

*Modeling and Simulation in Science, Engineering and Technology*

**Series Editor**

Nicola Bellomo  
Politecnico di Torino  
Italy

**Advisory Editorial Board**

*M. Avellaneda* (Modeling in Economics)  
Courant Institute of Mathematical Sciences  
New York University  
251 Mercer Street  
New York, NY 10012, USA  
avellaneda@cims.nyu.edu

*K.J. Bathe* (Solid Mechanics)  
Department of Mechanical Engineering  
Massachusetts Institute of Technology  
Cambridge, MA 02139, USA  
kjb@mit.edu

*P. Degond* (Semiconductor & Transport Modeling)  
Mathématiques pour l'Industrie et la Physique  
Université P. Sabatier Toulouse 3  
118 Route de Narbonne  
31062 Toulouse Cedex, France  
degond@mip.ups-tlse.fr

*A. Deutsch* (Complex Systems  
in the Life Sciences)  
Center for Information Services  
and High Performance Computing  
Technische Universität Dresden  
01062 Dresden, Germany  
andreas.deutsch@tu-dresden.de

*M.A. Herrero Garcia* (Mathematical Methods)  
Departamento de Matematica Aplicada  
Universidad Complutense de Madrid  
Avenida Complutense s/n  
28040 Madrid, Spain  
herrero@sunma4.mat.ucm.es

*W. Kliemann* (Stochastic Modeling)  
Department of Mathematics  
Iowa State University  
400 Carver Hall  
Ames, IA 50011, USA  
kliemann@iastate.edu

*H.G. Othmer* (Mathematical Biology)  
Department of Mathematics  
University of Minnesota  
270A Vincent Hall  
Minneapolis, MN 55455, USA  
othmer@math.umn.edu

*L. Preziosi* (Industrial Mathematics)  
Dipartimento di Matematica  
Politecnico di Torino  
Corso Duca degli Abruzzi 24  
10129 Torino, Italy  
luigi.preziosi@polito.it

*V. Prottopescu* (Competitive Systems,  
Epidemiology)  
CSMD  
Oak Ridge National Laboratory  
Oak Ridge, TN 37831-6363, USA  
vvp@epmns.epm.ornl.gov

*K.R. Rajagopal* (Multiphase Flows)  
Department of Mechanical Engineering  
Texas A&M University  
College Station, TX 77843, USA  
KRajagopal@mengr.tamu.edu

*Y. Sone* (Fluid Dynamics in Engineering Sciences)  
Professor Emeritus  
Kyoto University  
230-133 Iwakura-Nagatani-cho  
Sakyo-ku Kyoto 606-0026, Japan  
sone@yoshio.mbox.media.kyoto-u.ac.jp

# Mathematical Modeling of Biological Systems, Volume I

*Cellular Biophysics, Regulatory Networks,  
Development, Biomedicine, and  
Data Analysis*

Andreas Deutsch  
Lutz Brusch  
Helen Byrne  
Gerda de Vries  
Hanspeter Herzel  
*Editors*

Birkhäuser  
Boston • Basel • Berlin

## Pigmentation Pattern Formation in Butterfly Wings: Global Patterns on Fore- and Hindwing

Toshio Sekimura,<sup>1</sup> Anotida Madzvamuse,<sup>2</sup> and Philip K. Maini<sup>3</sup>

<sup>1</sup> Department of Biological Chemistry, College of Bioscience and Biotechnology, Chubu University, Kasugai, Aichi, 487-8501, Japan; sekimura@isc.chubu.ac.jp

<sup>2</sup> Department of Mathematics, University of Sussex, Mantell Building, Brighton, BN1 9RF, England, UK; a.madzvamuse@sussex.ac.uk

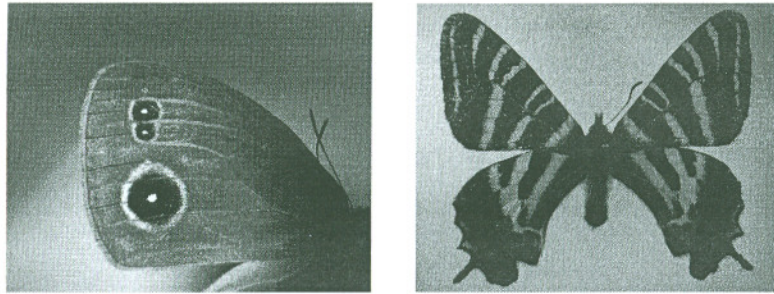
<sup>3</sup> Centre for Mathematical Biology, Mathematical Institute, University of Oxford, 24-29 St Giles, Oxford OX1 3LB, UK; maini@math.ox.ac.uk

