have described it. Some of these have been treated elsewhere (*12*). For instance, the all-important subject of phagocytosis has intentionally been omitted here. Metchnikoff, the founder of the phagocytic theory, as well as his followers, have treated very adequately this paramount and well-known subject, now considered to be a cornerstone of inflammation.

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Metamorphosis

A Physiological Interpretation

Morris Rockstein

During the past decade there has been evident an increasing number of cooperative efforts by scientists who represent research disciplines considered widely separated. However, a few areas of the biological sciences remain in which the techniques of the physical scientist and experimental biologist are generally overlooked. Thus, taxonomists continue to depend on gross morphological or anatomical criteria for their deductions (*1*). In the few cases in which experimental or analytic data have been so employed (*2*), this use has been through the efforts of a few biochemists and physiologists who have applied their findings to phylogenetic or taxonomic deductions. I should like to show here how recent findings by other physiologists and myself may serve as a basis for the critical examination, if not the revision, of the established concepts of insect metamorphosis.

Although the definition of metamorphosis includes all the changes in form that occur during postembryonic development, most entomologists tend to limit their concept of this phenomenon to the transformation from the juvenile form (the larva) to the adult, or imago. One result of this limited concept has been artificial grouping of various orders of insects into groups such as the Ametabola, Paurometabola, or Holometabola according to the extent to which the juvenile stages differ in outward appearance from their corresponding imagoes. A number of competent entomologists admit that such a classification is artificial, especially from the phylogenetic standpoint. In his excellent monograph, Snodgrass (*3*) writes that "insects cannot be classified taxonomically according to the type of metamorphosis they undergo" and that "true metamorphic characters are adaptive structures . . . that have no phylogenetic counterpart in the adult evolution." This point is best illustrated by insects with complete metamorphosis, for they can hardly represent a monophyletic group. A more likely hypothesis is that holometaboly arose independently on several occasions during the evolution of the different orders of insects (*4*). In the course of his discussion, Snodgrass (*3*) also cites postemergence metamorphic changes, of which several cases are known, and anamorphosis or body segmentation after hatching. Since entomologists consider metamorphosis to be complete, except for sexual maturation, when the juvenile characters are discarded, the usual interpretation of these changes is that they are exceptions to the rule.

My own investigations and those of other physiologists interested in metabolic pathways in insects at different stages of development indicate a different interpretation. These findings suggest that visible transformation to the adult should not be considered as a terminal event but as one in a series of changes

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that result ultimately in the mature adult. If my interpretation is correct, a number of more cryptic biochemical changes must occur following the emergence of the adult. I shall call this series of changes "postemergence maturation" and characterize this period as one of "metachemogenesis."

Patterns of Postemergence Maturation

Let me begin with a review of certain changes that I and others have observed in the adult forms of the worker honeybee, the housefly, and *Drosophila* sp. In my study of the cellular and biochemical changes that accompany the aging of the adult worker honeybee, I observed (*5*) that during the first week of adult life the cholinesterase activity of brain homogenates increased by 20 percent. In a subsequent investigation of the total body activity of the acid and alkaline glycerophosphatase system of adult worker bees, I found (*6*) that during the first week to 10 days of adulthood a reciprocal mechanism existed in which the activity of the acid enzyme rose by 90 percent, while that of the alkaline enzyme fell by about 50 percent.

In both studies, once the various levels of activity were reached, they remained constant through the remaining portion of the life of the bee. A study of the housefly, a species with a life span considerably shorter than that of the honeybee, reveals comparable data. Within 24 hours after the emergence of the adult, the brain cholinesterase activity may rise as much as 100 percent. This level is maintained for at least a week or longer (*7*). Studies of *Drosophila* have shown the occurrence of concomitant increments in wing-beat frequency and glycogen content during the first 7 days after adult appearance (*8*). Additional studies of *Drosophila* (*9*) have shown that both glycogen and fat accumulate rapidly during the first 2 days after adult appearance and then increase gradually to a maximum during the next 3 days. The maximum is maintained for at least 10 days.

