Unified Recursive Organization Theory: Toward a General Framework for Biological Holography

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Abstract

Organizational systems in nature span multiple scales, from crystals and living organisms to ecosystems. Despite differing in material composition, physical mechanisms, and functional properties, they commonly exhibit shared organizational features such as boundary formation, hierarchical organization, structural recurrence across scales, and whole–part organizational consistency. Existing theories largely explain these phenomena through discipline-specific physical or biological mechanisms, and a unified organizational theory capable of describing organizational formation, organizational continuity, and biological holography across different natural systems is still lacking.

To this end, this paper proposes the Unified Recursive Organization Theory, establishing a Domain–Boundary framework and further introducing two basic organizational mechanisms — structural recurrence and structural recursion — to provide a unified description of how organizational structures form, expand, and evolve. Building on this foundation, the paper establishes the recursive organizational unit (*SS*) and its intrinsic informational attribute $\Psi(SS)$, and proposes recursive holographic unfolding to describe the coordinated unfolding of organizational structure, organizational function, and organizational information throughout continuous recursive organization.

To test the generality of the theory, it is applied to non-living systems, the origin of life, and multicellular development, drawing on continuous cell lineages, germline continuity, asymmetric renewal, transgenerational germline pre-setting, vegetative propagation in plants, and somatic cell nuclear transfer to analyze how unified organizational information is continuously transmitted across hierarchical levels and generations. This paper further shows that this mechanism represents only one evolutionary pathway among several by which complex animals achieve biological holography; by examining how organisms across different levels of biological complexity — unicellular life, structurally simple multicellular animals, and plants — achieve whole–part consistency, the paper reveals that biological holography is in fact realized along a complexity-driven continuum, with structural recursion and asymmetric renewal as shared underlying principles throughout. A reductio ad absurdum argument further shows that living systems do not depend on mature individuals performing a reverse organizational compression of organizational information to produce the next generation; rather, continuity is achieved through the continuous recursive pre-setting of an initial-state organizational information source.

This paper argues that biological holography is an organizational outcome that naturally emerges from unified organizational information as it unfolds through continuous recursive organization, requiring no independent assumption. The Unified Recursive Organization Theory therefore provides a unified theoretical framework for understanding cross-scale organizational formation, organizational continuity, and biological holography.

Keywords Biological holography · Recursive organization · Domain–boundary framework · Organizational information · Germline continuity · Structural recursion

1 Introduction

Organizational systems in nature span dozens of orders of magnitude, from atoms, molecules, and crystals to living organisms and ecosystems. Despite marked differences in material composition, physical mechanisms, and functional properties, these systems commonly exhibit similar organizational structures — boundary formation, regional partitioning, hierarchical enclosure — and further give rise to shared organizational phenomena such as functional differentiation and structural recurrence across scales. Traditional natural sciences typically explain these phenomena through their own disciplinary principles: physics emphasizes interaction and energy, chemistry emphasizes bonding and self-assembly, biology emphasizes heredity, development, and evolution, and engineering emphasizes functional design and system integration. However, these explanations are largely confined within their respective disciplines, and a unified theoretical account of why disparate natural systems repeatedly display similar organizational regularities — and whether these regularities share a common organizational basis — remains lacking (Schaffer and Ideker 2021).

Living systems are the most representative and most thoroughly studied natural systems exhibiting cross-scale organization. Every multicellular organism originates from a single fertilized egg and, through continuous cell division, tissue formation, and organogenesis, gradually builds a highly complex yet coordinated and unified individual (Gilbert 2000). Although different tissues and cells differ markedly in morphology, function, and gene expression, nearly all somatic cells can be traced, through a continuous cell lineage, back to the same original germ cell (Stent 1985). Development is therefore not the successive accumulation of independent structures, but a continuous organizational process grounded in a unified cell lineage. Throughout this process, new organizational levels and functions continually emerge while organizational continuity is preserved, allowing living systems to maintain a stable whole–part organizational consistency even as they undergo ongoing differentiation and increasing complexity. This whole–part consistency is not only a defining feature that distinguishes living systems from typical artificial systems, but also a key scientific question for understanding how living organization forms and what overarching organizational regularities govern it.

Modern biology has already established a relatively complete body of theory concerning how living organization forms. Genetics has revealed the mechanisms of continuous transmission of genetic information; developmental biology has clarified the basic processes of cell division, cell differentiation, and organogenesis; morphogenesis theory has explained the rules governing the formation of complex biological forms (Turing 1952). Recent studies further emphasize that morphogenesis emerges through the integration of genetically programmed processes and self-organizing tissue dynamics (Collinet and Lecuit 2021). Research on stem cells, pluripotency, and somatic cell nuclear transfer has further demonstrated that most somatic cells retain the complete genetic information required to form an entire organism (Gurdon and Uehlinger 1966; Wilmut et al. 1997). Together, these lines of research explain how living systems form complex organization from the perspectives of heredity, development, morphology, and cellular potency, respectively, and collectively demonstrate that living systems possess a highly unified informational continuity.

However, existing theories focus primarily on specific biological processes such as genetic regulation, molecular mechanisms, cell signaling, and organogenesis, and a unified theoretical

account remains lacking for why living systems maintain whole–part organizational consistency throughout continuous organization, and whether this consistency reflects a more general organizational regularity.

Meanwhile, the development of the concept of holography has offered a new theoretical perspective on the relationship between whole and part. Since Gabor first proposed holographic theory in 1948, holographic thinking has gradually extended into neuroscience, theoretical physics, information science, and other fields (Gabor 1948, 1949; Pribram and Carlton 1986; Pribram 2007; 't Hooft 1993; Susskind 1995). Collectively, this body of work shows that, under suitable information organization and encoding mechanisms, a local part can retain important informational features of the whole. However, existing holographic theories are concerned mainly with wavefront reconstruction, information storage, information processing, and physical information encoding — their object of study remains information itself rather than organization itself. Thus, although the concept of "holography" has been widely applied across multiple disciplines, no organizational theoretical framework has yet emerged that can unify the explanation of living organizational formation, hierarchical organizational evolution, and whole–part organizational consistency.

It should be specifically noted that the "biological holography" discussed in this paper is neither an optical imaging method such as digital holographic microscopy (Lee and Park 2018), nor equivalent to existing applications of the holography concept in neuroscience or theoretical physics. Biological holography, as defined here, refers to the whole–part organizational consistency that living systems exhibit throughout continuous recursive organization. "Holography" in this sense does not imply a simple duplication of the whole's information within each part, but rather an organizational emergence arising as unified organizational information continuously unfolds and is realized layer by layer through recursive organization.

Nevertheless, the studies reviewed above share a common feature: most explain the formation of living organization from a specific level — genetic, molecular, cellular, or organ — while giving little attention to whether a unified organizational regularity holds across these different levels. Advances in organoid biology likewise demonstrate that, under appropriate developmental constraints, higher-order tissue organization can emerge through coordinated multicellular self-organization (Blatchley and Anseth 2023). Existing theories can explain how cells form tissues, how tissues form organs, and how organs form an individual, but no broadly accepted organizational theory has yet been established that applies simultaneously to non-living and living systems and unifies the description of organizational formation, functional emergence, and the continuous evolution of organizational information. A more fundamental question therefore remains: why do natural systems that differ in scale, composition, and physical mechanism repeatedly exhibit similar organizational structures and organizational relationships? Does the sustained whole–part consistency of living organisms stem from a more general organizational regularity, rather than merely from the combined action of several independent biological mechanisms?

Recent advances in multiscale biology, organoid research, developmental systems biology, and complex systems have greatly improved our understanding of how biological structures self-organize across different spatial and temporal scales (Schaffer and Ideker 2021; Collinet and Lecuit 2021; Blatchley and Anseth 2023). However, these studies remain largely focused on specific biological mechanisms, particular developmental stages, or individual hierarchical levels. A general organizational principle capable of describing organizational formation, continuity, and hierarchical expansion using a unified structural language across both living and non-living

systems has yet to be established. Rather than introducing another mechanistic model, the present work proposes such an organizational framework, emphasizing recursively organized domain–boundary relationships as a common structural regularity underlying cross-scale organization in nature, providing a common structural language for describing organizational formation across living and non-living systems.

To address these questions, this paper proposes the Unified Recursive Organization Theory. The theory first establishes a Domain–Boundary framework, describing natural systems uniformly as organizational systems composed jointly of domains and boundaries, and uses this as the basic framework for analyzing the organizational structure of different natural systems. Building on this, the paper further proposes two basic organizational mechanisms — structural recurrence and structural recursion — to provide a unified description of how organizational structures at different hierarchical levels form and evolve. The paper then establishes the recursive organizational unit (*SS*) and its informational attribute $\Psi(SS)$ — the informational content intrinsically carried by *SS* itself — and describes the specific composition of this attribute in terms of the bulk information potential Ψ_b and the surface information potential Ψ_s, providing a unified description of how organizational information is preserved, inherited, exchanged, coupled, and organized. $\Psi(SS)$ is driven by the continuous inheritance of the core genome and constitutes the intrinsic driving force behind the recursive unfolding of *SS*, rather than an independent counterpart external to *SS*. Based on this formulation, the paper proposes recursive holographic unfolding to describe the layer-by-layer unfolding and realization of unified organizational information throughout continuous recursive organization.

Within this framework, information is no longer treated as an abstract description independent of structure, but as the unified organizational information corresponding to the formation, maintenance, and evolution of organizational structure. As recursive organization proceeds, new organizational levels continually form, with organizational structure, organizational function, and organizational information realized in step with one another, establishing a unified and continuous organizational relationship among the three. Biological holography is therefore defined in this paper as the whole–part organizational consistency that emerges as unified organizational information unfolds layer by layer through continuous recursive organization, rather than as information duplication or optical holographic reconstruction in the conventional sense.

To test the generality of the Unified Recursive Organization Theory, the paper further applies it to different organizational levels — non-living systems, the origin of life, and multicellular development — drawing systematically on continuous cell lineages, germline continuity, asymmetric renewal, transgenerational germline pre-setting, vegetative propagation in plants, and somatic cell nuclear transfer to analyze how unified organizational information is continuously transmitted across hierarchical levels and generations. On this basis, the paper further shows that biological holography is not a living phenomenon requiring an independent assumption, but an organizational outcome that naturally emerges from unified organizational information through continuous recursive organization, and on this basis establishes a unified organizational theory applicable to different natural systems, offering a unified theoretical framework for understanding cross-scale organizational formation, organizational continuity, and biological holography in nature.

This paper further shows that this phenomenon is realized, across different levels of biological complexity, through at least two independent evolutionary pathways: beyond germline sequestration and transgenerational germline pre-setting, structurally simple multicellular

organisms and plants generally achieve the same whole–part consistency through a lifelong reservoir of totipotent cells, while unicellular organisms exhibit holography almost trivially, owing to the absence of any distinction between part and whole.

The Unified Recursive Organization Theory proposed here is methodologically related to several existing theoretical traditions, though its focus differs from each; this relationship is clarified below.

Hierarchy theory addresses the nature of level partitioning in complex systems. A significant divide exists within this field: Allen and Starr (1982) emphasize that hierarchical partitioning depends on the observer's chosen temporal/spatial scale, whereas Salthe (1985) and, earlier, Simon (1962) adopt a more realist position, holding that the partitioning of levels/domains depends on objective discontinuities in the strength of internal interactions within the system, rather than purely on the observer's subjective choice. The Domain criterion adopted in this paper (Section 2.1) aligns with the latter position: domain boundaries correspond to genuinely existing discontinuities in interaction strength; a change in observational scale merely changes which discontinuity falls within the current analytical view, without altering the objective existence of the discontinuity itself.

Autopoiesis theory (Varela et al. 1974; Maturana and Varela 1980) addresses how living systems maintain the self-enclosure of a single organizational identity amid continuous material turnover; its core question can be summarized as "how the system avoids falling apart," which is fundamentally a question of steady-state maintenance within a single level and a single identity. This paper is concerned with a different question: how living systems continue to unfold recursively toward higher organizational levels while preserving informational continuity, achieving nested transgenerational transmission of organizational information through the mechanism of transgenerational germline pre-setting (see Sections 4.9–4.12). The Unified Recursive Organization Theory and autopoiesis theory therefore address different kinds of stability — the latter concerns steady-state maintenance within a single level, while the former concerns developmental continuity across levels and generations.

Relational biology (Rosen 1958, 1991) holds that the causal relations within living systems possess a non-algorithmic, self-referential closure — a theoretical tension that the computable recursive expressions proposed in this paper (Equations 6, 8, 10, etc.) need to engage with directly. This paper takes the position that the structural recurrence and structural recursion introduced in Chapter 3 describe the spatial and temporal patterns of organizational information unfolding, rather than claiming to fully characterize the causal closure of living systems itself; the two need not conflict at the theoretical level, though this relationship still awaits further clarification in future work.

Bich and Skillings' organizational approach to development (2024) addresses a closely related question: how living systems maintain organizational viability through developmental change, without treating development as a linear progression toward a fixed adult endpoint. This paper's account of continuous recursive organization across levels and generations extends this organizational perspective by making explicit the informational mechanism—transgenerational germline pre-setting—through which such continuity is sustained, complementing an organizational characterization of development with a mechanistic account of how organizational information itself persists across the developmental and reproductive cycle.

2 Fundamental Concepts and the Domain–Boundary Framework

2.1 Fundamental Organizational Concepts

To establish the Unified Recursive Organization Theory, this chapter first defines the basic organizational concepts used throughout the paper and, on this basis, constructs the Domain–Boundary framework. Unless otherwise specified, all subsequent discussion is built on these fundamental definitions.

Traditional science typically describes natural systems in terms of matter, energy, or information, whereas this paper focuses on a more basic organizational fact: In the present theory any stable organization simultaneously possesses a bulk state and a surface/interface state. The bulk constitutes the main body of the organization and is responsible for preserving matter, energy, and organizational information; the surface constitutes the region of interaction between the organization and its environment, responsible for mass exchange, energy exchange, momentum transfer, charge transfer, and various forms of information exchange. The surface is therefore not a passive geometric boundary, but the starting point for organizational exchange, organizational coupling, and the formation of new organization.

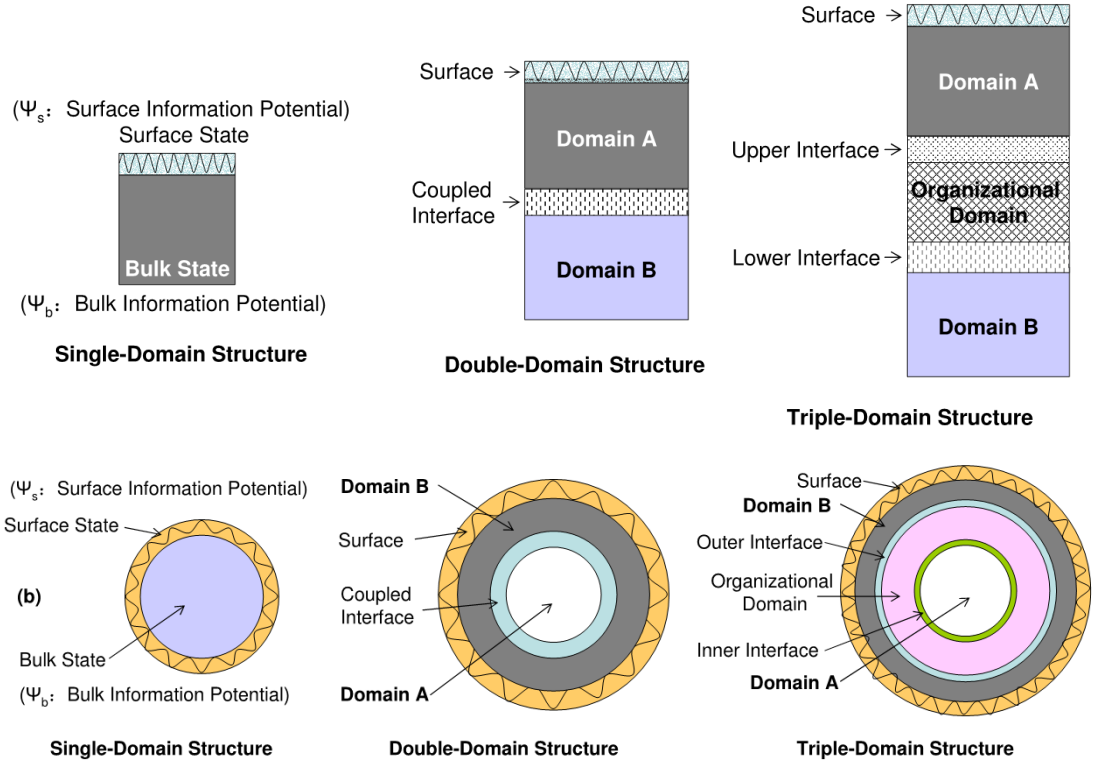

Fig. 1 General model of domain organization

The distinctive character of surfaces and interfaces arises from an electron distribution that differs from that of the bulk interior. Because different atoms, molecules, or material phases differ in electronegativity, charge density, and local structure, the electron distribution at a surface is generally in an organizational state distinct from that of the bulk phase. Since electron distribution is fundamentally governed by the laws of quantum mechanics, the electronic structure of a stable surface can be described by specific quantum states. This view is consistent with the matter-wave

theory proposed by Louis de Broglie (1924). Based on this organizational property, this paper uniformly represents the bulk as the bulk information potential Ψ_b and the surface as the surface information potential Ψ_s, describing, respectively, the preservation and the exchange of organizational information, as shown in Fig. 1. It should be noted that the term “in formation potential,” as used in this paper, follows the same usage as “potential” in physical chemistry (e.g., chemical potential): a potential is itself an attribute intrinsic to the system in a given state, rather than an independent entity external to and corresponding with the system; at the same time, it is precisely this attribute that drives the system’s spontaneous direction of evolution. This understanding underlies the use of Ψ throughout the paper.

Surface states belong to individual domains; their surface states couple to form an interface when adjacent domains interact. Under suitable conditions, a coupled interface may grow, stabilize, and eventually evolve into a new organizational domain. The rectangular model in Fig. 1 emphasizes organizational relationships among domains, whereas the circular model emphasizes structural enclosure and boundary architecture; both representations describe the same underlying domain organization principle from different perspectives.

Extending this analogy with "potential" further, one may speculate that if information content I is treated as an extensive variable, the information potential Ψ defined in this paper might, by analogy with chemical potential, be incorporated as its conjugate intensive variable into the fundamental thermodynamic equation for internal energy:

$$dU = TdS - PdV + \Sigma\mu_i dn_i + \Psi dI \qquad (1)$$

If I is measured in bits, Ψ then carries units of energy per bit, corresponding directly, in dimensional terms, to the minimum energy cost of information erasure given by Landauer's principle (kT ln2 per bit) (1961); Ψ might thus be understood as the value this bound takes in a specific organizational system. It should be made clear that this expression is, at present, only an exploratory extension based on a formal analogy with "potential," and is not empirically validated in this paper; a precise, operational definition of I — how "one unit of information" should be defined and measured in a specific biological or physical system — remains a question for future work. This expression is offered here solely to leave a formally self-consistent theoretical entry point for subsequent quantitative research.

