

PFN 2023

6th Yamada Symposium on "Diversity of Biological Patterns and Forms in Nature: toward a Comprehensive Understanding"

Tue. 1st - Thu. 3rd August 2023

Venue

Global Front, Meiji University, Tokyo Surugadai Campus



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Invited Speakers

Philip Ball	(Science writer, London, UK)
Haruhiko Fujiwara	(The University of Tokyo)
Sylvain Gerber	(Muséum National d'Histoire Naturelle, France)
Shigeru Kondo	(Osaka University)
Reiko Kuroda	(Chubu University)
Philip K. Maini	(University of Oxford, UK)
H. Frederik Nijhout	(Duke University, USA)
Hiraku Nishimori	(Meiji University)
Takao Ubukata	(Kyoto University)
Toshio Sekimura	(Chubu University)
Hiroyuki Shima	(University of Yamanashi)
Oliver Steinbock	(Florida State University, USA)

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Program

* Please click on the lecture title to open the abstract.

1st August

13:30-13:40	Opening Address Hiroshi Matano (Meiji University)
13:40-13:50	Welcome Greeting Ikuko Hara-Nishimura, D. Sc. (Director, Yamada Science Foundation)
13:50-14:00	Information from Organizing Committee
<i>Opening Session</i>	Diversity of Biological Patterns and Forms in Nature I Chair : <i>Philip K. Maini</i> (University of Oxford, UK)
14:00-15:00	Philip Ball (Science writer, London, UK) <i>Symmetry breaking from Physics to Biology</i>
15:00-15:30	<i>Break</i>
<i>Session 2</i>	Diversity of Biological Patterns and Forms in Nature II Chair : <i>Hiroshi Matano</i> (Meiji University)
15:30-16:30	Philip K. Maini (University of Oxford, UK) <i>Modelling collective cell behaviour in development and disease</i>
16:30-17:30	Shigeru Kondo (Osaka University) <i>How organisms transform 2D patterns into 3D forms</i>

2nd August

<i>Session 3</i>	Diversity of Biological Patterns and Forms in Nature III <i>Co-Chair :Toshio Sekimura (Chubu University) and Haruhiko Fujiwara (The University of Tokyo)</i>
10:00-10:45	Haruhiko Fujiwara (The University of Tokyo) <u><i>Mechanisms and evolution of Female-limited Batesian mimicry in Papilio butterflies</i></u>
10:45-11:30	Toshio Sekimura (Chubu University) <u><i>(1) A model for pattern formation and (2) population dynamics of the mimetic butterfly Papilio polytes in the Sakishima Islands, Japan: Mathematical analysis and Computer simulations</i></u>
11:30-11:45	<i>Break</i>
11:45-12:30	H. Frederik Nijhout (Duke University, USA) <u><i>The development and evolution of butterfly wing patterns: finding the primitive pattern</i></u>
12:30-13:30	<i>Lunch</i>
<i>Session 4</i>	Morphology and Evolution <i>Chair :Tomohiko Yamaguchi (Meiji University)</i>
13:30-14:15	Reiko Kuroda (Chubu University) <u><i>Snail coiling: CRISPR editing of a single gene turns righties into lefties</i></u>
14:15-15:00	Sylvain Gerber (Muséum National d'Histoire Naturelle, France) <u><i>Morphospace approaches to evolution: Geometric and developmental considerations</i></u>
15:00-15:45	Takao Ubukata (Kyoto University) <u><i>Functional morphospace analysis of molluscan shells</i></u>

15:45-16:00	<i>Break</i>
16:00-16:45	<i>Short talks</i>
16:45-18:00	<i>Poster Session</i>
18:00-20:00	<i>Banquet</i>

3rd August

<i>Session 5</i>	Mathematical modeling for Patterns and Forms in Nature <i>Co-Chair :Hiraku Nishimori (MIMS) and Ken-ichi Nakamura (MIMS)</i>
10:00-10:45	Hiroyuki Shima (University of Yamanashi) <u><i>Mechanical Optimality Hidden in the Structure of Plants</i></u>
10:45-11:30	Oliver Steinbock (Florida State University, USA) <u><i>Spiral patterns and morphology in chemical systems</i></u>
11:30-11:45	<i>Break</i>
11:45-12:30	Hiraku Nishimori (Meiji University) <u><i>Autonomous Workload Regulation Mechanism in Foraging Ants</i></u>
12:30-12:40	<i>Closing Address</i> Hiraku Nishimori (Meiji University)

Symmetry breaking from physics to biology

Philip Ball



What is the developmental source of biological form? The question preoccupied natural philosophers from Aristotle to William Harvey to Rudolf Virchow, and it remains debated today. Early ideas assumed that biological form was either already manifest in some way within the embryo – the preformationist idea, famously illustrated by the Dutch mathematician and microscopist Nicolaas Hartsoeker’s drawing of the homunculus in a sperm in the seventeenth century – or emerged via the guidance of a kind of life force or soul, as Aristotle asserted: the essentially teleological position called epigenesis. We might now regard both theories as sleights of hand designed to circumvent rather than to explain what is now seen as an example of symmetry breaking.

With the emergence of modern genetics, questions about form in biology became questions about genes: the phenotype of the developing organism was considered to be programmed by the genotype. DNA could in this view be regarded as a kind of informational homunculus: form already existed in the embryo, but in an encoded format, which Erwin Schrodinger famously called the “code-script” of life.

In his approach to the origins of embryogenesis, Alan Turing was thus going against the grain. It may be partly for this reason that his 1952 paper on morphogenesis had little impact for several decades. His approach follows the physical scientist’s instinct to express the problem at hand in the simplest possible terms, and then to explore what the minimal requirements are of a model that captures the essential phenomena. Turing pointed out that the question of how an embryo develops and acquires shape and form – bilateral symmetry, say, and the budding of limbs – seemed indeed to be one of spontaneous symmetry-breaking.

In this presentation I shall set out to explore how, by expressing the question in this manner, Turing aligned it with what is arguably the major theme of twentieth-century physics.

Perhaps the first intimation of the role of symmetry in physical processes was expressed in 1894 by Pierre Curie in a paper titled “On symmetry in physical phenomena”. Here he asked the question: what is the relationship between the physical and the symmetry properties of a system? Curie stated the fundamental principle of symmetry breaking by saying that some phenomena occur when a symmetry is *removed*: he said that “asymmetry is what creates the phenomenon”.

In Curie’s doctorate in the early 1890s on magnetism, he reported that ferromagnets such as iron will lose their magnetism when heated: this falls to zero at a temperature now called the Curie temperature. The onset of spontaneous magnetization by cooling through the Curie temperature occurs when random orientations of the atomic spins due to thermal motion switch to a collective state of mutual alignment.

This phase transition was studied in the 1920s using the Ising model, a lattice model developed by Wilhelm Lenz and his student Ernst Ising. It was soon appreciated that the

same model could be used to represent the transition between the gaseous and liquid states of matter, as investigated in the 1870s by Johannes Diderik van der Waals. Here the presence of a particle at a point in the lattice denotes the liquid, while its absence denotes a gas. Cooling a magnet through its Curie temperature then looks equivalent to cooling a fluid through its critical point, where the uniform symmetry of the supercritical state breaks to permit two distinct phases of differing density.

