Research and Review Insights

Research Article ISSN: 2515-2637

Buckling model for pancake and butterfly color patterns

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Abstract

Pancakes are probably one of the commonest foods on earth. Pancake color patterns are related with pancake anatomy and may be analogous to butterfly wing color patterns. Here we analyzed several pancakes for anatomical correspondence to surface color patterns to understand their development, and the results were discussed in light of the induction model for butterfly color pattern formation. The brown areas on the surface of a baked pancake were physically elevated and that the marginal/submarginal areas were distorted. Gas holes were indicative of expansion of the batter in response to heat. During cooking, a prospective brown area is likely heated from a pan surface and physically expand vertically and laterally to mechanically lift and push the surrounding prospective nonbrown areas through buckling stress. As a result, the surface color of a given area is expressed as either brown (attached to the pan) or nonbrown (detached from the pan) as a binary color code. This buckling model for pancakes was applied to butterfly wings, where lateral expansion force from mechanical organizers and subsequent cellular attachment to (or detachment from) a cuticular surface through buckling stress function to determine cellular expression of a black or white binary color code.

Introduction

Pancake is probably one of the most cherished foods around the world in the history of human beings [1]. According to Albara (2008) [1], "a pancake is here defined as a flat cake made of any starchy batter, normally cooked in a small amount of fat on a flat surface, with anything from a hint of leavening to positive fluffiness, yet retaining a soft pliable interior structure". Scientific studies on pancakes and other bakery products have been performed in the field of food science and engineering, in which bread baking has been investigated intensively [2,3]. Bread browning is also one of the important topics in the field [4,5]. There are many mathematical models for contact baking or oven baking of batter (dough), including pancakes and bread, where heat and mass transfer dynamics have been modeled [6-8]. Additionally, pancake batter spreads to optimal shape have been modeled [9]. Color development in bakery products is considered due to caramelization and the Maillard reaction [5,10], which is kinetically modeled [4,11]. In contrast, Rayleigh-Bénard convection [12,13] does not seem to be involved in color development of pancakes because of high viscosity and subsequent solidification of the batter during cooking.

Outside the field of food science and engineering, most likely because of its high popularity in daily life, the term "pancake" is figuratively used in many fields of sciences and engineering. For example, in astrophysics, pancake theory or the pancake model has been proposed to explain why the universe is flat [14-16]. In medicine, pancake kidney is diagnosed when both kidneys completely fuse together in the pelvic cavity [17-20]. In fluid physics, pancake ice indicates flat ice cover on liquid, and thus, in glaciology, pancake ice is a disc-like ice floating in the ocean with diameters from 300 mm to 3 m [21-23]. In organic chemistry, a stacking interaction is called a pancake bond [24-26]. In linguistics, pancake sentences are known in Scandinavian sentences [27-29]. In mathematics and computer science, the pancake problem is a nondeterministic polynomial (NP) problem called an NP-complete or NP-hard problem [30-33]. In superconductivity physics, Josephson vortices or pancake vortices of current emerge in response to angles of magnetic field applied to a layered high-temperature superconductor [34-37]. In electronics, a coil rolled into a flat circular shape is called a pancake coil [38]. In economics, pancake theory concerns the relationship between the pancake as growing economy and the pan as growth potential [39]. In most cases above, with a few exceptions, the word "pancake" is used in a figurative sense to describe the flat or stacking nature of something interesting. It seems that pancake has stimulated the imagination of scientists in many research fields. However, to the best of my knowledge, pancake analogy has not been introduced into the field of biological sciences yet. In this study, possible physical similarities between pancakes and butterfly wings are explored.

The brown color development of pancakes has been studied as an indicator to evaluate the heat transfer of cooking apparatuses with uniform or nonuniform heating sources [40]. A nonuniform heating source produces nonuniform color patterns on the surface of pancakes. It is known that cooking time, temperature, and water content are important factors in determining pancake color patterns [40,41]. Importantly, Eames et al. (2016) [41] categorized pancake color patterns into five types (island, ring, craters, smooth, and smooth with dark spots) and explained them by two factors, aspect ratio and water content in batter. Eames et al. (2016) [41] also mentioned that vapor escape routes from the heated side determine the color patterns.

Because the pancake color patterns are developed on the pan with good physical contact, I reasoned that there may be similarities between pancakes and butterfly wings when developmental dynamics

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Keywords: *browning, buckling stress, butterfly wing, color pattern, eyespot, morphogen, organizer, pancake*

Received: February 17, 2025; **Accepted:** March 06, 2025; **Published:** March 10, 2025

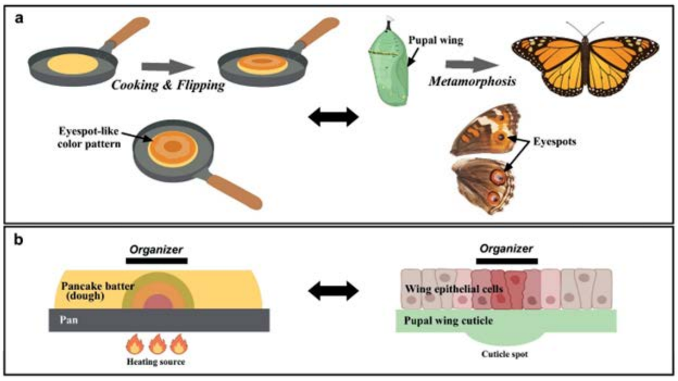

Figure 1. Correspondence between butterfly wing color patterns and pancake color patterns. (a) Comparison in color pattern development. In pancakes, color patterns are determined during cooking when pancake batter (dough) is attached to a pan (left). In butterflies, color patterns are determined at the pupal stage (right). In a pupa, a wing tissue is attached to exoskeletal cuticle. Both may develop eyespot-like patterns during a critical period. Color patterns are revealed after flipping in pancakes (right) and after metamorphosis in butterflies (left). (b) Schematic cross-sections of pancake batter (left) and butterfly pupal wing tissue (right). Pancake batter is attached to a pan (right). Heating source behaves as the organizer in pancakes. A butterfly wing tissue shows a pseudostratified epithelial layer attached to pupal wing cuticle (right). Cells on cuticle spot behave as the organizer (red cells) in butterfly wings. This figure was created with BioRender.com

is considered. Both are developmentally produced from flat objects resulting in binary color patterns as illustrated in Figure 1. As everybody knows, pancake color patterns develop from a handful of batter (dough) in response to applied heat from a pan. Batter on a pan here corresponds to a developing wing tissue on cuticle in a pupa. Both batter and wing tissues are flat objects attached to a hard surface. Other similarities may be found such as the presence of a source for changes (heating source in pancakes and developmental organizer in butterfly wings) and a virtual player for change (heat in pancakes and morphogens in butterfly wings).

In the present study, pancakes were anatomically analyzed to understand the brown color pattern development. Few anatomical observations in relation to color patterns of pancakes have been reported in scientific literature. Because there are a wide variety of pancakes in terms of size, thickness, water content, grain species, other ingredients, and cooking protocols, the present study focused on commercially available pancakes and homemade pancakes from commercially available pancake mixes for simplicity. It is important to examine various types of pancakes because they were made under different conditions. The location, size, and intensity of a heating source and heating duration are probably very important. Based on the information obtained in pancakes, the present study investigated analogies between brown color patterns of pancakes and eyespot color patterns in butterfly wings.

An important aspect of the pancake-butterfly comparisons is that both are transformed to become the final form with discrete color patterns during a critical period of cooking (in pancakes) or metamorphosis (in butterflies) (Figure 1). In pancakes, the trigger of the transformation is supplied by heat from a pan. Heating source is thus considered the "pancake organizer". The trigger of this transformation in butterflies is thought to be supplied by developmental organizers at the center of the prospective color pattern elements such as eyespots [42-44]. However, these important processes of color development are not well understood both in pancakes and butterflies. By analyzing the transformation process of pancakes initiated by heat, it would be possible to understand how brown color patterns develop in pancakes, which may also help researchers to elucidate how eyespot color patterns develop in butterfly wings. Furthermore, the present study discussed the relevance of pancakes to an important problem in developmental biology since the time of Spemann and Mangold (1924) [45,46]: functions of organizers and morphogens in fate determination during animal development [47].