Every independent organizational domain is defined by its boundary. A boundary may take the form of a surface, an interface, a membrane, or a layer; these are simply different manifestations of the same organizational concept at different scales, with different physical properties, or in different disciplinary contexts, rather than distinct organizational concepts. A region can be defined as an independent domain only if it has a relatively stable, repeatably identifiable boundary capable of maintaining organizational independence; a region undergoing continuous gradual change, without a stable boundary, does not constitute an independent organizational domain.

The basic organizational principle of this paper can be summarized as: the boundary defines the domain, the domain carries function, and function maintains the independence of the domain. When adjacent domains interact continuously, their surface information potentials Ψ_s couple with one another to form an interface; under suitable conditions, the coupled interface may further grow and stabilize, eventually evolving into a new organizational domain. Higher-level organization is therefore not a simple superposition of pre-existing organization, but a new organizational level formed recursively through the continuous coupling of existing organization.

Based on this organizational principle, this paper uniformly classifies natural organization into single-domain, double-domain, and triple-domain structures according to the number of organizational domains, rather than the number of boundary layers. A domain may be enclosed by one or multiple boundary layers, but a new domain is defined only when a new subject region with an independent organizational state is formed. Accordingly, all classifications of single-, double-, and triple-domain structures in this paper use the number of organizational domains as the sole criterion, rather than the number of membrane or boundary layers.

2.2 Informational Coupling

No natural system can exist in complete isolation. Every organizational domain continuously interacts with its surrounding environment, neighboring organization, or internal sub-domains, and these interactions occur first at its surface and interface. As shown in Fig. 1, when two independent organizational domains come into contact, their surface information potentials Ψ_s are not independent of one another but undergo continuous coupling through mass exchange, energy exchange, charge transfer, momentum transfer, and various forms of organizational information exchange. This organizational association formed through continuous interaction is termed informational coupling in this paper.

Informational coupling may be transient or stable over the long term. Transient coupling typically produces only temporary interactions, whereas sustained, stable informational coupling can gradually give rise to new organizational relationships. When coupling remains stable over an extended period, the original interface ceases to be merely an exchange region between two organizational domains and gradually evolves into a new organizational domain with its own organizational state. Organizational formation is therefore not simply the result of material aggregation, but the result of sustained informational coupling becoming progressively stabilized and recursively organized.

In the Unified Recursive Organization Theory, every organizational domain is jointly composed of two parts: manifest matter and unmanifest information. Manifest matter comprises mass and structure; unmanifest information comprises energy and organizational code. When information corresponds to a specific organizational domain, it is uniformly termed unified organizational information in this paper:

Domain = Matter (Mass, Structure) + Information (Energy, Organizational code)

In terms of organizational state, each organizational domain simultaneously possesses a bulk state and a surface state, corresponding respectively to the bulk information potential Ψ_b and the surface information potential Ψ_s. The unified organizational information of an organizational domain can therefore be expressed as:

$$\Psi(D) = \Psi_b(D) + \Psi_s(D), \tag{2}$$

Here, the bulk information potential Ψ_b is primarily responsible for the preservation, inheritance, and historical memory of organizational information, while the surface information potential Ψ_s is primarily responsible for organizational recognition, information exchange, organizational coupling, and the formation of new organization.

When two organizational domains A and B undergo sustained coupling, their surface information potentials interact nonlinearly to form a new coupled information potential:

$$\Psi_s(\text{Coupled interface}) = f(\Psi_s(A) + \Psi_s(B)), \tag{3}$$

Under suitable conditions, the coupled interface continues to grow and stabilize, eventually forming a new organizational domain. The newly formed organizational domain likewise possesses its own bulk information potential Ψ_b and surface information potential Ψ_s, and can therefore participate in the next round of organizational coupling. Organizational formation thus manifests as a continuous, recursive organizational process rather than a one-time structural combination. This continuous recursive organizational process constitutes the common organizational basis for structural recurrence, structural recursion, and recursive holographic unfolding, discussed in subsequent chapters.

Chemical reactions provide the most basic and universal natural example of boundary coupling. The formation of a chemical bond does not arise from the direct union of whole atoms, but primarily from the sustained coupling between boundary electrons. When this coupling reaches a stable state, a new molecular structure is formed. From the perspective of the Unified Recursive Organization Theory, a chemical bond can be regarded as a basic form of boundary coupling, and a molecule as a new organizational domain formed once informational coupling has stabilized over time. Informational coupling is therefore not unique to living systems, but a basic organizational regularity commonly followed in the formation of organization throughout nature.

2.3 Single-Domain Structure

Single-domain structure is the most basic and most common organizational form in nature. Its defining feature is that the entire organization contains only one independent organizational domain; all peripheral structures belong to the boundary of that domain, serving to maintain organizational integrity and to enable the exchange of matter, energy, and information between the organization and its environment, without forming a new independent domain. In the Unified Recursive Organization Theory, therefore, the criterion for single-domain structure depends on the number of organizational domains, not on the number of membrane layers, cell walls, or other boundary structures.

Single-domain structures are widespread in both non-living and living systems. In non-living systems, micelles, emulsion droplets, and various self-assembled structures formed by surfactants — although differing in composition and boundary form — each contain only a single continuous organizational body internally, and therefore all belong to single-domain structures. They illustrate that a single stable boundary is sufficient to maintain an independent organizational domain, without the need to form higher-level organizational structure.

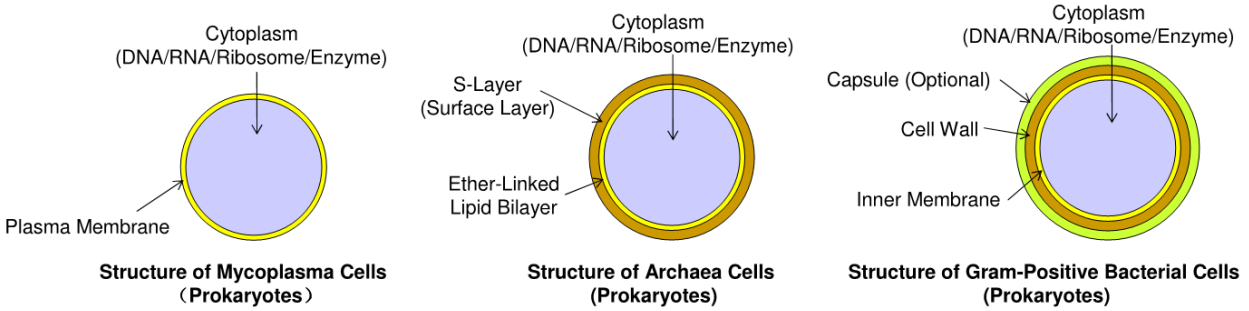

Fig. 2 Single-domain structure: unicellular prokaryotic microorganisms

Living systems follow the same organizational regularity. As shown in Fig. 2, Mycoplasma lacks a cell wall and is bounded solely by a cell membrane; Archaea possess a distinctive cell membrane composed of ether-linked lipids, often accompanied by peripheral structures such as an S-layer; and

Gram-positive bacteria have a relatively thick peptidoglycan cell wall. Although these three groups differ markedly in boundary composition, chemical structure, and environmental adaptability, each possesses only a single continuous cytoplasmic organizational domain; their outer membrane, cell wall, or S-layer all belong to the boundary of the same organizational domain rather than forming a new independent domain, and can therefore all be uniformly classified as single-domain structures.

This result shows that the Domain–Boundary framework describes an organizational classification rather than a structural classification in the conventional sense. Boundaries may differ in composition, number of layers, and physical properties, but as long as they jointly enclose the same organizational body, they still correspond to a single organizational domain. A new organizational domain arises, entering a higher-level organizational structure, only when a new boundary encloses a new subject region with an independent organizational state.

Single-domain structure is therefore not only the most basic organizational form of living organization, but also the starting point for the evolution of all higher-level organization within the Unified Recursive Organization Theory. The double-domain structure, triple-domain structure, and more complex recursive organizational structures discussed below can all be regarded as new organizational levels formed, on the basis of single-domain structure, through continuous organization.

2.4 Double-Domain Structure

Across biological, chemical, and engineering systems, the second widespread organizational form is double-domain structure. As shown in Fig. 3, a double-domain structure consists of two mutually independent organizational domains that continuously exchange matter, energy, and information through a stable interface. Unlike single-domain structure, double-domain structure does not simply add boundary layers; rather, it forms a new organizational domain on top of existing organization, thereby establishing a higher-level organizational relationship.

Two mutually immiscible organizational domains, if brought into direct contact, will typically separate rapidly and fail to form long-term stable organization. However, nature widely employs a mechanism — interfacial mediation — capable of simultaneously maintaining organizational independence and organizational exchange capacity. In physicochemical systems, surfactants serve as typical interfacial mediators, promoting the formation of a stable interface by lowering interfacial tension; in living systems, phospholipids, membrane proteins, glycolipids, and various natural biosurfactant structures serve the same role. From cell membranes and organelle membranes to pulmonary surfactant and lecithin in egg yolk, all illustrate that interfacial mediators are not unique to living systems, but a common material basis for the formation of double-domain organization.

Fig. 3 presents three representative types of double-domain structure. Gram-negative bacteria establish a stable double-domain organization through the periplasm formed between the outer membrane and the inner membrane; although metabolism in bacterial spores is nearly completely arrested, the core region remains enclosed by an inner membrane, forming a typical double-domain structure together with the cortex and outer coat; and fungal cells and fungal spores define, respectively, the nucleus and cytoplasm as two organizational domains bounded by the nuclear membrane and the plasma membrane. Although these three cases differ markedly in physiological state, metabolic level, and structural composition, they all follow the same organizational regularity: two independent organizational domains coupled continuously through a stable interface, jointly constituting a higher-level organizational system.

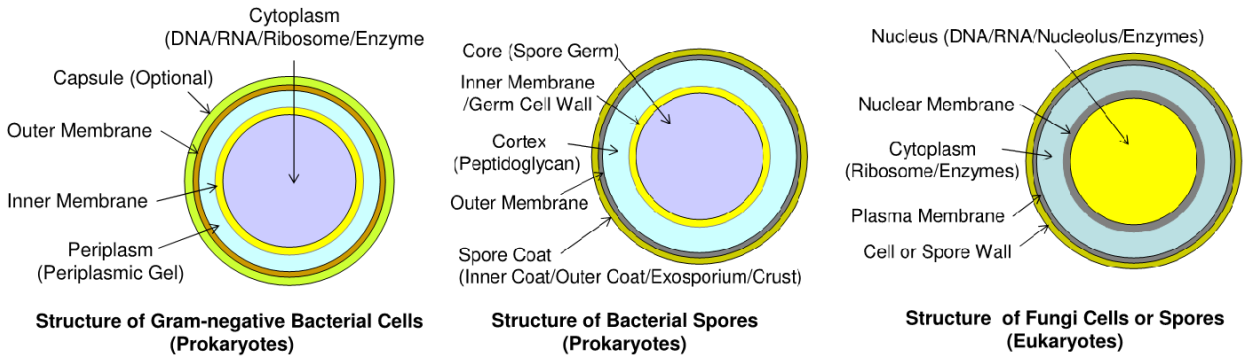

Fig. 3 Double-domain structure: Unicellular prokaryotic and eukaryotic microorganisms

Milk, cream, and butter offer the most familiar and intuitive everyday examples of double-domain structure. Milk is essentially a typical fat-in-water emulsion, containing approximately 3.6% fat and 3.2% protein. Milk fat remains stably dispersed in the continuous aqueous phase over long periods not because oil and water are naturally miscible, but because each milk fat globule is coated with an extremely thin milk fat globule membrane (MFGM). The MFGM consists mainly of membrane proteins and phospholipids; it maintains the independence of the milk fat organizational domain while allowing it to coexist stably with the surrounding aqueous phase, thereby constituting a typical interfacial mediator.

Cream typically has its fat content raised to 30–38%, close to the practical upper limit of fat concentration at which liquid cream remains stable without breaking during processing. Unwhipped liquid cream retains the same fat-in-water organizational structure, with fat dispersed in a continuous aqueous phase, except that the milk fat organizational domain is further enriched. Under sustained mechanical agitation, some fat globule membranes rupture, fat particles link together to gradually form a continuous fat network, and large amounts of air are introduced into the system to form a new dispersed phase, resulting in an air-in-fat-in-water (A/F/W) foam structure. Upon further separation, the fat content ultimately reaches approximately 80%, forming butter, whose organizational structure has transformed into a water-in-fat solid emulsion. The progression from milk to liquid cream, to whipped cream, and finally to butter is not four independent foodstuffs, but the result of the same emulsion system undergoing continuous organizational reconstruction under different interfacial conditions, reflecting the continuous organizational evolution among single-domain structure, double-domain structure, and a reorganized single-domain structure.

The examples above show that double-domain structure is not confined to living systems but is widespread among stable organizations throughout nature. Whether cell membranes, organelle membranes, biosurfactants, or milk fat globule membranes and industrial surfactants, their common function is to maintain, through interfacial mediation, a long-term stable organizational relationship between two organizational domains. The next section further uses industrial microemulsion and emulsion systems as examples to show how this organizational regularity extends to the more complex triple-domain structure.

2.5 Triple-Domain Structure

The previous section used milk, cream, and butter as examples to show that emulsion systems can undergo continuous organizational reconstruction as their interfacial organizational relationships change. These familiar food systems, however, illustrate only part of the organizational behavior of

emulsions. Industrial emulsion and microemulsion systems as shown in Fig. 4 display richer organizational forms, offering more representative non-living examples for analyzing the formation, stabilization, and transition of multi-domain organization.

Industrial microemulsions are highly thermodynamically stable dispersion systems with particle sizes of 10–100 nm. Unlike biological systems, microemulsions possess no life activity, yet they are capable of forming a highly ordered, liquid-crystal-like intermediate phase with a bicontinuous organizational structure, which may be either oil-in-water or water-in-oil in type. Surfactants serve as the interfacial mediator; the intermediate phase constitutes an organizational domain, while the oil phase and aqueous phase constitute the interacting subject domains, together forming a typical triple-domain/triple-interface structure, whose three interfaces are the upper interface, the lower interface, and the oil surface. Conditions such as ambient temperature and pressure, the concentration of inorganic salts in the aqueous phase, and the type or concentration of surfactant can all cause the microemulsion type to invert.

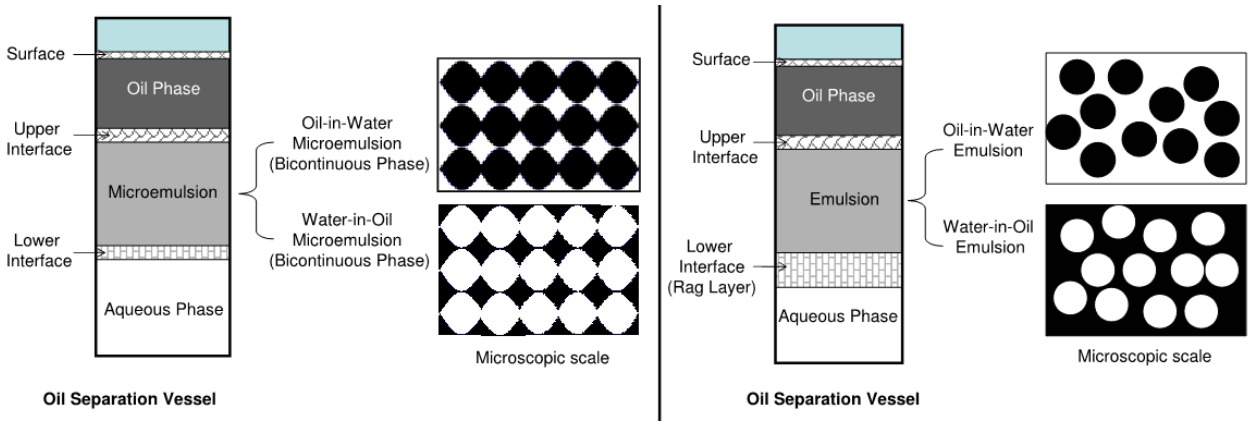

Fig. 4 Triple-domain structure: Microemulsion and emulsion systems

Industrial emulsions are dispersion systems in which most particle diameters range from 1–5 μm, with a small fraction of larger particles reaching up to 1000 μm. They differ considerably from industrial microemulsion systems in that their intermediate phase is thermodynamically unstable, yet displays considerable kinetic stability, remaining resistant to breaking over long periods. The interfacial layer beneath may be thin or, in industrial settings, quite thick — sometimes as much as ten feet — and is termed the rag layer. The rag layer is not simply a disordered mixture; it behaves as a highly viscous, highly damped, complex viscous fluid phase, forming a natural intermediate buffering and damping domain within industrial separators, with clearly organizational behavior: formation, evolution, collapse, reconstruction, and long-term stable existence. Within the framework of this paper, the rag layer can likewise be regarded as a representative intermediate organizational domain, whose behavior is influenced not only by material composition but also by ongoing informational exchange processes. Such complex emulsion systems spontaneously transition from a triple-domain to a quadruple-domain structure. Industrial oil–water systems thus provide an important real-world model for studying the mechanisms of organizational formation.

At the microscopic level, however, both conventional oil-in-water (O/W) and water-in-oil (W/O) emulsions also present a single-domain, single-membrane structure. Under special conditions, water-in-oil-in-water (W/O/W) or oil-in-water-in-oil (O/W/O) double-domain, double-membrane microstructures can also form.

The rectangular diagram is particularly well suited to explaining the macroscopic organizational structure of industrial oil–water separators, while the circular diagram is particularly well suited to explaining the microscopic organizational structure of emulsion systems.

Whether in food emulsions or industrial emulsions, organizational state is determined by interfacial organizational relationships rather than by specific material composition. Continuous organizational transitions between different organizational states, driven by interfacial reconstruction and phase inversion, show that the Domain–Boundary framework describes a general organizational regularity, not one confined to living systems. Building on this, the next chapter further discusses structural recurrence and structural recursion, analyzing how this unified organizational regularity continues to unfold across different scales.

3 Structural Recurrence Across Scales

3.1 Basic Topological Organization of Biological Tissue

If organization arises from informational coupling rather than from any particular material substrate, then the same organizational relationship may appear in entirely different systems. This phenomenon is termed structural recurrence. Structural recurrence does not imply that different systems share the same physical mechanism; rather, it emphasizes the similarity of their organizational relationships. Eggs, cells, microemulsions, and industrial oil–water systems, for example, differ completely in composition, yet all exhibit a domain–boundary organizational structure.