This connection was arguably the first glimpse of *universality* in physics: the idea that there is a deep parallel between systems that look superficially as though they share nothing in common. It stems from the fact that many-body behaviour often does not discriminate between the fine differences in the natures of those bodies: all that matters are the general features of how they interact, such as how many neighbours feel the influence of each body and the dimensionality of the system.

The 1956 proposal by Tsung Dao Lee and Chen Ning Yang that the weak interaction might break left-right symmetry (parity violation), experimentally confirmed by Chien-Shiung Wu that same year in experiments on beta decay, opened the path for the unification of the electromagnetic and weak interactions. The idea was developed in the 1960s by Sheldon Glashow and Abdus Salam, who had to introduce the symmetry breaking by hand. Their theory predicted three massive new bosons, later identified with the W and Z bosons that mediate the weak force, along with the massless photon. In the later 1960s Steven Weinberg showed how this symmetry breaking could happen spontaneously. The theory was verified by the discovery of the W and Z bosons in CERN's Proton-Antiproton Collider in 1983.

This Nobel-winning work on electroweak symmetry breaking was intimately tied up with the theory of the Higgs field and the Higgs boson. The fundamental insight here came in the late 1950s from theoretical physicist Yoichiro Nambu, who saw an analogy between the theory of superconductivity and quantum field theory. The idea won Nambu the 2008 Nobel prize for "the discovery of the mechanism of spontaneous broken symmetry in subatomic physics". But Nambu's work raised new problems, and it was by resolving them in the early 1960s that Peter Higgs and others concluded that space is permeated by the Higgs field, which exerts a drag on the particles and so affords them mass.

Turing's work on morphogenesis takes on a different complexion when considered against this context. Symmetry breaking is, one might say, nature's way of making many from one: of developing complexity out of simplicity. In this way it offers a kind of order and form for free: a distinction between a *here* and a *there* in what was initially a homogeneous system. Biology, it is now clear, exploits this source of organization to produce structure at scales well beyond the molecular. Turing's mechanism is just one among several now known to feature in the living world at scales ranging from the cellular to the ecological.

The broader question is how the palette of shapes and patterns available from spontaneous symmetry breaking interacts with natural selection. To what extent can evolution adapt and modify Turing structures, for example? Are all such structures necessarily adaptive at all? Or are we too readily tempted, when we see order and regularity in biology, to attribute a function to it? Might some of it, at least, represent nothing more than the intrinsic creative potential in the natural world?

Modelling collective cell behaviour in development and disease

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Synopsis: Understanding collective movement is a major and important challenge. In the context of cell movement, we present two case studies: (i) cancer and (ii) neural crest (normal development). Using partial differential equation models, and hybrid cell-based models, we show how modelling can increase our understanding of collective cell invasion and migration.

Collective movement occurs throughout nature across a multitude of scales, from the long-distance movement of whales, to flocking starlings, to bacterial pattern formation. Understanding what are the hallmarks of collective movement is still an open question. With colleagues, I have been studying this problem in the context of cell movement and I will present some results from this work in the context of disease spread and normal development. Understanding how cancer cells invade tissue is an important part of preventing the disease spreading. Several models have been proposed for this. Recently, we proposed a partial differential equation model for this phenomenon in which cells co-operate. That is, instead of having a generalist population that can overcome obstacles and invade, we consider two specialist populations. In this context, we consider two barriers to invasion: normal cells and the extracellular matrix, and we consider two cancer cell types: one that produces lactic acid that can kill normal cells, and one that produces matrix-degrading enzymes. We analyse the travelling wave behaviour of this system via linear stability analysis and numerical simulation. We then analyse in more detail show a simplified sub-model, with degenerate cross-diffusion and a continuum of steady states, and find that it poses challenging problems for travelling wave analysis.

We then study normal development in the context of the cranial neural crest. These are cells that leave the neural tube and migrate to form part of the skull. Neural crest cells give rise to many parts of the body and nearly one-third of birth defects arise from abnormal behaviour of neural crest cells. Moreover, neural cells are the precursors of melanocytes, which can form melanoma, one of the most aggressive cancers. We use a hybrid cell-based model as an hypothesis testing and hypothesis generating tool and, in a long-standing collaboration with experimental colleagues, we have uncovered new biological insights concerning this process. Some of these results will be presented.

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How organisms convert 2D patterns into 3D

*Keisuke Matsuda¹, Hiroki Gotoh², Haruhiko Adachi¹, Yasuhiro Inoue³ &
Shigeru Kondo^{1*}*



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ABSTRACT:

The question, "How are organisms formed?" is one of the central questions in developmental biology. In the past 30 years, embryological experiments and mathematical modeling studies have revealed the mechanisms by which individual genes are expressed in specific regions, the so-called principles of pattern formation. However, those principles deal, for the most part, only with the division of fixed fields into regions. In actual morphogenetic phenomena, pattern formation and the expansion and deformation of the field proceed simultaneously. As such, it is extremely difficult to model such a situation, because the two different elements affect each other.

To circumvent these difficulties, it is useful to study phenomena in which cellular changes and field deformation occur at different times. We believe that the deformations associated with molting in exoskeletal organisms serve this purpose.

Late morphogenesis in exoskeletons occurs through molting. During molting, (1) grooves are formed in the intracellular layer in advance, and (2) large-scale deformation occurs by expanding these grooves. The process (2) is a purely physical process because it occurs in a short time. By measuring the number, depth, and direction of the grooves, the final 3D structure can be calculated from the groove pattern.

On the other hand, process (1) is a biological process, in which the position and angle of the wrinkles are determined in a two-dimensional cell sheet, which is a kind of pattern formation. We first examined the beetle horn primordium. Beetle pupae have huge horns, but in larvae the horn primordia are compactly folded in the head. Reproducing the folding of the primordium from serial sections and extending it with physical calculations, the structure of the pupal horn emerged. This indicates that the three-dimensional morphology of the horns is already completed by the folding pattern of the primordium. Furthermore, by examining the wrinkle patterns corresponding to the various parts of the horns, part of the logic behind the creation of the three-dimensional form was revealed.

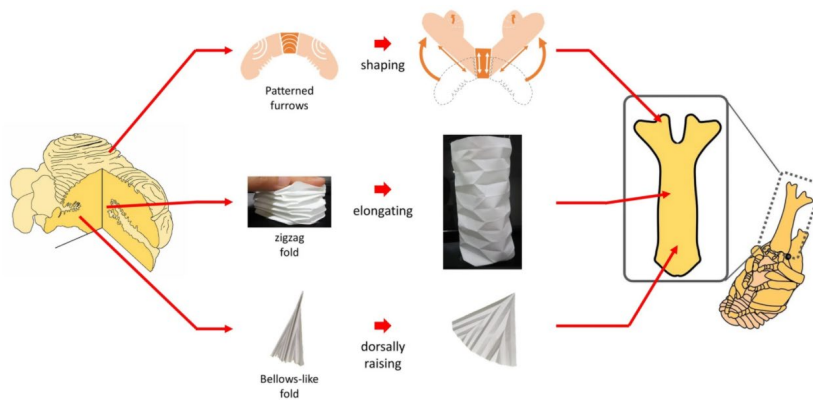
We are currently studying the folding patterns of the helmets of treehoppers, which have more complex and diverse three-dimensional structures, through which we expect to elucidate how the complex structures of insects are designed.

