1918 and 1919; the Scientific Novelties Exhibitions held at King's College, London, in connection with the King Edward's Hospital Fund in January 1923 and 1924, and experience at Wembley show that such displays of scientific work and results are much appreciated by the public. The desire for truth is at least as strong and as laudable an inspiration to the human spirit as the desire for beauty, and an event of this kind might well become to the world of science what the annual exhibition of the Royal Academy is to the world of art.

Such an annual exhibition would serve to maintain interest in the work of scientific inquiry, and help to keep it in the public mind in its just relation to the other activities in life. To men of science it might become a valuable auxiliary to the usual methods of publication of new scientific work, by reaching a wider public than the transactions of the scientific societies or the scientific periodicals can ever hope to do; and to the museums, it could be a source from which to obtain objects of interest from time to time, and thereby do much to prevent such national misfortunes as, for example, the dispersal, during the war, of the apparatus used by H. G. J. Moseley in his historic work on the X-ray spectra of the elements. It is to be hoped, therefore, that whatever facilities or funds are required to secure the continuance of the pure science exhibits and demonstrations now at Wembley will be provided.—*Nature.*

SPECIAL ARTICLES

PERIODIC REVERSAL OF HEART-BEAT IN A CHRYSALIS[1]

WHILE recently[2] studying two freshly formed chrysalids of *Colias eurytheme,* the cuticula of which was still transparent, I noticed that the heart was beating forward in one, as in insects generally, while in the other the direction of the beat was backward. This extraordinary phenomenon led me to watch the heart action of many pupae individually under a binocular dissecting microscope.

The profound internal changes in form of the mature caterpillar when it stops feeding and hangs itself up to shed its skin and become a chrysalis are accompanied by a periodic reversal in the direction of the peristalsis of the dorsal vessel. Beneath the larval skin the mature caterpillar is now wasp-waisted like the butterfly, and its wing buds are well formed. Its heart action then becomes essentially like that of the pupa, which, briefly, is as follows:

A period of rapid pulsation forward at the rate of approximately one wave of peristalsis per second is followed by a pause of 2 to 3 seconds. Then a slower pulsation at the rate of about one beat in two seconds and lasting for about 12 beats (25 seconds) occurs in *both directions,* forward from the third and backward from the fourth abdominal segments. Then the forward wave through the thorax usually stops altogether, and the whole dorsal vessel slowly pulsates backward at the same rate (about 0.5–0.6 beat per second). Toward the end of each phase just preceding reversal, the rate slackens slightly, but in the reversal to run *forward* there is little hesitation. The quick pumping forward is resumed without the noticeable pause that occurs at the end of the forward movement.

The number of beats forward and backward is subject to much variation, but in general the proportion of backward beats to forward increases with age.[3] Thus two larvae ready to pupate gave averages of 29.5 per cent. and 29.2 per cent. beats backward while two pupae, one fresh and one older, gave 41.3 per cent. and 59.2 per cent. backward. They beat as follows:

	Beats backward	Beats forward	Percentage backward	Temperature.
Mature larva	71	169	29.5	21° C.
" "	47	114	29.2	21° C.
Fresh pupa	78	111	41.3	25° C.
Older pupa	180	124	59.2	21° C.

It should be noted that in the two pupae just mentioned the first 10 to 15 strokes of the "backward" movements were mixed, including a forward pulsation through the thorax.

Another older chrysalis gave 238 beats backward to 196 forward (54.8 per cent. backward), the proportion of backward beats to forward showing no further increase but rather diminishing slightly as the number of beats in each phase lengthened; the backward beats in this pupa slackened to 0.33 beat per second, whereas the forward movement maintained a high rate (1.05 beat per second, temp. 24° C.)

The flow in the caterpillar up to the time when it stops feeding and prepares to pupate is always forward. This was true of every individual observed, but whether moulting affects the direction of circulation in the younger larval stages has not yet been determined. Since the hæmolymph is strongly colored, the outline of the dorsal vessel is clearly visible without a lens, as a dark green median-dorsal band against a paler green background. Closer examination shows that the dorsal vessel lies close to the

1 Research promoted by a grant from the Joseph Henry Fund.

2 October 21, 1924.

3 Exact counts with a stop-watch have been made upon eleven individuals. Thanks are due to Arthur M. Crosman, Joseph H. Berwick, K. W. Weeks, A. H. Lowell and L. J. Obermeier, who have served as timekeepers.

fairly transparent body wall and occupies a furrow traced through the whitish masses of dorsal musculature. The lateral outlines of the pericardium also can easily be distinguished. Mature larvae before the onset of pupation have regularly shown a *complete* reversal, that is, I have been unable to detect at the beginning of the backward phase any forward peristalis in front of the third abdominal segment.

