CC/NUMBER 6 FEBRUARY 8, 1982

This Week's Citation Classic ____

Shaaya E & Karlson P. Der Ecdysontiter während der Insektenentwicklung-II. Die Postembryonale Entwicklung der Schmeissfliege Calliphora erythrocephala Meig. J. Insect Physiol. 11:65-9, 1965. [Physiologisch-chemisches Inst., Univ. München, Fed. Rep. Germany]

The concentration of the moulting hormone ecdysone during the development of the fly Calliphora was determined by using the Calliphora abdomen bioassay. In the third and last larval instar, two peaks of the hormone were measured: a small one in the feeding larvae shortly before wandering, about 60 hours prior to pupariation, and a second main peak shortly before pupariation. During the pupal stage another hormone peak was measured on the eleventh to thirteenth day of the insect's life. These results were compared to the preliminary data of ecdysone levels determined for Bombyx mori. [The $SCI^{(0)}$ indicates that this paper has been cited over 135 times since 1965.]

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November 8, 1981

"In the early-1960s, there was great interest in studies related to the isolation and chemical characterization of insect hormones because of their important role in growth, moulting, and metamorphosis.

"In 1961, after receiving my MSc in biology from the Hebrew University of Jerusalem, I received a two-year scholarship from the World Health Organization (WHO) to work on insect hormones. This made it possible for me to go to Peter Karlson's laboratory at the University of Munich, Federal Republic of Germany.

"For the reader not familiar with hormonal control of insect development, the main facts will be explained here briefly. Moulting and metamorphosis in insects are controlled by two hormones: ecdysone and juvenile hormone. The larval moult producing a bigger larva from a smaller one is controlled by the joint action of ecdysone, which induces the moult, and juvenile hormone, which determines the larval character. Only when ecdysone is secreted alone will the larva moult to pupa, and the pupa develop to adult.

"In the early-1960s, our knowledge of the chemical nature of insect hormones was very poor, mainly because of the difficulties in the isolation of the hormones. Butenandt and Karlson¹ succeeded in 1954 in isolating the steroid hormone ecdysone, for the first time, in crystalline form. They had to use 500 kg of *Bombyx mori* pupae in order to obtain about 25 mg of the hormone.

"When I arrived at the University of Munich in November 1961 as a graduate student, Karlson, his students, and his postdoctoral fellows were working on the chemistry and mode of action of ecdysone. My main project was to develop a micromethod for the extraction of ecdysone, and to measure the concentration of the hormone during the life cycle of the blowfly, Calliphora ervthrocephala. As a biologist, I anticipated many difficulties, but after one and a half years of intensive work the project was successfully concluded. The extraction method which was developed facilitated the extraction of the hormone from 1 to 5 g of insect tissue. By biological tests it was possible to determine up to 0.1 µg of the hormone.

"I believe this paper has been cited frequently for two main reasons. One, it was the first paper of its kind which showed the ecdysone titer during the development of an insect. It remained as such for many years after its publication. A second reason is that the data served as a model to relate specific morphogenetic and biochemical changes during insect development to the changes in the hormone titer.

"The appearance in Calliphora of a small 'peak' of ecdysones, prior to the wandering stage, was later confirmed in a number of other insect species, and initiated the study of the role of this 'peak' in larval-pupal differentiation. From our knowledge today, the small 'peak' appears to be the signal for several subsequent events such as the initiation of wandering,² the cessation of feeding,³ HnRNA formation,⁴ and the change in epidermal commitment from larval to pupal cuticular proteins."²

Butemandt A & Karlson P. Ueber die Isolierung eines Metamorphosehormones der Insekten in Kristallisierter Form. Z. Naturforsch. Sect. B 96:389, 1954.

Riddford L M. Interaction of ecdysteroids and juvenile hormone in the regulation of larval growth and metamorphosis of the tobacco hornworm. (Hoffman J A, ed.) Progress in ecdysone research. Amsterdam: Elsevier/North-Holland Biomedical Press, 1980. p. 409-42.

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Shaaya E. Synthesis of giant HnRNA in the epidermal cells of Calliphora and the role of the ring gland. Hoppe-Seylers Z. Physiol. Chem. 360:445-9, 1979.