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蝶の魅力的な美しい生態を
科学の視点から探る

The Fascinating Beautiful Behavior of Butterflies
in View of Scientific Basis

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アゲハチョウのサナギの保護色

Protective coloring of the pupa in the common swallowtail butterfly

Q: 平賀さんは熊本大学教授を定年退職した後、自宅で蝶の研究をしていたと聞いたのですが、どんなことを研究したのですか？

A: アゲハチョウ（ナミアゲハ）のサナギの保護色に影響を与える環境要因について研究しました。アゲハチョウのサナギには緑色型と褐色型がありますが、自然界では緑色型は幼虫の食草であるカラタチやミカンの緑色の枝で見つかりますし、褐色型は枯れた茶色の枝などでよく見つかります。それは捕食者の鳥などに見つかりにくい保護色（カモフラージュ）になっているようです。

「サナギの保護色がどのようにして決まるのか」という疑問はアゲハチョウの幼虫を飼育したことがある人なら誰もが思うことでしょう。昆虫少年であった僕は中学1年生のときにこの疑問を解き明かそうとして実験をしたことがありました。幼虫がサナギになる場所の周りの色を見てカメレオンのようにサナギの色を決めるのではないかと考えていろいろな色紙を使って実験を行ったのでした。しかし、周りの色とは関係がないらしいことはわかりましたが、それ以上のことはわかりませんでした。それから58年後、熊本大学の教授を定年退職し、京都大学で昼は大腸菌を使った分子生物学の研究を続けていましたが、夜は自宅でこの保護色の問題を研究していたのです。

Q: I head that you were studying for butterflies at home after mandatory retirement from the professorship of Kumamoto University. I wonder what kind of research you were doing then.

A: I had been studying the environmental factors influencing/determining the coloration of pupae in common swallowtail butterfly (*Papilio xuthus*). There are two types of pupa color: green type and brown type. The green pupa is usually found on green twigs of orange trees, and the brown one on withered brownish twigs of the orange trees. Therefore, the pupal coloration that mimics the surrounding color may let them camouflage to escape from predatory animals, for example, birds.

People who had raised the common swallowtail butterflies starting from the larvae stages might wonder how the coloration of pupa could be determined knowing the coloration is not destined to a single one. When I was a first-year student in junior high school, I tried to find out the mechanism of the protective coloration. I first guessed that larvae of the butterfly have an ability to recognize the color surrounding the larvae on pupation stage to mimic the color as a chameleon does. Therefore, I tested the possibility by placing a variety of colored paper sheets one by one whether the coloration of pupae would be affected. The results were negative in supporting the possibility, however. Accordingly, this interesting subject will have been left unexplored until I retired from the professorship at Kumamoto University over five decades later.

After I retired from Kumamoto University as mentioned above I moved to Kyoto University to continue my molecular biological study on the bacterium *Escherichia coli*. On this occasion I reopened the research at home mainly at night to explore the mechanisms underlying the coloration of pupa in response to the environmental conditions on larval development of butterfly.



アゲハチョウ♀ Common swallowtail butterfly ♀



アゲハチョウのサナギの2型

Two types of pupae of the common swallowtail butterfly

Q: 実験に使ったアゲハチョウの幼虫はどんなにして集めたのですか？

A: 京都大学本部の近くにある吉田神社の参道にはカラタチの長い生垣があり、そこでアゲハチョウの卵や幼虫を採集して、食草のためにカラタチの小枝をハサミで切り取り、毎日通勤電車で宇治市の自宅に運びました。幼虫はプラスチックの箱で飼育していましたが、この実験には述べ 700 匹の幼虫を飼育しました。

Q: How were you able to obtain the larvae of common swallowtail butterfly for your study at home?

A: Larvae of common swallowtail butterfly feed on leaves on trifoliate orange trees. There is a long hedge of trifoliate orange along the front approach to the Yoshida Shrine, which locates close to the

head office of Kyoto University building. So, I collected eggs and larvae of common swallowtail butterfly there everyday and also some cutoff-shoots with leaves to feed them, and brought them back with me to home in Uji City by trains everyday. Thus, the number of larvae I raised in plastic boxes amounted up to 700 in total.



アゲハチョウの終令幼虫

A final instar larva of the common swallowtail butterfly

Q: どんな実験をやったのですか？

A: この研究では大学の研究室で使うような高価な実験機械を使わずに、一般家庭でも使えそうな器具だけで研究したいと考えていました。アマチュアが自宅でもできる研究を目指したのです。それがアマチュア研究者を励ますことになると思ったからです。

最初に行ったことは、サナギになる場所の色彩は色彩決定にどのような影響を与えるかを白色蛍光灯の 200 ルクス of 光の下で調べることでした。両面がスベスベした名刺大の光沢紙（写真用紙）を細い針金の一端に固定し、ガラス瓶に立てます。光沢紙にはジェットプリンターで各種の色を塗って

おきました。成長した終令幼虫はサナギになる前に腸内の食べた物を全て排出するために下痢便をしてから、サナギになる場所を探して急いで歩きまわります。そういう幼虫をこの装置に止めて逃げ出さないようにポリエチレンの袋をかぶせます。装置には番号をつけてサナギになる過程を記録しました。

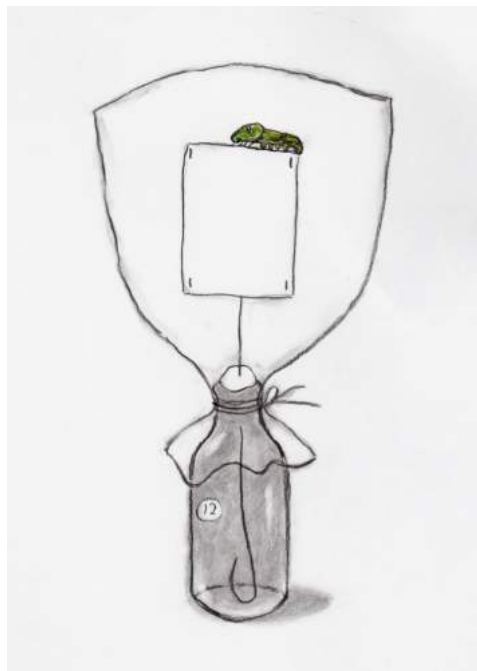
こういう実験で重要なことは、台紙の色彩以外の条件は全て同じにしておくことです。ですから、部屋の白色蛍光灯を1日中点けたままにしておきました。明るさは200ルクスでした。エアコンも実験を行った4月から9月までの6ヶ月間（2004・2005年）点けっぱなしで温度を26°Cに保ちました。また生物を使った実験では多数の個体を使って結果を出すことが必要です。他と違う生理的状态（病気？）の個体が混じることもあるからです。

Q: Now, what kind of experiments have you done in resuming your old research on the protective coloration of pupae once you had stopped some decades ago?

A: I tried to design experiments that even amateurs can perform at home simply using materials and tools that are available as low-cost household products. I thought that this way of designing should encourage amateurs to perform experiments at home without being restricted to use expensive equipment for professionals.

First, I tried to examine if color environment influences the pupal coloration by placing the final instar larvae on a sheet of colored paper. As illustrated in the Figure, a sheet of visiting-card-sized glossy photo-paper with smooth surfaces on both sides, which had been painted in a differing color of choice by use of an inkjet printer, was fixed to a wire terminus and the other end of the wire was set in the glass bottle. Larvae that have finished the final evacuation (gut purge) prior to pupation, were characterized by

bustling around to finally perch on a fixed-spot for pupation. I placed such a bustling larva on each of the colored card, which had been connected to a wire at an end and stood in a bottle, and covered with a transparent polyethylene bag to restrict the bustling larvae within the handmade apparatus. Each bottle was numbered and the pupation phase progress of larva was individually recorded. These experiments were all performed under 200-lux intensity of white fluorescent light and room temperature were kept constantly at 26°C throughout the experimental period for 6 months from April to September in 2004 and 2005. I should emphasize that, for a biological experiment in general, a certain number of subject individuals to be used should be proper enough for statistical analysis, as the population is not always homogeneous. They might be mingled with somewhat physiologically abnormal animals, for example, having diseases.



自作の実験装置

A hand-made experimental apparatus.

実験結果はどの色の台紙でも緑型のサナギの方が圧倒的に多くでした。褐色型は48匹中わずか4匹(8%)でした。すなわち台紙の色はサナギの保護色と無関係のことがわかりました。

The results showed that out of 48 larvae used, 44 metamorphosed into green pupae and 4 into brown ones regardless of the color of card on which the larva was placed, i.e., the brown pupae corresponded to only 4% of the total.