In my interpretation, the changes in the worker honeybee, the housefly, and *Drosophila* represent fragments of integrated patterns of postemergence maturation at the cellular level. These changes are related to the final development of certain adult characters which in turn are related to various neuromotor activities, particularly those concerned with flying.

The enzyme cytochrome oxidase has been studied by investigators interested in the role of this enzyme and the entire cytochrome system in insect development. Obscured, if not hidden, in a number of reports there is repeated evidence that this system is also involved in postemergence maturation in a number of species of flies. In houseflies (*10*), its activity declines steadily during the first 2 days of pupal life and then rises sharply in a U-shaped curve resembling the oxygen consumption patterns of pupae of many holometabolous insects. Of particular interest is the fact that after adult emergence, the activity of this enzyme continues to rise, reaching a maximum by the third day of adult life, the value of which is 2 to 3 times that of an adult less than 1 hour old. In *Drosophila virilis* (*11*) a remarkably similar pattern is exhibited in the pupal and adult stages. The high level of activity of the late prepupal larva is reached again in the newly emerged adult. The enzyme continues to increase in concentration and reaches a maximum 3 days after emergence, the value of which is 80 percent above that of the young adult.

In a singularly well-planned study of certain moths, Carroll Williams and his coworkers have extended our understanding of the endocrine-enzymatic mechanisms that underlie and coordinate the differentiation, the growth, and the development of the adult from the pupal form. Thus, in the pupa of the cecropia moth, the onset of adult development is marked by the initiation of secretion of a growth and differentiation hormone by the prothoracic glands. This secretion has been triggered, in turn, by a stimulating hormone released from certain neurosecretory cells of the brain, as a result of exposure to low temperature. Concomitant with the burst of mitotic activity, signaling initiation of adult development, there occurs a rapid rise in cytochrome *c* synthesis. Conversely, during the early stages of adult development, the concentrations of cytochrome *b* and cytochrome oxidase, as well as the concentrations of two dehydrogenases, fall precipitously (*12*).

Of particular importance is the fact that rapid synthesis of cytochrome oxidase is begun on the second day of adult development. This marks a shift from a cyanide-insensitive system in the diapausing pupa, with a flavoprotein as the terminal oxidase, to a cytochrome system, the shift being essential to the metabolism of morphogenesis in the adult. It is not clear from Williams' reports, however, exactly how long the cytochrome system continues to play a dominant role in metamorphosis after the adult emerges. Evidence obtained in certain studies of *Drosophila virilis* (*11*) suggests that in insects such as the cecropia moth this dominance may also continue into the adult life.

This inference is strengthened by a recent study of the Japanese beetle (*13*), in which is reported a comparable pattern, from diapause through early adulthood, of changes in cytochrome oxidase activity. Despite certain differences between these findings and those for other species, a characteristic U-shaped activity curve during pupal "metamorphosis" is followed by an increase in cytochrome oxidase in the adult beetle, the maximum value of which is 2.5 times that of the highest activity observed in the last hours of pupal life. It is germane to these considerations to remark that in the early reports by Keilin of the occurrence of cytochrome compounds in animals (*14*), although generally unnoticed, the observation is to be found that the "cytochrome" concentration in insects rises during the early days of adult life.

Sites of Action

The series of interrelated changes reflected in the obviously limited set of data summarized here must ultimately be defined more precisely at the tissue and cellular levels. Indeed, a few investigators have been engaged in describing the biochemical properties of the discrete cytoplasmic particles located in the flight muscles of certain orders of holometabolous insects (Diptera and Hymenoptera); these particles are the sarcosomes or giant mitochondria. In one species of fly, *Phormia regina,* the activity levels of cytochrome oxidase and catalase in isolated sarcosomes show a rapid drop during the first 4 days following adult emergence (*15*). More recently, as reported in a personal communication, Levenbook found that, during the first week of adult life in *P. regina,* not only the dry weight of the sarcosomes but also the concentration of cytochrome *c* triples in value. Moreover, other cytochrome components appear to rise proportionately during this same period. The concomitant rise in wing-beat frequency, reaching a maximum by the seventh day of adult life, points to the cytochrome system as playing an important role in the metabolism of wing action. At least in the case of this species of fly, a well-defined site of action of postemergence maturation, related to the full development of a particular adult function, appears to have been precisely located within the sarcosomes of the appropriate muscles.

