PHYSIOLOGICAL COLOUR CHANGE IN THE ELYTRA OF THE HERCULES BEETLE, *DYNASTES HERCULES*

H. E. HINTON and G. M. JARMAN

Department of Zoology, University of Bristol

Abstract—The male of the hercules beetle, *Dynastes hercules*, is able to change the colour of its elytra from yellowish to black and back again to yellowish within a few minutes. The epicuticle of the elytra is transparent and about 3 μm thick. Below it is a yellow spongy layer that is usually about 5 μm thick. The cuticle below the yellow sponge is black. When the layer of yellow sponge is air filled it becomes optically heterogeneous, and the light reflected from the elytra is yellow. When the yellow sponge is liquid filled it becomes optically homogeneous, and the black cuticle below is seen.

If a beetle that has yellowish elytra is placed in a saturated atmosphere, the elytra become black. When the relative humidity is appreciably reduced, yellow patches begin to appear on the elytra, usually within 30 sec to 2 min. However, if the beetle is kept at a constant relative humidity that previously caused yellowing, it will become black given enough time. Most colour changes observed were clearly in response to changes in the ambient humidity and were not affected when the beetles were kept in the light or in total darkness nor by blackening their eyes or prodding them or exposing them to sounds of different intensities or frequencies.

If an elytron is removed from a live beetle, it changes colour in response to changes in relative humidity exactly like the elytron left attached. When a restricted area of the elytra is subjected to a humidity that normally causes blackening and an adjacent area to a humidity that normally causes yellowing, both change colour in the expected way. This local control of colour change seems to preclude hormonal control. It is suggested that the epidermal cells or both the epidermal and blood cells in the elytra are responsible for the hydration and dehydration of the layer of yellow sponge.

INTRODUCTION

THE HERCULES beetle, *Dynastes hercules* L., can change the colour of its elytra from black to yellowish and back again to black all within a few minutes. That there are two colour forms of this species, one with black and the other with yellowish elytra, has been repeatedly noted by collectors from the eighteenth century onwards, but BEEBE (1947, p. 111) appears to have been the first to note that the same individual could rapidly change the colour of its elytra. Beebe said nothing about the way the colour change was effected. HINTON and JARMAN (1972) pointed out that there is a yellowish spongy layer below the transparent epicuticle. When the spongy layer is flooded it becomes optically homogeneous and the black cuticle below the yellow sponge is seen. However, when the spongy layer is filled with gas instead of liquid,

light is reflected from the sponge and the beetle is therefore yellowish. In this account we have referred to the colour when the spongy layer is gas filled as yellow or yellowish. The yellowish colour of different individuals differs. BEEBE (1947) notes that the elytra may be pale brownish olive, greenish yellow, buffy brown, Dresden brown, or cold buff citrine.

It seems that the only other insects that can rapidly and reversibly change the colour of their elytra by varying the level of hydration are some chrysomelid beetles of the subfamily Cassidinae. The iridescent colours of these arise from multiple-layer interference. As first noted by MASON (1929), *Deloyala guttata* (Oliv.) and *Metriona bicolor* (F.) change the colour of their elytra by varying the moisture content and thereby the thickness of the thin films responsible for the interference colours. Since then it has been found that *Aspidomorpha tecta* Boh., *Eurypepla calochroma* Blake, and a number of other Cassidinae can quickly and reversibly change the colour of their elytra (HINTON, 1973).

It now appears that in the family Scarabaeidae there are more different ways of producing colour than in all other insects. As in other insects, colour may be produced by pigments, or by structural colours or by a combination of both. Structural white caused by scattering as well as colours arising from multiple-layer interference in optically inactive cuticles have long been known. Optically active cuticles that reflect circularly polarized interference colours are confined to the Scarabaeidae (GAUBERT, 1924; MATHIEU and FARAGGI, 1937; NEVILLE and CAVENEY, 1969), and colour produced solely by diffraction gratings occurs in many groups of the subfamily Melolonthinae (HINTON, 1970b). Many scarabaeids of the subfamily Cetoniinae have ultraviolet patterns produced by patches of micro-trichia that contain a pigment that reflects ultraviolet (HINTON, 1970a). Such patterns are thought to serve in species and sex recognition. The only structural colours known in insects and not so far found in the Scarabaeidae are Tyndall blues such as occur in some dragonflies.