図の説明：いろいろな色の光沢紙の台紙の上のアゲハチョウの緑色型サナギ。

Figure legend: The green type of pupae of the common swallowtail butterfly on smooth surface cards of various colors.

Q: ほとんどの幼虫が光沢紙の台紙の上では緑色のサナギになったそうですが、表面がザラザラした台紙ではどんなことが起こるのですか？

A: サンドペーパー (No.100) の台紙を 200 ルクスの光の下で使ってみま

した。すると驚いたことに 27 匹が全部 (100%) 褐色型のサナギになりました。そして、光沢紙とサンドペーパーの中間の表面の濾紙 (ろし) の台紙では褐色型が 80% で緑色型が 20% でした。これらのことから台紙の表面からの触覚刺激が褐色型を生じさせていると結論できます。このような実験からはカラタチの葉から出る匂い化合物などはサナギの色彩決定には無関係であることもわかります。

緑色型サナギの緑色は終令幼虫が持っていた色素のためです。一方、褐色型サナギの褐色はメラニン色素がサナギの表皮にできたためです。メラニン色素はチロシンというアミノ酸から幾つかの化学反応を通して合成される化合物です。サンドペーパーの粗粒面からの触覚刺激が脳に蓄積するとメラニン色素の合成が誘導されると考えられます。

Q: You obtained the results above using the glossy photo-paper with smooth surfaces on both sides. I wonder what's about when you used paper with coarse surfaces?

A: Yes, I used cards of sandpaper (No.100), as shown in the Figure, in place of the colored smooth surfaced glossy paper cards under otherwise the identical conditions including 200-lux intensity of light and room temperature at 26°C. In this condition, surprisingly, all of 27 larvae used metamorphosed into the brown pupae by 100%. When I used filter paper cards, which had moderate rough surfaces in the both sides, i.e., the conditions corresponding to the in-between surface features with respect to the above two conditions, the larvae metamorphosed into the brown pupae by 80% and the green pupae by 20%. From these results one may conclude that the larvae sense surface tactile stimuli on the site for pupal settlement. Also, one may exclude a possibility that smell substances generating from the leaves of the trifoliate orange trees influence the pupal coloration.

The green color substance of the green pupae has been shown to

be the remains of the green substance present in the final instar larvae. The brownish coloration of the brown pupae is due to melanin, which is newly synthesized upon pupation from tyrosine via several synthetic steps. Accumulation of the tactile stimuli having received from the coarse structural surface on the settled site is considered to induce melanin synthesis in the larvae.



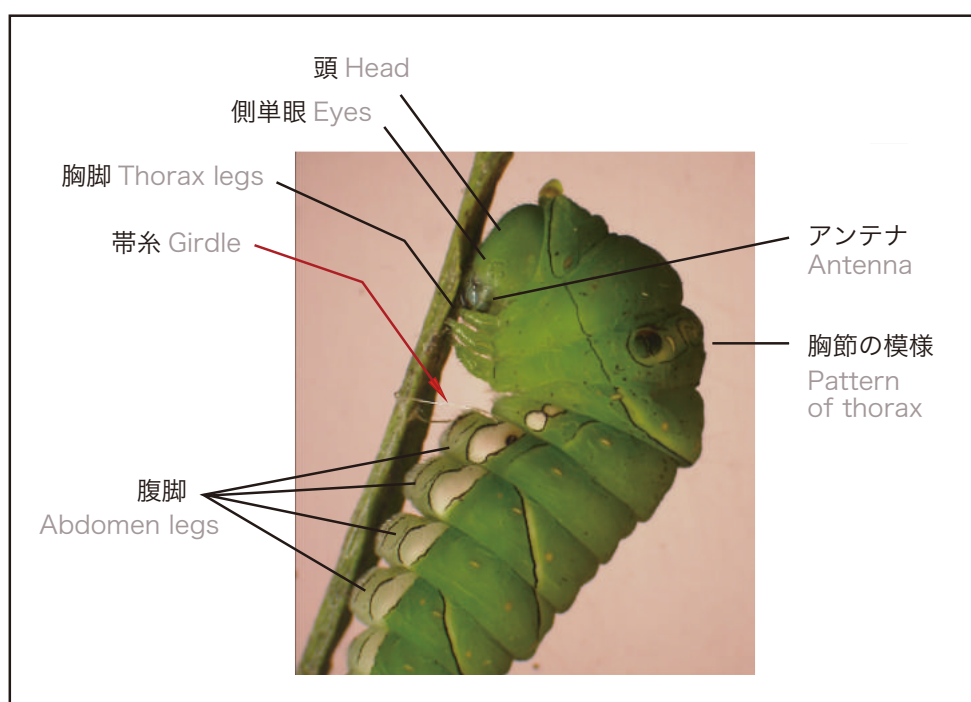
サンドペーパー上の褐色型サナギ

The brown type of pupa on a sandpaper card.

Q: 触覚刺激はどこで感じるのですか？

A: 幼虫の口の両側に触角（アンテナ）があり、その先端には剛毛が生えています。この剛毛の根元には機械刺激を感じる細胞があり、剛毛が何かに触って動くとその刺激が神経細胞を通過して脳に伝達されるのです。ネコの

ヒゲと同じように働くのです。この剛毛の他にも頭部の前面には機械刺激を感じると予想される剛毛がありますし、胸脚にも剛毛があります。体に帯糸を巻付けて前蛹になると下の写真のように頭部の向きが変わるのでアンテナの剛毛はもう台紙に触らなくなります。したがって台紙に触っている頭部前面の剛毛や胸脚の剛毛からの触覚刺激も重要であることが分かります。前蛹になると腹脚（成虫になると退化）を台紙から離しますので腹脚の剛毛はサナギの色の決定には関係しないのではないかと考えられます。



アゲハチョウの前蛹

A larva in the prepupa stage.

Q: Which organ of the final instar larvae is particularly responsible for sensing the tactile stimuli on the coarse structural surface during pupal settling?

A: The larva has a pair of antennae at the mouth side and the antennae have apical bristles connecting to the sensory cells that

transmit mechanical tactile stimuli to the brain. You can imagine the function similar to the cat's whiskers. The final instar larvae also possess other bristles besides those near the mouth in the front of head, which may also supposedly have the same function, and also those of unknown function on the thoracic appendages.

Among the three candidate for sensory organs involved in coloration of pupae, the antenna bristles no longer attach to the pupation card in the prepupa stage as shown in the above photo. Accordingly, the rest of two sensory bristles should play important roles in determining coloration of pupae. Prepupae remove their abdominal legs, which degenerate in adult butterfly, from the pupation card as shown the photo, therefore bristles of these legs do not presumably effect the pupal coloration.

Q: それではサナギになる場所のツルツルかザラザラかでサナギの色が決まってしまう、他の環境因子は関係ないのですか？

A: もちろん他の環境因子も調べてみなくてはなりませんね。それで次に光の影響を調べてみました。サナギになる装置を暗箱の中に置いて実験してみたのです。すると光沢紙の台紙ではサナギの 80%が褐色型で、残りの 20%が緑色型でした。一方 200 ルクスの光を当てていた時には光沢紙の台紙ではサナギの 8%が褐色型で残りの 92%が緑色型でしたので、200 ルクスの光は褐色型の出現を抑える働きをしていることがわかりました。しかし 1 ルクスの弱い光の時には褐色型サナギの出現を抑えることはできませんでした。

またサンドペーパーの台紙を使った時には、1,000 ルクスの強い光を使っても褐色型のサナギは 100%でした。すなわち触覚刺激が強すぎる時には 1,000 ルクスの強い光でも褐色型サナギの出現を抑えることはできないのです。

Q: You have shown above that the coloration of pupae for

common swallowtail butterfly will be determined by the surface structure of the settling site for the larvae to be metamorphosed whether the surface structure is smooth or coarse. One may wonder if any other environmental factors remain to be checked in determining the color.

A: Yes, you are right. I have checked other possible factors I can think of. First, I checked the effect of light, that is, I have repeated the above experiments under otherwise the identical conditions except the experiments were performed in a dark box during pupation. The larvae metamorphosed to brown pupae by 80% even on the glossy photo-paper with smooth surfaces while the rest to green pupae by 20%. I should emphasize that under 200-lux intensity of white fluorescent light the value was only 8%, suggesting that the light would suppress the synthesis of melanin. In support of this possibility, One-lux intensity of white fluorescent light could not suppress the high frequency of brown pupae generation.