Materials and methods

2.1 Commercially available pancakes

Nine kinds of commercially available pancakes were purchased. They were mass-produced and likely baked on an evenly heated flat pan. They all contained leavening (baking powder) as an ingredient, but leavening is not essential in pancake baking [1,48]. Among these pancakes, the following three kinds of pancakes belonged to a series from the same production line (Okiko, Nishihara, Okinawa, Japan): "Fluffy, yummy! hot cake (maple & margarine)" here called the Pancake Okiko-MM, "Strawberry hot cake (strawberry jam & strawberry whipped cream)" here called the Pancake Okiko-SB, and "Maccha hot cake (kuromitsu & maccha whipped cream)" here called the Pancake Okiko-MC. Similarly, the following two kinds of pancakes belong to a series from the same production line (Ise-mochi collaboration association, Yokkaichi, Mie, Japan): "Outlet pancake made from Japanese wheat flour" here called the Pancake Ise-OW and "Outlet pancake with cocoa made from Japanese wheat flour" here called the Pancake Ise-OC. Additionally, the following three kinds of pancakes were purchased: "Bite-size pancakes" (ICHIEI FOODS, Asakura, Fukuoka, Japan) here called the Pancake Ichiei-BS, "Butter flavor pancakes" (Royal Confectionaery, Ginan, Gifu, Japan) here called the Pancake Royal-BF, and "Imperial Hotel kitchen pancake" (Marin food, Osaka, Japan) here called the Pancake Marin-IH. Lastly, a different kind of pancakes (i.e., voluminous or thick pancakes) were purchased: "Pancakes with ricotta cheese" (NH Foods, Osaka, Japan) here called the Pancake Nipponham-RC.

2.2 Homemade pancakes

In addition, pancakes were cooked by the author. To bake pancakes, "Hot cake mix with whole-wheat flour and brown sugar" (Natural Kitchen, Nagoya, Japan) was used, which contains wheat flour, whole-wheat flour, sugar, and baking powder (aluminum free). These homemade pancakes were called the Pancake NK-WB. Batter was made by adding soy milk, water, and eggs. Additional flour was added to adjust the viscosity of the batter. Sesame seed oil was poured onto a stainless-steel pan (240 mm in inner diameter) (Zwilling J. A. Henckels, Solingen, Germany) heated on a standard Japanese gas stove. The batter was then poured on the pan. The heat level was kept low throughout cooking. After one side (defined as the upper side) was lightly baked for a few minutes, the batter was flipped and baked for a few minutes. This step was repeated several times. Five pancakes were made in a row. At the time of cooking the Pancake NK-WB, the author was not aware of any analogy between pancake and butterfly wings; there was no experimental manipulation of ingredients or cooking procedures.

Another set of pancakes was also cooked by the author. At that point, the author was aware of the potential analogy between pancakes and butterfly wings, but instructions from the manufacturer were simply followed except that milk was replaced with water. To do so, "Organic pancake mix" (Natural Kitchen, Nagoya, Japan) was used. These homemade pancakes were called the Pancake NK-OG. Its ingredients are organic wheat flour, organic sugar, dietary salt, organic sunflower oil, baking powder (aluminum free), and natural vanilla essence. The cooking tools and procedures were the same as above, but an induction heater (instead of gas stove) was used to heat the pan more evenly, and olive oil was used (instead of sesame seed oil). The heat level was kept low throughout cooking. Three pancakes were made in a row.

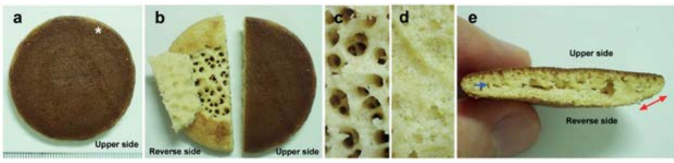

Figure 2. Pancake Ichiei-BS. (a) Upper side. An asterisk indicates wrinkle patterns in the marginal area. (b) Upper and reverse sides. A part of the reverse-side layer is lifted. Large gas holes are present only on the upper-side layer. Note also patchy lightly baked brown areas on the reverse side. (c) Magnification of the upper-side layer. (d) Magnification of the reverse-side layer. (e) Cross section. A blue arrow indicates a boundary between the upper-side and reverse-side layers. The double-headed red arrow indicates a trapezoidal cline

2.3 Anatomical analyses

We examined the morphology and anatomy of commercially available pancakes. Although how these pancakes were made is not exactly known, it can be reasonably assumed that they were produced in a reproducible manner in a factorial production line. Anatomical structures discovered in a given commercially available pancake are thus likely to be reproducible at least in the same commercial product.

The pancakes were pictured using an Olympus Stylus TG-4 digital camera (Tokyo, Japan). The surface that was baked first in contact with the pan was defined as the upper side because this surface is often presented upside when served. The surface that was baked second after tuning over was defined as the reverse side. After observing surface structures visually, cross sections were cut with a kitchen knife, and their anatomical structures were visually observed. Pancakes used for this study were consumed by the author and the family members after the analyses as much as possible.

2.4 Quantification of physical expansion

For quantification, the Pancake NK-OG was cooked. The batter was made in accordance with the manufacturer's protocol, but milk was replaced with soy milk. The mix and soy milk were mixed in the ratio of 200 g to 160 mL. The batter (approximately 120 mL) was poured at once over the pan covered with olive oil at room temperature before heating the pan. Thickness was measured at the center of the batter using a piece of toothpick. The width of the batter was measured by placing a scale and taking a picture of the entire batter. After the measurements, the pan was heated at the lowest possible heat. The batter was baked for approximately 10 min until the reverse-side surface became dry. The batter was not moved or flipped. After one-side baking, the thickness and width were measured as before. Thickness and width values before and after backing were compared by bi-sided paired *t*-test using Microsoft Excel (Microsoft Office 365).

Results

3.1 Commercially available pancakes: Pancake Ichiei-BS

The pancake Ichiei-BS was first examined (*n*=28). This pancake was relatively small, with a diameter of approximately 40 mm (Figure 2a). It may be called a small-sized pancake. Its upper side was almost evenly backed, but the submarginal areas exhibited wrinkle patterns (Figure 2a). A cross-sectional view revealed that the whole structure was more or less trapezoidal (i.e., the marginal/submarginal area of the reverse side formed a weak cline to connect to the upper side) and that the upper and reverse sides were separate (Figure 2b). These two sides appeared to have different coarseness, forming two separate layers (Figure 2b). When an upper or reverse layer was lifted, an upper-side layer contained relatively large gas holes, whereas a reverse layer did not (Figure 2b-d). The structural difference between the upper and reverse layers suggests different degrees of expansion of the batter in response to heat from the upper surface. In contrast to the upper side, the reverse side had patchy light browned areas (Figure 2b), suggesting that the reverse side was not heated much during the production process. Likely, for production efficiency, a pancake was heated strongly at the upper side first and turned over just once. The reverse side was probably heated for a short period of time.

3.2 Commercially available pancakes: Pancake Royal-BF

Here, another commercially available pancake, Pancake Royal-BF, was examined (*n*=20). This pancake had a diameter of approximately 70 mm (Figure 3a). It was larger than the previous Pancake Ichiei-BS (Section 3.1) but smaller than the next Pancakes Okiko (Section 3.3). Overall, the anatomical results of the Pancake Royal BF were similar to those of the previous Pancake Ichiei-BS (Section 3.1). Its upper side was almost evenly backed, but the marginal/submarginal areas exhibited wrinkle patterns (Figure 3a). The reverse side had very light browned areas at the center (Figure 3b), suggesting that the reverse side was not heated much during the production process. When a part of the upper-side or reverse-side layer was removed, an upper-side layer contained relatively large gas holes, whereas a reverse layer did not (Figure 3c). A cross-sectional view revealed that the whole structure was trapezoidal (Figure 3d). The upper and reverse sides were not very separate (Figure 3d). Interestingly, numerous gas bubble signatures were found between wrinkles (Figure 3e), which was not clearly seen in the Pancake Ichiei-BS (Section 3.1). The centers of these gas bubble signatures were nonbrown, suggesting that they did not have good physical contact with the heated pan.

3.3 Commercially available pancakes: Pancakes Okiko

Here, three kinds of commercially available pancakes (the Pancakes Okiko-MM, Okiko-SB, and Okiko-MC) from the same manufacturer (Okiko) were examined (*n*=4 for each pancake type). They were approximately 90 mm in diameter, middle-sized pancakes. The Pancake MM showed that its upper side was baked almost evenly, but the marginal/submarginal areas were somewhat discontinuous from the rest of the body in terms of height and color patterns (Figure 4a). The reverse side showed a dark area only at the central portion, and the peripheral area exhibited the color of the batter (Figure 4b). Removal of the upper-side layer revealed that the reverse layer had minute gas holes (Figure 4c), suggesting that the reverse side was baked for a relatively short time. In contrast, removal of the reverse layer revealed that the upper-side layer had relatively large gas holes (Figure 4d).

