an agent is a system with spontaneous activity that selects actions to pursue goals." Kull, who quotes the Sharov's concept of agentivity in 2020, rightly makes the difference between selection and choice, the first qualifier pertaining to purely sequential algorithmic operations, while the second concerns the presentation of non-sequential options constantly arriving in the present (simultaneous interactions in place of stochastic or deterministic ones), which corresponds to the case of plants rooted in the soil and subjected to permanent and changing stimuli. This point of view caught my attention because, like Uexküll's initial observation previously noted about the meaning theory, it strongly supports our discovery of the presence of a spontaneous bioelectrical activity permanently emitted at the level of the whole plant (recorded by electrophytography). Indeed, as previously shown, EPGs correspond to biological signals of low amplitude and voltage that are an integral part of the plant electrome that we had detected very early (Debono and Bouteau 1992),[25] hypothesizing that they would have a functional role, and in particular an essential function as a radar or discrimination window for all the environmental stimuli in order to allow the plant to develop optimally in an environment that is often adverse, stressful, and that requires minimal cognition to survive.

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[25] See Sect. 10.4.2.

Ongoing field experiments following the validation of our results by several teams are now projected with Souza's team (Debono and Souza 2019; de Toledo et al. 2019; Parise et al. 2020, 2021) and would confirm this hypothesis.

10.5.3 Semiosis, Uexküll's Primary-Meaning Making and Functional Circle: An Ecosensitive Complexion?

As shown in two synthesis done by Kull about Uexküll's work in Semiotica (2001) and more recently in Kull (2020) about the study of primary-meaning-making and evolutionary biology, Uexküll's great contribution related to classical genetic considerations about mutations and natural selection concerns the introduction of subjectivity and biosemiotics. Choice-making done by living beings is described as a necessary interpretation of the environment by living beings (mainly animals and humans) and not as a nervous or conscious prerogative. Meaning-making is then considered here as a semiotic process using signs and the Umwelt to survive and evolve. Uexküll has modelled it as a functional circle. This circle means that any cell or multicellular organism having enough complexity is able to use functional circles in which its subjectness or subjectivity can emerge as relation signs in "the phenomenal present" (the here and now singular milieu). This interpretation constituted by the reciprocal link Umwelten- Umwelt established between living beings and their singular milieu is essential to describe any semiosis, joining classical assertions about logical or literary languages by Pierce (1979) or De Saussure (1995).

Quoting Deacon (1997, 2012), Eco (1979), Sebeok (1997), von Uexkull (1986), or Hoffmeyer (1996), Kull (2020) recalls us that "semiosis is co-extensive with life." Thus, rather than focusing on the Eco's semiotic thresholds, he suggests to pay attention to perceptual and action signs that are included in meaning-making operations defining functional circles that could be related or differentiated to functional cycles or closed sequences (Sebeok 1994), or also in another context to the operational close described by Maturana and Varela for self-organization and autopoiesis (Maturana and Varela 1980; Varela 1983). Gestalt, feedback, or situationist approaches were also adopted by Dewey following Pierce primeity, by Thure von Uexküll and Wesiak (1997) concerning elementary sensations linked to receptor–effector relationships and emergent perceptual properties and also by von Weizsäcker (1985) introducing the temporal factor or Plessner, the ontogenetic one. The time factor is indeed essential to insure the operability of the functional circle for agency and the dynamical pair formed by living beings as subjects incorporated into a singular milieu and a present moment. This unique conjunction allows the simultaneous elaboration of a semiogenesis and an Umwelt in a given environment. Now, a fundamental difference between animals and plants resides in this limited and conditioned time factor for the former and almost unlimited and indeterminate for the latter, which may constitute at first sight an obstacle in the operability of the functional circle. Another potential obstacle raised by Plessner (1940, see review 2019) at the ontological level: the "open form" of plants which are divisible, are never finished and live in immediacy, directly incorporated into the external environment compared to the "closed form" (or completed form) of animals or humans whose embryogenesis follows precise stages, whose organs are positioned in the body, and who acquire an autonomy and an individuality of their own with regard to their learning and their indirect experience (passing through representation) of the external world. This experience of the lived world, if it is not internalized, individuated, and even less conscious or existential in plants, is not absent for all that at the sensitive level where it is on the contrary exacerbated (plants are hypersensitive to the environment) and embodied cognitive (in the post-cognitivist sense of the term). It corresponds to minimal cognition (Calvo and Keijzer 2011), extended or distributed cognition according to the authors and the behaviors observed among the thousands of plant species. With regard to extended cognition, Parise et al. (2020) have, for instance, recently shown that the root system of plants would constitute, as the whole body of the spider weaving its web, an extension of the environment where external physical objects are part of the cognitive system.

The model of mesological plasticity describes more precisely three stages at the level of the plant plastic interface, including: (1) an active binding directly resulting from the dynamic coupling between the plant and its singular milieu; (2) a medial organism by excellence (body rooted in the soil and in permanent interaction with aerial elements) and (3) an ecosensitive complexion allowing a trajective access to experience. This experience is not subjective as in the animal, capable of projecting targeted actions in relation to the object of its instincts or life projects, or introspective and represented (image) as in the human being, but it constitutes a subjectity following Imanishi as noted by Berque (2015). Moreover, our mesological and plastic approach is a counter-argument to the Plessner's considerations linked to the open form of plants, where precisely their immediacy and direct incorporation into the external environment are presented as a handicap to acquire an autonomic or ontological status. Their subjectivity and open source behavior in close interaction with the interactive ecosystems from which they cannot extract themselves constitute, on the contrary, the signature of their specificity or otherness and are guarantors of their unique mode of exchange with the environment.

Namely, many authors associate the complexity of certain plant behaviors to minimal agentive capacities without mental representation. For instance, Barandiaran memorization or perceptual learning (2009), deriving in part from Simondonian perception's level assimilated to sensibility (2006) and Gibsonian affordance or direct perception phenomena (1986) showing the direct contribution of the action to the perceptual process, introduces the concept of *perceptual systems* like the dynamic touch (Turvey 1996) or the visual system. It means that perception may be active and not only driven by external stimuli giving rise to a cognitive representation or a mental reconstruction. This direct access to the experience or perception–action loop concerning here an animal doing a motor exploration of his environment does not exclude learning and memory processes but describes another mode of cognition close to the mesological relationship linking the subject and its singular milieu.

A lot of works about mesology (Berque 2014a, b, 2016, 2019) or biosemiotics (Kull 2020) show indeed that Uexküll, as an anti-behaviorist, had clearly anticipated the anthropocentric tendency separating the notion of *Umgebung* (unique consideration of the raw data of the environment) from that of *Umvelt* where living subjects are in strong interaction with their singular environment (milieu or habitat for animals) and the other species of its ecosystem. In this sense, they interpret the environmental data and make them their own milieu, establishing specific links that the other species do not have. Numerous examples of specific flora or fauna support these observations, which ensure the dynamic couple established between a living being and his singular environment, an optimal growth, and cooperative links. Indeed, mutualistic exchanges are observable at the level of many plant species and by extrapolation could be the symbol of a symbiotic planet (Margulis 1998). So, they are for us not only included in the Uexküll's functional circle, but also have an Umwelt. A recent study of Clements (2016) compared the circle and the maze with an ecosemiotic grid of lecture showing that Uexküll's functional circle corresponds more to a solipsist view of ecological relations, while Peirce's drawing maze is more chaotic and not predictable, both concepts being linked to a subjective factor—causality for Uexküll and self or man as signs for Peirce (1979).

Indeed, if we consider the historicity of the theory, the teleological view of Uexküll (the bauplan), the idea that plants were inferior beings, lacking sophisticated receptors, sensory organs, and mobility, incapable of exchanging or co-constructing with the environment, we understand that Uexküll did not give them an Umvelt status. We all know, however, that the scientific discoveries that followed have shown, on the contrary, that the sensitiveness of plants was flagrant and their communication capacities, even learning, very extensive. This is why it is important to reconsider these pioneering works in the light of current knowledge in biochemistry, electrophysiology, genetics, ecology, and epigenetics, where the extent of phenotypic as well as developmental plasticity is widely demonstrated. In addition, there are numerous semiotic, philosophical, and phenomenological approaches that take plants as subjects of study today (from a metaphysical to a political point of view, respectively, for Coccia 2016; Marder 2013a, b).

Among the major findings of these fields of research is the fact that all forms of life, however elementary, need to exchange with the environment in order to grow, reproduce, and survive. This evidence, on which everyone can agree, has gone unnoticed, as is often the case with the obvious, although it alone justifies the status of subject anchored in a meaningful reality granted to plants by transdisciplinary researchers. This status is linked to their active perception of the environment, which is volitional or intentional in this primitive sense, that is to say capable of discerning an inside from an outside, of distinguishing their own entity from the otherness of the world. An informal identity, blurred, internalized, without nervous system, a form of ipseity or radical otherness (Hallé 2014) differentiating itself clearly from the subjectivity, the marked individuality and the implicit self-consciousness of the animal or the man, but which leads the plant kingdom, in spite of its fundamental differences with these species (timelessness, divisibility, sessility, autotrophy...), to establish perception–action loops and to develop, not only "intelligent" behaviors proper to all living beings (reactivity, problem solving, etc.), but efficient and significant exchanges with the environment which are its own.

For instance, plants mobilize their whole bodies in an environment spatially constrained but which they do everything to optimize, widen, develop by all the means: chemical communication via odorous or volatile substances, co-evolution with insects, propagation of electrical signals at long distance via the electrome, development of the mycorrhizae within gigantic root networks, proprioception (perception of their own deformation by plants or trees), elementary cognition, cellular or biological memory (habituation in sensitive plants like Mimosa P., motor response in the carnivorous plant Dionea M.), developmental and epigenetic plasticity (often transgenerational), remediation, meaning-making, local memories, and learning abilities approaching animal procedural memories (Gagliano et al. 2016; Thellier 2017). The concept of interface and plastic complex to the mesological approach that we develop puts forward this inextricable link between the living being and its environment, widely described at other levels of organization of the living being (neuroplasticity) and of reality (biophysical, energetic).

The notions of plasticity of the living being that we develop, on the one hand, and of morphosis and semiosis or semiophysics (Thom 1988), on the other hand, best translate this consideration of plant phenomenology, which ensures in a simple and efficient way the optimal growth of the plant, without the need to have recourse to an integrative and centralized nervous system. This is possible through the trajection of living forms or a sensitive reality which, since the dawn of time, establishes an unconditional and inextricable link with nature, which we tend to over-interpret or anthropize, but which has no less value as a sign. Such a sign marks in an indelible way the singularity of the living compared to artificial intelligences (Benasayag 2017) and translates a ternary reality plant–environment–world, which leads to an anoetic highly sensitive reading of the reality of the world. This essential reading on the scale of self-organized evolutionary processes allows relativizing the predominant and self-centered vision of humanity on the world. It is a matter of taking into account the ecoplastic and ecosensitive nature of the world in all its dimensions (Debono 2022)[26] and this requires a transdisciplinary approach and methodology. The sensitive experience means being for Nietzche (1878). And that concerns all the living beings. There is apart from us, an intelligible and sensitive world that lives in an autonomous way, has its own codes and cognitive borders, or of access to the experience founded on its interactions with this world. The plant body represents a major one, because contrary to the sectorized and indivisible animal body secured by shelters or habitats, it lives constantly in an open environment and does not have separate cells, but a diffuse body with zones of exchanges from near to near (some of which are purely electrogenic) that can typically activate genes coding for receptors emitting defense molecules which will induce a local response and can be propagated at long distance via the electromic field (de Toledo et al. 2019).

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[26] Debono (2020a, b) Plant cognition: when science requestions the ecosensibility of the world. IIIrd World Congress of Transdisciplinarity. Planned conference on the topic at Mexico City, Nov. 3–7, 2022. See Nicolescu 1996, 2011 for details regarding the chart and methodology of transdisciplinary.

So, elementary life (from protists like amoeba to bacteria, fungi, plants, and animals) not only can but need to feel. This notion of primary "feeling" differentiated from emotions and the basic intelligence of any living being by Damasio (2021) that could be linked to direct perception and meaning-making in plants is important to take in consideration in evolutionary biology and studies considering homologies vs semiosis or ontologies when comparing animal to vegetal behaviors. Indeed, some arguments are oppose to the consideration of the sensitivity of plants and the reality of the lived experience, confining them to a simple reactivity to a given stimulus. However, this ignores the medial and trajective effectiveness of plants (their mesological plasticity), which are by definition extremely sensitive to their immediate milieu (they are anchored in it and totally dependent on it), capable of movement, of developing advanced defense or communication strategies and high degrees of cognition relatively to their biological constraints in a hostile environment.

10.5.4 Phyto- vs Ecosemiotics as an Experimental Field of Mesological Plasticity: Evolutionary Biology and the Umvelt of Plants

One potential issue to assess plant biosemiotics could be to consider the field of phytosemiotics. Kull (2000) made a nice synthesis on the subject, comparing the concept of biological need as "the primary holistic process in living systems" to that of semiosis, where signs, according to their categories (respectively, cellular, vegetative, animal, linguistic, and cultural) are considered as meronomic entities and plants as semiotic systems. Excluding the presence of semiotic thresholds (Eco 1979), he shows, quoting a lot of biosemioticians like Deely (1986, 1990) that semiosis is a general process in biological systems from unicellular cells to fungi, protists, and multicellular organisms and asks "whether there may be anything special in plant semiosis in order to justify its distinction from the other fields of biosemiotics?". Phytosemiotics is often mentioned, he said, quoting mainly Krampen that lunch the term in Semiotica (1981) and also Nöth (1990, 1994, 1998), but not clearly defined and differentiated. He banishes then the generic semiotic attributes of living organisms to search the specificity of evolved plants (like bryophytes and vascular plants) excluding algaes and differentiates phytosemiotics from human–plant interaction studies (plant as signs to communicate) belonging to the ecosensitive field. The Krampen (1992, 1997) in-deep analysis of von Uexküll's statements about autonomy and semiosis in plants has several phases, first agreeing with him (neither Umwelt nor effector/receptor relationships, feedback cycles but not functional circles and meaning factors only) and then admitting their specificity (plants' signs being considered as indexes, sensing, meaning used by plants via their forms, chemosensitive responses) compared to the iconicity of animals and humans as symbols, on condition of detaching from any anthropomorphic or phytocentric enterprise (Krampen 1986).

This assertion is at minima in adequation with the Uexküll's Wohnhülle of plants describing their singular relationships to the habitat and corroborates a lot of plant behaviors using via bioelectrical or chemical networks, insects, fungi, other plants and their own form as signs or meaning factors. However, Thure von Uexküll (1986) assimilates plants to solipsistic systems using only iconic signs and not able to discriminate objects (only self and nonself) because they are not subjects and use only vegetative signs. For him, indeed "they are not signs for occurrences outside the plants, as there is no "outside" for vegetative systems." Kull (2020) rightly points out in his synthesis about phytosemiotics clear contradictions between these positions and the attribution by many of the same authors, Uexküll in first place, of an Umwelt to fungi (Hoffmeyer 2008a) but also protists and unicellular organisms like the paramecium or other flagellates provided with a plasma membrane, receptors, and effectors inducting body movements characteristic of the animal kingdom. We can thus better understand the historical genesis of these classification battles including few botanists, the outcome of which is clearly in favor of plants, which have no reason, whether it is at the cellular or organic level, not to have their own Umwelt.

A lot of plant signalization and behavior studies attests to it (Baluška et al. 2006) and as we discussed before, functional circles are most likely present in plants, knowing their ability to move (even slowly), to show an important phenotypic, developmental, and epigenetic plasticity, to recognize and answer specifically to a lot of external signals. They treat them by means of differentiated and specialized structures showing mechanosensitivity, gravi- or proprioception (Moulia and Fournier 2009), direct intercellular junctions or root networks, and the electrome between themselves or other species (pollination, reproduction, mutual exchanges, symbiosis) They also have defense strategies based on hormonal or chemosensitive receptors, present some degree of memory and learning (Thellier 2017; Gagliano et al. 2016) and perhaps more specifically in relation to the Umvelt of plants, and show, as previously evoked, a morphogenesis directly acting as phytosemiotic agent. Kull (2020) says in this way that a "correspondence between the spatial placement of leaves and roots will be achieved due to a functional relationship that has originated from a specific biological need," where the need is not a feedback process but a semiotic and universal one using meronomy—objects as parts of a whole—in place of taxonomy as typological vegetative sign recognition (compared to the Sebeok's zoosemiotic system 1994). To conclude, phytosemiotics is reinforced by this analysis.

10.6 Assessments of in Loco Mesological Plasticity Using Monitored EPG Kits: A Key Approach to Study Electrome Patterns in Natural Conditions

Let us come back to our experimental results in this perspective. Previous bioelectrical experiments have quantified spontaneous electrophytographic activities and shown the presence of specific patterns related to certain types of stimuli on long-term EPG recordings (Pereira et al. 2018). They constitute specific signatures of the electrome (Souza et al. 2017; Simmi et al. 2020) validating our key hypothesis about the role of these micropotentials in plant communication (with their milieu as for interspecies exchanges). The next step is to plan monitoring experiments using miniaturized EPG kits or sensors in natural environments, which is challenging and very important to understand the behavior of plants outside the constraints of the laboratory. The aim is to find specific patterns of electrome responses highlighting the cognitive capacities of plants, especially in terms of operational mode of communication at long distance (Debono and Souza 2019; Debono 2021a, b; Gimenez et al. 2021). These patterns could include synchronization among electrical signals at the level of single plants (Debono 2013a, b; Masi et al. 2009) and discrimination of environmental stimuli or propagated defense signals (Reissig et al. 2021)

This still ongoing methodological part related to the operability and nature of in situ mesological plasticity of plants constitutes a key point of our experimental approach. As a matter of fact, the electrome signatures, addressed in a new way in this book, are related to the plant Umwelt (their eco- and phytosemiotics) and the lessons that can be drawn from Uexküll's succinct approaches to the plant kingdom in the context of current research. We show here that our field of research on the plant electrome and the particular role of EPGs could corroborate or at least support the reality of a plant Umwelt characterized by a cognitive access to its singular environment. This environment taken into account at the plant mesological interface is not a habitat as in animals, but can be seen as a somatotopic mapping of plant spatiotemporal evolution. Its self-organization and dynamic coupling with the milieu (or its mediation) open up trajective perspectives describing precisely the mesological interface that they form intimately with it, especially since plants are anchored there and must necessarily develop elaborate and interactive defense and communication strategies with regard to both the elements (aerial, terrestrial, aquatic, etc.) and the surrounding species (insects, fungi, etc.).

These perspectives characterize the Umwelt or the proper world of plants in relation to their singular environment.[27] Starting from the idea that matter, and thus the living, are semiotized, biosemiotics, which can be criticized,[28] imply a stable imbalance or homeostasis on the scale of a territory where each species is the sign of another. Finally, scientific ecology, which is necessary, but whose perverse effects on agricultural policies, excessive urbanization, or the use of biodiversity as an argument for the Capitalocene (Haraway 2003, 2008) tend to anthropomorphize

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[27] Uexcküll, who, as we have seen, was little concerned with plants, distinguishes in an interesting way in his work of 1934 on the animal and human worlds the Umwelt of the "higher" animals able to internalize (to replicate, to represent) the external world (Gegenwelt), to perceive it (Merkwelt) finely (landscape, intention, danger...) with the proper notion of animal affect or stimmung, notably developed in comparison to the man by Buytendijk, one of his pupils and to act (Wirkwelt), drawing up there clearly a classic loop perception-action of the Umwelt of the lower animals (molluscs, insects, etc..) whose Merkwelt only perceives the stimuli of the environment, without relating them to a sense or a function.

[28] As we have seen in the chapter speaking of the differences between cycle and functional circle: for instance on its understanding of function and the biologization it sometimes grants itself in excess can lead to contradictions such as Uexcküll attributing an Umwelt to unicellulars and not to plants or Umwelt-Umwelten semiotic configurations that are ambiguous to say the least.

the notion of the environment. Hence, the birth of an ecocritical watches wishing to counteract the nature–culture opposition by using biosemiotics or Piercean and Uexckülian ecosemiotics as a field of investigation. Vignola (2017) thus reminds us that "Jakob von Uexküll developed the concept of Umwelt, a key concept in biosemiotics that refers to the fact that each species, that each individual within each species, perceives its environment according to what is significant to it for the purposes of its survival and according to the senses conferred on it by its anatomy." This Umwelt is particularly marked in man where the influence of the environment—of the habitat, the ecumene in particular, of the geography, of the climate, of the city—has a direct impact on his behaviors (whether they are individual or group) and the culture they convey. Kull (1998) relied in particular on the Lotmanian concept of the semiosphere to describe specifically the human Umvelt, characterized by a place, a language, a psyche that can induce biases and an imaginary. It forms a powerful network of exchange whose semiosphere corresponds to "the whole of all the interconnected Umwelten."

This large-scale network includes the ecosystem and all the Umwelten that it contains, some of the species concerned. Plants are consequently in the sensing or the sensitiveness, a form of sentience in opposition to the intellecting[29] and have obviously, like all living organisms a non-explicit intelligence (neither representational, nor affective or conscious), anchored in a territory or an environment, a milieu whose dynamic coupling has given rise to a biodiversity and an ecosensitivity like no other, the explosion of life on Earth and the rise in complexity that we know with the advent of consciousness and mind.[30] Several authors in this way show that plant (specifically roots that use homeobox proteins able to control the morphodynamics of the shoots) could use sensing to draw up spatial and even cognitive maps of the soil and the environment. They use as well qualitative as quantitative informations directing growth or other behaviors like fitness, following local conditions (light conditions, moisture, drought, mechanical stress, temperature, attacks of pathogens and insects, pollution, gravity, symbionts, nutrients), competitive or mutualistic strategles with other species, abiotic inputs or obstacles (Falik et al. 2005; Trewavas 2005). Memory and learning processes or proprioception (Gagliano et al. 2016; Hamant and Moulia 2016) are also widely described in the literature in plants showing their ability to control the environment and growth optimally. The electrome of plants including cellular action potentials, systemic responses, calcium waves, and EPGs have a key role in long-distance signal propagation as we stated before (Masi et al. 2009; Debono 2013a; Souza et al. 2017), but could also act at the level of defensive responses and biological rhythms (Volkov 2012, 2014). More generally, sensitiveness, otherness, or ipseity of plants could be considered as sufficient to explain their cognitive abilities whose nature is under study to interpret the world in a sensible and agentive mode without the need

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[29] In another context, Deleuze and Guattari (2004) interestingly compare plant behaviors to the intellective process.

[30] What I called protoneural dynamic networks in my paper referenced in 2013a.

for a nervous system. Parise et al. (2021) have in this way recently shown in Cuscuta R. that electrical signaling of dodders could change according to host species perceived in patterns recorded by machine learning, suggesting a recognition system but also for the first time a vector of “attention” in plants.

Deacon (1997, 2012) clearly shows that sentience is an emergent property of teledynamic systems, but distinct emergent forms of sentience found in animals and humans (higher-order forms) from that found in plants and other multicellular organisms (lower forms). He shows however about the sentience of individual neurons compared to the brain that we cannot reduce the former to the latter because teledynamic processes are irreducible to the thermodynamic processes that they depend on and that higher forms could not exist without lower levels of sentience serving. This level-specificity can be attributed to any emerging teleodynamic processes from the molecular level to auto-organized systems such as single-cell organisms, multicelled plants and animals having brains. So, for Deacon, lower sentient forms like those of all cellular-level adaptive responsiveness permit the higher forms to emerge. The interesting report concerning our considerations at the plant level is that the author assimilates this second-order operation related to brain–neurons interactions to “the way that the teleodynamics of interacting organisms with an ecosystem can contribute to a higher-order population dynamics, including equilibrating (homeodynamic) and self-organising (morphodynamic) population effects.” It includes morphodynamic processes as well as self-recognition by teleogenic closure, but also the key notion of Bateson (1979)[31] opposing the neuronal matter–energy (firing pattern) constitution to the informational one of the mental worlds embodied by distributed dynamical attractors. Yet, network activity patterns and attractor forms are present in many non-linear dynamical systems, including in particular the electrome of plants which can relay the microstates constituted by permanent spontaneous low-voltage EPG’s regularities to macrostates involving “large-scale global attractor dynamic produced by an extended interconnected population” of plant cells (neurons for Deacon). Indeed, for him there is no need for a brain to accomplish this qualitative leap, as long as we examine the whole homeodynamic process and that we “disregard the level of complexity reached in mental operations due to the synchronization of hierarchical and highly specialized structures.” The result obtained in plants would be different, being limited to a minimal cognitive access to experience and to a specific interaction with its environment, which is already far from being negligible!

10.7 The Plant Mesological Plasticity: A Unique Cognitive, Electromic, and Ecosemiotic Interface

To sum up our discussion, we can say that the way in which plants exist is based on sessility, unlike animals, which implies a dependence on environmental constants and their variations. It is thus a question of playing on other factors than movement

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[31] See also Hoffmeyer (2008a, b).

and immediacy, of composing with the physical forces in presence and their spatiotemporality. Although chemistry and taxonomy have long occupied botany, the essential role of bioelectricity in all motor phenomena, communication and exchange with the environment and other species has long been underestimated.

The first objective of this chapter was therefore to introduce this prevalence by describing in detail the plant electrome and the potential of mesological plasticity as a new theoretical model of self-organizing evolutionary systems considering the plant and its environment as inseparable. Indeed, this framework of analysis combines two distinct concepts: the plasticity complexes and the dynamic coupling between living beings and their environment (their mesological link). It has the advantage of not being limited to a reductionist, dualistic or, conversely, too permissive or deviant reading grid, but of giving the clearest possible vision of the place, the role and the prerogatives that can be granted to new plant signaling and behavior discoveries (Brenner et al. 2006) in the context of the Anthropocene.

Our second objective was to highlight the fundamental role of spontaneous low-voltage variations or electrophytograms (EPGs) within the whole plant's electrome dynamics and more generally of systemic plant electrophysiology (Volkov 2012). These bioelectrical activities are indeed directly linked to their singular continuum via symplasms and plasmodesmata as well as the progressive establishment of efficient non-linear dynamic systems that occur during evolution (Debono 2013a, b; Souza et al. 2017, 2018). The resulting operational and cognitive modes allow establishing a precise mapping of ecosensitivity and complex processing of information within a plant or between plants in their natural environment. These behaviors and ways of communication are currently under studies focusing on new patterns of electrome responses in natural conditions (Debono and Souza 2019; Reissig et al. 2021; Parise et al. 2020, 2021). We show more precisely here that the plant electromic reading grid integrates the key role of EPGs as early markers, permanent scans, and discrimination tools for environmental stimuli or stresses, allowing the whole plant reaching self-organized critical states or SOCs to have vigilance systems and an active perception of their milieu.

As for the architectural relationships between these systems or interfaces, we describe them through plasticity complexes set up during evolution. More precisely, we have established plastic links between the matter and the form, the non-linear dynamic systems linked to the plant electrome, and the activation of operational ternary models during some of these evolutionary processes. The resulting plant electrome signatures will allow us to identify how plants survive and grow optimally in their interactive ecosystem as well as in their singular milieu. Similarly, it will allow the description of a specific flora, of the close interactions between an environment or milieu and a particular species as well as its relations with other animal or plant species.

Our third goal was to clarify for the first time key points about the Uexküllian gap or positioning on the Umwelt and the primary-meaning making of plants showing as a new reading grid to study ecosensitive complex systems and to question plant evolution and emergent cognitive or intelligent behaviors (Debono 2022).[32] More precisely, the selective role of EPGs at plant electromic interfaces and mesological plasticity is proposed as the best bottom-up approaches of co-evolutionary and ecosemiotic processes. Indeed, they cover two essential fields: the intrinsic cognitive capacities of plants to internalize without representing it the external world by quantifying and discriminating the stimuli of the environment (biotic or abiotic, degree of humidity or dryness, rate of luminosity...) and their high sensitivity to the milieu (singular mesological link) by means of morphogenesis and semiosis (Sebeok 1997; Kull 2000; von Uexküll 1986; Deacon 2012), in other words of the direct relation between form and function or form and environment (epigenetic plasticity). In this way, new experimental fields like phytosemiotics or mesological plasticity will permit to support fundamental research areas questioning the sensitive and cognitive nature of plants.

To conclude, evolutionary biology is particularly illustrated at the scale of the action–perception loop and of the communication established within a species or between the species. This is precisely what is operated at the plant's electromic interface that irreversibly binds form and matter, the living being and its environment, subject and object with a single purpose: to express the singular existence of plants in their alterity (Hallé 2014) or simplexity (Berthoz 2009): a mesological and cognitive relationship to the world which does not have an equivalent in the animal and human world.

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[32] Reference to the last book of the author questioning in a transdisciplinary way plant intelligence, Hermann, Paris, 2020.

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11

Quantum Fractal Thermodynamics to Describe the Log-Periodicity Law in Species Evolution and Human Organizations

Diogo Queiros-Condé, Jean Chaline, and Ivan Brissaud

Abstract

We propose a physical representation of the log-periodicity law which has been evidenced in the field of seismic physics, species evolution, astronomical systems, economy, history, and human organizations. Calling "fractal state" a truncated fractal obtained for a finite number of iterations, i.e., defined for a finite scale range, we define a fractal length, a fractal time of interaction, and finally a fractal mass for the fractal states of a fractal. The introduction of the mass of a fractal allows showing the existence of a quantum structure due to the fractal structure which leads to a Planck–Einstein-like law. Inspired by the work of Louis de Broglie on the "hidden thermodynamics of the particle," we introduce a "kinetic chain temperature" which gives access to a thermodynamical description of log-periodicity. We found that log-periodic systems are characterized by a constant entropy production between two consecutive fractal states. The parameter g of log-periodicity finds here a clear and simple physical interpretation. It quantifies the increase of fractal length or fractal time with the number of iterations of the fractal state.

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_11

Keywords

Quantum fractal dynamics · Log-periodicity law · Species evolution · Human evolution

11.1 Introduction

As a geologist working on the physics of earthquakes, Sornette evidenced a log-periodic structure in a temporal seismic signal probably linked to an underlying fractal structure (Sornette and Sammis 1995; Sornette 1998). Inspired by this log-periodic structure, Chaline et al. (1999), convinced by the fractal nature of evolution, showed that a log-periodic structure was existing in species evolution. Making use of paleontological data giving the major dates T_n of the evolutive jumps of a species, Chaline et al. (1999) discovered that these dates are linked by a log-periodic law.

$$T_n = (T_0 - T_{\mathrm{c}})g^{-n} + T_{\mathrm{c}}, \tag{11.1}$$

where T_0 is the first date of the series giving the birth (emergence) of the species, T_{c} is a critical date interpreted as the date at which the species loses all its evolutive capacity, and g would be a parameter, a sort of "time-scale ratio" linked to a fractal structure in time. The parameter g is interpreted in the framework of a "temporal fractal tree" as being the ratio between lengths L_{b-n} and diameter r_n of two consecutive branches of the tree: $g = L_{b-n}/L_{b-n+1} = r_{b-n}/r_{b-n+1}$. In the case of a fractal tree, we thus have $g = k^{1/D_{\mathrm{f}}}$, where k is the mean number of branches at the level $n + 1$ coming from the level n and D_{f} is the fractal dimension. Assuming a fractal dimension equal to 2 and a trichotomic tree ($k = 3$) the authors calculated $g = 3^{1/2} = 1.73$, which is close to the value found in a wide variety of data. Since this work, a great number of studies in the field of the economy (Johansen and Sornette 1999; Nottale et al. 2009) and in human ontogenesis (Cash et al. 2002), demography (Johansen and Sornette 2001; Nottale et al. 2000, 2009), history (Brissaud et al. 2012), arts (Brissaud 2007; Brissaud and Chaline 2013), monastic structures (Brissaud 2009), and information systems (Guillen 2001) have shown a similar log-periodic structure. This points to a universal behavior that deserves to be investigated and explained more deeply. These studies are mainly based on treatment of data which are dates. Log-periodicity is thus a temporal phenomenon. The fundamental problem is that it is difficult to grasp what can be its fractal nature, what can be the length and the diameter of a temporal tree. This is the major problem raised by J. Dubois concerning the log-periodic law (Dubois 1995). After all, species evolve in space so this log-periodic temporal dynamics should have a spatial explanation (Queiros-Condé et al. 2015). Moreover, the studies on the economy (Nottale et al. 2009) and empire expansion (Brissaud et al. 2012) clearly suggest an important spatial component. In this chapter, our main objective is to propose a geometric and spatial approach to this time log-periodic structure.

11.1.1 Length of a Fractal Interaction: Homogeneous Time and Entropic Fractal Time

Let us consider a homogeneous field of characteristic size L crossed by a phenomenon or a mobile having a velocity V. The crossing time is simply $t_L = L/V$. Let us now assume that this limited field develops some local heterogeneous structures which will slow the crossing phenomenon. This is the case if the field displays some defects, or obstacles, which deviate or perturbate any crossing trajectory. Let us consider that the sum of these perturbations will increase the crossing time by a term denoted t_Z. The total crossing time is thus $t = t_L + t_Z$. To illustrate this simple idea, let us consider the general case of a field as in Fig 11.1 which displays a homogeneous part and a heterogeneous component which can be defects, obstacles, vortices, loops, or anything that perturbates a regular and linear trajectory through the field. The heterogeneous set can have some multi-scale features and even a fractal structure. But for the moment let us work with a simple system as in Fig. 11.1.