Sequential photos of Japanese beetle pupation. Giant horns emerge in just 100 minutes. Because of the extremely short time, this deformation is thought to be due to the physical unfolding of the folded cell sheet.



Scientific Reports volume 11, Article number: 1017 (2021)

Relationship between wrinkle patterns in cell sheets of horn precursors and 3D morphology after unfolding.



Zoological Letters volume 6, Article number: 3 (2020)

Scientific Reports volume 7(1), Article number13939 (2017)

Mechanisms and evolution of female-limited Batesian mimicry in *Papilio* butterflies

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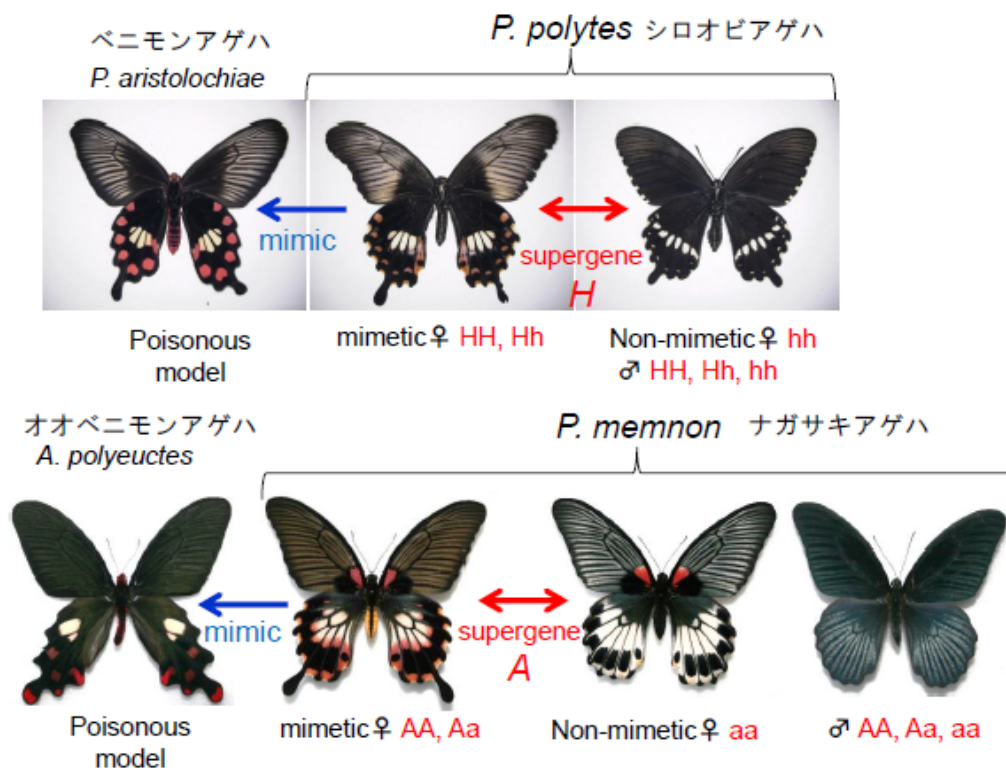


To deceive predators, palatable species often resemble color patterns and morphology of unpalatable species, which is called Batesian mimicry. Many animals employ the Batesian mimicry, which mechanisms and evolution remain largely unknown. In two closely related swallowtail butterflies, *Papilio polytes* and *P. memnon*, there are two types (mimetic and non-mimetic coloration) females, while males show non-mimetic pattern. The female-limited Batesian mimicry of these butterflies attract public interest from Darwin and Wallace's era. In both species, mimetic phenotype is superior to non-mimetic and known to be controlled by a single autosomal locus (*H* in *polytes* and *A* in *memnon*). Thus, the mimetic female genotype is HH or Hh (AA or Aa) and non-mimetic is hh (aa), while all males with any genotype are non-mimetic. Fisher RA (1930) suggested that this polymorphic female-limited mimicry is regulated by “supergene”, which is a cluster of multiple genes tightly linked together.

Recent genome projects revealed many supergenes involved in various complex adaptive phenomena, but the functional unit of supergene has not been clarified in any cases. We have identified the mimicry supergene locus (*H* for *P. polytes* and *A* for *P. memnon*) in a region around *doublesex* (*dsx*) of chromosome 25 (1): The region includes several genes, *dsx*, *UXT*, *U3X* (only for *polytes*) and *Nach-like*, which sequences are highly diversified between *H* and *h* (*A* and *a*) due to recombination suppression, caused by chromosomal inversion in *P. polytes* but probably by repetitive sequences without inversion in *P. memnon* (2, 3). To identify the functional unit of mimicry supergene, we performed knock-down of candidate gene function by electroporation mediated RNAi in mimetic female wings of *P. polytes*. We found that *dsx-H* was responsible for switching from the non-mimetic to mimetic traits, and that not only *UXT* within highly diversified region (HDR) but also *sir2* adjacent to HDR affected the wing pattern (4). Furthermore, it was suggested that *U3X* regulates both *dsx-H* and *UXT* expression. These results indicate that *dsx-H* works as a mimicry gene and other flanking genes as modifier and that functional unit of mimicry supergene is expanded to a wider region than we thought before. In the symposium, I also discuss how two mimicry supergenes in *Papilio* species have evolved.

References

- (1) Nishikawa, H. et al. (2015) [A genetic mechanism for female-limited Batesian mimicry in *Papilio* butterfly](#). *Nat Genet* 47, 405-409.
- (2) Iijima, T. et al. (2018) [Parallel evolution of Batesian mimicry supergene in two *Papilio* butterflies, *P. polytes* and *P. memnon*](#). *Sci Adv* 4, eeao5416.
- (3) Komata, S. et al. (2022) Genomic architecture and functional unit of mimicry supergene in female limited Batesian mimic *Papilio* butterflies. *Philos Trans R Soc Lond B Biol Sci.* B 377 (1856), 20210198.
- (4) Komata, S. et al. (2023) Functional unit of supergene in female-limited Bastian mimicry of *Papilio polytes*. *Genetics* 223, iyac177.



Female limited Batesian mimicry in *P. polytes* and *memnon*

(1) A model for pattern formation and (2) population dynamics of the mimetic butterfly *Papilio polytes* in the Sakishima Islands, Japan: Mathematical analysis and Computer simulations

Toshio Sekimura

Chubu University, Japan



(1) A model for pattern formation

Butterfly wing pigmentation patterns are one of the most spectacular and vivid examples of pattern formation in biology. They have attracted much attention from experimentalists and theoreticians, who have tried to understand the underlying genetic, chemical and physical processes that lead to patterning. In this paper, I present a brief review of this field by first considering the generation of the localised, eyespot, patterns and then the formation of more globally controlled patterns. We present some new results applied to pattern formation on the wing of the mimetic butterfly *Papilio dardanus* and *Papilio polytes*.