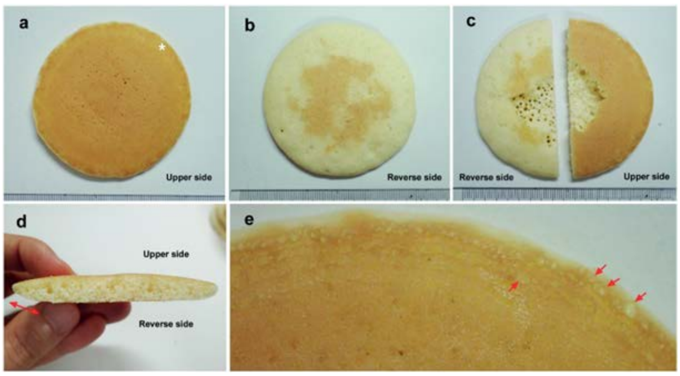

Figure 3. Pancake Royal-BF. (a) Upper side. An asterisk indicates wrinkle patterns in the marginal/submarginal areas. (b) Reverse side. (c) Upper and reverse sides. A part of the upper-side layer is removed. Similarly, a part of the reverse-side layer is removed. Large gas holes are present only on the upper-side layer. (d) Cross section. A double-headed red arrow indicates a trapezoidal cline. (e) Magnification of marginal/submarginal areas. Wrinkle patterns are associated with numerous gas bubble signatures (red arrows)

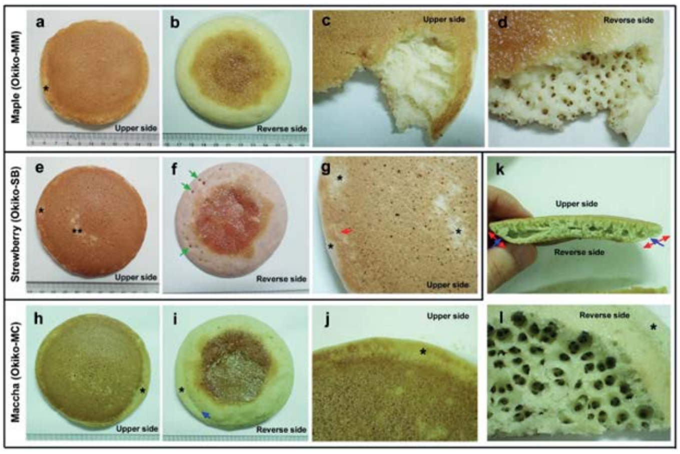

Figure 4. Pancakes Okiko. Asterisks indicate nonbrown areas on the upper side (or its corresponding areas on the reverse side). (a-d) Pancake Okiko-MM. (a) Upper side. (b) Reverse side. (c) Reverse-side layer exposed by removing the upper-side layer. (d) Upper-side layer exposed by removing the reverse-side layer. (e-g) Pancake Okiko-SB. (e) Upper side. More surface holes are found in the central area. (f) Reverse side. Green arrows indicate relatively large surface holes in the submarginal area. (g) Magnification of a portion of the upper side. A red arrow indicates a wrinkle structure in a nonbrown area. (h-l) Pancake Okiko-MC. (h) Upper side. More surface holes are found in the central area. (i) Reverse side. A blue arrow indicates a height gap. (j) Magnification of a portion of the reverse side. (k) Cross section. Double-headed red arrows indicate a trapezoidal cline. Blue arrows indicate a boundary between the upper-side and reverse-side layers. (l) Upper-side layer exposed by removing the reverse-side layer

The Pancake Okiko-SB on the upper side showed an outlook similar to the previous one with marginal/submarginal structures, but there seemed to be more notable surface holes in the central area (Figure 4e). In addition to the marginal/submarginal areas, a small central area had a nonbaked area with the color of the batter (Figure 4e). The reverse side of the Pancake Okiko-SB was similar to that of the Pancake Okiko-MM except that there were relatively large surface holes (craters) in the submarginal area (Figure 4f). A magnification image of the upper side revealed that relatively large surface holes were distributed in the more central area and that the marginal area did not have any noticeable surface holes (Figure 4g), showing a difference in distribution patterns between the upper and reverse sides.

The Pancake Okiko-MC in the upper side showed that more surface holes were located in the more central area and that the discontinuous marginal/submarginal areas were notable (Figure 4h). Its reverse side also showed a step-like uneven structure (Figure 4i). A magnification image of the upper side showed marginal/submarginal areas without surface holes and without brown color (Figure 4j), suggesting that the marginal/submarginal areas did not make direct contact with the pan. A cross-sectional view revealed a trapezoidal shape and a double-layer structure (Figure 4k). Removal of the reverse layer exhibited many large gas holes in the upper-side layer (Figure 4l), probably more extensively than other types of pancakes. The color of the nonbrown areas was different among the three types of pancakes, but the color of the brown areas was also affected due to superimposition of additives. These results suggest that additives may affect the anatomy of pancakes in a minor way because there were minor differences among these three pancakes.

3.4 Commercially available pancakes: Pancakes Ise

Here, the Pancake Ise-OW was examined (*n*=24). It was approximately 70-80 mm in diameter and was a middle-sized pancake. It was evenly baked on the top surface at first glance, but marginal/submarginal wrinkle structures were observed (Figure 5a,5b). When it was placed on a light box, the central area and the marginal/submarginal areas were slightly darker than the area in between, and many surface holes were aligned along winkle lines in the submarginal area (Figure 5c). A cross-sectional view was almost oval but slightly trapezoidal, and there were no clear double layers (Figure 5d,5e), suggesting that the Pancake Ise-OW was baked relatively well from both sides. Indeed, the reverse side was as brown as the upper side, although the brown area was not evenly distributed (see below). Many gas holes were aligned perpendicular to the surface (Figure 5d).

The Pancake Ise-OC (*n*=12) contained cocoa powder, which masked the baked brown colors (Figure 5f). Nonetheless, the central area and the submarginal area appeared to be slightly darker than the area in between (Figure 5f,5g), as in the Pancake Ise-OW (Figure 5c). Most structures showed no noticeable difference from Pancake Ise-OW, including marginal/submarginal wrinkles (Figure 5g) and gas bubbles in the upper and reverse layers (Figure 5h,5i). However, there were more surface holes (craters) on the reverse side than on the upper side (Figure 5j). There seemed to be more large surface holes in the Pancake Ise-OC than in the Pancake Ise-OW (see below), which is reminiscent of the case of the Pancake Okiko (Figure 4). These results suggest that an additive (i.e., cocoa powder) changed the behavior of other ingredients in a minor way, if any.

Interestingly, Pancake Ise-OW showed various browning patterns on the reverse side (Figure 6a). In other pancakes examined in this study, the reverse side had unclear light brown areas and was not baked well. In the Pancake Ise-OW, the central part had a brown color similar to that of Pancakes Okiko, but the brown area was not circular but irregular, which was different from that of Pancake Okiko. It seemed

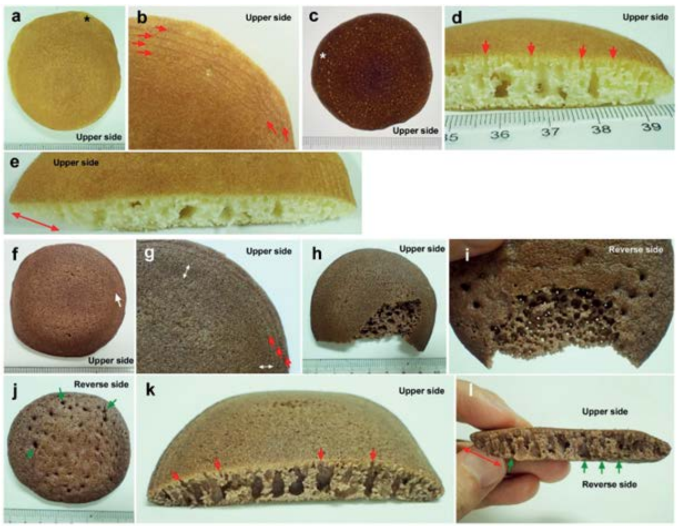

Figure 5. Pancakes Ise. (a-e) Pancake Ise-OW. (a) Upper side. An asterisk indicates a marginal/submarginal area with multiple wrinkle structures. (b) Magnification of a marginal/submarginal area. Red arrows indicate multiple wrinkle structures. (c) Upper side lighted from the bottom upward. An asterisk indicates a marginal/submarginal area with multiple wrinkle structures. Large surface holes are seen along the wrinkles. Small surface holes are numerous in more central areas. Note that the central area is slightly darker than its neighboring area. (d) Cross section. Red arrows indicate vertical gas holes from the surface. (e) Cross section. A double-headed arrow indicates a trapezoidal cline. (f-l) Pancake Ise-OC. (f) Upper side. The central and submarginal areas are slightly darker than their neighboring areas. A white arrow indicates the submarginal band. Note the similarity to (c). (g) Magnification of a marginal/submarginal area. Red arrows indicate wrinkle patterns. Double-headed white arrows indicate the width of the submarginal band. (h) Reverse-side layer exposed by removing the upper-side layer. (i) Upper-side layer exposed by removing the reverse-side layer. (j) Reverse side. Green arrows indicate large surface holes. (k) Cross section. Red arrows indicate vertical gas holes from the upper surface. (l) Cross section. Green arrows indicate large surface holes, which are connected with large gas holes in the body. A double-headed red arrow indicates a trapezoidal cline