The phenomenon undergoes deviations and curvature of the trajectories which increases the crossing length. The length of the interaction of order 0 denoted L_{F0} is the total length of the loops of level zero. This interaction frontier can be interpreted as a kind of "buffer layer" in which all the physical interaction between the system and its environment takes place. But due to statistical repeating over time associated with a sort of "memory effect," the loops of order 0 can organize themselves to form a larger loop of order 1 having a smaller length: this can be interpreted as an evolution, an improvement, or optimization of the system. The interaction length is now denoted L_{F1} and represents the sum of all the loops of order 1. These order 1 loops can again organize together and it gives a loop of order 2. Let us note L_{Fn} the length of interaction for the order n. If we assume now that the local velocity V remains unchanged, it is then possible to associate a time of interaction t_{Fn} for a

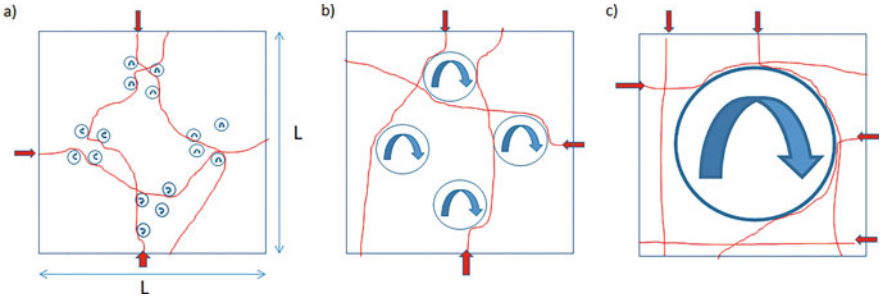

Fig. 11.1 (**a**) The field displays some loops of order 0 which deviates the trajectories and increases the length of interaction relatively to the size L. The arrows indicate the direction of an energetic perturbation. (**b**) The field displays now loops of order 1: the smaller loops of order 0 have been integrated into a loop of order 1. The length of interaction is smaller; (**c**) The loops of order 1 are integrated into a larger loop of order 2. The length of interaction is reduced again. The length of interaction can decrease beyond this value if the loop or order 2 loses some of its spatial extension at it can be seen in Fig. 11.2

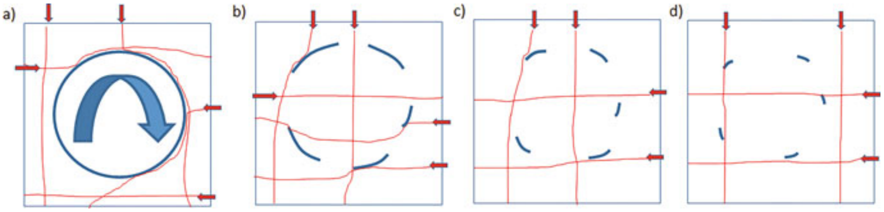

Fig. 11.2 (**a**) The system of Fig. 11.1 has reached the largest integrative loop. The length of interaction has its minimum value. (**b**, **c**) This loop is submitted to fragmentation and loses some of its spatial extension: this reduces the entropic time, i.e., the internal deviation of trajectories. (**d**) The largest loop is now completely erased. The crossing time tends to the homogeneous time $t_L = L/V$

given order n. We just write $t_{Fn} = L_{Fn}/V$. The loop of order 2 represents the largest scale of the system, but the system can evolve beyond this state if the loop is fragmented and loses its spatial extension as can be seen in Fig. 11.2.

11.1.2 The States of a Fractal: Application to the Generalized Surface Cantor Fractal

We present our approach by taking, as an example and to make easier the presentation, the case of the generalized surface Cantor fractal. This set is very interesting when we are studying multi-scale distributions in ecosystems and natural patterns because it recalls some kinds of natural clustering of vegetation or animal distribution in space. Figure 11.3 explains how the set is built. We start from an initial square which is fragmented in k smaller squares by a scale ratio r. By definition, the fractal dimension of the set is thus $D_\mathrm{f} = \ln(k)/\ln(1/r)$. For $r = 1/3$ and $k = 4$ which is the classical Cantor set, we obtain $D_\mathrm{f} = \ln 4/\ln 3 = 1.26$. But the scale ratio r can vary from 0 to ½.

We are here interested in the length of the fractal set for a given number of iterations: we will work with truncated fractals that we call "fractal states." Let us note the interaction length L_{Fn} as the length of the fractal at the level n. But for some reasons of coherence in the notations, we will consider that the level $n = 0$, i.e., $L_{F0,}$ corresponds to the set having the largest number of iterations denoted n_0. The fractal length at level 0 is thus $L_{F0} = {g_F}^{n_0} L_{B,}$ where avec $g_F = kr$. The case of the classic surface Cantor is recovered for $k = 4$ and $r = 1/3$, i.e., $g_F = 4/3$. Since the fractal dimension is $D = \ln k/\ln(1/r)$, we thus can write

$$g_F = kr = r^{1-D} \,\text{or}\, g_F = kr = k^{(D-1)/D}. \tag{11.2}$$

The quantity g_F is the ratio of the lengths of two consecutive fractal sets, i.e., $g_F = L_{Fn}/L_{F(n+1)}$. The specific case $D = 2$ implies $g_F = 1/r$ which means that this parameter, only for $D = 2$, is a scale ratio. At the level $n = 1$, the fractal length is $L_{F1} = {g_F}^{n_0-1} L_B$. At the level $n = 2$, $L_{F2} = {g_F}^{n_0-2} L_B$; then we have $L_{F3} = {g_F}^{n_0-3} L_B$

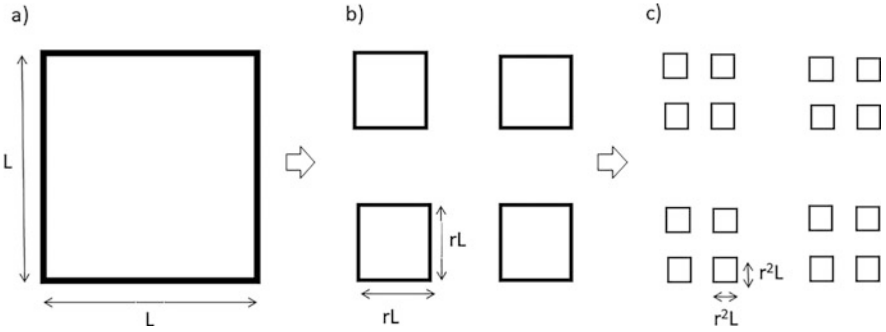

Fig. 11.3 Sketch of the surface Cantor; (**a**) The zero iteration is a square of side L; its total length is $L_B = 4L$. (**b**) Iteration $n = 1$: the initial square is reduced by a scale factor r and k reduced squares are placed in the corners of the initial square. The total length is now $4rL_B$. (**c**) Iteration $n = 2$: the same reduction procedure is made. The total length is now $L_B(4r)^2$. The classical surface Cantor corresponds to $r = 1/3$, but r can take values between 0 and ½

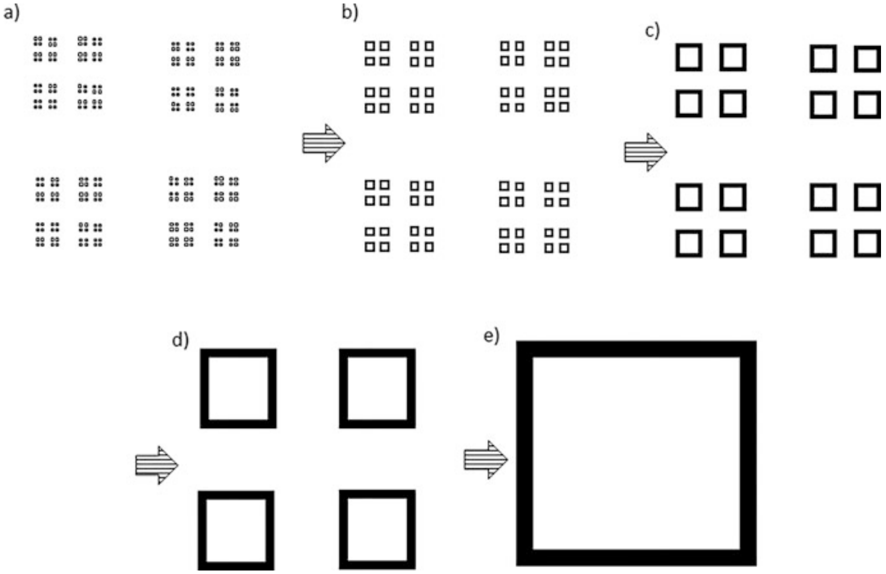

Fig. 11.4 (**a**) The Cantor surface fractal for $r = 1/3$ and $n_0 = 4$ iterations (**b**) The previous fractal set is smoothed, the smallest scale are eroded, and the fractal has now 3 iterations. (**c**) Again the fractal is submitted to a smoothing procedure and loses its smallest scale. It becomes an order 2 fractal. (**d**) The fractal displays now one iteration after new smoothing. (**e**) Finally, we get a simple square after new smoothing. Let us note that the fractal becomes thicker as it is simplified suggesting a more massive object after each smoothing procedure

and the level $n = 4$ gives the basis length L_B with $L_{F4} = L_B$. We thus can write for n varying from $n = 0$ to n_0 the following relationship (Fig. 11.4):

$$L_{Fn} = L_{F0}{g_F}^{-n} \quad \text{with} \quad L_{F0} = {g_F}^{n_0} L_B. \tag{11.3}$$

What happens when the fractal set has been smoothed until to its largest scale? The general relationship $L_{Fn} = L_{F0}{g_F}^{-n}$ remains valid for n larger than n_0. If $n > n_0$, the length L_{Fn} becomes smaller than the basic length L_B corresponding to the largest scale. If $n \to \infty$, the length L_{Fn} tends toward zero. This means that the fractal interaction is smoothed beyond this largest scale and that entropic time becomes null.

Let us observe that the interaction lengths L_{Fn} are linked to each other by

$$\frac{L_{Fn} - L_{F(n+1)}}{L_{F(n-1)} - L_{Fn}} = 1/g_F \quad \text{with} \quad \lim_{n \to \infty} L_{Fn} = 0. \tag{11.4}$$

Moreover, between two fractal states n et $n + 1$, it can also be written

$$\frac{L_{Fn}}{L_{F(n+1)}} = g_F. \tag{11.5}$$

To make our presentation easier, we need to give some precisions of vocabulary. This is now clear that we are not working here with infinite mathematical fractals but with truncated fractals at some level n having for smallest scale (internal cutoff). The scale characterizes the smallest scale of the truncated fractal of order n: its scale range is thus $[l_{c(n)}; L]$. That is why we call "fractal state of order n" the truncated fractal at the level n.

11.2 Interaction Time of a Fractal State

Let us remind that we defined the minimum crossing time t_L as the time obtained for a homogeneous field without any heterogeneity, without any friction or entropy production. If a phenomenon interacts with this field, the time of interaction will be larger than t_L and frequency smaller than $\nu_L = 1/t_L$. We assume now the existence in the field of a heterogeneous fractal set that creates blockage, deviations, and frictions which can be called "entropy production." If the fractal heterogeneous set generates a time interaction t_{Fn} (called entropic time), then the total crossing time is the sum

$$t_n = t_{Fn} + t_L, \tag{11.6}$$

where t_L is the homogeneous time (without entropy production). Let us make some remarks on the entropic time. It is clear that the more the fractal set displays iterations, i.e., an increasing scale range, the more the entropic time is high with a fractal set. The evolution of entropic time through scale-space is given by the parameter $g_F = kr$ since (Fig. 11.5).

It is easily shown that the crossing time can be written

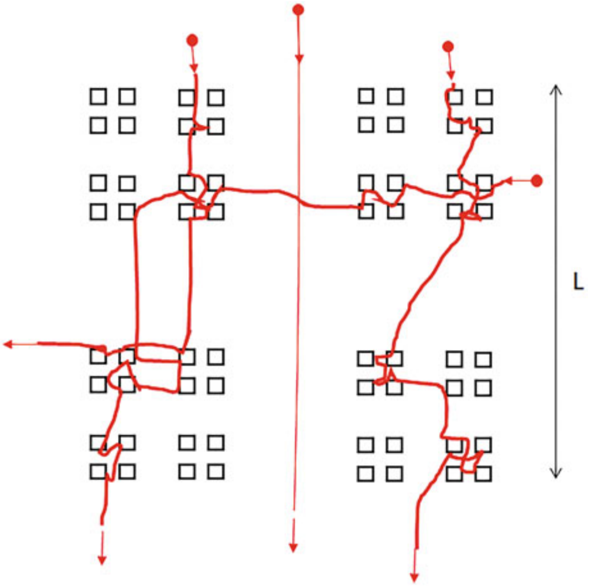

Fig. 11.5 The fractal set of heterogeneities deviates the trajectories and increases the crossing time relatively to the homogeneous time $t_L = L/V$

$$t_n = (t_0 - t_L){g_F}^{-n} + t_L. \tag{11.7}$$

We thus derive the following relationships:

$$\frac{t_n - t_{n+1}}{t_{n-1} - t_n} = 1/g_F \text{ and } \frac{t_{n+1} - t_L}{t_n - t_L} = 1/g_F. \tag{11.8}$$

One recognizes here a log-periodic equation linking crossing times. Crossing time tends toward a minimum interaction time which is the homogeneous time, a time obtained for a perfectly smoothed field. The homogeneous time defines a field without entropy production. It can be associated with a critical time at which evolutive capacities saturate. The system has thus reached a sort of rigid dynamical state as if the mass of the system had increased becoming more difficult to move from its kinematical state.

11.3 Energy of a Fractal State

Let us now define the energy E_{Fn} of a fractal state. Its length being L_{Fn} and the crossing time being t_{Fn}, the simplest way to define an energy is first to define an acceleration $a_{Fn} = L_{Fn}/t_{Fn}^2$ and then to introduce a mass m_{Fn} that would lead to the force. The work done by this force over the length of interaction is then $E_{Fn} = m_{Fn}a_{Fn}L_{Fn}$, i.e.,

$$E_{Fn} = m_{Fn}(L_{Fn}/t_{Fn})^2. \tag{11.9}$$

If we define a velocity c_F such as $c_F = L_{Fn}/t_{Fn}$ we thus have $E_{Fn} = m_{Fn}c^{2}{}_{F}$. Such an equation is of course reminiscent of the field of relativity and quantum mechanics. To go forward, i.e., to be able to link mechanics and geometry, we need to understand what can be the mass of a fractal state.

11.4 The Mass of a Fractal State: The Variation of Mass with the Order of the Fractal State

To define the mass of a fractal state, let us come back to the "scale smoothing" between two fractal states. When the fractal set jumps from the fractal state of order *n* to the fractal state of order *n* + 1, it loses some length in a precise ratio. It also loses interaction time such as $g_F = t_{Fn}/t_{F(n+1)}$. Can we consider this smoothing effect differently? If there is smoothing during a jump from *n* to *n* + 1, what happens to the lost interaction length? If we say that there is a smoothing phenomenon, how can we reduce the interaction length and at the same time how can we increase the quantity of smoothed length? One solution is to define geometrically the smoothed length. One way to do this is to define a sort of "thickness of the fractal" by wrapping along with the fractal set of order *n* + 1 the smoothed length coming from the fractal set of order *n*. Let us consider an example of the surface Cantor fractal. To make the presentation clear let us start from the fractal in Fig. 11.6 displaying only two iterations. Its fractal length is $L_{F0} = g_F{}^{n_0} L_B$ with $n_0 = 2$ and the smoothing procedure leads to the fractal or order one having a fractal length. The segments along the main lines of the normal fractal set represent the segments lost in the smoothing procedure, the total length leading to the length jump $L_{F0} - L_{F1}$. If we consider that this smooth length along the main fractal contributes to making easier some flux existing on the

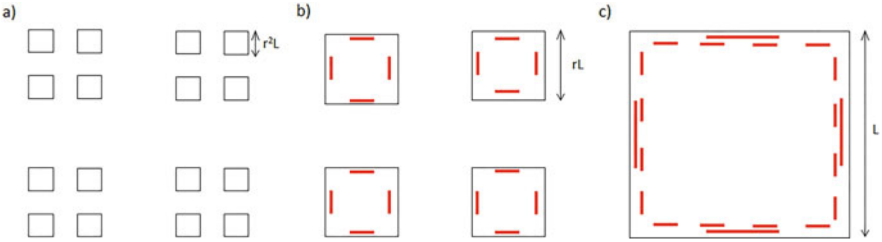

Fig. 11.6 Sketch explaining the wrapping process of mass which increases the mass of a fractal. (**a**) A surface Cantor fractal state of two iterations. It has no wrapped length. (**b**) The initial fractal state is smoothed to one single iteration. The internal segments correspond to the wrapped length. (**c**) A new smoothing leads to a final square of size L: the internal segments represent all the length that has been wrapped from the initial fractal state (**a**). This wrapped length makes the increase of the mass of the fractal state. We consider that the sum of the fractal length and wrapped length is conserved from (**a**–**c**). Fractal length is transformed into the wrapped length which gives an increase of mass

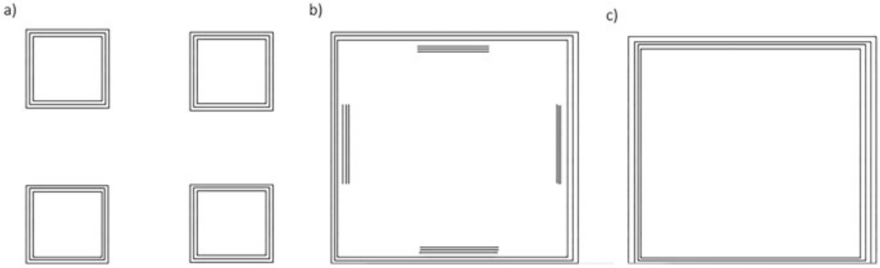

Fig. 11.7 Sketch illustrating how smoothing a fractal generates wrapped length which increases the number of circulating lines and thus the mass of the fractal set

set, then the main thickness should be proportional to the mass of the set. The smoothed length appears to be wrapped in the main fractal structure. If we note L_{Wn} the wrapped (smoothed) length at the level n, we have $L_{Wn} + L_{Fn} = L_{F0}$. This means that we consider that the intrinsic length L_{F0} is conserved through the smoothing procedure. The length of interaction decreases, but the wrapped (smoothed) length increases in such a way that their sum is conserved.

The mass of a body can be defined by the measure of the resistance of the body to a change in its kinematical state. Let us now consider the different levels of a fractal set by taking into account their wrapped lengths. If there is a phenomenon circulating on the fractal, along with and around its frontier, we can easily see that more the fractal is “thick” in terms of wrapping lengths more circulation on the fractal is possible. We also understand that if more circulation occurs on the fractal it will be more difficult to change its kinematical state. This means that the wrapped length is linked to the kinetic mass of the body. In other words, the increase of wrapped length corresponds to the increase in mass. We will assume that there is a proportionality between the increase of mass and wrapped length. If m_{F0} is the mass corresponding to the fractal set of order 0 which has a fractal length L_{F0} and a wrapped length $L_{W0} = 0$, then the fractal set of order n with L_{Fn} and a wrapped length L_{Wn} will be associated with a mass

$$m_{Fn} = m_{F0}(1 + L_{Wn}/L_{Fn}). \tag{11.10}$$

This leads to a simple and remarkable relationship between the masses at different orders.

To understand more clearly how the wrapped length can generate an increase of the mass, let us consider Fig. 11.7 representing a simple surface Cantor for $r = 1/3$. The basic elements of the initial fractal of order 0 in (a) are made up of three lines: this is the initial “thickness” of the fractal. The smoothing of the fractal obtained with its wrapped length represented in (b) generates a system with four lines which is represented in (c). The system in (c) being thicker in terms of internal smoothed lines is more massive than the one in (a).

11.5 A Planck–Einstein-Like Law for the Fractal State Energy

Having now a geometrical definition of the mass of a truncated fractal, we can come back to the energy of a fractal written through $E_{Fn} = m_{Fn}L_{Fn}^2/t_{Fn}^2$. Since $L_{Fn} = L_{F0}g_F^{-n}, t_{Fn} = t_{F0}g_F^{-n}$ and $m_{Fn} = m_{F0}g_F^n$ it is easily shown that the quantity $m_{Fn}L_{Fn}^2/t_{Fn} = m_{F0}L_{F0}^2/t_{F0}$ does not depend on n and should be a constant when n changes. This quantity has the dimension of action. Let us note $h_F = m_{Fn}L_{Fn}^2/t_{Fn}$. We thus have $E_{Fn} = h_F/t_{Fn}$ which leads to a remarkable Planck–Einstein's law-like formula

$$E_{Fn} = h_F \nu_{Fn}. \tag{11.11}$$

What is here very interesting in this approach is that a constant of action is emerging naturally from a simple fractal system. The constant of action exists because there is compensation between mass, length, and time which destroys the dependence with n: the energy then becomes proportional to the frequency. The action is a fundamental quantity in physics. There is no quantum physics without the concept of action. Action is an energy multiplied by a time, but it is interesting to observe that it is also a mass multiplied by a diffusivity. In our case, diffusivity is equal to $\alpha_F = L_{Fn}^2/t_{Fn}$ and defines the capacity of the system to diffuse energy. We thus have $h_F = m_{Fn}\alpha_{Fn}$. The action is constant because mass and diffusivity display inverse evolutions with order n of the fractal state. When mass increases which means also an increase of energy, the internal diffusivity decreases which also means a decrease of spatial extension denoted here Δx which can be associated with a decrease of temporal extension denoted by Δt; the system is thus more localized in space and in time. The opposite case, i.e., a decrease of mass, implies a decrease of energy; the internal diffusivity becomes higher, which implies a higher spatial extension. It seems that we have here a geometrical way to visualize the uncertainty principle of Heisenberg. To our knowledge, this is the first derivation of Planck–Einstein's law using simple and direct fractal ideas. This model has certainly a lot to say in the field of quantum mechanics and the origin of Planck–Einstein's law. This will be developed in a future book entitled *Creative Entropy* (Queiros-Condé et al. 2022).

11.6 Kinetic Chain Temperature, Exergy, and *Dispergy* of a Fractal State

At this stage, inspired by the pioneering work of Louis de Broglie on the "hidden thermodynamics of the particle" and the "temperature of the photon," we introduce a temperature $\overset{\circ}{t}_{Fn}$ such as $E_{Fn} = h_F\nu_{Fn} = k_{BF}\overset{\circ}{t}_{Fn}$ where k_{BF} is a constant having the dimension of an entropy which can be interpreted as the quantum of entropy and of course linked to a sort of macroscopic constant of Boltzmann. Pay attention: k_{BF} is different from the fractal geometrical parameter k. How can we interpret the temperature? This temperature defines the intensity of kinetic chaining. For $n = 0$, the temperature is at its smallest value: the chaining between quanta is relatively small and displays high dispersive features. For increasing values of n, the chaining between quanta is very intense leading to some internal rigidity and strong linkage corresponding to a high kinetic mass. For all these reasons, we will call this temperature the "kinetic chain temperature." We observe that for low values of n, i.e., for highly developed and spatially extended fractal states, the chain temperature is low, while for high values of n (i.e., for highly localized fractal states) the chain temperature is high.

We would like now to distinguish in the fractal state energy E_{Fn} two forms of energy that appear through the second principle of thermodynamics: (i) the exergy content of energy denoted X_{Fn} which is simply the maximum work that can be realized by using the energy E_{Fn} and (ii) the complementary energy which represents the rest of energy that is not available for mechanical work and has an entropic nature. This energy Z_{Fn} displays dispersive features which cannot be transformed into mechanical work. For these reasons, it is called "dispergy." In some thermodynamical books, this quantity is sometimes referred to as "anergy," but this term is ambiguous since it suggests a quantity without energy or positive feature. This is not the case. Dispergy is of course linked to the entropic features of energy, but this does not mean that dispergy is linked to "disorder" or does not have a useful function. Dispergy must not be seen as disordered energy. It rather can be interpreted as the energy necessary to make possible the transfer of exergy, a kind of "energy of canalization" which is also correlated to the information necessary to this canalization. Moreover, it certainly displays a damping (buffer) function which gives stability to the system: this means that systems with low dispergy relative to exergy can deliver a high quantity of work (this means a high efficiency) but are highly unstable and vulnerable to internal or external perturbations because there is not enough dispergy to maintain the stability and to display a buffer or a damping function. We thus will keep the term *dispergy* (Queiros-Conde and Feidt 2018). Let us take a temperature of reference $\overset{\circ}{t}_0$. If an energy E is transmitted at the temperature $\overset{\circ}{t}_E$ with, the exergy content of E denoted X_E is expressed through the Carnot factor $\theta_E = 1 - \overset{\circ}{t}_E/\overset{\circ}{t}_0$. It gives $X_E = E\left(1 - \overset{\circ}{t}_E/\overset{\circ}{t}_0\right)$. The dispergy is thus $Z_E = E\left(\overset{\circ}{t}_E/\overset{\circ}{\mathrm{t}}_0\right)$.

Let us come back to the energy E_{Fn} of a fractal state. We would like to quantify its exergy and dispergy contents, i.e., X_{Fn} and Z_{Fn} with $E_{Fn} = X_{Fn} + Z_{Fn}$. It is easy to see that the dispergy content is constant with n, since by definition we thus have

$$Z_{Fn} = Z_{F0} = k_{BF}\overset{\circ}{t}_0 = Cte. \tag{11.12}$$

This implies that the energy jump $E_{F(n+1)} - E_{Fn}$ is an exergy jump and that it can be written $\delta W_n = X_{F(n+1)} - X_{Fn}$. This means that the fractal state changes with n due to its exergy content X_{Fn} which increases. It can be shown that the exergy content is

$$X_{Fn} = E_{Fn}\left(\frac{g_F^n - 1}{g_F^n}\right). \tag{11.13}$$

A fractal state jumps from n to $n + 1$ by an equivalent of mechanical work δW_n. What is exactly this equivalent work? This quantifies all the improvements, the innovations, and the increase of information which makes the fractal length and the fractal time shorter from n to $n + 1$. These changes have a smoothening effect on the smallest scales which are orientated along the direction given by the larger scales. The fractal length L_{Fn} becomes shorter, but the kinetic mass m_{Fn} increases as it has been illustrated in Figs. 11.6 and 11.7. The scale smoothening is thus associated with an internal mass roughening. The kinetic chain temperature also increases because $\delta W_n = E_{F(n+1)} - E_{Fn} = k_{BF}(t_{F(n+1)} - t_{Fn})$. Since $g_F = t_{Fn}/t_{F(n+1)}$ we have $\delta W_n/E_{Fn} = g_F - 1$. The system seems thus evolving by a sort of compression from n to $n + 1$ where δW_n would be the compression work. As in a classical compression, this work is transformed into heat ($\delta W_n \rightarrow \delta Q_n$) which makes an increase of kinetic chain temperature with $\delta Q_n = k_{BF}(t_{F(n+1)} - t_{Fn})$: the constant k_F can thus be interpreted as linked to an elementary calorific capacity.

11.7 Entropy Production Between the Fractal States: The Kinetic Chain Temperature

Let us calculate the production of entropy when the structure jumps from the state n to the state $n + 1$. By definition

$$\delta S_n = \frac{\delta Q_n}{\overset{\circ}{t}_n} - \frac{\delta Q_n}{\overset{\circ}{t}_{n+1}}. \tag{11.14}$$

By using $h_F/t_{Fn} = k_{BF}\overset{\circ}{t}_{Fn}$ and $h_F/t_{F(n+1)} = k_{BF}\overset{\circ}{t}_{F(n+1)}$ we can derive

$$\delta Q_n = k_{BF}\left(\overset{\circ}{t}_{F(n+1)} - \overset{\circ}{t}_{Fn}\right) \tag{11.15}$$

and then

$$\delta S_n = \frac{k_{BF}(g_F - 1)^2}{g_F}. \tag{11.16}$$

The entropy production we calculated so far is for one single elementary event ("a geometrical quantum") on the fractal set. But the fractal set does not jump from state n to state $n + 1$ with one single quantum. To change the state, it will need the action of a great number of geometrical quanta: let us note this number of quanta N_n. If T_n is the date at which starts the state n and T_{n+1} is the date at which ends the state n and begins the state $n + 1$, the difference of time $T_{n+1} - T_n$ gives the time needed for the transition. The question now is: how many quanta the system needs to go from n to

$n + 1$? Since $t_{Fn} - t_{F(n+1)}$ is the quantum time between two states, the number of quanta can be expressed by

$$N_n = \frac{T_{n+1} - T_n}{t_{Fn} - t_{F(n+1)}}. \tag{11.17}$$

The total entropy production becomes now

$$S_n = N_n \delta S_n = \frac{k_{BF} N_n (g_F - 1)^2}{g_F}. \tag{11.18}$$

The previous formula can be written

$$\frac{S_n}{N_n} = \frac{k_{BF}(g_F - 1)^2}{g_F}. \tag{11.19}$$

Our last result means that the entropy per quantum is conserved when n changes. We will see just hereafter that this is in agreement with the entropic-skins theory (Queiros-Condé 2000) used to describe log-periodicity in species evolution and based on a fractal approach of the phenomenon of intermittency in turbulence. If we assume that the number of quanta does not depend on n ($N_n = N_S$) then it implies that the entropy production is also a constant between two fractal sets, i.e., $S_n = N_S k_{BF}(g_F - 1)^2/g_F$.

We observe that for this case, the entropy becomes null which means a reversible evolution without entropy production. The other limit $g_F \to \infty$ gives $S_n/N_n \to k_{BF} g_F = k_{BF} rk$. This means that in this limit the quantity $k_{BF} rk$ becomes a new quantum of entropy k'_{BF} and that we have $S_n = N_n k'_{BF}$. This is the simple well-known equation giving the entropy of a number N_n of particles in a perfect gas.

By writing $N_S(t_n - t_{n+1}) = T_{n+1} - T_n$ for n increasing from 0 to n and by summing all the equations, we simply obtain for any value of n

$$N_S(t_0 - t_n) = T_n - T_0. \tag{11.20}$$

By taking the limit $n \to \infty$, it gives $N_S(t_0 - t_L) = T_L - T_0$ where T_L is the critical time of T_n when $n \to \infty$. We thus recover the famous log-periodic equation

$$T_n = (T_0 - T_L) {g_F}^{-n} + T_L. \tag{11.21}$$

11.8 Irreversibility and the Structuration Efficiency of a Log-Periodic Phenomenon

We thus found that the entropy production between two consecutive fractal sets is a constant when n changes. The entropy production is null for the specific case $g_F = 1$ which is characteristic of a reversible evolution. The change in the fractal structure is thus associated with the same amount of entropy. We recover here the result we obtained in the context of "entropic-skins theory" in the paper entitled "Principle of conservation of the flux entropy in species evolution" (Queiros-Condé 2000). Let us recall that the parameter g was interpreted as $\gamma = 1/g$ where the factor of reversibility quantifies the level of intermittency. Intermittency is a phenomenon (namely in turbulence) that is characterized by the fact that energy dissipates through a clustered structure: a non-intermittent system is defined by a homogeneous and space-filling dissipation without clustering. The case $\gamma \to 1$ (i.e., $g \to 1$) corresponds to a purely reversible evolution without entropy production and thus without intermittency. The system does not display internal differentiation. In other words, it has no internal structure since it is characterized by homogeneity. The opposite extremal case $\gamma \to 0$ (i.e., $g \to \infty$) corresponds to an infinite irreversible case where all the energy is transformed in entropy very rapidly when n varies. All the energy is dissipated (dispersed) in entropy within the system. We can define an efficiency of internal structuration $\eta = 1 - \gamma$. We see that when $\gamma \to 1$ the structural efficiency tends to zero and when $\gamma \to 0$ the structural efficiency is equal to one. Working with frequencies, it takes the form $\eta_F = 1 - \nu_{Fn}/\nu_{F(n+1)}$ which implies $\eta_F = \delta Q_n / E_{F(n+1)}$. Working with temperatures, it takes the form

$$\eta_F = 1 - \frac{\overset{\circ}{t}_{Fn}}{\overset{\circ}{t}_{F(n+1)}}. \tag{11.22}$$

The structuration efficiency between two fractal states n and $n + 1$ is a sort of Carnot efficiency corresponding to a thermal machine working between the low temperature $\overset{\circ}{t}_{Fn}$ and the high temperature $\overset{\circ}{t}_{F(n+1)}$. The log-periodic law implies that this efficiency is a constant when the order of the fractal state varies.

11.9 Conclusion

We developed a thermodynamical explanation of the log-periodic law based on a simple quantum fractal model. The parameter g of the log-periodic law is interpreted as linked to the increase of the length of the fractal with its number of iterations which defines its scale range. By introducing a "kinetic chain temperature," we show that the log-periodic law corresponds to a log-periodic increase of temperature converging toward a critical temperature. We defined an efficiency of structuration and found a production of entropy which are constant through the fractal states of the phenomenon. The critical time T_L represents thus a state having the maximum kinetic chain temperature. The system is thus in its hottest state, which is defined by internal strong links, a minimum evolutive capacity, and thus a low potential of adaptation. Around its critical time or equivalent critical temperature, due to its low dispergy (or entropy) content which displays a damping function to internal and external fluctuations, the system becomes highly unstable and vulnerable. It can thus collapse very rapidly since it has no damping (no "escaping") possibility. The revenge of dispergy (entropy) against exergy (mechanical power) lies precisely in this simple idea: without enough dispergy (entropy) there is no stability in time, no adaptation, and thus no survival.