**Summary.** Pigmentation patterns in butterfly wings are one of the most spectacular and vivid examples of pattern formation in biology. In this chapter, we devote our attention to the mechanisms for generating global patterns. We focus on the relationship between pattern forming mechanisms for the fore- and hindwing patterns. Through mathematical modeling and computational analysis of *Papilio dardanus* and *polytes*, our results indicate that the patterns formed on the forewing need not correlate to those of the hindwing in the sense that the formation mechanism is the same for both patterns. The independence of pattern formation mechanisms means that the coordination of unified patterns of fore- and hindwings is accidental. This is remarkable, because from Oudemans's principle [10], patterns appearing on the exposed surface of fore- and hindwing at the natural resting position are often integrated to form a composite and unified adaptive pattern with their surrounding environment.

**Key words:** Color pattern formation, global patterns, butterfly wing, *Papilio dardanus*, *Papilio polytes*, reaction-diffusion, Gierer–Meinhardt.

### 12.1 Introduction

One of the most striking phenomena about wing color patterns is the close match between patterns of fore- and hindwing when wings are held at their resting position. This phenomenon is known as the Oudemans principle [10]. The overall unified pattern of both wings is usually explained through their functional significance, i.e., the adaptation to the environment [8]. We have investigated color pattern formation of butterfly wings from a mathematical modeling point of view [7,9,14]. In this paper, using *Papilio dardanus* and *polytes* as examples, we discuss the close match between fore- and hindwing patterns from a mathematical modeling point of view. In the following sections, we discuss butterfly wing color patterns focusing on: (i) current research activities on wing color patterns, (ii) ground plan of global patterns, (iii) global pattern of fore- and hindwing, (iv) *Papilio dardanus* and *polytes* as model butterflies, and



**Fig. 12.1.** Local and global patterns: local eyespot patterns of the forewing of *Mycalesis gotama* (left) and global patterns of fore- and hindwings of *Luehdorfia japonica* (right).

(v) mathematical modeling and numerical simulations on geometrically accurate wing shapes. In Section 12.5 we conclude with a comparison of the pattern on the hindwing with the forewing pattern.

## 12.2 Global and Local Patterns

Butterfly wings are composed of two monolayers (upper and lower) of epidermal cells which are separated by an extracellular space. After pupation, a fraction of the epidermal cells on each wing surface differentiates into scale cells, which then arrange their positions to form parallel rows in the proximal-distal direction of the wing [12, 13]. The colors on wings are due to the colors of scale cells that cover the entire wing surface. Currently, there exist two different research directions on color pattern formation (Fig. 12.1). The first one is that of localized patterns such as eyespot patterns. The second one is of global patterns which cover the whole dorsal or ventral wing monolayer. The best-understood mechanism of color pattern formation is that of local eyespot patterns in which the spatial patterns of expressions of the gene *Distal-less* and several other genes have been detected and examined [1, 2, 4, 5]. Little is known about genes for global patterns except for a few cases such as the butterfly *Papilio dardanus* [3]. Our mathematical model is a reaction-diffusion model for global pattern formation, which is analyzed mathematically and simulated computationally. Our research interest in this chapter is concerned with global patterns of the fore- and hindwing which we discuss below.

### 12.2.1 Ground Plan of Global Pattern

Global pigmentation patterns of butterfly wings are very complicated in structure and are sometimes used for identification of butterfly species. When looking at global wing patterns it is difficult sometimes to understand the rules governing diverse wing patterns. However, because of the pioneering work of Schwanwitsch [11] and Süffert [16] on the nymphalid ground plan, the complicated patterns on the wing can be understood

as a composite of a small number of pattern elements. The ground plan is not really a pattern existing in nature, but a hypothetical one from which a large number of real wing patterns on the Nymphalidae butterflies could be generated by some organizing principles such as dislocation of pattern elements along the veins [8].

### 12.2.2 Global Patterns of Fore- and Hindwings

A close match between global patterns on fore- and hindwings when these are held at rest occurs on the dorsal sides of many species. It is usually assumed that dorsal patterns have evolved independently from ventral patterns in the vast majority of species and are adapted for a wide variety of functions. Oudemans pointed out that when a butterfly settles to assume its natural resting position, patterns appearing on the exposed surface of the fore- and hindwings, head, thorax, abdomen, and even the legs are very often integrated to form a composite but unified pattern. This phenomenon is generally known as Oudemans's principle [10]. The integrated pattern of both the fore- and hindwing is often suggested as evidence of a unified adaptive pattern just like we see in *Kallima inachus* [8]. However, at the same time we find a mismatch between patterns of fore- and hindwing on the ventral wing surface. For example, the integrated pattern of living Lepidoptera fitted to Oudemans's principle seems to break this match when insects feed [15]. We are thus faced with the dilemma of having to interpret the adaptive significance of the consistency and diversity of these patterns.