Since the larvae placed on glossy photo-paper with smooth surfaces under 200-lux light became brown pupae only by 8% and all of the rest were green ones, we can suspect that the 200-lux light suppresses the generation of brown colored pupae.

I should also emphasize that all of the larvae settled on sandpaper cards metamorphosed into the brown pupae by 100% even under 1000-lux intensity of white fluorescent light. Even excessive amounts of the strong mechanical tactile stimuli received from the coarse structural surface were accumulated, the induction of the melanin synthesis was not suppressed even by such strong light.

Q: 湿度の影響はどうか？

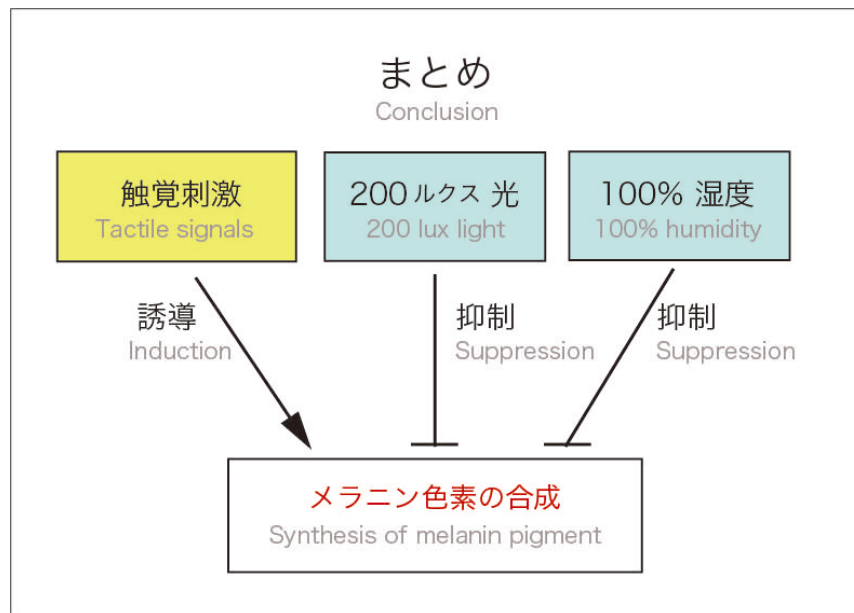
A: 湿度も調べてみました。光沢紙の台紙をつけた装置と一緒に水を含んだティッシュペーパーを暗箱の中に入れてみました。暗箱の内側には水滴がたくさんついていましたから、湿度は 100%になっていたはずですが、光沢紙の場合、湿度が高いと褐色型は少なくなりました (40%)。水のない暗箱の対照実験では褐色型は 80%でしたから、100%湿度はメラニン色素の合成を抑制したと言えます。

以上のことをまとめると、触覚刺激はメラニン色素の合成を促進して、200-lux の光と 100%の湿度はメラニン色素の合成を抑制すると結論できます。

Q: How was the effect of humidity?

A: In the dark box of plastic in case of larvae on the glossy photo-paper with smooth surfaces, I placed damped sheets of tissue paper with water in the box to increase the humidity. Since many drops of water were recognized on the inside surface of the box, humidity should have reached to 100% inside. In this case, the larvae metamorphosed to brown pupae by 40% in contrast to 80% obtained when I did not placed water-damped sheets of tissue paper. The results suggested that 100% humidity environment suppressed the synthesis of melanin.

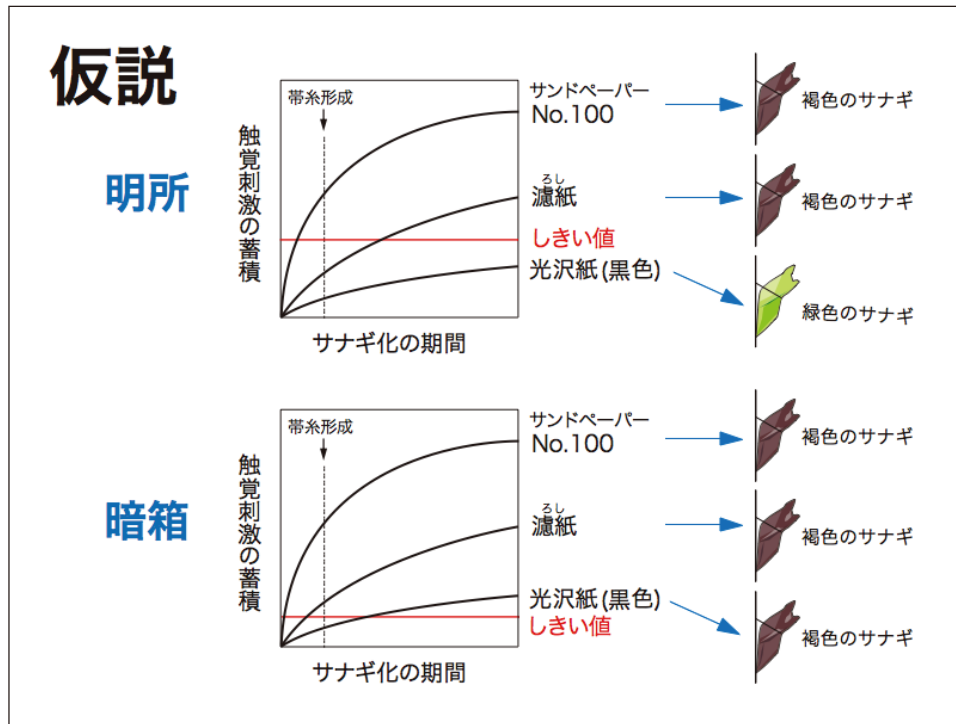
In conclusion, the larvae that received strong mechanical tactile stimuli from the coarse structural surface were stimulated to synthesize melanin, whereas the 200-lux intensity of light or the saturated humidity suppressed the melanin synthesis as shown in the figure below.



Q: 得られた結果はなかなか複雑ですね。これをどのように理解したら良いのでしょうか？

A: このように説明できるのではないのでしょうか。触覚刺激の情報が脳内に蓄積されて或る閾値（いきち、しきい値、限界点）を越えるとその情報が胸部にある内分泌腺に伝達されてホルモンが放出され、そのホルモンが全身に血液によって拡散され皮膚細胞でのメラニン色素の合成を誘導することになるのでしょうか。一方強い光（200ルクス以上の照度）や高い湿度（100%）はその閾値を低下させると考えられます。このように3つの環境要因はサナギの色彩決定に協調的に関与しているのです。

もし触覚刺激の蓄積が閾値とほぼ同じレベルになったときには、緑色と褐色のサナギの両方が現れることに注意してください。



図の説明：横軸は最後の脱糞をしてから幼虫の皮を脱いでサナギになるまでの時間。縦軸は触覚刺激の蓄積量を表す。縦の点線は帯糸を作った時間を示す。触覚刺激の蓄積が『しきい値』を越えるとメラニン色素の合成が誘導される。明所と暗箱では『しきい値』の高さが異なることに注意。

Q: The results you have obtained are somewhat complicated. How would you clear them up and explain in a collective view?

A: I made a working hypothesis to explain the results in the following way. When mechanical tactile stimuli are transmitted to the involved brain via sensory cells with bristles and if the amount of accumulated stimuli will exceed a certain threshold level, the brain cells would send certain direction to an endocrine gland to start secreting some hormone. The hormone will reach the cuticle cells of the larvae via blood stream and induce the synthetic pathway of melanin. In this line of information transmission pathway, the role of light intensity stronger than 200-lux or high humidity (100%) could lower the

threshold level of accumulated stimuli that enable the brain cells to direct the endocrine gland to secrete hormone. Thus, these three factors are thought to cooperate in controlling the coloration of pupae.

Please note that if the level of accumulated stimuli in the brain cells fluctuates above and below the threshold level, either the brown colored or green colored pupae would generate accordingly in support of my above hypothesis.