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Sapiens and Cognition: The Optimal Vertical Nervous System—The Last Threshold of Self-Organized and Self-Memorizing Increasing Complexity from Gametes to Embryo

12

Anne Dambricourt Malassé

> « Teilhard wrote, “we are not lost in the Universe, on the contrary” (...). This phenomenon is of course observable only in the long term, but it translates a logic of astonishing stability, an irreversible time, writes Anne Dambricourt Malassé, who memorizes! I am not far from her thought. The sense (in all the senses of the term) of the history of the inert, alive, thinking matter, in its race to the complexity, is an observation (. . .). —*Y. Coppens (1996)*

Abstract

From Antiquity to the nineteenth century, the human being was seen as an archetype from the metaphysical origin organized in the physical world around the verticality, monkeys belonged to another archetype able of quadrupedalism and bipedalism. In 1801 and 1802, Jean-Baptiste de Lamarck proceeded to a rupture by seeking a natural and functional explanation of human verticality since extinct monkeys in relation to climate changes. He opened the mind to self-organized processes between living systems and their environments. In 1868, Charles Darwin took up the Lamarckian theory with the gemmules hypothesis, looking for an explanation for the transmission of the macroscopic changes and their memorization at the microscopic scale of the sex cells. Memorization and

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_12

self-organization were the implicit processes of transformism, the natural selection being a general concept waiting for better knowledge in bio-physicochemistry, i.e., in thermodynamics. This double evolutionary problematics, (1) the memorization of the transformation processes and (2) the neural straightening from quadrupedal primates to bipedal *Homo sapiens,* is confirmed but as a consequence of the macroevolution of the embryonic body plans and not as the result of postnatal biomechanical constraints. I have demonstrated for more than 30 years that the straightening was a progressive embryonic and phylogenetic process, saltationist and reiterated four times, starting systematically from the horizontal direction of the notochord. This process followed increasing complexity and duration of the neurulation with morphological reorganization along the cephalocaudal axis. The stability of the evolutionary trajectory over 40 million years up—despite successive emergent angular discontinuities separated by million years—allowed us to infer a new family of gametogenesis attractors which correspond to evolutionary properties transmitted since the emergence of unicellulars: the self-memorization of self-organized processes. In other words, self-organization which includes simultaneously its own memorization is the complex process that allowed the emergence of life whose principles are self-reproduction. Prokaryote diversification generated environmental increasing complexity. Then, eukaryotes and multicellulars became possible thanks to the increasing diversity and complexity of the environment but also thanks to self-memorization properties able to create and transmit the first ontogeny. Later, macroevolution could develop with a coherent reorganization of the body plan according to the rules of internal increasing complexity. The phylogenetic straightening of the central nervous system allows us to induce that gametes have inherited these macroevolutionary properties acting during embryogeny along the craniocaudal axis. This paradigmatic shift is coherent with the sciences of self-organization and opens debate on the future of our species because the verticality is reaching a physical limit for the vocal tract, the dental occlusion, and the cerebellum with psychomotor and cognitive consequences, whereas the relationships between the environmental complexity, the sex cells, the reproductive organs of the females, and the exponential complexification of the neurogenesis are still unknown.

Keywords

Verticality · Hominization · Central nervous system straightening · Embryonic body plan · Gametogenesis · Increasing complexity · Self-memorization · Modeling · Attractors · Instability · Axial skeleton · Basicranio-facial contraction · Cerebro-cerebellar Rubicon · Psychomotor balance · Cognition

12.1 The Premises

The theory of biological evolution was formulated in 1801 by Jean-Baptiste de Lamarck and developed in 1802 with the concept of the inheritance of characters modified by the function (Lamarck 1801, 1802). His mentor Georges Buffon (1707–1788) had already described the major stages of the planetary transformations which reached 10 million years (Buffon 1785) or even several hundred million years (Giraud-Soulavie 1780–1784). The natural history of organisms, or the natural order of their places in the environment, remained that of Aristotle. The history was recognizable thanks to the fossil records, from the least to the most complex organization illustrated by the human nervous system. The planet was irreversibly committed to a state of stable internal equilibrium, with the cooling of the lava (the magma) and its tectonic consequences (shrinking of the earth's diameter), so the fauna and flora had necessarily been replaced by new species as geochemical and climatic changes took place. The cooling tendency of the earth and the natural order of the animals in their environment were thus linked, as confirmed by the extinct species. The variation of subspecies according to latitudes and continents was accepted, but only within the limits of a metaphysical archetype, an "inner mold" as proposed by Georges Buffon (1749). These archetypes were no longer embodied in the matter as soon as the climatic and/or geophysical conditions did not allow the molecular inputs necessary for their development, from fertilization to adult form. The environment was, therefore, influential insofar as the same mold had adaptive plasticity to different environments (Buffon's "organic molecules" of the mold). But global environmental changes were the cause of their massive extinction according to the planetary extent of geophysical changes, as Georges Cuvier maintained later with the catastrophism paradigm. Aristotle's gradation of the animals had thus followed the history of the Earth, according to the internal diversification and complexification of their organizations until the modern human encephalon. It should be noted that man appears not only as the most complex organism in the history of the animal kingdom but also the only animal whose nervous system is vertical from the brain stem. The Greek philosophers already reasoned on this cognitive capacity, but without the long durations, since the cosmos and the earth had neither beginning nor end.

The varieties of a species were seen as adaptations of the same archetype, but the environment was not conceived as the master-builder capable of creating an archetype with molecules or atoms. The origin of an animated organization from the embryonic germ with the transmissible memory of its construction was out of the field of natural history and the observation tools. Thenceforth how to understand that atoms or molecules could have organized themselves to generate the ancestors of sexual cells, or male and female animalcules (spermatozoids and oocytes)? In other words, how could free molecules and atoms have generated an autonomous organization which will simultaneously be its self-memorization, since the consequence is to reproduce in itself, from itself? For the origin of the animalcules, the naturalists thus relied on the metaphysics of the Greek philosophers, nature was the physical dimension (space-time-energy) of a being (ontos) and accessible to the human reason by the senses of observation and the measurements. The organization was thus the visible part, physically observable and measurable, of the beings. Their beginning and end were their physical dimensions in the duration. The study of fossils, or paleoontology, was the science of extinct beings whose animate, or physical, organization would have been a kind of terrestrial incarnation of abstract entities (mathematical forms at the base of archetypal structures). Such was the intellectual context in Europe, only 220 years ago, when Jean-Baptiste de Lamarck began teaching in 1793 at the new chair of invertebrate zoology of the National Museum of Natural History in Paris (Dambricourt Malassé 2021a).

12.2 Lamarck and Darwin, Pioneers of the Self-Organized Evolution

Lamarck had developed the first reflection on metabolism or the internal equilibrium of organisms and their death, in terms of physical processes (Lamarck 1794). The zoologist was thinking on the origins of life, the very beginning of the first unicellular cycles, but without pushing the reasoning until its logical consequences that implied self-memorized processes. The emergence of life, or a unicellular cycle, is more than the replication of a cell. The cycle is the reproduction of the process organization, it has self-memorized. Nevertheless, the zoologist reasoned on the adult term of ontogeny and added a conceptual difficulty for the transmission of the modifications to the sexual cells. Abandoning the chronology of the development, he reversed the direction of the reasoning from the macroscopic toward the microscopic scale, whereas he should have logically followed that of the physical and chemical laws at the terrestrial surface. But the spontaneous formation of replicative cells from physicochemical processes was inconceivable. Thirty years later, in 1830, his audacity reached the European community thanks to the debate at the Academy of Sciences between his fervent defender Etienne Geoffroy Saint-Hilaire and his contradictor Georges Cuvier. The first argued that there was only one “unity of organic composition plan” in the animal kingdom, which was therefore capable of becoming more complicated, while the second distinguished four, without any possible transition. The environment as a factor of variability within the limits of the species had already been disseminated by Buffon, but seeing the environment as the motor of the evolution of the “chain of beings” including *Homo sapiens*, was the audacity of Lamarck. Charles Darwin recognized the historical reality:

> The conclusion that man is the co-descendant with other species of some ancient, lower, and extinct form, is not in any degree new. Lamarck long ago came to this conclusion (. . .) as the progenitors of man became more and more erect (. . .) owing to a change in its manner of procuring subsistence or in the conditions of its native country, to live somewhat less in trees and more on the ground, its manner of progression would have been modified: and in this case, it would have had to become either more strictly quadrupedal or bipedal (Darwin 1871).

Darwin was a Lamarckian and he extrapolated the reasoning until its limits, postulating the existence of gemmules (Darwin 1868), a kind of molecule capable of recording modifications on the macroscopic scale of the adult animal and transmitting them to the microscopic scale of the internal organization of sex cells. Then looking for an explanation for the successful transmission from generation to generation, he applied his concept of natural and sexual selection: the transmission could only be explained by the crossing of females and males which shared the same functional modifications and the same gemmules able to transmit them to the sex cells. Individuals unfit for change, because the gemmules were deficient, should end up not having any descendants, in accordance with the model of extinction defended by Georges Cuvier.

The gemmules hypothesis was already obsolete because of Gregor Mendel's laws of inheritance. On other hand, Darwin's nephew Francis Galton tried to explain to him that the gemmules—the molecules able to record or memorize changes—could be conceivable only for the reproductive cells.[1] But Darwin's merit, rarely mentioned, was to set an implicit condition for the environment to be able to modify organisms: they had to be endowed beforehand with physical and chemical properties on the scale of adult organization and transmissible to the sex cells. This conception was already one of the self-organized systems with their internal logics, the organism possessing the necessary properties to reorganize itself and transmit them to the sex cells. The individuals endowed with these self-organized internal properties and interbreeding with each other transmitted them. But without such self-organized organic properties, natural selection alone would have made no sense. Darwin did not solve the chicken-and-egg dilemma, since the gemmules had to come from the sex cells first and match with the cellular specialization of an organism completed in its development while not yet existing in the zygote stage.

Neither Lamarck nor Darwin discovered the biological processes of the transformist evolution, but they raised the real question: the transmission of its complex mechanisms.

In France, therefore, natural selection was not welcomed by naturalists as Charles Darwin expected, because the concept could not be compared to a discovery of physicochemical processes that generate embryogenesis more complicated than that from which it was supposed to emerge. The physician Armand de Quatrefages, inventor of the Cro-Magnon race and an astrogeophysicist (PhD on lunar gravitation), had a solid grounding in physics and mathematics and was in the position to note the absence of scientific content in the formulation of transformism, aware that the skeletal structures subject to gravitation, form a whole whose vital parts are in reciprocal coherence. The morphological plan of organization was necessarily in conformity with the physical and chemical laws since the sex cells.

The transformation of an internal structure could not be conceived by gradual and isolated changes within the organism and even less in the direction of the most

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[1] Correspondence between Charles Darwin and Francis Galton. http://galton.org/letters/darwin/correspondence.htm

complex organization toward the least complex sex cell necessary for their hereditary transmission. The naturalists could not conceive a morphogenetic body plan otherwise than as the completion of a process toward the achieved archetype at the adult stage, a metaphysical being without duration.

Armand de Quatrefages was a metaphysicist, so natural selection was not a scientific discovery able to invalidate the use of the metaphysical concept of the archetype, defended in paleontology by Richard Owen (1848). And many naturalists agreed with Quatrefages, even Paul Broca, the French founder of biometric anthropology and the free-tinkers society because this doctrine did not consider the structural and functional unity of the organism. French naturalists were looking for a vaster multidisciplinary theory taking into account the laws of physics and the forces of attraction at the inframolecular scale (Dambricourt Malassé 2021a).

The successive appearance of prosimians,[2] monkeys, great apes, and man in the geologic strata raised this problem. Anthropologists familiar with the primate's comparative anatomy did not conceive the vertical anatomy of man as the result of the slow transformation of the semierect organization of apes. Paul Broca has studied orangutan skeleton and concluded:

> But then it is not by slow and gradual evolution, by a selection with a secular march, that the species of the orang was produced? The change took place suddenly, without transition; it is not a progressive transformation, it is a complete transfiguration, carried out at once, contrary to all the Darwinian laws or others (...). The Darwinian doctrine is therefore inseparable from the idea that the evolution of species has been gradual and excessively slow. This is, one can say, its fundamental axiom. And yet, when we apply the rules of natural selection to the example of the orang, we come to recognize that the type of this animal could not have been produced gradually, that it must have appeared suddenly, without any transition. I find, on the contrary, that if the species have evolved, which is probable, they are arranged as if natural selection had not been the agent of their transformation. (Broca 1870).

Thus, Georges Cuvier's heirs rejected the transformism and consequently Charles Darwin's theory, because the hypothesis granting to sex cells properties of remodeling organogenesis more complex than those of the ancestor had no physicochemical modeling. Moreover, these properties of increasing complexity would have been transmitted from the first unicellular organisms, the origins of which were misunderstood. The acceptance of Lamarck's ideas in his own institution dates from the accession of Albert Gaudry to the chair of paleontology in 1872 where one century later Yves Coppens will pursue his research with the discovery of *Australopithecu*s *afarensis*, a hominin in permanent verticality but, to the general surprise, still arboreal.

The fundamental mechanism that Charles Darwin was confronted with, was the origins of life, in other words, the self-memorization of self-organization processes and this very abstract problem is still relevant today:

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[2] We keep this classical terminology coherent with the embryonic data.

> We will also hypothesize that living organisms are not palimpsests that have erased all memory of their past, but that they still contain today archives from the past. Also, we will restrict our quest to the atom of life, the cell, leaving aside multicellular organisms. The physicist Freeman Dyson (1999) demonstrates that in a realistic scenario of the origins of life, the reproduction of primordial processes must predate the emergence of a replicative process and then associate them into a coherent whole. In a chemical world such as the Earth's surface, this implies both the reproduction of chemical flows and the emergence, from this metabolism, of entities that can replicate themselves. In short, it takes at least two chemically distinct origins to explain the origin of life (. . .). This functional scenario of the origins of life is very abstract. (Danchin 2022)

The memory of the cellular construction is the memory of the evolutionary process that created the cell cycle as such; otherwise, it would not transmit itself. So, the process has therefore put itself in memory. This paradox is one of the complexity solved by the emergence of an unedited organization not reducible to its parts, but without having understood emergence as such (Morin 2022). The self-organized process which created the very first living system—a unicellular—included itself in the logic for its own transmission. This fundamental problem is found again with the process formerly called "orthogenesis", i.e., reproducible over very long geological times with morphogenetic trajectories forming phylogenetic lineages. The stability of the trajectory implies the reproduction of the evolutionary process, e.g., its memorization. By inference, these properties of memorization are necessarily constitutive of gametogenesis properties since the origins of life.

12.3 Orthogenesis, Macroevolution, and the Synthetic Theory (Princeton, 1947)

Such evolutionary mechanisms were beyond comprehension and they remained so in the middle twentieth century when the neo-Darwinian doctrine developed thanks to the discovery of genes and statistical calculations. The new Synthetic Theory was formulated in January 1947 during the Princeton conference taking into consideration the chromosomes but with a new postulate according to with only mistakes of electronic bonds—or covalency—during their replication could change the species. In April 1947, the French National Center for Scientific Research (CNRS), the *Muséum national d'Histoire naturelle* and the Sorbonne University organized a symposium with the Rockefeller Foundation hosted at the *Institut de Paléontologie Humaine* to debate on the insufficiency of the new synthesis (Piveteau 1950). Many researchers did not agree because of the incapacity of such molecular randomness to explain orthogenetic processes of the macroevolution but also those of microevolution described with mole rats of China.

For the paleontologist George Gaylord Simpson, orthogenesis was an "optical effect", the trend was only the combination of statistics and the natural selection of favorable random mutations, i.e., chemical processes occurring during the chromosomic replication:

> The reconstruction of orientations, geologically long, in a single direction, is subjective (...). The postulates inherent in one form or another of the orthogenetic theory (...) by unknown factors are neither required nor probable according to the present data (...). The driving role of natural selection, in this synthetic view, is not merely channeling, without a restrictive sense, but is also creative, bringing about a progression in a definite direction, orthogenesis, as it occurs, is ortho-selection. (Simpson 1950).

His colleague Pierre Teilhard de Chardin opposed him to three lineages of mole rats emerging from the same ancestral population over 20 million years he had studied in China. These species were distinguished by their skulls, but they have evolved with the same dental trend statistically improbable by the mere accumulation of electronic bond mistakes during the chromosomic replications.

> Elongation of the crowns, loss of the roots, which betrays a continuous process affecting the phylum itself, in its totality, and each of its components (...). The Siphnae confronts us with a certain case of directed morphological transformation that is to say of orthogenesis. The phenomenon can no longer be denied. But it remains to find a good explanation of the phenomenon. (Teilhard de Chardin 1950).

The statistics would not explain such improbability; the new paradigm did not take into consideration possible mutagenic effects with amplification or autocatalysis which will be developed later (e.g., Moore and Pearson 1981).

12.4 Posing the Evolutionary Problem: The Embryonic Trajectories of the Nervous System Versus Locomotion

12.4.1 Locomotion

The mammal skeleton is divided into axial and appendicular territories. The axial skeleton is composed of the skull, the laryngeal structures, the vertebral column, and the thoracic cage, whereas the appendicular skeleton is formed by bones attached to the vertebral column with the shoulder and pelvic girdles and the limbs. The neurocranium is formed by the vault and the base with three internal fossae, the anterior under the frontal lobes, the medial containing the temporal lobes, and the posterior with the brainstem and the cerebellum (Fig. 12.1).

The nervous system is surrounded by the meninges formed by three membranes, the outermost of which, the dura mater, is attached to the endocranial surface from the vault to the base, before extending to the end of the spinal cord forming the dural sac. The dura mater separates the two cerebral hemispheres as well as the occipital lobes from the cerebellum, by forming respectively the cerebral falx and the cerebellar tentorium. The membrane in contact with the nervous system is the pia mater, separated from the dura mater by the arachnoid membrane. Cerebrospinal fluid circulates in the cavities of the nervous system and spreads outward under the arachnoid, suspending the encephalon above the bony skull base and cushioning shocks.

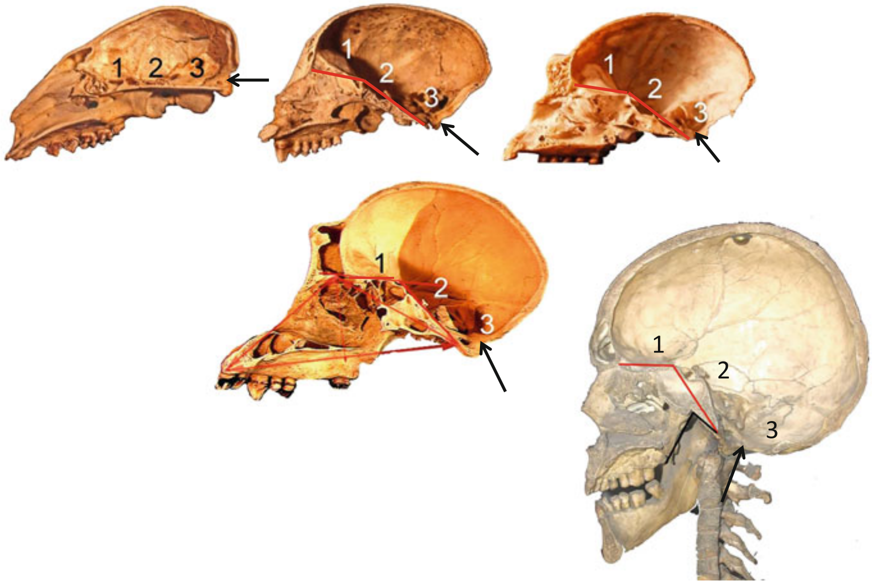

Fig. 12.1 Median sagittal section of adult skulls of extant species showing the staging of the three cerebral fossae (1, 2, 3) according to the classification of primates: top from left to right: prosimian (*Indri*), platyrrhine simian (*Cebus*), catarrhine simian (*Hylobates*), bottom from left to right, great ape (*Pan*) and *Homo sapiens*. The arrow indicates the orientation of the occipital foramen (different scales, © Dambricourt Malassé)

Since the nervous system has no contact with bone or cartilage tissues, their reciprocal relationships during morphogenesis imply necessarily these membranes. The cranial skeleton is a discontinuous bony system with sutures and a continuity solution with the first vertebra (atlas), but the membranes form a unified support system from the vault to the dural sac which is inserted at the level of the sacral vertebrae (S2–S3). A coccygeal ligament of the dura mater attaches it to the last vertebra of the coccyx. This membrane thus forms a guy wire unifying the endocranium to the sacrum.

Lamarck had not studied the comparative anatomy of skulls and did not know the complex internal organization of the skull base. His reasoning, therefore, assumed that the constraints were applied on the exocranium by the muscular insertions between the nape and the neck. But Lamarck did not verify whether his hypothesis was realistic given the organization of the vascular-nervous orifices of the base coming from the nervous system and the orientation of sutures showing that strains are internal and coming from the mesenchymal tissue. Due to a lack of knowledge in comparative anatomy, he missed the true problem of the straightening which becomes obvious when the axial skeleton is sectioned in the median sagittal plane (Fig. 12.1). No muscular strain can force the posterior fossa (the clivus and the pyramids, S-Ba and R in Fig. 12.2) to straighten. Later anthropologists will be looking for pressures coming from the cerebral hemispheres.

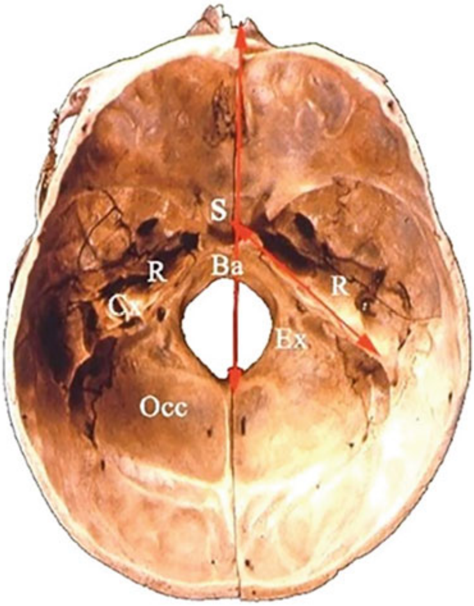

Fig. 12.2 Internal view on the adult *Homo sapiens* skull base. Ba: basion, Cx: semicircular canals of the vestibular system, Ex: exo-occipital, Occ: occipital squama, R: petrous pyramids, S: body of the sphenoid bone (© Dambricourt Malassé)

Until the 1950s, the internal comparisons of the cranial base were rare because they need the destruction of the skull. The stomatologist Robert Gudin (1952) had demonstrated the utility of the profile radiography applied to different primate species including *Homo sapiens*, for a PhD thesis of the Sorbonne University in Comparative Anatomy with Jean Piveteau. He enlightened dynamical basicranio-facial links modeled with a pantograph (Fig. 12.3).

The geometrical analysis of Gudin was necessary for the nonchirurgical orthopedic treatments and announced a revolution in anthropology with the highlighting of dynamic balances between the occlusion, the spine and the posture, putting in light a self-organized system with its inner logics, able to maintain its global equilibrium. But the dynamic trace was still unknown in paleontology and anthropology when 30 years later, in 1983, I committed myself to PhD thesis of the *Muséum national d'Histoire naturelle*, on the mandible and skull base of extant and fossil catarrhine primates (Dambricourt Malassé 1987). The emergent question was: when and how the verticalized craniocaudal equilibrium took place during ontogeny and phylogeny.

12.4.2 More Precise Vocabulary to Clarify the Problem: The Endoskeleton of the Axial Skeleton

Comparative anatomy distinguishes the exoskeleton of arthropods and the endoskeleton of vertebrates. In the former, the skeleton is outside and protects the body, in the latter the skeleton is inside the organism. The vertebrate skull is an endoskeleton but

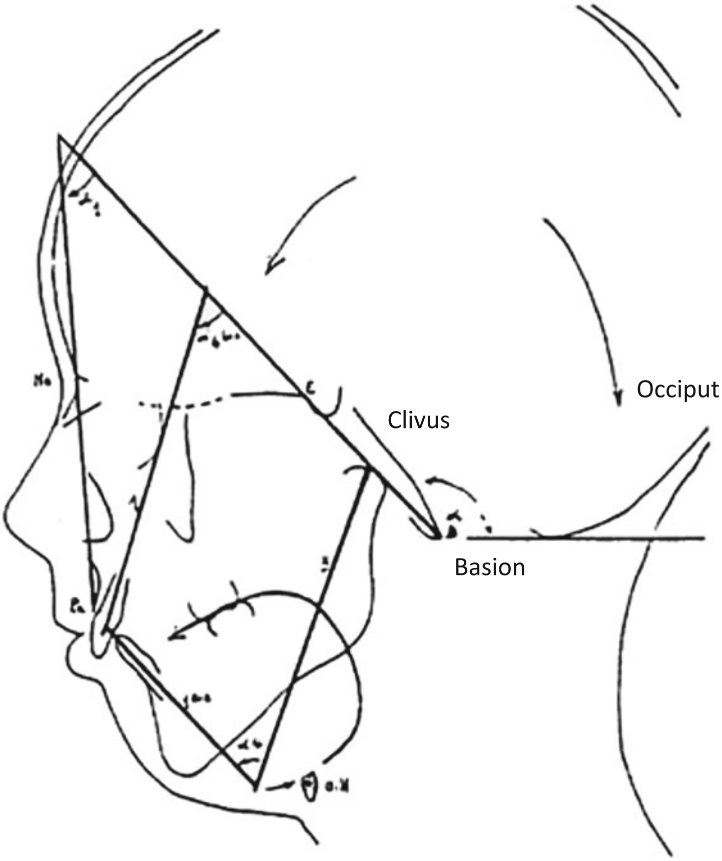

Fig. 12.3 Geometrical trace of Gudin, or “pantograph”, drawn in the 1950s thanks to the X-rays, linking for the first time, the inclination of the clivus, the posterior part of the mandible (ascending branch), and the prognathism of the middle face (angle α1), and modeling dynamical basicranio-facial relationships in opposite direction, with a rotation axis in the middle of the skull base (after Godard and Ducasse 1973; Gudin and Godard 1989)

anatomists distinguish the exocranium and the endocranium surrounding the brain. On the other hand, anthropologists divide the endoskeleton into two territories: the cranium and the postcranium. This dichotomy has no embryonic reality, but its impact is considerable in human paleontology which divides the body into two evolutionary approaches which fail to unify; the first studies the cranial cavity and the imprints of the cerebral hemispheres, and the second studies external constraints due to the locomotion. This creates a clash between the internal approach of cerebral growth and the external study of adult and locomotion. Both disregard the embryonic organization of the craniocaudal axis and especially the skull base and the distinction in zoology between the axial and the appendicular skeletons and not the division in cranial and postcranial skeletons.

As soon as the term endocranium is used, such a distinction can be generalized to the whole axial skeleton, which is why I distinguish the axial exoskeleton and the axial endoskeleton lined by the dura mater from the vault to the dural sac. This inner craniocaudal unification by the dura mater allows a better understanding of the ontogenetic and phylogenetic processes that generated the straightening of the nervous system, before the locomotor functions of the vertebral column, the pelvis and the appendicular skeleton, especially those of the lower limbs. As we will see, the endoskeleton is submitted to constraints from neural embryogenesis, whose primordial environment is the amniotic fluid and the body of the mother.

In the past, males and females lived in environments beneficial for reproduction, starting with the survival of the mother-new born couple. We have always insisted on two conditions: (1) the environment was known to mothers and clans for the protection of parturient and (2) rich in water necessary for the production of the amniotic fluid and breast milk. At the threshold of the verticalized neuroaxial system, i.e., hominin emergence, the way of life was adapted to mixed environments of forest and savannah. Recent studies confirm that the arid East African environment of prehominins (*Ardipithecus*, 5.5 Ma) and oldest known hominins (*Australopithecus*, ca 4 Ma) offered a wide variety of microhabitats with wetlands maintained densely forested by groundwater, such as palm forests (Barboni et al. 2019).

12.4.3 The Straightened Axial Endoskeleton: The Result of an Internal Evolutionary Process

The straightening involves the axial skeleton since the center of the cranial base, i.e., the sphenoid, a composite bone with a central body with extensions that form laterally the temples, the back of the orbits, and, underlying, the back of the nasal cavities. Its central body is formed by an anterior segment, the presphenoid and a posterior segment, the basisphenoid. The basisphenoid is the part that straightened during evolution step by step, given the geometrical direction which matches the classification starting from most primitive primates before reaching *Homo sapiens*. The basisphenoid is prolonged by the basioccipital which ends on the large occipital foramen. Both are separated by a cartilaginous suture or synchondrosis and together form the clivus, bordered on each side by a massive bone called the “petrous pyramid”. The pyramid has two parts, the first belongs to the medial fossa supporting the temporal lobe and the second belongs to the cerebellar fossa. The cerebellar part of the pyramid and the clivus form the anterior wall of this lower fossa, a complex puzzle assembled by sutures (Fig. 12.2).

As soon as the skull base shows an angulation at birth, the three fossae are stepped from front to back. The clivus and the cerebellar surface of the pyramids form the straightened territory, the angulation of which is measured by their inclinations regarding the presphenoid planum (Dambricourt Malassé and Lallouet 2021). This fossa is the territory dedicated to the control of locomotor movements and balance with the brainstem for the nervous connections between the cerebellum and the brain informed by neurosensory receptors. The pyramids contain the vestibular system, a sensory organ in the inner ear related to the cerebellum for the control of head movements (Fig. 12.2, Cx). This proximity is all the more understandable as the cerebellum is immediately concerned.

A new paradigm was established in the 1920s, with the fetalization theory developed by Louis Bolk (1926). The Dutch anatomist started from the principle that the plication between the presphenoidal planum (see Fig. 12.1, line 1 of *Homo sapiens*) and the clivus-coccyx axis was the ancestral embryonic conformation, so the straightening would never have been an evolutionary reality. However, the cranial base of the most primitive primates, or prosimians, is horizontal at birth; the clivus is a little straightened in monkeys, a little more in great apes and verticalized in humans. Bolk assumed that the ontogenetic tendency of the cerebellar fossa was to join the horizontal according to the spine. The increasing volume of the fetal brain over millions of years and especially its development according to a superoinferior winding would have progressively prevented the skull base to tend toward the horizontal. *For Bolk, hominization was not the acquisition of verticality but its embryonic conservation* and the main process was the development of the cerebral hemispheres, called telencephalon. *Homo sapiens* would have preserved the hypothetical vertical embryonic ancestral configuration because of the pressure of the cerebral hemispheres applied on the cerebellar tentorium inserted on the pyramid and the periphery of the occipital squama. This pressure would have kept the clivus and petrous pyramids upright in humans. The search for internal physical constraints of neural and fetal origin was already more coherent than the external adult constraints transmitted by the appendicular skeleton to the vertebral column.

12.4.4 Human Paleontology and the Neural Straightening: One Century of Dilemma Between Locomotion and Encephalon

The fetalization hypothesis coincides with two major paleontological discoveries of the fossils which seemed intermediate between extinct apes and *Homo sapiens*. The first was the skull and endocranial cast of a child found in South Africa in 1924, in the Taung karst, named *Australopithecus africanus* dated 2.3 Ma. The second is a sub-adult skull collected in 1929 in the Zhoukoudian karst in Northern China, named *Sinanthropus*, then later *Homo erectus pekinensis*, and dated to 800,000 years. The physician Franz Weidenreich (1943) studied a dozen skulls of *Sinanthropus* extracted from the karst and described the curvature of the vault around a transverse axis passing through the center of the skull base (Fig. 12.4b), this curvature was more advanced than the living great ape but less than *Homo sapiens*. The paleoanthropologist disagreed with Bolk and concluded that the clivus straightened around this transverse axis under the effect of the encephalization. But nothing is evocated concerning the primordial conformation of the embryonic skull base if this one was flat or flexed.