## 12.3 *Papilio dardanus* and *Papilio polytes*

In this chapter, we choose the Papilionidae butterflies *Papilio dardanus* and *Papilio polytes* as model butterflies for mathematical analysis and computer simulation. We briefly describe these two butterflies in the following subsections.

### 12.3.1 *Papilio dardanus*

A species of *Papilio dardanus* is widely distributed across sub-Saharan Africa and is well known for the spectacular phenotypic polymorphism in females. The females have evolved more than a dozen different wing color patterns of which several mimic different species of unpalatable danaiids, other butterflies and moths (Fig. 12.2). The males, on the other hand, are monomorphic and strikingly different from the females, exhibiting a characteristic yellow and black color pattern and tailed hindwing. The female wing patterns look very complicated in their appearance and at first glance it seems difficult to find an underlying logical relationship between the patterns even in the single species. However, Nijhout [8] proposed the idea that the black color pattern elements in the wing constitute the principal pattern elements, even though the background color attracts our attention most. The elements differ in size depending on the mimetic form and this can have dramatic effects on the overall appearance of the pattern. For this reason, our problem then simplifies to presenting a mechanism that can account for only the black pattern elements (see Fig. 12.3).

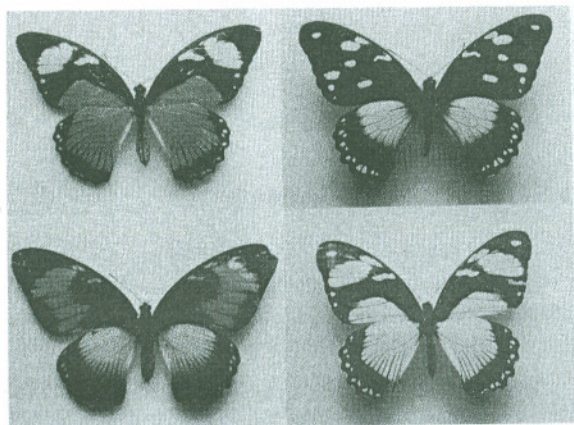


Fig. 12.2. Polymorphism in mimetic females of *Papilio dardanus*: *trophonius* (top left), *cenea* (top right), *planemoides* (bottom left), and *hippocoonides* (bottom right).

### 12.3.2 *Papilio polytes*

A species of *Papilio polytes* is widely distributed across India and Southeast Asia including the southern islands of Japan. *Papilio polytes* has monomorphic males and several female forms. The male-like female is nonmimetic and resembles the male. Other female forms are mimetic and mimic different species of unpalatable *Aristolochia*-feeding swallowtail butterflies.

The forewing pattern of the male has a white band along the distal wing margin in the entire black-colored wing. The hindwing pattern has a white band passing through

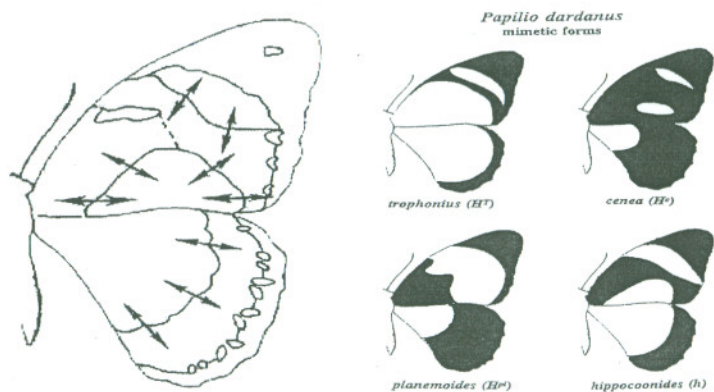


Fig. 12.3. Ground plan and the black pattern elements in mimetic forms of *Papilio dardanus* (reproduced with permission of Fred Nijhout, Duke University).

