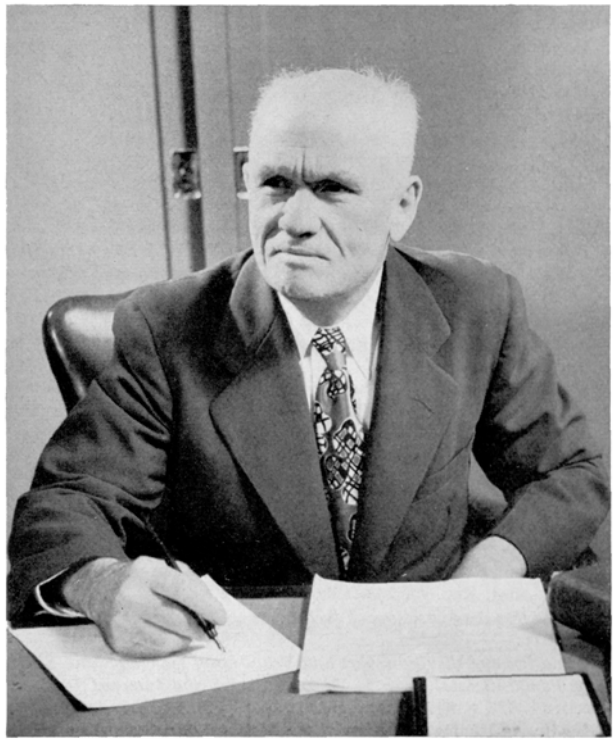
IN MEMORIAM

Carl G. Hartman's Contributions to the Physiology of Reproduction*

Few people know that CARL HARTMAN was immortalized when two species of fungus growing ants were named after him: *Atta Hartmanni Wheeler*, and *Trachymyrmex turrifex Wheeler caroli* Sub. sp., Wheeler. He is best known, however, for his basic contributions to the embryology of the opossum (Didelphis virginiana) and the reproductive physiology of the monkey (*Macacus rhesus*).



In 1912 Professor J. T. PATTERSON offered HARTMAN an instructorship in his department of zoology with the request to study the embryology of the opossum. Why the opossum? 'For the same reason that PATTERSON selected the armadillo: the prairie and the creek bottoms were full of both species and nobody had yet bothered to study the development of these, the most bizarre of all American mammals. It was, therefore, at the University of Texas that the essential characteristics of their mode of reproduction was cleared up.' (HARTMAN.) For thirteen years, he relates in a biographic sketch, 'I hunted the animals in the field. I also took care of them (at first at my home), operated on them, secured, fixed, sectioned, and stained their eggs and photographed the sections myself.'

Based on a thorough study of nearly 1000 females from which several thousand eggs were obtained, HARTMAN established the important stages in the intra- and extrauterine development of the opossum. He found that the opossum is polyestrous with a modal length of the cycle between 28 and 30 days. During its tubal journey, the ovum of the opossum first acquires a heavy albuminous coat, and later, in the distal parts of the tubes, a soft shell. He tagged ova at ovulation with Ascaris eggs and recovered them 25 h later in the uterine folds. He thus proved that the ovocyte of the opossum travels through the oviducts at a higher speed than do the eggs of the mouse, rat, rabbit, or pig. From these experiments HARTMAN generalized that there must be a close and critical time relationship between ovulation and fertilization in mammals. Incidently, HARTMAN brought to the attention of the gynecological world the experiments of L. L. LEWIS, published in 1911, on timed matings in the sow, which supported a limited viability of the mammalian ovum. HAMMOND has later supplemented precise data for the short period of viability of the ovocyte in the rabbit. Together with the facts learned from the primates the notion of a restricted viability of the opossum egg has given great momentum to the research of the fertile and sterile days in the menstrual cycle of women.

The opossum was the first wild species to yield the complete story of its embryology and reproductive physiology. Most females were caught while already pregnant and, fortunately, mating dates were not known. To establish the chronology of successive stages in fetal development HARTMAN modified Bischoff's technique of timed and repeated uterotomies with fetal evacuations in the course of the same pregnancy. He discovered that, in the opossum, in each estrous cycle many more eggs are ovulated than ever become fertilized. In addition, 10 to 20% of the ovocytes fertilized degenerate at different stages during pregnancy. From observed matings and from timed operations on the pregnant opossum he learned something about the large degree of variability in the course of fetal development. Dating mammalian embryos as to their 'coital age' or as to specified 'days of pregnancy' is possible only with allowance for a wide margin of variability. This important fact has too often been neglected, even by present workers in the field.