Furthermore, a considerable paradox was already visible: the skulls of Eurasian Neandertals contemporary with Proto-Cromagnoids from the Near East (Skhul 115,000 years and Qafzeh 92,000 years in Israel) had a larger endocranium and

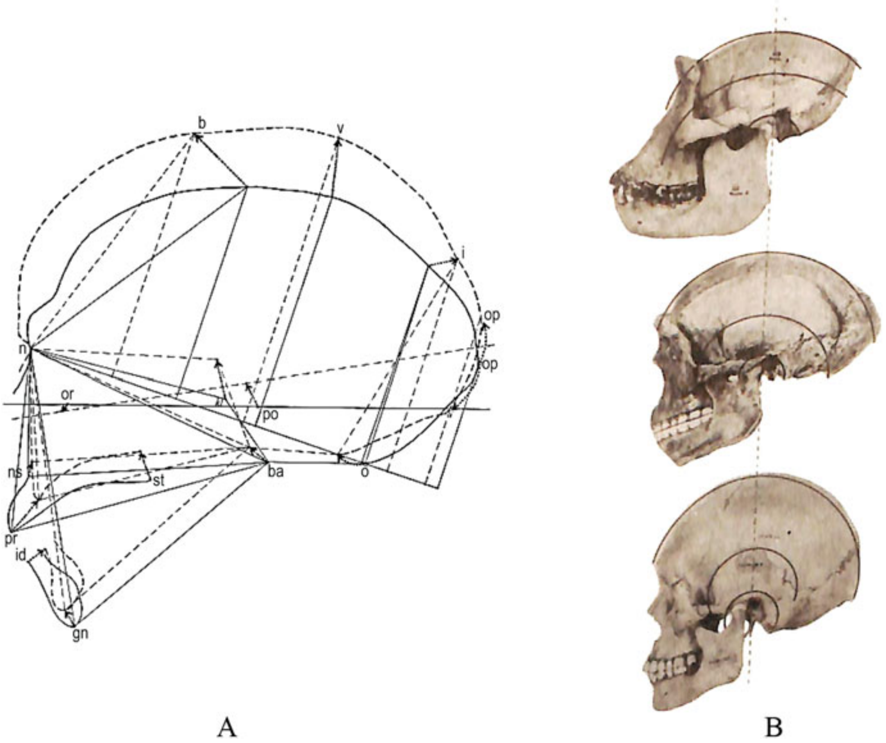

Fig. 12.4 (**a**) Comparative sagittal midsection diagrams of *Sinanthropus* III and *Homo sapiens* centered on the porion showing homologous point displacements. (**b**) Exocranial profiles of adult skulls from top to bottom: *Gorilla*, *Sinanthropus* III, *Homo sapiens*, aligned on a vertical and centered on a transversal axis of rotation passing just before the external auditory meatus, showing the curvatures of the vault and the temporal squama forming almost a circle in *Homo sapiens* (according to Weidenreich 1943)

more developed neocortical imprints than *Sinanthropus*, while the occipital lobes were not farther down. Instead, their growth was directed backward forming the occipital bun. In other words, the growth activity of the basicranial synchondroses was not influenced by the growth of the cerebral hemispheres; the vectors were oriented in the direction of least resistance. The contradictions will accumulate with the Australopithecines. In 1948, the most complete adult skeleton of *Australopithecus africanus* showed a verticalized clivus, the cerebellar fossa was tilted forward and downward above a short and wide pelvis supporting the viscera of a verticalized axial skeleton. The animal was in permanent bipedal locomotion on the ground, but the brain, with a volume of 485 ml, was no larger than a chimpanzee with a semierect base. In opposite, with a brain volume of 915 ml, the cerebellar fossa of *Sinanthropus* was no more verticalized than *Australopithecus*. *The brain (cerebrum) volume had nothing to do with the verticalization of the clivus and* *petrous pyramids*. A closed-angle between the anterior cerebral fossa and the neuraxis imposes the erect posture of the axial endoskeleton and its locomotion in an exclusive bipedal mode. But how this orientation has been acquired since the prosimians if the increasing volume of the cerebral hemispheres was not the mechanical cause?

In 1974, nothing goes further: a new species of *Australopithecus* was discovered in Ethiopia (East Africa), showing adaptation to an arboreal way of life. Thus, not only the encephalization was not the mechanical cause of the verticalization of the clivus and the petrous pyramids, but arboricolism was still practiced while the axial skeleton was in permanent bipedalism on the ground. The bipedal walking of *Australopithecu*s did not substitute arboricolism. If brain growth and locomotion were not the explanation of this closed angle in the young and the adult stages, what could be the cause? The fetalization was invalidated by fossils. It was necessary to ensure that the embryonic axis was formed verticalized with respect to the presphenoidal territory.

12.5 The Straightening, an Embryonic Dynamical Reality

12.5.1 A Bibliographic Rediscovery

The skull base is the only cranium formed during embryogenesis, named chondrocranium because of its cartilaginous nature. It is located under the nervous system in a rudimentary state of organization, that of a neural tube, the vault does not exist since the cerebral hemispheres (telencephalon) are not yet formed. The doctoral thesis I had supported at the *Muséum national d'Histoire naturelle* tested the fetalization hypothesis. When the research began in 1983, no publication on the chondrocranium of nonprimate mammals and prosimians described a flexed conformation. The chondrocranium was always flat, hence its name *planum basale*. But what about *Homo sapiens*? Embryological studies on human embryogenesis cited a work published in 1900 in a German journal (Levi 1900). By chance, the article was available at the Central Library of the Museum. The reproductions of the cartilaginous structures were of remarkable quality. The Italian physician and surgeon Guiseppe Levi (1872–1965) had pursued embryological research in 1899 at the University of Berlin with Oscar Hertwig (1849–1922), a former student of Ernest Haeckel. Levi described four stages, the first two are the earliest ever observed, at 13- and 14-mm crown-rump. *And the conformation of the human chondrocranium is flat like all mammalian embryos.*

Louis Bolk and Franz Weidenreich never referred to this article and therefore probably never knew about it. Levi returned to the University of Turin and devoted his work to neurogenesis, giving a boost to molecular and cellular biology awarded by three Nobel prizes, Salvatore Luria in 1969, Renato Dulbecco in 1975, and Rita Levi Montalcini in 1986. This article described the verticalization of the clivus in two steps, but the chondrocranium was isolated from its context and the anatomist did not give a dynamic explanation.

12.5.2 The Mandible, the Double Pantograph, and the Craniofacial Contraction

The PhD thesis was dedicated to the ontogeny and phylogeny of the mandible in its cranial context in extant and fossil catarrhine primates. The morphogenesis has been studied in the three planes replaced in the basicranial context. As shown by the Gudin's pantograph, the mandible has two spatial determinisms: the first is cranio-rachidial; it depends on the vertical position of the cerebellar fossa with which it articulates on each side of the petrous pyramids and the second is facial, with the maxilla and their articulation via the alveolar and dental arches (see *Homo sapiens* Fig. 12.1). Moreover, the mandible has the incomparable advantage of being the most frequent fossil in the paleontological record, whereas the base is rarely preserved. Thus, its position relative to the posterior part of the base changes during embryogenesis because it depends on the straightening of the clivus and the pyramids. The maxilla, on the other hand, is integrated into the anterior part of the cranium and is not mobile. Thus, the adequacy between the two mandibular and maxillary arches implies particularly complex coordination between the "mobile" posterior base and the fixed anterior base of the cerebral skull as soon as the straightening begins. This coordination is a research topic in infantile dento-maxillo-facial orthopedics since the 1950s. The highlighting of the dynamic relations between the cranial base and misplacements of the dental arches is teaching in the French school of Nantes (Delaire 1978, 2003; Deshayes 1986; Deshayes and Deshayes 2013) and allowed collaborations in infant dento-maxillo-facial orthopedics (Dambricourt Malassé and Deshayes 1990, 1992; Deshayes et al. 1990; Deshayes and Dambricourt Malassé 1991). These principles are applied by different orthodontic schools (e.g., Bhattacharya et al. 2014; Monirifard et al. 2020).

The morphological growth of the mandible of extant and fossil species was measured with angles in the sagittal and transverse planes and placed in its basicranial context. The objective was the 3D modeling with a double pantograph (Figs. 12.5 and 12.6). We have called this morphogenetic process "craniofacial contraction" (Dambricourt Malassé 1987, 1988).

12.5.3 The Embryonic Origin of the Neural Straightening

In the nineteenth century, the leader of "human embryogenesis" was Alfred Velpeau (1795–1867), an obstetrician and physician who held the chair of surgery at the Faculty of Medicine in Paris, where he established the first large collection of human embryos. It took him 8 years to constitute this collection by eliminating the malformations, which totaled 200 specimens until the end of the third month. He published this collection in 1833 with lithographs of very high quality made by the painter-engraver Antoine Chazal (1793–1854), professor of drawing at the *Muséum national d'Histoire naturelle*. The earliest embryonic stage had been described by Gilbert Breschet (1784–1845), Velpeau reproduced the illustration which shows the axis of the embryo entirely horizontal. Thirty years later, the Russian embryologist

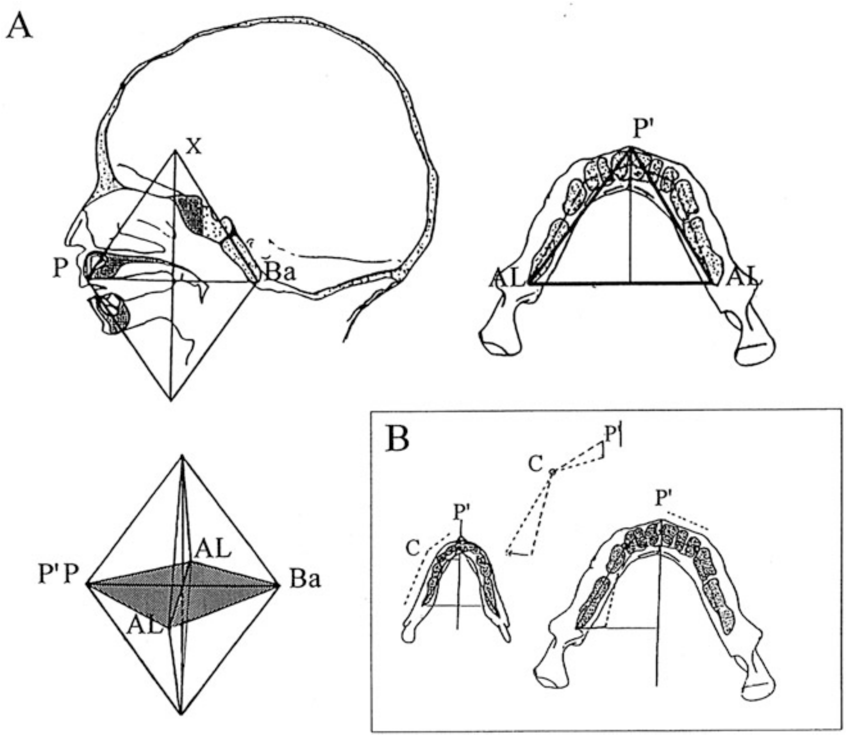

Fig. 12.5 Basicranio-facial double pantograph applied to a human newborn. In the box: comparison of the mandibular shape between 3 and months, same scale (drawing © Dambricourt Malassé 1987)

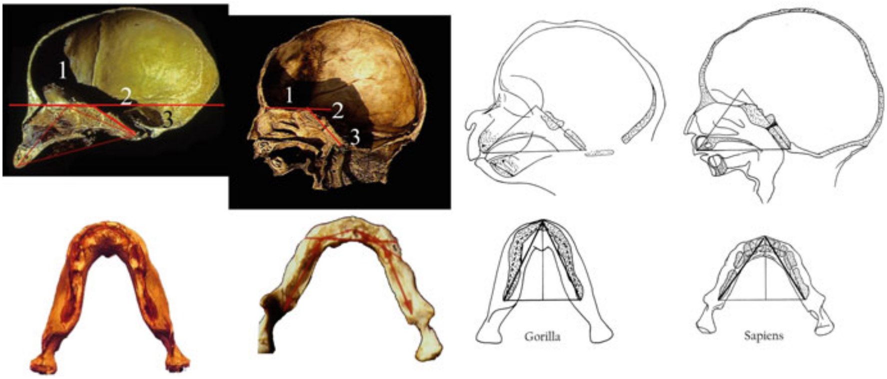

Fig. 12.6 *Gorilla* and *Homo sapiens* newborns. Left: Mid-sagittal section of the skull and superior view of the mandible. Right: Geometric traces in sagittal and transversal plans containing the alveolar arch, a part of a double pantograph which prolongs with the skull base (collection *Muséum national d'Histoire naturelle*, photos and drawings are not at the same scale, © Dambricourt Malassé 1987)

Alexander Kowalevsky discovered an axial embryonic structure, the notochord, located under the neural tube. The notochord is common to Tunicates (Urochordates), Cephalochordates (*Amphioxus*), and Chordates which include Agnatha and Vertebrates.

At the beginning of the twentieth century, a collection was built up by the Carnegie Institution of Washington, which allowed describing the chronology of neurulation and organogenesis during the 8 weeks following ovulation. George Streeter (1873–1948) described the collection at the beginning of the 1940s by defining "horizons", then Fabiola Müller and Ronan O'Rahilly took it up again in the 1980s by defining the 23 stages of the Carnegie (CS) since fertilization.

At the end of the twentieth century, the rapid progress of medical imaging made it possible to create a scan library. Researchers from Hopkins University (Baltimore, north of Washington) applied Microscopic Magnetic Resonance Imaging (MIR) to the embryos of the Carnegie collection and realized an animation in the framework of the Virtual Human Embryo program (Paidas et al. 1999; Smith 1999).

In the twenty-first century, the new imaging technologies are the Episcopic Fluorescence Image Capturing (EFIC) and the High-Resolution Episcopic Microscopy (HREM) which generate digital volume data and three-dimensional (3D) images. They were applied by the Congenital Anomaly Research Center of Kyoto University to 101 human embryos from stage 13 to stage 23 without malformation (Shiraishi et al. 2015). All these technical advances have made it possible to progressively verify what we have been describing since 1987 and whose major observations we recall here.

The linear shape of the neural tube is acquired at the end of the neural gutter closure at stage 13 (4–6 mm, 28 days postovulatory). This shape progressively curves around the voluminous heart to form a circle where the caudal and cephalic ends tend to join. Neurulation and organogenesis take place in this context of folding common to all mammals. When it is completed, the coiled axis which has grown from a few millimeters to several centimeters straightens out with its human conformation. We will therefore follow the spatial formation of the human cephalic neural tube in this coiled configuration and place the four stages of Levi in the succession of these stages. Figures 12.7 and 12.8 illustrate the geometric landmark that we have defined and the stages described by Levi (Dambricourt Malassé et al. 2006).

The cephalic part of the neural tube is initially formed by three vesicles from front to back: the prosencephalon, the mesencephalon, and the rhombencephalon. The neural area on which the observation focuses is the rhombencephalon, located above the notochord. Its upper part is formed by a thin membrane of cells (neuroblasts) and its thicker floor; it is separated by the cerebrospinal fluid. This space is the fourth ventricle. The horizontal axis x is given by the notochord, the origin 0 is its apex, and the vertical axis y is the perpendicular passing through the origin. This geometrical frame is sufficient to place the different stages in the sagittal median section, to follow the vectors of the neural tube and then to replace the four stages of Levi.

At stages 16–17 (37–41 days postovulatory), the chondrocranium is formed by the presphenoid, postsphenoid, and basioccipital aligned. The notochord is embedded in the basioccipital and postsphenoid where it ends.

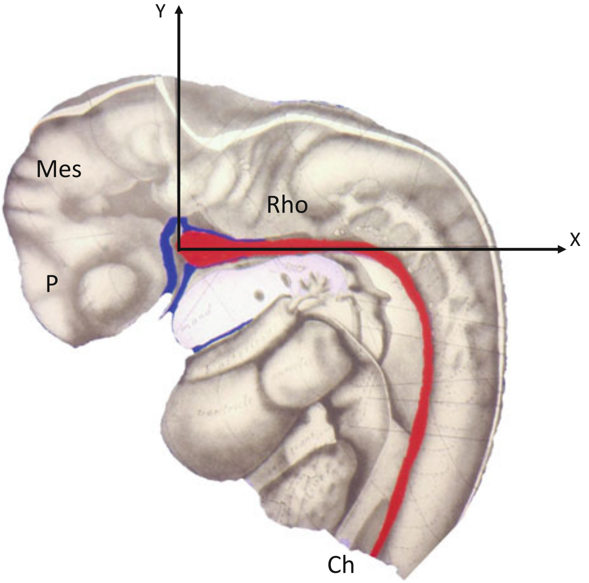

Fig. 12.7 Cephalic end of the human embryo in median sagittal section. X horizontal axis aligned with the cephalic termination of the notochord, Y vertical axis passing through the notochord apex. Ch: notochord, Mes: mesencephalon, P: prosencephalon, Rho: rhombencephalon, after Susanna P. Gage (1905) modified (© Dambricourt Malassé et al. 1999)

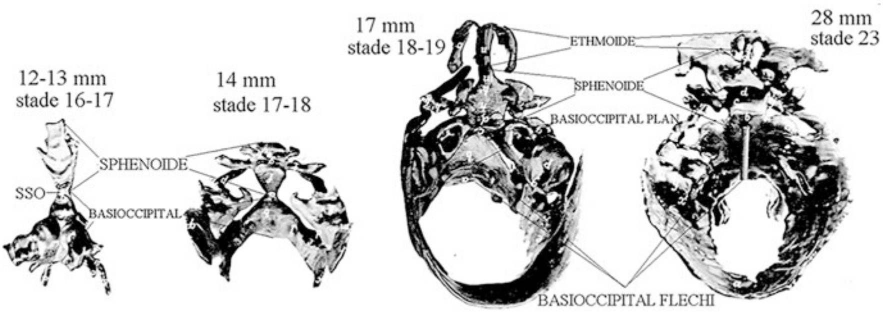

Fig. 12.8 After Levi (1900) modified: the human chondrocranium in superior view at four stages of embryogenesis, from the flat conformation (stadium 16–17 and 17–18) to the final verticalization (stadium 23). The straightening happens at the stadium 18–19 and concerns only the postsphenoid (© Dambricourt Malassé et al. 1999)

At the following stages 17–18 (41–44 days postovulatory), the morphogenesis develops in the transverse direction, and the petrous pyramids (see R in Fig. 12.2) begin to form, as well as the cartilaginous occipital squama. The cartilaginous skeleton of the mandible is formed by two stalks (Meckel's cartilages), one per half jaw. Each posterior end is in connection with the otic capsule and will be integrated into the petrous pyramids which belong to the dynamical part (Fig. 12.9).

At stages 18–19 (44–47 days postovulatory), the ethmoid is visible in front of the presphenoid, the postsphenoid is verticalized, it has tilted around its axis from top to bottom, the basioccipital is thus lowered but a segment remains horizontal. The otic

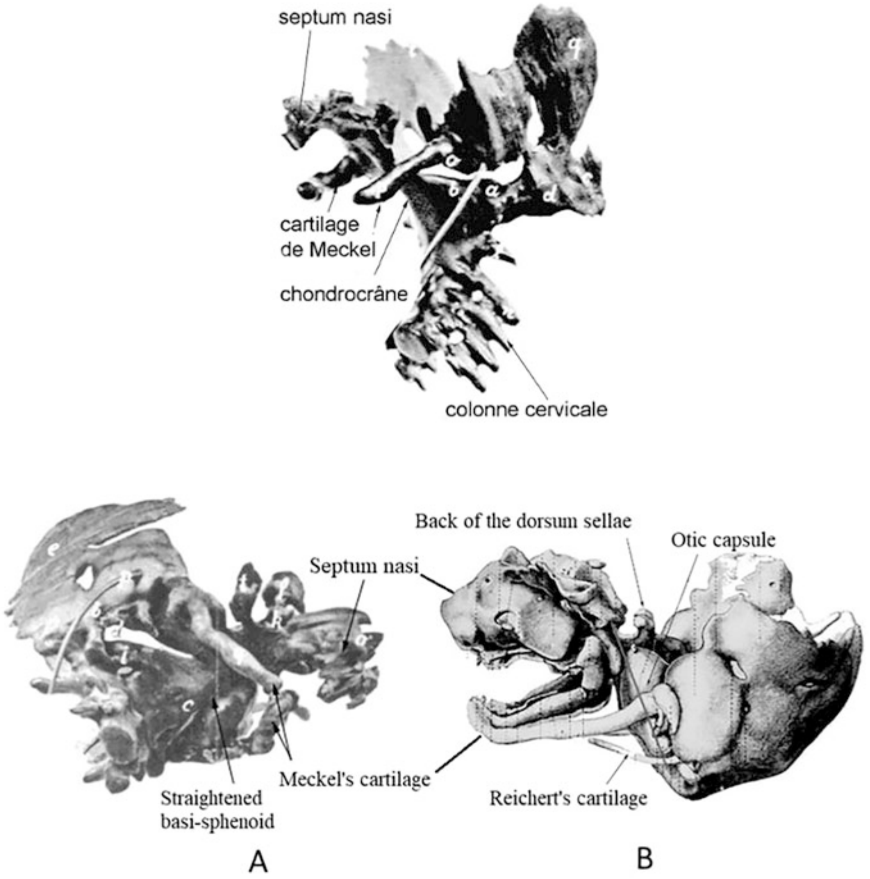

Fig. 12.9 Three stages of the human chondrocranium with the mandibular cartilage in connection with the otic capsule. Top: stage 17–18 before the verticalization (after Levi 1900). Bottom: (**a**) stage 18–19, the first straightening of the basisphenoid and the forward and downward projections of Meckel's cartilage (after Levi 1900). (**b**) stage 23, the second straightening with both basisphenoid and basioccipital and the verticalization in opposite sense of the Meckel's hook (after Macklin 1914). © Dambricourt Malassé

capsules attached to the postsphenoid are thus dragged into its downward and forward movement. The two ends of the mandibular cartilage are therefore also displaced downward and forward. The vertical dimension has just become part of the axial skeleton. The face will develop in the verticalized configuration. The verticalization thus finds its axis of rotation in the body of the postsphenoid.

Stages 20 to 22 are not described. The fourth is stage 23 (56 days) which marks the end of embryogenesis. The postsphenoid and the basioccipital have aligned, they form the erect clivus. The sella turcica is visible and the wings of the sphenoid begin to develop. The cartilaginous cerebellar fossa is well-formed. The sphenoid angle is acquired. The two mandibular cartilages have joined in their ventral end forming an arch, named “Meckel’s hook” or *hamulus Meckeli*. Under the arch is a space visible in the human fetus and called the symphyseal void. It will give its triangular shape to the chin.

These four morphologies correspond to different stages of neural tube development. For the early stages, our description observes the prechordal territory (Fig. 12.10). The last synthesis has been enriched and became more precise (Fig. 12.11). The sequence is as follows:

1. The anterior segment of the rhombencephalon elongates in front of the notochord apex forming the metencephalon (the futures cerebellum and annular protuberance) while its floor begins an upward rotation that brings it above this apex, clearing a space in front of the notochord. The two small vesicles of the telencephalon, which were in contact with the heart, are dragged into the upward rotational movement. The space freed in front of the sphenoid allows it to continue its morphogenesis in a rostral direction (forward). The ethmoid is differentiated in the median sagittal plane and the floor of the future frontal lobes begins to form. This conformation is acquired when the floor of the metencephalon has rotated by 90° and is merged with the y-axis (stage 16, Fig. 12.10). Up to this stage, the chondrocranium is plane, the origin 0 is in the center of the chondrocranium. The segment of the neural tube that remains above the notochord becomes the myelencephalon, it will form the elongated medulla and the segment in front of the notochord becomes the metencephalon: the floor will form the protuberance and the ceiling will develop in the cerebellum.
2. From stage 17 onwards, the chondrocranium enlarges between the two otic capsules due to transverse myelencephalon enlargement which can be seen very well on medical imaging (see Fig. 12.1 in Shiraishi et al. 2015[3]).
3. From stage 18 (Fig. 12.11), the floor of the myelencephalon begins to rotate toward the vertical apex of the notochord in the opposite direction to the metencephalon so that the two floors meet above the notochord termination at stage 20. The space filled with cerebrospinal fluid is compressed, the fluid is pushed upwards, and the ceiling of the fourth ventricle swells. The rhombencephalon thus forms two floors, one remained above the notochord, the other developed in front of the notochordal termination. They join at its apex, closing the fourth ventricle with the rotation axis located at the termination.

However, it is at stages 18–19 that Levi described the verticalized postsphenoid. This last one is separated from the other cartilaginous territories, anteriorly by the intrasphenoidal synchondrosis and posteriorly by the spheno-occipital synchondrosis. The cartilaginous blastema that forms the postsphenoid has rotated on its axis between these two synchondroses. Microscopic Imaging shows the

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[3] Morphology and morphometry of the human embryonic brain: A three-dimensional analysis—ScienceDirect.

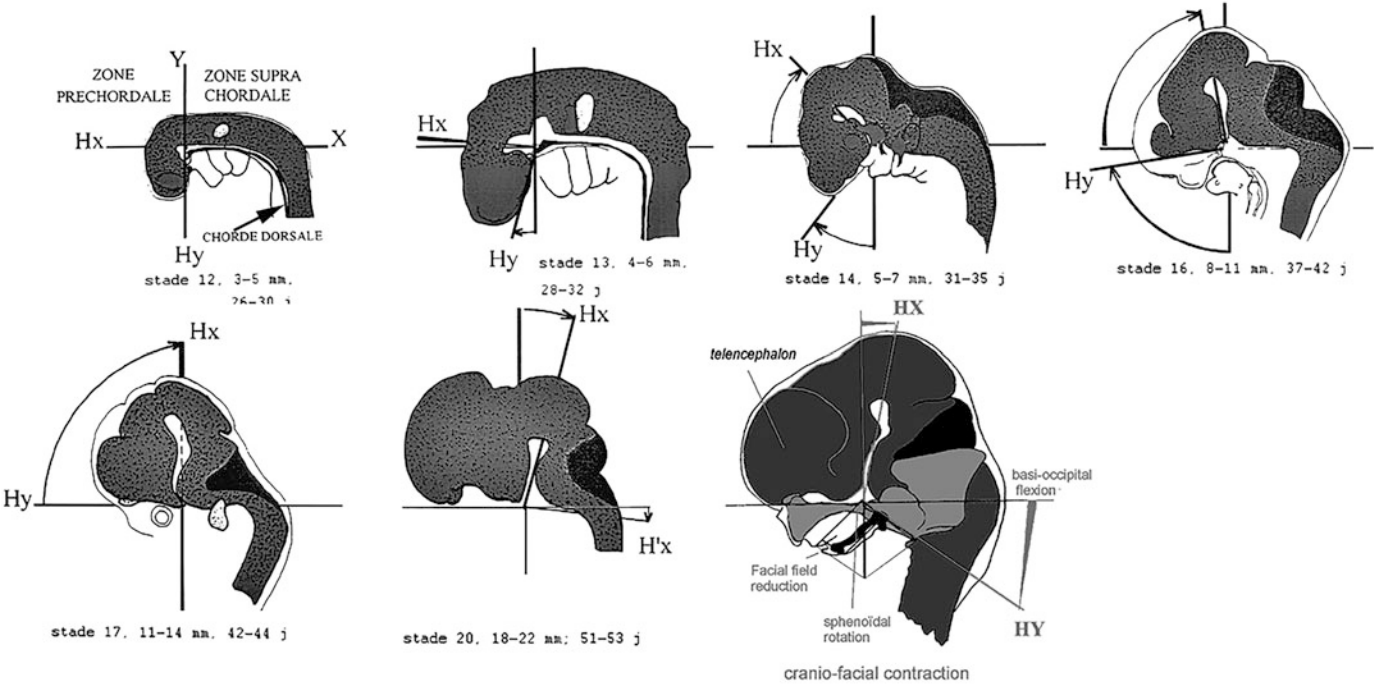

Fig. 12.10 Trajectories of the neural tube in the geometric frame aligned on the notochord and centered on the notochord apex. The last stage illustrates the straightening of the clivus. The drawings are scientific illustrations of different articles (© Dambricourt Malassé 1993)

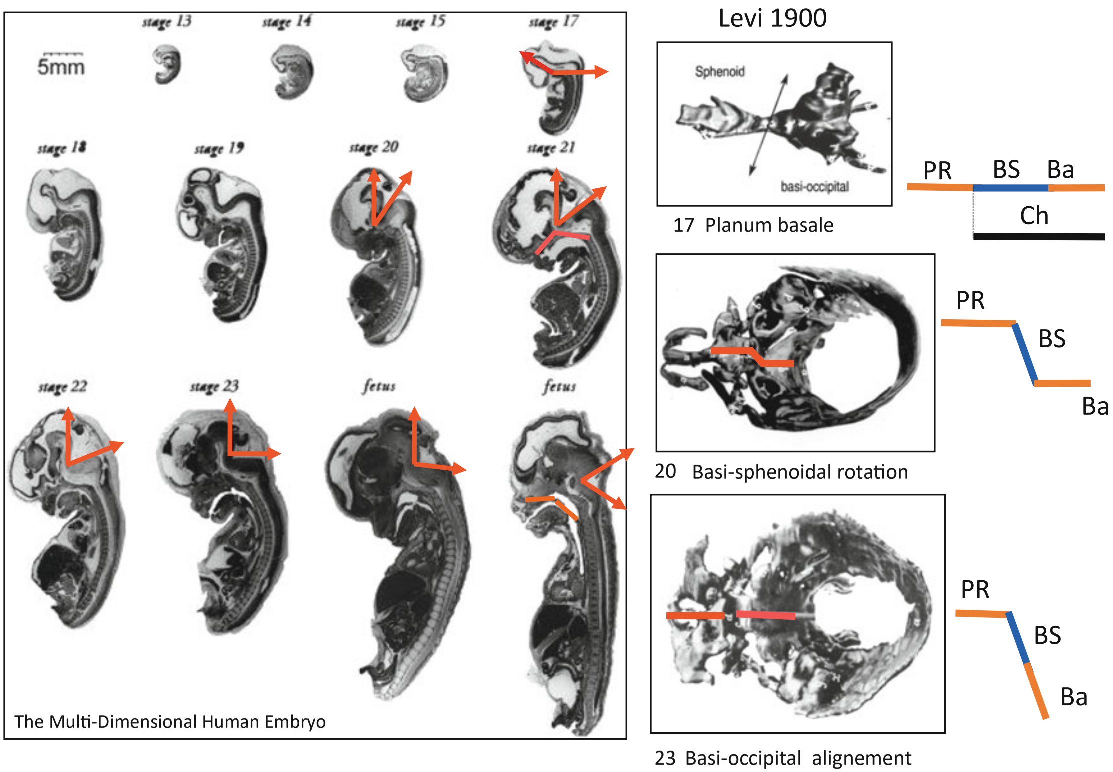

Fig. 12.11 Left: Sagittal midline section of the Carnegie embryonic stages scanned in magnetic resonance microscopic imaging (MRI) for the Multidimensional Human Embryo project (source: http://embryo.soad.umich.edu/). The neural dynamics are visible online. We have added arrows to visualize the directions of movements. Right: Three stages of Levi in correspondence with the neural dynamics on the left. The lines illustrate the profile in the median sagittal section of the chondrocranium, this comparison shows the correlations between the closure of the IV ventricle and the rotation of the *basisphenoid*. Ba: *basioccipital*, BS: *basisphenoid*, Ch: notochord, PR: presphenoid (Dambricourt Malassé 2022)

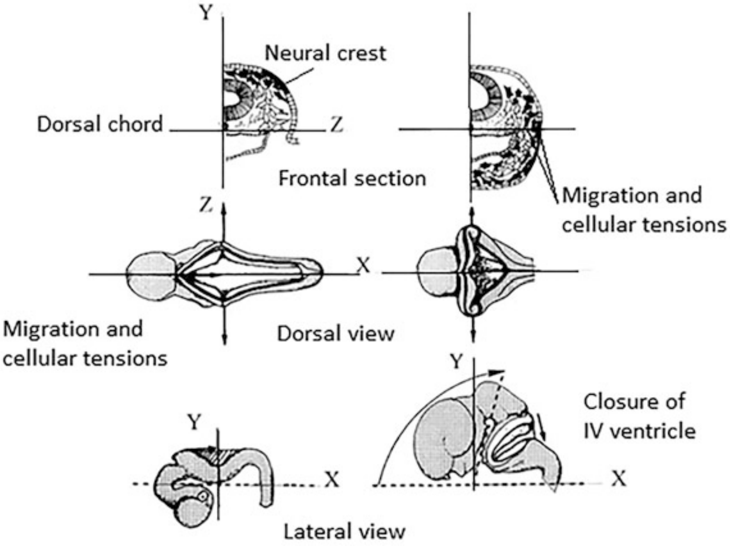

Fig. 12.12 Dynamics of the rhombencephalon in the three planes showing the relationship between the migration of neural crests at the cephalic end of the notochord and the closure of the IV ventricle by the get closer together of the metencephalon and myelencephalon. Vectors and orthonormal planes have been added (Langman 1984 modified, in Dambricourt Malassé et al. 1999)

closure of the fourth ventricle at stage 20. Then, the movement of the myelencephalon's floor returns backward and does not stop until the optimal straightening. The basioccipital then aligns with the tilted postsphenoid and together they form the clivus.

Figure 12.11 highlights with more detail, the phenomenon of neural dynamics that generate the rotation of the basisphenoid, the stage 20, with the complete closure of the IV ventricle, when the pressure of the cerebrospinal fluid and tensions due to the neural crest cell migration toward the floor, are maximal. This double movement can be understood in 3D by resuming the chronology (Fig. 12.12): we observe an enlargement of the rhombencephalon on both sides of the sagittal plane of symmetry. This is due to the migration of the membrane that covers the fourth ventricle and stretches laterally with a maximum tension at the aplomb of the notochord termination.

The dynamic trajectories of the rhombencephalon floor associated with the rotation of the postsphenoid are visible between stages 19 and 20, then 20 and 21 (Fig. 12.11).

After stage 23, the fetal period begins, the head straightens with the cerebral trunk in a vertical orientation (see the morphing referenced Fig. 12.11).

The postsphenoid supports the pons (bridge) while the basioccipital supports the medulla oblongata (elongated spinal cord).

The observation of the embryonic straightening in two steps is still unknown, although it enlightens the understanding of the Hominins' emergence according to parallel evolutions and not to the linear model "great ape-*Australopithecus*-*Homo*" as we will see (12.6). So we have concluded that the macroscopical event which reveals the microscopical evolutionary processes that occurred during gametogenesis and which changed the body plan, is the closure of the IV ventricle.