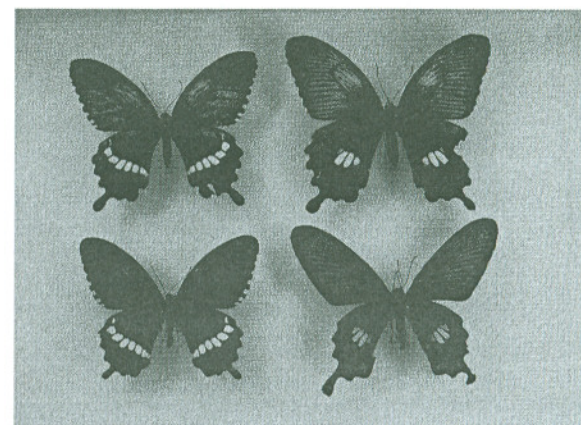


Fig. 12.4. Male and two different female forms of *Papilio polytes* with a typical unpalatable swallowtail *Pachliopta aristolochiae*: male-like female of *P. polytes* (top left), a mimetic form of *P. polytes* (top right), a male of *P. polytes* (bottom left), and a model *Pachliopta aristolochiae* (bottom right).

the middle of the wing in the anterior-posterior direction which appears to link continuously to the forewing white band when both wings are held at rest. On the other hand, a mimetic form shown in Fig. 12.4 has a different and characteristic hindwing pattern in which the white band is shortened in the central area of the wing and red-colored spots appear along the wing margin just like the model butterfly *Pachliopta aristolochiae* (see Fig. 12.4).

### 12.4 A Reaction-Diffusion Model and Numerical Results

The model is based on the idea that a system of reacting and diffusing chemicals could evolve from an initially uniform spatial distribution to concentration profiles that vary spatially by what is called the diffusion-driven instability [17]. We solve the non-dimensionalised reaction-diffusion system with Gierer–Meinhardt [6] reaction kinetics

$$u_t = \gamma \left( a - bu + \frac{u^2}{v(1 + ku^2)} \right) + \nabla^2 u, \quad v_t = \gamma (u^2 - v) + d \nabla^2 v$$

using the finite element method [14] on fixed two-dimensional wing domains. Here  $u(x, t)$  and  $v(x, t)$  represent chemical (morphogen) concentrations at spatial position  $x$  and time  $t$ .  $a, b, d, k$ , and  $\gamma$  are positive parameters.

In all simulations we fix the parameter values of  $a = 0.1, b = 1.0, d = 70.8473, k = 0.5$ , and  $\gamma = 619.45$  to isolate the specific (3,0) mode pattern. Initial conditions are taken as small random perturbations around the uniform steady state and mixed

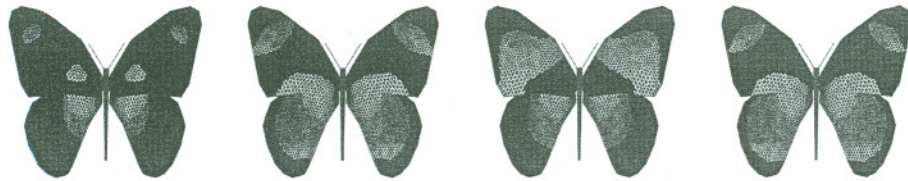


Fig. 12.5. Numerical results illustrating global patterns for cenea, hippocoonides, planemoides, and trophonius [14].

boundary conditions applied. Shading is according to a gradient threshold function of the form of a plane  $\alpha y + \beta x + c_0$  where  $\alpha$  or  $\beta$  or both are non-zero and  $c_0$  is a non-negative constant (see [14] for further details).

Figs. 12.5 and 12.6 illustrate computational results corresponding to global patterns of *Papilio dardanus* and *polytes*, respectively. For *Papilio dardanus* these correspond to observed patterns of the butterflies cenea, hippocoonides, planemoides, and trophonius. In all our simulations small changes in the gradient threshold give rise to a variety of different observed patterns. We have observed in simulations that wing geometry, model parameter values, gradient threshold, and boundary conditions are key factors in obtaining the global patterns illustrated.

## 12.5 Conclusions and Discussion

We showed that a Turing model [17] could account for the global pigmentation patterns on butterfly wings by solving the model equations on geometrically accurate adult wing shapes of *Papilio dardanus* and *polytes*. Our results suggest that the global wing coloration is essentially due to underlying stripe-like patterns of some pigment-inducing morphogen [14]. Computations on the fore- and hindwing shapes were carried out separately. Except for a small change in a parameter value of the threshold function, we used the same parameter values to obtain both fore- and hindwing patterns. This means that from a mathematical modeling point of view, global pigmentation patterns of the fore- and hindwing are independent in the sense that they are