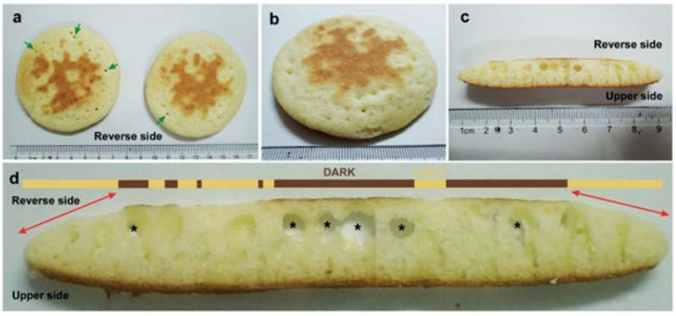

Figure 6. Reverse side of the Pancake Ise-OW. (a) Two pancakes as examples of baked brown color patterns. Green arrows indicate large surface holes. (b) One of the pancakes shown in (a) pictured from obliquely upward. Note the bumps and dents on the reverse surface. (c) A cross-section of a pancake. (d) Enlarged thin cross section of the pancake shown in (c). Note the bumps for baked dark (brown) color and dents for less baked light color. Additionally, note that there seems to be more large gas holes (asterisks) under the dark areas than under the light areas, although not quantified. Double-headed red arrows indicate trapezoidal clines

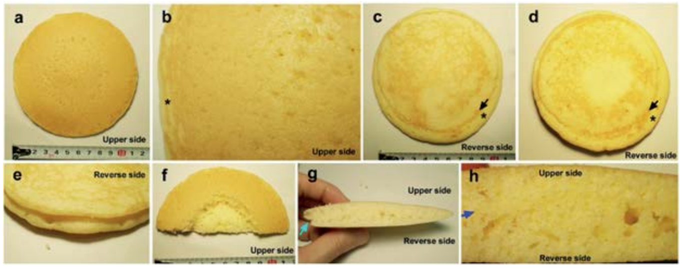

Figure 7. Pancake Marin-IH. (a) Upper side. (b) Magnification of the upper side. Marginal wrinkles are indicated by an asterisk. (c,d) Reverse side. The low height area is indicated by an asterisk. The margin of the high height area is indicated by an arrow. Web-like mesh patterns are seen in both (c) and (d), but in (d), the central portion was blank. (e) Side view of a double-decking structure. This is a single pancake. (f) Reverse-side layer exposed by removing the upper-side layer. No large gas holes. (g) Cross section. A height gap (deck gap) is indicated by a cyan arrow. (h) Magnification of the cross section shown in (g). The middle boundary layer is indicated by a blue arrow

that the brown area was physically elevated (Figure 6b,6c), and this trait has not been observed in other pancakes examined thus far. In the nonbrown area, large surface holes (craters) were found, and they were physically dented compared to the brown areas (Figure 6b,6c). This is probably because gas was not produced much there. In contrast, where gas was produced much, the volume increase was inevitable. Cross sections confirmed this finding; brown areas on the reverse side were elevated, and brown areas had relatively large gas holes underneath (Figure 6c,6d). Relatively large surface holes on the reverse side, mostly in the submarginal area (Figure 6a), coincided with a lack of relatively large gas holes underneath the submarginal area (Figure 6d).

3.5 Commercially available pancakes: Pancake Marin-IH

Here, the Pancake Marin-IH was examined (n=4). It was approximately 110 mm in diameter (Figure 7a). It was a middle-sized pancake, but the largest among the commercial ones examined thus far. The upper side appeared to be smoother than the other pancakes examined before, and the brown color was not very dark, suggesting that relatively low temperatures were applied for longer baking times. There were identifiable marginal wrinkle patterns despite small numbers (Figure 7b). Surface holes were not numerous but were circularly arranged as a circle that surrounded a central area (Figure 7a,7b). The reverse side was not evenly baked; web-like mesh patterns were observed, but the brown color was not dark (Figure 7c,7d).

Importantly, there was a difference in the height (thickness) of the whole pancake between the central and marginal areas, and their boundary was clear (Figure 7c). In one case, the central area was not baked well (Figure 7d). In another case, a clear double-deck structure was observed (Figure 7e). This structure probably suggests a lateral expansion of the pancake in addition to a vertical expansion due to gas (vapor) bubbles from water and leavening. Somewhat surprisingly, removal of the reverse side revealed no extensive gas holes underneath the upper side (Figure 7f). A cross-sectional view confirmed a double-deck structure (Figure 7g), and there was no clear difference between the upper and reverse layers in terms of gas hole structures (Figure 7h), suggesting that leavening may be put modestly and/or that this pancake may be baked at low temperatures to retain moisture for better taste. It should be noted that this pancake is supposed to be of high quality in taste, according to the manufacturer. There was a middle boundary layer that physically separated the upper and reverse layers (Figure 7h).

3.6 Commercially available pancakes: Pancake Nipponham-RC

Here, the Pancake Nipponham-RC was examined (n=6). It was approximately 100 mm in diameter and 15 mm in thickness. It was a middle-sized pancake. This pancake was unique among the commercially acvailable pancakes examined thus far in terms of hight (thickness) and softness because of use of meringue as one of their ingredients. Different pancakes are important because they are likely cooked under different conditions including the intensity of a heating source, corresponding to different oragaizers in butterfly wings.

The upper side of the Pancake Nipponham-RC was evenly baked and largely smooth but with many small nonbrown dents; that is, brown areas were physically elevated from nonbrown areas (Figure 8a). There was no marginal/submarginal wrinkle in any of these pancakes in the upper side as if there was no mechanical distortion at the marginal and submarginal areas, which was different from other commercial ones examined thus far. In contrast, the reverse side showed unevenness; there were brown areas along the margin and in the inner area (Figure 8b). Like the upper side of this pancake and like the reserse side of the Pancake Ise-OW (Section 3.4), the brown area in the revese side was physically elevated from the surrounding nonbrown area. Numerous gas bubble signatures were observed in the brwon areas in the reverse side (Figure 8c), suggesting volume expansion associated with the brown areas. A cross sectional view showed a trapezoidal cline on the side, and there was no clear layered structures (Figure 8d). The double-deck strucrtures were clearly seen (Figure 8a,8b) like the Pancake Marin-IH (Section 3.5). On the upper side of another sample, there

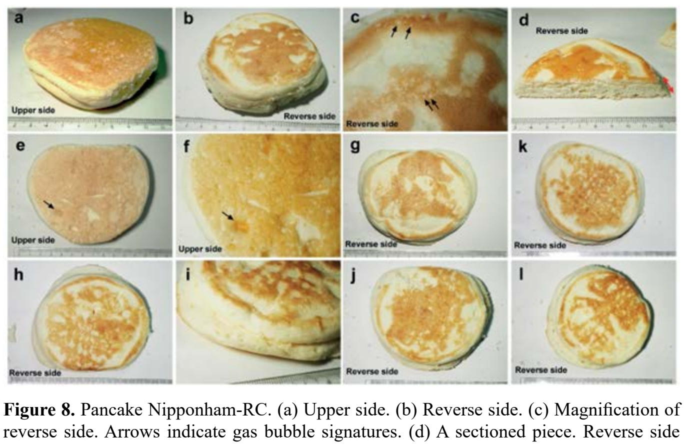

Figure 8. Pancake Nipponham-RC. (a) Upper side. (b) Reverse side. (c) Magnification of reverse side. Arrows indicate gas bubble signatures. (d) A sectioned piece. Reverse side up. A trapezoidal cline was indicated by a double-headed arrow. (e) Upper side. An arrow indicates a dent with dark color. (f) Magnification of (e). (g) Reverse side of another sample. (h) Reverse side of an additional sample. (i) Side view of (h). (j-l) Reverse side of further additional samples

were some brown dents (Figure 8e,8f), but they may be exceptions in contrast to elevated brown areas around them. The reverse side of this sample clearly exhibited elevated brown areas along the margin and in the inner area (Figure 8g). Additonal four samples all showed similar structural features (Figure 8h-8l).