HARTMAN established for the opossum what J. P. HILL had discovered in the kangaroo: at the time of parturition a temporary direct canal forms between the uteri and the distal vagina. The lateral vaginal canals participate in the changes of the estrous cycle. They, probably, serve as organs for semen activation and they facilitate the rapid transport of the sperm cells into the proximal parts of the fallopian tubes.

The span of gestation in the opossum lasts 12 to 13 days. At birth the newborn opossum weighs approximately 0·13 g. This tiny baby, by the force of his forepaws, crawls from the urogenital sinus into the maternal pouch and, for the next two months, affixes himself at one of the 13 teats. From his report the reader will sense something of the fascination HARTMAN experienced when he and his wife first witnessed the birth of the opossum (February 6, 1920).

By unilateral oophorectomy at specified intervals after mating HARTMAN demonstrated that one ovary alone suffices for the maintenance of pregnancy in both uteri. Bilateral oophorectomy interrupts pregnancy at any stage. Castration does not interfer with lactation.

When HARTMAN began to study the opossum, very little was known about this 'most stupid animal' (HARTMAN). The only monograph of some importance was E. SELENKA's *Studien über die Entwicklungsgeschichte der Thiere*, Vol. 4, *Das Opossum*. Thirteen years later, HARTMAN had described the main features of the anatomy of the sex organs, the estrus, ovulation and fertilization, the early embryology, the birth and postnatal development in the pouch of the opossum. His findings have been verified in-

* Paper read at his eightieth birthday, June 3, 1959.

dependently – and supplemented in a few details – by the work of E. MCCRADY (1938).

After he was through with the opossum HARTMAN felt ready for similar studies in the reproduction of primates. In 1925 he, therefore, planned an expedition to the philipine islands to gather monkey embryos. But G. L. STREETER of the Department of Embryology of the Carnegie Institution of Washington invited him 'to join his laboratory and study the monkey embryology the safe and sane way, bringing the monkey to the laboratory' (HARTMAN). G. W. CORNER, in continuation of his investigations on the corpus luteum of the sow, had already begun to study the menstrual cycle in a few rhesus monkeys. In 1923 he demonstrated the first living primate egg. In Baltimore, then, HARTMAN took over CORNER's monkey cages. He 'got acquainted with the monkey' and succeeded in raising and maintaining a large rhesus colony. Thus, for the first time, a primate became a laboratory animal.

By daily rectal palpations of the monkey ovaries HARTMAN estimated the time of ovulation and its relationship to the phases of the menstrual cycle. Through timed matings he produced the embryological material on which G. L. STREETER and CH. H. HEUSER based their *Developmental Horizons*, the first complete embryological series in a primate. With G. W. CORNER, HARTMAN worked out the histogenesis of the corpus luteum. With G. B. WISLOCKI he indulged in the development of the primate placenta. With INES DE ALLENDE he studied the cytology of the vagina in the course of the menstrual cycle. He provided timed specimens for G. W. BARTELMEZ' detailed study of the histology of the mucosa uteri.

HARTMAN showed that the frequency of anovulatory cycles explains the relative sterility during adolescence in the primates. The bleeding which frequently occurs at the time of implantation, in the monkey as well as in women, carries his name (HARTMAN's sign).

In 1932 he summarized his monkey work in the now classic monograph: *Studies in the Reproduction of the Monkey*. His general review *Time of Ovulation in Women* (1936) marks a milestone in the search for facts in human reproduction.

HARTMAN holds a central position among the workers on reproductive physiology during the first half of the twentieth century. His broad approach to the special subject and his inexhaustible industry secured lasting results. Many workers in the field owe to him research suggestions, material help, and friendly advice or sound criticism. He contends that he never said to himself: 'I am going to be a scientist... I never bothered to consider: is there any use in this study? The main thing was that I was having fun doing the experiments.' This, the essayist feels, is the secret why his 'researches were to occupy his waking hours to this good day ...'.

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Zusammenfassung

Der Bericht schildert die Entwicklung des Philologiestudenten CARL G. HARTMAN zum Naturwissenschaftler. Studien über pilzzüchtende Ameisen und über die Ökologie solitärer Wespen folgten embryologische Versuche bei Fledermäusen. Mit hier anschliessenden Untersuchungen zur Fortpflanzungsphysiologie und frühen Embryonalperiode des Opossums und des Rhesusaffen hat HARTMAN einen grundlegenden Beitrag zur modernen Fortpflanzungsphysiologie geleistet.

Selected Bibliography of Carl G. Hartman's 253 Publications

'Anybody who is industrious can get results in research. Only once in a while do we have a basic idea that can be stated in a few pages ...' (HARTMAN).

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