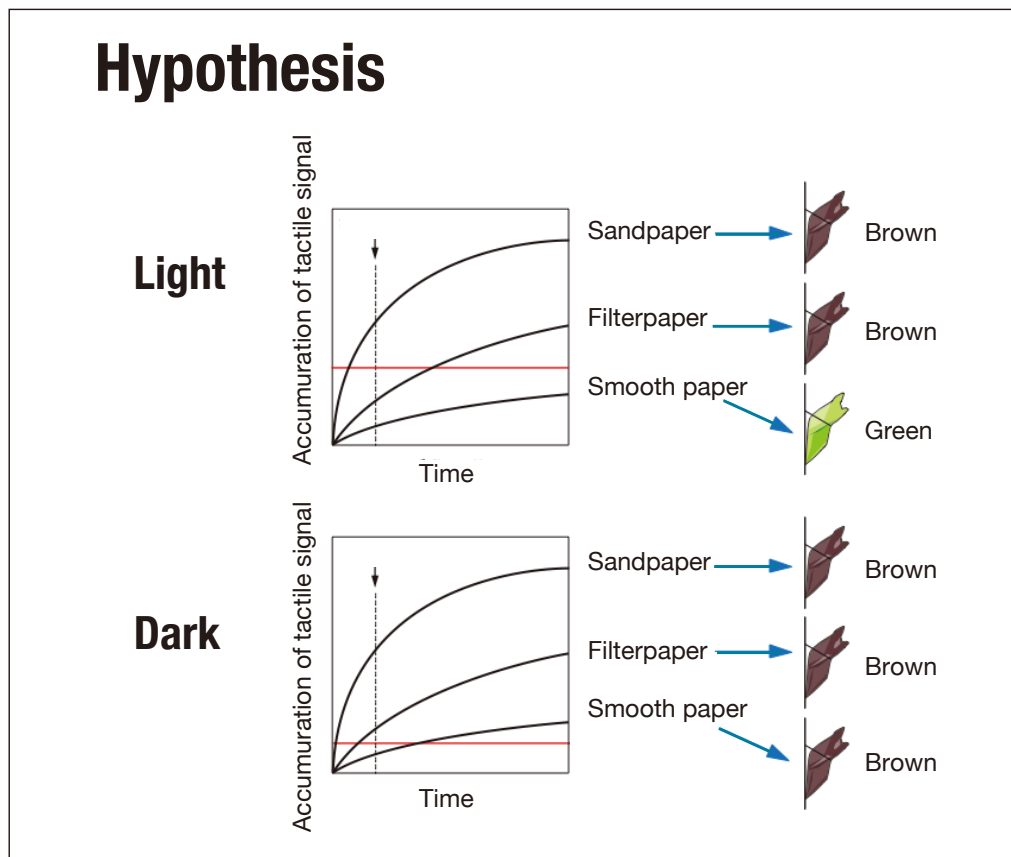


Figure legend: The horizontal axis represents the time required for the larvae to metamorphose to a pupa after the final evacuation followed by taking off the larval skin (ecdysis). The vertical axis represents the accumulated level of tactile signals. The vertical dotted line shows the time the girdle formed. The red horizontal line

shows the threshold level of tactile signals required for induction of the melanin pigment synthesis. When tactile signals accumulate beyond the threshold level, the synthesis of melanin pigment is induced. Note that the threshold level differs when the larvae were placed under the strong light or kept within the dark box throughout.

Q: このような環境要因は絹糸で帯糸を体に巻く前と後でどのように働くのですか？

A: 幼虫が光沢紙の上でサナギになる準備をして帯糸（絹糸）を体に巻いた直後に頭と胸の間にサンドペーパーの小片を挟んだ場合はその切り替えの効果が表れて褐色のサナギが多くなります。その逆にサンドペーパーの上でサナギになる準備をして帯糸を体に巻いた直後に光沢紙の小片を挟んだときには褐色のサナギが少なくなります。すなわち、帯糸を作った後も触覚刺激はサナギの色彩決定に関係するのです。

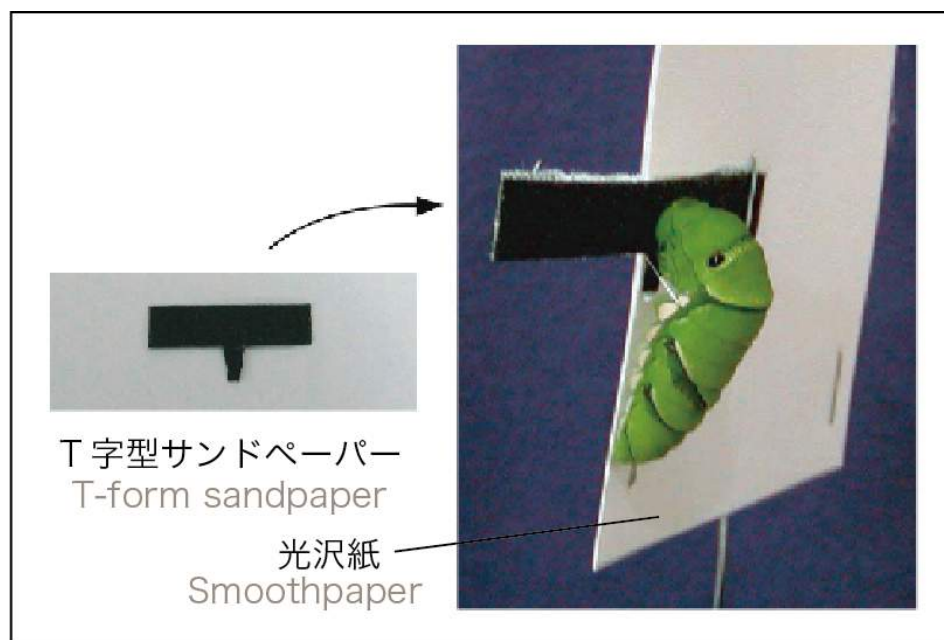
さらに帯糸形成の後と前で光があるか無いかの切り替え実験をやりましたら切り替えの効果が現れました。すなわち、帯糸形成後の「前蛹」（ぜんよう）のステージでも光はサナギの色彩決定に影響するのです。

Q: I wonder if these environmental stimuli/factors affect differentially in determining the pupal coloration before and after the girdle formation with silk strings?

A: When I inserted a small T-form piece of sandpaper to separate the surface of smooth paper and the head-and-thorax portion of larvae that had just finished the girdle (body band) formation with silk strings on the smooth paper, increased number of brown pupae was generated probably because of the sandpaper insertion. Conversely, when sandpaper was used for pupation site, insertion of a small T-form smooth piece decreased number of brown pupae was generated. The results indicate that tactile signals can affect the

pupal coloration even after the girdle was formed, i.e., in “prepupa stage.”

Furthermore, the same was true for the effect of lightening in the prepupa stage, i.e., intense lighting decreased the pupal coloration even after the girdle was formed toward prepupa stage.



図の説明：光沢紙の上で帯糸をかけた前蛹の頭と胸のところにサンドペーパーの小片を挟む実験。

Figure legend: Insertion of a small T-form sandpaper piece between the smooth paper card and the head-and-thorax position of the larva just after the girdle formation.

Q: メラニン色素の合成が誘導されるのは何時でしょうか？

A: 褐色型のサナギになる前蛹の背中に黒い模様が薄っすらと透けて見えてくるのは幼虫の皮を脱ぐ2～3時間前ですので、少なくともそれまでにメラニン色素を合成することが決定されているものと考えられます。そして幼虫の皮を脱いでサナギになった後でもメラニン色素は作られ続けられます

ので、サナギの色の判定は 24 時間後に行いました。
実験に使ったサナギは全て休眠することなく約 10 日後には羽化しました。

Q: When is the synthesis of melanin pigment induced?

A: Since some see-through pale black pattern is observed under the larval skin in the dorsal part of the brown-type prepupa 2 to 3 hours before they start taking off the larval skin, melanin synthesis should have been induced before that stage. As the synthesis of melanin will continue and melanin is accumulated throughout the pupal stage, therefore I judged the color-type of pupae 24 hours after the larvae took off the skin.

All the pupae used in the experiments metamorphosed to adult butterflies after about 10 days without diapause.

Q: 自然界ではいつ前蛹になるのでしょうか？

A: その質問に答えるためには、人工的な照明の無い自然光の下で飼育した幼虫を観察しなければなりません。太陽光の昼と夜のリズムが繰り返される条件で幼虫を飼育すると幼虫の体内に体内時計（生理的な時計）ができます。このような実験条件で幼虫がサナギになる時間帯を調べました。この実験では夜でも 1 時間ごとに目覚まし時計を掛けて起きて観察しましたが、こんなことを 1 ヶ月も続けたので拷問を受けているようでした。

36 匹の幼虫を使ったその実験結果から、終齢幼虫は夜になると最後の下痢便をして、真夜中 24 時頃に帯糸を体に巻き「前蛹」の状態での日の日中を経てから夜になると幼虫の皮を脱いでサナギになることがわかりました。すなわち、「前蛹」の状態です。ですから、暗箱中の実験は自然界の条件とは異なるのです。一方、蛍光灯を点けっぱなしで飼育した 36 匹の幼虫は、サナギになる時間はめっちゃめっちゃでした。正しい体内時計ができないのですから当然ですね。

Q: In nature, what time of the day do larvae become prepupae?