The set of data I have cited emphasizes the continuity of the pupal and imaginal stages of holometabolous insects. As such, the data lend strong support to the theory of Poyarkoff, which interprets the pupa as a preliminary imaginal stage and not as the last nymphal instar, a theory for which Snodgrass (*3*) has ably presented a considerable body of evidence of an embryological, comparative morphological, and endocrinological nature. In certain flying insects, this continuity has been markedly manifest in a well-integrated pattern of postemergence development of the neuromotor mechanism, reflected in the heightened activity of the cholinesterase system, in the enhanced storage of glycogen, and in the increased activity of enzymes concerned with respiration and energy release within the flight muscles. This period of cryptic metachemogenesis, through which the newly emerged adult must pass in order to complete its development, I consider to be, at the very least, a characteristic feature of holometabolous insects.

That a period of metachemogenesis may characterize all insects possessing *any* kind of metamorphic growth is suggested by other recent studies. In these studies (*16*), succinoxidase activity of the thoracic flight muscles in both sexes of the woodroach and in the male American cockroach, insects with gradual metamorphosis, has been observed to rise continuously after the final molt to a maximum by the tenth day of adult life. Moreover, Brooks (*17*) found that changes with age in succinoxidase activity in the basal leg and wing muscles of this insect are correlated with changes in color. In male cockroaches, for example, muscle color is white at the last nymphal molt and changes to pink shortly after emergence. The pink hue, as well as the enzyme activity, then increases rapidly in intensity and reaches a maximum at about 1 month after adult emergence. These findings for insects with gradual metamorphosis correspond closely to those presented earlier for holometabolous insects. They raise further doubts concerning the validity of the taxonomic separation of insects with metamorphic growth into three major categories, an otherwise arbitrary separation based on superficial criteria and with no great phylogenetic significance (*18*).

References and Notes

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18. A. G. Richards has called my attention to the early (but little emphasized) recognition by V. B. Wigglesworth, *Insect Physiology* (Methuen, London, 1934), p. 41, that different types of metamorphosis are physiologically untenable, that the Hemimetabola and Holometabola represent differences in morphological transformations accompanying molting, and that at the final molt some hemimetabolous (like holometabolous) insects undergo transformations far more extreme than those at preceding molts.

R. W. Marriott, Astronomer

Ross Walter Marriott was born in Paxton, Illinois, on 30 December 1882, and died at Hahnemann Hospital in Philadelphia on 19 October 1955. He entered the University of Indiana in 1902, obtained the bachelor's degree in 1906, and came to Swarthmore College that same year with the late John A. Miller, professor of mathematics and astronomy. Marriott received the master's degree at the University of Pennsylvania in 1911. He taught mathematics at Swarthmore College for 46 years, as an instructor (1907–10), assistant professor (1910–22), associate professor (1922–27), and professor of mathematics and astronomy (1927–52). He took an active part in making the adjustment of, and early observations with, the Sproul 24-inch refractor after it was installed at Swarthmore in 1911.

From 1923 to 1932 Marriott participated with Miller in the Swarthmore eclipse expeditions, and owing to his zeal and care Swarthmore College possesses a collection of fine coronal photographs. In the director's office of the Sproul Observatory hangs an oil painting of Miller and Marriott studying a solar eclipse photograph, painted by the late Owen D. Stephens, well-known artist of astronomical subjects.

Mariott was a perfectionist and was very critical of the results of his own observational efforts. He did not publish the measurements and discussions of some of his best plates, because he was not satisfied with the results.

The definition of Marriott's eclipse photographs is excellent; solar astronomers recognize the value of his large-scale photographs of the solar corona, which he generously shared, together with his unique knowledge about them. Outstanding are his large-scale photographs of the inner and outer corona at the time of the eclipse of 21 October 1930 at Niuafoou, Tonga ("Tin Can Island"), which are of exquisite quality and have been analyzed by several astronomers, particularly for the "jets," or small spicules.

The fruits of his long period of service in the teaching profession and his valuable collection of eclipse photographs remain as a monument to Ross W. Marriott of Swarthmore College.

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