3.7 Homemade pancakes: Pancakes NK-WB and NK-OG

Here, the Homemade Pancake NK-WB was examined (*n*=5). Homemade pancakes are important in that they were cooked in response to a restricted heating source. The Pancake NK-WB was approximately 180 mm in diameter. It was a large pancake. Its baking conditions were not controlled, in contrast to the commercially available ones, resulting in various color patterns (Figure 9a-9d). The color patterns were mostly circular, which may be because the batter was not pored quickly at once. Nonetheless, the central area was mostly brown (Figure 9a-9c), and the very marginal portions were mostly colored dark (Figure 9a-9c). Submarginal bands were also identified (Figure 9a-9c). In one exception, no such structures were observed (Figure 9d). There was no marginal/submarginal wrinkle in any of these pancakes, which was different from the commercial ones.

A cross-sectional view revealed that brown (dark) areas were relatively thicker than their neighboring nonbrown (light) areas (Figure 9e,9f). Upper-side and reverse-side layers were not very different in gas hole distributions in the cross section, and a thin boundary layer was observed between the upper-side and reverse-side layers (Figure 9e). The cross section showed a trapezoidal cline on the upper side (Figure 9e), which was different from commercial ones.

Another type of homemade pancake, the Pancake NK-OG, was cooked (*n*=3), which likely contained much leavening to result in thick ones. It was approximately 120 mm in diameter. It was a relatively large middle-sized pancake. During cooking, vertical expansion of the batter was observed visually, resulting in relatively thick pancakes (Figure 10a). Perhaps because of the pancake mix, bumps and dents were not extensive compared to the previous commercial and homemade ones. Indeed, both the upper and reverse sides were made almost smoothly baked. A trapezoidal cline was observed in the cross section (Figure 10a), which is likely due to a lateral expansion of the batter. The cross section revealed that the pancake was thicker in the relatively large central brown area than the peripheral nonbrown area (Figure 10a). The cross section further revealed that the upper and reverse surfaces constitute a layer of relatively large vertical gas holes, and the relatively thick central layer contained smaller gas holes (Figure 10a-10c). Despite the smooth baking, small bumps and dents were found on the upper surface (Figure 10b,10c). The bumps were brown, the dents were nonbrown; the brown areas were physically elevated in comparison to the nonbrown areas (Figure 10b,10c). Importantly, the brown bumps were connected with vertical gas holes inside (Figure 10b,10c).

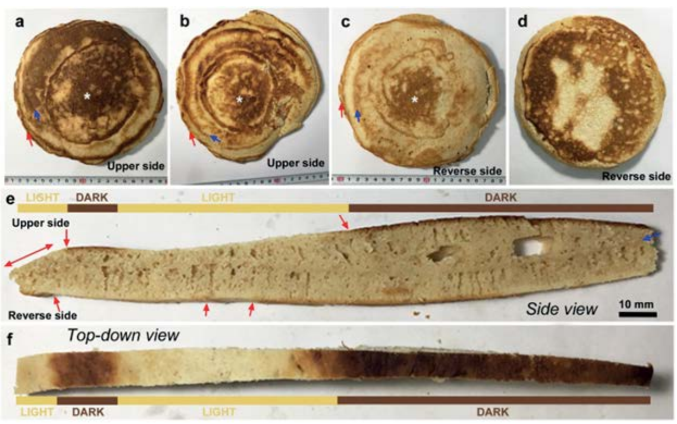

Figure 9. Homemade Pancake NK-WB. (a-d) Upper side in (a,b) and reverse side in (c,d). These are different pancake samples. The central areas (core disk) (asterisks), the submarginal bands (blue arrows), and the marginal bands (red arrows) are indicated. (e) Cross-sectional side view. The boundary basal layer is indicated by a blue arrow. Boundary points between dark and light areas are indicated by red arrows. Trapezoidal cline is indicated by a double-headed red arrow. Dark (brown) and light (nonbrown) areas are indicated by a lateral bar. (f) Top-down view of the section shown in (e). Dark (brown) and light (nonbrown) areas are indicated by a lateral bar

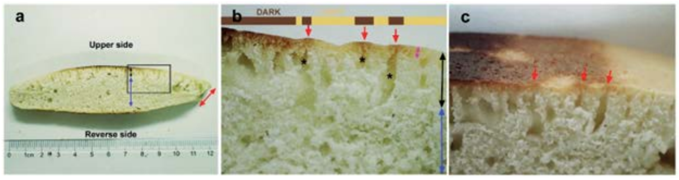

Figure 10. Homemade Pancake NK-OG. (a) Cross section. Surface layers at the upper and reverse sides are similar to each other with vertical gas holes and are different from the central portion with small circular gas holes. The magnified portion in (b) is indicated by a black rectangle. The upper surface layer is indicated by a double-headed black arrow. The central layer is indicated by a double-headed blue arrow. A trapezoidal cline is indicated by a double-headed red arrow. (b) Magnification of a portion of (a). The apical layer (indicated by a double-headed pink arrow) is a thin layer with or without brown color. The surface layer (including the apical layer) is indicated by a double-headed black arrow. The basal layer is indicated by a double-headed blue arrow. Miniature brown areas are connected with vertical gas holes (asterisks) underneath and form bumps (red arrows) relative to neighboring nonbrown areas. Dark (brown) and light (nonbrown) areas are indicated by a lateral bar. (c) The same portion of (b) from a different angle. Brown bumps are indicated by red arrows

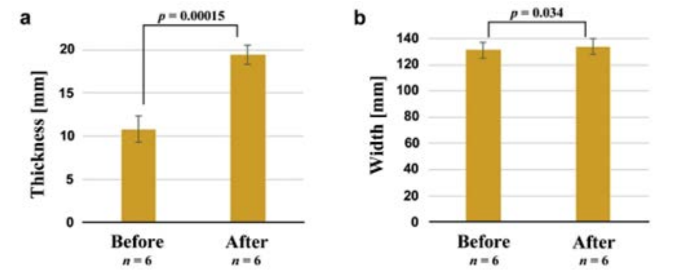

Figure 11. Size changes from batter to pancake before and after baking. Statistically significant differences are indicated by *p*-values (bi-sided paired *t*-test). (a) Thickness. (b) Width

3.8 Experimental quantification of expansion

Using the mix for the Pancake NK-OG, the thickness and width of the batter and the baked pancake were quantified to examine vertical and lateral expansion (*n*=6). The thickness at the center of the pancake significantly increased from 10.8 ± 1.5 mm (mean ± standard deviation) to 19.4 ± 1.1 mm (*p*=0.00015) (Figure 11a), demonstrating the vertical expansion of the batter. The width of the pancake also increased significantly from 131 ± 6 mm to 134 ± 6 mm (*p*=0.034) (Figure 11b), demonstrating the lateral expansion of the batter. The lateral increase (3 mm) was much smaller than the vertical increase (8.6 mm).

Discussion

4.1 Anatomical traits of pancakes

In this study, several commercially available pancakes were anatomically examined. The pancake surface had a few traits: brown (or nonbrown) color, surface holes, and three-dimensional height differences. Brown color is a product of caramelization and the Maillard reaction caused by heat [5,10]. There were small nonbrown areas in the middle of the upper surface, although not numerous, and the marginal areas were often nonbrown. These nonbrown areas indicate that they did not make good contact with the heated pan due to height differences despite that heat was supposed to be evenly applied to the batter. Gas holes are produced by heat in the batter, and gas (water vapor) may merge and be ejected from the surface, creating surface holes. The distribution of surface holes on the upper side suggests the degree of baking and seems to be related to the brownness of the upper surface. The surface holes on the reverse side were much fewer in number than those on the upper side, were much larger than those on the upper side, and were distributed more in the submarginal area. The marginal brown ring was also found in the Pancake Nipponham-RC.

In addition to the pancake surface, the pancake body also showed a few traits. Not necessarily related to the surface holes, the cross sections exhibited large and small gas holes inside the pancakes. Gas holes were often vertically arranged at the surface layer and sometimes formed large holes in the body. Gas holes are important in that they are evidence for volume expansion. The upper-side and reverse-side layers were often separated clearly with or without a middle boundary layer. All the pancake traits discussed above are primarily caused by heat. This is no doubt because batter without heat application cannot be transformed spontaneously to pancakes. In this sense, the importance of heat cannot be overemphasized.