## STRUCTURE OF OUTER LAYERS OF ELYTRA

The outermost layer of the cuticle is transparent, and in most areas it is about 3 μm thick. Below this transparent layer is a yellowish spongy layer, generally about 5 μm thick. The cuticle beneath the yellow sponge is black by reflected light and reddish by transmitted light: spectrophotometer measurements show it to be highly transparent to infrared. Transmission electron micrographs (Figs. 3–4) show that the layer of yellow sponge consists of columns or pillars normal to the plane of the surface and usually about 0·5 to 1·0 μm thick. The pillars are connected to each other by irregular branches normal to their major axes (Fig. 6). When the elytra are yellowish, the spaces between the pillars are filled with air; when.the elytra are black, the spaces between the pillars are filled with liquid. Scanning electron micrographs of 10 μm thick sections (Figs. 7–8) show that the spongy layer is much more irregular than would appear from transmission micrographs. The interstices or spaces between the branches of the pillars usually vary from 0·01 to 0·5 μm in width. Columns that are oval or circular in section and up

FIGS. 1–2. Live Hercules beetles. In one the elytra are in the yellow phase when the spongy layer is air filled, whereas in the other they are in the black phase when the spongy layer is liquid filled.
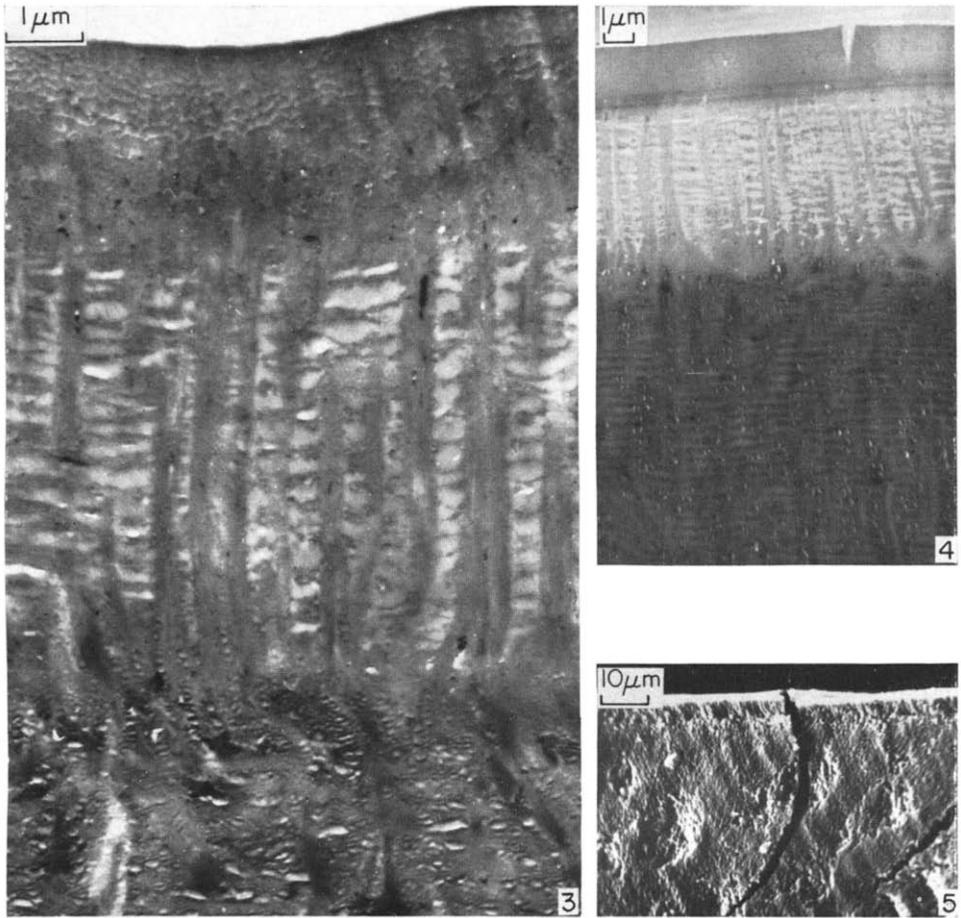
FIGS. 3–5. Transmission (3–4) and scanning (5) electron micrographs of the outer part of the cuticle of the elytra of *D. hercules*.
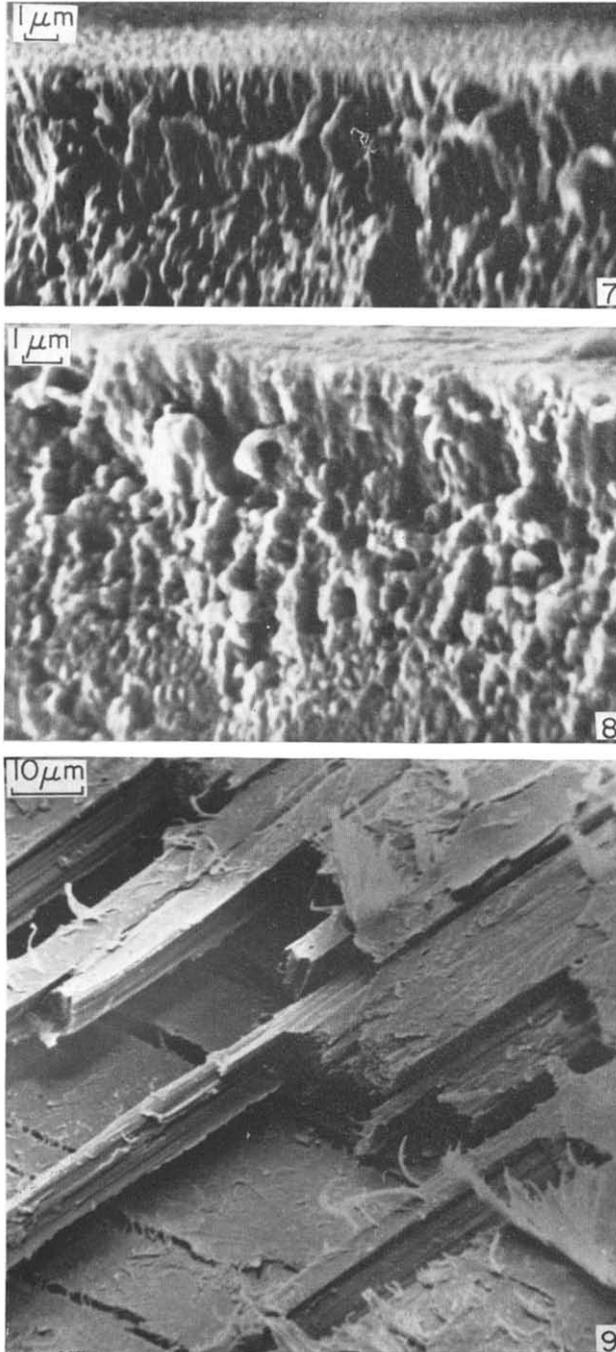
FIGS. 7–9. (7–8) Scanning electron micrographs of 10 μm thick sections of the yellow spongy layer of the elytra of *D. hercules*. (9) Laminated procuticle of the elytra.
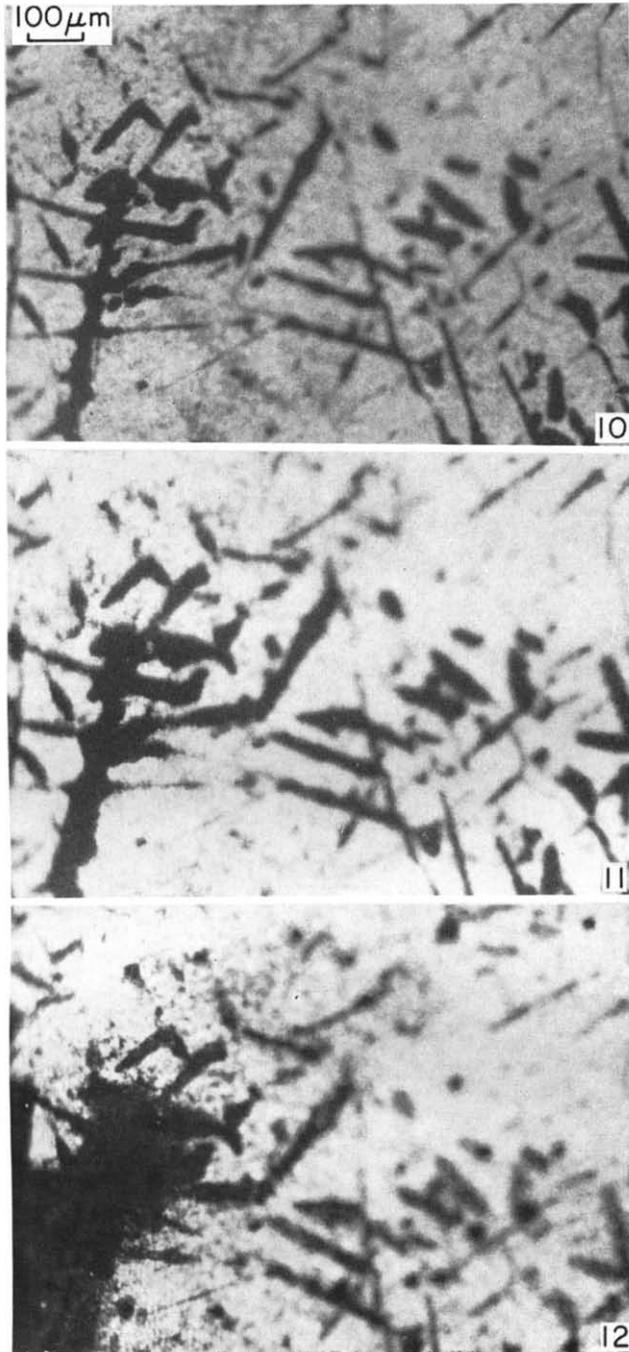