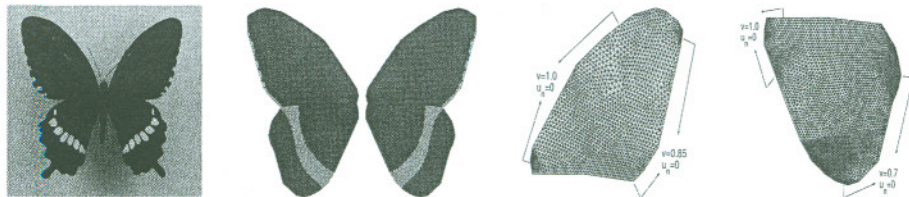


Fig. 12.6. Numerical solutions of the model equations computed on a geometrically accurate fore- and hindwing of *Papilio polytes*. Parameter values for the gradient threshold are  $a_0 = -0.00111$ ,  $b_0 = -0.005$ , and  $c_0 = 0.56$  (forewing) and  $c_0 = 0.645$  (hindwing).

produced or controlled independently by the same mechanism. This result suggests that the close match between global pigmentation patterns on both wings is logically reasonable and somewhat accidental, but need not be explained by an unknown adaptive or functional viewpoint. This might solve the dilemma noted in Section 12.2.2, namely, that of the close match and mismatch between fore- and hindwing patterns.

## Acknowledgments

A.M. would like to acknowledge travel support from the College of Science and Mathematics, Auburn University.

## References

- Beldade, P., Brakefield, P.M.: The genetics and evo-devo of butterfly wing patterns. *Nature Rev Genet*, **3**, 442–452 (2002).
- Brakefield, P.M.: The evolution-development interface and advances with eyespot patterns in *Bicyclus* butterflies. *Heredity*, **80**, 265–272 (1998).
- Clarke, C.A., Sheppard, P.M.: Interactions between major genes and polygenes in the determination of the mimetic pattern of *Papilio dardanus*. *Evolution*, **17**, 404–413 (1963).
- Dilão, R., Sainhas, J.: Modelling butterfly eyespot patterns. *Proc. Roy. Soc. Lond., B* **271**, 1565–1569 (2004).
- French, V., Brakefield, P.M.: Pattern formation: A focus on Notch in butterfly wings. *Curr. Biol.*, **14**, R663–R665 (2004).
- Gierer, A., Meinhardt, H.: A theory of biological pattern formation. *Kybernetik*, **12**, 30–39 (1972).
- Madzvamuse, A., Maini, P.K., Wathen, A.J., Sekimura, T.: A predictive model for color pattern formation in the butterfly wing of *Papilio dardanus*. *Hiroshima Math. J.*, **32**, No.2, 325–336 (2002).
- Nijhout, H.F.: The development and evolution of butterfly wing patterns. Smithsonian Institution Press, Washington and London (1991)
- Nijhout, H.F., Maini, P.K., Madzvamuse, A., Wathen, J.W., Sekimura, T.: Pigmentation pattern formation in butterflies: experiments and models. *C. R. Biologies*, **326**, 717–727 (2003).
- Oudemans, J.T.: Etudes sur la position de repos chez les Lepidopteres. *Verhandelingen der Koning-klijke Akademie van Wetenschappen*, **10**, 1–90 (1903)
- Schwanwitsch, B.N.: On the ground plan forewing-pattern in nymphalids and certain other families of rhopaloceros Lepidoptera. *Proc. Zool. Soc. Lond., B* **34**, 509–528 (1924).
- Sekimura, T., Maini, P.K., Nardi, J.B., Zhu, M., Murray, J.D.: Pattern formation in lepidopteran wings. *Comments Theor. Biol.*, **5**, No. 2–4, 69–87 (1998).
- Sekimura, T., Zhu, M., Cook, J., Maini, P.K., Murray, J.D.: Pattern formation of scale cells in lepidoptera by differential origin-dependent cell adhesion. *Bull. Math. Biol.*, **61**, 807–827 (1999).
- Sekimura, T., Madzvamuse, A., Wathen, A.J., Maini, P.K.: A model for colour pattern formation in the butterfly wing of *Papilio dardanus*. *Proc. R. Soc. Lond., B* **267**, 851–859 (2000)

15. Sibatani, A.: Oudemans' principle and its extension in pattern formation on the wing of Lepidoptera (Insecta). *J. Lib. Arts, Kansai Med. Uni.*, **11**, 1–10 (1987).
16. Süffert, F.: Zur vergleichende analyse der schmetterlingszeichnung. *Biologisches Zentralblatt*, **47**, 385–413 (1927).
17. Turing, A.M.: The chemical basis of morphogenesis. *Phil. Trans. Roy. Soc. Lond.*, B **237**, 37–72 (1952).