12.5.4 Nonhuman Primate Embryogenesis

Nonhuman primate embryos are rare, some are kept at the Hubrech Laboratorium (Utrecht, the Netherlands) but to age for a comparison with the stages 17 and 20, nevertheless, the youngest *Tarsius* (22.9 mm) described by Jeffery et al. (2007, see Fig. 12.3) matches with the human neural stage 23 and its postsphenoid is not straightened, that can be observed with X-ray at an oldest fetal stage (Dambricourt Malassé 2022). We can therefore conclude that the neural tensions of the tarsiiformes and their omomyiformes ancestors, never exceeded the amplitude of the older mammals in the same way as the extant lemuriformes and lorisiformes. For this reason, the creation of the taxonomic group Haplorhinian based on adult characteristics to classify them with the simiiformes is a counter-sense (Dambricourt Malassé 2011a). This was confirmed by genomic analysis:

> Despite numerous morphological and molecular studies, there has been weak support for grouping tarsiers with either strepsirrhine primates in a prosimian clade or with anthropoids in a haplorrhine clade. (Jameson et al. 2011).

The best nonhuman primate species illustrated by embryos is the monkey *Macaca* (*Cercopithecidea*), but they have never been scanned in Magnetic Resonance Microscopic Imaging. The comparison between a fetus of *Semnopithecus* (*Cercopithecidea*) and the embryonic human stage 23 shows clearly the differences in the amplitude of the cerebellar fossa's tilt and the cranial termination of the Meckel's cartilage higher than in *Homo sapiens* and without a ventral (facial) hook. The human craniofacial contraction and the lowering of the cerebellum fossa are obvious (Fig. 12.13).

Great ape's embryos are unknown but the fetus allows the comparison of the postembryonic dynamics and to verify that the lowering of the cerebellar fossa is greatest than in monkeys and lesser than in *Homo sapiens* (Fig. 12.14).

For the clarity of purpose, I keep the name prosimian to qualify primate organizations older than simians.

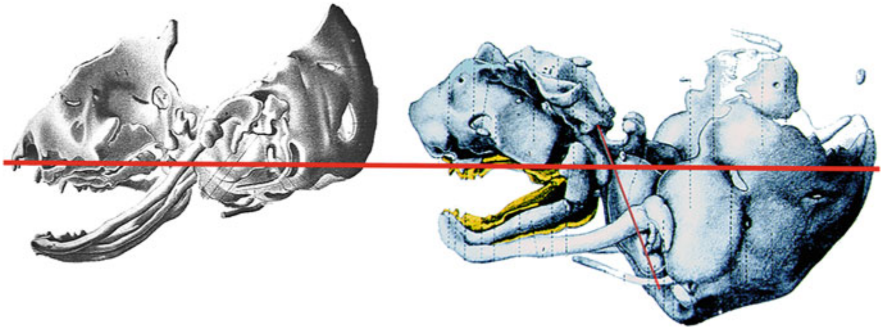

Fig. 12.13 Fetal chondrocranium with the mandible of a *Cercopithecidae* (*Semnopithecus maurus*) (TS of 53 mm, according to Fischer 1902) (left) and *Homo sapiens* (TS 40 mm, according to Macklin 1914) (right). The horizontal line is the tangent at the septum nasi; the red asterisk locates the contact of the cranial termination of the mandibular cartilage, with the otic capsule. Both highlight the lowering of the human cerebellar fossa. The drawings are not at the same scale (Dambricourt Malassé 1987, 2006) © Dambricourt Malassé

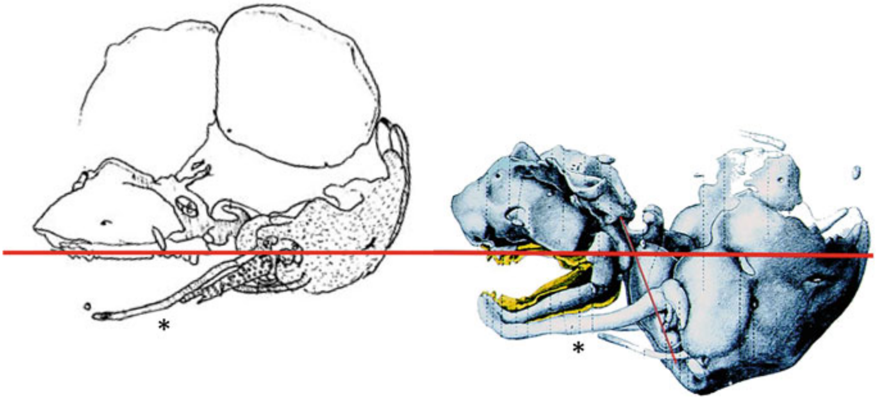

Fig. 12.14 Comparison of a very young chimpanzee fetus (TS 71 mm according to Starck 1960) (left) and a human embryo (TS 40 mm according to Macklin 1914). Same legend than Fig. 12.13 (Dambricourt Malassé 1987)

12.5.5 Embryogenesis, Homeotic Genes, and Viscoelastic Dynamics

12.5.5.1 Hominins Verticality and Homeotic Genes

We have seen that craniofacial contraction is an embryonic process related to the amplitude of the tensions that close the IV ventricle. These tensions lead to a pivoting of the postsphenoid around the axis located at the apex of the notochord and laterally, to the bascule forward and downward of the otic capsules which contain the three semicircular canals of the inner ear. Spoor et al. (1994), Spoor and Zonneveld (1997) observed these canals for the first time in *Homo erectus* and South African *Australopithecines* thanks to the CT scanning and the results were

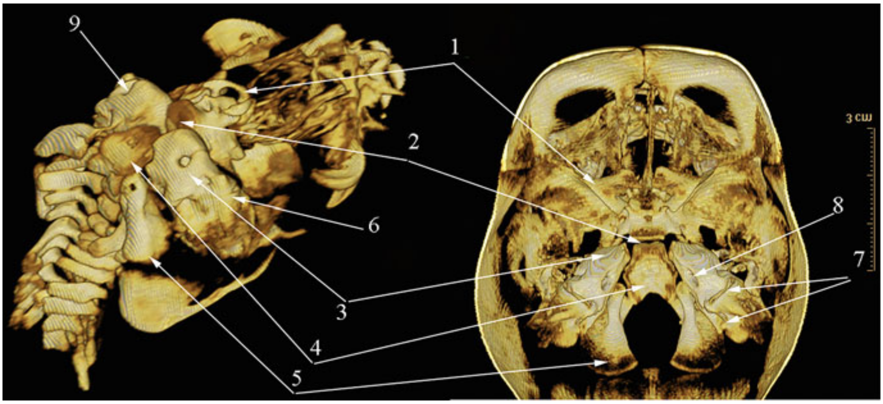

Fig. 12.15 CT scanning of 5-month-old human fetus. Left: anencephaly without rotation of the *basisphenoid*, the petrous pyramids (3) and the *basioccipital* (4). Right: normal fetus. The skulls are not at the same scale. Collection of *Musée de l'Homme—Muséum national d'Histoire naturelle* (Dambricourt Malassé and Lallouet 2009, © Dambricourt Malassé)

surprising. Paleoanthropologists were waiting for a human-like morphology in *Australopithecus* because of their bipedal locomotion (Dambricourt et al. 2000). It was the opposite, the canals are similar to extant African great apes. More recently two specimens of South African *Australopithecus* have been scanned (StW 573 "Little foot" and StW 578) and authors reach the same conclusion (Beaudet et al. 2019).

I have studied a rare case of anencephaly with spina bifida (absence of neural tube closure) from the *Musée de l'Homme*,[4] a human fetus 5-month-old which does not show the rotation of the postsphenoid (Fig. 12.15) and compared it to a *Gorilla* and a normal human fetus of the same age. Despite the lack of rotation, the semicircular canals are human (Dambricourt Malassé and Lallouet 2009).

This observation had huge consequences for the validation of the embryonic and phylogenic origins of hominins. Since 1987, I suspected that what had changed in the great ape embryonic body plan was the regulation of the embryonic craniocaudal gradient (Dambricourt Malassé 1987, 1988, 2011b, 2022). As soon as the homeotic genes were recognized in the genetic control of early embryonic development (Duboule 1994), it seemed obvious that they have played a major role in the hominization process and that the dynamic of the neural straightening was an epiphenomenon without relation with the necessity to walk on the two posterior limbs. For the semicircular canals, the role of homeotic genes has been confirmed in the control of apoptosis acting with cartilage tissue (Merlo et al. 2002) and this was our conclusion (Dambricourt Malassé and Lallouet ib.). It, therefore, appears that neither the function nor the shape and the volume of the cerebrum or the cerebellum, are the causes of these morphogenetic changes.

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[4] The *Musée de l'Homme* is a site of the *Muséum national d'Histoire naturelle*.

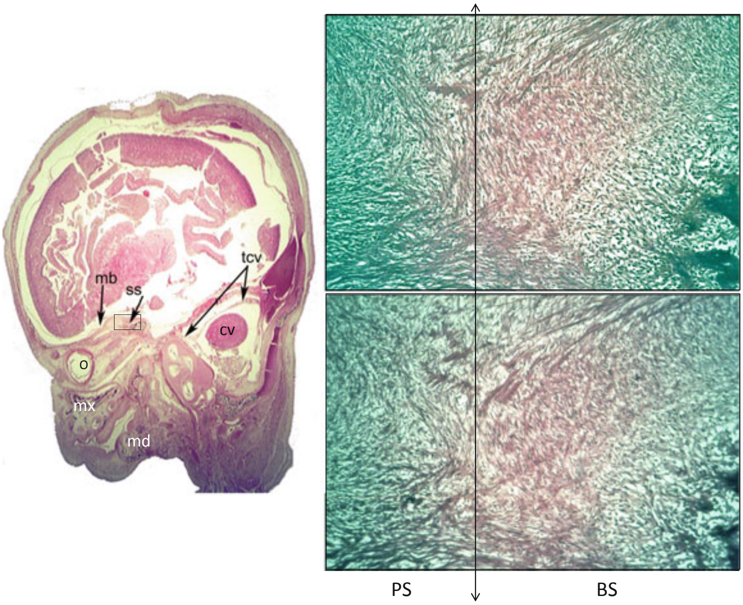

Fig. 12.16 Parasagittal histological sections of a 4-month-old human fetus. cv: cerebellum, mb: basement membrane, md: mandible, mx: maxilla, o: eye, ss: intrasphenoid synchondrosis, tcv: cerebellar tentorium. The histological sections on the right show the spatial organization of collagen fibers between the presphenoid (PS) and the basisphenoid (BS), the double arrow marks the physical limit between the two dynamic territories (photos and © Dambricourt Malassé 1989)

12.5.5.2 Embryonic Straightening and Viscoelastic Dynamics

Finally, the histological observation of the synchondrosis that separates the basisphenoid and the presphenoid confirmed the organization of the interstitial matrix by a dynamic of rotation, training by the mesenchymal tissue formed before the chondrification and which will become the ectomeninge (dura mater). Indeed, the collagen fibers are organized in "convection cell" from bottom to top (Dambricourt Malassé 1989) (Fig. 12.16).

It was necessary to integrate forces and thus the microphysics of microfibrils or molecular structures which confer the forms and spatial organization to synchondroses, sutures, and cellular tissues. Experiments performed on newts in the 1970s (Jacobson and Gordon 1976; Jacobson 1978) showed that, since the embryo is 95% water, the summation of neuroblast cell behaviors obeys viscous and elastic properties. The neuroblasts are made up of collagen fibrils that link them together, contract to the maximum under the induction of notochord. In 2008, modeling went further: "One of the fundamental challenges of current embryo modeling is the profound lack of relevant mechanical property data" (Chen and Brodland 2008):

> How that embryonic tissues are fundamentally viscous or plastic, unlike mature tissue, which is basically elastic or viscoelastic. This fundamental difference arises because

> embryonic cells are relatively free to flow past one another and rearrange. Strictly speaking, embryonic tissues do exhibit viscoelastic characteristics when the constant interfacial tension between their cells interacts with the viscous cytoplasm, but the resulting viscoelasticity is best described by a fluid-like Maxwell model, not the solid-like Kelvin–Voigt model more commonly used for mature tissues (Chen and Brodland 2008).

The works of Fleury et al. (2016) also shed light on the physical constraints of embryogenesis since fertilization:

> The oocyte is spherical at the base, before flattening into a disc of concentric rings of cells as it matures into the blastula stage. Researchers have shown, through micromechanical studies on chicken embryos, how to change from this shape to that of cylinders. The alignment and difference in plasticity between the specialized cells in each ring create tensions within the embryo, forces that cause it to bend exactly at the boundaries between these rings until it forms nested cylinders. But the team went even further by demonstrating that the fold of the amniotic sac is triggered by the previous fold, which forms the body of the animal, itself caused by the folds that precede it. Thus, there is a cascading fold phenomenon entirely due to deterministic physical phenomena, and not controlled solely by genetic information. If morphogenesis could be perceived as a phenomenon with a strong element of arbitrariness or randomness, these works place it in a true dynamic explanation, linked to clearly identify physical phenomena.[5]

Works on embryonic morphogenesis confirm that tissue is viscoelastic material in accordance with biorheology:

> Tissue morphogenesis in multicellular organisms is brought about by spatiotemporal coordination of mechanical and chemical signals. Extensive work on how mechanical forces together with the well-established morphogen signaling pathways can actively shape living tissues has revealed evolutionary conserved mechanochemical features of embryonic development. More recently, attention has been drawn to the description of tissue material properties and how they can influence certain morphogenetic processes. Interestingly, besides the role of tissue material properties in determining how much tissues deform in response to force application, there is increasing theoretical and experimental evidence, suggesting **that tissue material properties can abruptly and drastically change in development**. These changes resemble phase transitions, pointing at the intriguing possibility that important morphogenetic processes in development, such as symmetry breaking, and self-organization, might be mediated by tissue phase transitions (. . .). We posit that abrupt changes of tissue rheological properties may have important implications in maintaining the balance between robustness and adaptability during embryonic development. (Petridou and Heisenberg 2019).

DNA does not code for the synthesis of water molecules, while water is indispensable for the kinetics of organogenesis. Intracellular circulation of organelles would be impossible without the viscous properties of the matrix that limit friction, or resistance. So, it is clear that factors involved in the morphogenesis of the chondrocranium and the splanchnocranium, both unified by the dynamics of rotation, are combinations between microbiophysics including water, organic molecules,

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[5] Le rôle de la physique dans le développement des embryons enfin dévoilé | INSIS (cnrs.fr).

and homeotic genes. The question is now the natural factors that have changed the hereditary memory of the embryonic body plan of extinct species.

12.6 Embryogenesis and Paleontology: Consequences for the Recognition of Extinct Taxa in the Fossil Records

12.6.1 Craniocaudal Discontinuities in Phylogenetic Continuities

Fossil mandibles are arranged into four groups, prosimians (lemuriforme, lorisiforme, tarsiiforme), monkeys, great apes, and *Homo sapiens*, except fossil specimens which fill a geochronological gap between the two last. These mandibles match with verticalized skull bases and transverse growth of the middle fossa superior to the great apes. These primates are *Australopithecus* (the oldest fossils are known ca 4 Ma), *Paranthropus* (known for 1.8 Ma), *Homo* (nothing comparable with Sapiens more verticalized) and of which the present approach predicts fossils as old as the first *Australopithecus*. The geometrical modeling of the postsphenoidal rotation confirms greater amplitude in *Australopithecus*, or contraction of the IV ventricle during embryogenesis (Fig. 12.17b, d) (Dambricourt Malassé 2022).

The postsphenoidal straightening is very close to the oldest known *Homo* skull base (*Homo habilis* ER 1813, 1.9 Ma) but the basioccipital is not aligned with it, the pyramids are less verticalized and the foramen magnum is still oriented dorsally and not ventrally (Fig. 12.18), the ontogenetic divergences increase in *Homo* with the gracilization of the masticatory apparatus and the facial growth, the whole engaged in a verticalization that transforms the vocal tract.

The oldest cranial fossil allocated without a doubt to *Homo* is a mandible of 2.4 Ma (Malawi). The skull base of the oldest *Homo* species is less straightened than in *Sapiens*, the cerebellum as well as the vocal tract, are higher (Fig. 12.19).

Paranthropus, known in East and South Africa (OH 5, KNM ER 406, SK 48) shows a postsphenoid straightening greater than in *Australopithecus* and *Homo sapiens* but as in *Australopithecus*, the basioccipital did not align with it (Dambricourt Malassé 2005, 2022, Fig. 6.23). Aiello and Dean (1990) observe the same greater verticalization for the cerebellar surface of the pyramids. I have concluded that the complexification of *Australopithecus* gametogenesis has evolved in an unprecedented acceleration which amplified the IV ventricle closure, the pons having reached the physical limit of verticality but not the medulla oblongata and without increasing telencephalization.

Australopithecus and *Homo* were permanent bipedal because their endoaxial skeleton was verticalized at the end of the embryonic period, which can be explained only by a recrudescence of gametogenesis increasing complexity which had generated the great apes 15 million years ago. As illustrated by Paranthropus, the increasing embryonic complexity of Australopithecus did not change the spheno-basi-occipital trajectories, whereas that was not the case with *Homo*. This fact added to the great proximity between Australopithecus and *Homo* embryonic straightenings, allows us to infer contemporaneous polycentric foci in tropical, or

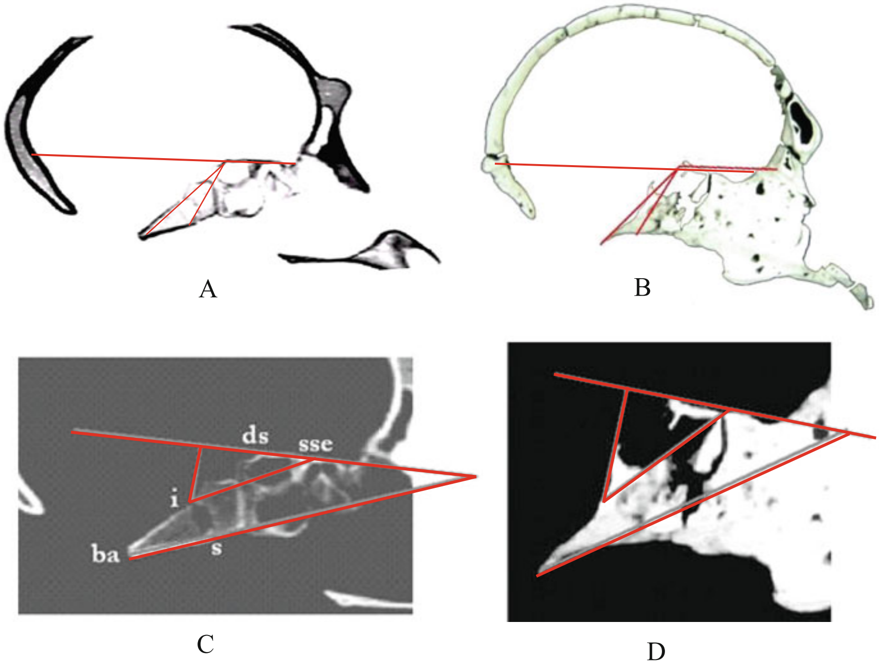

Fig. 12.17 Comparison between adult chimpanzee (**a**, **c**) and *Australopithecus africanus* (**b**, **d**) from Sterkfontein (Sts 5), showing the straightening of the postsphenoid in hominin. ba: basion, ds: dorsum sellae, i: internal section of the spheno-occipital synchondrosis, s: external section of the spheno-occipital synchondrosis, sse: spheno-ethmoidal synchondrosis. The skulls are aligned on the planum sphenoidal. (**c**, **d**) Caro 2004 (photos A. Dambricourt Malassé, CT scanning of Sts 5 courtesy from P.V. Tobias in 2003)

sub-tropical forests, with independent emergences starting from different sub-species of the same great ape genus (see Sect.12.6.2).

The taxonomical determination is largely influenced by two doctrines, the oldest which postulates since the 1950s a gradual transition from *Australopithecus* to *Homo and* then, the Rift Valley seen as the cradle of *Homo* emergence with a geologic glass-ceiling not oldest than 3 Ma. The first doctrine was not supported by Pierre Teilhard de Chardin who has been appointed as the expert of the Wenner-Gren Foundation in the 1950s to evaluate the funding for new excavations in South Africa. Moreover, the necessity of australopithecine ontogeny to generate *Homo* has never been demonstrated. Paleoprimatologist Brigitte Senut (2020) is also in favor of the independence of the australopithecine and human lineages that supposes a divergence of the two phyla at least 4 Ma ago. This view is supported by the appendicular and vertebral skeleton of Kadanuumuu (Ethiopia, Afar, 3.58 Ma) close to modern human with long legs. Unfortunately, the skull with semicircular canals is missing. Paradoxically, the fossil is allocated to *Australopithecus afarensis* (Haile-Selassie et al. 2015) while the anatomy has no common features with the genus; Zeresenay

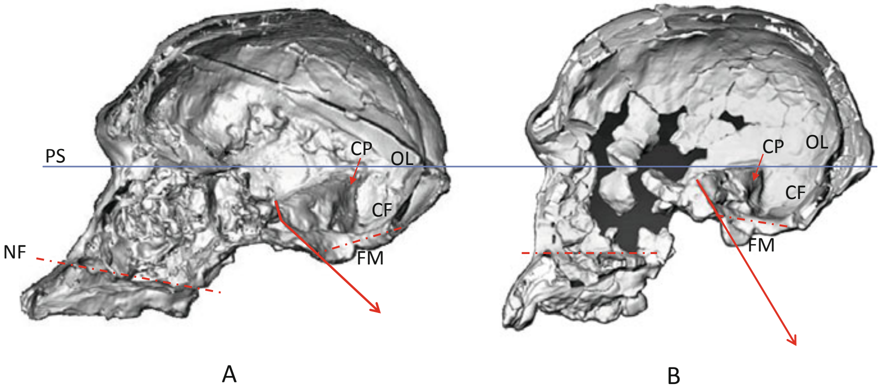

Fig. 12.18 Comparison between *Australopithecus africanus* from Sterkfontein (Sts 5) (**a**) and *Homo habilis* KNM ER 1813 (**b**) showing the less straightening of the *basioccipital* (arrow) and foramen magnum (FM, dotted line) and the less verticalized vocal tract in *Australopithecus* (inclinations of the arrow and nasal floor NF, dotted line). CF: cerebellar fossa, CP: the cerebellar face of the pyramid, FM: foramen magnum (dotted line), OL: occipital lobe. The skulls are aligned on the planum sphenoidale PS. CT scanning of the UMR 7194 CNRS database. Figure © Dambricourt Malassé

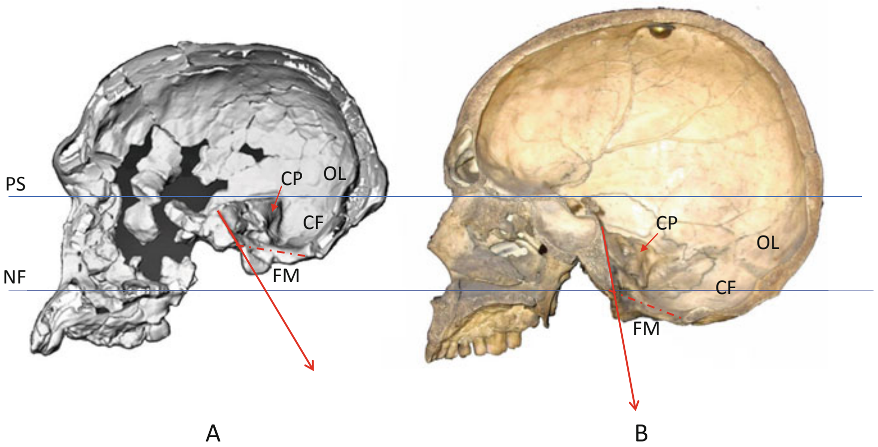

Fig. 12.19 Comparison between *Homo habilis* KNM ER 1813 (**a**) and present-day Sapiens (**b**) showing the less straightening of the *basioccipital* and foramen magnum (dotted line) and the less verticalized cerebellar surface of the pyramids in *Homo* (*habilis*). CF: cerebellar fossa, CP: the cerebellar face of pyramid, FM: foramen magnum, OL: occipital lobe, PS: tangent to the planum sphenoidal. The skulls are aligned on the planum sphenoidal. CT scanning: the database of the UMR 7194 CNRS and skull of the IPH collection. Figure and photo © Dambricourt Malassé

Alemseged who have collected the skeleton of a child, disagrees,[6] the conclusion is the existence of another hominin in Afar very close to *Homo* and oldest than *Australopithecus afarensis* (3.2 Ma).

These African phyla become extinct while *Homo* has known an important diversification and reached Asia long before the Quaternary (Pleistocene, 2.58 Ma) as evidenced in sub-Himalayan floodplain (Dambricourt Malassé et al. 2016; Dambricourt Malassé 2021b; Chapon Sao et al. 2016; Cauche et al. 2021; Dambricourt Malassé and Cauche 2022). The genus gathers mandibles and skull bases of African and Eurasian species: *habilis*, *ergaster*, *rudolfensis*, *erectus*, *heidelbergensis*, *and neanderthalensis*. In 30 years, the number of species illustrated by their mandibles have increased with *georgicus* in Caucasia (1.8 Ma), *antecessor* in Spain (1.22 Ma), *denisovensis* in Eastern High Asia (Tibetan plateau, 160 ka), *floresiensis* in Indonesia (80 ka), *naledi* in South Africa (335–236 ka), and a controversial taxon in Northwestern Africa (300 ka, Jebel Irhoud). They have in common a receding mandibular symphysis or the absence of a chin. The skull bases associated with the mandible are rare (e.g., the four skulls of *Homo georgicus*), their correspondence is allowed either because the fossils are extracted from the same karstic deposits (South Africa), or the same geologic layers (lake or river terraces, East Africa) and thanks to their morphological coherences. These mandibles correspond to cerebellar fossa in a higher position than Sapiens, corroborated by the inclination of the clivus and pyramids less verticalized, whatever their geologic age and their cranial capacity as well as their complexity of brain convolutions (imprints on the endocranium) (Fig. 12.20). These different lineages share the same embryonic straightening and became extinct, but after gametogenic lineages have generated the last embryonic verticalization, Sapiens, or the last threshold of increasing complexity whose axial and appendicular skeletons differ from *Homo* regardless of species.

Jebel Irhoud allows putting the question of the axial straightening well diffused since 1996 (Coppens 1996).[7] If the vault from the frontal squama to the occiput gives the impression of a progressive evolution within the *Homo* genus that is not the case for the chondrocranium which has evolved according to modalities of emergence with punctuated equilibria after million years of stability. Contrary to recent claims, Jebel Irhoud cannot be seen as the oldest member of *Sapiens*:

> This evidence makes Jebel Irhoud the oldest and richest African Middle Stone Age hominin site that documents the early stages of the H. sapiens clade in which key features of modern morphology were established. (Hublin et al. 2017).

Unfortunately, this "evidence" has no ontogenetic support. The skull base is sufficiently preserved with the pyramids to see that not only the chondrocranium has not exceeded the embryonic straightening of *Homo habilis*, but also that its

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[6] "Lucy" Kin Pushes Back Evolution of Upright Walking? (nationalgeographic.com).

[7] Invitation at his professorial chair of the *Collège de France* for the magisterial conference « Les fondements modernes de la pensée de Pierre Teilhard de Chardin face au chaos déterministe », March 1996.

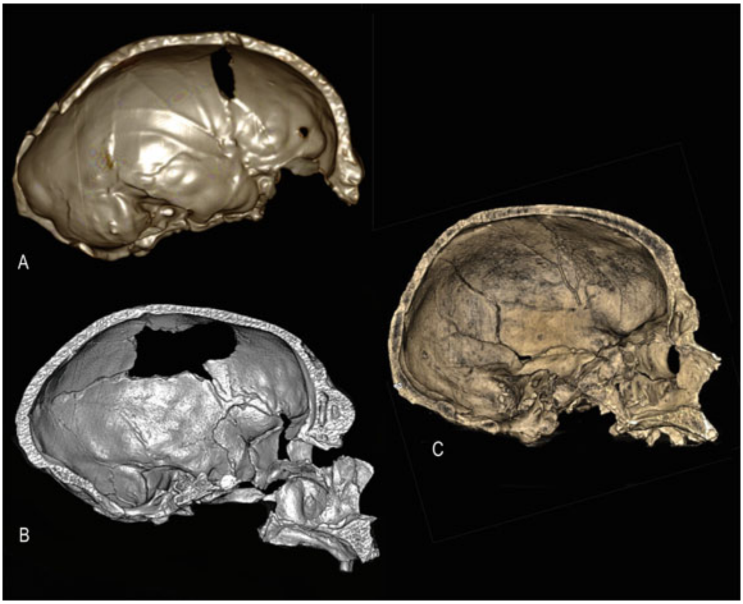

Fig. 12.20 CT scanning of mid-sagittal cranial section. (**a**) Jebel Irhoud, (**b**) *Homo neanderthalensis* La Chapelle-aux-saints, and (**c**) fossil *Homo sapiens* (Cro-Magnon 1). The horizontal line is parallel to the sphenoidal planum, starting from the foramen caecum; the inclined line is the tangent to the cerebellar surface of the petrous bone, Ol: imprint of the occipital lobe. (**a**) cast from the collection of the *Institut de Paléontologie Humaine*, CT scanning American Hospital of Paris with Dr Fabienne Lallouet; (**b**, **c**) original skulls, CT scanning collection of *Musée de l'Homme* (photos and © A. Dambricourt Malassé)

dynamic was in extension as did later *Homo neanderthalensis* (Fig. 12.20). The occipital lobe was higher than in *Homo sapiens* and extended dorsally.

Moreover, the mandibular symphysis has no more chin than the Neandertal La Quina H9 (Dambricourt Malassé 2022). Then a "discrete" character that supports the separation of Jebel Irhoud lineage from the one common to Sapiens and *Homo neanderthalensis* is the occlusal pattern of the first upper molar. In Sapiens and Neandertal, the pattern is rhomboidal (in a shape of a rhombus), the posterior relief on the lingual side (hypocone) is particularly prominent and is not older than 1 Ma, whereas on the oldest known maxillae of Africa and Western Asia, of at least 1.8 Ma, it is poorly developed and the shape is square. Jebel Irhoud developed the square shape (Dambricourt Malassé et al. 2018). These Northwestern African populations, therefore, belong to a lineage separated since 1 Ma at least of the lineage common to Neandertal and Sapiens.

The emergence of the new embryogenesis is the overcoming of the angular threshold of *Homo*, regardless of species. A neurocranium with an occiput as high as a *Homo habilis* cannot be called *sapiens*, even when approaching the geologic age of emergence with a complexified brain. Sapiens is organized around a more verticalized endoskeleton with a complexified cerebral vascularization (Saban

1984) and neocorticalizations (e.g., Holloway 1996; Grimaud Hervé 1997), regularly confirmed by paleontological discoveries. *The taxonomic criteria are thus read 1° in the chronological order since embryogenesis and 2° from the base to the vault and not from the face, the vault and the base after birth only*. So, reasoning about the adult vault before considering the developmental chronology from embryogenesis and overriding the sphenoid and the petrous pyramids can generate phylogenetic counter-sense like for Jebel Irhoud (Neubauer et al. 2018) and misunderstanding of the evolutionary process because Sapiens is not a variability within the limits the genus *Homo*, the changes are at the level of the genus.

Neither the brain, nor the cerebellum and the endoskeleton *Homo sapiens* Linnaeus, 1758, match with any previous taxon. Sapiens is the last emergent ontogenetic unit complexified and reorganized during embryogenesis, with anatomical and neural changes all along the craniocaudal ontogeny and reorganization of the cerebro-cerebellar loop. So, giving the name sapiens to Jebel Irhoud is the application of gradualism allowing interpreting of more recent fossilized bones, such as the mandible with a chin, as a simple variation or gracilization within the limits of a morphotype (Bergman et al. 2021). Human paleontology has fallen far behind the sciences of self-organization by ignoring the dynamics of systems, such as embryogenesis and dentofacial orthopedics (Gudin, Delaire, Deshayes. . .), which explains why concepts such as body plan, emergence, thresholds, and sciences of nonlinear dynamic systems are still missing. This great lacuna has consequences for the understanding of the current occluso-postural disorders as well as for maxillary dental agenesis (Héloret 2015) which cannot be replaced in a correct interpretation of the evolutionary processes doing no distinction between microevolutions and macroevolutionary changes.

The oldest Sapiens' skulls have been collected in Ethiopia. Interesting cases are coming from the Member 1 of the Omo Kibish Formation (Ethiopia), with the fragmentary skeleton Omo I and the neurocranium Omo II. The first is Sapiens while the cerebellar fossa of Omo II is as high as in *Homo erectus*. Fragments of mandible and neurocranium of Omo I are associated, which implies a fast burial of the corpse after death. The mandible developed a projecting chin as Skhul V excavated from the oldest intentional burial (115 ka, Israël) but the supraorbital arch is significantly less developed by comparing with Herto (160–155 ka, Ethiopia). The bones have been collected on the outcrop of a lithostratigraphic disconformity within a sedimentary series of deltaic deposits and in which "mottles follow root structures of reed and seed vegetations" and match with a temporarily emerged period (Butzer 1969). Overlaying tuff has been recently dated to 230 ka (Vidal et al. 2022), Omo I is then claimed as the oldest "modern" *Homo sapiens*. But the corpse was neither covered by river silts nor disarticulated by carnivores, which remains intriguing and raises the question of an ancient intentional burial after the erosion of the Kibish Formation, recalling the case of the skeleton of Asselar (Mali) (Vialet et al. 2013).