4.2 Marginal/Submariginal areas and lateral expansion

In some pancakes, the marginal/submarginal areas had winkle patterns. They were found only on the upper side. This fact suggests that there was a lateral force generated due to expansion of the heated batter on the upper side. Differential binding of the batter to the pan due to a temperature (heat) gradient probably makes lateral even expansion difficult, causing wrinkle formation. This interpretation seems to be correct because of the lack of wrinkles in the homemade the Pancake NK-WB, which was flipped frequently. Moreover, the Pancake Marin-IH had a relatively small number of wrinkles compared to other commercial pancakes (excluding the Pancake Nipponham-RC). The Pancake Nipponham-RC did not have any marginal wrinkle. This is probably because the whole batter was able to slowly expand laterally and vertically due to slow cooking, as shown in the double-deck structure of the Pancake Marin-IH and the Pancake Nipponham-RC. In addition, the Pancake Royal-BF had gas bubble signatures between wrinkles at the marginal/submarginal areas. Indeed, during cooking of the homemade pancakes, active bubbles at the periphery of the batter were observed. The center of the gas bubble signature in the Pancake Royal-BF was nonbrown, suggesting that bubbles pushed up the surface of the batter from the heated pan. The wrinkle patterns are reminiscent of the ripple patterns in butterfly wings, which are occasionally seen in association with eyespots in nymphalid butterflies [43].

In some other cases, the marginal/submarginal areas were not colored well. This fact indicates that the nonbrown marginal/submarginal areas did not make direct physical contact with the pan. That is, as the central area vertically expands, the marginal/submarginal areas are physically detached from the pan. This is probably because the marginal/submarginal areas are heated later (because poured later) than the central area. Considering that the cross-sectional anatomy of pancakes appeared to be generally independent of starch species [48], the double-deck structures and the marginal/submarginal nonbrown areas can be interpreted as a result of physical expansion of the batter at the whole pancake level due to water vapor and leavening heated at the first contact surface. In accordance with this interpretation, the present study quantitatively demonstrated vertical and lateral physical expansion of the batter during cooking (Section 3.8).

The trapezoidal structure was observed in most pancakes but not in the Pancake Marin-IH, which instead showed the double-deck structure. In the Pancake Nipponham-RC, both the trapezoidal and double-deck structures were observed. This trapezoidal structure may originate from the original structure of the batter before baking; the bottom of the batter tends to expand further by gravity. The trapezoidal structure may be enhanced during baking by the vertical expansion of the central areas of the batter. The trapezoidal structure may also be enhanced by the lateral expansion of the batter during cooking, but such lateral enhancement may not be extensive, considering that the level of lateral expansion was a few millimeters in the middle-sized pancakes (Section 3.8).

In addition, the marginal area is often thinner and dries faster than the central area. As a result, temperature may rise quickly in the marginal area. This feature inherent to the marginal area may result in a marginal brown ring pattern, which was not observed in commercial pancakes but was observed in homemade pancakes. These results suggest that heating a relatively small central area of the batter, such as a cooking process of homemade pancakes, may be required to obtain a marginal brown ring pattern.

4.3 Vertical expansion

The upper-side and reverse-side layers were anatomically different in many pancakes. In some cases, gas holes were seen extensively under the brown area in the upper-side layer, indicating their contribution to the expansion of the batter. In different cases, extensive gas holes were not observed, and a relatively thin but identifiable boundary layer was seen between the upper-side and reverse-side layers. The difference between these two cases may depend on the heating conditions (heating temperature and duration) and contents of water and leavening in the batter. Many commercially available pancakes are not being paid attention to the reverse side. This is understandable from the standpoint of production efficiency, considering that the reverse side is not seen from outside when two pancakes are stacked together on their reverse sides.

The vertical expansion of the heated brown area at smaller levels was suggested in the Pancake Ise-OW. Its reverse side showed that the brown areas were vertically elevated compared with the surrounding nonbrown areas. This feature was also observed clearly in the Pancake Nipponham-RC. This elevation may be caused by surface distortion of the reverse side initiated by baking the upper side first. When flipped, slightly bumped areas that had direct contact with the pan may be heated more than the dented areas; the bumps are amplified to be more bumped. This explains the fact that the Pancakes Ichiei-BS, Royal-BF, and Okiko-MM, Okiko-SB, and Okiko-MC did not clearly show elevated brown areas on the reverse side. This is likely because the reverse side of these pancakes was not baked enough to induce elevation of brown areas. To be sure, the physical elevation of brown areas were also observed in the upper side, but it was not easy to recognize because most upper side areas were brown in most commercial pancakes.

This elevation tendency was also observed in homemade pancakes. In the Pancake NK-WB, the thickness of a pancake appeared to be related to the surface color; the brown areas were thicker than the nonbrown areas. There seemed to be a physical height gap at the transition positions between the brown and nonbrown areas. In the Pancake NK-OG, at smaller levels, the brown areas were bumped and had relatively large vertical gas holes underneath. These results suggest that the brown areas expanded vertically more than the nonbrown areas. It is important to stress that these small brown bump structures are a scaled-down version of the entire brown area. They are self-similar

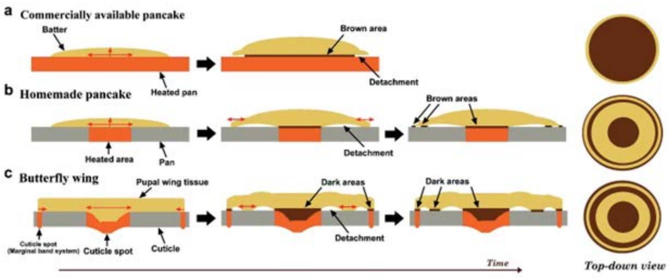

Figure 12. Mechanisms of color pattern development in pancakes and butterfly wings. Mechanical forces are indicated by red arrows. (a) Commercially available pancakes. Heat is applied evenly to the batter. Marginal/submarginal wrinkles are not depicted. The marginal area is detached from the pan, resulting in a nonbrown color. (b) Homemade pancakes. Heat is concentrated in the central area of the batter. Detachment emerges around the heated area due to buckling stress, and a submarginal brown ring emerges. A marginal ring emerges because the marginal area is thin and dries fast. Other rings may also emerge but are not depicted for simplicity. (c) Butterfly wings. For simplicity and comparison, the butterfly wing here is shown to be circular. The primary organizers have a thick cuticle and are located at the center and at the margin of the wing tissue in this figure. Detachment emerges between the two organizers due to buckling stress, and the nondetached area differentiates into the secondary organizer

to each other like butterfly color patterns [49,50]. It is important to note that homemade pancakes had a restricted heating source, which is more similar to butterfly wings than commercially available pancakes.

Together with the discussion in the previous section (Section 4.2), these results indicate that the batter expanded both vertically and laterally during baking. Vertical expansion was visually noticeable in the homemade pancake NK-OG without quantification, but lateral expansion was difficult to detect visually. Experimental quantification demonstrated both vertical and lateral expansion of the batter, consistent with the interpretations of the anatomical results. The level of lateral expansion was much less than that of vertical expansion (Section 3.8), which may be because of the tight binding of the batter to the pan. Further studies are needed to investigate the factors that determine the ratio of vertical and lateral expansion.

4.4 Minor changes by additives

The effects of additives on the brown color development in pancakes seem to be minimal, but there may be minor effects on batter expansion, considering the larger gas holes in the pancakes containing maccha (Pancake Okiko-MC) or cocoa (Pancake Ise-OW). More importantly, in the cocoa pancake (Pancake Ise-OW), although the cocoa color masked the brown color, the color contrast appeared to be enhanced. That is, the central and submarginal brown areas were slightly darker than the area in between, although the color contrast was still low. This eyespot-like arrangement in commercial pancakes is somewhat unexpected, considering that they were likely baked on an evenly heated pan. Different levels of brownness may originate from the fact that the central portion of the batter was poured first on the pan, and the marginal portion was poured last. Then, color development might have occurred according to the model discussed below as if the heat source was limited to the central area of the batter (Section 4.5). Cocoa powder contains fats, which may be easily oxidized to enhance browning reactions.

In a sense, pancake color patterns are depicted in black and white (binary colors), and additives in the batter (such as cocoa powder) produce color changes in the background area. This is similar to butterfly wing color patterns, which are basically depicted as black or white according to the binary rule [49-51]. In addition to the background area, the dark brown areas appear to be modified due to superposition of brown and additive colors. This is also similar to butterfly wing color patterns, in which an original color pattern may be overpainted [52].