FIGS. 10–12. Time-lapse photographs of a piece of yellow elytron of *D. hercules* immersed in De Faures medium. (10) Shortly after immersion. (11) About 15 min after immersion. (12) About 30 min after immersion when the flooding of the spongy layer on the left side is much more extensive.
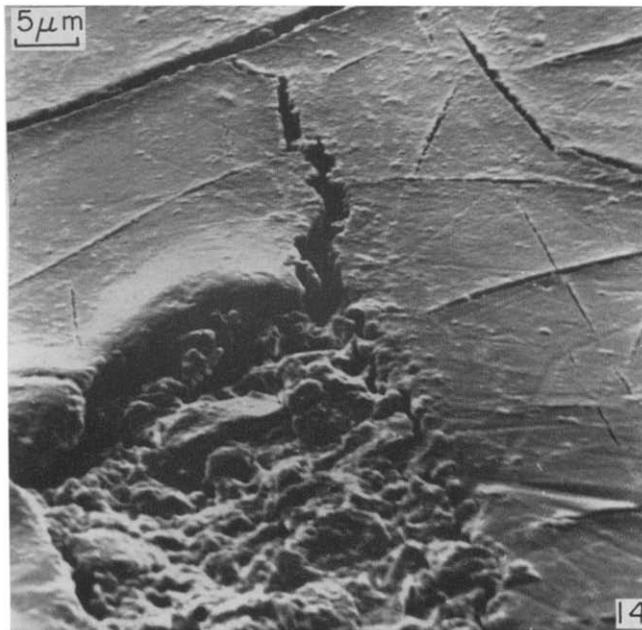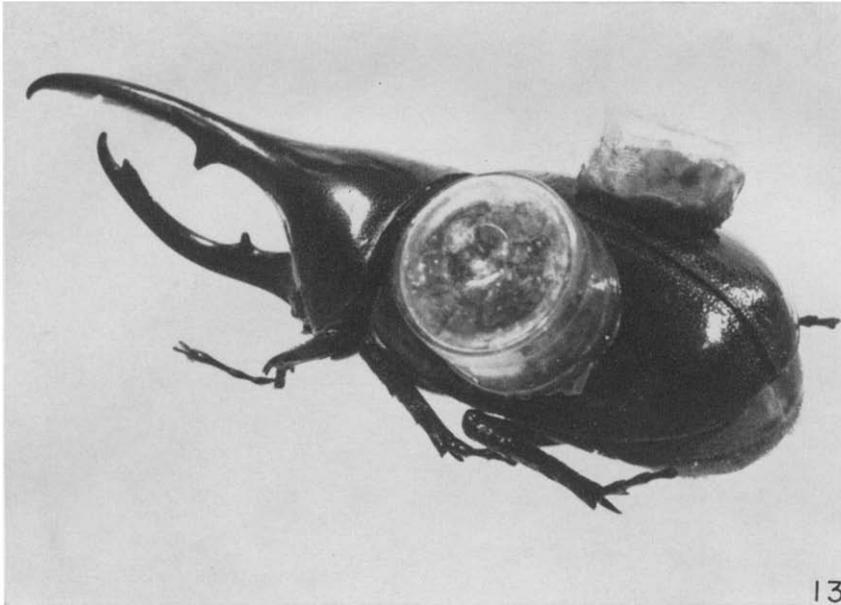
FIGS. 13, 14. (13) Glass tubes 20 mm in diameter attached with chewing gum to the elytra of the Hercules beetle. One tube contains dehydrated silica gel and the other damp filter paper as a control. (14) Scanning electron micrograph of the surface of an elytron showing numerous scratches and a small section on the left side where the epicuticle was removed in order to expose the spongy yellow layer below.
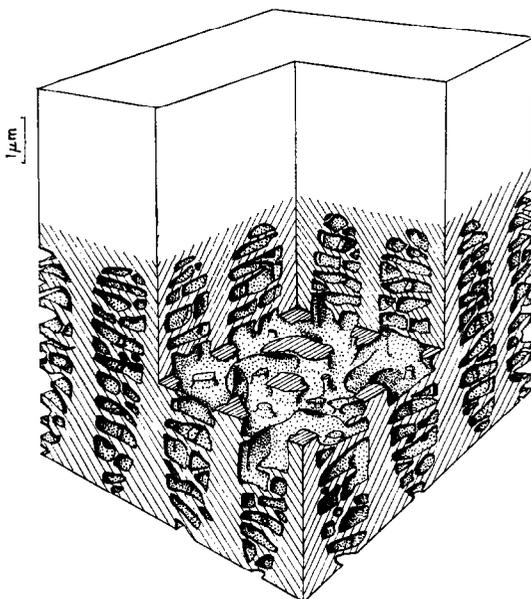
FIG. 6. Diagram of the structure of the yellow spongy layer of the elytra of *D. hercules*. The outer transparent layer is unshaded.