12.6.2 A Key Distinction: Different Appendicular Adaptations for a Same Embryonic Axial Straightening

This lack of consideration of embryogenesis does not allow distinguishing between two evolutionary problematics, generating confusion between the verticality of the axial endoskeleton, which is part of the macroevolution of the organization plan and the large diversity of adaptations of the appendicular skeleton, of a same notochord organization plan. The classical reasoning consists in comparing the adaptations of the adult posterior appendicular skeleton to detect traces of bipedalism which would be the "ancestor" of hominin's bipedalism, whereas this bipedalism has no locomotor origin. *Hominin bipedalism is the displacement of the verticalized endoaxial skeleton due to the straightening of the embryonic notochordal axis*. Therefore, there can be no human or hominin "type" of bipedalism in semierect primates, but occasional bipedalism is possible within the limits of the semierect embryonic plan. Brigitte Senut rightly recalls that the appendicular skeletons of the extant great apes, *Gorilla*, *Pan,* and *Pongo*, are not identical to the fossil species in their specialization (Senut ib). However, the morphogenesis of their notochordal cephalic extremity is the same and is found again with the mandibles in Europe, Asia, and Africa until 20 Ma ago. In other words, these species have adapted their appendicular skeleton to different ecosystems within the limits of the same embryonic axial dynamics, or, of the same notochordal straightening.

The axial inclination is distinguishable with the canines and premolars. The occlusal balance of a semierect axial skeleton is blocked by the four canine crowns higher than premolars, as well as deciduous than permanent teeth. This is the case in Africa with the Miocene fossils *Sahelanthropus* (7.2–7 Ma, Chad), *Orrorin* (6.1–5.7 Ma, Kenya), and *Ardipithecus ramidus* (5.6–5.2 Ma, Ethiopia) while the lock has disappeared in Pliocene Hominins. Miocene fossils show that occasional bipedalism was more developed than in the living *Gorilla*, *Pan,* and *Pongo*, with *Orrorin* and *Ardipithecus,* but also in South China 6 Ma ago, in Yunnan with *Lufengpithecus lufengensis*.

Then, it became clear that the genus *Orrorin* lived in the tropical Miombo woodland[8] with areas particularly wet (Senut ib). In other words, the use of bipedalism for a semierect axial skeleton appears as a frequent locomotor mode, whereas lineages such as those of *Pongo* became specialized in arboricolism and dependent on forest ecosystems. In the end, it is important to note that the occasional use of bipedalism was viable in wet woodland so that "mutants" newborns in these populations with a verticalized axial skeleton were not unsuitable. Occasional bipedal walking and tree climbing were the maternal behavior. So, the first environment of the "hominin mutant" was the mother's body, her behavior and that of the clan toward parturients and their nutritional needs. I have concluded that the verticalization of the supranotochordal neural tube, both in Australopithecus and

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[8] Miombo woodlands can be classified as dry or wet based on the per annum amount and distribution of rainfall.

Homo, was two neural dynamic effects due to increasing complexity occurring during gametogenesis of great ape species. The two lineages would have emerged because of different changes in the homeotic regulation along the cephalocaudal axis. The postnatal anatomical differences developed in an educational context transmitted by the mothers, with the disappearance of quadrupedal balance and canine lock, hormonal delay, and longer psychomotor development (Dambricourt Malassé 2010, 2022). The child could learn arboreal locomotion with an endoaxial skeleton in permanent verticality.

12.6.3 Wet Woodland and the Role of Females in Hominization Processes

Since the endoaxial verticality is not a consequence of bipedalism and because the embryonic angular straightening of *Australopithecus* and *Homo* is very close, I argue for many years that their emergences occurred at the same geologic period, in different great ape populations and environments controlled by the females (Dambricourt Malassé 2022). If the species were arboreal, then the births occurred in the forest environment chosen by the females to feed themselves during gestation, lactation, and psychomotor development, these were the priorities that conditioned their behavior for their protection as well. Thus, to the first environment which was the placenta and not the trees, then the second which was the body of the mother who carried her child, was added the maternal and social behavior of the clan. It was normal that females have sought the best conditions, by instinct, by experience, and by reflexive consciousness to preserve their own equilibrium. The embryonic and biodynamical approach allows us to support that *Australopithecines* and *Homo* emerged from different great ape's lineages in wet woodland long before the population density allowed the conservation of a sufficient number of fossils and in conditions more favorable than the acidic forest soils (Dambricourt Malassé 2011b, 2022).

There remains a conceptual difficulty in paleoprimatology with the prevalence of the XIXth century Lamarcko-Darwinian model that limits the reasoning at the gradualist vision and the posture at biomechanics influenced by a ratio between arboreal and open environments. These studies are necessary but insufficient. Paleontologists feel compelled to postulate intermediate stages as the very ancient and saltationist emergence of anatomy considered as human (but different from Sapiens), is contrary to the collective imagination for two centuries. But the distance of walking between trees will not explain the emergence of the verticalized endoaxial skeletons with cerebro-cerebellar loops more complex (Leiner et al. 1987). Only mechanisms transmitted by the gametogenesis could reorganize and complexified the embryogenesis in a coherent and coordinated manner along the craniocaudal axis and sustainably to the stage of reproduction. Thus it is not by reasoning in terms of environmental pressure on locomotor behavior that the anatomical origin of hominins will be better understood, but by considering embryogenesis, its dynamics, and their consequences for the geometry in space of the central nervous system. They are the ontogenetic roots of behavioral changes concerning mother-newborn relationships, psychomotor development with more complex cerebro-cerebellar loops, and social interactions between the females.

12.6.4 Cerebro-Cerebellar Rubicon, Psychomotricity, Mother-Infant Interactions, and Cognitive Implications

Mothers and their newborns constituted the first level of reflexive consciousness with the transmission of knowledge, experiences, care, and the search for the best living conditions. As a result, this is not the environment that selected the little hominins more vulnerable with a less "biting" jaw, delayed psychomotor development, and the permanent struggle against the fall, but the mothers who welcomed them in their hands, on their chest, and certainly already with emotion and affection and empathy between the adults. I then distinguish between intrauterine biological hominization and development to the adult stage and this phase of "humanization" of behavior for these more vulnerable children, the construction of the self-reflexive consciousness. All this is a matter of several levels of self-organization in interactive loops.

Of course, adaptations will differentiate species, with different dental adaptations, depending on the diet; the development of the nervous system and cognitive functions will also depend on nutrients, but it is essential to distinguish between adaptive microevolution, on one hand, and macroevolution, on the other, which generated the two embryonic straightenings, *Australopithecus* and *Homo*. The cradles of hominization were the territories known for by females well before the extension into unknown territories without behavioral references in the collective memory. Socialization and innovative cognitive abilities were, from our point of view, the previous conditions of the extension in new biotopes and to extend territories.

In this cadre, I have developed the concept of cerebro-cerebellar Rubicon, or the sudden instability of the cerebellum due to the verticality of the endoaxial skeleton (see more in Dambricourt Malassé 2022). The cerebellum that controls the equilibrium is forced to be simultaneously informed on its own balance, i.e., the position of the cerebellar fossa, while it cannot inform itself and control itself the head posture. The nervous system composed of networks of interconnected neurons was constrained to self-reorganize and self-complexify in order to allow the cerebellum to receive information about the stability from the cerebellar fossa and for sending back information to maintain the muscular tone of the neck. The cerebro-cerebellar loop necessarily experienced a leap in the complexity of its interconnections. This was not the consequence of bipedalism, widespread in primates, but of the threshold of verticality reached by the mesencephalon, the myelencephalon, and the spinal cord at the end of the embryonic period. This threshold of complexity, or the cerebro-cerebellar Rubicon, would explain the emergence of operating chains such as the Lomekwan dated 3.3 Ma produced by nonhuman hominins (Harmand et al.

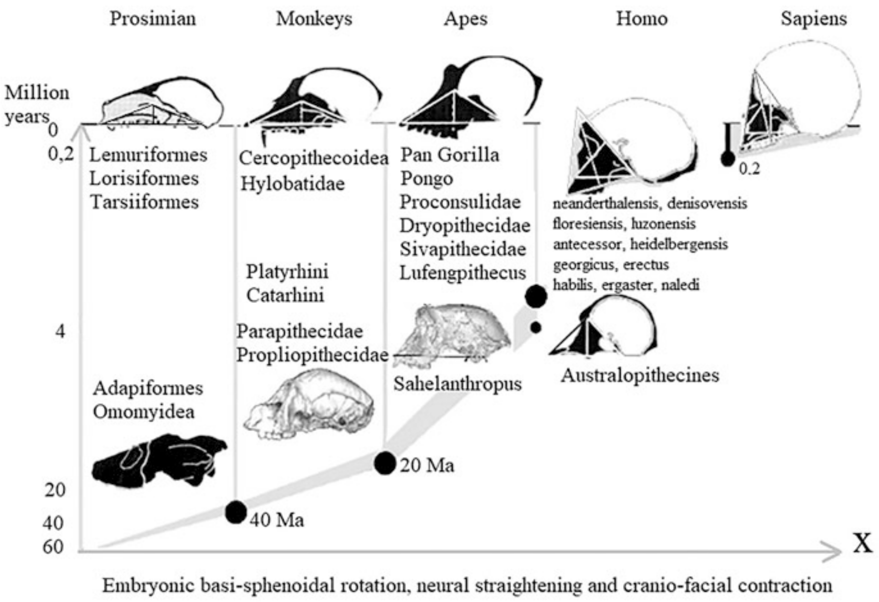

Fig. 12.21 Phylogenetic succession of the neural tube straightening illustrated by the adult basicranio-facial pantograph and regularly tested by paleontological discoveries of skull bases and mandibles (Dambricourt Malassé 1993, 1996, 2011b, 2022; Dambricourt Malassé et al. 1999; Chaline et al. 2000). © Dambricourt Malassé

2015) and in the sub-Himalayan floodplains before Pleistocene (Masol, ca 2.8 Ma) by unknown hominins (Dambricourt Malassé and Cauche 2022).

No geo-paleontological data allow excluding the hypothesis of a tropical cradle of *Homo* emergence ca 4 Ma in Central Africa and then slowing dispersions in borderlands exposed to the global climate cooling with biological and behavioral adaptations. To the climate model forcing biomechanical changes allowing walking in open spaces, it seems interesting to consider environmental contexts much more complex since the issue concerns the complexity of the central nervous system and the control of its embryonic development memorized in the gametes.

12.7 An Emerging Evolutionary Problematic

Basicranio-facial morphogenesis and mandibular growth of the extant primates match with the classification in prosimian, monkeys, great apes, and *Homo sapiens,* and the phylogenesis (Fig. 12.21). The succession of adult skulls in internal view, illustrated by the pantograph, is the same as in external view published in The Cambridge Encyclopedia of Human Evolution (2009).

The Evo-Devo approach allowed cooperation with Jean Chaline and his team at the University of Burgundy, familiar with heterochrony and the formalization of evolutionary processes modifying skeletal or dental morphologies over long geologic periods (Chaline et al. 1996, 1998, 2000; Dambricourt Malassé et al. 1999; Chaline and Marchand 2010). We asked the question if the climate was the engine that could explain such iteration on 40 million years regarding the organization level concerned, the embryonic body plan and its evolution in increasing complexity (Chaline et al. 2000). Finally, *the evolutionary problematics of changes in shapes and positions measurable by angles can be modeled and formalized thanks to the spatio-temporal trajectories characteristic of self-organized and emergent processes*. In the present case, mathematics is that of nonlinear dynamical systems far from equilibrium such as the dissipative structures developed by the Brussels School of thermodynamics and Ilya Prigogine. For this reason, the research has turned in 1995 for a collaborative project with the astrophysicist Eric Bois (2010) to substantiate the use of mathematical languages such as attractors, basin of attraction, and bifurcations, or singularities, acting during gametogenesis (Dambricourt Malassé 1992, 1995, 1996, 2011b).

12.7.1 Environments and Self-Memorizing Evolutionary Processes

12.7.1.1 Dissipative Structures and Unpredictability

Chance in evolutionary biology is seen as random flows of information, coming either from outside the gametes (mesological influence) or generated during gametogenesis (Brownian motion, Grandcolas 2021). The dominant trend in the natural system is the search for equilibrium; a biological system tends to maintain itself "alive", or its stability, through its energetical exchanges and informative signals with the environment. Studies of the early embryonic stages of the *Drosophila* show that the developing dynamic system has properties allowing it to maintain its internal coherence:

> Extensive variation in early gap gene[9] expression in the *Drosophila blastoderm* is reduced over time because of gap gene cross regulation. This phenomenon is a manifestation of canalization, **the ability of an organism to produce a consistent phenotype despite variations in genotype or environment**. The canalization of gap gene expression can be understood as arising from the actions of attractors in the gap gene dynamical system. (Gursky et al. 2011).

Ilya Prigogine developed the model of dissipative structures in biochemistry (Prigogine and Stengers 1979), according to which the system opens on its environment and which dissipates energy, can increase its organization if it is far from its initial state of equilibrium. At the threshold of instability, its state bifurcates toward a

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[9] "Drosophila "gap" genes provide the first response to maternal gradients in the early fly embryo. Gap genes are expressed in a series of broad bands across the embryo during first hours of development. The gene network controlling the gap gene expression patterns, includes inputs from maternal gradients and mutual repression between the gap genes themselves" (Papatsenko and Levine 2011).

new equilibrium, but its innovative reorganization is unpredictable. The mathematical modeling explains that at the bifurcation point, a singularity or a critical point, the system is under the control of internal attractors called "chaotic". Nonlinearity is seen in the contrast between the scale of the instability threshold, a local constraint, and its exponential effects on the global scale of the system. The chaos theory differs from the neo-Darwinian paradigm, in which all are stochastic, because of physical determinism which refers to an underlying order proper of the dynamical system:

> The two main components of chaos theory are the ideas that systems—no matter how complex—rely on an underlying order, and that very simple or small system and events can give rise to very complex behaviors or events. While chaos is often thought of as a reference to randomness and lack of order, it is more accurate to think of it as an apparent random state that results from complex systems and interactions between systems. (Techtarget 2021).[10]

But despite the underlayer order due to complex interactions, the sensibility to initial conditions, or Brownian agitation, remains the physical cause of the search for a new equilibrium, with unpredictable modifications. This paradigm can integrate the critics of the "all genetics" dogma by Henri Atlan (1999) who put forward epigenetics, or the cellular self-regulation that has shifted the determinism of DNA to its nucleic, cellular, or extracellular environment. Thus, the chaos theory shares with the neo-Darwinian doctrine the pre-eminence of random fluctuations even internal determinism cannot allow any reorganization, the causality which allows innovation with a new state of equilibrium is not the reproducibility of the principles which constructed the system.

In such cases, the self-organized dissipative structures are not replaced in their phylogenetic context, or the gametogenic filiation over the very long geologic durations. This is the reason why internal properties of self-regulation controlled by references in memory are not evocated, whereas, with such hindsight, they would be highlighted as in the case of three lineages of *Siphnae* described by Teilhard de Chardin. The theory of deterministic chaos thus reverses the roles between determinism and random, because of the lack of the historical understanding of the gametogenesis, or (1) the encoding processes of the principles of construction and (2) the memorization of these encoding processes. The chaos theory does not correspond to the stability of the evolutionary straightening over 40 million years. The circumstances in which the gametes have been forced to maintain their equilibrium during duplication were unpredictable, but their responses to these unforeseen conditions were already memorized, preserved, and transmitted.

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[10] Que signifie théorie du chaos ?—Définition IT de Whatis.fr (techtarget.com) in French: Les deux principaux constituants de la théorie du chaos sont l'idée que les systèmes—quelle que soit leur complexité—s'appuient sur un ordre sous-jacent, et que des systèmes et événements très simples ou de faible envergure peuvent engendrer des comportements ou événements très complexes. Si le chaos est souvent considéré comme une référence à un caractère aléatoire et à l'absence d'ordre, il est plus précis de le considérer comme un état aléatoire *apparent* qui résulte de systèmes complexes et d'interactions entre systèmes.

Yet, fossil and extant primate species attest to reproducibility and nonlinear amplification of the effects: increasing complexity of the nervous system and axial straightening show retrospectively an iteration, not of the form as in a fractal such as the Koch snowflake, but of the dynamics and self-reorganization processes.

12.7.1.2 Self-Memorization, Conservative Dynamics with Innovative Organization

Life is understood as an organization of molecules, atoms, and ions integrated in autonomous dynamic systems, capable of maintaining their equilibrium with the environment as described in thermodynamics, and capable of reproducing. But, as recalled previously, this cycle is not only the replication of a cell; it is first the self-transmission of the memory that builts itself as an autonomous dynamical system open on its environment. During abiogenesis, such processes had to be capable of being self-memorized; otherwise, they would not be able to transmit themselves. So it is possible to conclude that the best chance for replicative processes to stay stable on long geological durations are those keeping the self-memorization properties. The emergence of such properties poses the problem of their abstract representation as recalled previously (Danchin 2022). Appearing 3770 billion and possibly 4280 billion years ago (Dodd et al. 2017), these unicellular properties remained in equilibrium with their aqueous environment before the Cambrian explosion or the “explosive” emergence of multicellular organisms—or the metazoans—around 2.3–2.1 billion years ago in relation to a threshold oxygen concentration (El Albani et al. 2014). These evolutionary phenomena allow inferring primitive memories’ necessaries for the transmission of self-complexified systems and unexpected attractors regarding the chaotic attractors better known in the living systems (Uthamacumaran 2021). These primitive attractors match with conservative properties, or self-memorization, and seem hidden by the past of current gametogenesis. So, the difference between orthogenetic macroevolutions visible only on very long geological periods, and bushy microevolutions observed in shorter periods, allow inferring different levels of organization in gametogenesis. The oldest would be composed by metamemory necessary to explain the stability of phylogenetic lineage despite the more and more complex changes acquired at each new emergence. This principle of self-reproduction of the complexification process is found again at the origin of our verticality inseparable from the complexification of the central nervous system, essential to ensure the psychomotor control of its balance.

12.7.2 Self-Organization, Self-Memorization, and Predictability

Our embryogenesis emerges from fertilization in continuity with internal orthogenesis characterized by the neural straightening and craniofacial contraction, but in a nonlinear way: for 20 million years, monkeys reproduce monkeys; 20 million years later, great ape embryogenesis emerges and again gametogenesis stabilized with species reproducing great ape embryogenesis till today. Then 4 million years ago that was the threshold of the verticality and since then, the process follows an unprecedented acceleration, with the last threshold emerging around 200,000 years ago. The stability of the trajectory despite its acceleration does not correspond to the predictions of the chaos theory. If chaotic attractors were the regulators of the gametogenesis evolution, great apes and a fortiori hominins would never have appeared. With the chaos theory, it would be impossible to predict retrospectively a bifurcation 20 million years after the first simian, yet this bifurcation was a first iteration of the embryonic complexification with an amplification of the straightening. It would be not possible to predict again, 20 million years later, a second iteration with the hominins and the two very close states of equilibrium, *Australopithecus* and *Homo*. These to last iterations amplified the previous straightening and reached the unstable threshold of verticality that generated the loss of quadrupedalism. The third iteration is Sapiens, our stage of verticality which tends toward a physical limit and develops occluso-postural disorders.

The meiotic attractors that enabled bifurcation at a threshold of complexity are not chaotic. Other attractors have the property of preserving the logic of a process that reaches a threshold of disequilibrium and causes it to shift into a new state of organization. Such attractors are different from the chaotic attractors because they preserve the internal logic at the threshold of the bifurcation, whereas the latter would have reacted to fluctuations that modify it without reference to the identity of the phylogenetic process in memory. They go back to the origin of the first cellular cycles. I have called them “harmonic” attractors because of the conservation of internal evolutionary properties which have not been deviated by random fluctuations (Dambricourt Malassé 1992, 1995, 1996, 2011b).[11]

Innovations have emerged within the limits allowed by the memory of the reconstruction process of ontogeny when the metabolic equilibrium of gametes has reached limit conditions of complexity. This amounts to conclude that gametes produce their complexity and keep in memory the mechanisms of regulation of a state of equilibrium became too unstable. These processes are auto-catalytic, self-organized, self-controlled, and complexity-producing. Thus it is possible to predict the morphological effects on the axial skeleton due to the iterations of the straightening amplification and heterochronic effects at the cephalic pole. For instance, the mesenchymal cells of the dental buds are formed with neural crests derived from the mesencephalon and from the rhombomeres 1 and 2 of the rhombencephalon. The mandibular molars form five cusps in the great ape except the deciduous teeth which form only two, whereas they form five in all hominins (*Australopithecus*, *Paranthropus*, *Homo*). In other words, the deciduous germs had time to form the five cusps and thus to complexify the occlusal surface. In contrast, the morphological

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[11] *The allusion to the chaos theory instead of the stochastic theory shows the change of paradigm in Mrs. Dambricourt. Harmonic attractors play a stabilizing role like chemical clocks that oscillate between two color*s, Jacques Vauthier (2011), mathematician, Emeritus Professor of Sorbonne University, former director of the unit of research “Pure mathematics” at Pierre et Marie Curie University (Paris VI). Report for the Accreditation to Direct Research.

changes of the appendicular skeleton due to the cascade effect of the homeotic genes, for instance, the shape of the pelvis, are not understood.

Similarities have been observed with the mathematics of forms, the topology, developed by René Thom (1977) with the "general theory of the models" known as the catastrophe theory (TC).

> Thom discovered with astonishment that, unlike stable applications, some unstable applications cannot be described in simple terms, because of the presence of a hidden dynamism. The text around which this talk will be organized is a 1962 paper in which Thom described the first example of such hidden dynamism. It marks an important milestone in the development of his reflections on the general problem of the birth and destruction of forms—morphogenesis—employing the qualitative study of the applications of one variety on another. This is the germ of the catastrophe theory, which he developed from the middle of the 1960s, which was much publicized in the 1970s, and which continues to inspire many researchers in the theory of singularities. (Popescu-Pampu 2021).

His work gives a mathematical description of spatial phenomenology in which discontinuities are singularities of a continuous medium. They have highlighted the primacy of internal logic in the control of threshold effects or hidden dynamics. These mathematics are consistent with the stability of the morphogenetic trajectory over 40 million years, whereas chaos theory would never have supported the appearance of Sapiens 40 million years away from the first monkeys. In conclusion, chaotic attractors are not consistent with the properties of gametogenesis that controlled the reorganization of the embryonic body plan. Other attractors dating from the origins of life are highlighted over the very long geological periods and without which the phylogeny of primates, from the prosimian to Sapiens (*Homo sapiens*), would never have been possible, thus joining the transdisciplinary curve of increasing complexity synthesized by Pierre Teilhard de Chardin in the 1950s.

12.7.3 Examples of Memory in Nonlinear Systems

Memory phenomena are observed in physics. Gleick (1987) in "Chaos: Making a New Science" recalls the discovery and theory of the soliton or collective solitary waves:

> Bifurcation points are the milestones of system evolution; **they crystallize the history of the system**. Hidden in all the forms and processes that make us unique—in the chemical reactions of our cells and the shape of our nerve networks—are thousands upon thousands of bifurcation points constituting **a living chronology of the choices by which we have evolved as a system, from the primordial single cell to our present form**. Systems are highly sensitive near these areas, which **constitute the crystallized "memory" of past bifurcations**. (Gleick 1987).

Self-memorizing processes called gray models have been modeled by Guo et al. (2014) and have allowed researchers to conclude, which is basically logical, that the best of them have a memory in reference. During the same years and closer to cells and interstitial tissues, mathematical equations have been published dedicated to viscoelastic medium and behaviors, attractors, and memory, for instance, Conti et al. (2014, 2016), Boldyrev and Zvyagin (2019), Zvyagin and Orlov (2021). In physics as well as in mathematics, the nonlinear behaviors of dynamical systems can thus be associated with memory. In biology, recent studies on the unicellular *Physarum polycephalum* have deduced such properties with the transmission of memory (Vogel and Dussutour 2016).

12.7.4 Macroevolutionary Straightening and Self-Memorization Versus Random Ecological Epiphenomenon

The succession of angular thresholds generated its theoretical formalization which does not match with the neo-Darwinian doctrine of accidental mutations; this is the first statement (Dambricourt Malassé 1993, Chaline et al. 1996, 1998, 2000, Chaline and Marchand 2002). The emergence of new embryogenesis does not reflect a random dissipation of covalent bonds between DNA atoms. If this had been the case, this would have resulted in disorganization and not in **an amplification of the effects keeping the correlations**, which are the neural straightening, the craniofacial contraction, and the complexification of the cerebro-cerebellar neuronal networks. The innovations are reorganizations according to (1) the internal coherences of the cellular dynamics and (2) the conditions of equilibrium of the cellular divisions with the immediate environment formed by the ovaries, then the uterine tubes after the ovulation until the implantation in the intrauterine mucosa.

The stability of the phylogenetic trajectory and its exponential curve since the first hominins have allowed us to induce harmonic attractors which match with a metalevel of memory, that of the reconstruction rules of the embryonic body plane. These attractors control the morphological innovations and their coherence (1) with the previous body plan and (2) with the rules of the previous craniocaudal reorganization. This deduction is contrary to the paradigm according to which hominin ontogeny is a mere environmental epiphenomenon that does not take into account the necessary hereditary rules for the craniocaudal reorganization. For many years I make a distinction between, on one hand, the microevolution of the body plan with its different adaptations, and on the other, the macroevolution with the increasing complexity of the embryo. The mutant populations were adapted to their ecosystems, but as Teilhard de Chardin (1921) developed after he discovered primitive primates collected in the Quercy phosphorites (Eocene, France, 37–34 Ma), it should be necessary to make a distinction between specialized and generalized species. He considered that the phylum from the oldest primates to *Homo sapiens* was the trunk formed by generalized species, while extant species are divergent branches from the trunk. So, I sustain for more than 30 years in the scientific lineage of Pierre Teilhard de Chardin and his intellectual successors, professors holding chairs at the *Muséum national d'Histoire naturelle*, Yves Coppens, and Henry de Lumley, that hominization is in continuity with terrestrial phenomena of increasing complexity since the first unicellular cycles and that without these very old and primitive attractors associated to the production of complexity, never hominins could have emerged. Environmental conditions are necessary but they are not the complex processes that increase the complexity of embryogeny and control it without disorganizing the internal coherence of the ancestral embryogeny. A unicellular is a living organism that is no more the case for the gamete in continuity with the first cells. Nevertheless, maybe, this could be the case when attractors inherited from these unicellular ancestors have been activated because of thresholds of complexity. The question remains why gametogenesis increased irreversibly the complexity of embryonic memory.

12.8 Conclusion: The Emergence of Life Helps to Understand the Phylogenetic Neuraxis Straightening

Natural selection was a fecund concept as long as the properties of physics such as thermodynamics escaped the knowledge. But this concept could not explain the processes of memorization necessary for the reproduction of the first cellular cycle that stays the problem of the emergence of life. As recalled in this chapter, the cellular cycle would have been impossible if the rules of the construction of the dynamic system did not integrate themselves for their transmissible sustainability. Attractors of such properties have been called “harmonic”. These properties of self-memorization prove as the initial conditions for the emergence of the first level of complexity, without which, the increasing complexity of organisms, the metazoans—or the “Cambrian” explosion—could not have been transmitted until the first primates and their central nervous systems, the most complex among vertebrates. Physical, geophysical, and geochemical conditions constitute the matrix of biodiversity and local indetermination has contributed to adaptive innovations. But harmonic attractors are necessary for the understanding of the neural straightening and the stability of the irreversible trajectory up to our verticality, psychomotricity, social behaviors, and complex cognition emerging through the cerebro-cerebellar reflexive loops, waiting for a better understanding of the mesological conditions to complete the synthetic theory of the self-organized hominization.

Acknowledgments I thank Prof. Valeria Isaeva and Dr Sandra Joffroy for accepting the invitation to review the chapter.

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Evolutionary Creativity

13

Edgar Morin

> The fabulous bushy developments of the plant and animal kingdoms show us what Bergson called “creative evolution” and which we could also call “evolutionary creativity”.
> —*Morin (2017)*

Abstract

Fifty years of reflection on the modes of thought of scientists and transdisciplinary synthesis allow the philosopher of science and the sociologist to understand how much life cannot be reduced to biochemistry. Its creative capacities open the consciousness of *Homo sapiens* to the recognition of emergence, considered here as the mystery of life unceasingly renewed by the progress of knowledge.

Keywords

Life · Evolution · Self-organization · Creativity · Recursiveness · Autonomy · *Genos* · *Phenon* · *Autos* · Individuality

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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_13

13.1 Introduction

This chapter looks back on a life committed to the exploration of the ways of knowledge of Man by Man, and on the need for a method to apprehend the complexity emerging from the evolutionary creativity at the origin of life and its unfolding. The method of complexity makes it possible to integrate antagonisms by conferring on them a creative unity that has allowed the prodigious inventions of plant and animal life. Since the 1960s, complexity has never ceased to animate my curiosity as an anthropologist, in sociology, philosophy of science, and cogniscience. It led me to discover the theories of self-organization, notably "On self-organizing systems and their environment" by Heinz Von Foerster (1960) and "The Laws of Form" by George Spencer-Brown (1969) which emphasizes the use of self-referential paradoxes.

There is a double creativity in the "history of life", the first and that of any organization which associates diverse elements, produces qualities unknown to the isolated elements, qualities named emergences. Thus, the birth of the living organization has produced remarkable emergences which are autonomy, self-reference, self-reproduction, cognition, mobility. Self-reference constitutes a recursive loop whose products are necessary for its own production, a typical phenomenon of living complexity (which Artificial Intelligence (AI) lacks), it is this primum movens that unites life, knowledge, and creativity.

The second creativity is that of invention, or rather of the innumerable inventions of life, such as sexuality in the two kingdoms, the chlorophyll function, the germ, the flower in the plant world, the legs, wings, organs, and brains in the animal world. As Anne Dambricourt Malassé (1992) has shown us, this creativity is carried out at the time of reproduction after self-reorganized gametogenesis and whereas human creativity is carried out in the cerebral process and thought.

13.2 The Complexity of *Autos*

Let us recall at the beginning this principle: The object of study metamorphoses according to the type of vision that beholds it. Either one considers that there is nothing under, above, or outside the phenomena, that what is mere potential is purely and simply unreal, and therefore, everything that is alive is phenomenal, including the *genos*,[1] which is inscribed in the *phenon*[2] (productive activity) in the form of the genome. Or one considers as worthy of attention only the organizing principles that generate visible things, and then, phenomenal life is only the expression of the deeper reality of the *genos*. Here, I have consistently rejected this type of alternative. I will try to link the two points of view which deny each other, that is to say to

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[1] Genos: everything that is genetic and therefore generic and generative referred to in general as genotype.

[2] Phenon: the concrete phenomenal existence designated by phenotype.

relativize them into a meta-point of view that respects the complexity of *auto*[3]*s*. We will thus see that everything that is generative is, in one sense, phenomenal, and that everything that is phenomenal participates, in another sense, in what is generative.

Everything that is generative is phenomenal: DNA is molecular in nature, like protein; although more stable than protein, it is not immune to degradation and disintegration. The genetic memory, inscribed in this physico-chemical entity, can be corrupted, and in fact, it is protected and repaired by ad hoc enzymes. Conversely, everything that is phenomenal is also generative, since exchanges and activities bring energy, materials, work, and synthesis necessary for the reorganization/regeneration of the organism.

It is not enough to notice that, under a certain angle, the *genos* is phenomenal and that the *phenon* is generating. It is also necessary to see that each one contains the other in specific ways. The phenomenal being contains within itself its matri-patrimonial heritage, and the *genos*,[4] for its part, contains within itself the potentiality of all new phenomenal beings. The *genos* is in the *phenon* which is in the *genos*. More still: The organization of the one comprises the organization of the other. It is not only the phenomenal organization that requires the generative organization; it is also the generative organization that requires the phenomenal organization. DNA always needs a phenomenal envelope to reproduce itself. When, in the cell, the two chains of the DNA double helix separate from each other, it is the cytoplasm that provides the complementary nucleotide opposite each nucleotide that has become accessible. The virus, an autonomous RNA or DNA capsule, becomes active, i.e., reproductive, only in the cell it parasitizes.

Thus, genes only operate as genes in living cells. In order for their configuration to become "information" and for their "information" to become "program", they need the living cell, not only as a nourishing environment, but above all as an organizing being of which they themselves are a part. Specialized enzymes have even been discovered, arranged along the strands of DNA, which detect breaks, excise the fractured parts, and repair accidents. These enzymatic repair mechanisms seem universal. They indicate to us not only that phenomenal organization plays a co-organizing role in genetic organization, but also that in a way *it regenerates the regenerator*.

All reproduction is always carried out in and by geno-phenomenal activity. It is the cell, not the gene, that self-reproduces (Dumitrescu 1976, p. 25). The egg resulting from the fusion of two gametes is not the food reservoir of a genome, but a cellular organism from which a complex ontogeny will be organized. Moreover, any embryogenesis needs phenomenal conditions of protection and development, which can be organismic (the intra-uterine gestation of mammals), peri-organismic (the brooding of eggs by birds), sociological (where the eggs of an ant or a bee are

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[3] Autos: the (dependent) autonomy of the species/individual complex specific to the living.

[4] It does not replicate itself in a test tube; enzymes and substrates must be added under specific conditions; and when it replicates chemically, there is no duplication of the entire DNA–enzyme–substrate system (the enzymes degrade, the substrates run out).

entrusted to the social organization), or ecological (where, for example, the eggs of fish are fertilized in a shelter). We see therefore that at each level of existence—cellular or muticellular—and at each stage of existence—birth, ontogenesis, adult state—*genos* and *phenon* ineluctably call on each other. Every phenomenon of life constitutes in a way a geno-phenomenon, a pheno-genomenon.