A: To answer the question, I raised the larvae under natural light, but not under any artificial light, in harmony with the inherited circadian rhythm (biological clock). Then, I carried out a plan: I kept watching the larvae for the time course of metamorphosis every hour for a whole month by setting up an alarm clock that forced me to wake up. This job was really a hard one as if I was tortured for sleep-deprivation.

The observations in 36 larvae revealed that the larvae in the final instar stage finished the final evacuation in early night and formed a girdle at midnight. The larvae thus entered the prepupa stage stayed unchanged overnight and next daytime until early evening when each of them started to take off the larval skin to metamorphose to a pupa. Thus, the larvae in the prepupa stage received sunlight sufficiently during daytime before metamorphosis in nature. Therefore, The experiment performed in dark box was obviously the artificial conditions, which differs from those in nature. On the other hand, 36 larvae were raised under constant exposure to artificial light (200 lux), the larvae formed girdles randomly in terms of time as expected because the inherent biological clock did not seem to work in harmony in the absence of natural alternating day-and-night rhythm.

Q: それでは、自然界ではどの環境因子がサナギの保護色にもっとも重要なのでしょうか？

A: それを調べるためには、自然界と同じ環境で実験をやってみなければなりませんね。自然光の下で飼育した幼虫を光沢紙とサンドペーパーの台紙を使って比較してみました。光沢紙の台紙では褐色型は10%でしたが、サンドペーパーの台紙では60%でした。このことは、自然界ではサナギになる場所が平滑面であるか、粗粒面であるかが色彩決定に最も重要である

ことを示しているのです。なぜなら、自然界では全ての前蛹が昼間の太陽光を1日中十分に浴びていますし、大気の湿度が100%になることは実際には滅多にありませんのですから、サナギになる場所の触覚刺激が最も重要な環境要因になるのです。

自然界を注意深く観察してみましょう。カラタチやミカンの緑色の小枝は表面がツルツリしていますが、枯れた小枝は褐色でザラザラしています（5ページの写真を参照）。したがって、自然界ではサナギになる場所からの触覚刺激の蓄積量の違いでサナギの色彩が決定される結果、捕食者の鳥から逃れる保護色になれるのです。

Q: Well, what is the most influential factor in natural environments that determines the protective coloration of pupa?

A: To answer the question, experiments should be performed under natural daylight conditions. In such conditions, when larvae were placed on smooth paper cards only 10% of them metamorphosed to brown type, while larvae were placed on rough sandpaper cards 60% of them metamorphosed to brown type. The results indicated that the surface of texture at the pupation site was most important for the coloration in nature, because all the prepupae should have received sufficient sunlight during daytime and 100% humidity that was used in the previous experiment is actually rare in nature.

Considering the natural environments with respect to the above results, the surface structure of green twigs of trifoliolate orange trees is smooth, whereas that of withered brown twigs is coarse (see photos in 5 page). Therefore, accumulation of the tactile stimuli having received from the coarse surface on which prepupae settled is considered to induce melanin synthesis in the larvae. In other words, the accumulated level of tactile signals from the texture of pupation site would determine the pupal color, thus pupae in

camouflaged color could escape from predatory birds in nature.

Q: 以前、何かの本で「アゲハチョウの幼虫は生きた植物の匂いがあると緑色型のサナギになる」ということを読んだことがありますが、それは誤りですか？

A: その本の著者はおそらく日高敏隆博士（京大名誉教授、昆虫学）が1975年に発表した説を無批判に引用したのでしょう。日高博士は暗箱内では褐色型が多く出るが、その箱の中にカラタチの葉（食草）やブタクサの葉（食草ではない）を入れておくと緑色型が多くなることからそのような結論をだしたのです。暗箱の中では植物は光合成をしません呼吸はしていますから、水蒸気と炭酸ガスを放出しています。水蒸気によって湿度が高くなった効果を匂い物質と勘違いしたのでしょう。植物の匂いはサナギの色彩決定に関係ないことは、先ほど話した僕の実験結果から明らかですね。暗箱の実験は人工的な条件であり、自然界の太陽光のある条件とは異なることにも注意が必要だったのですが、日高博士は自然光下での実験はやっておられません。昆虫学の専門家でさえもこのような間違っただ結論を出してしまう難しい研究課題だったのです。

Q: I once read in a book that some odor substances of live plants that give off are said to largely affect the larvae of common swallowtail butterfly to become green type pupae. Is the description correct?

A: I would say it is not. The author of the book might have uncritically cited the work of Prof. Toshitaka HIDAKA (Professor emeritus of Kyoto University, an expert in entomology) published in 1975. He found that, when he placed the larvae in the dark boxes together with live leaves of trifoliolate orange (food plant) or ragweed (*Ambrosia artemisiifolia* (not the food plant for the butterfly larvae) most of the larvae became green type pupae, whereas in the absence of those live leaves the larvae became the brown type pupae in dark boxes.

Hence he explained his results as odor substances of the living plants determine pupal color and he proposed the “odor theory.” However, as you may know that within dark boxes, living plants cease photosynthesis but continue cellular respiration. Consequently, the plants effuse moisture and carbon dioxide in the boxes. Since Prof. HIDAKA did not repeat his above experiments but in the natural conditions under sunlight, he might have ignored or misunderstood the effect of humidity as an odor substance of living plants. As you recall my experiments mentioned earlier, it is clear that odors of plants are not the determinant of the pupal coloration, if at all. Thus, the issue of the pupal color determinants is so very difficult one even in entomology experts.

コーヒブレーク

Coffee break



アオスジアゲハのサナギの保護色

Protective coloring of pupa in the blue streak butterfly

Q: ところで、平賀さんはアオスジアゲハについても研究していたと聞いてきたのですが、どんなことがわかったのですか？

A: アオスジアゲハの保護色決定の仕組みを研究しました。アオスジアゲハはアゲハチョウと同じくアゲハチョウ科に属しているのですから、アゲハチョウと同じような保護色決定機構を持っているのではないかと思い実験を始めたのですが、全く異なる決定機構を持っていることを発見したのです。

Q: By the way, I understand that you had also studied about the blue streak butterfly. Could you tell me what you have found out in the butterfly?

A: Yes, I have also studied on the pupal coloration in the blue streak butterfly (*Graphium sarpedon nipponum*). This species belongs the *Papilionidae* family as same as the common swallowtail butterfly (*Papilio xuthus*). Therefore, I first imagined that this species also has the same mechanism of pupal coloration as that of the common swallowtail butterfly. However I have found out that the blue streak butterfly has a mechanism quite different from that of the common swallowtail butterfly.



アオスジアゲハ Blue streak butterfly

Q: アオスジアゲハの幼虫は何を食べているのですか？

A: クスノキの葉です。クスノキは大木ですので根元に生えた「ひこばえ」から卵や幼虫を採集するのですが、何百匹も集めようとする大変な仕事になりました。休みの日に自家用車であちこちの団地のクスノキの並木道を走り廻って探すのですが、「ひこばえ」の生えている木自身が少ないので多数の卵や幼虫を集めることは大変でした。

アオスジアゲハの幼虫は通常クスノキの葉の上で緑色のサナギになります。次の写真のように見事なカモフラージュになっています。

Q: What do larvae of the blue streak butterfly feed on?

A: They feed on leaves of camphor tree (*Cinnamomum camphora*). I collected eggs and larvae of the butterfly on basal shoots grown

from the stump of the trees, as the camphor trees are usually so big. Though the camphor tree-lined streets are commonly found in the apartment complexes, these trees are usually not aged enough to grow basal shoots. So, it took many days to collect hundreds of the eggs and larvae as I could search them around only on weekends and holidays by driving my car. Larvae of the butterfly became usually the green type of pupae on green leaves of the plant. As shown in the photo below, the pupae camouflaged themselves admirably.



クスノキの葉の上のアオスジアゲハの緑色型サナギ
The green type pupa on a leaf of camphor tree.