The African female limited mimetic butterfly *Papilio dardanus*

(2) Population Dynamics of the mimetic Butterfly *Papilio polytes* in the Sakishima Islands, Japan

I next present a mathematical model for population dynamics of the mimetic swallow butterfly *Papilio polytes* in the Sakishima Islands, Japan.

(Introduction) *P. polytes* is a mimetic swallowtail butterfly species widely distributed across India and Southeast Asia, including Southeast of China, the Philippines, Taiwan, and the Ryukyu Islands of Japan (Clarke and Sheppard, 1972). *P. polytes* exhibits the female limited polymorphism, that is, the female is polymorphic, whereas the male is monomorphic and exhibits a white bar on the black hind wing. In the Ryukyu Islands located in the southwest of Japan, the female of *P. polytes* has two different forms, the mimetic form f. *polytes* and the non-mimetic form f. *cyrus* resembling the monomorphic male in appearance. The form f. *polytes* mimics the unpalatable butterfly *Pachiliopta aristolochiae* as a mimetic model, which has a large white area in the center, and a row of submarginal red spots on the black hind wing. Mimicry in the female of *P. polytes* is known to be Batesian mimicry. Batesian mimicry is one of the most interesting biological phenomena in nature.



Papilio polytes and the numerical simulation result of fore and hind wings

The development and evolution of butterfly wing patterns: finding the primitive pattern

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Synopsis: The color patterns of butterflies and moths constitute a highly evolved system of visual communication used in sexual signaling, camouflage, warning, territoriality and mimicry. These patterns are based on extensive modifications of a groundplan of three pairs of bands. The ancestors of this pattern can be found as far back as the dragonflies, which are among the first winged insects, and model simulations will illustrate how this could have happened.

Outline: The development and evolution of butterfly wing patterns have been extensively studied over the past 30 years. Much of our understanding of the structure of these color patterns derives from the classical work of Schwanwitsch (1924) and Suffert (1927). These authors independently derived the diversity of color patterns in the butterfly Family Nymphalidae, from a common "groundplan" composed of three parallel pairs of bands that run from the anterior to posterior margin of the wing. Each pair of bands has a characteristic pigmentation pattern and is called a symmetry system because the pigments of the bands mirror each other. Subsequent work by these authors and their associate showed that the "nymphalid groundplan" (Figure 1) applies widely to other Families of butterflies and to many moths as well.

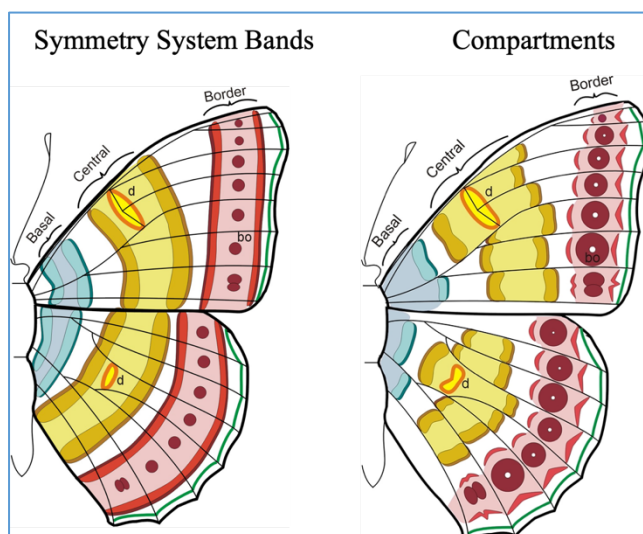


Figure 1. The **Nymphalid Groundplan** is composed of 3 sets of bands called the basal-, central- and border- symmetry systems. In some butterflies and moths the bands are un-interrupted, as in the left panel, but in most cases the bands are disrupted by the vein system (as in the right panel), which compartmentalizes the pattern into semi-independent developmental units (after Nijhout, 1991).

A long-standing question in this field is whether the Nymphalid Groundplan somehow represents the primitive butterfly wing pattern from which all others were derived. The butterflies are phylogenetically within the moths, so if there is a primitive pattern of Lepidoptera, it needs to be sought among the moths. Recently, Schachat and Brown (2016) studied the color patterns of the Micropterigidae, the most basal group of moths, and deduced that their color patterns were based on a system of 5-6 parallel bands. In many moths and butterflies the crossbands are interrupted by the wing veins and appear as a row of spots, and it is still an open question whether bands arose from rows of spots or whether rows of spots came from broken bands.

In my presentation I will show that the primitive color pattern from which the moth patterns evolved arose long before the evolution of the Lepidoptera. Color patterns of the caddis flies (Trichoptera) and scorpion flies (Mecoptera) all resemble those found in the basal moths. I will show that these patterns are all based on variations on a set of 6 parallel bands, and that this basic patterning system can be found in the earliest winged insects, represented today by the dragonflies (Odonata).

A simple reaction-diffusion system can readily generate three symmetry systems, that can be visualized as either 3 pairs of bands or 6 identical bands (e.g. the yellow stripes in Figure 2).

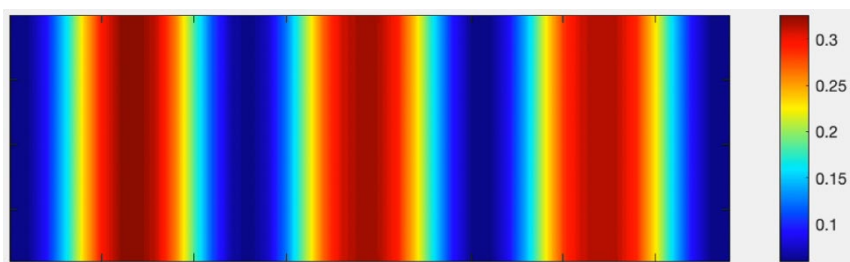


Figure 2. Pattern of three symmetry systems formed by a substrate-depletion model of reaction-diffusion.

I will show that from this banding system, a lateral inhibition mechanism can, in turn, generate much of the diversity of spotting and banding patterns that we see in the dragonflies and other patterned insect wings, including the Lepidoptera.

References:

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Snail coiling: CRISPR editing of a single gene turns righties into lefties

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Synopsis

The establishment of left-right (l-r) body asymmetry is a key biological process which is strictly regulated genetically. We have demonstrated unequivocally that the handedness of the freshwater snail *Lymnaea (L.) stagnalis* is determined by the single maternal diaphanous gene *Lsdial*. The gene operates at the one-cell stage to set the chirality and dictates the entire chiromorphogenesis programme across the levels of biological hierarchy. We have also revealed that mechanical micromanipulation during the 3rd cleavage to reverse the spiral-cleavage direction creates mirror-image animals.