to 1·6 mm in diameter extend vertically through the elytra to the outermost layer. When the elytra are yellowish because the interstices of the spongy layer are filled with air, the areas occupied by the columns appear as black spots.

OBSERVATIONS ON MUSEUM SPECIMENS

The yellow elytra of museum specimens blacken reversibly when wetted with water and other liquids. From time-lapse photographs of elytra in De Faures mounting medium (Figs. 10–12), it seems clear that the liquid is, in the first instance at least, entering the yellow sponge through numerous scratches (see Fig. 14) in the transparent layer. Unlike live elytra, those of specimens that have been dead for a long time do not change colour when placed in atmospheres of different relative humidities. However, when kept for several days in a saturated atmosphere, some dead elytra became partly or almost entirely black. We suppose that this is because water condensed on the surface over a long period eventually floods the yellow sponge.

By exerting a little pressure with a rounded point so that the outer transparent layer is not broken, black lines may be made on the yellowish elytra of museum specimens. The pressure exerted compresses the coloured layer below sufficiently to exclude the air spaces in it with the result that it becomes optically homogeneous and the black layer below becomes visible. Such black lines made visible on museum specimens appear to be more or less permanent and only occasionally do

small flecks of yellow appear in the black lines. However, if the elytra are then flooded with water which is next allowed to evaporate, the black lines become yellow like the adjacent areas of the elytra. Evidently the water absorbed by the spongy layer restores its original form and its interstices reappear, but the lines remain black until the water evaporates and the interstices fill with air so that the coloured layer beneath the lines once again becomes optically heterogeneous.

If a drop of liquid nitrogen is placed on the black elytra of a live beetle, a yellow spot immediately appears as the liquid in the spongy layer is frozen and the layer made optically heterogeneous. As soon as the nitrogen has evaporated the yellow spot becomes black as the spongy layer once more becomes optically homogeneous. When a yellow elytron of a dead beetle is made black by soaking it in water, a drop of nitrogen placed on the upper surface immediately produces a yellow spot that vanishes as soon as the nitrogen has evaporated.

When drops of water are placed on the outer surface of the yellow elytra of either dead or live beetles, blackening occurs at the site of the drops within a few minutes. The elytra of both the dead and live beetles used were extensively scratched. This seems evident from Fig. 9, in which black lines caused by wetting the spongy layer with gum chloral are orientated at random in the plane of the surface. Hardly any of the lines and spots in Fig. 10 are isolated from adjacent ones by more than about 100 μm. From Fig. 10 it is also evident that some of the scratches are deeper and wider than others: in a given unit of time the spongy layer below some is more extensively wetted than below others. When Fig. 10 is compared with the stereo-scan micrograph (Fig. 14) of the surface above and to the right of the piece of epicuticle removed, a similar series of scratches can be seen, and these differ both in length and depth in the manner that might have been expected from the way in which the yellow sponge is wetted (Fig. 10). Although water may enter through the unbroken epicuticle, we have obtained no clear evidence that it does so. As shown in the experiments in which tubes filled with silica gel are attached to the elytra (p. 546), transfer of water can be prevented through scratches and other minor damage to the epicuticle, presumably by translocation of lipids to these areas.

In the experiments in which pieces of the elytra of dead beetles were immersed in De Faures medium (gum chloral), flooding of the yellow sponge was to some extent reversible. For instance, if the middle right-hand side of Figs. 11 and 12 is compared with the same area of Fig. 10, it will be seen that some of the black markings have become fainter or have altogether disappeared. Although the pieces compared with the same area of Fig. 10, it will be seen that some of the black of elytra remained completely immersed in the gum chloral, evaporation from the exposed surfaces of the medium causes its retraction from some of the parts of the sponge previously wetted by it. Gum chloral was used for these experiments because it is less mobile than water and so makes time-lapse photography easier.

By the kindness of Mr. R. D. Pope, the collection of *Dynastes* in the British Museum (Natural History) was examined. None of the African or Oriental species of the genus appear to be able to change colour, and they appear to lack the yellow spongy layer in the outer part of the elytra. One American species, *D.*

neptunus Quenzel, also does not appear to be able to change colour. In the other American species, *D. granti* Horn, *D. hyllus* Chevr., and *D. tityrus* L., the structure of the elytra is like that of the Hercules beetle. In *D. granti*, *D. hyllus*, and *D. tityrus* the outer layers of the cuticle of the pronotum are similar to those of their elytra. A few simple experiments suggest that they are able to change the colour of their pronotum from black to yellowish and back again: water added to the surface of the pronotum causes blackening by flooding the yellowish spongy layer, and black marks can be caused by exerting pressure on the pronotum just like they can be caused by exerting pressure on their elytra or on those of the Hercules beetle.

From what has been said above, it would seem that every dried museum specimen of the Hercules beetle should have yellowish elytra. However, 1 male of a total of 37 seen had entirely black elytra, and in about a third of all females the elytra were black instead of mottled with yellowish. Black or nearly black males and females were also found among museum specimens of *D. granti*, *D. hyllus*, and *D. tityrus*. In these the pronotum was usually also black. In 1 male of *D. hyllus* and 1 of *D. tityrus* the left elytron was entirely or nearly entirely black and the right elytron was extensively mottled with yellowish. Two females of *D. tityrus* also had the left elytron black and the right elytron mottled. The fact that dry specimens can be black, and particularly that the left and right elytra can differ so much in colour, is unexpected. It may be that in these specimens the yellow sponge is filled with a lipid, but no tests were made.