This recurrence suggests that organizational structure may be governed by regularities deeper than specific material composition. This paper therefore does not treat structural recurrence as coincidental, but regards it as the natural outcome of long-term informational coupling. If this view holds, cross-scale organizational similarity is not accidental but may reflect an organizational principle that is universal in nature — one that would be expected to produce similar organizational relationships across systems differing in scale, composition, and functional level. Similar multilevel organizational behavior has also been discussed from the perspective of biological network hierarchies and multilevel organization (Uversky and Giuliani 2021), although the present theory emphasizes recursive domain formation rather than network topology. The representative organizational structures are the single-domain, double-domain, and triple-domain structures discussed above.

In animal tissue, cells are not simply stacked together but are jointly organized into a boundary system through intercellular junctions (ICJ), the extracellular matrix (ECM), the basement membrane, and related structures. This boundary system not only anchors cells in place but also provides mechanical support, mediates material transport and information transfer, and maintains tissue integrity.

Theoretically, although ICJ, ECM, the basement membrane, and related structures differ in form, they perform the same class of function — establishing the boundary, coupling, and topological constraint between adjacent structures. This paper therefore abstracts them uniformly as the generalized boundary matrix (*BM*).

The generalized *BM* represents the boundary matrix of a domain — a generalized boundary system that achieves connection, support, stabilization, and functional coupling between adjacent cells or core domains. *BM* does not correspond to any single fixed biological structure, but is a collective

term for the class of structures that perform a boundary function across different biological systems. Fig. 5 illustrates *BM* in animal cellular tissue.

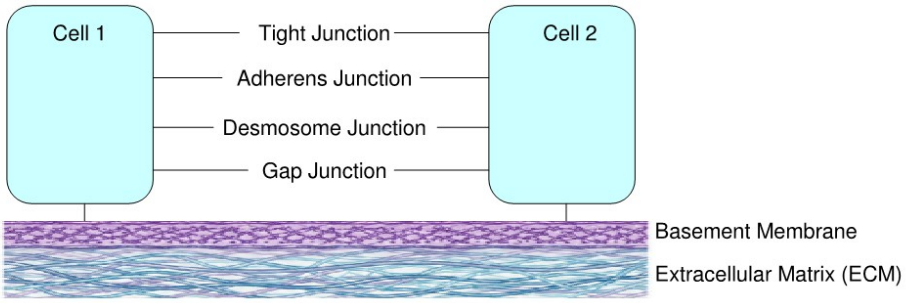

Fig. 5 Schematic boundary matrix (*BM*) in animal tissue

(*BM* = Intercellular junctions (ICJ) + Basement membrane (Basal lamina) + Extracellular matrix (ECM)).

The generalized *BM* mainly includes ICJ, ECM, the basement membrane, cell adhesion structures, the basal lamina, synapses, integrin-mediated adhesions, and other boundary structures. In plants, *BM* corresponds to the cell wall and plasmodesmata; in fungi, to the chitinous cell wall; and in bacteria, to the cell wall and biofilm, among others. *BM* may therefore differ in specific composition across different levels and different biological systems, while performing the same topological function throughout.

Although biological tissues and organs display extremely complex spatial forms, their basic modes of construction can, from a topological standpoint, be reduced to a small number of fundamental types. To establish a unified descriptive framework independent of any specific biological structure, this paper abstracts any biological structure into the following three basic topological elements.

(1) Core (*C*)

Core (*C*) represents the core constituent unit at the current level of analysis, as shown in Fig. 6. At the cellular level, *C* typically corresponds to a core functional region within the cell, such as the nucleus. At the tissue level, *C* corresponds to a single cell. As the level of analysis rises, *C* may represent any core domain at that level — a muscle fiber, a fascicle, a lobule, an organ, and so on. is therefore a relative concept whose specific meaning depends on the chosen analytical starting point, rather than fixedly denoting a cell.

In Fig. 6, *C* denotes the Core (cell or core domain), *E* the Envelope, P_f the functional pore space, and P_e the local environmental space; the circular geometry shown is schematic and represents a generalized closed topology rather than the actual anatomical shape.

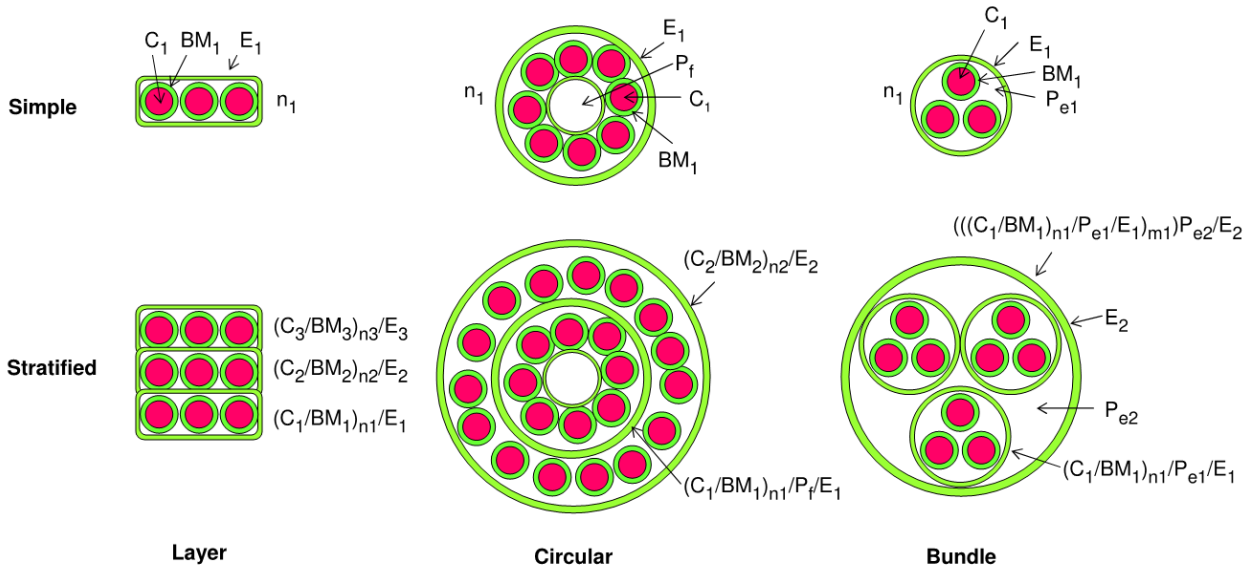

Fig. 6 Three fundamental topological organizations of biological domains

This relativity can be illustrated with a straightforward example: when the object of observation is a tissue or organ, the cell itself constitutes the Core at that level; when observation shifts down to the interior of a single cell, the nucleus becomes the new Core at that level. Notably, whatever the level, the object designated as Core always has an independent, repeatably identifiable physical and functional boundary — the cell is bounded by the cell membrane, the nucleus by the nuclear membrane. The relativity of Core therefore does not mean its definition can be chosen arbitrarily: only a region that satisfies both functional independence and a repeatably identifiable physical boundary can be designated as Core at the corresponding level of analysis (Simon 1962). This criterion is consistent with the more realist strand of hierarchy theory (Salthe 1985; Simon 1962), which holds that the partitioning of levels/domains depends on objective discontinuities in the strength of internal interactions within the system, rather than purely on the scale chosen by the observer (Allen and Starr 1982).

(2) Envelope (*E*)

Envelope (*E*) represents the outermost enclosing boundary of an entire domain, defining the overall outer boundary of the current Domain and serving as the interface for interaction with the external environment or with a higher-level Domain. *E* may be realized by the same structure as *BM*.

(3) Pore space (P_f, P_e)

Pore space (*P*) represents the spatial region contained within a domain. Based on its topological function, it can be further divided into two types: functional pore (P_f) and environmental space (P_e). P_f refers to the spatial region enclosed by the inner boundary of a circular structural domain, forming a core functional domain that serves functions such as storage, processing, transport, exchange, or flow — for example, the vascular lumen, the gastric lumen, the intestinal lumen, glandular lumina, and the Haversian canal. P_e refers to the local environmental space between multiple sub-domains, such as the extracellular matrix, tissue fluid, and local microenvironment between fascicles, nerve bundles, and other modules. P_e does not itself constitute an independent Domain, but rather the local environment required to sustain interaction among multiple sub-domains.

Based on the four basic topological elements — Core (*C*), Boundary matrix (*BM*), Envelope (*E*), and Pore space (*P*) — three basic topological structures can be further formed by combination: Layer, Circular, and Bundle.

Layer and Circular structures

Layer structure is generally regarded as the most basic mode of spatial organization; this paper treats layer structure as a local representation, or local section, of a continuous circular structure. A circular structure is a closed-loop topology with a closed boundary, and is not limited to a circular geometry. It may be composed of one or more concentric layers, with a functional pore (P_f) forming at the center. In this model, a forward slash "/" denotes physical adjacency and direct contact between the organizational structures on either side. Its general recurrence form can be expressed as:

$$(C_1/BM_1)_{n(1)}/P_f/E_1,\ i = 1 \text{ (circular)}, \quad (4)$$

$$(C_i/BM_i)_{n(i)}/E_i,\ i > 1 \text{ (circular)},\ i \geq 1 \text{ (layer)}, \quad (5)$$

Here, the Core (C_i), Boundary matrix (BM_i), Envelope (E_i), and quantity parameter $n(i)$ of layer i may be identical to those of the adjacent layer — e.g., $C_{i-1} = C_i = C_{i+1}$, $BM_{i-1} = BM_i = BM_{i+1}$, $E_{i-1} = E_i = E_{i+1}$, $BM_i = E_i$ — representing a continuous homogeneous region that increases tissue thickness and enhances overall transport capacity, though its topological role remains distinct: *BM* is primarily responsible for the connection, support, and coupling between adjacent *C*'s, whereas *E* defines the outer boundary of the entire Domain. *BM* and *E* should therefore be distinguished by their topological function rather than by specific biological material. Alternatively, C_i, BM_i, and E_i may differ entirely from one layer to the next, indicating substantive functional change in that region, primarily achieving functional differentiation and coordination. Both cases conform to the unified topological model proposed in this paper.

This model applies both to a simple structure and to a stratified structure (*SS*). *SS* refers to a composite structure recursively built from multiple simple structures or lower-level stratified structures; it does not specifically denote stratified epithelium in the conventional histological sense. Its general recursion expression is as follows:

$$SS_{i+1} = SS_i/(C_{i+1}/BM_{i+1})_{n(i+1)}/E_{i+1},\ i \geq 1, \quad (6)$$

where $SS_1 = (C_1/BM_1)_{n(1)}/E_1$ (*L*ayer), $SS_1 = (C_1/BM_1)_{n(1)}/P_f/E_1$ (*C*ircular). (7)

Moreover, this model does not depend on cell morphology. Core may correspond to squamous, cuboidal, or columnar cells, or equally to muscle cells, neurons, or any other cell type. The Layer and Circular models thus describe the spatial topological structure of tissue rather than the conventional histological classification of cell types. Layer primarily characterizes layered organizational structures with an open boundary (Fig. 7); Circular primarily characterizes organizational structures that form a closed boundary around a functional space (Fig. 8). Circular chiefly characterizes ductal or luminal tissues and organs across the animal body, with representative examples including blood vessels, the stomach, the small intestine, the colon, bone, and glands.

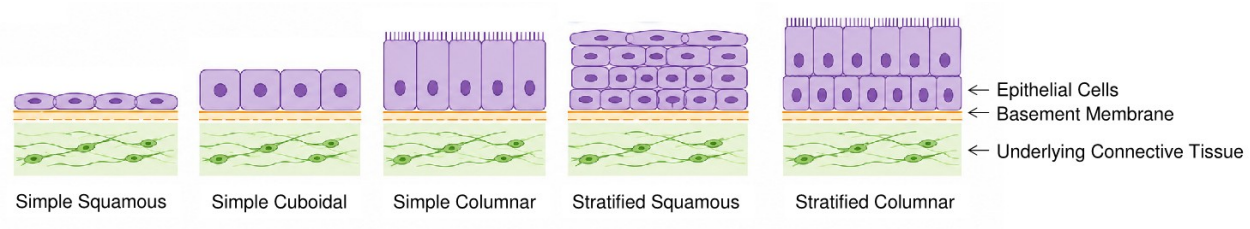

Fig. 7 Schematic layer structures of epithelial tissue

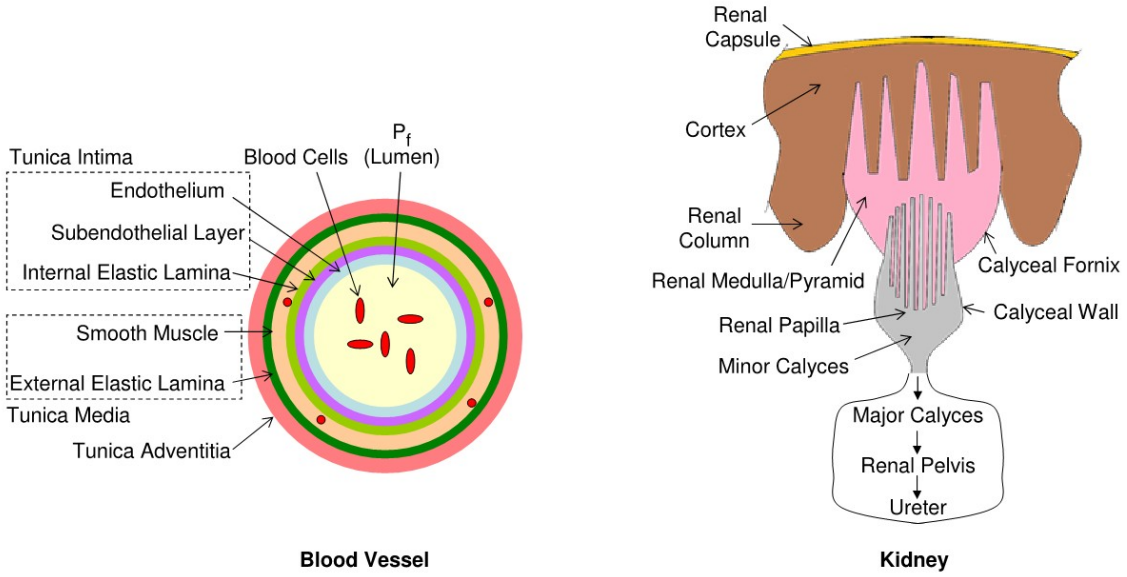

Fig. 8 Schematic circular structures of blood vessel and kidney

Simple squamous epithelium lines body cavities, the cardiovascular and lymphatic systems, and the surfaces of the lungs and kidneys, serving gas and fluid diffusion and filtration. Simple cuboidal epithelium presents an approximately square cross-section; it lines many ducts and renal tubules within the body and performs secretory and absorptive functions. Simple columnar epithelium consists of cells taller than they are wide, with nuclei typically located at the cell base and arranged in a single row in cross-section; it lines the stomach, intestine, and certain large ducts within the body, and its surface is often modified with cilia or microvilli, serving secretory and absorptive functions.

The blood vessel exemplifies a typical double-domain/double-boundary circular structure, comprising two nested functional-domain/boundary units: the vascular lumen (P_f)/tunica intima, and the smooth muscle/tunica adventitia (external elastic lamina + tunica adventitia). Fig. 8 follows conventional vascular nomenclature in classifying smooth muscle as part of the tunica media, a treatment that obscures the function of the tunica media as an independent organizational domain — a domain that in fact governs luminal pressure regulation, mechanical deformation, and the delivery of nutrients to the vessel wall.

The structure of the kidney may not appear to be a circular structure at first glance, but it is, in essence, likewise a double-domain/double-boundary circular structure — only its boundary takes the form of a folded, nested structure. The renal lumen constitutes a long, continuous, closed functional channel domain (P_f):

Renal papilla → Minor calyces → Major calyces → Renal pelvis → Ureter,

extending all the way to the exterior via the urethra. The other functional domain is the renal medulla/pyramid, which, together with the well-developed cortex as its boundary layer, performs the core function of filtration and purification — filtering waste and excess water from the blood, maintaining water and electrolyte balance, regulating blood pressure, and secreting hormones that stimulate red blood cell production. Although anatomically subdivided into the renal papilla, minor calyces, major calyces, renal pelvis, ureter, bladder, and urethra, these structures together constitute a single continuous P_f enclosed by a continuous Boundary. The anatomical subdivisions above reflect functional differentiation rather than topological separation.

Bundle structure

A bundle structure may be composed of one or multiple nested bundles. At the current level, multiple "bundle" structures from the level below share a continuous local environmental space (P_e), enclosed by the Envelope of the current level. Its general recursion expression for a stratified structure (SS) is as follows:

$$SS_{i+1} = (SS_i)_{m(i)}/P_{e(i+1)}/E_{i+1},\ i \geq 1, \tag{8}$$

$$\text{where } SS_1 = (C_1/BM_1)_{n(1)}/P_{e(1)}/E_1, \tag{9}$$

As shown in Fig. 9 for skeletal muscle and peripheral nerve, the continuous functional region between fascicles is defined as the environmental space (P_e) at that level, composed jointly of ECM, tissue fluid, microvasculature, nerves, lymphatics, and other interstitial components. Likewise, in peripheral nerve structure, the continuous functional region between nerve fascicles corresponds to the environmental space (P_e) at that level. The specific mapping is as follows: C_1 = axon, BM_1 = axolemma, $P_{e(1)}$ = myelin sheath, E_1 = endoneurium, $n(1) = 1$, $SS_1 = (C_1/BM_1)_{n(1)}/P_{e(1)}/E_1$; $m(1) = 13$, $P_{e(2)}$ = the internal environment within the perineurium and outside each endoneurium, E_2 = perineurium, $SS_2 = (SS_1)_{m(1)}/P_{e(2)}/E_2$; $m(2) = 4$, $P_{e(3)}$ = the internal environment within the epineurial sheath and outside each perineurium, E_3 = epineurial sheath, $SS_3 = (SS_2)_{m(2)}/P_{e(3)}/E_3$. Skeletal muscle and peripheral nerve are each quadruple-domain/quadruple-boundary bundle structures, in which C_1 is the first-level core domain and BM_1 is its boundary.