Abstract

Most animals display external bilateral symmetry, but the structure and position of the visceral organs show asymmetries that are determined genetically. To reveal the still unknown mechanism of the establishment of left-right body asymmetry, we have chosen to work on the freshwater snail *L. stagnalis*, which has several unique characteristics. 1) Both the dextral and the sinistral strains within a species are found in the wild with 98% of the snails dextral and 2% sinistral. 2) The asymmetry is displayed both externally and internally. 3) Snail handedness depends on the direction of spiral cleavages of the embryos, as was reported as early as 1894.¹⁾ 4) The snail is a hermaphrodite, and hence both self-crossing and crossing can occur. This makes the genetics more versatile and informative.

Fig. 1 shows three left-right pairs of *L. stagnalis*: **a)** a pair in the wild, **b)** one created by mechanical manipulation and **c)** the sinistral one is created by CRISPR/Cas9 genome editing of the dextral one. Contrary to what has been believed, temporal and spatial cytoskeletal dynamics for the left- and right-handed snails within a species are not mirror images of each other. Thus, during the third cleavage, helical spindle inclination (SI) and spiral blastomere deformation (SD) are observed only in the dominant dextral embryos at metaphase-anaphase, whereas in the recessive sinistral embryos, helicity emerges during the furrow ingression (Fig. 2)²⁾. We have constructed the congenic F10 strain that on average has inherited 99.9% of the sinistral-derived genome and only 0.1% of the dextral strain-derived genome. All the dextral embryos oviposited by F10 animals that inherited the dextrality gene(s) within the 0.1% of the dextral-derived genome exhibited dextrotropical rotation with SD/SI at the 3rd cleavage and without exception grew to possess dextral body shape. Equally, all the sinistral embryos oviposited by F10 animals that do not inherit the dextrality-determining gene(s) showed levotropical rotation without SD/SI, and grew to possess the sinistral body shape,

again without exception. These findings strongly suggested that dextrality is determined by a single gene or by genes at closely linked loci.³⁾

We carried out positional cloning and identified that *Lsdial* is the strongest candidate gene for the handedness determination. There are tandemly duplicated *Lsdial* and *Lsdia2* genes whose proteins share 89.4% amino acid similarity. In the sinistral strains, both *Lsdial* alleles had a frameshift mutation early in the coding region (c.184delC) that leads to protein truncation.⁴⁾ Further, knocking out the *Lsdial* gene using CRISPR/Cas9 produced sinistrally-coiled offspring generation-after-generation in the otherwise totally-dextral genetic background, if biallelic frameshift mutations had occurred (**Fig. 1c**).⁵⁾ We could show that the gene sets the chirality at the one-cell stage, the earliest observed symmetry-breaking event linked to body-handedness in the animal kingdom. The gene dictates the entire chiromorphogenesis programme across the levels of biological hierarchy wherein the early intra-cellular chirality is superseded by the inter-cellular chirality during the 3rd cleavage, leading to asymmetric *nodal*/*Pitx* expressions and then to organismal body handedness.⁵⁾

In parallel, we revealed that mechanical micromanipulation during the 3rd cleavage to reverse the spiral cleavage direction creates mirror-image animals (**Fig. 1b, 2**). The expression site of the *nodal*/*Pitx* genes was inverted by mechanical micromanipulation. (**Fig. 2**).⁶⁾

Diaphanous genes are present in all the Eukaryotes, and therefore, our work featuring formin-controlled early onset of chirality in *L. stagnalis* may provide new insight on unifying mechanisms of l-r body plan formation in animals.

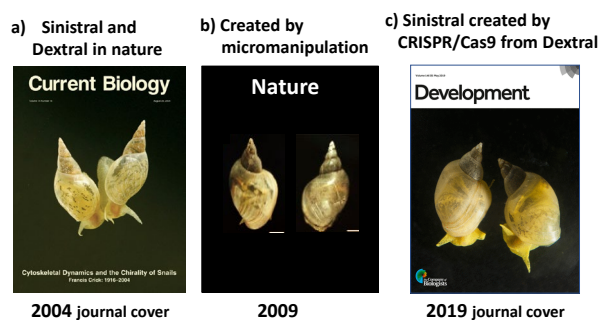


Fig.1 Three l-r pairs in the wild (a) and created (b, c).

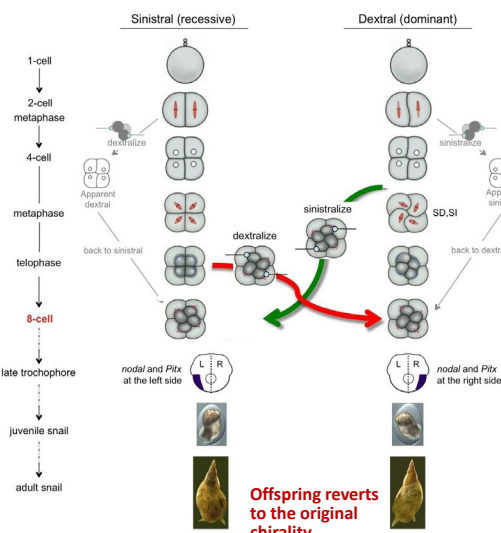


Fig.2. Breaking of mirror-image relationship, and l-r inversion by mechanical manipulation.

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Morphospace Approaches to Evolution: Geometric and Developmental Considerations

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Synopsis

The biological notion of morphospace is examined from its conceptual and analytical dimensions. We review the diverse morphospace geometries encountered in the literature and their implications for the interpretations of morphological patterns. We also show how considerations of organismal development suggest novel mathematical structures to endow the set of morphological variants with evolutionarily meaningful notions of accessibility.

Main text

The notion of morphospace is both of conceptual and empirical importance in biology and paleobiology. Conceptually, it has entailed critical discussions about the relative prevalence of selective forces, variational constraints, and historical contingencies in shaping patterns of morphological evolution. Empirically, morphospaces have proven powerful quantitative tools to document and analyze morphological patterns in various research areas, from comparative anatomy and systematics, to functional morphology and large-scale studies of clade dynamics.

A morphospace is generally understood as the depiction of morphological variants as points in an abstract space in such a way that the relative proximity of points expresses the morphological similarity of variants. Here, we discuss whether this way of conceiving morphospace is always warranted in empirical studies or even adequate for all research questions. Two main aspects pertaining to morphospace geometry are considered: (i) the potential misinterpretation of the geometry induced by some morphometric descriptors and (ii) a notion of evolutionary accessibility among variants derived from the developmental representation of morphological traits.

Morphospace narratives often include statements about distance (between morphological variants) and direction (of morphological change) indicating that an inner-product geometry (generally the dot product of Euclidean geometry) is assumed for the morphospace. However, not all morphospaces are equipped with the metric properties that one tends to intuitively attach to the notion of 'space' [1,2]. So-called 'theoretical morphospaces' are particularly

prone to such non-metric geometries [2]. Raup's iconic shell coiling morphospace is taken as an example to illustrate this phenomenon and discuss its implications for biological inferences.

In paleobiology, the use of discrete character data does lead to metric morphospaces (assuming no missing data), but their Hamming-like geometry is sometimes overlooked [3]. In particular, the morphospace and its multivariate ordination are often confused for one another, inviting the use of inappropriate methodologies for their analyses (Fig. 1A).