EXPERIMENTS WITH LIVE BEETLES

Over a period of nearly a year 8 living beetles were obtained, 5 males and 3 females. Most were maintained between experiments in a glass container $60 \times 40 \times 30$ cm kept at 21 to 22°C and approximately 70% r.h. They were fed on peeled bananas and honey and water. In most of the earlier experiments (HINTON and JARMAN, 1972) 2 males from Venezuela were used, and these were kept between experiments in warmer and more humid conditions.

Females change colour, but the colour changes of the 3 specimens available were not as complete nor as obviously and immediately related to changes in ambient humidity as were colour changes in males. Only males were used in the experiments described below, all of which were done at 25°C unless otherwise indicated.

In order to obtain a numerical measure of the tendency of the elytra to yellow when the ambient relative humidity was reduced, tests were done according to the following schedule.

(1) The beetle was placed in a container at approximately 100% r.h. for a recorded period that was never less than 20 min after the disappearance of the last trace of yellow from the previous test.

(2) The now black beetle was transferred to a lower relative humidity for exactly 10 min. During this interval, the time taken for the first trace of yellow to appear, the 'yellowing time', was noted.

(3) After 10 min in the drier atmosphere, the beetle was returned to the container at about 100% r.h. and the time taken for the last trace of yellow to disappear, the 'blackening time', was noted. Usually a run of six such '10-min tests', using a variety of relative humidities, was completed during the day and the beetle was then returned to the container at 70% r.h. for the night.

Both the blackening time and the yellowing time were often difficult to judge, and errors up to 20% may have been made. Factors that have a slight influence on colour change are therefore hard to recognize and are ignored in the comparatively crude experiments which are only concerned to clarify some of the grosser features of the phenomenon.

When the beetle was exposed to increasing differences in relative humidity, the time for the first appearance of yellow decreased and the time for the last trace of yellow to disappear increased. A typical relation between yellowing time and a change in relative humidity is shown in the line for day 1 in Fig. 15. This also shows the considerable scatter of the results typical for this type of experiment. When the yellowing time was shorter, the total area of the elytra that became yellow in the 10 min test period was clearly greater.
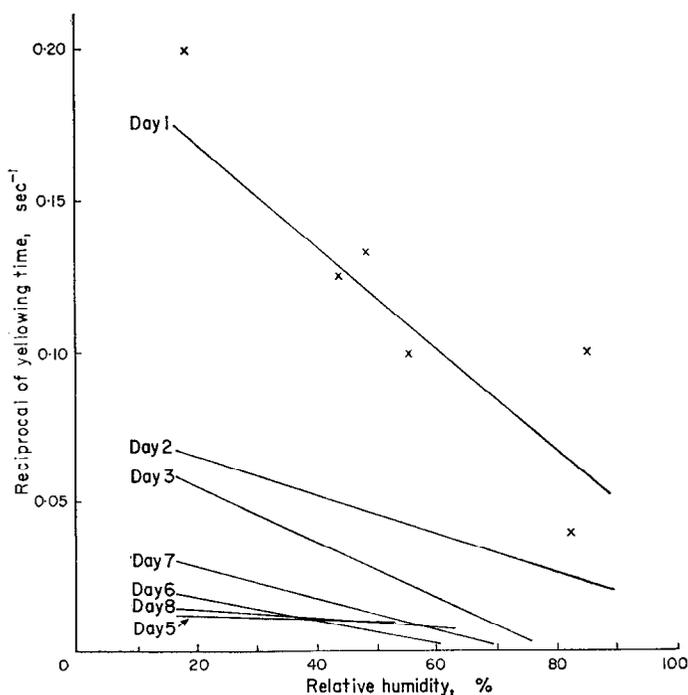

Fig. 15. Speed of yellowing (as reciprocal of yellowing time) against changes in relative humidity in 8 consecutive days. Points are indicated only for day 1. A marked yellowing had taken place on day 0. Tests were done at 25°C, but the beetle was kept at 21°C and 70% r.h. between the end of tests on one day and the start of tests on the next day.

There was a rather inconsistent relation between t_y, the yellowing time in seconds, when the relative humidity was reduced from 100% to some lower value and t_b, the blackening time in seconds, when the beetle was returned to 100% r.h. after 10 min in the lower humidity. Assuming a relation

$$\log t_b = a \log t_y + b,$$

the figures in Table 1 were obtained. The numerical value of a was consistently less than 1, clearly indicating that blackening time was less dependent on humidity change than was yellowing time.