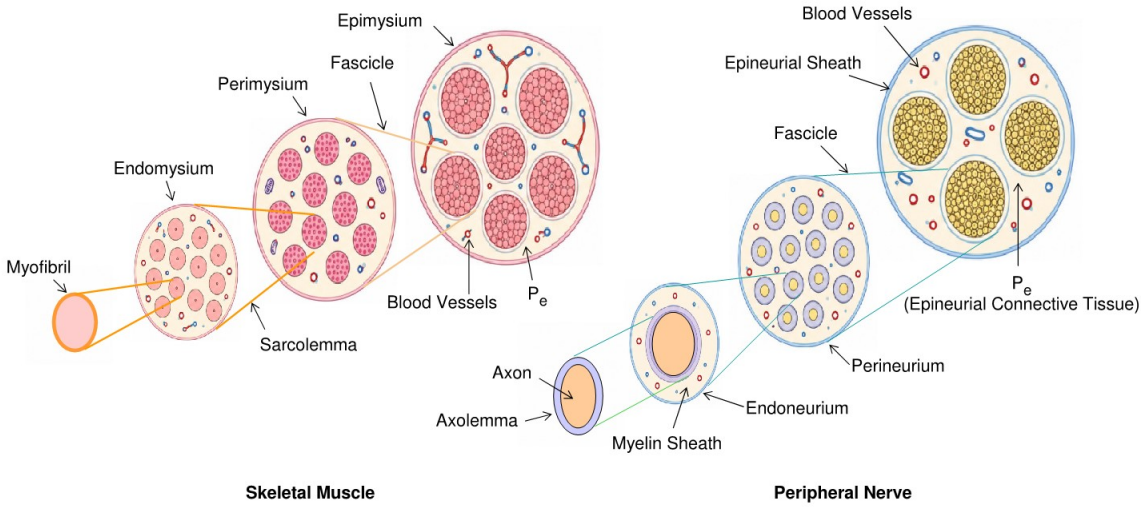

Fig. 9 Schematic bundle structures of skeletal muscle and peripheral nerve

The specific composition of P_e may differ across tissues, but its common role is to maintain the continuous functional environment required for the overall function of the bundle at that level. As the bundle structure nests recursively, each level of bundle structure has an environmental space (P_e) corresponding to its level, whose specific composition and function vary with the level and tissue type. Unlike P_f, P_e does not itself constitute an independent Domain, but rather the local environment necessary to maintain internal stability and functional coupling within the Bundle. Representative examples of bundle structure include skeletal muscle, cardiac muscle, peripheral nerve, and various glandular tissues.

Based on the unified topological expressions (8) and (9) above, the complete organizational structure SS_i at any level inherently contains the full structural information from level 1 through level i. Applying Equation (2) directly, the overall organizational information potential accumulated upon recursion to level i is expressed as:

$$\Psi(SS_i) = \Psi_b(SS_i) + \Psi_s(SS_i), \tag{10}$$

This shows that, in terms of static spatial structure, the overall information of the system continues to consist of a conserved element fixed at that level (bulk information Ψ_b) together with an outward-facing open element (surface information Ψ_s). Consistent with Section 2.2, $\Psi(SS_i)$ is the information potential intrinsic to SS_i at that level — an intrinsic attribute of SS_i itself, rather than an independent counterpart external to SS_i; this attribute derives fundamentally from the continuous inheritance of the core genome and drives the recursive unfolding of SS_i into SS_{i+1}.

The three topological structures above are not a conventional histological classification, but the three most basic modes of spatial organization in the construction of biological tissue. Different tissues and organs may be formed by one or a combination of these topological modes. Epithelial tissue, for example, is mainly expressed as Layer; blood vessels and the digestive tract are mainly expressed as Circular; and skeletal muscle, cardiac muscle, and peripheral nerve are mainly expressed as Bundle.

It should be noted that, in the recursive expressions for the three topological structures above, SS_i does not denote the structure of level i alone, but the complete structure formed upon recursion to level i. SS_i therefore inherently contains all recursive information from level 1 through level i, rather than representing only the newly added level. Correspondingly, the structure newly added at level can be expressed as SS_i/SS_{i-1}, which includes the Boundary, P_e, or P_f newly added at that level, but not the additional function arising from the combination of these structures (gain of function).

This model describes topological organization rules rather than a specific histological classification. Multiple adjacent, homogeneous *SS* units may together constitute an extension of a continuous Domain (or continuous Boundary). *SS* itself denotes a recursive structural unit, whereas the delineation of a Domain depends on whether new structural and functional differentiation has occurred.

The same topological structure therefore allows different levels to have different Core, Boundary matrix, Envelope, and Pore space, and allows different biological systems to employ different specific biological structures to achieve the same topological function. Layer, Circular, and Bundle thus constitute a unified topological language, providing a common structural basis for the recursive construction model of Domain.

In a broader sense, circular recursion is a special case of bundle recursion, in which $m(1) = 1$, P_e degenerates to P_f, and the recursion formulas (8) and (9) degenerate to recursion formulas (6) and

(7). Layer structure can be regarded as a local representation, or local section, of a continuous circular structure. As a result, all three nested structures can be expressed using a unified bundle structure model. Within the framework of this paper, the bundle model can be regarded as a general recursive form that unifies the description of the layer, circular, and bundle topological structures. From the perspective of recursive structural organization, different biological tissues can all be uniformly described as a bundle recursive construction process.

This nested relationship does not introduce a new basic principle at each level, but simply replicates the minimal structural unit of "bulk + boundary + information" onto a higher level; it not only explains the process but also encodes the level-generating mechanism directly into the expression itself. This is precisely the manifestation of what this paper calls "structural recurrence" in the construction of an organism, and it forms the structural basis for the discussion of holographic properties later in the paper. A nested structure not only generates hierarchical levels but also preserves the rule that generates them, and thereby naturally gives rise to a holonomic/holographic property.

3.2 Structural Recurrence, Structural Recursion, and Gain of Function

According to Equations (6) and (8), SS_i represents the complete organizational structure formed upon recursion to level i, not the organization newly added at level i. The structure newly added at level i is therefore defined as

$$L_i = SS_i/SS_{i\text{-}1},\ i \geq 2, \tag{11}$$

where L_i denotes the recurrence organizational unit newly added at the current level, and SS_i denotes the complete organizational structure formed upon recursion to level i.

Substituting Equation (11) into Equations (6) and (8), respectively, gives

$$L_i = SS_i/SS_{i\text{-}1} = (C_i/BM_i)_{n(i)}/E_i,\ i \geq 2\ (\text{Layer or Circular structure}); \tag{12}$$

$$L_i = SS_i/SS_{i\text{-}1} = (SS_{i\text{-}1})_{m(i\text{-}1)\text{-}1}P_{e(i)}/E_i,\ i \geq 2\ (\text{Bundle structure}). \tag{13}$$

This shows that structural recurrence and structural recursion are not two independent processes, but two descriptions of the same organizational construction process. Recurrence describes the organization newly added at the current level, while recursion describes the overall organization formed once the newly added organization is incorporated. Each occurrence of recurrence simultaneously forms a new recursive structure; the two therefore always occur synchronously, with no temporal precedence between them.

For all three topological structures — Layer, Circular, and Bundle — each instance of recurrence corresponds to a new instance of recursion. As recurrence proceeds, organizational levels continue to rise, organizational relationships become increasingly rich, and organizational complexity increases accordingly.

Recurrence may occur between homogeneous organization or between heterogeneous organization. When C_i, BM_i, and E_i at level i remain identical to those of the previous level, recurrence mainly manifests as an expansion of organizational scale, thickness, capacity, and transport ability; when any of these topological elements changes, new organizational differentiation forms, giving the overall organization new organizational characteristics after recursion. Recurrence can thus produce either quantitative accumulation or qualitative change, while recursion fully preserves the overall organization resulting from these changes.

As organizational complexity increases, system function increases correspondingly. The overall function after recursion is generally not equal to the simple sum of the functions of its constituent parts, but rather a new system function that forms on the basis of new organizational relationships. This paper terms this additional system function arising from organizational recursion the gain of function.

Gain of function may manifest either as an enhancement of existing function or as the emergence of new function. Homogeneous recurrence mainly enhances existing function, whereas heterogeneous recurrence establishes new organizational relationships through new organizational differentiation, giving the system new functions that did not previously exist. Gain of function can therefore arise either from quantitative accumulation or from organizational differentiation.

It should be noted that gain of function is not a property possessed by any single newly added organization in isolation, but a systemic property exhibited by the entire recursive organization as a whole. Gain of function therefore depends on how organizational units are organized, not on the organizational units themselves.

Taking the vascular structure in Fig. 8 as an example, the vascular endothelium, smooth muscle, and outer membrane each perform distinct functions, and together they form the complete blood vessel through recursive organization. The endothelium alone cannot accomplish blood transport, nor can smooth muscle alone accomplish circulatory regulation; only once the three together form the complete vessel are the overall functions of pressure bearing, transport, contractile regulation, and material exchange achieved.

Multiple blood vessels further recurse to form arteries, veins, and capillary networks, which together with the heart constitute the circulatory system. The circulatory system not only accomplishes blood transport but also carries out the transport and regulation of oxygen, nutrients, metabolic waste, hormones, and immune cells throughout the body.

At a still higher level, the circulatory system recurses further together with the respiratory, digestive, urinary, nervous, and other functional systems to form a complete animal individual. The movement, metabolism, homeostatic maintenance, and vital activity exhibited by an animal are likewise not the function of any single functional system, but an overall function formed through the further recursion of multiple functional systems. Structural recursion thus continually forms not only new organizational structure but also new system function. As the recursive level continues to rise, gain of function accumulates progressively, ultimately giving rise to the overall function possessed by the complete living organism.

Furthermore, at the informational level, the “gain of function” brought about by structural recursion is essentially an emergent result of nonlinear informational coupling between the newly introduced recurrence unit L_i and the pre-existing overall structure $SS_{i\text{-}1}$. When the overall recursive structure at level i-1 comes into boundary contact with the newly added recurrence unit at level i, their outward-facing surface information does not simply add linearly, but interacts through a nonlinear coupling potential f, generating the interface information $\Psi_s(\text{Interface}(i))$ at the current level:

$$\Psi_s(\text{Interface}(i)) = f(\Psi_s(SS_{i\text{-}1}) + \Psi_s(L_i)). \tag{14}$$

As the organization moves from “contact” to “growth” under self-organizing dynamics, the interface information generated by this nonlinear coupling potential further consolidates and differentiates over time, ultimately transforming into the overall informational state of the new level SS_i:

$$\Psi(SS_i) = \text{Growth}[f(\Psi_s(SS_{i-1}), \Psi_s(L_i))] \rightarrow \Psi_b(SS_i) + \Psi_s(SS_i). \quad (15)$$

Because every organizational structure is accompanied by corresponding structural information, structural recurrence and structural recursion manifest not only as the continual expansion of organizational structure but also as the continual accumulation of organizational information. Each instance of recurrence introduces new structural information, while recursion retains both pre-existing and newly added information together within the new organizational level. As the recursive level continues to rise, organizational information therefore becomes correspondingly richer, forming an informational hierarchy that corresponds to the organizational structure.

How structural information is preserved, replicated, and transmitted across different organizational levels is discussed further in subsequent chapters.

4 Evolution of Structural Information and Universal Validation

4.1 Organizational Structure of Non-living Matter

Although non-living systems lack cells, they likewise possess Domains, Boundaries, and recursive organizational structure, and are therefore equally amenable to the unified topological model proposed in this paper. In inorganic systems, processes such as the precipitation and growth of single crystals in solution, the formation and growth of micelles in surfactant solutions, solid–liquid phase transitions, and solution crystallization all involve the formation of single- or double-domain structures. When the surrounding medium is considered together as an environmental domain, these organizational forms can all be uniformly described as topological structures jointly composed of Domain and Boundary.

Crystal growth offers a representative example of the preservation of structural information in inorganic systems. Once a nucleus has formed, atoms or ions in solution do not deposit randomly, but are guided by the existing lattice structure, entering the crystal layer by layer in the same spatial arrangement, so that the entire crystal maintains a consistent lattice orientation and periodic structure. As the crystal continues to grow, each newly added portion continually recurs the organizational pattern of the existing lattice; each instance of structural recurrence therefore increases not only the size of the crystal but, correspondingly, the structural information it carries.

It should be noted that structural information in a crystal always exists attached to the pre-existing lattice, and is continually preserved and perpetuated through the process of crystal growth. When new atoms or ions join the crystal, they do not establish a new organizational rule, but inherit the spatial arrangement already fixed by the existing lattice. Crystal growth can therefore be regarded as a process of continuous preservation and recurrence of structural information in inorganic systems. However, this information remains confined to the structure itself and does not yet possess the capacity for independent preservation, replication, and active transmission; it therefore remains a primitive form of structural information.

As system complexity increases further, multicomponent crystallization, metal smelting, ceramic sintering, and colloidal systems progressively form double-domain, triple-domain, and even higher-domain organizational structures, continually undergoing formation, disintegration, and reconstruction. From simple micelles and solubilization systems to industrial oil–water systems such as emulsions and microemulsions, organizational levels continue to rise, while the mode of organization consistently follows the same recursive regularity.

Crystal growth shows that structure itself is not only capable of remaining stable, but can also continually guide the formation of new structure through pre-existing structure, so that structural information is preserved and recurs throughout the growth process. This information, however, remains attached to pre-existing structure and does not yet possess the capacity for independent replication and active transmission apart from that structure. The next section further discusses how structural information gradually evolves into an information system capable of replication and propagation.

4.2 Non-cellular Biological Systems

Non-cellular biological systems include prions, viroids, and viruses as illustrated in Fig. 10. All lack a complete cellular structure and an independent metabolic system, and cannot replicate autonomously apart from a host; whether they qualify as true living entities therefore remains debated. From the standpoint of informational organization, however, they represent an important stage in the gradual evolution of structural information into genetic information.

Prions possess neither DNA nor RNA and consist solely of misfolded protein, constituting a unit of structural information encoded by protein conformation. A prion can induce the same conformational change in a host's normal protein, allowing structural information to propagate and recur continually among different protein molecules. Much as an existing lattice guides the formation of new lattice during crystal growth, a prion directs the folding of new protein molecules through its existing conformation, showing that structural information can not only be preserved but also propagate across hosts. This demonstrates that the preservation and propagation of information need not depend on DNA or RNA; structure itself can equally serve as an information carrier.

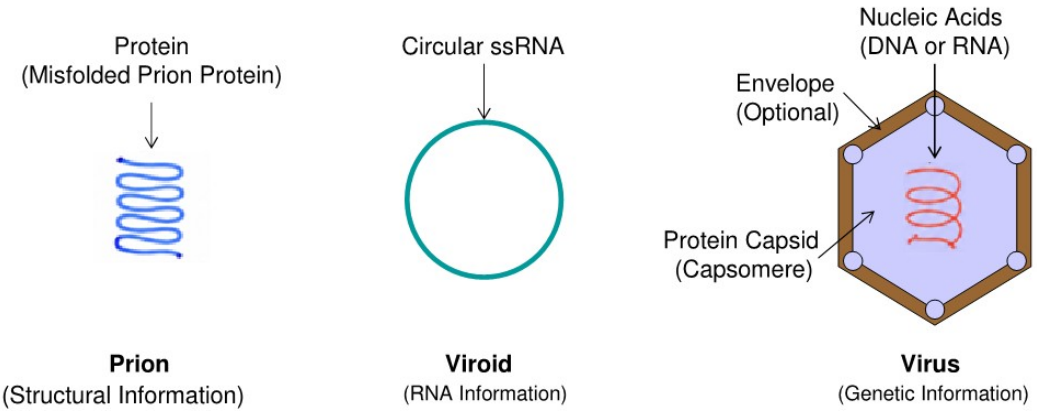

Fig. 10 Representative non-cellular biological systems illustrating the evolution of information carriers

Viroids consist solely of a circular single-stranded RNA molecule, lack a protein coat and any complete cellular structure, and must rely on a host cell to replicate. Compared with prions, the information carried by a viroid is no longer attached to protein conformation but is jointly preserved by its RNA sequence and spatial structure. This marks the beginning of a transition from information as a structural state to information as nucleic acid encoding, providing a more stable information carrier for the eventual formation of genetic information.

Viruses further develop an organizational form of information composed of DNA or RNA together with a protein capsid. Genetic information is preserved in the nucleic acid, while the protein capsid

protects and delivers this genetic information, relying on the host cell to accomplish replication, expression, and assembly. Although a virus still cannot metabolize independently, it has already formed a relatively complete informational organizational system, with organizational complexity and informational expression capacity markedly exceeding those of prions and viroids.

Prions, viroids, and viruses are therefore not three mutually isolated classes of biological entity, but successive stages in the continual development of informational organization. From the protein-conformational information of prions, to the RNA information of viroids, to the DNA/RNA genetic information of viruses, the mode of information preservation progressively develops from structural information into sequence information, with the stability, replicative capacity, and transmissibility of information continually increasing. This continuous evolutionary progression shows that the evolution of life reflects not only the increasing complexity of organizational structure, but also the continual development of the capacity to preserve, replicate, and transmit information.

They are best understood as surviving "information fossils," recording how structural information gradually evolved into genetic information and further developed boundaries, organization, and increasingly complex informational organizational systems — offering important clues to the formation of complete cellular life.

4.3 Organizational Structure of Structural Organelles

A complete cell requires not only genetic information to direct protein synthesis, but also the capacity to restore complex spatial organizational structure. At the cellular level, therefore, information manifests not only as DNA or RNA sequence, but also as the structural information needed to preserve and restore spatial organization. After cell division, a new cell can re-form complex structures such as the endoplasmic reticulum, Golgi apparatus, lysosomes, vacuole, and cytoskeleton — showing that what life inherits is not only genetic information, but also the organizational information required to restore these structures.

Compared with crystal seeds in non-living systems, structural organelles not only preserve an organizational template but also possess a degree of active organizing capacity. They participate in processes such as structural sorting, packaging, transport, renewal, and spatial organization, and can therefore be regarded as an intermediate functional level between a purely structural template and a functional organelle.

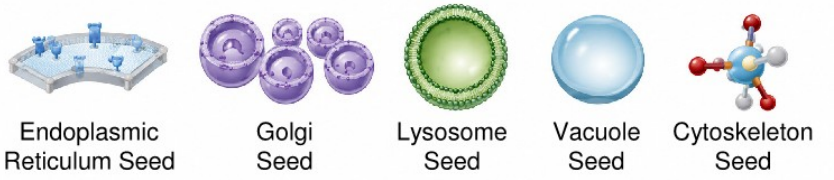

Fig. 11 The five structural organelles of a cell

This paper refers to the endoplasmic reticulum, Golgi apparatus, lysosomes, vacuole, and cytoskeleton collectively as structural organelles. Together they constitute the internal spatial organizational network of the cell and can be regarded as structural organelle seeds, as illustrated in Fig. 11, required to restore the corresponding structures. These seeds do not directly determine the expression of genetic information, nor are they the primary producers of cellular structural components; rather, they preserve the organizational template needed to restore their own structure and provide a stable spatial organizational platform for the various functional modules.