Self-organization is thus both double and one—*unidual*—that is to say, self-(geno-pheno-)-organization. *Geno-phenomenal uniduality means first of all that every geno-organization and every pheno-organization needs the dynamism of the other, and that both need the dynamism of the self-organizing whole that they co-constitute.*

The progress of biology, starting with the discovery of the evolution of the living world, reveals to us the mystery of plant and animal creativity, but the fear of creationism has produced an explanatory flattening with the notions of (random) mutation and adaptation. Nevertheless, I need this term, creativity, without which biological evolution and human history are seen trivially as due to mere determinism and/or chance.

13.3 Our Reality Is Not Primary, It Is Emergent

How could the reality of our universe emerge from that which is devoid of all criteria that define reality? Here, the notion of emergence provides a decisive clarification, even if the notion itself is inexplicable. Emergence is a surprising systemic notion that the sciences are beginning to integrate. Emergence is a type of new reality, endowed with its own qualities and properties, and which is formed, constituted, and concretized from the organizing assembly of elements not endowed with the qualities and properties of this reality. Thus, living organization was constituted and is constituted unceasingly starting from physico-chemical molecules which in themselves do not have any property of life. Nevertheless, the organizing complexity of living beings gives them qualities unknown to the molecules in isolation: self-repair, self-reproduction, cognitive aptitudes. The reality of life is the result of the complexity of its self-organization, which is in fact self-eco-organization; it needs its environment from which to draw the necessary energies for its uninterrupted work (which this work degrades unceasingly).

Our reality as individual beings with bodies and minds in a world of material objects—plants, animals, houses, machines, cars, supermarkets—is emergent in its very reality. This emergence is permanently ongoing from microphysical constituents devoid of locality and where our time and our space are non-existent. So the notion of emergence can help us to understand our doubly antagonistic feeling of an absolute reality and the relative or weak reality of our reality. The reality of our world emerged 15 billion years ago from a self-organizing process. The material universe emerges unceasingly from microphysical elements, devoid of materiality, but whose combination makes our materiality emerge.[5] Matter is not a primary reality, but an emergent reality. What we call decoherence is the phenomenon by which the association of a large number of microphysical elements, past a certain threshold, makes our spatio-temporal universe emerge.

Our spatio-temporal, physical, and biological reality is therefore obviously an emergence from a strange reality that we apprehend with our words, our instruments of detection, our observation and experimentation, but which escapes our logic. This microphysical reality has very little reality compared to ours, but the latter depends on this reality without reality. Microphysics gives us only indirect or metaphorical approaches to something inconceivable and unnamable.

Time and space are emergences that appeared in and through the formation of the universe. They are real, while having a reality depending on an unknown which is neither time nor space (a “void”?) and which remains beneath our reality. At the same time, our reality is absolute, in our pain as in our love (in our affectivity, as Stéphane Lupasco has said), because the emergence of our world is a reality, although very dependent on an “infra-world” endowed with another reality where our time and our space have not yet emerged. This emergent reality constitutes a literal reification (at least to our senses and to our minds): “real”, from the Latin *res* for “thing”. The notion of reality is reified in itself; our universe is a gigantic thing made up of things separated from each other by time and space. Our reality is a process of thingification.

However, and here I take up an idea of Niels Bohr, which I have developed elsewhere, where key paradoxes from microphysics are found as well in our physical, biological, and human reality. Thus, the inseparability of what is separate is found in a particular way in our world and at our scale; it is not only the separate particle of microphysics that is inseparable from the “inseparable” wave; it is the individual separated from the species and society that is at the same time inseparable from the species and society. We are humans separated from our biological ancestors, but we are also inseparable from them; we are separated from the animal world, but we are inseparable from the process that stretches all the way from the unicellular organisms to us, just as we are inseparable from the physical history of the cosmos from which life originates. The most astonishing thing is that the astrophysical conception of our cosmos not only supposes an underlying chaos, but that this cosmos is supposed to have issued from what seems to have the least reality: the quantum vacuum. Now this vacuum is said to be constituted by virtual and infinite energies, which, when actualized (following some strange event or accident) produced the thermal deflagration metaphorically called the Big Bang. Thus, what seems the least real, the vacuum, would be the source of our reality.

Thus, there is no reality in itself. There is, however, a self-organization of the universe which produces its reality.

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[5] Let us recall that for philosophy and materialist science, as well as for common sense, matter seemed the first fundamental reality.

As Basarab Nicolescu[6] affirms, there are levels of reality, totally heterogeneous among themselves, but also inseparable and interdependent. Moreover, there would seem to be a permanent and invisible level of pre-reality, an infra- or super-reality that is co-present with our universe, which for Buddhism, under the name of emptiness or nirvana, is the supreme reality and which for us is that which escapes reality but grounds realities. A Taoist-Buddhist thinker, such as Fang Yi Zhi, speculated that *samsara* (our world) and *nirvana* were not two separate worlds, but two polarities of the same reality. Nagarjuna went so far as to say, "As long as you make a difference between *samsara* and *nirvana* you are in *samsara*", as if to indicate that *nirvana* is within *samsara*, just as *samsara* is within *nirvana*. If all realities form reality, then reality is multidimensional (Pierre-André Terzian[7]). I would say otherwise: We must hypercomplexify the idea of reality.

Hypercomplex Reality

The continuous and the discontinuous, the separate and the inseparable are themselves inseparable. Illogically, the real and the unreal are each contained in the other. The fabric of our reality comprises layers, holes, and emergences which are sub-logical, supra-logical, a-logical, extra-logical, one really does not know what else...

Emergence is logically non-deducible: We can only observe it. It is not an explanation, but a mystery proper to physical reality. Chaos is not only anterior to cosmos; it is interior to the cosmos. Our cosmos is not only order: It is a permanent, retroactive, and recursive dialogue between order, disorder, and organization. Chance, this unknown, is omnipresent. Even in our perception of the human universe, reality only obeys classical logic if we cut it into separate pieces.

The important question remains: Are we bound to, exiled or separated from, indescribable realities? Do we participate in them without knowing it? In flashes? What relation could our minds have with an unknowable and ineffable reality? Verified thought transmissions, premonitions, and verified predictive clairvoyances are like holes in time (premonitions, clairvoyances) or in space (telepathy) which suggest that our brains have the ability to participate tangentially or in flashes in this non-separated reality without time or space.

We exist between two infinities, said Pascal. Human knowledge is carried out in a middle band between these infinities, a zone of shadows and flickering light. It is by holding to this band that we sense in our depths how the real exceeds the thinkable, which fragments and dissolves into it. Outside this middle band, we cannot establish our distinctions, our logic, our separations, and this extra-reality takes on the face of chaos before sinking into emptiness, which itself enfolds a plenitude of potentialities.

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[6] Basarab Nicolescu is the founder of the International Center for Transdisciplinary Research and Studies (CIRET).

[7] Pierre-André Terzian is a poet and playwright.

Reality is indeed hypercomplex: It comprises plurality, even heterogeneity, reification, the imaginary, uncertainties, the unknown, and finally, mystery.

The mystery is in the real, perhaps in the two senses of the word mystery:

1° something unknowable, 2° a secular/sacred ceremony where our lives play out and are played out. In any case, within a reality woven of unreality, a reality both absolute and illusory, suffering, enjoying, being born, living and dying, these realities, so fleeting and ephemeral, are our true human reality.

13.4 *Autos* Revealed and Hidden

It is by wanting to reduce living processes to physical–chemical processes that molecular biology makes us discover the astonishing organizational autonomy of cellular life and gives us access to the idea of an organization that organizes itself—that is, self-organization. It is the approach that seeks to annihilate any idea of autonomy of living *matter* that allows us to discover the autonomy of the living *machine*. It is the search for elementary simplicity that leads us to a fundamental complexity.

At the same time, however, we see that this biology neglects the self-organization that it has revealed. Danchin's book is telling in this respect. No other work better demonstrates how molecular biology has been able to reconstitute a good portion of the myriad cogs of the prodigious cellular machine and will undoubtedly reconstitute its entire economy (Danchin 1978, pp. 107–263). Everything is there, almost: The fact of self-organization is present, but what is missing is the idea of self-organization.[8]

Thus, biology, and molecular biology in particular, brings to light the central problem of the organization of living autonomy and of the autonomy of this living organization, only immediately to fall back to the level of chemical interactions. It brings to light processes of self-assembly, but remains at the level of molecular

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[8] Let us recall (Morin 1977, *Method* 1, pp. 95–96) that the reductive conception proper to classical physics atomizes beings and existence into their elementary units and makes of them "objects" devoid of autonomy: It does not grasp the phenomenon of self-organization proper to natural machine-beings, and which grounds the autonomy of physical beings like stars, atoms, and whirlpools. Biological theory exceeds this understanding when it calls upon the organizational framework of cybernetics (Morin 1973, p. 257). But the model used is that of the artificial machine which is produced, constructed, and programmed from the outside (by humans). However, as we have seen (Morin 1977, *Method* 1, pp. 165–166), "life includes the idea of machine in its strongest and richest sense: a form of organization which both produces and reproduces itself. We can conceive of living beings, from unicellular organisms to animals and humans, at once as heat engines and chemical machines which produce all the materials, all the complexes, organs, and features, all the behaviors, all the emergences of this multiple quality called life.... Life is a polyvalent machine-like process that produces machine-beings, a process which is maintained by self-reproduction.... The living being fulfills and brings to fruition the idea of machine, while overflowing it existentially and exceeding it biologically."

configurations. It brings to light a self-organization which, while presupposing them, exceeds in richness and complexity any systems or cybernetic notions, but at the same time it cannot provide an autonomous foundation for autonomy: *it cannot theoretically link together autonomy and dependence*, and it emphasizes in extremis the non-autonomous factors of autonomy. It recognizes and emphasizes the problem of organization, but it lacks the organizational paradigm that would allow it to give consistency to the ideas of feedback, emergence, and therefore of autonomy. It retains only half of this fundamental two-sided truth: (1) All elementary phenomena of life are strictly physico-chemical, and all global phenomena are organizational emergences; (2) the organization produced by the elementary interactions retroacts on them, controls them, governs them and produces an overall reality endowed with its own qualities.

This organization, which depends on physico-chemical processes, is not produced by any external super-organization, which would be its *deus pro machina*: It is a self-organization. It is indeed this self-organization that molecular, cellular, and genetic biology shows us. But biological thinking does not manage to comprehend the meaning of the prefix "self-". And as long as we cannot conceive what "self" means, the organizing autonomy of the living being is condemned, either to float in the vacuum like a ghost, or to let itself be dissolved by heteronomous determinations.

13.4.1 *The Emergence of* Autos

An obviousness and a mystery lie hidden in the prefix "self-". What is the autonomy of organization and action that is both productive and produces the autonomy of an individual being and of a living existence, while constituting a trans-individual process of self-reproduction? Here is a problem deprived of a name, which has only a prefix, and this prefix is most often asleep or forgotten. We lack a key concept for the most obvious, most banal character of all life, from bacteria to *Homo sapiens*. This concept exists in germinal form in the prefix "self-". We must therefore first transform this prefix into a concept: *autos*. From then on, *autos* becomes the sphinxlike word which poses us the great enigma of life.

The notion of *autos* must awaken and regenerate the prefix "self-"(*auto-* in French), restoring to it its two vitally inseparable meanings: its direct meaning, "the same" (*idem*), and its reflexive meaning, "oneself" (*ipse*). It thus designates both the return of the same through the cycles of reproduction (*idem*) and the emergence of individual beings (*ipse*), the identical (*idem*) which defines a species, and the identity (*ipse*) which defines an individual. It gives a living meaning to the terms of organization, production, reproduction: self-organization, self-production, self-reproduction.

autos	
the same (*idem*)	oneself (*ipse*)
the identic	identity
auto-reproduction	auto-organization
species	individual

Even before recognizing the concept, the problem of *autos* arises in the 1950s, not in the heart of biology, but in a no man's land patrolled by the advanced reflection of cybernetics, the theory of systems, and the theory of automata.

1. The notion of self-organization appears as a key problem in three symposia on the theme of Self-Organizing Systems (Yovits and Cameron 1960; Yovits et al. 1962; von Foerster 1962).
2. von Neumann's reflection on natural (living) automata had already led in the 1950s to the idea of self-reorganization. Going beyond the problem of self-reproduction [cf. the posthumous publication of von Neumann (1966)], von Neumann had discovered that what opposes natural automata to artificial automata is the complexity of an organization which, tolerating, reabsorbing, and correcting disorder, repairs and regenerates itself.[9] Atlan was to draw the fundamental consequence of the Neumannian discovery (Atlan 1972): Permanent disorganization/reorganization is a constitutive character of living self-organization. Thus, a two-sided process emerges:

3. The idea of self-production emerges from the work of Maturana, Varela, and Uribe (Varela et al 1974). These authors consider that *auto-poiesis*,[10] i.e., the capacity to self-reproduce in a permanent way, constitutes the central property of living systems (Maturana and Varela 1972).
4. Finally, and perhaps most importantly, the logic of living organization has raised various questions since the 1960s (Gunther 1962; von Foerster 1974) and has given rise to the problem of self-reference [cf. the formalization of Varela (1975) based on the arithmetic of Spencer-Brown (1969)].

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[9] Let us recall: von Neumann wondered why an artificial machine, whose constituents are extremely reliable, is less reliable than the living machine whose constituent proteins are extremely degradable. He discovered that this was due to the always degenerative character of the former (a disturbance or an error is the cause of stoppage or irreversible degradation) and to the provisionally non-degenerative character of the latter, which is capable of tolerating, fighting, and rectifying the error by carrying out repairs and reorganizations.

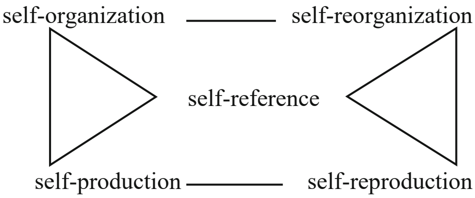
[10] I have defined production in the strong sense of "bringing to being and existence" (Morin 1977, La Méthode 1, p. 157) and I use *poiesis* whenever I give a creative connotation to the term production (ibid. p. 158).

The notions of self-organization, self-reorganization, self-production, and self-reference emerge separately, without much communication between them. Although they concern a fundamental problem, they remain marginal and peripheral to the theory of life. The idea of self-organization remains at the crossroads between thermodynamics and biophysics, without having made a strategic breakthrough in biological thought. After its emergence at the end of the 1950s, it has only attracted the interest of a small number of adventurous minds and remains ignored in the great theoretical and epistemological debates.

How can we explain the neglect and persisting marginality of such a fundamental notion? It is because, unlike cybernetics, which can be effectively applied to computing machines, theoretical models of self-organization cannot produce any living machine, nor can they fertilize research in molecular biology which aims at identifying chemical units and their interactions. The nascent idea of self-organization is still too abstract for empirical research, too premature for practical application. Moreover, it is not yet itself conceptually self-organizing. Nevertheless, however late its birth, however old it may seem, self-organization remains a new idea, hardly recognized and explored. The idea of *auto-poiesis* is still too localized in one school of thought. It has isolated itself by insisting on the idea of closure, at a time when, on the contrary, the idea of the openness of living systems was spreading.[11] The idea of self-reference, in its necessarily formalizing elaboration, still hovers over life without knowing how to embody it.

13.4.2 *The Constellation of* Autos

All these notions—self-organization, self-reorganization, self-reproduction, self-referentiality—have not yet attained to a real existence. They are still separate, with little or no communication. In fact, however, they call for and imply one another, and ask to be associated in a macro-conceptual constellation. This constellation is indeed constitutive of the macro-concept of *autos*, which gives principle and consistency to what is at the same time:



We will explore and elaborate on the notion of *autos*, taking care:

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[11] I have already indicated (Morin 1977, La Méthode 1, p. 210) and I will show again later that openness and closure are two inseparable notions and cannot be posed as alternatives.

- not to confine *autos* to one of these terms,
- to conceive in *autos* both the dimension of reproduction (*idem*) and that of the individual being (*ipse*), but without reducing *autos* to the Linnean cut of species/individual,
- not to forget the relation of independence/dependence between *autos* and *oikos*, that is to say the self-eco relation.

From Self to *Autos*

We have now to make the conceptual leap from the physical to the bio-logical where at the same time:

- Self becomes *Autos*;
- existence becomes life;
- being becomes an individual;
- the living generates itself from the living.

13.5 The Unity of geno → phenomenal Duality

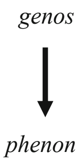
13.5.1 The *geno* → *phenomenal* Organizing Loop

Weiss emphasizes the idea of global dynamism when he notes that the correspondence between differences in the arrangement of DNA sequences and differences in the morphological characteristics of an organism does not explain the morphogenetic dynamism by which configurations such as eyes, hair, etc., are constituted: "How can discrete units such as genes (...) lead to an organization if they are not nested in a reference system (itself already) organized, of which they are the constitutive elements, but the global dynamism of which they must undergo in return?" (Weiss 1974, p. 117).

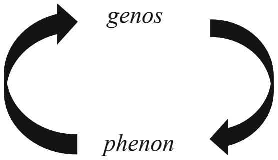
We must grasp the inseparability of *genos* and *phenon*, not only in terms of interaction and interdependence, but also in the dynamic totality of a recursive organization. Let us recall (Morin 1977, p. 187): Any process is recursive whose final states or effects produce the initial states or causes. A recursive organization is an organization that produces the elements and effects necessary for its own (re)-generation and existence. It is thus organizer-of-itself. Living organization is a machine-like organization; it is recursive in the sense that its organized products are necessary to the reconstitution and operations of this very organization, and are therefore organizing. From this point forward, the idea that the product co-produces its producer takes on a non-absurd meaning. In this double organization, the organized is not only organizer, but necessarily contributes to the organization of its organizer. Generative organization is in a sense the organization of the phenomenal organization, which co-organizes the organization that organizes it.

The whole consists precisely in an auto-(geno-pheno)-organization, *where the generated is necessary to the (re)generation of the generating*.

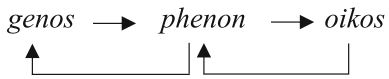
We must therefore not think in linear terms:



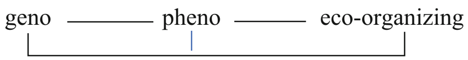
but in a loop:



and enlarge this loop further by including *oikos*:



which constitutes the



relation, where each of the terms participates in the regeneration of the others. This does not mean that there is symmetry or equivalence of the action of *genos* on *phenon* and that of *phenon* on *genos*. Thus, there is no informational marking of the protein on the DNA (contrary to the "Lyssenkian" idea), but there is co-organizing feedback of the proteins on the DNA, in particular in the case of DNA repair and excision proteins. More broadly, it is not only the protein envelope, but the whole phenomenal organization of the living being that is indispensable to the action, duplication, repair, and regeneration of genes. So we see the recursive process whereby the action of the genes is regulated by cellular organization, which is regulated by the action of the genes.

Everything that is self-organizing is grounded in a recursive geno-phenomenal dynamism. Thus, living machinery includes the regulation of the regulated on the regulator (homeostasis being necessary for the regeneration of the loop that generates it) as it includes the productive action of the product on the producer.

If we now consider not only the living being, but also the cycle of reproductions, we see that this cycle produces individuals which, while constituting themselves by means of relatively autonomous geno-phenomenal loops, are indispensable moments for the continuation of this cycle. There is thus a double loop: The generative loop is inscribed in the phenomenal loop that it produces, but the same phenomenal loop, while producing the continuation of the generative cycle, is inscribed in the generative loop that precedes and succeeds it. Thus, the generative (cycle of reproductions) produces the phenomenal individuals which produce this generative cycle.

Finally, generative autonomy depends on the existential autonomy of the *phenon*, which depends on generative autonomy. *The autonomy of living self-organization is the product of this double organizational dependence of the generative on the phenomenal and of the phenomenal on the generative, a mutual dependence which builds the autonomy of the whole, and thereby of both. Each one, in this sense, constitutes a capital moment of the other, while accomplishing its own loop.* Thus, *genos* and *phenon* are not only inseparable, but co-organizers of each other in a process of self-organizing recursion.

13.5.2 Computing Apparatus and Geno-Phenomenal Transformations

The "biological revolution" has revealed to us that living organization is informational/communicational; DNA contains hereditary "information"; this information "programs" the activities of the cell via a DNA RNA protein communication device. But the notions of information, memory, knowledge, and program only make sense within an apparatus that resurrects memory, organizes knowledge, transforms information into a program, and decides on action, and this computing apparatus cannot be dissociated from the organizing activity of the entire living being. Thus, the genes are part of the computing apparatus, which is an integral part of the cellular being. It is the whole of every cell that constitutes a being, a "machine", and a computing apparatus.

The computing apparatus of the cellular being becomes generative by transforming information (potential negentropy) into programs and strategies (organizational negentropy) that govern the phenomenal actions and performances, which, themselves essential to the existence of the generative apparatus, participate in the regeneration of the generator. Thus, starting from the computing apparatus, an unceasing cycle of conversion of generative praxis into phenomenal praxis and vice versa takes place, is generated and regenerated.

The unity of duality: Let me recapitulate what makes their unity: *genos* and *phenon* belong to a unity, the *autos*, of which they are, by their association in a loop, the two necessary constituents; the recursive unity that is born from their conjugation makes them indissociable. Moreover, each in its own way is constitutive of the other, participates in the nature of the other, and each, via permanent computation, is transformable into the other. Living self-organization constitutes indeed a geno-phenomenon, a pheno-phenomenon.

13.6 The Duality of the Unity

The deep unity of *autos* should not hide from us the deep duality between *genos* and *phenon*. Let us recall what has already been said. On the side of *genos*, the terms: species, *germen*, *phylum*, genotype, DNA, reiteration, reproduction, invariance, stability, closure; on the side of *phenon*: individual, *soma*, phenotype, protein, existence, death.

The duality does not appear only between nucleic acids and proteins (the one as long polymers with an always identical helical structure, the other as molecules with very varied three-dimensional structures; the one stable, the other unstable; the one able to duplicate itself, the other to combine itself); it is not only in the structural/functional difference between karyoplasm and cytoplasm. It is not, in short, only substantial and organizational. It is also an apparently ontological duality between two dimensions of reality.

The realm of *genos* is a realm of the virtual, of potential, of the past, of the future; it is below and beyond life itself; it is below and above phenomena; it is, in Castoriadis's words, “much more than real without being real” (Castoriadis 1978, pp. 47–48). The realm of the *phenon* is in the present, the actual, the immediacy of existence; in it emerge individuality, subjectivity; however, precarious and condemned to death from birth, it emerges for a moment between two nothingnesses and seems therefore to be only epiphenomenon.

The time of *genos* is at the same time the slow time of indefinite becoming and the time of the return to the infinite. The time of the *phenon* is that of instants which follow one another irreversibly and it is inscribed in finitude... With phenomena, there is enjoyment and suffering, but where there is only gene, there is no delight...

It seems therefore that there are in *genos* and in *phenon* two ontologies, two heterogeneous logics. And yet these two ontologies, these two logics communicate in and through the uninterrupted translation between two languages, the language of the “code” of the four purine and pyrimidine nucleotides of DNA and the language of the twenty amino radicals. It is in this ongoing communication between genosphere and phenosphere that the geno-phenomenal uniduality, that is to say the self-organization itself, is woven.

13.6.1 Symbiotic Uniduality

The first cellular beings came from a very long pre-biotic history associating nucleotides and amino acids in an increasingly stable and functional way (Eigen 1971; Danchin 1978, pp. 301–316): the former, duplicating, becoming capable of regenerating and reproducing the association; the latter, transformable, ensuring its exchanges and nutrition; and the whole, having become one, found itself endowed with a bundle of emerging qualities unknown to each of the associates: life. We can thus see that the idea of symbiosis (complementary interdependence of two partners of different nature) corresponds to a certain extent to the type of complementarity that is instituted between *genos* and *phenon*, the difference with symbiosis itself being that it is not a question of two living "beings" associating, but of two heterogeneous entities whose symbiosis precisely constitutes one living being.

This reservation being made, *autos* can be considered as a quasi-symbiotic complementarity between these two entities, each of which has become indispensable to the being, existence, and organization of the other. As we have seen, the *phenon* is necessary for the generativity of the *genos*, just as the *genos* is necessary for the phenomenality of the *phenon*. The one brings its invariant capital, the other its thermodynamic machinery. The one brings the principle of duplication; the other brings the aptitude to metamorphoses. One brings closure on the generic identity; the other brings opening to the environment. It is what opposes the *genos* to the *phenon* which unites them, the closure of the first on its hereditary capital, the opening of the second on the external universe. The one brings its resistance to random agitation, the other brings its sensitivity to events. The generative is paralytic, the phenomenal, blind. The generative preserves, the phenomenal consumes; the generative conceives, the phenomenal consumes and is consumed. This leads to an extreme fragility of existence and an extreme constancy of regeneration and reproduction. Hence, the *autos* is at the same time open and closed, invariant and variable, at once uniting and dissociating the ephemeral and the durable through the conjunction/disjunction of two temporalities, hence the rebirth of the ancestral past in the individual present, which is at the same time the production by the present of a future reflecting the past.

In this symbiosis, the virtual *genos*, escaping from "reality", enjoys a kind of infra-supra-mortality, neither immortality nor amortality, but transmortality; the *phenon*, on the other hand, is all "reality" but also all mortality and their union is thus a fighting union against and through death.

13.6.2 Internal Competition and Antagonism

Genos and *phenon* are united in an almost symbiotic way and, in unicellular organisms, the two processes—one dedicated to reproduction, the other dedicated to individual autonomy, one "altruistic", the other "egoistic"—seem to be indistinct, and differentiate only when sexual reproduction takes place. They will differentiate themselves more and more clearly when reproduction will be carried out by specialized organs and when individual autonomy will have a neuro-cerebral apparatus. From then on, they become competitors, not only in the sense that they will "run together" without merging, but also in the sense that they can enter into competition.

However, already at the cellular level, it is conceivable that the symbiotic *genos*/*phenon* relationship originally and structurally includes features of mutual subjugation and parasitism.[12] One can even think that in the double enslavement that has become symbiotic, the nucleic entity is in a way “master”; it monopolizes the genetic memory, the organizing knowledge, and its trans-mortal character is based on the mortality of proteins that degrade and renew themselves unceasingly. The protein complex thus seems dedicated to work, obedience, and death. Is this already the model of the domination of knowledge/power over work and execution—the immemorial source of our social hierarchies? Or is it rather our anthroposocial hierarchical model that I am projecting onto cellular organization? We must note here that, at the cellular level, the symbiosis is so strong that the unity of the being transcends the subjugation of the proteinic by the nuclear. And, in any case, the antagonistic potentiality included in the association between the two entities is necessary to the constitution of this unity itself. Thus, from the “opposition” between rigid order, of which DNA is the citadel, and the turbulent agitation of the *Kutos* is born and reborn unceasingly the recursive organization of the cellular being: In the same way, the opposition between the closure of the *genos* and the opening of the *phenon* generates the necessarily open/closed character of living organization.

13.6.3 The Struggle to the Death

The *genos*/*phenon* antagonism can even take, in animal life, the face of a struggle to the death. Whereas unicellular organisms, and even many multicellular organisms, could live indefinitely and only die from the accumulation of “noise” and disorder within their organization, it seems that for insects, fish, birds, and mammals, death is genetically determined, either by a “programming” for aging, or by a “deprogramming” of the processes of resistance to aging. Everything seems to indicate that beyond a certain time (two years for the mouse, fifteen years for the dog), the *genos* abandons the *phenon* to its disintegration and even triggers the process of physical liquidation.

Conversely, mammals show anti-reproductive states or behaviors in conditions of food shortage or demographic excess: famine amenorrhea, the almost automatic interruption of procreation, the devouring of the eggs by the genitors. The devouring of their own litter by female dogs or cats are perhaps “aberrations” resulting from the denaturing conditions of domestication, but these aberrations can also be revealing of the deep virtual conflict between *genos* and *phenon*. Besides, in apparently normal conditions for the observer, lynxes, lions, or male baboons have been seen devouring their newborns.

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[12] Thus, it is conceivable that RNA, a kind of self-replicating proto-virus, could have enslaved an enzymatic ensemble, allowing it to reproduce and making this proto-cytoplasm (cyto—*kutos* = cavity) its ecological niche; it is reciprocally conceivable that this proto-cytoplasm would have been able to use the organizing potential of P RNA for the maintenance in memory of the processes of exchanges and transformations that are necessary for it.

In any case, we see that, in mammals, primates, and finally in humans, there can be an oscillation between the tendency to sacrifice oneself, even to death, for one's offspring, and the tendency to sacrifice one's offspring to oneself, even to death.

13.6.4 Dialogical Unity

It is not enough to recognize the unity or the complementarity of *genos* and *phenon*. It is also necessary to realize that self-organization, like any organized unit or system (Morin 1977, pp. 118–123), comprises in itself antagonism, virtual or active, among its components and between its components and the whole. Here, we must conceive at the same time the extraordinary ontological unity (because constitutive of a living being) and the antagonism, which can become radical, between the logic of *phenon* and the logic of *genos*. We must conceive at the same time that the antagonism between these two logics is not only disintegrating of their unity, but constitutes a necessary ingredient of it.

Let me repeat: The term of *autos* takes its unity, its stability, its distinctive features only if we give it the recursive movement that assembles these different, heterogeneous, symbiotic, competing, parasitic, complementary, and enemy terms into its own loop-unity. The problem is not so much to recognize the inseparable character of *genos* and *phenon*, which is not disputed by anyone. It is to be able to consider without prejudice the biological mystery of their unity and duality which, like the sacred mystery of *homoiesis*, always risks being betrayed by simplification, either when the two are reduced to one, or when the one is split into two. It is therefore necessary not to cease conceiving one in two, two in one: This is why I speak of uniduality and introduced the idea of a dialogic, a logic of one in two, a double logic in one, whose two terms are at the same time irreducible to one another and inseparable one from the other.

13.6.5 The Republic of the Complex: Between the Empire of the Genes and the Empire of the Environment

Geneticism and environmentalism, while fighting each other, have in common the annihilation of the phenomenal autonomy of the individual. The more they fight over causal authority, the less they leave to the living being itself, which, laminated between *genos* and *oikos*, is no more than a thin film that separates them. Incapable of recognizing self-determination and self-causality, their simplifying logic crushes *autos*, either under the determinism and external chance of the empire of the Environment, or under the determinism and superior chance of the empire of the Genes. Living beings thus appear as toys and puppets whose spring and strings always come from elsewhere than themselves. It is certainly true that genetic determinism comes from the past and that ecological determinism comes from the external universe. But this means rather that self-causality is produced, not *ex nihilo*, but by and through external determinism and determinism from the past, both of which, in the very game of self-organization, transform each other into self-determination without the one ceasing to remain anterior and the other external. *Thus the problem is not only to recognize the phenomenal autonomy of living beings. The problem is especially to think this autonomy in the paradox of its dependence relative to the Empire of the Genes and the Empire of the Environment, both of which not only crush self-causality with their own dominating causality, but allow it and co-produce it.*

It is not a question of reducing or underestimating the capital importance of *oikos* and *genos*. I have indicated that eco-causality is not just an anonymous external causality and that it plays a co-programming and co-organizing role in self-causality. I indicated that geno-causality is interior to self-causality while being prior to the individuals who succeed each other in the chain of generations. Moreover, I have begun to indicate that living individuals constitute emergences that retroact on the conditions of their formation, that they are endowed with the quality of being, that some of them, having a neuro-cerebral apparatus, develop their autonomy by becoming capable of acquiring, capitalizing, and exploiting experience as well as elaborating strategies of knowledge and behavior. But I have also already indicated that this autonomy is based on a geno-dependence, since the neuro-cerebral apparatus produced in an innate way functions in and through genetically conditioned cellular interactions, as well as on the basis of an eco-dependence, since learning can only be formed in an environment.

Living autonomy, whether considered from the point of view of the individual or of the *autos* as a whole, requires a double dependence. It is the closure of the *genos* which, by locking out individual experience from the matri/patrimonial inheritance, prevents the invasion of determinism and external chance and ensures the autonomy of the being with regard to the environment. Conversely, it is the opening of the *phenon* to the environment which allows individuals, especially if they have a neuro-cerebral apparatus, to build up their own experience. It is this closed/open neuro-cerebral apparatus which uses external determinism and chance for its strategies. Thus, geno-dependence and eco-dependence feed the production and the development of the autonomy of the individual being, without the latter ceasing to depend on it.

13.7 Generativity and Genesis

There is in *genos*, in living generativity, something both repetitive and genesis-like, which corresponds to the two aspects under which we conceive of genetic capital: memory and program.

13.7.1 Generativity and Genesis

Genesis is what gives birth to organization from non-organization; it transforms agitation into motricity, the dispersive into the concentric, contrary movements into loops, and turbulence into being (Morin 1977, p. 225 ff.). Living generativity, for its part, constantly overcomes disorganizing processes, uses them and transforms them into reorganizing processes and, in this sense, it can be considered as an indefinitely renewed, organized, and regulated genesis. But it is obviously in reproduction that the genesis-like character of living generativity is vividly manifested. Asexual cellular self-reproduction creates two beings from one. Sexual reproduction creates a being that is not only new, but new in relation to its ancestors. Although it unites two genetic heritages, the recombination of this dual heritage is original. Thus, the developments of *genos*, via the developments of sexuality, are at the same time the development of the powers of genesis.