Q: アオスジアゲハはどんな保護色決定機構を持っているのですか？

A: アオスジアゲハの場合には触覚刺激はサナギの色彩決定には関係しませんでした。光 (200 lux) のある明所では、台紙が白色なら緑色型になり、台紙が黒色ならば褐色型になりました。灰色の台紙の時にも褐色型になり

ました。

そして興味あることには暗箱の中では台紙の色には関わらずに全部緑色型サナギになったのです。幼虫の頭の両側に6個ずつ側単眼 (stemmata) があります。この12個の側単眼を全部黒いアクリル絵具で塗りつぶすと200ルクスの光の下で黒い台紙の上でも緑色型のサナギになりました。すなわち、側単眼から入ってくる光刺激が保護色決定に大切なのです。

Q: What mechanism did you find that determines the protective pupal coloration in the blue streak butterfly?

A: I found that tactile signals were not involved in determining protective pupal coloration in the blue streak butterfly. Under the 200-lux light, the larvae became green type pupae on white cards, while they became brown type pupae on black cards. Larvae became brown type pupae also on gray cards. Surprisingly enough, in dark boxes, all the larvae became green type pupae regardless of the card colors.

The larva has six eyes (stemmata), each on both sides of the head. When all the 12 eyes were painted over with black acryl paint, the larvae became green type pupae on a black card even under the 200-lux light. Thus, the stemmata receiving the light were critical to the determination of the pupal coloration.



図の説明： 白い台紙の上の緑色のサナギと黒い台紙の上の褐色のサナギ。両者ともに 200 ルクスの光の下で。

Figure legend: A green pupa on a white card and a brown pupa on a black card under the 200-lux light.

Q: アオスジアゲハの場合には側単眼から入る光がサナギの色彩決定に大切なのですね。

A: そうです。このような結果を基にして考えると、幼虫の背側からの光の強さと腹側からの台紙からの反射光の強さの差を感知しているのではないかと推測されます。黒色の台紙では光が吸収されてしまい反射光は少ないはずです。

Q: Do I understand that light received specifically via stemmata is essential as the stimulus to determine pupal coloration in case of the blue streak butterfly?

A: You are right. I would speculate such specific role of stemmata as

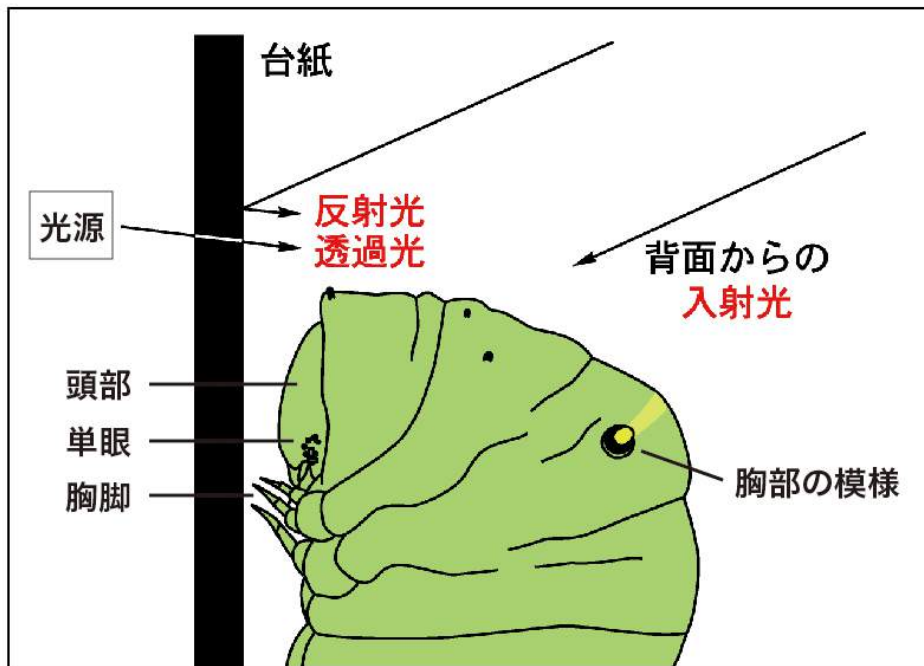
follows, based on my experimental results. The stemmata could be able to distinguish the strength of light that comes from dorsal side from that comes from ventral side as a differential. Consequently, in case of the larvae on the black card, the reflected light strength from the ventral side should be less than that in case of the white card. Accordingly, the differential value should differ between the two cases.

Q: 背中側からと腹側からの照度の差を識別しているのではないかという仮説は平賀さんの新しい仮説ですか？

A: そうです。僕の新しい仮説です。アオスジアゲハの幼虫は光源に対して反対側の台紙の裏側でサナギになる性質があります。照度計で実際に明るさを測定してみました。200ルクスの白色蛍光灯を当てた場合には部屋の壁などから台紙の裏側に当たる散乱光は100ルクスでした。したがって、幼虫が背面から受ける光は100ルクスです。幼虫が腹側から受ける光（台紙の反射光と透過光の和）は、白色台紙では約100ルクスですので照度差はほとんどありません。

一方、黒色台紙の場合は腹側からの光は約25ルクスでしたので、背側からの光と腹側からの光の差は75ルクスでした。灰色の台紙の時には腹側からの光は60ルクスでしたので、背中側からの光と腹側からの光の差は40ルクスでした。すなわちこの差が40ルクス以上だとメラニン色素の誘導が起こり褐色型のサナギになるのです。

黒い台紙を使って光源の光の強さを段階的に200ルクスから0.03ルクスまでに減少させる実験を行ったら、背側からの光と腹側からの光の差が40ルクス以上の時にだけメラニン合成が誘導されることが明らかになりました。一方、暗箱の中では背中側と腹側の照度の差はないのですから当然緑色型になるのです。



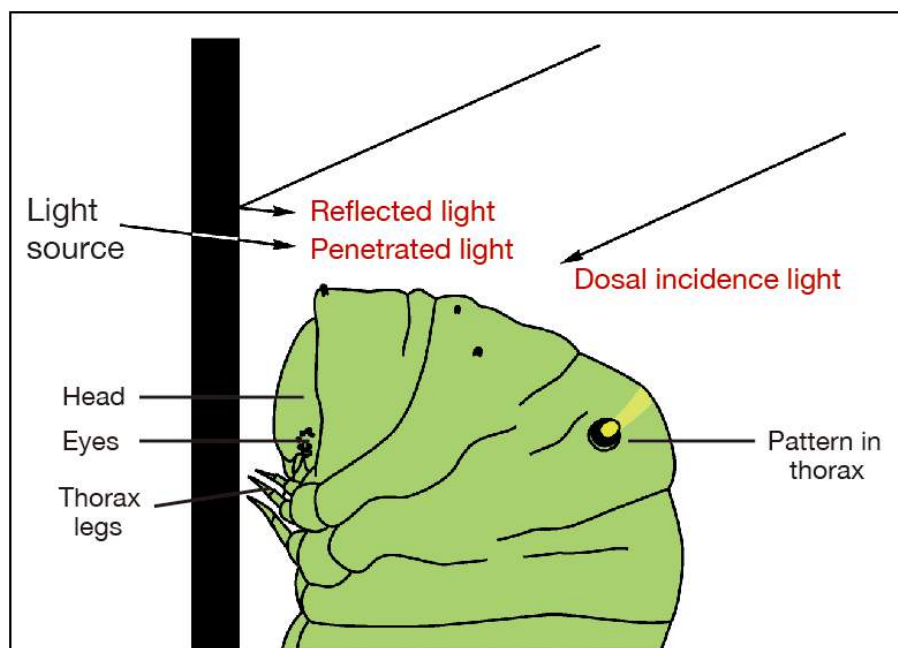
背側からの光と腹側からの光

Q: Are you the first to propose a new working hypothesis to explain the differential coloration of the pupae of the blue streak butterfly in terms of a differential strength of light between those come from dorsal and ventral sites?

A: Yes I am. Let me describe my experimental results more in details. Larvae of blue streak butterfly tend to stay on the reverse side of the card against the light source to become pupae, i.e., the side on which the light illuminates indirectly. Indeed, when I used an illuminometer the 200-lux white fluorescent light reached the reverse side of the card as diffused light via reflection on the wall in the room, the light value decreased to 100-lux. Accordingly, the larvae should receive 100-lux light from dorsal side. In the case of using white card, the light value received from the ventral side was 100-lux (the reflected light on the card plus the light comes through the card), apparently no or a little difference would be detected when compared between the dorsal and ventral sides.