The main organizational roles of the five structural organelles are as follows:

1. **Endoplasmic reticulum (ER):** provides a continuous membrane network, offering a spatial organizational platform for protein folding, membrane lipid formation, and intracellular transport.
2. **Golgi apparatus:** sorts, packages, and directs the transport of proteins based on the molecular recognition information they carry, coordinating internal structural organization of the cell.
3. **Lysosome:** responsible for structural degradation, recycling, and renewal, maintaining the dynamic equilibrium of cellular structure.
4. **Vacuole:** responsible for material storage and intracellular homeostasis, providing a stable internal environment for cellular structure.
5. **Cytoskeleton:** provides spatial support, an organizational framework, and transport tracks, serving as an important template for maintaining the overall structure of the cell.

Although these structural organelles possess a degree of active organizing capacity, their primary responsibility remains the maintenance and restoration of the cell's spatial organizational structure, rather than the reading of genetic information, large-scale protein synthesis, or energy conversion. The relevant structural components are produced mainly by the functional organelles and, guided by the structural template, are progressively restored into a complete structural system through transport, self-organization, and assembly.

4.4 Organizational Structure of Functional Organelles

A complete cell requires not only a stable spatial organizational structure but also the vital activities of preserving and interpreting genetic information, producing structural components, supplying energy, and regulating cell division. Beyond the structural organelles, therefore, another class of organelle responsible for these core life functions must exist. This paper refers to the nucleus, ribosome, mitochondrion — and, in plants, the chloroplast — together with the centriole, collectively as functional organelles as illustrated in Fig. 12.

Unlike structural organelles, which are mainly responsible for establishing and maintaining the cell's spatial organization, functional organelles are mainly responsible for preserving, interpreting, and executing life's information and for energy conversion, supplying the driving force and material basis for the cell's continued growth, self-renewal, and autonomous replication. Together they constitute the core of the cell's functional system.

Functional organelles can be divided, according to their primary function, into four basic functional modules.

1. **Nucleus: Information storage and regulation.** The nucleus is the core of a cell's genetic information. It preserves not only DNA sequence information but also multiple layers of structural information, including that of chromosomes, chromatin, and nuclear architecture, and governs the cell's vital activities through DNA replication, RNA transcription, and gene regulation. The nucleus therefore serves as both the primary repository of sequence information and an important organizing center for structural information, providing a long-term, stable informational foundation for the entire cell.

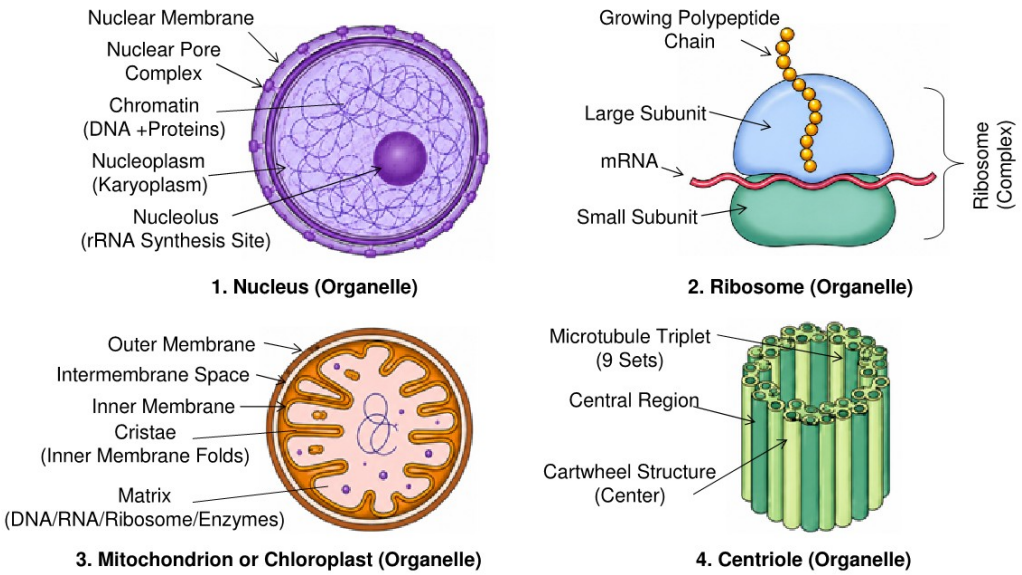

Fig. 12 The four functional organelles of a cell

2. **Ribosome: Information interpretation and component production.** The ribosome interprets the genetic information carried by mRNA and synthesizes proteins according to the codon sequence, serving as the direct executor that translates genetic information into cellular structure and function. Nearly all structural components and functional proteins within the cell depend on the ribosome for their synthesis; the ribosome thus links genetic information to cellular structure and constitutes a core functional module in the execution of life's information.

3. **Mitochondrion and chloroplast: Energy conversion.** The mitochondrion carries out cellular respiration and ATP synthesis, supplying continuous energy for all of a cell's vital activities; the chloroplast in plant cells converts solar energy into chemical energy through photosynthesis, providing the primal energy source for the entire biosphere. Notably, both mitochondria and chloroplasts possess their own DNA, RNA, and ribosomes and can carry out part of their protein synthesis, giving them a degree of genetic independence. This distinctive feature further illustrates that the functions of life are not concentrated in a single structure but are accomplished through the coordination of multiple functional modules.

4. **Centriole: Cellular organization and division.** The centriole participates mainly in microtubule organization, cytoskeletal reconstruction, and the formation of the mitotic spindle, playing an important role in the spatial organization and division of the cell. Although it is not directly involved in the expression of genetic information or protein synthesis, it coordinates the establishment of the cell's spatial organization, enabling the cell to maintain stable organizational order throughout division; it is thus an important functional module linking spatial organization to cell replication.

These four functional organelles each perform a distinct role — preserving genetic information, interpreting genetic information, converting energy, and regulating cellular organization — dividing labor while cooperating with one another, and together with the fifth category, the structural organelles, constitute the structural and functional system of the complete cell. At this point, structure, function, and information achieve, for the first time, complete coupling within the same living system, enabling the cell not only to maintain its existing structure but also to

continually generate new structure, preserve and transmit genetic information, and carry out vital activities such as autonomous growth, self-maintenance, and cell replication.

A complete cell is therefore not a simple collection of organelles, but a unified organizational system formed by the tight coupling of multiple structural and functional modules. From this level onward, structure, function, and information no longer evolve independently, but together constitute an inseparable whole underlying vital activity, laying the foundation for the subsequent formation of multicellular tissues, organs, and complete organisms.

4.5 Co-evolution of Structure, Function, and Information

This chapter has proceeded from non-crystalline matter through crystals, prions, viroids, viruses, structural organelles, and functional organelles, tracing the continuous evolutionary path along which the basic capacities of life progressively formed. Unlike conventional biological classification or phylogenetic research, this chapter is concerned not with the classificatory relationships among different life forms, but with how nature progressively acquired the three basic capacities of life — structure, function, and information — ultimately forming a complete cell capable of autonomous vital activity. This evolutionary process can be summarized as:

Non-crystalline matter → Crystal → Prion → Viroid → Virus → Structural organelles → Functional organelles → Cell

Throughout this process, each new evolutionary level retains the basic capacities already acquired at the preceding level while further acquiring new structural organization, more refined function, and new forms of information, so that the entire system continually evolves toward higher organizational levels rather than simply replacing the preceding stage. Table 1 summarizes the developmental trends of structure, function, and information across this continuous evolutionary process.

Table 1. Progressive evolution of structure, function, and information from non-living matter to a complete cell

Evolutionary stage	Structure	Structural information	Functional capability	RNA	DNA
Non-crystalline matter	×	×	×	×	×
Crystal	✓	✓	✓	×	×
Prion	✓✓	✓✓	✓✓	×	×
Viroid	✓✓	✓✓	✓✓✓	✓	×
Virus	✓✓✓	✓✓✓	✓✓✓	✓✓✓	✓✓
Structural organelles	✓✓✓✓	✓✓✓✓	✓✓✓	×	×
Centriole	✓✓✓✓	✓✓✓✓	✓✓✓✓	×	×
Ribosome	✓✓✓✓	✓✓✓✓	✓✓✓✓✓	✓✓✓✓	×
Mitochondrion / Chloroplast	✓✓✓✓✓	✓✓✓✓✓	✓✓✓✓	✓✓✓	✓✓✓
Nucleus	✓✓✓✓✓	✓✓✓✓✓	✓✓✓✓✓	✓✓✓✓	✓✓✓✓✓
Complete cells	✓✓✓✓✓	✓✓✓✓✓	✓✓✓✓✓	✓✓✓✓✓	✓✓✓✓✓

Table 1 shows clearly that nature first acquired stable structure and its corresponding structural information, then progressively established more complex organizational function, and further developed sequence-based information systems such as RNA and DNA. As structural complexity continued to increase, functional capacity continually strengthened and the means of information preservation and expression continually matured, culminating for the first time in the unification of all three within the complete cell.

The complete “Cell” referred to in Table 1 denotes the cellular organizational unit that, for the first time, possesses complete organizational structure, basic metabolic capacity, and unified

organizational information, thereby achieving continuous recursive organization and autonomous reproduction. Among present-day organisms, Mycoplasma represents the structurally simplest complete cell currently known, while prokaryotic cells — Gram-positive bacteria, Gram-negative bacteria, and Archaea — and eukaryotic cells of animals, plants, and fungi each represent different organizational realizations of the complete cell. In this paper, Cell therefore does not denote any particular organism or evolutionary stage, but the unified organizational level reached once living organization first crosses the threshold of a complete cellular organization — realized at different levels within present-day living systems, yet all conforming to this paper's definition of a complete cell.

Along this path, crystals established a stable structural template, providing the physical basis for the long-term preservation of structural information; prions demonstrated that structural information alone can achieve replication and propagation without the involvement of DNA or RNA; viroids introduced RNA sequence information for the first time, expanding life's information from pure structural information to the coexistence of structural and sequence information; and viruses further established a more complete RNA and DNA genetic information system. Structural organelles subsequently established a stable spatial organizational system, while functional organelles further accomplished the core vital functions of preserving and expressing genetic information, converting energy, and regulating cellular organization. At this point, structure, function, and information achieved, for the first time, complete coupling within the same living system, together constituting a complete cell capable of autonomous vital activity.

From the standpoint of materials physics, the liquid crystalline state represents an important transition from rigid order to flexible order. Although the liquid crystalline state is not itself living organization, nor a distinct stage in this paper's evolutionary chain, it embodies the unification of ordered structure with dynamic reorganizing capacity, offering an important physical insight into the subsequent formation of flexible biological templates such as prion protein conformations, biological membranes, and cellular tissue.

It should be noted that this chapter addresses the formation and accumulation of life's basic capacities, whereas the Unified Recursive Organization Theory established in Chapter 3 addresses the organizational mechanism of living systems; the two are descriptions operating at different levels. The progression from non-crystalline matter to a complete cell does not strictly correspond to the structural recurrence and structural recursion formulas introduced in Chapter 3, but is instead a continuous evolutionary process in which life's basic capacities are progressively formed and refined.

Once structural and functional organelles have progressively formed, however, and structure, function, and information achieve complete coupling, life's evolution undergoes a fundamental transition, at this point, from capability acquisition to unified recursive organization. From this stage onward, structural recurrence and structural recursion no longer act on physical structure alone, but simultaneously on structure, function, and information together, so that all three recur and recurse in coordination, ultimately forming the complete cell.

Modern biology generally takes the cell as the basic dividing line between the living and the non-living. This paper further proposes that, from the standpoint of the Unified Recursive Organization Theory, the cell is not only an important marker of the formation of life, but also the recursive structural unit (*SS*) at which structure, function, and information first achieve unified coupling. This paper accordingly defines Cell as: a living organizational unit that, for the first time, possesses

unified organizational structure, basic vital function, and unified organizational information, and is capable of autonomous recursive organization and the continuous transmission of unified organizational information.

In the Unified Recursive Organization Theory, this living organizational unit is defined as SS_0 — the initial condition of unified recursive organization. From this point onward, all higher-level living organization can be uniformly expressed as SS_i ($i \geq 1$). SS_i denotes a new organizational level continually formed from SS_0 through structural recurrence and structural recursion, which may manifest either as the continued expansion of homogeneous organization or as the formation of a new organizational level between heterogeneous organization. SS_i therefore does not correspond to a fixed biological classification, but denotes a recursive organizational level within the Unified Recursive Organization Theory.

As recursion continues, organizational structure, organizational function, and organizational information increase in step with one another, ultimately forming more complex tissues, organs, organ systems, and, eventually, the complete individual. The Unified Recursive Organization Theory proposed in Chapter 3 thus explains not only the formation of the complete cell, but also provides a unified theoretical framework for the continued formation and evolution of living organization across scales.

The formation of the complete cell marks not only the first unification of life's three basic elements — structure, function, and information — but also the transition of the living system from a capability-formation stage to a unified recursive stage. From that point on, the three constitute an inseparable whole, together driving the continued recursion and evolution of living organization toward higher organizational levels. The Unified Recursive Organization Theory therefore applies not only to multicellular life, but, taking the complete cell (SS_0) as its starting point, establishes a theoretical framework capable of uniformly describing the cross-scale formation and continued evolution of living organization.

4.6 Microscopic Organizational Structure of Single-celled Microorganisms

The vast majority of organisms in the microbial world consist of a single complete cell, estimated at approximately 99% of all microbial species by number. For a single-celled microorganism, its microscopic organizational structure is therefore simultaneously the macroscopic structure of its complete living organization. In other words, a single-celled microorganism can itself be regarded as a complete recursive organizational unit (SS_0). The preceding sections have already introduced the single-domain/single-membrane structures of Mycoplasma, Archaea, and Gram-positive bacteria (Fig. 2), as well as the double-domain/double-membrane structures of Gram-negative bacteria, bacterial spores, and fungal spores (Fig. 3). Although these different types of single-celled microorganisms differ in boundary structure, organizational complexity, and functional differentiation, all are complete cells and can therefore all serve as instances of SS_0 within the Unified Recursive Organization Theory.

4.7 Multicellular Microorganisms

The great majority of microorganisms are unicellular, with multicellular microorganisms constituting only a small minority. From the standpoint of the Unified Recursive Organization Theory, however, multicellular microorganisms hold special significance, as they represent the earliest instances of living organization developing from the complete recursive organizational unit (SS_0) toward higher-level recursive organization.

Compared with single-celled microorganisms, the individual cells of multicellular microorganisms undergo no essential change. Whether in filamentous cyanobacteria, filamentous fungi, or certain multicellular algae, the constituent cells retain a complete cellular structure, including the cell membrane, cytoplasm, genetic information system, and various functional organelles. Each cell can therefore still be regarded as a complete SS_0.

What genuinely changes is the addition of a higher-order organizational relationship between cells. Multiple cells, each originally capable of independent survival, form a stable cellular assembly through cell junctions, intercellular material exchange, the extracellular matrix (ECM), and related modes of organization — marking the first extension of living organization from the development of intracellular complexity to the establishment of intercellular organizational complexity.

Taking the filamentous cyanobacterium Anabaena as an example, its basic cellular structure does not differ essentially from that of ordinary bacteria, yet multiple cells connect end to end to form filaments, and further functional differentiation — such as the heterocyst — arises, achieving coordination among different cells. Filamentous fungi, in turn, consist of a continuous hyphal network formed from large numbers of hyphal cells, each of which retains a complete structure including nucleus, mitochondria, endoplasmic reticulum, and Golgi apparatus; the increase in complexity here arises mainly from the higher-level mode of organization among hyphae, rather than from any marked change in the internal structure of individual cells.

Slime molds further illustrate another form of organizational recursion. Their life cycle can transition between a unicellular stage and a multicellular aggregate stage, in which large numbers of cells self-organize into a collective capable of migration, foraging, and environmental response. This capacity, likewise, arises mainly from the establishment of organizational relationships between cells rather than from any change in the structure of individual cells.

The most important change in the evolution of multicellular microorganisms is therefore not the appearance of new cell types, but the establishment of an organization layer between cells. The focus of living evolution begins to shift from increasing intracellular structural complexity toward increasing intercellular organizational complexity.

From the standpoint of the Unified Recursive Organization Theory, a multicellular microorganism can be regarded as the first higher-level organizational unit formed from multiple SS_0 through structural recurrence and structural recursion. Each cell retains a complete system of structure, function, and information, while multiple cells together form a new organizational level through boundary structure, the extracellular matrix, and functional division of labor, acquiring new functions that no single cell possesses. Multicellular microorganisms thus represent not only an important transitional stage in the development of life from unicellular to multicellular organization, but also the first direct validation, within a living system, of the Unified Recursive Organization Theory: higher-level living organization is not formed by altering the cells themselves, but progressively formed through the continual establishment of new organizational relationships among multiple complete recursive organizational units (SS_0), in a process of coordinated recurrence and coordinated recursion of structure, function, and information — the unified recursive stage $SS_0 \rightarrow SS_i$ ($i \geq 1$).

4.8 Microscopic Organizational Structure of Complex Multicellular Organisms

Although complex multicellular organisms ultimately form highly differentiated tissues, organs, and organ systems, their vital activity almost always begins with a single complete fertilized egg. In

both animals and plants, the earliest stage of development involves a single cell undergoing continual division, growth, and differentiation, ultimately forming the complete individual. From the standpoint of the Unified Recursive Organization Theory, complex life therefore does not alter the basic regularity of living organizational formation, but instead continually forms higher-level organizational structure through sustained structural recurrence and structural recursion, building on the complete recursive organizational unit (SS_0).

Fig. 13 presents six representative double-domain organizational structures found in complex multicellular organisms: the mammalian egg cell, the fertilized mammalian egg, an ordinary animal cell, the egg of an oviparous animal, its fertilized form, and the plant seed. Although these differ markedly in outer boundary, nutrient source, and mode of development, they can each be resolved into the same basic organizational unit — a Cell or Embryo constituting the living subject, jointly enclosed by peripheral supporting tissue that forms a complete developmental system. The mammalian egg cell, for example, is surrounded by protective structures such as the zona pellucida and corona radiata; birds and other oviparous animals form an egg membrane, yolk, and, in some species, an eggshell; and plant seeds further form peripheral tissues such as the endosperm, aleurone layer, and seed coat — together constituting the organizational boundary of these different types of living organism.