13.7.2 The Resurrection of the Past

While involving production, generation, and genesis, *genos* is at the same time repetition of the same, a restarting of the old, a resurrection of the bygone. The new and original being of which I have just spoken is certainly singular in its genetic combination, but there is no element of this combination which (except for accidental mutations) does not come from its ancestors. All reproduction, asexual or sexual, cellular or organismic, is the result of a memory; it takes on the character of remembrance, that is to say of reproduction/resurrection of the past, and reproduces this memory.

The ontogeny of a multicellular being even constitutes a kind of remembrance, from the cellular state, of the history of the phylum. Of course, ontogeny does not "reproduce" phylogeny, but one cannot say that its process has no analogy with that of phylogeny. Everything happens as if the still extremely obscure process of ontogeny (where the ideas of "program" and "chreodes"[13] are still only indicative arrows) included a dimension of recollection which, like any recollection, includes failures, errors, shortcuts, and abbreviations. We can use this term of recollection since we can consider genetic inscription as a kind of memory. But it is a completely different recollection from that of our cerebral recollections, which are imaginary representations. Genetic recollections are not images, but practical actions, which are carried out in the image of past actions. Thus, ontogenetic "recollection" produces, not the unreal image-memory of a dead past, but a real living being where this past is resurrected.

Everything happens, therefore, as if ontogenesis produces, in the case of parthenogenesis, the resurrection of the progenitor in another being, and in the case of sexual reproduction, the resurrection by snippets and fragments, associated with chance, of traits proper to each ascending lineage whose assembly determines a new and original being.

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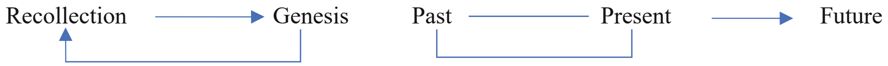
[13] Waddington so names the moving morphogenetic paths that embryonic development seems to follow (Waddington 1977, pp. 106–112).



Any living act, in its genetic character, produces a present referring to the past and propelled toward the future. Every living act involves both recollection and genesis, including genetic mutation, which does not abolish all memory, but modifies it. Each birth is the re-presentation—the presentification—of a past, its reinscription in becoming, and in a way produces the regeneration of time in and through the genesis of a being.

13.8 Biological Oscillation, a Principle of Uncertainty

Instead of retreating from the challenge, we must ceaselessly confront the problem of the individual, which is at the same time focal point and field, particle and system, nothing and everything. We must conceive of the individual which, totally dependent on *genos* and *oikos*, is at the same time the most autonomous, the most individualized of beings.

As Simondon put it, "the individual cannot give an account of itself from itself" (Simondon 1964, p. 71). But one neither reduce the individual to the non-individual, because, as Simondon also says, "the individual is at the same time result and medium of individuation" (Simondon 1964, p. 272). Here, we have a dazzling paradox of complexity, where the individual demands simultaneously to be conceived intrinsically (as an individual) and extrinsically (in relation to the non-individual).

The insufficiencies and weaknesses of our understanding, i.e., our tendency either to confuse or to simplify, lead us to make of the individual either everything or nothing. But the key notion of the individual must remain something rather flickering.

13.8.1 Biological Individuality and the Living Individual

Everything that tends to neglect the discrete in favor of the continuous, the random in favor of the determined, emergence in favor of initial conditions, autonomy in favor of dependencies, self-organization in favor of external determinism, being and existence in favor of pattern and schema, tends to neglect the individual.

Every approach that tries to escape from uncertainty and ambiguity (that is to say, from complexity) tends to bypass and forget the problem of the individual. From that point on, the individual always tends to be reduced to the external general or to the superior generic.

Until the middle of the twentieth century, individuality was anesthetized where it was most immediately evident: in behavior and the animal organism. The individual seemed to have to be reduced—or dissolved—into its components and determinants.

However, while ethology rediscovered the individual in the observation of higher animals within their natural environment, molecular biology discovered individuality at levels of unsuspected radicality: the cell, the molecule; it made it appear where it was not sought: in the gene; and it finally resurrected the individual where it was no longer seen: in the organism.

We know today that in any living population, including unicellular organisms, no two individuals are exactly alike, even when they have an identical genotype. Each individual therefore has, as a constitutive trait of individuality, at least one tiny but irrefragable difference that makes it original among its fellow creatures. Individual difference increases with the evolution of multicellular beings. The environment (which plays an ever greater role in individual development), sexuality (which renews and varies the gene combinations) are both machines for making difference and singularity. Singularity increases and differences unfold in the higher animals. Each being is singular in its genetic capital and can be unique forever within its species.[14] Each being is singular in its morphology, in its anatomy, physiology, temperament, behavior, and intelligence. With *Homo sapiens*, differences of all kinds, from individual to individual, are extremely strong, even in extremely closed isolates, much stronger than the statistically established differences between ethnic groups or races (Neel 1970).

Individual singularity does not only concern the morphology, anatomy, and physiology of the organism, but its molecular constitution as well. Each protein has its singularity in relation to other proteins in the same cell, in relation to the same protein in other species, and finally in relation to the same protein in individuals of the same species.

We thus see this character of individualization and individuality, which is singularity, emerging and imposing itself at all levels of organization and constitution of the living being, whether molecular, genetic, organismic, or behavioral. We even see that this singularity produces, not only biological individuality, but chemical (molecular) individuality.

This singularity is inseparable from a constellation of features of individuality. To say singularity is at the same time to say originality, even unicity. It is also to say difference—the difference of one individual from another, the difference/gap compared to an average or ideal type. As I have just said, these remarkable features of individuality—singularity, difference, originality, uniqueness—concern all levels of self-(geno-pheno)—organization. However, given the theoretical inconsistency of the notion of the individual, simplifying principles tend to pump them out of the individual as a whole and to attribute them either to the *genos*, to the environment, or to randomness.

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[14] "By considering only a very small segment of our genome (1/300), we can already affirm that each man is unique on earth. (...) If we consider the sixty other genetic systems that also have variants, we see that there have probably never been two similar men" (Dausset 1978, p. 7).

Certainly, we have here not only recognized, but affirmed genetic, random, and environmental determination in the very constitution of the individual. But is it necessary for all that to withdraw individuality from the individual?

13.8.2 Individuality and Individual

The general drives out the individual. The generic, by monopolizing individuality, hides the individual. The problem here is not to remove the singularity/originality from the *genos* to restore it to the *phenon*. The original/singular determination of the gene must be fully recognized in the originality/singularity of the individual. The old conception of the species made it a general term whose principles and rules apply to all the individuals belonging to it. The new conception, resulting from the progress of genetics and molecular biology, links the general and the singular by emphasizing generic singularity. The generic is singular because it is the perpetrator and perpetuator of singularity. Genes constitute a capital and a source of singularities, and this is why the *genos* carries within it a principle of individuation.

However, it is necessary to recall again that this genetic individuation is not only the producer, but also the product of the individual, who is therefore not only the product, but also the co-producer of the individuation. That is to say that we cannot return individuality exclusively to the camp of *genos*. It is necessary to conceive in recursive terms the articulation between the two different levels (*genos* and *phenon*) of singularity/originality: The individual accomplishes and actualizes the singularity of a genetic heritage, which in turn preserves, transmits, and multiplies the singularity of individuals. The individual is not the singular specimen of a general type; it is the concrete accomplishment of a process of individuation. The individual is specific in the same movement that the species is individualizing. It is not only the individual that has the characters of the species, it is the species that has the characters of the individual.

On the other hand, and especially, one should not confuse singularity and individuality. Singularity, originality, and difference constitute only one dimension of living individuality and this dimension, though certainly necessary, is completely insufficient to give an account of the living individual. The individual is not only the singularity of a singularity. It is also a living being existing in the phenomenal world. The individual is not defined only, even mainly, by differences and originality. It is also defined by qualities of being and existence, themselves inseparable from qualities of organizing autonomy. In other words, one cannot reduce the individual to singular individuality.

Thus, the individual possesses within itself a capital of singularities and a principle of individuation which precede and exceed it, but its quality of individual rests also on its autonomy of being and existence.

13.8.3 Individual Autonomy

The biological notion of the individual is thus inseparable from the self-organizing and existential autonomy of the living machine-being. This autonomy is quite original in the physical universe, and (although and because it is much more eco-dependent) it is much more autonomous than that of other physical machine-beings, both natural and artificial. Now, when physiology focused on the animal body to recognize its organization, it effected an initial dissociation between the idea of organism and the idea of individual. Claude Bernard admirably expressed, in the same sentence, both the unity and the dissociation between the two terms: “The living being forms an organism and an individuality”. It would be enough to push the unifying virtue of this “and” to conceive the living being as an organismic individuality, an individual organism. In fact, this “and” constituted a frontier for a whole century. In these conditions, the isolated idea of organism remained marked by a profound insufficiency: the organism as corporality deprived of individuality, even if it has, according to Cannon’s expression, a “wisdom of body”. The individual dissolves all the more when one considers the organism as a sample of a generic type, obeying a program that precedes and transcends it. The organism becomes from then on the concretized species. The individual disappears in favor of an anonymous machinery and an abstract dependence. However, the fundamental progress of physiology allowed us not only to know the organization of the organism, but also, from Claude Bernard to Cannon, to recognize the autonomy of this organization.

On the other hand, the individual autonomy of behavior was for a long time repressed by behaviorism, even for higher animals.[15] But this autonomy came back in force under the joint effect of the development of genetics and ethology. The self-causality of animal behavior was finally emphasized when ethology broke with behavioral experiments in artificial environments (zoo, laboratory) to observe natural behavior. At first, it was only the *genos* (the “instinct”, the “genetic program”) that was credited, and the genericity paradigm took over from the external causality paradigm to make the individual the puppet of a genetic program. Then, in the sixties, a more complex ethological vision finally put the accent on the individual qualities of intelligence, sensitivity, and affectivity.

While the individual comes back from above (superior animals endowed with an evolved neuro-cerebral apparatus), it emerges at the lowest level of living existence. But this level is at the same time the fundamental level. Indeed, we discover in the unicellular organism not only traits of singularity which differentiate it from its fellow creatures, but also an individual being computing and deciding by itself and for itself.

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[15] Behaviorism emphasized external determinism and not internal elaboration: In the stimulus/response pair, the response is seen more as the product of the stimulus than as the fruit of individual computation. Of course, the existence of an inner causality is not denied and is sometimes even highlighted in the processes of behavioral reinforcement, but it remains secondary to exocausality, which has led contemporary ethologists to denounce behaviorism as the doctrine of the empty organism (cf. in particular Lorenz 1977).

13.8.4 The Individual Being

Self? This word both points to and brings about the reunification between the idea of autonomous living organization and the idea of individual being.

Who says "Self"? It is immunology which finally brings to light (Grabar 1947) and develops (Jerne 1969) this notion of Self, a notion which, though absent from biological theory until then, is fundamental for any conception of the living individual. The Self is not only an idiosyncrasy (a particular disposition which makes each individual react in a personal way to the action of external agents) in the response to microbial aggressions; it is not only an individual originality in the production of individualized antigens; it is not only the singular unity of individual molecules in an individual being. The immunological idea of the Self manifests itself as a self-affirmation of identity, not only molecular, but global, of a character not only defensive, but possibly offensive and fundamentally organizing, of a being that recognizes itself as itself, and organizes itself from itself and acts for itself (Dausset 1978, p. 7).

From this point on, the idea of autonomy (of organization, of computation, of decision, of action, of behavior) must no longer be juxtaposed to the idea of the individual. These two ideas henceforth call each other forth, combine, and identify with one another. By revealing the Self, immunology reunites the organism and the individual. In this way, the individual being rightfully forces its way into the biological sciences. But it is still only in the immunological compartment, and communications are rarefied from compartment to compartment.

13.8.5 The Non-Elementary Individual

We have seen the emergence of non-elementary—that is to say complex—aspects of living individuality at all the levels of self-(geno-pheno)-organization. They are inscribed in the heart of *genos*, which is conservative of singularities and generator of individuation. But they also concern the individuality of the individual.

The individuality of the individual is not merely a matter of discontinuity, spontaneity, randomness, and actuality; it is not only singularity, originality, and difference with regard to other individuals, including members of the same or similar species; it is not only the individuality of the organism and its behavior. The individuality of the individual is also in the being and existence of oneself. This "oneself" cannot be identified with *autos*, although the latter includes it. What is this "oneself"?

13.9 Reason and Unreason in Life

13.9.1 The First Level of Rationality

At the first level, life appears to us as a marvel of rationality: As compared with all our industrial and administrative enterprises, the living being presents itself as an automated combination superior in economy, efficiency, functionality, and reliability. The environment is the permanent spur of this rationality in the form of “natural selection”: The latter eliminates not only the “bad” genes, but also the second-choice genes, and privileges high profitability along with the extra-quality genes: savings in the time budget, excess birth-rate compared to mortality, minimization of effort and risk...

13.9.2 The Second Level of Irrationality

However, at second glance, we realize that the living economy contains and produces not only competitions, antagonisms, egoisms, and disorders which seem very irrational, but also wasteful, useless, luxurious, parasitic, and harmful... Does mating really need colors and ornaments, cock’s crests, peacock’s feathers, or incredible and endless courtship rituals? Is it necessary for sexual reproduction to indulge in a senseless waste of germinal cells, seed, and sperm, and for each ejaculation to disperse one hundred and eighty million spermatozoa? Couldn’t all these insects, agitated by Brownian motion, proceed in straight lines, or at least take a few precautionary zigzags? Isn’t the marvelous process of chlorophyll assimilation, which is so far ahead of our technologies, nevertheless underproductive, fixing as it does only one percent of solar radiation as chemical energy?

13.9.3 The Third Level: Complex Rationality

However, it would be just as superficial to substitute the vision of a generalized functionality with that of a generalized waste.

We have seen that the integration of antagonisms, competitions, disorders, freedoms, and egoisms produced an organization richer and superior to that of the most rationalized artificial automatons. One can guess or verify that the waste caused by egoistic competition can be paradoxically less than that of a programmed/planned/unified organization, but where the latter stifles individual initiative and reacts very slowly to randomness. This means that it is more rational to tolerate/use disorders/waste as by-products or components of complexity than to want to eliminate them totally, which amounts to hyperwaste.

The bio-economy does not necessarily need high profitability. The low energy yield of chlorophyll assimilation is in fact a more rational “laziness” than a maximalist activism would have been: Where there is full abundance of resources and absence of competition, there is no need to improve systems largely sufficient to the needs.

Moreover, it appears that many characteristics which, from the point of view of a narrow rationality, are useless, luxurious, and expensive can, in a broader vision, prove to be necessary and vital. Thus, unused devices, or even activities that are parasitic in normal circumstances in bacteria, can prove to be salutary in dangerous situations or become a source of progress (Ninio 1979). Diversity, as we have seen, has a greater selective value, because of the qualities it brings to a population, than a selection that would homogenize this population according to what is most efficient (cf. p. 40 f.). Let us remember that diversity, which abhors all homogenizing rationalizations, is a source of evolution, development, and complexity.

More amply still, when one is situated at a complex level of vision, many apparently irrational features are transformed into constituents of the only rationally conceivable behaviors within a world that includes irrationality.

It is by dealing with randomness, not by ignoring it, that strategy becomes rational. It is by living with disorder that living organization surpasses in rationality an organization without disorder, but that is incapable of living.

It is therefore quite "reasonable" to squander as much seed as possible, to minimize regulation... An apparent irrationality becomes the open rationality of a system that must constantly confront the forces of destruction and death.

Finally, it is necessary to notice that life is not economy, on the one hand, and waste on the other, but is played out at the same time on the double ground of economy and waste. Thus, any living organization knows at the same time how to save (accumulation of energy reserves) and to spend (useless movements and actions). In the same way, the mad squandering of seed is at the same time an economic operation. It accumulates informational redundancy by multiplying generative memory. This multiplication is not a hoarding of the most precious capital, the genetic capital, in a closed box, but an all-out investment via dissemination.

13.9.4 The Fourth Level: The Reverse Side of Rationality: Infra? Meta? Rationality

At the same time, complex rationality has a flip side. It cannot totally absorb all of the expense, waste, competition, conflict, antagonism, and disorder, although the expense/waste is complementary to the economy, and the competition, antagonism, and disorders are co-organizers. The complex economy of life integrates what disintegrates it, without what disintegrates it ceasing to be disintegrating.

More deeply, life contains within itself the irrationality of the random situations that it finds itself in and of the universe of which it is part. The hecatombs paid by the survivors are not totally rationalizable. The fabulous expenditure of life is not totally functional. It was discovered that "natural selection" retained not only useful traits, but also useless traits, even handicaps, but which were drowned among other traits.

What's more: There is something irrationalizable in the idea of being, of existence, and of living:

- being and existence are irrationalizable, not in their determinations, processes, structures, and organizations, but intrinsically, as being and existence: There is no reason why there should be something rather than nothing;
- individual egocentrism has something absurd, necessary though it is to the "will to live";
- the absence of any external and superior purpose to living concentrates irrationality in the heart of life itself: Why live? Why struggle? To be defeated? Why

> develop for death? So much effort, so much expenditure of energy, of work, of strategies, of intelligence for a few moments of life, a few flea jumps for the fleas, a few wing beats for the swallows...

Life is a strange and unstable mixture of rationality, a-rationality, irrationality, and the unrationalizable, where each of these terms inter-communicate and inter-contaminate. Life defies the old rationalism that enclosed it in a merely functional and economic vision or that rejected it as unworthy irrationality. But we must understand that the elimination of the irrational is ultimately non-rational: To remove the unreason of living is to remove the reasons for living.

13.9.5 Inoptimization

All this brings us back to a capital idea: the impossibility of defining in an obvious and clear way, as well as of governing in a "rational" way, what could be considered a "real life", a good life, the best of lives. Optimization is a technological concept coming from the artifact and adapted to the artificial machine: It allows one to determine a rational program according to clear and precise ends and an economy functionality of the means. But as we have seen, it is impossible to optimize complexity, and especially living complexity:

1. As complexity intrinsically involves chance and uncertainties, it is necessary to link program and strategy: However, everything that involves chance and innovation cannot be pre-optimized; the strategy can only randomly self-optimize in the course of its development.
2. As the ends are uncertain, diverse, competing, and antagonistic, optimization loses its foundations: How can these ends be satisfied together? Why favor one over another? And when the ends change, wither away, are born, optimization becomes pessimization, favoring obsolete ends and thwarting new ends that want to be born.

An optimum can only be based on a clear and unequivocal distinction between the good (*optime*) and the bad (*pessime*). Now, if the "evil" of life is disorder, disintegration, and death, this "evil" is also an ingredient of life, and therefore also a "good", and it is impossible absolutely, totally, and always to oppose evil and good, which maintain complex relations. Thus, Boltzmann's demon works diabolically for disunity (*diabolo*: that which disunites), but it works at the same time, without wanting to, for Maxwell's demon, which restores order from disorder, which in return works for Boltzmann's demon, since it spends energy... In the same way Mephisto accomplishes, without wanting to, or rather by wanting the opposite, the designs of the Lord, who on his side works as much for Mephisto as this one works for him. Thus, just as it is very poor theory absolutely to oppose order and disorder, it is very poor rationality absolutely to oppose the benign to the malignant. Finally, one cannot optimize according to the present alone (to enjoy, to consume) or the future alone (to survive, to give life). The present/future relation is uncertain, and their compromise is inoptimizable. It is thus impossible in the unequivocal and simple sense of the term that concerns the complexity of the living.

13.9.6 Toward an Open Rationality

Here, I merely want to raise the problem of rationality. Let us note some questions that emerge at this point:

1. Neither the physical universe nor life can be totally translated into a coherent system of ideas. This impossibility of enclosing reality in the ideal must be conceived as irrationalizability.
2. Can we know if this irrationalizability involves irrationality, infra-rationality, meta-rationality, or supra-rationality?
3. Rationalization is what obscures and covers the problem of irrationalizability; it identifies the real and the rational, that is, the real and the ideal: It is the height of idealism. The real escapes rationalization on all sides.
4. Life, like *physis*, but in its own way, unites in it the rationalizable and the irrationalizable.
5. A low rationality rejects the irrationalizable. High rationality must recognize it: It must work with/against the a-rational, the irrational, and perhaps contribute to the supra-rational. The new rationality must be open, that is, open to the non-rational.
6. The new rationality must dissociate itself from and oppose rationalization which, although it comes from the same source, is its real enemy: Rationalization is closed ideation, closed coherence, closed logic; it wants to find a "reason for being" for all existence, all reality. It is more insane than irrationalism, since the latter knows that it is irrational and that the madness of rationalization is to believe that it is rationality.

13.9.7 Open Life

Complexity is not only the fundamental character of the organizational logic of life. It is the only one that allows us to conceive of the living. Life cannot be reduced to utility,[16] economy, homeostasis, or adaptation, although it includes all these dimensions. Living bursts through, not rationality, but any closed conception of rationality.

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[16] Von Bertalanffy said: "We must conceive that a large part of biological conduct (...) is beyond the principle of utility, of homeostasis, of stimulus-response" (Bertalanffy in Buckley 1968, p. 26).

13.10 Living Creativity

The creativity of the physical universe is systemic: Its systems, resulting from the organizing association of diverse constituents, create emergences and new qualities unknown to the isolated elements. Life is born from such systemic creativity, from the organizing association of innumerable and diverse molecular constituents and its own qualities, including self-organization itself, are born from systemic creativity. But once born, living self-organization has a new creativity, one able to create organs and to transform organisms: living creativity.

13.10.1 Life Is a Creator of Creativity

There is a dialogic specific to living self-organization: One logic ensures the invariance of the species as well as of the individual; the other allows creative genetic reorganizations at the heart of the reproductive system, from which have emerged the innumerable innovations of evolution: eukaryotic cells, multicellular organisms, chlorophyll assimilation in plants that allows them to capture solar energy, the floral explosion and, in animals, fins, legs, wings, brain, nervous system, liver, kidneys, etc.

Apparently, starting from reproduction, which perpetuates the identical and opposes any modification, the law of life should exclude any creative invention. However, let us note that if, in relation to identical reproduction, which is a normal phenomenon, innovative creation is a deviant, marginal, and rare phenomenon, it has become the decisive motor of a bushy and luxuriant biological evolution, that is to say of the very history of life.

Creativity manifests itself in the course of reproduction, that is to say in the re-creation of a new living being; it can be stimulated by chance, by the integration of a virus in the DNA that brings innovative information; it can above all be stimulated by challenges from the environment. As soon as a new quality or a new organ is created, these will spread by reproduction which, “normally” prohibiting the new, puts itself at the service of the new, multiplying it, hence the myriad of plant and animal species.

There are in nature, not only with animals but also with plants, prodigious forms of knowledge linked to a form of creativity, such as the invention of flowers which “know” how to attract foraging insects, but this is also true for insects, as for birds and many other species. The remarkable cases of plant cognition/creativity without a brain or nervous system reveal to us that the cognition/creation link (where cognition enables a creation that brings a new cognition) is inherent to living self-eco-organization, although it is only activated in extreme situations, almost always, it seems, in response to a deadly challenge or a deep aspiration.

Creativity is carried out by associations and combinations. The intimate union of two unicellular organisms, or rather the absorption of one by the other, will create the eukaryotic cell with a double heredity, the second one in the mitochondrion, a vestige of the absorbed cell. Single cells will unite durably in multicellular organisms, which will then diversify their cells. Chance, or the constraints of an environment, must have played a role in the formation of multicellular organisms, a collective grouping better armed against chance. Creativity is manifest in the invention of an organ or an innovative reorganization with its own emergence. The fabulous bushy developments of the plant and animal kingdoms show us what Bergson called "creative evolution" and that we could also name "evolutionary creativity".

Since the first cells, life has generated a proliferation of millions of species, of which perhaps 8.7 million living species remain, including 2.2 million in the aquatic environment. It has invented the most incredible shapes, of turtles, snails, octopuses, scorpions; the most shimmering colors, the most extreme sizes, from bacteria through aphids to elephants, from blades of grass to giant sequoias; the most ingenious devices, such as the spider's web; the most imaginative weapons, such as the venom of the snake or hornet or the horn of the rhino. Through births, including those of cells within a living organism, life is a permanent renewal), a restart of the same (the return is the movement of life: the *Dao*), a reproduction of the identical, which, at certain decisive moments of external or/and interior origin, is modified or transformed. The dialogical union of a principle of invariance and a principle of transformation is an essential character of life.

13.10.2 The Challenge

Living creativity has often been a response to a mortal challenge. And it has manifested itself by an ability to solve a vital problem. The first great invention of living beings was made without a brain or nervous system. It is the invention of photosynthesis by chlorophyll, already present in certain unicellular organisms (diatoms, microalgae), which was generalized to the immense plant kingdom. This marvelous invention allows the plant to draw its energy from sunlight. Moreover, the roots were created to absorb mineral juices.

Creativity has manifested itself in the art of metamorphosis: from seed to plant, from egg to adult animal, from mammalian embryo in its placenta to adult, and finally, from crawling caterpillar to butterfly and dragonfly. This creativity has reached a complexity and ingenuity that human genius has not (yet?) reached: The latter, which has invented so much, has not yet succeeded in making a bacterium, nor the slightest plant, nor the slightest animal. As the animal kingdom has not been able to capture solar energy, it has had to invent the means of locomotion to seek its food and escape its predators: fins, legs, wings. It had to invent a jaw or a beak to catch food, to lengthen the beak of the stork or the toucan, to lengthen the neck of the giraffe or the trunk of the elephant; it invented an extraordinary digestive system to assimilate food and to reject the waste. It invented sense organs, sight, hearing, olfaction, nervous system, brain. It invented shapes, colors, and smells to make itself beautiful, to frighten its enemies, to attract members of the opposite sex.

The diffusion of oxygen from plants into the atmosphere was a poison transformed in the animal world into a cellular detoxifier through respiration and blood circulation. The lowering of sea levels gave rise to amphibia in fish that transformed their gills into lungs. Cataclysms and catastrophes have stimulated living creativity. Thus, the Permian–Triassic extinction event, which destroyed 90% of the species, gave rise to the creation of new species. Creativity is not only a response to a challenge or a problem. It can also be the satisfaction of an aspiration. Could it be that what has so often given rise to wings in earthbound beings comes from an aspiration to experience the lightness and exhilaration of flight? Certainly, one can think that flight allows the predator to better find its terrestrial prey and the prey to better flee its terrestrial predator, but it seems to me that unlike legs and fins, wings do not respond to a primary locomotor necessity for living or surviving. It seems rather that the desire to fly has produced the wings of innumerable insects, has given wings to a branch of reptiles that have become birds, and has even given wings to mammals in the form of bats. We might forever contemplate the astonishing metamorphosis that transforms a crawling caterpillar into an aerial dragonfly or a shimmering butterfly.

Would not an obscure, unconscious, but deep desire coming from the whole being be at the source of so many creations?

The luxury of so many ornaments and colors, from the small beetle to the peacock, cannot be reduced to the sexual seduction of congeners, and in any case, such seduction comprises an aesthetic component. Adolf Portmann proposes the concept of *Selbstdarstellung*,[17] "self-presentation", the inherent tendency of the living to present itself, not only as congener or enemy, but for itself, which corresponds to the desire for beautification among humans.

In fact, we humans extend animal aesthetics with our tattoos and colorful ornaments by endowing ourselves, through our clothes, with a variety of removable skins.

It is not very plausible to reduce so many creative inventions to simple genetic mutations due to chance, although chance can intervene.

Researchers in molecular biology, geneticists, and Darwinians attribute all the inventions of life to mutations due solely to chance and limit themselves to seeing only adaptation in what was more than adaptation: invention. Invention can create adaptation to an environment; it can also create adaptation of an environment to itself (as in the formation of birds' nests or in the architecture of beavers, building lodges and dams). Many scientists are afraid that living creativity refers only to creationism, i.e., to the design of a creator God, whereas creativity is, as Spinoza thought, at the

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[17] 1. Adolf Portmann, La Forme animale (1948), reed. La Bibliothèque, 2013.

Self-presentation (*Selbstdarstellung*) expresses the idea that living being feel the need to present itself, to present itself to its fellow creatures and to the world that welcomes it and with which it interacts. The animal form expresses a vital need to exhibit itself, to show itself: "Self-presentation is thus a kind of requirement which falls to any life: to appear, to show only what one is. The pure and simple being (simple positive existence) is not enough: it is necessary moreover 'to appear', that is to say to give form, in the field of the visible (but it can be also about acoustic or olfactory manifestations), to the singularity of what one is—not, in this case, of its individual existence, but of its singularity as a species, of its specific particularity."

very heart of living nature. There is, I believe, a dormant creative potentiality within living beings that awakens to a challenge, a desire, an aspiration. Inventive creativity operates in the embryonic phase of development, where the work of the species becomes the formation of the individual.[18]

I cannot end this passage on creativity by forgetting my own body, that is to say the body of all *Homo sapiens/demens*. This organism is the fruit of a creative evolution from the vertebrates, then the mammals, and finally from the primates to our species. It is an incredible machine which, as I have said, possesses me more than I possess it. And what ingenuity, what complexity, to consider only digestion where, without wanting to, I secrete saliva around the food that my teeth grind, then through the digestive tract, soaked in gastric juices, where it goes on a prodigious journey that ends up in the large intestine. Such complexity in the production of hormones by the brain! What a hypercomplex machine this brain is and, while it produces feelings and thoughts, we only know its electrochemical manifestations! The most sophisticated machines that we can manufacture are still crude and rudimentary next to this machine that has manufactured us and that remakes us moment by moment.

13.10.3 Generalized Life

Molecular biology eliminates the notion of life, whereas, in my opinion, it should be generalized beyond strictly biological beings (single cells, plants, animals). Planet Earth is a geo-bio-physical entity with a life of its own. It is perhaps endowed with intelligence... Might the true "flying saucers" not be travelers from outer space, but emanations of Earth? Ecosystems are living self-organizations arising from the conjugation between the living beings of a given environment and the geoclimatic determinants of this environment. Human societies are living beings endowed with self-eco-organization (Morin 1985, p. 236 ff.). They are at the same time physical machines, living machines, and social machines. Language exists as the first necessity of communication in any human society; at the same time, it has certain characteristics of life: evolution, metamorphoses; words die, are born, and drift; turns of phrase change. Language tends to spread out into two branches, the prosaic branch with a utilitarian function and the poetic, creative branch, which provides aesthetic emotion. Slang is a poetic sub-branch very alive in its inventiveness. The prosaic branch tends to lose all vitality, becoming empty and formulaic, especially in the case of administrative, technocratic, and economic discourse.

The way in which languages have been formed, organized, and have evolved is proof of a formidable creative power, a power nourished by innumerable speaking minds. Finally, the human minds of a given society produce and nourish entities—gods and ideas—endowed with a life that exercises power over the minds that created them. Gods are anthropomorphic or biomorphic, their power such that they

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[18] Since there is obviously creativity in life, we cannot exclude other creativities elsewhere, but at this point no one can be certain.

demand from humans adoration, obedience, and sacrifice, including the sacrifice of their lives and the murder of the impious or unfaithful. Ideas can also be sovereign and despotic: Thus, communism was an imperious religion of earthly salvation (Morin 1991). It is our minds and activities that produce and nourish all these lives that feed us and that sometimes, like gods and ideas, enslave us.

13.11 Conclusion

The most fertile fields for discoveries concerning the nature of living organization, molecular biology and genetics, have obscured the very idea of life, which has become invisible to those who only see molecules, genes, programs, random mutations, and natural selection, all of which allow creativity to be concealed for fear of the creationist illusion.

Life has been trivialized and made banal.

However, since the 1960s, ethology has allowed us to recognize the complexity of the behaviors and interrelationships between mammals, birds, and fish, not to mention the work on bees, ants, and termites. A new botany has revealed that the complexity of plant evolution is no less than that of the animal world, and on this occasion, I salute the memory of Jean-Marie Pelt.[19] This new botany has begun to discover the intelligence and sensitivity of plants that I mentioned previously.

We must detrivialize life and be astonished by it. Life surprises by its complexity, its autonomy, and its creativity that appeared so suddenly and marginally in the physical universe. In this universe without apparent aim or goal, obeying only the dialogic of order/disorder/organization, life has introduced its dual purpose in a loop: to reproduce itself to make living individuals, to make living individuals to reproduce itself.

If we cannot conceive of a great goal proper to such a diverse and bushy evolution, we must notice myriads of goals that are simultaneously divergent and convergent (in ecosystems and the biosphere), both complementary and antagonistic. Once again, we find the Heraclitean insight into the union of concord and discord.

We are coming to know more about life, but it remains more and more mysterious.

Life is emergence, that is to say, a set of qualities.

Life is made of nucleoprotein molecules but its emergence due to their organization cannot be reduced to its constituent elements.

As a sociologist and philosopher of science, I can only note how much creativity is a mystery for the sciences. It might be stimulated or triggered by as yet unknown interactions between our level of physical reality and the level of the quantum, and these interactions are likely to give rise to creativity in biological evolution as well as in the human creativity of the mind/brain. Above all, I believe that the creative force

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[19] Jean-Marie Pelt (1933–2015) is the founder of the European Institute of Ecology.

eludes all naming and remains, in the final analysis, an “unspeakable mystery” (Klee) encouraging scientists to never forget the models and equations that allow us to build machines and robots are not life.

Acknowledgments My special thanks go to Anne Dambricourt Malassé without whom the article would never have seen the light of day, and to Sean Kelly who translated it with his benevolent friendship.

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