Violent changes in circulation occur at the moment of pupation when the last larval skin is being stripped backward off the body. Relatively long periods then occur when the blood flows rapidly *in both directions,* backward and forward from the third and fourth abdominal somites where it appears to well up from a ventral sinus and to collect as in a transitory ventricle, alternating with much shorter periods of forward movement. While a strong aortic peristalsis directed forward is occurring in the thorax, an extremely strong flow backward occurs in the abdomen, where the dorsal vessel is now much dilated. Periods of flow in both directions lasted, in the caterpillar observed in the act of pupation, at first for about five minutes, alternating with periods of forward motion which were very short (25 seconds); then the forward phase became longer (68–70 seconds). The rate for all movements at first was about one beat per second, becoming only slightly more rapid in the forward phase (1.09 beat per second). During the first hour after shedding the larval skin the period of beating in both directions fell from 5 down to 3 minutes and the rate to 0.77 beat per second (139 beats in 180 seconds). The phase of forward motion, on the contrary, by one count had increased in extent to 111 seconds (113 beats), without further increase in the rate.

After the first day or two of pupal life the cuticula becomes so thick and opaque that it is usually impossible any longer to follow clearly the beating of the heart, but, in a chrysalis of *C. eriphyle* 60 hours after pupation, I observed 123 beats *forward* in 225 seconds (rate, 0.54 beat per sec.), then a very long pause of several minutes without detectable peristalsis, followed by a *backward* phase of 26 beats in 110 seconds (rate, 0.23 beat per sec.). Another backward phase included only 9 beats in 36 seconds (rate, 0.25 beat per sec.). Thus at 60 hours the forward and backward rates have each decreased by one half, though retaining with each other the same relation, and two successive phases are regularly separated by a long period of inactivity. I have not yet been able to determine whether periodic reversal of direction still occurs in the butterfly.

An Explanation of Periodic Reversal

To reach from behind the dome-shaped mesothoracic receptacle for blood at the base of the wings, the aorta is sharply bent ventrad and then like a siphon rises into the huge dorsal sinus, which is cut off from behind by high vertical walls. Into this relatively large hæmolymphatic reservoir for the wings, the fluid is pumped at the rate of one beat per second, till it is full to overflowing. The blood pressure in the wings is now probably at its greatest. Then something happens to relieve the pressure. Up to the time of pupation, immediate reversal of the peristalsis occurs in the thoracic aorta. Then the intense muscular activity of the pupa in relieving itself of the larval skin opens wide the longitudinal ventral sinuses between the thoracic-abdominal muscles; the blood rushes backward into the base of the abdomen where it wells up like a fountain into the pericardial sinus, thence into the heart, and we have, usually for 25 seconds, blood directed forward in the aorta and backward in the abdominal part of the dorsal vessel. Soon the aorta likewise reverses, and the whole dorsal vessel slowly siphons off, so to speak, the accumulated blood distending the bag-like wings. The pressure then being relieved, rapid forward peristalsis (of one beat per second) is once more resumed until the pause comes before the backward phase.

This pause may be interpreted as a period of maximum blood pressure in head and wings. The last forward strokes preceding it were somewhat languid, warning the observer that the pause was coming, that is, pressure was reaching its limit.

The hæmolymph in flowing backward to relieve the pressure meets obstructions. The contracted base of the abdomen, filled with cords of longitudinal muscle crowding upon the sinuses, and probably the smallness of the open ends of the arteries, make back-action difficult and slow. The "aortal chamber," described by Burgess[4] in the adult of *Colias philodice* and recently found by me there and in the chrysalis of *C. eurytheme,* undoubtedly helps largely in sucking in and driving backward the haemolymph.

I have observed in a pupa with aborted wing buds (affected either by disease or a noxious hereditary factor) that the backward phase was almost entirely omitted, being exceedingly short as compared with the forward phase. This shortness of the forward phase I interpret to mean that owing to the small capacity of the wings there is less blood to be pumped backward, so that the pressure is soon relieved and the free movement forward is quickly restored.

Periodic reversal to beat backward, in brief, means better irrigation of the wings, which in the pupa I regard as organs of excretion of uric acid products

4 Burgess, E., 1881, "Note on the aorta of lepidopterous insects," *Proc.* Boston Soc. Nat. Hist. 21: pp. 153–156.

and probably of carbon dioxide. Reasons for this view will be set forth in detail in a later paper. Moreover, periodic reversal to beat backward means directing the main stream of hæmolymph toward the reproductive organs. This would seem to be a condition most favorable for the growth of the ovaries, which later in the female so fully fill the abdominal cavity.