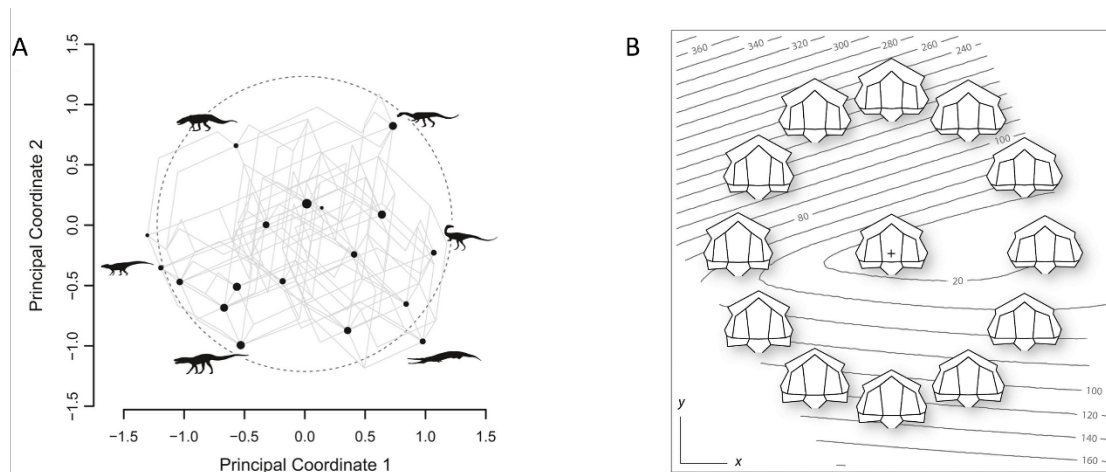


Figure 1. (A) Morphospace representation from discrete character data; (B) Accessibility structure mapped onto a morphospace.

Historically, methodological approaches to morphospace construction have typically aimed for metric topologies defined at the morphological level, organizing variants according to their morphological similarity. This choice may be suboptimal for addressing some important evolutionary questions however, since morphological distance among variants can be a poor predictor of their evolutionary accessibility (Fig. 1B). We show how a genetic or developmental representation of morphological characters allows the definition of accessibility among variants and enriches the explanatory power of morphospace with regards to the role of constraints and selection in morphological evolution [4].

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Functional morphospace analysis of molluscan shells

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Morphospace is a powerful tool for large-scale comparison of morphology across a number of species. Morphospaces are geometric spaces in which a particular organic form can be plotted with reference axes chosen to represent morphological parameters. Abstraction of essential morphological traits allows us to summarize complex morphological variation into a few dimensional morphospace. If a functional performance can be assessed for a set of organic shapes accommodated in the morphospace, the relationship between the functional performance and morphological traits can be visualized as a surface on the morphospace which mimics an adaptive landscape. The functional morphospace allows us to predict which shape is common or rare from the view point of functional morphology. Such a prediction can be readily tested for paleontologists by referring actual fossil records. The present talk introduces a couple of case studies on evolutionary morphology of fossil and extant molluscan shells using morphospaces based on theoretical morphologic models.

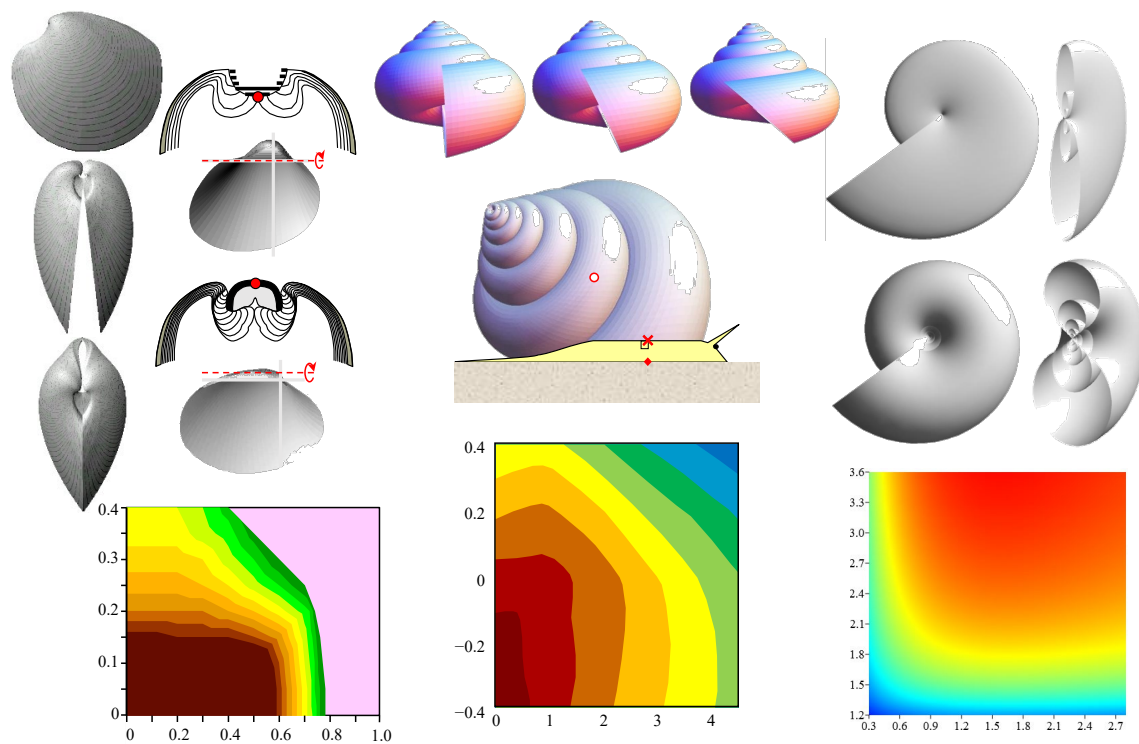
In the first topic on bivalve shell morphology, geometric constraints of bivalve shell form derived from space conflict between umbones of both valves are discussed. A functional morphospace analysis of bivalve shells using a theoretical morphologic model revealed that the space conflict between umbones restricts morphological diversity of bivalve shell of each group depending on hinge morphology. A characteristic type of ligament evolved in a heteroconch bivalve in the late Mesozoic may have allowed the clams to develop an adaptive shell shape for burrowing through their macroevolution.

The second topic on shell form of gastropod snails focuses on a functional trade-off between postural stability and efficiency of shell construction. The result of a functional morphospace analysis of gastropod shells revealed that mechanical stability of a snail while creeping and the amount of shell material necessary for shell construction both depend on shell shape and are hardly compatible with each other. The aperture of snail is often inclined to the coiling axis particularly in the species living in the environment with less buoyancy and calcium carbonate. The results

suggest that the aperture inclination downward relaxes the functional trade-off between postural stability and efficiency of shell construction.