TABLE 1—CONSTANTS IN THE RELATION $\log t_b = a \log t_y + b$ FITTED TO VALUES OBTAINED IN 152 10-min TESTS

	Temperature (°C)	a	b	Coefficient of correlation	P	No. of tests
Beetle B	25	−0·52	+3·93	0·75	<0·001	17
Beetle C	21	−0·48	+2·81	0·67	<0·01	19
Beetle D	21	−0·37	+3·23	0·32	<0·05	40
Beetle D	25	−0·57	+3·25	0·71	<0·001	76

The relative humidity in the drier atmosphere ranged from 15% to 90%.

The yellowing was obviously faster at 25°C than at 21°C for the same change in relative humidity. In one set of tests on the same day, the rate at 25°C was three times faster than at 21°C, in another eight times. At 16°C the rate was three-fourths that at 21°C. This may be partly because the same relative humidity change represents a slightly greater humidity change in grams of water/litre at the higher temperature. Blackening times at 25°C were not clearly distinguishable from those at 21°C because of the large scatter of the results. The relation to be expected between blackening time and temperature is not obvious; on a purely speculative basis it might be supposed that at the higher temperature a greater volume of spongy layer has to be rehydrated, but at the higher temperature the rehydration mechanism may move water faster.

The effect of the previous experience of an individual beetle on the results of an experiment was hard to predict. Occasionally the elytra would remain black for several days at relative humidities between 60 and 80% and then rather suddenly become yellow. Nevertheless, with few exceptions the elytra of a beetle kept long enough at any constant relative humidity above 60% (lower humidities for long periods were only tried on small areas of the elytra (Fig. 13), but the results were similar) eventually became black, however extensively yellow they were before and for whatever reason. However, while this gradual bias towards black was taking place, the 10 min tests showed that the yellowing time was lengthening and the blackening time shortening. This gradual bias towards black, as distinct from the

blackening in the 10 min tests, was clearly faster at 25°C than at 21°C. Fig. 15 shows graphs illustrating the dependence of yellowing speed on relative humidity change for the same beetle in a series of days. An abrupt and extensive yellowing had taken place on day 0. The subsequent reduction in yellowing speeds during the next few days is evident, as is the reduction in dependence of yellowing speeds on changes in relative humidity.

The yellowing tendency can be increased by rubbing an elytron gently for a minute or so with a filter paper wet with either water or chloroform. It may be supposed that this treatment removes the lipids on the surface of the epicuticle as well as those sealing the scratches through the epicuticle.

It was quite clear that the yellowing and blackening responses were locally mediated. One simple and conclusive experiment consisted of removing one elytron from a beetle and then submitting both the beetle and the detached elytron to identical humidity changes. Before the experiment, the two elytra were yellowing and blackening similarly. For 21 hr after the removal of the right elytron the two elytra continued to yellow and blacken with identical times, to the nearest 5 sec, in a series of 13 changes of relative humidity. After that, the detached elytron became more and more biased towards yellow, presumably as the epidermal cells died.

Other experiments showed that the response need not involve the whole of one elytron. A short glass tube was attached with chewing gum to each elytron and separated from the epicuticle only by the thickness of a fine gauze (Fig. 13). One tube contained dehydrated silica gel and the other damp filter paper as a control. The beetle so treated was always kept overnight at 25°C and 100% r.h. Initially the area beneath the tube of silica gel yellowed and then slowly blackened; 8 hr at 25°C was enough for it to blacken completely in the particular beetle used. The beetle was then transferred to a room at 25°C but at *ca.* 70% r.h., whereupon the elytra outside the areas covered by the tubes yellowed. Removal of the tube with filter paper revealed a black circle that yellowed at the same rate as did the surrounding area of the elytron. Removal of the tube with silica gel revealed a black circle that stayed black: it was being subjected to a considerable increase in relative humidity. The sharp boundaries of the black circles suggest that control of the colour change must be very localized: hormonal control of colour change seems to be precluded.

As may be seen in Figs. 10 and 14, the epicuticle tends to have a great many scratches, some of them extending to the spongy layer below. The area enclosed by the tube of silica gel obviously included many such scratches. The fact that it blackened after some hours despite the very low ambient relative humidity maintained locally suggests that lipids were translocated to the site of each scratch in sufficient quantity so that after a time transfer of water to the silica gel ceased.* A difficulty about this explanation that we have not resolved is that each time the

* It is possible that a little water is continuously taken up by the silica gel, but the entry of liquid into the sponge makes up for the loss incurred so that the sponge remains flooded.

experiment was repeated on the same area of the elytron, the area under the tube of silica gel initially yellowed. This suggests that if the scratches were indeed temporarily sealed by translocation of lipids, they must again become permeable to water in the intervals between experiments. That scratches can do so is also suggested by the fact that when water is placed on the surface of the epicuticle of a living beetle it enters the spongy layer, and it is hard to believe that in all our experiments it did so only through very newly made scratches. However, if the possible effect of scratches through the epicuticle is disregarded, all of the results obtained can be accounted for by assuming that changes in the colour of the area covered by the tube of silica gel are mediated only by local humidity receptors.