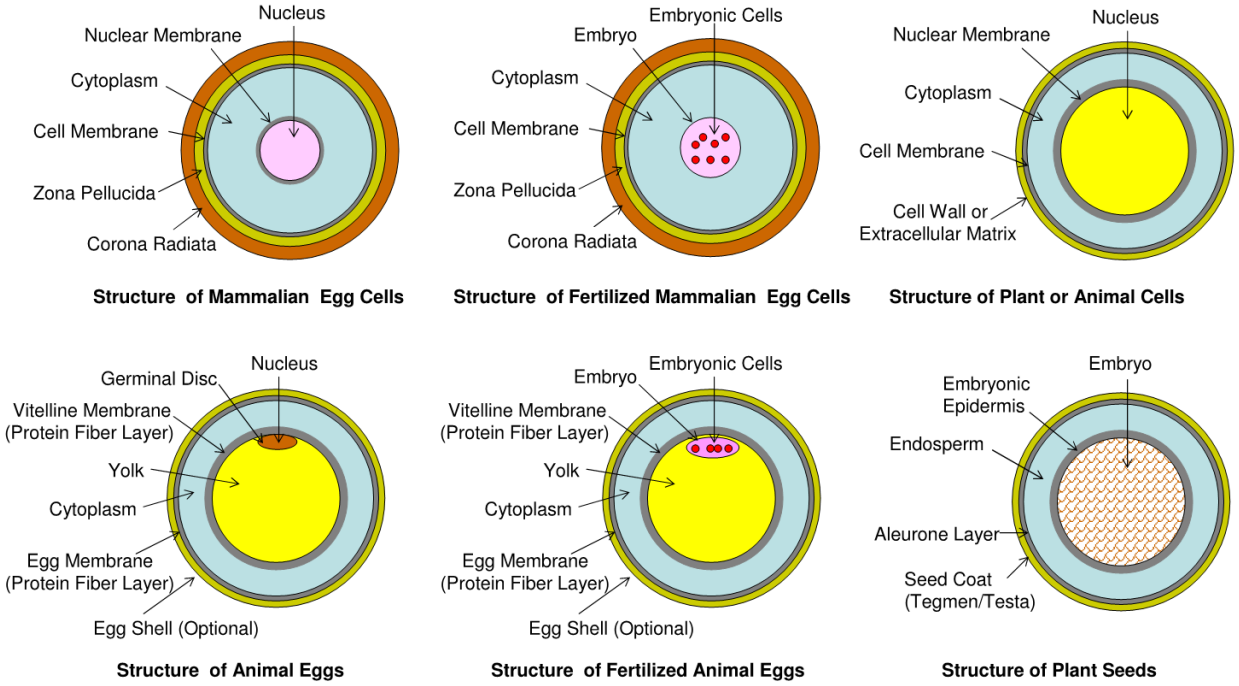

Fig. 13 Double-domain structure: Cells or eggs of complex multicellular organisms

Oviparous animals are widely distributed across different evolutionary lineages of the animal kingdom, including marine invertebrates, insects, fish, amphibians, reptiles, and birds. The scale of their eggs varies enormously, from microscopic insect and fish eggs to chicken, goose, and ostrich eggs, and even the fossilized eggs of extinct dinosaurs, yet all follow the same basic organizational pattern: the embryo as the living subject, surrounded by the yolk, which supplies nutrition, and protected mechanically by the egg membrane and, in some species, the eggshell. This organizational consistency, spanning vastly different animal groups and an enormous range of scales, shows that living organization follows a highly conserved basic organizational regularity.

Mammals adopt a different mode of development. Because the embryo develops within the maternal uterus and continually obtains oxygen and nutrients through the placenta, the mature egg cell no longer stores substantial yolk, retaining only protective structures such as the zona pellucida and corona radiata. In other words, mammals have not lost the yolk domain, but have transferred its primary nutritive function to the maternal placental system — effectively "outsourcing" the nutritional system. Animal embryonic development is therefore, in general, an open embryo strategy, in which vital activity remains continuously coupled to an external nutritional environment.

Plants have developed another representative organizational strategy. Once mature, a plant seed must separate from the parent, undergo prolonged dormancy, and germinate anew under suitable conditions. Plants therefore not only form a complete embryo, but also establish an encapsulating system — nutrition supplied by the endosperm, germination regulated by the aleurone layer, and environmental protection provided by the seed coat — enabling the embryo to withstand drought, cold, and other environmental stresses. This mode of organization can be regarded as an encapsulated embryo strategy, in sharp contrast to the open embryo strategy of animals.

Although plants and animals adopt different developmental strategies, both follow the same organizational regularity: life first forms a complete cell (SS_0), then continually forms higher-level living organization through continuous cell division, cell differentiation, and organizational recursion. As recursion proceeds, what is newly added is not a new basic cell type, but continually new organizational relationships between cells, giving rise to new organizational function, new informational organization, and new levels of life.

From the standpoint of the Unified Recursive Organization Theory, the developmental process of a complex multicellular organism is therefore essentially a continuous process in which the complete recursive organizational unit (SS_0) undergoes continual recurrence and recursion to form higher-level recursive organizational units SS_i ($i \geq 1$). Whatever the resulting organism — plant or animal — the increase in its organizational complexity arises mainly from the sustained establishment of organizational relationships, rather than from continual changes in the basic structure of individual cells.

Complex multicellular organisms thus constitute the most direct and complete validation of the Unified Recursive Organization Theory. Beginning with the fertilized egg, structure, function, and information remain in coordinated recurrence and coordinated recursion throughout, continually forming new organizational levels and ultimately establishing a complete organism with highly differentiated tissues, organs, and organ systems. This process demonstrates clearly that the source of biological complexity is not any single cell becoming progressively more complex, but the continual formation of new organizational relationships among multiple complete recursive organizational units (SS_0), further recursing to form higher-level organizational units SS_i ($i \geq 1$).

4.9 Germline Continuity and Unified Recursive Organization

It should be noted that germline sequestration and transgenerational germline pre-setting, discussed in this section and in Sections 4.10–4.12, represent one evolutionary pathway among several by which complex animals achieve biological holography — a pathway found primarily among bilaterian animals with highly differentiated organ systems that reproduce via oviparity, viviparity, or ovoviviparity. Other pathways are discussed together in Section 5.5.

Complex multicellular organisms exhibit not only the continual expansion of organization across spatial scale, but also informational continuity across generations. The preceding sections addressed the spatial organizational process by which the complete cell (SS_0) continually recurs and recurses to form higher-level organizational structure (SS_i); the capacity of life to continue evolving over the long term, however, depends on another continuously maintained informational thread — the germline.

Fig. 14 illustrates the unified organizational pattern of multicellular organisms along two dimensions: spatial organization and temporal continuity. The black branches in the figure represent the process by which the fertilized egg undergoes continual cell division, tissue differentiation, and individual development to gradually form a complete organism — the process of organism expansion. The red continuous lineage, on the other hand, represents the sustained transmission of germ cells across generations — germline continuity. These two principal threads correspond, respectively, to the spatial expansion and temporal continuation of living organization, together maintaining the long-term stability of the living system.

In Fig. 14, the fertilized egg corresponds to the initial recursive organizational unit of the individual, Initial SS_0, constituting Level 0 of the entire continuous cell recursive lineage. Thereafter, every cell can be traced, through the continuous recursive lineage, back to this common origin.

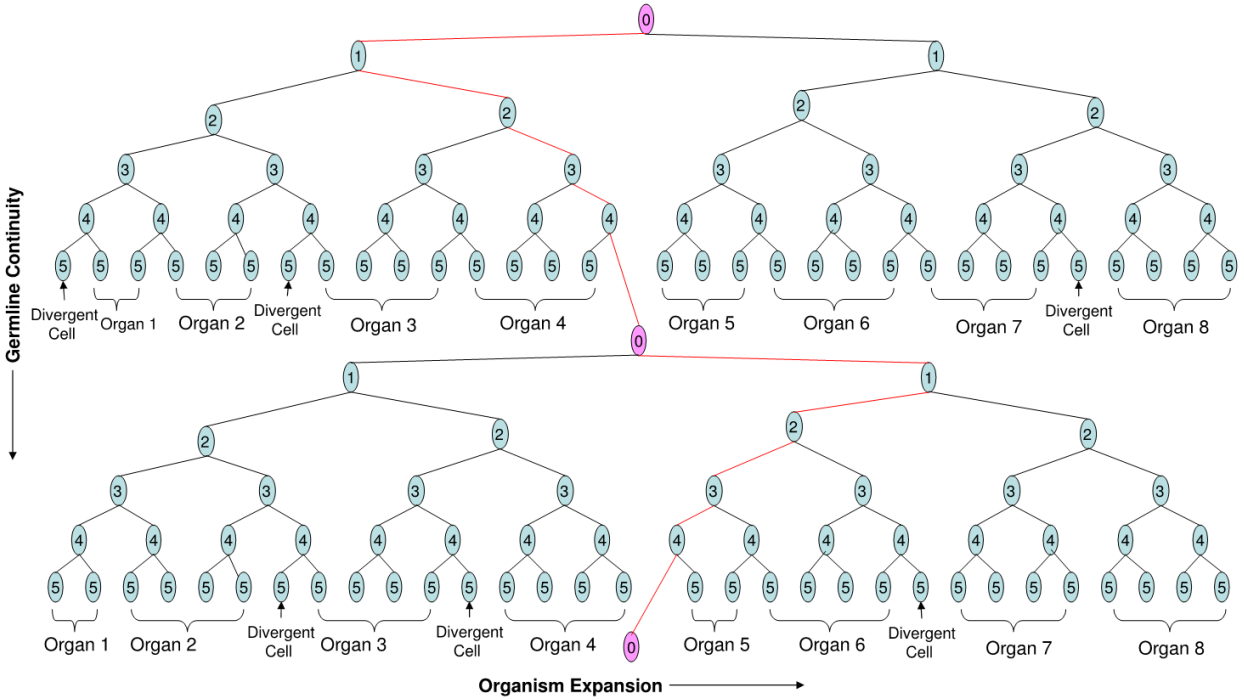

Fig. 14 Germline continuity in multicellular organisms

Notably, although every individual of every generation eventually ages and dies, a continuous germ-cell lineage is preserved throughout. Every offspring egg cell can be traced back to the egg cell of its mother, grandmother, great-grandmother, and still earlier ancestral germ cells. This continuous lineage is not maintained by the individual as a whole, but perpetuated by the germline itself. From the standpoint of biological evolution, therefore, a new life is not a fresh start of genetic information, but simply a new node on this continuous reproductive lineage.

At the same time, once each generation's fertilized egg forms, it goes on to form new tissues, organs, and a complete individual through continuous cell division. Spatial organization thus continually expands, while temporal information remains continuously unbroken. Living individuals are continually renewed, yet the living system itself remains continuous throughout — an important reason why life has been able to continue evolving for billions of years.

From the standpoint of the Unified Recursive Organization Theory, every fertilized egg can be regarded as an Initial SS_0. Once formed, it continually forms higher-level recursive organizational units (SS_i) through structural recurrence and structural recursion, ultimately establishing the complete organism. Once life completes reproduction, however, a new Initial SS_0 is again generated, entering the next round of organizational recursion. Multicellular life is therefore not a one-time act of organizational construction, but a continuous process cycling through $SS_0 \rightarrow SS_i \rightarrow SS_0 \rightarrow SS_i$.

This cycle has two salient features. First, living organization continually expands toward higher levels, achieving individual development (expansion). Second, the germline remains continuously unbroken across generations, allowing life's information to be preserved over the long term (continuity). At the same time, throughout each generation, large numbers of somatic cells are continually renewed, age, and undergo apoptosis, while only a very small number of cells enter the germline of the next generation — a selective process of retention and renewal that embodies the asymmetric renewal of living organization.

Living systems can therefore be summarized in terms of three interrelated and complementary basic organizational principles:

- **Expansion** — continually forming higher-level tissues, organs, and the complete individual through structural recurrence and structural recursion, achieving the sustained growth and increasing complexity of living organization.
- **Continuity** — maintaining the continuity of life's information through the transgenerational transmission of the germline.
- **Asymmetric renewal** — not all cells within living organization share the same fate; the recursive process continually generates divergent cells with different fates. Most somatic cells undertake tissue formation, functional execution, and the maintenance of the individual, ultimately undergoing senescence, apoptosis, or programmed elimination; only a very small number of cells enter the germline, bearing the task of transmitting life's information continuously across generations. This asymmetric retention together with asymmetric elimination constitutes the basic mechanism of life's continual renewal.

  It should be noted that asymmetric renewal is not a strategy exclusive to complex multicellular organisms, but an organizational principle of general significance. In both unicellular and multicellular organisms, cell division is the shared underlying mechanism through which organizational renewal and informational transmission are achieved; asymmetric renewal is simply the organizational expression of this shared mechanism, holding equally in unicellular and multicellular organisms alike — the division of unicellular organisms follows the same principle, differing only in what is asymmetrically partitioned, which varies according to the type of organism

  Oogenesis is a representative example of asymmetric renewal. Through two successive meiotic divisions, a single primary oocyte ultimately gives rise to one mature ovum and

three polar bodies. Although all four cells derive from the same initial oocyte (Initial SS_0), only the mature ovum retains the great majority of the cytoplasm and organizational resources required for development, continuing on into the germline of the next generation, while the three polar bodies fail to obtain the organizational conditions required for continued recursive organization; their life cycle terminates rapidly, and they exit the continuous recursive lineage. Life does not retain all products of division equally, but achieves the continuous inheritance of organizational information through selective retention, while achieving optimal allocation of resources through selective elimination.

Similar instances of asymmetric renewal are widespread across every level of life. During embryonic development, for example, large numbers of transient cells undergo programmed apoptosis; the immune system continually generates and eliminates large numbers of immune cells; intestinal epithelial and skin cells are continually renewed; and the nervous system retains certain cells over the long term while continually renewing its supporting cells. Living organization exists perpetually in a dynamic equilibrium of "partial retention, partial renewal," rather than having all its components renew in synchrony.

Asymmetric renewal is therefore not an isolated developmental phenomenon, but an organizational principle followed universally by living organization. Without selective retention, transgenerational continuity could not form; without selective renewal, new organizational function and adaptive evolution could not arise. Asymmetric renewal is thus an indispensable basic mechanism for the continued evolution of life.

4.10 Boundedness of Structural Recursion and the Regulatory Role of Asymmetric Renewal

The expressions for structural recurrence and structural recursion given by Equations (5), (6) and (8) in Chapter 3, considered in isolation from their biological context, carry no inherent termination condition and could in principle unfold indefinitely. In real living systems, however, structural recursion never occurs independently of its genetic context — it is always synchronized with, and jointly determined by, the same genetic program as asymmetric renewal. Structural recursion in actual living systems is therefore not a process that first expands without restraint and is only afterward brought under the control of a separate mechanism; rather, it is, from the very outset, a bounded expansion process that is genetically controlled and runs in parallel with asymmetric renewal. The stability of the recursive system is jointly maintained by three mechanisms of a different nature.

The first layer is asymmetric renewal itself, which is not a corrective adjustment applied after structural recursion has "gone astray," but an intrinsic program sharing the same genetic origin as structural recursion: each successive layer of cells, in inheriting the genetic program of the original cell (Core), likewise inherits the pre-set rules governing the assignment of division fate. Structural recursion and asymmetric renewal are therefore two outputs given simultaneously, at every step, by the same recursive program — some progeny continue to recurse, while others terminate or differentiate according to pre-set rules — rather than a sequence of events in which one corrects the other after the fact. This is directly supported by empirical work on the invariant lineage of Caenorhabditis elegans: its embryonic development follows an almost entirely determinate sequence of cell divisions, with the fate of the two daughter cells produced at each division determined by the lineage program itself — deterministic from the very first division, rather than triggered by environmental feedback in the course of development (Sulston et al. 1983).

It should be noted that this genetically pre-set character further manifests, in the context of adult stem cells maintaining tissue homeostasis, as a conditional form of genetic programming: whether a cell divides symmetrically depends on an extrinsic input signal — the orientation of its mitotic spindle relative to the stem-cell niche — yet the molecular machinery responsible for sensing the niche signal and orienting the spindle accordingly remains a fixed, genetically encoded, evolutionarily conserved apparatus, rather than a capacity acquired postnatally or shaped by adaptive evolution (Morrison and Kimble 2006). The facultative symmetric/asymmetric switching seen at the adult stage therefore does not constitute a counterexample to the “genetic pre-setting” argument, but rather an extension of that argument to the more complex situation of reading positional information.

Between the deterministic program of genetic pre-setting described above and the immediate environmental correction carried out by the immune system lies a second layer of regulatory mechanism of a different nature: epigenetic loading and adaptive fine-tuning. Unlike the fixed division fate provided by asymmetric renewal, this layer allows the parental generation, during gametogenesis, to convert environmental stresses it has experienced (such as nutritional status, temperature fluctuation, or pathogen exposure) into non-coding RNA fragments and DNA methylation marks, which are imprinted into the gametes and carried forward into the offspring’s initial organizational information source. This process neither alters the DNA sequence itself nor touches the lineage-differentiation program on which asymmetric renewal depends; rather, while leaving the genetically encoded core intact, it pre-sets for the offspring a bounded, reversible degree of adaptive fine-tuning in response to the parental environment (Fitz-James and Cavalli 2022; Carone et al. 2010; Stringer et al. 2013). In terms of its operating timescale, this layer sits between asymmetric renewal (fixed for nearly the entire lifespan, spanning the whole recursive lineage) and immune surveillance (an immediate response to specific damage encountered by the individual in the present), constituting an independent third pathway within the regulation of structural-recursion stability.

The third layer is environmental correction, carried out by a separate, dedicated subsystem — the immune system. The immune system is itself an organizational structure that arises once structural recursion has unfolded to a certain level, and its function is to continually monitor for, and eliminate, cells that deviate from the genetically pre-set trajectory (mutated, damaged, or otherwise abnormal cells), constituting a genuine feedback loop, with continual monitoring and a corresponding elimination response (Burnet 1970; Dunn et al. 2002).

The stability of structural recursion therefore does not depend on a single regulatory mechanism, but is jointly maintained by three mechanisms of a different nature and successively broader operating timescales: asymmetric renewal provides an intrinsic, deterministic pre-setting of division fate, forming part of the recursive program itself, with an operating timescale spanning nearly the entire recursive lineage; epigenetic loading and adaptive fine-tuning provides a bounded environmental response intermediate between the other two, allowing parental experience to permeate the offspring's initial organizational information source at an extremely low proportion without altering the genetically encoded core; immune surveillance provides external feedback, arising from recursion itself and dedicated to addressing environmental deviation. The three correspond respectively to self-selection at the level of design, bounded adaptation at the transgenerational scale, and an immediate corrective subsystem derived from recursion — complementary to one another, and not to be conflated.

It is worth noting that this architecture — a fixed, genetically pre-set circuit that receives a triggering input from the environment — is structurally consistent with the immune surveillance mechanism itself: the immune system is likewise a fixed, genetically encoded apparatus (its recognition and elimination pathways) that determines when to initiate elimination based on an extrinsic input, namely, the presence of abnormal antigens. Together, these two cases suggest that a living system's capacity to respond to its environment is achieved not through postnatally learned or adaptively modified genetic programs, but through conditional response devices that are pre-constructed by the genome — perhaps another concrete instance, at the level of regulatory mechanism, of what this paper terms "structural recurrence."

Together, structural recursion, asymmetric renewal, epigenetic loading and adaptive fine-tuning, and immune surveillance ensure that life can continually form new organizational levels while maintaining informational continuity across generations, thereby achieving the long-term, stable evolution of living systems.