The subject of the third topic on cephalopods focuses on the functional properties for their nektonic mode of life. The functional morphospaces constructed using a theoretical model representing planispiral cephalopod shells clearly shows a functional trade-off between hydrostatic and hydrodynamic efficiencies: a shell form which minimizes a form drag acting on the shell while swimming readily maximizes the density of the totally produced shell. The results of morphometric analyses indicates the followings. Nautilids tend to be optimized for hydrostatics in comparison with other groups. Some ammonoid groups seem to be optimized for hydrodynamic efficiency. Tarphycerid cephalopods tend to have high scores of postural stability. The results suggest that the macroevolutionary pattern is clearly different among cephalopod phylogenies.

Morphospaces constructed through geometric morphometric and multivariate analyses appear to be potentially useful for a functional morphospace analysis. Evolutionary morphology based on morphospace analysis can be facilitated by big-data analyses using morphological databases. Combining the conventional functional morphospace analyses and their potentially relevant techniques is an interesting subject of future research.



Mechanical Optimality Hidden in the Structure of Plants

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Plants of various morphology (shape) can be found in nature. These diverse shapes are believed to be the result of the evolution of plants, which cannot move, to adapt to the surrounding environment. In this talk, I will particularly focus on the shapes of three plant types: i) bamboo [1-4], ii) butterbur, and iii) muskmelon [5]. First, I will demonstrate how the shapes of bamboo and butterbur, which are both tall and hollow plants, are optimal for supporting their own weight. Next, I will explain that the rind of muskmelons develops a mesh pattern with a certain geometric property, which may be used by farmers as a visual indicator of optimum sweetness of flesh; this is a consequence of a farmer seeking the optimum sweetness of the flesh.

i) Optimal structure of bamboo

Bamboo is the fastest-growing plant worldwide. This rapid maturity stems from their hollow structures, which require less material to develop, thereby promoting rapid growth. One critical disadvantage of hollowness is the propensity to easily collapse under external forces such as wind, rain, and self-weight. To overcome this limitation, bamboos generate a sequence of “circular plates” within the long cavity. The plates stiffen the culm locally; therefore, numerous plates from the bottom to the top of the bamboo enhance the stability of the culm. However, this is not a case of “the more, the better”, because an excessive number of plates will inhibit the growth rate of the bamboo plant. Therefore, the number of plates has to be “neither too many nor too few”. This trade-off between stability and growth rate implies an optimum number of stiffening plates that bamboo has acquired over millions of years of evolution.

Against this backdrop, our research group has explored the optimum solution to this issue by investigating wild bamboo groves in Japan. Analysis of the measurement data showed that a single universal law explaining the interdependence between the preferred number of stiffening plates and their ideal arrangement along the culm governs the growth of bamboo [3]. Specifically, the density at which fibers are embedded increases as it gets closer to the outer skin. This universal law thus provides a design criterion, endowing less material and high strength to wild bamboos, which are advantageous for survival over competing tree species.

Surprisingly, another mechanism lurks in the cross-section of the bamboo to increase its stability as a whole. It is bamboo fiber. Inside the bamboo, many long fibers are embedded in the longitudinal direction. These fibers are called “vascular sheaths” in biological terminology, and they act as straws that convey water and nutrients vertically. The structural mechanics theory revealed that this fiber plays an important role in the mechanical properties of bamboo. If a part of the cross-section of bamboo is cut and observed using an electron microscope, it can be seen that the fibers are not evenly

distributed over the entire cross-section. Specifically, the closer it is to the outer skin, the more fibers are embedded. We were able to prove within the scope of the elastic approximation theory that by gathering many reinforcing fibers near the outer skin of the bamboo, the bamboo as a whole is less likely to bend [4]. This result indicates that the bamboo makes its own body stronger by efficiently arranging a limited number of reinforcing fibers inside the cross-section.

ii) Optimal cross-section of butterbur petiole:

There are many plant species with hollow stems and petioles, including those belonging to the family Poaceae. One of the reasons why many plant species have hollow tubular structures is thought to be the structural stabilization provided by hollowness. A tube with a hollow cross-section deforms less than a solid tube (filled) with the same cross-section. Thus, it can support its own weight by using minimal resources. In addition, by choosing the optimal cross-sectional shape (circular, polygonal, etc.) according to the growth environment, the resistance to the most influential mechanical loads (crosswind, self-weight of stems, weight of petals, etc.) increases.

From this perspective, the plant that we focused on in this study was the Japanese butterbur, a type of wild grass. A close examination of the cross-section of the stem of the Japanese butterbur reveals that it has a shape similar to that of a horse's hoof, which is rarely seen in other plants. We hypothesized that this peculiar horseshoe-shaped stem cross-section is the optimal structure for supporting large leaves at the tip of the stem. We have verified this hypothesis both experimentally and theoretically.

iii) Geometric law of mesh pattern of melon skin:

The surface of muskmelons, which is representative of high-grade melons, has a fine mesh pattern (net). It is empirically known that the appearance of this mesh pattern correlates with the quality of melons and is used as an important indicator for quality evaluation at production sites. However, only a few studies have investigated the geometric properties of melon nets.

Our research group took photographs of several muskmelons sold at a retail store (for quality assurance) and investigated the shape and size of the small green peel fragments separated by white reticular stripes. Calculating the areas of these small peel fragments, obtaining the probability distribution curves of the areas, and normalizing them, it was found that the distribution curves were on a common curve regardless of the type and size of individual melons [5]. Furthermore, this common probability distribution curve was derived from fracture mechanics theory. This discovery suggests the possibility of non-destructive identification and evaluation of melon quality using mesh pattern imaging.

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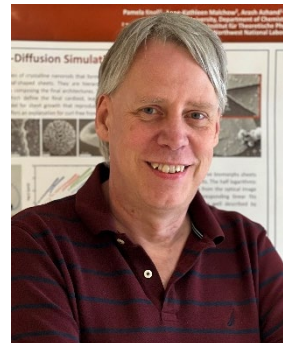
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Spiral patterns and morphology in chemical systems

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Synopsis

This talk will showcase different examples of chemical systems undergoing self-organization far from the thermodynamic equilibrium. Starting with a brief look at the history of chemical waves and the work of the field's pioneers, we will discuss similarities to the growth of unusual polycrystalline solids called biomorphs and go beyond to the self-propulsion of chemical garden tubes.

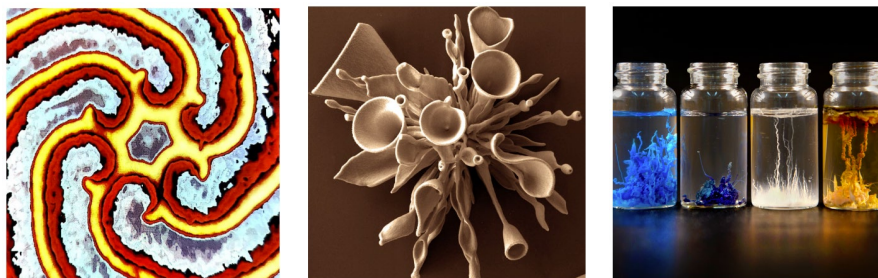
Abstract

Living systems masterfully program molecular events to create macroscopic shapes and dynamics. Can the same be done with inorganic chemistry? I believe the answer is yes if reactions are kept far from the thermodynamic equilibrium (and your expectations are not too high). In my talk, I will introduce several self-organizing chemical systems including the Belousov-Zhabotinsky (BZ) reaction, chemical gardens, biomorphs, and self-propelled catalytic units capable of swarm-like cooperativity. These examples will illustrate unexpected behaviors if reactions are allowed to unfold in space and time. Perhaps not surprisingly, similar processes are used by living systems suggesting system-level interpretations of important biological phenomena (e.g. cardiac arrhythmia) and novel approaches to materials science and engineering.