In contrast, the larvae on the black card, they received about 25-lux from the ventral side, i.e., the difference between the dorsal and ventral sides was 75-lux. When gray card was used, the light intensity from the ventral side was 60-lux, i.e., the difference between dorsal and ventral sides was 40-lux. Therefore, one may speculate that the differential value of 40-lux is a threshold: the difference value of more than 40-lux may allow the synthesis of melanin in the larvae to become the brown type pupae.

I additionally performed experiments using black cards in a dark room. I lowered the illumination from the white light source stepwise from 200-lux to 0.03-lux. When the difference between the dorsal and ventral sides was more than 40-lux, melanin synthesis occurred to become the brown type pupae. These results indicated that melanin synthesis requires the differential value of more than 40-lux. Lowering the illumination to zero resulted in dark condition. Therefore, it was reasonable that all the larvae became green type pupae in dark boxes as described above.



Dorsal and ventral lights.

Q: 自然の太陽光の下ではどんなことが起こるのですか？

A: 先に述べたように蛍光灯を使う実験では、光源の反対側でサナギになりましたが、自然界でもアオスジアゲハの幼虫は太陽光の反対側の葉の陰でサナギになる性質があると考えられます。晴れた日の太陽からの直射光は約10万ルクスですが、光源にたいして葉の裏側にいる幼虫の背中側には空からの散乱光約1万ルクスが当たります。腹側からは葉からの反射光と透過光との和の約1万ルクスの光が当たります。このように背中側からの照度と腹側からとの照度はほぼ同じになりますから、自然界では緑の葉の上で緑色型のサナギになると説明できます。太陽光のような強い光のもとでは、40ルクスの「差」ではなく、背側と腹側の光度の「比」を幼虫は感知しているのではないかと推測されます。

Q: What happens really under the natural sunlight?

A: As I said in the above experiments under the fluorescent light, larvae tend to move to the reverse side of pupation cards to stay for pupation sites where they can avoid the direct rays from the light source. Similarly, in nature, larvae presumably determine the pupation site the reverse side of leaves to avoid the direct sunlight. Therefore, although the direct rays of the sun was about 100,000-lux in a fine day, the larva staying on the reverse side of camphor leaves received about 10,000-lux of diffused light from the sky at the dorsal side. The ventral light, which was the sum of reflected light from the leaves plus penetrated sunlight through the leaves, was actually about 10,000-lux in a fine day. Thus, the light intensity from ventral side was nearly the same as that from dorsal side. Under the strong sunlight, larvae presumably recognize the 'ratio' of lights of the ventral side and the dorsal side rather than the differential value of 40-lux. Therefore, all the larvae might become the green type pupae on green leaves in nature.



自然光の下のサナギ
A pupa under natural light.

Q: 褐色型のサナギはどのようなところで見つかるのですか？

A: 褐色型のサナギは自然界では極めて珍しいためか、記載された論文は見つかりませんでした。クスノキは常緑広葉樹ですから秋になっても落葉はしませんが、春に新葉が出た後、古い葉が散発的に赤くなり枯れて落葉します。この赤く紅葉した葉や赤茶色に枯れた葉を使って実験したら 200ルクスの光の下で褐色型のサナギになりました。赤い葉は2～3日で枯葉になりましたので、サナギの色は次の写真のように枯葉の色と全く同じ見事な保護色ですね。

Q: I was wondering if one can find brown type pupae of blue streak butterfly in nature.

A: You rarely see the brown type pupae of blue streak butterfly in nature. In fact, to my knowledge, nobody has published a paper describing about the brown type pupa. Camphor tree is an evergreen broad-leaved tree, so leaves don't fall down in winter. However, in spring as the new leaves start growing, old leaves sporadically turn red followed by withering and fall down. I tried to use red leaves and withered reddish brown leaves for experimental analysis of the pupal coloration. All the larvae became the brown type pupae on these leaves under the 200-lux light. After 2 to 3 days red leaves withered and turned reddish brown. The pupal color of brown type was completely the same as the color of withered leaf as shown in the following photo. It presumably works as a fine camouflage color for them to escape from predatory animals in nature.



赤い葉があるクスノキ

A camphor tree with red leaves.



枯葉の上のアオスジアゲハの褐色型サナギ

A brown type pupa of the blue streak butter on a withered leaf.

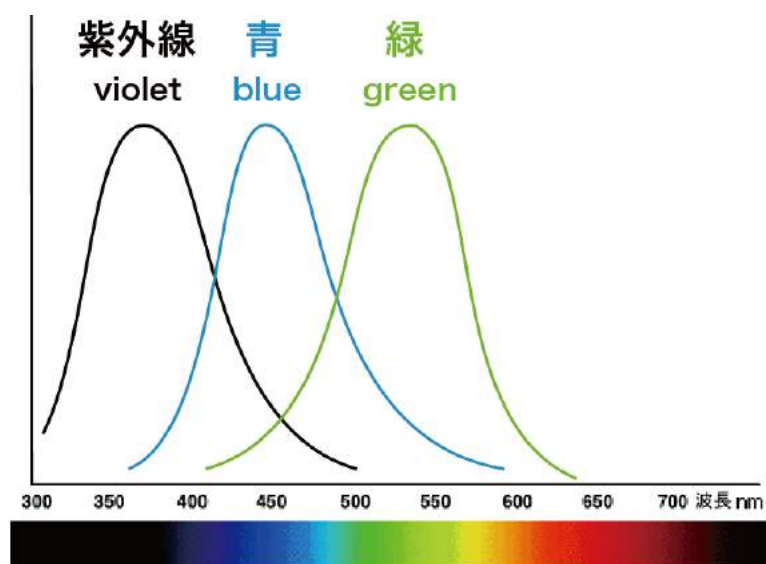
Q: どうして赤い葉の上で褐色のサナギになるのですか？

A: 先ほど話したように幼虫の頭部の両側に6対ずつ側単眼があります。そして、それぞれの側単眼の中には3種の視細胞があり、それぞれ紫外線、青色、緑色を感知することができるそうです。しかし、赤色を感知する視細胞はありませんので、赤い葉や枯れた赤褐色の葉では黒い台紙の場合と同じように褐色型のサナギになったものと考えられます。幼虫はサナギになる前に葉と小枝の間に絹糸をかける習性があるので、葉が枯れても落葉することはないのです。そしてアオスジアゲハの幼虫は朝に最後の脱糞をして昼の間に帯糸をかける性質があるので昼の間に色彩決定を行うことができます。このように色彩決定機構と生態との間に見事な連携がありますね。

Q: How does a larva of the blue streak butterfly become brown type pupa on a reddish camphor leaf?

A: The larva has six eyes (stemmata) each on both sides of the head as told earlier. It is known that there are three types of photoreceptor cells in each stemma. The cells can receive respectively the wavelength of ultraviolet, blue, and green. However, there is no cell that can receive the wavelength of red. Therefore, the larvae presumably recognized a red leaf as a black leaf, resulting in the brown type of pupae.

The larvae that are going to stay at the pupation site of leaf have a behavior to fix themselves to the twig by secreted silk strings before pupation, so that even if the leaf with a pupa withers, the leaf will not fall down. In addition, I found that larvae finish the final evacuation in the morning and form the girdle in daytime, so that the larvae can see the color of leaf to determine the pupal color during daytime. Thus, there is such a fine reasonable cooperation between these behaviors and the mechanism of pupal coloration.



図の説明：幼虫の単眼にある3種の視覚細胞はそれぞれ紫外線・青・緑の波長を感じるが、赤の波長を感じ視覚細胞は存在しない。

Figure legend: Three types of photoreceptor cells in the larval eyes can receive respective wavelength of ultraviolet, blue, and green, but there is no photoreceptor cell that can receive the red wavelength.

このアオスジアゲハのサナギの保護色決定機構についての私の英語論文の外には、*Graphium* 属に属する世界の蝶のサナギの保護色決定機構について記載した論文は今までにありませんでした。

To my knowledge, except my paper published in English describing about the pupal coloration mechanism in the blue streak butterfly, there has been no paper reported about the mechanism of pupal protective coloration in butterflies in the world belonging to the *Graphium* genus.