In summary, the Unified Recursive Organization Theory describes not only the formation of living organization in the spatial dimension ($SS_0 \rightarrow SS_i$), but also reveals its regularity of continuity in the temporal dimension. Spatial recursion continually generates new organizational structure, while temporal continuity continually sustains life's information; together, the two constitute the complete spatiotemporal organizational framework of living organization. This also lays the theoretical foundation for the next chapter's further discussion of the intrinsic relationship — "informational attribute driving structural realization" — between organizational structure (SS_i) and holographic informational organization $\Psi(SS_i)$.

Life is not a succession of mutually independent individuals, but a single, continually perpetuated, unified recursive organizational system — one that begins at SS_0, takes SS_i as its organizational form, and is bound together across time by the germline.

Expansion endows life with the capacity to continually form higher organizational levels; continuity ensures the stable transmission of life's information across generations; and asymmetric renewal drives the continual optimization and ongoing evolution of life. Together, the three constitute the basic organizational principles underlying life's long-term perpetuation and continued evolution.

Life has already crossed the organizational threshold of the complete cell. The next chapter further discusses how this complete cell, as the initial SS_0, continually unfolds through continuous recursive organization to ultimately form the complete living individual and its biological holographic properties.

4.11 Transgenerational Germline Pre-setting

This paper defines transgenerational germline pre-setting as follows: while the grandparental generation ($G1$) continues to support the embryonic development of the parental generation ($G2$), the organizational information source of the offspring generation ($G3$) is established simultaneously, thereby forming a continuously nested recursive organization spanning three generations. By contrast, if $G1$ withdraws its support for $G2$'s recursive organizational process immediately after laying eggs or giving birth, so that the transfer of organizational information between $G2$ and $G3$ no longer overlaps with $G1$, this is classified as intergenerational continuity rather than transgenerational germline pre-setting. The criterion distinguishing the two is not the timing of $G3$ germ-cell specification within $G2$ (a process that occurs very early in most

vertebrates), but rather whether *G*1's own recursive organizational process is still organizationally enveloping and supporting *G*2 at the moment *G*3's information source is established. This criterion underlies the discussion of different reproductive modes throughout this section.

Structurally, transgenerational germline pre-setting takes the form of nested recursion rather than sequential recursion, and this nesting is not confined to adjacent generations but can compound across layers, allowing three generations to coexist simultaneously within a single individual (Fig. 15). Under a sequential-recursion interpretation, the initial recursive unit of the parental generation (*G*2), SS_0^2, would only be established after the grandparental generation (*G*1) has completed its recursive unfolding to its final state, SS_{final}^1 (i.e., after *G*1's individual development is complete); similarly, the starting point of the offspring generation (*G*3), SS_0^3, would not appear until *G*2's development is complete. The three generations would follow one another end to end, each independent. However, living systems actually follow nested recursion: when *G*1's own recursion has unfolded to some intermediate level SS_i^1 (i.e., *G*1 has already developed into an adult and is now carrying *G*2, the initial recursive unit of *G*2, SS_0^2, is already established as a substructure within *G*1's SS_i^1. And before *G*2's own recursion, $SS_0^2 \rightarrow ... \rightarrow SS_j^2$, has unfolded to its final state (i.e., while *G*2 itself is still at the fetal stage of development), the initial recursive unit of *G*3, SS_0^3, is already established as a substructure within G2's SS_j^2. Consequently, at the same time slice, SS_0^3 (*G*3) is nested within SS_j^2 (*G*2), and SS_j^2 (*G*2) is in turn nested within SS_i^1 (*G*1), the recursive units of all three generations coexist simultaneously within the same *G*1 individual. This is precisely the meaning of transgenerational germline pre-setting in recursive-structural terms, and it corresponds exactly to the phenomenon of transgenerational oocyte formation in humans: during *G*1's pregnancy, her body already simultaneously carries the recursive starting points of both *G*2 and *G*3.

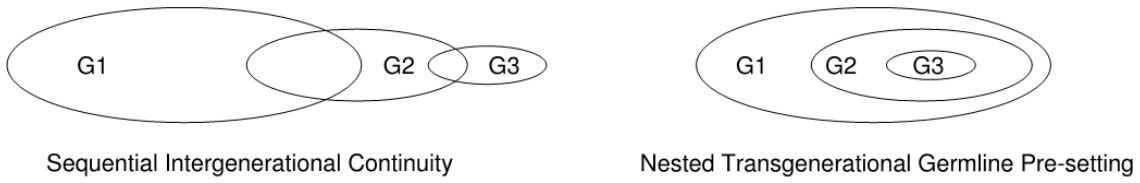

Fig. 15 Comparison of two organizational modes of generational continuity

Taking humans as an example: a new life begins with a fertilized egg (SS_0). After fertilization, the zygote develops through continuous recursive organization into an embryo, a fetus, and eventually a mature individual. Yet before that individual is even born, the information source of the next generation has already begun to be established. For instance, by around 5–6 months of gestation, a female fetus's ovaries have already formed several million primary oocytes. These cells are retained for decades after birth and gradually mature, eventually forming gametes that give rise to the next generation. In other words, before a woman is even born, the initial-state pre-setting of her future offspring's organizational information source has already been completed; and when she later becomes pregnant with a female fetus, that fetus will in turn simultaneously establish the oocytes of the generation after that. Thus, a single pregnancy already connects grandmother, mother, and grandchild across three generations through continuous recursive organization.

One detail worth elaborating is that the transgenerational pre-setting of oocytes is not a simple two-stage sequence of "structure first, information migrating in later." Rather, it is a process in which two lineages within *G*2's own cells unfold along their own separate timelines before later converging — it is not the case that *G*1's cell division produces the germ cells, which are then implanted into *G*2. Developmental biology evidence shows that primordial germ cells are first

induced and specified within early embryonic cells as early as weeks 2–3 of *G*2's own embryonic development, becoming the starting point of *G*3, while the remaining cells proceed toward *G*2's own somatic development. This differentiation event precedes the formation of the genital ridge (the primordium of the ovary): the genital ridge does not independently develop from the intermediate mesoderm until around week 4, and at that point still contains no germ cells at all. It is not until around week 5 that the cells already specified as the *G*3 germline complete their migration and reach the primordial gonad of *G*2; only then do the two begin true coordinated differentiation, culminating around weeks 11–20 of *G*1's pregnancy in the assembly of primordial follicles jointly composed of *G*3 oocytes and the surrounding *G*2 ovarian granulosa cells (Ramakrishna et al. 2025). This pattern, in which the soma and germline diverge early within *G*2's own lineage, develop separately, and are only later co-constructed together, is precisely a molecular-level instantiation of Weismann's germ plasm–soma separation thesis (Weismann 1889), and it corroborates the core thesis of Section 4.5, “Co-evolution of Structure, Function, and Information.”

This organizational principle is not unique to viviparous animals but is broadly present across different modes of reproduction; what differs is where the three-generation recursive overlap occurs, and the specific means by which *G*1 sustains this organizational support.

In **viviparous animals**, while *G*1 is pregnant, *G*2 is still at the fetal stage of development, and the initial germ cells of *G*3 have already been established within *G*2's body. Thus, during a single pregnancy of *G*1, three generations (*G*1, *G*2, and *G*3) already coexist simultaneously within the same individual, forming the typical three-generation nested recursive organization; the human case described above is an instance of this category.

In **ovoviviparous animals**, this organizational relationship holds equally. For example, in some sharks, rays, and vipers, *G*1 retains the fertilized eggs internally for development, while *G*2 relies mainly on yolk to complete its own development. When *G*2 is female, the initial germ cells of *G*3 likewise begin to be established within her body. Thus, regardless of whether *G*2's nutrition comes mainly from a placenta or from yolk, as long as *G*2 has not yet completed her own development while *G*3's organizational information source has already begun to be established, a three-generation nested recursive organization is likewise formed.

In **oviparous animals that require incubation by *G*1**, three-generation nested recursion likewise holds, except that the site of overlap shifts from within *G*1's body to the egg or brooding structure that *G*1 continues to incubate up until hatching — examples include birds incubating eggs on the nest, certain pythons that coil around and actively warm their eggs, mouthbrooding fish (e.g., some cichlids that incubate fertilized eggs in the mouth), and male seahorses' brood pouches. In these species, *G*1 does not withdraw immediately after laying eggs; instead, it continues to organizationally envelop the developing *G*2 through incubation, guarding, or a brood pouch, up until hatching. Before hatching is complete, during *G*2's embryonic development, the initial germ cells of *G*3 have likewise already been established. Thus, the recursive units of *G*1, *G*2, and *G*3 likewise coexist simultaneously; the physical site of coexistence is simply the egg or brooding structure that *G*1 continues to incubate, rather than within *G*1's own body. By contrast, in oviparous animals where *G*1 withdraws immediately after laying eggs and hatching depends entirely on the natural environment, such as most broadcast-spawning bony fish, most amphibians, insects, and most turtles, the organizational support between *G*1 and *G*2 is severed as soon as the eggs are laid. Although *G*3's information source is still established early in *G*2's embryonic development, it no longer overlaps with *G*1's recursive organization; such species are therefore classified as intergenerational continuity rather than transgenerational germline pre-setting.

Although this paper classifies plants under sequential intergenerational continuity rather than nested transgenerational germline pre-setting, during plant development the seed coat tissue from *G*1, the plant body tissue of *G*2, and the floral bud primordia of the future *G*3 may nonetheless coexist for a time on the same plant. However, this spatiotemporal coexistence of three generations of tissue should not be conflated with transgenerational germline pre-setting, because *G*1's seed coat tissue no longer continues to perform an organizational support function for *G*2's embryonic development at that stage. Plants therefore remain classified under intergenerational continuity rather than under the transgenerational germline pre-setting defined in this paper.

Animals and plants both follow the same underlying organizational principle: in animals, the germline is established early in embryonic development and, under the continued organizational support of *G*1, maintains the continuous transmission of organizational information; in plants, the apical meristem is likewise established early in individual development and maintains organizational continuity over the long term, eventually giving rise to new gametes and the next generation. Although the two follow different developmental modes, both fundamentally follow the same organizational strategy, establishing the next generation's organizational information source concurrently with the unfolding of unified organizational information, rather than relying on a mature individual to reorganize the information of life anew.

Is this mechanism merely a contingent strategy of biological development, or is it an organizational constraint that unified recursive organization must satisfy to maintain long-term stability? The next section addresses this question through a reductio ad absurdum analysis.

4.12 Necessity of Transgenerational Germline Pre-setting

To further show that transgenerational germline pre-setting is not an incidental strategy in the course of biological development, but a necessary organizational constraint for the long-term stability of unified recursive organization, the following discussion proceeds by way of a *reductio ad absurdum* argument.

Suppose that living systems possessed no mechanism of transgenerational germline pre-setting; the next generation’s gametes could then form only after the mature individual has completed its development. This would require the mature individual to reorganize its entire living system — one that has already undergone extensive recursive holographic unfolding — and re-compress it into a unified organizational information source capable of initiating the next generation of life. This paper terms this process reverse organizational compression.

It should be noted that the reverse organizational compression discussed here is not lossless data compression in the computational sense, but the reverse reconstruction of the organizational state of a mature living system. A mature living system is a complex dissipative system that has existed for a long time within an open environment; its organizational structure has already undergone sustained organizational differentiation, environmental perturbation, energy dissipation, and information exchange, such that its initial organizational state has irreversibly evolved into a highly complex organizational state. Reverse organizational compression would therefore inevitably introduce new organizational noise, and would also result in organizational information loss — a loss that is not a change in how organizational information is represented, but the irreversible loss of the initial organizational information itself.

If living systems depended on this kind of reverse organizational compression to generate each new generation’s organizational information source, every generational transition would carry

organizational noise and organizational information loss into the new starting point of life. As generations continued, this organizational drift would accumulate progressively, causing unified organizational information to diverge increasingly from life's initial state, with organizational continuity and organizational consistency declining generation after generation — ultimately rendering continuous recursive organization unable to remain stable over the long term.

Living systems in nature, however, show no sign of this kind of generation-by-generation degradation. On the contrary, both animals and plants establish the next generation's organizational information source early in individual development, so that the next generation directly inherits the unified organizational information of the preceding generation's initial-state node, rather than deriving it from reverse organizational compression late in a mature individual's life. Human development is a representative example of this organizational regularity: by the time a female fetus reaches approximately 5–6 months of gestation, large numbers of primary oocytes have already formed within its ovaries, cells that will go on, decades later, to form gametes and give rise to the next generation. That is, while the mother herself is still at the fetal stage of development, the organizational information source of her future offspring has already completed its initial-state pre-setting; and should the next generation likewise be female, the informational source for the generation after that will be established simultaneously within it — forming an informational chain of continuous recursive organization across generations.

The true key to a living system's continuity, therefore, is not the capacity of a mature individual to reorganize the whole of its life's information anew, but the establishment of the next generation's organizational information source in step with the continuous unfolding of unified organizational information. Transgenerational germline pre-setting avoids the accumulation of organizational noise and the loss of organizational information that reverse organizational compression would entail, allowing unified organizational information to be transmitted across generations continuously along the recursive organizational pathway, and preserving the long-term continuity and consistency of organizational structure, organizational function, and organizational information. Transgenerational germline pre-setting is thus not a special developmental phenomenon, but a necessary organizational constraint by which unified recursive organization sustains biological holographic continuity over the long term.

This argument resonates in several respects with existing theories of system reliability and the biology of aging, worth noting here. Rosen (1958) proved mathematically that within any self-repairing system there must exist at least one component that the system cannot itself repair or replace — a logical limit on "complete self-maintenance." Gavrilov and Gavrilova (2001) further showed that even when biological systems delay the exposure of this limit through large numbers of redundant elements (such as functionally equivalent cells or copies of repair enzymes), the redundant reserve itself is inevitably depleted over time, causing the individual failure rate to rise inescapably with age. The disposable soma theory (Kirkwood 1977) explains, from the standpoint of evolutionary resource-allocation economics, why organisms tend to invest limited resources preferentially in the germline rather than in somatic maintenance — an idea traceable to Weismann's (1889) classic account of the separation of germ plasm and somatoplasm.

The argument for transgenerational germline pre-setting advanced in this paper addresses a different, complementary question: the architectural division of labor between redundancy and asymmetric renewal in maintaining a system's organizational continuity. Redundancy delays the exposure of individual-level failure through parallel, substitutable elements, functioning essentially as an online contingency strategy — it cannot prevent the redundant reserve from being gradually

depleted (Gavrilov and Gavrilova 2001), only postpone the onset of failure. Asymmetric renewal (Section 4.9 of this paper), by contrast, establishes, through germline sequestration and transgenerational germline pre-setting, an independent informational source with minimal accumulated damage before the individual's redundancy is exhausted — achieving not a delay of failure, but a renewal of the entire organizational information carrier at the scale of generations. Redundancy and asymmetric renewal are therefore not two expressions of the same mechanism, but complementary organizational strategies operating at two different scales — individual maintenance and generational continuation — the former a contingency measure, the latter a system-level renewal.

5 Biological Holography

5.1 Recursive Unit and Information

Chapter 4 has already established the basic framework of the Unified Recursive Organization Theory and shown how living systems, through continuous recursive organization, germline continuity, asymmetric renewal, and transgenerational germline pre-setting, achieve the continuous transmission of unified organizational information across hierarchical levels and generations. On this basis, biological holography ceases to be a living phenomenon requiring an additional assumption, and instead becomes an organizational outcome that naturally arises as unified organizational information continually unfolds through continuous recursive organization. This chapter therefore proceeds, on the basis of the Unified Recursive Organization Theory, to systematically analyze the organizational nature of biological holography and the mechanism by which it forms.

The Unified Recursive Organization Theory uniformly denotes the recursive organizational unit at any level as SS_i. Here, i denotes the recursive level; SS_0 denotes the initial recursive unit formed once living recursive organization begins; and SS_1, SS_2, …, SS_i denote the organizational units formed at each successive level of continuous recursion. Recursive units at different levels may differ entirely in material composition, spatial scale, and organizational function, yet all follow the same organizational regularity.

Recursive organization manifests not only as the continuous formation of organizational structure, but also as the continuous formation of information. $\Psi(SS_i)$ is the informational attribute carried by SS_i itself, encompassing structural information, DNA/RNA sequence information, and all other informational content, whose composition is already given by Equation (10) ($\Psi(SS_i) = \Psi_b(SS_i) + \Psi_s(SS_i)$). $\Psi(SS_i)$ is not an independent entity external to, and corresponding with, SS_i, but the expression of SS_i's own informational content; this informational content derives fundamentally from the continuous inheritance of the core genome — structure, function, and information unfolding in step at every recursive level (see Section 4.5) — and constitutes precisely the intrinsic driving force behind the recursive unfolding of SS_i into SS_{i+1}.

5.2 Recursive Holographic Unfolding

As an intrinsic information attribute of SS_i, $\Psi(SS_i)$ unfolds in step with continuing unified recursive organization into the informational content of the new level, $\Psi(SS_{i+1})$. As new recursive organizational units continually form, their informational content forms new organizational levels in step — the two are two aspects of the same recursive process, rather than evolving independently and only subsequently corresponding with one another. The development of living organization

therefore manifests not only as the continuous formation of organizational structure and organizational function, but also as the continual unfolding of unified information throughout continuous recursive organization.

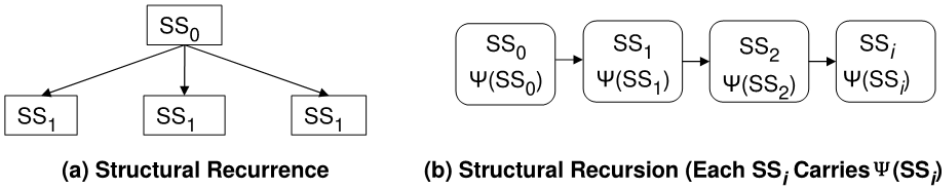

Fig. 16 Two fundamental organizational mechanisms in the unified recursive organization theory

In Fig. 16, panel (a) shows structural recurrence generating multiple recursive organizational units at the same hierarchical level, and panel (b) shows structural recursion progressively forming higher-level recursive organizational units; in both panels, each recursive organizational unit SS_i carries a unique organizational information potential $\Psi(SS_i)$ as an intrinsic attribute of its own state.

The process of recursive holographic unfolding is shown in Fig. 16. Structural recurrence continually extends recursive organizational units at the same level, as in the repeated formation $SS_0 \rightarrow SS_1$. Structural recursion continually forms higher-level recursive organizational units, as in $SS_0 \rightarrow SS_1 \rightarrow SS_2 \rightarrow \ldots \rightarrow SS_i$. Throughout this process, each recursive organizational unit continually carries its own informational attribute; the two form new organizational levels in step, rather than evolving independently and subsequently being brought into correspondence.