Our discussion of the BZ reaction will focus on three-dimensional patterns and discuss them in the context of pioneering work by Profs. Stefan Müller, Benno Hess, and Art Winfree. These and other prominent scientists studied two-dimensional spirals, the basic building blocks of scroll waves that provide the foundation for understanding 3D dynamics. While spiral waves rotate around point singularities, scroll waves rotate around 1D filaments that move according to their local curvature. Today tomographic methods, numerical simulations, and controlled manipulations are used to obtain deeper insights into the local pinning to heterogeneities as well as scroll behavior in gradients. Many of these studies, including the results to be presented, are motivated by similar phenomena in the ventricles of the human heart and their link to sudden cardiac death.

Similar nonlinear wave dynamics appear to rule the growth of certain polycrystalline assemblies known as biomorphs. The smoothly curved and life-like biomorphs form when aqueous solutions of BaCl_2 and silicate react with CO_2 . The shapes are about $100\text{ }\mu\text{m}$ in size and include helices, funnels, and urns. The entirely abiotic biomorphs can form from natural spring waters and constitute intriguing problems for the identification of Earth's earliest microfossils as well as the search for life's remnants on Mars and other planetary bodies.

Lastly, we will present novel results on chemical gardens (CG). In the classical CG experiment, these colorful, hollow precipitate tubes form when a salt crystal is placed into an alkaline sodium silicate solution. Specific aspects to be covered include a cellular automaton model of CGs, the involvement of colloidal particles in their growth, and applications as self-propelled micro-rockets. Our model considers, CG growth based on a simple $\text{A}+\text{B}\rightarrow\text{C}$ reaction and a lattice for which each site is exactly one of these three species. We show that the aging of the material modulates the likelihood of mechanical changes in the position of the solid product C and that a strong preference for changes in the fresh material causes filament (2D) and tube (3D) growth. The self-propulsion of CG tubes is demonstrated for Mn-containing units in H_2O_2 solutions. The tubes are propelled forward by the rhythmic ejection of O_2 microbubbles formed in the catalytic tube cavity. We also observed a characteristic acoustic signature of this propulsion that allows detailed analyses of the bubble dynamics. These analyses reveal that the tube speed is determined by the tube diameter (which approximates the step size per bubble) and the bubble ejection frequency (which is nearly proportional to the H_2O_2 concentration). Lastly, we will discuss the swarming behavior of the CG tubes and their interactions with bubble rafts.



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Autonomous Workload Regulation Mechanism in Foraging Ants

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As the basic mechanism to enable task allocation in ant colonies without a leader, the primary role of the caste system has been discussed [1], through which system, specific tasks are autonomously assigned to individual workers according to their size, age, and other factors. Even among specialized ants that are involved in the same task, a hierarchical structure, namely, a heterogeneity of workload is observed.

In the present study, we introduced an experimental system to observe the statistical behavior of colonies of ants, *Camponotus japonicus*, using tiny RFID tags attached to the bodies of all ants in 5 colonies (Fig.1) [4]. By analyzing the “big data of ant society” focusing on foraging behavior obtained through more than three months of continuous measurement, we found various kinds of statistical characteristics of the ant society; i)The emergence of the foraging workload hierarchy, namely, the heterogeneity of the diligence on foraging task, that obeys a simple mathematical form of distribution, ii)Autonomous workload compensation after

the separation of each colony into two different groups; the diligent half before separation, and, the lazy half, and, iii)The slowly decreasing correlation of rank-order of diligence with a characteristic duration of a month.

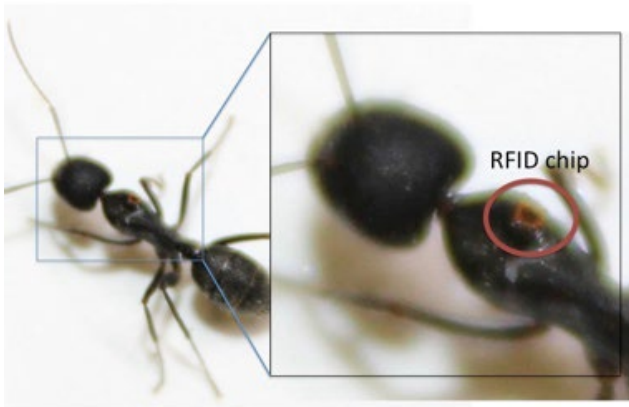


Fig.1 RFID tag is affixed to the center of the red circle in the enlarged image.

As a mathematical model to numerically reproduce the characteristic behavior of social insects; ants and bees, the response threshold model [3] is widely known. To analytically treat the response model, we introduce a corresponding master equation. In conjunction with foraging behavioral data obtained through the above-mentioned long-term observation using tiny RFID tags [4], we found that a master equation approach is effective in quantitatively describing the statistical features of the collective foraging-task engagement of ants. Specifically, the following two kinds of statistical characters related to the autonomous workload compensation in ant colonies were indicated; i) Response threshold θ for starting the foraging task is not uniformly nor normally distributed but largely skewed among ants in each colony(Fig.2). ii)Foraging-task in a colony is carried only by a small fraction of workers in a colony.

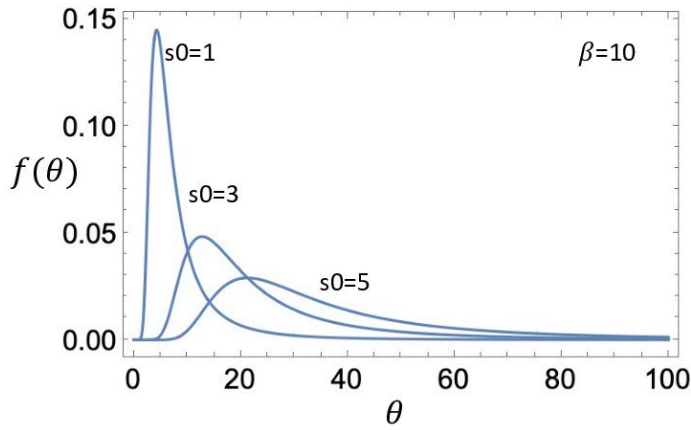


Fig.2 Estimated distributions of the response threshold $f(\theta)$ of the foraging task through the combinatory analysis of master equation and the experimental outcomes of the foraging activity of *Camponotus japonicus*'s colony. The shape of $f(\theta)$ varies according to the experimentally unconfirmed values of parameters, α , β , and δ . However, if β is fixed, the change of α and δ is reflected in s_0 , then, all graphs overlap after rescaling.

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