4.5 Buckling model for pancake color patterns

Based on the findings and interpretations above, a mechanistic model for color pattern development in pancakes is proposed, which may be called the buckling model (Figure 12a,12b). The location of the heat-generating apparatus underneath the pan defines the location of the "organizer", which locally heats up the batter to let it brown. Simultaneously, the heated part of the batter expands vertically as well as laterally due to gas bubbles generated by heated water and leavening such as baking powder. In the case of the commercial pancake (Figure 12a), heat is applied to the whole area, and almost all areas of the batter expand vertically and laterally. However, the lateral expansion is limited due to binding to the pan, which causes physical distortions in the marginal/submarginal areas, and these areas were wrinkled and/or detached from the pan because the marginal/submarginal areas are less baked at that time point and are flexible enough and hard enough to be detached. This model is applicable to the upper side of the commercially available pancakes. Both the vertical force for lifting and the lateral force for buckling together may mechanically contribute to the wrinkles and detachment of the marginal/submarginal areas.

It is important to note that the homemade pancakes are more similar to butterfly wings in that their organizers are restricted in terms of location, size, and intensity. In the homemade pancakes (Figure 12b), only a central area is heated, producing vertical and lateral forces in the batter. The vertical force for lifting and the lateral forces for buckling detach the nonheated surrounding area of the batter from the pan. A distant area that is not detached from the pan differentiates into the submarginal ring due to heat on the pan. A similar mechanism may operate in some commercial pancakes with central and submarginal brown areas (Section 3.4). It is important to stress that the submarginal ring is induced by the central brown area but can behave independently to induce a tertiary brown area around it, at least theoretically. In addition, the marginal ring is developed in homemade pancakes. This model may also be applicable to the reverse side of the commercially available pancakes with small modifications. Because the surface of the reverse side is not smooth at the time of a direct heat application when flipped, elevated areas make direct contacts with the pan surface, making the elevated areas more elevated and causing vertical and lateral expansion of the batter like the upper side of the batter of the homemade pancakes (Figure 10b).

Detachment from the pan during cooking has been noted in previous reports and is thought to produce nonbrown areas [40,41]. Detachment is thought to be caused by gas bubbles of water vapor that form a narrow physical space between the batter and the pan [40,41]. In accordance with these studies, gas bubble signatures were observed between wrinkles in the Pancake Royal-BF. It is speculated that expansion of the batter and the production of the vapor (gas) layer in a space between the batter and the pan may cooperate for regional detachment of the batter from the pan.

4.6 Pancake for butterflies

The color pattern development of pancakes is now applied to the color pattern development of butterfly wings, considering that the butterfly wing tissue is approximately a flat sheet like a pancake. Potential analogous points between the two systems including those discovered in this study are summarized in Table 1. To understand these analogous points, one should know the following features of butterfly wings and the induction model. The butterfly wing tissue at

Table 1. Potential analogies between pancakes and butterfly wings in color pattern development

	Butterfly wing	**Pancake**
Trigger of transformation	Organizer	Heating source
Color pattern	Binary, Inside-wide, and Self-similar	Binary, Inside-wide, and Self-similar
Attachment object	Cuticle	Pan (Metal or its coating)
Lubricant	Hemolymph	Gas (Vapor) and Cooking oil
Object character	Flexible flat sheet (Epithelium)	Flexible flat sheet (Batter)
Force origin	Polyploidization (Volume increase)	Gas bubble (Volume increase)
Expander (Force generator)	Cell	Water (Vapor) and Leavening
Distribution of expander	Even	Even
Organizer height (Thickness)	Higher (Thicker) than surroundings	Higher (Thicker) than surroundings
Initiator	Molecular morphogen (e.g., Wnt)	Heat (and Gas)
Effects of diffusible	Color development, polyploidization, and binding to the cuticle	Browning, gas (vapor) release, and binding to the pan
Output code (Prepattern)	Attachment/Detachment (Binary)	Attachment/Detachment (Binary)
Secondary organizer	Induced	Induced
Minor patterns	Ripple patterns	Wrinkle patterns
Note: This table includes theoretical possibilities, and they have not necessarily been demonstrated experimentally		

Table 2. Comparison of molecular and mechanical morphogens in butterfly wing color pattern development

	Action	**Range**	**Direct/Indirect**	**Function**	**Analogy to pancake**
Molecular morphogen (Wnt-family proteins)	Self-activation (activator)	Short	Indirect action for morphogenesis	Glue (binding aid) to initiate downstream transduction	Heat
Mechanical morphogen (Lateral force)	Lateral inhibition (Inhibitor)	Long	Direct action for morphogenesis	Pressing (or being pressed) to initiate differentiation	Volume increase

the pupal stage is an epithelial (epidermal) sheet in which the locations of organizers for color pattern elements such as eyespots are clearly "marked" as the pupal cuticle spots and marks [53,54]. Organizers are physically distorted [54,55]. Organizing cells may become larger through polyploidization and generate lateral force onto surrounding cells [50,56] because the eyespot focal scales are larger than other scales [57,58]. In this way, the mechanical force generated at the primary organizer induces secondary distortion at the distance, which becomes the secondary organizer [50,56]. To transduce mechanical force to surrounding cells, the wing tissue must be attached to the extracellular cuticle [59-61].

4.7 Buckling model for butterfly wing color pattern development

Similar mechanisms may operate in butterfly wing color pattern development (Figure 12c). In this buckling model, the pan and the batter correspond to the cuticle and the wing tissue, respectively (Figure 1, Table 1). After the determination of the position of the primary organizer, relatively tight binding of the prospective organizer to cuticle is realized by active secretion of cuticle from organizing cells. At the same time, molecular morphogens are secreted to enhance the binding. Molecular morphogens also cause color pattern development (pigment synthesis), and lateral force may be supplied by active polyploidization of the primary organizing cells. Lateral force generated by polyploidization detaches the surrounding tissue from the facing cuticle via buckling stress. Polyploidization may require tight binding to the facing cuticle.

The settlement position of mechanical signals may be determined by the two opposing forces generated by the central and marginal organizers [62,63]. This settlement position becomes the secondary organizer, which is almost always smaller than the primary organizers, following the inside-wide rule [49-51]. The settlement position should have good physical contact with the cuticle. Importantly, once settled, this secondary organizer can behave independently to induce a tertiary organizer around it at least theoretically, following the self-similarity rule [50]. In other words, terminal differentiation into dark-scale cells accompanies differentiation into secondary organizing cells.

According to this model, molecular morphogens may function as a glue (or a binding aid) to the facing cuticle or other extracellular matrix (ECM) because morphogenic signals are sensitive to chitin-binding inhibitors such as FB28 [61]. A group of representative molecular morphogens in butterfly wings, Wnt family proteins [64-70], is known to interact with heparin and heparan sulfate proteoglycan [71-75]; indeed, butterfly wing color patterns are modified by the injection of sulfated polysaccharides [76]. Such cellular binding to the cuticle or other ECM may be necessary to transduce force signals. It is to be noted that molecular morphogens are not expected to establish a concentration gradient, although heat in pancakes forms a gradient. Rather, molecular morphogens are considered initiators of the downstream biological reactions.

In contrast, lateral force itself may be called mechanical morphogen (mechanical morphogenic signal) because it is lateral force that positionally determines and generates morphological structures. Comparisons between molecular and mechanical morphogens in butterflies are shown in Table 2. Possible comparative dynamics of pancakes and butterfly wing tissues are schematically described in Figure 13. This figure shows that heat in pancakes and molecular morphogens such as Wnt family proteins in butterflies initiate binding enhancement, volume increase, and color development simultaneously, and these three factors are interrelated, producing vertical and lateral forces that cause buckling of the batter or butterfly pupal wing tissue. Distortion of the batter or butterfly pupal wing tissue specifies the secondary heating point in pancakes or the secondary organizer in butterflies.

In the buckling model of butterfly wings above (Figure 12c), the position of the primary organizer is predetermined (by the previous organizer), and organizing cells may be activated by their own morphogen molecules. That is, they are "self-activated" (Figure 13). This autocrine mechanism may be considered a process of self-

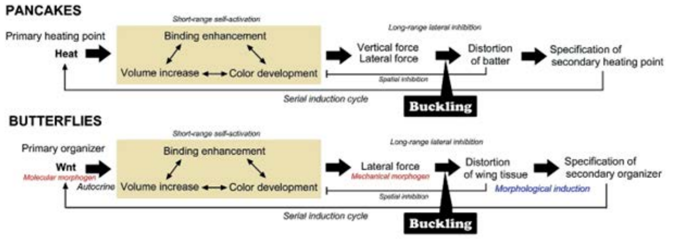

Figure 13. Comparative schematic diagrams for possible development of pancakes and butterfly wing tissues. In this scheme, Wnt is supposed to be a molecular morphogen. Expression of Wnt corresponds to a dark area in a butterfly wing. Heat or Wnt induces binding enhancement, volume increase, and color development simultaneously both in pancakes and butterflies. The volume increase produces lateral force, causing a distortion of the batter or wing tissue and specifying the secondary heating point or the secondary organizer

activation proposed by Meinhardt and Gierer [77-79]. There is no direct long-range effect of molecular morphogen on surrounding cells, but a downstream process of signal transduction initiated by molecular morphogens, which is a force transduction process in butterflies, spatially inhibits lateral expansion of self-activating cells through the detachment of epithelium from the facing cuticle. Thus, this process may be considered a process of long-range lateral inhibition (Figure 13) proposed by Meinhardt and Gierer [77-79]. In the case of pancakes (Figure 13), a heated brown area is more heated via stronger binding to the pan, which is considered a process of short-range self-activation. Also in pancakes, neighboring areas without a direct heating are detached from the pan via buckling stress, which is considered a process of long-range lateral inhibition. Thus, both butterflies and pancakes likely follow the principles of pattern formation proposed by Meinhardt and Gierer [77-79].