It should be noted that the formation of a new recursive organizational unit does not mean that the living system is continually generating new underlying information. On the contrary, as unified recursive organization proceeds, the same unified information continually acquires new organizational realizations, progressively forming new organizational structure, new organizational function, and new organizational relationships. The continual increase in biological complexity is not the result of a continual increase in underlying information, but the result of unified information continually unfolding and being realized.

This paper defines this layer-by-layer realization of unified information throughout continuous recursive organization as recursive holographic unfolding. Here, *Recursive* indicates that the unfolding of information always follows the regularity of unified recursive organization; *Holographic* indicates that unified information continually maintains a continuous connection between whole and part; and *Unfolding* indicates that unified information continually acquires new organizational realizations, rather than continually generating new underlying information.

The process of 3D printing offers an intuitive analogy. Once the printing program is fixed, the printing process as a whole does not continually generate new programs, but rather realizes the same program, step by step, into a complete structure through material deposition. As printing proceeds, the structure becomes increasingly complex, while the underlying program remains unchanged. The unfolding of information within unified recursive organization is analogous: unified information remains continuous throughout, while recursive organization continually realizes it as new organizational structure, organizational function, and organizational relationships. The continual increase in biological complexity arises from the continual unfolding of unified information, not from a continual increase in underlying information.

Recursive holographic unfolding is not a process independent of the Unified Recursive Organization Theory, but the natural manifestation, in the process of living organizational formation, of $\Psi(SS)$ as an intrinsic information attribute of SS, as established in Equation (10).

5.3 Continuity of Unified Organizational Information

The fundamental reason recursive holographic unfolding can proceed continuously is that unified information maintains continuous inheritance throughout. Every recursive organizational unit possesses its own informational attribute $\Psi(SS)$ (Equation 10). As living organization continually recurses to form new organizational levels, organizational structure continually expands and organizational function continually strengthens, while unified information runs continuously through the entire recursive organizational process, forming a continuous system of informational inheritance. The development of living organization therefore manifests not only as the continuous formation of recursive organizational units, but also as the continuous inheritance of unified information.

For any given living individual, every cell can be traced, through a continuous cell lineage, back to the same fertilized egg. This fertilized egg is therefore not only the starting point of biological development, but also the common origin of that individual's unified information. Although this paper defines every complete cell uniformly as a recursive unit (SS_0), the fertilized egg holds a special theoretical status for any given individual: it is the Initial SS_0 to which all of that individual's cells can be traced in common. Every somatic and germ cell within a living individual derives from this common origin and continuously inherits its unified information.

Modern biology has already demonstrated that the genome remains highly continuous throughout normal biological development. However, the structural differences, functional differences, and organizational relationships that form among different cells cannot be fully explained by the genome alone. In the Unified Recursive Organization Theory, unified information remains continuous throughout, and these differences can be understood as different organizational realizations of unified information formed under different recursive organizational conditions. After continuous cell division, for example, the same fertilized egg can give rise to many different cell types — neurons, muscle cells, hepatocytes, and epithelial cells among them. These cells share the same genome, yet form entirely different organizational structures, organizational functions, and organizational relationships. These differences do not arise from any change in the genome, but from different organizational realizations of unified information formed under different recursive organizational conditions.

As continuous recursive organization proceeds, new recursive organizational units continually form, giving rise correspondingly to new organizational structure, organizational function, and organizational relationships. This does not, however, mean that mutually independent informational systems have formed, but rather that unified information has further unfolded at the new recursive organizational level. Although living organization continually forms new organizational levels, unified information remains continuous throughout, running through the entire developmental process of living organization.

The continuous inheritance of unified information can explain many natural phenomena in plant life. In cutting propagation, for example, a single stem segment can redevelop into a complete plant; in air layering, a local tissue can re-form its own root system and grow independently. These phenomena show that local tissue continues to retain unified information. Once appropriate

recursive organizational conditions are re-established, unified information can once again enter the process of recursive holographic unfolding.

Similarly, experiments involving somatic cell nuclear transfer (SCNT) in animals, tissue culture, and induced pluripotent stem cells (iPSCs) likewise show that tissue differentiation does not entail the loss of unified information, but rather that unified information has formed a different organizational realization under different recursive organizational conditions. Once appropriate recursive organizational conditions are re-established, unified information can unfold once again. These phenomena do not mean that local tissue has reacquired new information, but rather show that unified information remains continuous throughout, simply re-entering the unfolding process under new recursive organizational conditions.

5.4 Biological Holography

The preceding analysis shows that the formation of living systems manifests not only as the co-evolution of structure, function, and information, but, still more fundamentally, as the sustained unfolding of unified organizational information throughout continuous recursive organization. Unified organizational information runs continuously through the formation, development, and evolution of living organization, maintaining whole–part consistency across the different levels of life. Living systems therefore possess a holographic character intrinsically. This paper defines this whole–part consistency, naturally arising from unified recursive organization, as biological holography.

Biological holography is a natural product of recursion, and this holds equally at the informational and the structural level; the two are not related as principal and subordinate, but constitute two parallel lineages of continuous inheritance. DNA semiconservative replication ensures that sequence information is transmitted completely at every step of recursion (Meselson and Stahl 1958); at the same time, cell membranes and every kind of membranous structural organelle — whether or not they carry their own DNA/RNA — are never generated de novo, but always grow and expand by inheriting pre-existing membrane structure as a template (Cavalier-Smith 2000). This mechanism of membrane heredity has operated in parallel with, and as a mutual precondition of, DNA heredity since the origin of life. What is transmitted through structural recursion is therefore not only the gene sequence, but also the membrane seed that serves as a structural template; structure, function, organizational relationships, and information achieve co-evolution precisely through these two parallel lineages of inheritance, neither of which tolerates interruption — rather than information unilaterally driving structure to follow passively. The physical mechanism underlying each of these two lineages of inheritance is set out below.

The mechanism of semiconservative replication dictates that the two daughter cells produced by every division, whatever their respective fates, each receive a copy of the complete genome, rather than a partial inheritance. This means that the continuity of the informational attribute $\Psi(SS_i)$, which drives the recursive unfolding of SS_i, is not conferred by this paper's definition of the relationship between $\Psi(SS)$ and SS, but is instead a matter of physical fact: the replication mechanism itself simply does not permit a break in continuity.

This point already has direct empirical support. Nuclear transfer experiments show that even highly differentiated somatic cells — corresponding to the terminal branch reached through asymmetric renewal within structural recursion — retain, within their nuclei, the complete genomic information needed to direct the development of an entire individual (Gurdon and Uehlinger 1966; Wilmut et al.

1997). Differentiation terminates a cell's continued unfolding along its original recursive path, but does not truncate the completeness of its informational attribute Ψ.

It should be noted that a small number of cell types — mature red blood cells, lens fiber cells of the eye, and lymphocytes that have undergone V(D)J recombination, among others — actively eliminate their nucleus or rearrange their gene sequence during differentiation. These cases do not constitute a counterexample to the argument above: they are terminal events pre-arranged by the genetic program itself, not an informational discontinuity caused by a failure of the replication mechanism or by external damage, and thus still fall under the basic regularity of "structure, function, and information recursing in step" (see Section 4.5) — the unfolding form of the informational attribute Ψ undergoes a predetermined transformation along that particular terminal branch, rather than being lost by chance.

Structural inheritance follows an equally strict requirement of continuity. It is an established principle in cell biology that only two classes of cellular component are never generated de novo: chromosomes and membranes. Structures such as ribosomes and microtubules can reassemble from free molecules through self-assembly, but the endoplasmic reticulum, Golgi apparatus, mitochondrial membrane, cell membrane, and every other membranous structure can only ever grow and expand by inheriting a pre-existing membrane fragment as a template (Cavalier-Smith 2000). This is entirely consistent with the phenomenon described in Section 4.3, in which structural organelles retain only 1–10% of their core components at division, the remainder being restored through self-organized regrowth — the retained core component is precisely the inherited membrane seed, not a dispensable remnant. Even structural organelles that carry no DNA/RNA of their own therefore owe their continuity not to a fortuitous assembly of environmental conditions, but to membrane heredity, a mechanism as fundamental as DNA heredity and equally intolerant of interruption.

Biological holography therefore does not depend on this paper's formal definition of $\Psi(SS)$ in order to hold, but is rooted in two more fundamental physical facts: at every step of structural recursion — whether toward continued expansion or asymmetric termination — its sequence information is transmitted continuously and without interruption by DNA semiconservative replication, and its structural information is likewise transmitted continuously and without interruption by the parallel mechanism of membrane heredity. Biological holography is the natural manifestation, at the organizational level, of these two parallel physical continuities, rather than the outcome of either one acting alone.

It should be emphasized that the biological holography proposed in this paper is not built upon optical holographic theory. Optical holography serves only as a physical analogy for understanding the relationship between whole and part, whereas the theoretical basis of biological holography in this paper derives from the Unified Recursive Organization Theory itself — including SS as the structural realization of its intrinsic informational attribute $\Psi(SS)$ (Equation 10), recursive holographic unfolding, and the continuous inheritance of unified information.

Nor does biological holography imply that any local part of a living system can restore a complete individual under any conditions. Whether unified information can continue to unfold still depends on whether appropriate recursive organizational conditions are re-established. A plant cutting can re-form a complete plant because it is able to re-establish continuous recursive organization — roots, stems, and meristematic tissue; a mature animal somatic cell generally cannot re-form a complete individual, not because unified information has been lost, but because it lacks the

organizational conditions needed to restart continuous recursive organization. Once appropriate recursive organizational conditions are met, unified information can continue to unfold, forming new organizational structure, organizational function, and organizational relationships.

The novelty of this paper's treatment of biological holography lies not in rediscovering already-known biological facts such as continuous cell lineage, continuous genomic inheritance, tissue regeneration, or cloning, but in proposing the Unified Recursive Organization Theory and, on this basis, clarifying the driving relationship between a recursive organizational unit and its intrinsic informational attribute — further demonstrating how unified information continually unfolds through continuous recursive organization to ultimately produce the whole–part consistency of a living system. Biological phenomena that were previously understood independently of one another thereby receive a unified explanation within the framework of the Unified Recursive Organization Theory.

5.5 Asymmetric Renewal and the Continuum of Biological Holography

The germline sequestration and transgenerational germline pre-setting discussed in Sections 4.9–4.12 represent only one evolutionary pathway among several by which complex animals achieve biological holography. Broadening the view across different levels of biological complexity reveals that biological holography is in fact realized along a continuous spectrum, ranging from cases in which holography holds almost trivially, with no dedicated mechanism required, to cases in which it must be actively and elaborately maintained. This section examines that spectrum in order of increasing complexity.

Unicellular organisms: holography as a trivial consequence

Unicellular organisms admit no distinction between part and whole: cell division does not involve part of the body becoming offspring while the remainder is sacrificed as soma; the entire organism itself becomes the next generation. Biological holography is therefore not a conclusion requiring a dedicated mechanism at this level, but the only possible mode of existence for this level of organization.

As discussed in Section 4.9, asymmetric renewal is a general organizational principle running through both unicellular and multicellular organisms, differing only in what is asymmetrically partitioned across organism types. In yeast that reproduce by budding (such as *Saccharomyces cerevisiae*), the mother cell and the newly formed bud are morphologically asymmetric from the outset: the mother cell undergoes progressive senescence with each successive division (replicative aging), while the bud begins its own division cycle in a near-"reset" state. Existing research suggests that this asymmetry in aging is not a passive outcome but the result of active, asymmetric partitioning by the cell — aging-associated factors such as extrachromosomal ribosomal DNA circles and aggregates of damaged protein tend to be retained preferentially in the mother cell rather than distributed randomly to the bud (Shcheprova et al. 2008). It should be emphasized that this asymmetric partitioning acts on damage and metabolic byproducts, not on genomic information itself: the mechanism of DNA semiconservative replication (see Section 5.4) ensures that both mother and bud receive a complete copy of the genome at every division. Yeast budding therefore does not constitute a counterexample to the trivial holography of unicellular organisms, but is instead a concrete instance of the same principle of asymmetric renewal holding at the unicellular level.

Structurally simple multicellular animals and plants: lifelong totipotency

Multicellular animal lineages with a relatively simple body plan and a low degree of organ differentiation — including both radially symmetric cnidarians such as *Hydra* and bilaterally symmetric but structurally simple flatworms such as planarians — rely on multipotent cells distributed throughout the body to maintain tissue plasticity for life, differentiating germ cells from this pool only when reproduction is required, rather than sequestering a germline early in development as complex animals do. The clearest expression of this strategy is the remarkable regenerative capacity such organisms typically display — a planarian cut into multiple fragments can regenerate a complete individual from each fragment independently, offering perhaps the most direct empirical demonstration of holography's defining claim: that a part contains sufficient information to reconstruct the whole.

Vascular plants likewise generally rely on the apical meristem to maintain lifelong stem-cell activity, sustained through hormonal concentration gradients and a feedback regulatory network (such as the WUSCHEL–CLAVATA feedback loop) (Mayer et al. 1998; Schoof et al. 2000) that keeps this population of cells continuously dividing without over-proliferating. Vascular plants (ferns, gymnosperms, and angiosperms) account for over 90% of all land plant species, making them the dominant group within the plant kingdom rather than a marginal branch.

The totipotency of plant somatic cells was first proposed as a theoretical prediction by Haberlandt (1902), and was first experimentally confirmed by Steward et al. (1958) through somatic embryogenesis in carrot root tissue: ordinary, differentiated plant tissue can, under appropriate hormonal induction, autonomously re-initiate an embryo-like developmental process — without requiring the cytoplasmic environment of an egg cell at all — and ultimately develop into a complete plant. This capacity is now understood to be a general property of plant cells. The ease of experimental induction varies considerably across species and cell types — cereal crops and other monocots, for instance, have historically shown lower regeneration efficiency and stronger genotype dependence — but this variation more plausibly reflects the limitations of current induction protocols than any absence of the underlying capacity: viable regeneration protocols have, in fact, been progressively established even for monocot crops once considered recalcitrant, as induction techniques have continued to improve. In a sense, somatic embryogenesis offers an even more direct empirical demonstration of holography than animal somatic cell nuclear transfer, which still requires the cytoplasmic environment of an egg cell to re-initiate development, whereas somatic embryogenesis requires no such vessel at all.

An evolutionary trade-off: why complex animals adopted the more costly strategy

The strategy of lifelong totipotency is not without cost. Because floral buds and germ cells differentiate late, from ordinary meristematic tissue that has already undergone years of growth and countless rounds of mitotic division, rather than being specially sequestered and protected early in development, somatic mutations accumulated over the plant's lifetime could, in principle, infiltrate the germline and be transmitted to offspring — a sharp contrast to the germline of animals, which is shielded by the Weismann barrier (Weismann 1889), though this barrier has since been revisited in light of epigenetic evidence (Nilsson et al. 2020)

This contrast offers a plausible evolutionary rationale for the germline-sequestration mechanism of complex animals argued for in Sections 4.9–4.12: animals with a complex body plan and highly differentiated organ systems likely evolved the comparatively more "costly" mechanism of transgenerational germline pre-setting precisely to circumvent the risk of somatic-mutation infiltration inherent in the lifelong-totipotency strategy — sequestering and specially protecting the

germline early, at the cost of sacrificing the flexibility of being able to reconstruct the whole organism from any part at any time, in exchange for higher informational fidelity.

This continuum, spanning unicellular organisms, structurally simple multicellular animals, plants, and complex animals, lends further support, across the full range of biological complexity, to this paper's central thesis in Section 5.4 — that biological holography is a natural outcome of unified organizational information unfolding through continuous recursive organization, rather than a living phenomenon requiring an independent assumption. Whichever pathway is taken, the same two underlying organizational principles — structural recursion and asymmetric renewal — are present throughout.

6 Conclusion

This paper has proposed the Unified Recursive Organization Theory, establishing a Domain–Boundary framework applicable to natural systems, and further introducing two basic organizational mechanisms — structural recurrence and structural recursion — to provide a unified description of how organizational structure at different scales forms, expands, and evolves. On this basis, the paper has clarified the informational attribute Ψ of the recursive organizational unit (*SS*) and its intrinsic relationship in driving recursive unfolding, and has proposed recursive holographic unfolding to describe the mechanism by which unified organizational information unfolds and is realized, layer by layer, throughout continuous recursive organization.

Building on this theoretical framework, the paper has further analyzed the mechanism by which organizational continuity forms in living systems. Drawing on representative biological phenomena — continuous cell lineage, germline continuity, asymmetric renewal, and transgenerational germline pre-setting — it has shown that living systems do not rely on mature individuals to reconstruct the next generation's organizational information anew, but instead achieve continuous transmission of unified organizational information across hierarchical levels and generations through the synchronized establishment of an initial-state organizational information source within continuous recursive organization. A further *reductio ad absurdum* argument shows that, were living systems to rely on mature individuals performing reverse organizational compression to generate a new organizational information source, organizational noise and organizational information loss would inevitably accumulate generation after generation, undermining organizational continuity and organizational consistency. Transgenerational germline pre-setting is therefore not a special developmental strategy, but a necessary organizational constraint by which unified recursive organization sustains its stability over the long term.

The paper further shows that germline sequestration and transgenerational germline pre-setting are not the only pathway to biological holography. By comparing how unicellular organisms, structurally simple multicellular animals, plants, and complex animals achieve whole–part consistency at different levels of biological complexity, the paper reveals that biological holography is realized along a continuous spectrum — from the near-costless, trivial holography of unicellular life, to the direct holography enabled by lifelong totipotent cells, to the high-fidelity holography enabled by germline sequestration — with structural recursion and asymmetric renewal serving as shared underlying organizational principles throughout, differing only in the cost and fidelity of their realization as a function of complexity.

Within this theoretical framework, biological holography is no longer regarded as a living phenomenon requiring an independent assumption or additional proof, but an organizational property that naturally presents itself as unified organizational information continually unfolds

through continuous recursive organization. Whenever unified organizational information sustains organizational continuity and organizational consistency across hierarchical levels and generations, a holographic correspondence between whole and part necessarily follows.

This paper has attempted to establish a unified organizational descriptive framework for natural and living systems, proceeding from organizational regularity rather than from any specific biological mechanism. Although many questions remain to be further refined and validated — the quantitative description of the organizational information potential Ψ, the mathematical expression of organizational evolution, and unified validation across different natural systems, among others — the Unified Recursive Organization Theory offers a new theoretical perspective for understanding cross-scale organizational formation, organizational continuity, and biological holography in nature, and lays a unified theoretical foundation for further exploring the informational evolution of complex organizational systems.

Biological holography is therefore not an assumption that the Unified Recursive Organization Theory must additionally introduce, but a result that naturally emerges from the continuous recursive unfolding of unified organizational information.

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