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Considerable amounts of ecdysteroids are produced during each ovarian cycle in adult females of *Locusta*. The hormonal molecules are synthesized at the end of the maturation of the terminal oocytes during each cycle, at the time when vitellogenesis is almost completed. [The SCI® indicates that this paper has been cited in over 140 publications.]

Steroid Hormones and Ovarian-Embryonic Development of Insects

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Our study on ecdysone in adult females of the insect *Locusta migratoria* started off unconvincingly. We, as others, held the firm belief that ecdysone, which had been isolated and fully characterized as a polyhydroxylated steroid hormone some 10 years previously (1965), was the molting and metamorphosis hormone of insects. So strong was this belief that we used adult insects, which neither molt nor undergo metamorphosis, as negative controls in the initial bioassay tests for ecdysone and in studies on the metabolic fate of the molecule. It was probably this decision that put us on the track of the ecdysone story in the adult female of *Locusta*. But, in contrast to our assumption, such females contained at some stages in their reproductive cycles large amounts of material that behaved in bioassays as the molting hormone. Within six months we established that adult females of *Locusta* produced molecules cross-react-

ing with ecdysteroids in radioimmunoassays (RIAs) and showed that the synthesis took place in the ovaries at the end of each gonotropic cycle.

Our preliminary data met with skepticism about the bioassay and RIA results that might have indicated molecules close to ecdysone but not identical to it. Mass spectrometric analysis demonstrated that they were identical to the molt and metamorphosis hormone of larvae and pupae.

Our 1977 paper raised many questions: the first, of course, concerned the function of the ovarian ecdysteroids. Henry H. Hagedorn¹ showed during the same time that ovaries of the adult female of the mosquito produce ecdysteroids, and some of his experimental evidence pointed to the role of these molecules in the control of the synthesis of yolk proteins. This clearly could not be the case in *Locusta*, as ovarian ecdysteroid biosynthesis occurs in the adult female well after the onset of vitellogenin synthesis. Our investigation of the destiny of ovarian ecdysteroids in *Locusta* then led to the surprising observation that these molecules accumulated inside the oocyte where they were tightly bound to the major yolk protein, vitellin. Each synthesis of an embryonic cuticle was preceded by or coincident with a concentration peak of ecdysone. Our observations probably represent the best documented example of a transfer of steroid hormones of maternal origin to the embryo in egg-laying animals.

Ecdysteroids have been confirmed in ovaries of reproductively competent female insects of some 120 species since 1977. Similar results have been obtained in the three other arthropod classes, i.e., crustaceans, spiders, and millipedes. Ecdysone biosynthesis and metabolism has been explored as a potential target for insect growth regulation.²

1. Hagedorn H H, O'Connor J D, Fuchs M S, Sage B, Schlaeger D A & Bohm M K. The ovary as a source of α -ecdysone in an adult mosquito. *Proc. Nat. Acad. Sci. USA* 72:3255-9, 1975. (Cited 230 times.) [See also: Hagedorn H H. Ecdysone production by insect ovaries. *Citation Classic. Current Contents/Agriculture, Biology & Environmental Sciences* 20(13):14, 27 March 1989.]
2. Hoffmann J A & Lagueux M. Endocrine aspects of embryonic development in insects. (Kerkut G A & Gilbert L I, eds.) *Comprehensive insect physiology, biochemistry and pharmacology*. Oxford, England: Pergamon Press, 1985. Vol. 1. p. 435-60.