For the possible mechanical transduction to work in butterflies, the epithelial (or epidermal) sheet should be devoid of noncellular space; otherwise, forces would not be signaled. Accordingly, all epidermal cells may become larger (or then divide) at the early stage of color pattern determination until cellular gaps are mostly filled with cells, although regional differences in cellular size can be expected in a single wing. Epithelial cells at the prospective organizers likely secrete more cuticle than other epidermal cells at this point, forming pupal cuticle spots. Cells at the prospective organizers tightly bind to these thick cuticular structures. Simply because these cells cannot be moved in response to lateral pressure, they tend to receive and "collect" lateral compressional forces around them. These lateral forces from surrounding cells stimulate the organizing cells to become even larger to push back the surrounding cells. Such mechanical signals may behave like decelerating rolling balls [80].

There may be additional force-generating and transducing mechanisms in butterfly wings. It is known that butterfly pupal wing tissues at the early stages show physical expansion and shrinkage [52,81-83]. Moreover, an organizer (and other areas of a wing tissue) appeared to be subdivided into "clusters" of cells [82,83]. A cluster may be a unit of mechanical signal generation and reception and hence a unit of functional differentiation.

4.8 Attachment or detachment

Mechanical signal transduction in butterfly wings is further clarified in Figure 14. The importance of binding (attachment) to the cuticle has been demonstrated by pharmacological experiments, in which inhibitors of cuticle formation and/or cuticle binding inhibit morphogenic signals from traveling [61]. Moreover, the cuticle surface can be replaced with other covering materials for morphogenic signals to travel; without such materials, morphogenic signals cannot travel [59,60].

Importantly, butterfly wing tissues can generate an ectopic spot or eyespot at an injury site when an injury is made at the background area [84-88]. It is likely that physical injury causes tissue distortion and tight attachment to the cuticle to repair the injury site. It is unlikely that specific molecular morphogens become available immediately after physical injury at that site. In other words, molecular morphogens can be skipped for color pattern development as long as distortion and attachment are realized. In contrast, the lateral force signal and attachment/detachment signal may not be skipped. In this sense, attachment (and detachment) itself may be considered another mechanical signal for differentiation in addition to the lateral force. In this line of argument, what is essential for color pattern formation is distortion (lateral force) and attachment/detachment (vertical force) in the system, both of which are found in both pancakes and butterflies. Lateral force is converted to vertical force via buckling.

Butterfly color patterns are constructed by the binary rule in dark (black) and light (white) colors [49,50]. Dark and light colors correspond to attachment and detachment to the facing cuticle, respectively. Because a scale cell having a single scale on a wing is a unit of color expression, butterfly color patterns may be considered a digitized array of binary code (attachment/detachment), although various colors are produced in the areas of light colors later in real butterflies.

4.9 Limitations of the pancake analogy: The white focal spot

This study explored analogies of pancakes to butterfly wings, and such analogies seem to help understand the butterfly system. However, there are likely liminations in this approach. Many butterfly eyespots have a white focal spot at the center, which was not considered in this study. Importantly, the focal spot can be diverse in shape and can be located at the edge of the eyespot body or even outside the body as indicated by the uncoupling rule [89]. In contrast, other color pattern elements generally do not have such focal spot (althuogh there are some exceptions), and damage-induced eyespots have never shown any white focal spot at the center [84-88]. More studies are requred to resolve this issue.

4.10 Other potentially analogous systems

This study explored analogy of pancakes to butterfly wings, but there may be other systems analogous to these systems. When lateral force stresses a flat object, it produces bumps, dents, and bends at mechanical weak points. Such buckling-like examples can be found in architectural engineering [90]. Concrete is highly resistant against compressional force but relatively weak against tensional force. These

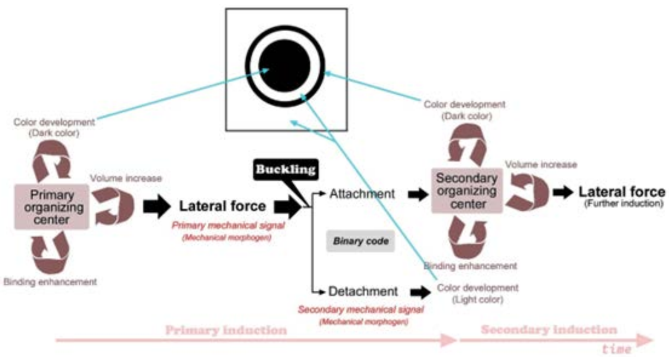

Figure 14. Schematic diagram for possible mechanical signal transduction in butterfly wings. Lateral force causes attachment or detachment of epithelial cells to the cuticle. The attachment/detachment mechanical signal is translated into color expression. Cyan arrows indicate the positions of color development in an eyespot. Light color is not shown in this eyespot

two kinds of forces are produced simultaneously at the two opposing surfaces, for example, when a lateral beam is stressed vertically. This is a general mechanism of cracking in concrete, and there are various mechanisms that induce cracking in concrete. A case can be found in the alkali-aggregate reaction. This reaction produces expansion inside the concrete. Because the expanding part of concrete should find an extra space outside the concrete beam, cracks are created between the expanding and nonexpanding areas. If a concrete beam were more flexible, bumps and dents would be created instead of cracks. Similar insights into force dynamics in a flat object are found in plate tectonics in earth science [91]. Earth's surface is covered with several plates, and plates are expanding at certain places. At the site where these plates are crashing together, mountains may be produced as a result of buckling, one of which is the Himalayan Mountains. To be sure, buckling phenomena are also found in many biological morphogenesis [92-97].

The dynamics of pancakes and butterfly wings may be understood from the viewpoint of interactions between two facing surfaces, i.e., batter and its facing pan in pancakes and an epithelial tissue and its facing cuticle in butterflies. Attachment and detachment correspond to colored and noncolored areas, respectively, in both pancakes and butterflies. In general, two facing surfaces generate friction, which has been studied in tribology (friction physics) [98]. Tribological view may be important for understanding developmental processes of foods and animals in the future.

Conclusions

On the basis of anatomical observations, it is concluded that mechanical expansion of the batter contributes to the development of the surface color patterns of pancakes. This buckling model was applied to the butterfly system. Both systems appear to follow the principles of pattern formation proposed by Meinhardt and Gierer [77-79]. Both systems appear to employ mechanical forces, especially buckling stress, for color pattern determination. Both systems appear to operate under the binary code for color development. And both systems appear to initiate serial induction. Because both systems use physically flat object on a hard surface, their comparisons appear to be reasonable and likely advance the understanding of how color patterns are determined in pancakes and butterfly wings.

Logical reduction of color pattern development to two physical factors, lateral force (distortion) and vertical force (attachment/detachment), in both pancakes and butterflies may not be just a coincidence. Cooking process on a pan is a series of physicochemical reactions, initiated by regional heat, that physically construct new morphology from an initial flat object. Similarly, morphological development in animals is, after all, a physical construction process of a flat cellular sheet that requires physical factors for regulation. Biological molecules might have evolved to assist and enhance a physical construction process for morphogenesis.

Funding

This research was funded by the basic research fund from the University of the Ryukyus and by the Ohsumi Frontier Science Foundation (OFSF), Yokohama, Japan. The APC was funded by the OFSF.

Data availability statement

This paper contained all data obtained in this study.

Acknowledgments

The author is grateful to the laboratory members of the BCPH Unit of Molecular Physiology for discussions. The author would like to dedicate this paper to embryologists, lepidopterologists, and developmental biologists who care about organizers and morphogens at the centennial anniversary of their discovery by Spemann and Mangold.

Conflicts of interest

The author declares no conflict of interest.

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