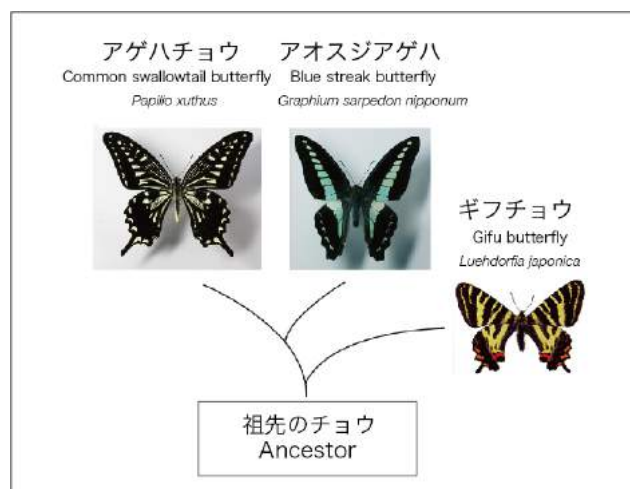
Q: アゲハチョウとアオスジアゲハは異なるやり方でサナギの色を決めたのですね。 どうしてこんな異なる色彩決定機構を持つようになったのでしょうか？

A: アゲハチョウ科の祖先のチョウの幼虫はおそらく背丈の低い草植物を食べて地面で褐色のサナギになったと推測されます。 なぜなら、原始的なチョウといわれているギフチョウはカンアオイの葉を食べて落ち葉の下で褐色のサナギになるからです。 DNA 解析からアゲハチョウとアオスジアゲハは 8500 万年ほど前の恐竜時代に互いに分岐し進化してきたことが知られています。 木の上でサナギになる性質を発展させる過程でそれぞれ別々の保護色決定機構を捕食性動物から逃れるために進化させてきたと考えられますね。 このような巧妙な機構や生態はダーウインが唱えた『自然選択（自然淘汰）』によって 8500 万年の間に徐々に進化してきたのです。

Q: It is quite interesting that you have shown different mechanisms of the pupal coloration between the common swallowtail butterfly and the blue streak butterfly. How and why did these butterflies develop into those acquired different

mechanisms?

A: Larvae of the oldest ancestral butterfly in the Papilionidae family are thought to feed on short herb plants and form only the brown pupae on the ground. These speculations were based on the fact that larvae of the primitive species called gifu butterfly (*Luehdorfia japonica*) feed on the short herb wild ginger (*Asarum*) and form only the brown pupae on the reverse side of brown leaves fallen on the ground. DNA analysis revealed that the common swallowtail butterfly (*Papilio xuthus*) and the blue streak butterfly (*Graphium sarpedon nipponum*) were diverged each other about 85 million years ago (corresponding to the dinosaur period). During the evolution, these butterflies presumably developed independently each other in terms of time and environments the different behaviors of pupation on trees and the different mechanisms of the protective pupal coloration to escape from predatory animals. These appropriate mechanisms of pupal coloration and behaviors in pupation might have developed gradually during 85 million years by the 'natural selection' proposed by Charles Darwin.



アゲハチョウ科のチョウの系統樹

The phylogenetic tree of butterflies in the Papilionidae family.



Book: "Butterfly: Mystery of Pupa" by Hiraga Sota.



書齋 兼 昆虫研究室 兼 アトリエ (2016)
Library /insect research room /atelier (2016).

インタビュー後記

平賀さんにインタビューして、普通種の蝶でもまだこんな未知の面白いことがたくさんあったことには驚きました。平賀さんが選んだ研究課題は蝶のサナギの保護色がどのようにして決まるのかという問題でした。捕食者の鳥などから身を守るカモフラージュです。あたかも自然が蝶に与えたフアインアートのような生態です。平賀さんはこの巧妙な美しい生態を明らかにしたのです。研究者としての粘り強い探求心に私は深く感動し、そして自作の簡単な装置を使って複雑な生命現象を手際よく解析したやり方が印象に残りました。使った道具類は温度計、湿度計、照度計、デジタルカメラ、エアコン、蛍光灯スタンドなど、どれも一般家庭でも見えそうなものばかりです。こんな研究を平賀さんは夜中に自宅で一人こつこつとやって結構楽しんでおられたのではないのでしょうか。目覚まし時計をかけて夜1時間ごとに起きて1ヶ月間観察したとか、200ルクスの蛍光灯を6ヶ月も点ければなしにした部屋でアイマスクをしてたくさんの幼虫やサナギに囲まれて眠っていたなどというエピソードを皆さんは想像できますか？これこそ研究者魂ですね。羽化した蝶がたくさん飛び回っていた自室はまるでインセクタリアム（昆虫園）のようだったとのことでした。

この研究結果を2つの英語の論文にまとめて海外の昆虫生理学の学術誌 (Journal of Insect Physiology) に発表されたとのこと。また単行本「蝶・サナギの謎」(トンボ出版社)も上梓されました。文・絵・イラスト・写真・研究・ブックデザイン・レイアウトなど全部平賀さんが一人で作成した本だそうです。平賀さんが描かれた蝶・鳥・魚・人物などのイラストや油絵も見せていただきました。京都市美術館で毎年開催されるLINK展では社会的メッセージを含んだ大きな油絵の作品を多数発表しているそうです。研究における熱狂的パワーに圧倒された楽しいインタビューでした。

(Y. K. 記 2017)

Interviewer's Notes

After the interview with Prof. Hiraga, I was surprised to find out that there had remained so many such interesting problems to be explored even in these common species of butterflies. The subjects he chose among them to study were the physiological mechanism of protective coloring of pupae in butterflies so that the pupa can mimic its color to that of pupation sites resulting in camouflaging to escape from predatory animals, for example, birds. I was really fascinated that butterflies behaved as if nature gave them a gift of fine artist. And Prof. Hiraga explored the behavior in view of scientific basis. I was deeply stirred by his researcher's spirit of inquiry and also impressed that he performed experiments using experienced skills with the use of apparatus simply consisting of only household utensils like thermometer, hygrometer, illuminometer, digital camera, air conditioner, fluorescent lamp, and so forth so that one could perform experiments at home. He must have enjoyed his all the experiments he planned including the hard one in which he had to keep watching the larvae for the time course of metamorphosis every hour for a whole month by setting up an alarm clock. Can you imagine the scene he told me episodes where he is wearing a sleep eye mask under the 200-lux strong fluorescent light at nights for "6 months" surrounded by many larvae and pupae, and he had to wake up every hour at nights for 1 month using an alarm clock. I just couldn't help smiling or laughing, but for him it was no laughing matter overwhelmed by spirit of inquiry. Many butterflies emerged were flapping round anywhere. The room was like an insectarium.

He has published two papers in English about the results mentioned in the interview in International journal 'Journal of Inset

Physiology. In addition, he published a book on his own work, entitled “Mystery of Butterfly Pupa” in Japanese (2007, TOMBOW Publishing Co., Ltd.). In this book he did by himself all the editing including drawings, illustrations, photos, book design, and layout. I remarkably enjoyed his illustrations of butterflies, birds, fishes, figures, and others by oil painting. In fact, he has sent his many large oil painted pictures in exhibition including social messages in LINK Exhibition, which has been held in the Kyoto Art Museum in every year. I really enjoyed the interview, in which I was overwhelmed by his powered enthusiasm on his research.

(Y. K. wrote in 2017)

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平賀壯太のホームページ: www12.plala.or.jp/s3t45h86a9g8xyz6/

平賀壯太 | 京都大学ウイルス研究所ウイルス研アーカイブ研究者:
www.virus.kyoto-u.ac.jp/archive/interview/s-hiraga.html

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1936 新潟県生まれ

1965 大阪大学大学院理学研究科博士課程終了 理学博士

1965-1984 京都大学ウイルス研究所 助手

1970-1972 スタンフォード大学 特別研究員

1985 京都大学ウイルス研究所 助教授

1985-2002 熊本大学大学院医学研究科 教授

2002-2008 京都大学大学院理学/医学研究科 非常勤研究員

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1970-1972 Stanford University, Special Researcher

1985 Kyoto University Institute for Virus Research, Associate Professor

1985-2002 Kumamoto University Graduate School of Medicine, Professor

2002-2008 Kyoto Graduate School of Science/medicine, Part-time Researcher

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Kumamoto University, Honorary Doctor

Japanese Society of Genetics, Honorary Member

Japanese Society of Genetics, KIHARA Hitoshi Award

Japanese Society of Molecular Biology, Former Member

Japanese Society of Lepidoptera, Former Member

Society of Insect DNA Research, Member

American Academy in Microbiology, Former Member

Specialty: Molecular Biology

Hobby: Research for insect and oil painting