"One swallow does not make a summer," and pupal circulation in this genus of butterflies may or may not be typical of that in all the different forms of higher insects with complete metamorphoses which make up such a large part of the animal kingdom. Few of them have colored blood, an unfortunate circumstance which is probably responsible for the fact that so little is known of periodic reversal of heart-beat. It has been described in the pupa of the silk-worm, however, by Bataillon.[5]

Periodic reversal in the direction of the heart-beat occurs, therefore, not only in Ascidians but is also an important characteristic of the metamorphosis of some and possibly most butterflies and moths. Wingless female moths are likely to prove an exception.

In the genus *Colias* periodic reversal of circulation is a most important feature in metamorphosis, as it may prove to be in other holometabolous insects.

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THE AGE OF THE PAYETTE FORMATION AND THE OLD EROSION SURFACE IN IDAHO[1]

THE Payette formation, of continental origin, underlies extensive areas in the Snake River Valley south and west of Boise and in neighboring parts of southwestern Idaho and southeastern Oregon. The age of these strata is a matter of interest because they are the principal key to the Tertiary history of this region, and because beds correlated with them have been used in recent years by Umpleby, Lindgren, Blackwelder, Mansfield and others in attempts to establish the age of the widely recognized old erosion surface of central Idaho.

Lindgren,[2] in 1900, divided the Tertiary sediments of the lower Snake River Valley into two formations. The younger, comprising nearly horizontal strata, he termed the Idaho formation, after Cope, and assigned it to the Pliocene. Merriam[3] has since studied and determined a mammalian fauna from the Idaho beds as representing a late stage of that epoch.

The name Payette was applied by Lindgren[4] to the older more deformed strata underlying the Idaho. The formation was originally considered to be upper Miocene in age on the basis of its flora, studied by Knowlton, but in 1900 Lindgren assigned the Payette to the Eocene because of a revision of the flora by Knowlton. In later years, in discussions of the age of the Idaho Erosion Surface, Umpleby has considered the Payette as Miocene and Lindgren has referred to it as "Miocene (or Eocene)." Chaney,[5] in 1918, on the basis of additional plant remains, said ". . . at this time the writer is satisfied to make the reference to the Miocene without further specification." It thus appears that difference of opinion has existed regarding the age of the Payette.

In the course of field studies in the Snake River region the writer secured remains of two mammalian faunas from the Payette. One occurs in the lower part of the formation, in beds beneath the interbedded rhyolite, about one mile north of Rockville, shown on the Silver City Quadrangle of the U. S. Geological Survey. The second was found in the same section in strata overlying the rhyolite, probably disconformably, near Sands, about 11 miles northeast of Rockville. The beds at both localities dip to the north beneath the nearly horizontal Idaho formation, from which they are easily discriminated by their attitude and lithology.

The Rockville or lower fauna includes a proboscidean of the *Tetrabelodon* type, a species of *Hypohippus* resembling other forms in that genus from middle and upper Miocene formations of the Great Basin province, *Merycodus* sp., a large camel, a rhinoceros, fish bones and freshwater shells. Proboscidean remains first occur in North America in the middle Miocene; they are not abundant until upper Miocene time. This fauna may represent the middle Miocene, but it is more probably of upper Miocene age, and possibly even lower Pliocene.

The small fauna from Sands consists mainly of fragmentary *Hipparion* teeth and rodent teeth. The former resemble most closely in their complicated enamel patterns *H. anthonyi* from eastern Oregon and the hipparions from the lower Pliocene Ricardo formation of the Mojave Desert described by Merriam. The age of the fauna is approximately lower Pliocene.

5 Bataillon, E., 1893, "La métamorphose du ver à soie et le déterminisme évolutif," Bull. Sci. France et Belgique. Tome 25. (Quoted from Henneguy, L. F., 1904. Les Insectes, p. 533).

1 Published with the permission of the director of the U. S. Geological Survey and the secretary of the Idaho Bureau of Mines and Geology.

2 Twentieth Ann. Rept., U. S. Geol. Surv., Pt. 3, pp. 93–99, 1900.

3 *Bull. Geol. Soc. Amer.*, Vol. 29, p. 162, 1918.

4 Eighteenth Ann. Rept., U. S. Geol. Surv., Pt. 3, pp. 632–634, 1898.

5 *Am. Jour. Sci.*, Vol. IV, p. 220.