DISCUSSION

KEY and DAY (1954a, b) have discussed the possible selective advantages of physiological colour changes in acridis and O'FARRELL (1963, 1971) the advantages of similar changes in dragonflies. A discussion of the selective advantage that may be conferred on the Hercules beetle because it is able rapidly to change the colour of its elytra is necessarily speculative because so little is known about its biology. Its chief predators are not known: the only predator that appears to be recorded is a screech owl, *Otus chilba srusigerus* (BEEBE, 1947). The beetle on which experiments were begun had entirely black elytra when taken by one of us (H. E. H.) at about 9 p.m. in Nirgua, Venezuela. The only specimen found during the day by BEEBE (1947) had yellow elytra.

In most situations at night there is enough light so that a beetle with yellow elytra will be more easily seen by predators than one with black elytra. During the day this is reversed, and a beetle with yellow elytra, particularly if it is still feeding on fruit, will be less conspicuous than an entirely black one (Figs. 1–2). At night the humidity is high, but during the first part of the morning it falls steeply. The beetle would therefore be expected to be entirely black at night but its elytra would become yellow during the morning as the humidity decreased.

The change in colour may have a slight advantage in thermoregulation: a beetle with black elytra will heat up more quickly and to a greater extent than one with yellow elytra. The solar radiation coming through the atmosphere in low latitudes amounts to about 1.3 cal cm^{-2} min^{-1} when the sun is in zenith, but only about a quarter of this at low angles. About 62 per cent of solar radiation is in the visible, and about 6 per cent in that part of the visible spectrum most strongly reflected from the yellow elytra. Taking the reflectivity of white filter paper as 1, the reflectivity of yellow elytra is about 0.14 and black elytra 0.07. A beetle with yellowish elytra will therefore not warm up as much nor as quickly as one with black elytra. In the morning a beetle with black elytra will warm up more quickly than one with yellow elytra. If it happens to be exposed to the sun during the day, the yellow elytra will prevent it from getting as hot as it would with black elytra. It may thus gain a dual advantage from the change in colour irrespective of any advantage gained by altering its degree of visibility to predators. The transparency of the elytra to light up to 1000 nm is shown in Fig. 16. Beneath the elytra is an

air pocket partly occupied by the folded hind wings, and so far as heating is concerned a 'greenhouse effect' may be produced.
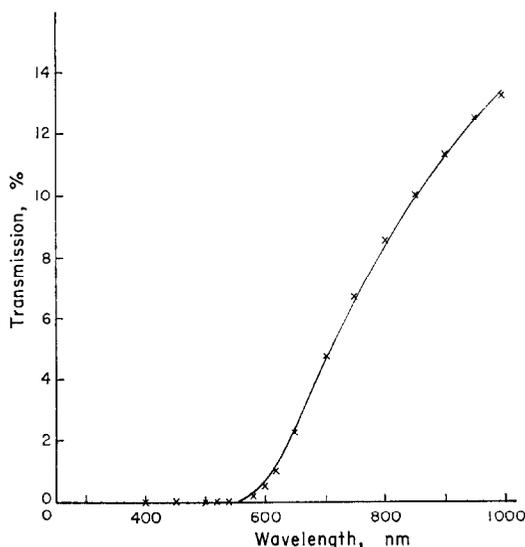

FIG. 16. Light at normal incidence transmitted through the intact yellowish elytron
of a museum specimen of *D. hercules*.

BEEBE (1947) records the colour of 16 freshly caught specimens that came to light at night during the rainy season at Rancho Grande, Venezuela. Two of these were entirely black or nearly so, but no less than 9 had elytra that were extensively yellow. Rancho Grande is a subtropical cloud forest, and during the rainy season the relative humidity is over 95% from 4 p.m. to 6 or 7 a.m. (BEEBE and CRANE, 1947). There is no reason to doubt Beebe's records, and we do not do so, but they cannot be reconciled with our experiments and the conclusions we have drawn from them unless in the natural state colour changes are sometimes triggered in some way other than we have found. For instance, it may be that the colour of the elytra is also mediated by the CNS so that when flying towards light the elytra are not their normal night-time colour. We have noted the fact (p. 545) that just occasionally the elytra of a beetle kept at constant relative humidity would suddenly become extensively yellow for no determined cause. It is hard to imagine circumstances that confer a selective advantage on having yellow elytra at night when black ones are possible.

Note added in proof:
    After this paper was in press Mrs. J. H. Quay called our attention to a paper by M. E. PROKOP (1969, *Col. Bull.* 23, 20–23). Prokop found that a male of *Dynastes tityrus* L. was

dark when provided with food and greenish or yellowish when left without food. His experiments would be consistent with ours if the humidity rose when food was provided (peaches, pears, grapes, apples) and fell in the absence of food. Although we think we have established beyond cavil the autonomous control of colour change, some of our observations clearly suggest central control. In other arthropods colour changes are known to be local and autonomous in some circumstances and under central nervous control in others, *e.g.* in some dragonflies.

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