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(WITH 12 PLATES)

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(PUBLICATION 4148)

CITY OF WASHINGTON  
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# THE REPRODUCTION OF COCKROACHES<sup>1</sup>

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## INTRODUCTION

Cockroaches are important for several reasons. As pests, many are omnivorous, feeding on and defiling our foodstuffs, books, and other possessions. What is perhaps less well known is their relation to the spreading of disease. Several species of cockroaches closely associated with man have been shown to be capable of carrying and transmitting various microorganisms (Cao, 1898; Morrell, 1911; Herms and Nelson, 1913; and others). Recently there has been a resurgence of interest in this subject, and some workers have definitely implicated cockroaches in outbreaks of gastroenteritis.

Antonelli (1930) recovered typhoid bacilli from the feet and bodies of *Blatta orientalis* Linnaeus which he found in open latrines during two small outbreaks of typhoid fever. Mackerras and Mackerras (1948), studying gastroenteritis in children in a Brisbane hospital, isolated two strains of *Salmonella* from *Periplaneta americana* (Linnaeus) and *Nauphoeta cinerea* (Olivier) that were caught in the hospital wards. Graffar and Mertens (1950) isolated *Salmonella typhimurium* from *Blattella germanica* (Linnaeus) captured in a hospital in Brussels. These latter workers were only able to check the epidemic of gastroenteritis among children by ridding the hospital nursery of cockroaches. Bitter and Williams (1949) have isolated three species of *Salmonella* from the hind gut of *P. americana* captured in a hospital, private home, and sewer manholes.

It is significant that four strains of poliomyelitis virus have recently been isolated from *Periplaneta americana*, *Supella supellectilium* (Serville), and *Blattella germanica*, which were collected on the pre-

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<sup>1</sup>This study was made by the Army Quartermaster Corps as part of a research program that includes the investigation of the biologies of insect pests of economic and medical importance to the armed services.

ises of paralytic poliomyelitis patients (Syverton et al., 1952). In addition to harboring bacteria and viruses, cockroaches also harbor pathogenic protozoans and nematodes. The Surinam cockroach, *Pycnoscelus surinamensis* (Linnaeus), is the vector of the eyeworm of poultry (Fielding, 1926), and the American cockroach can carry, mechanically, hookworm of man (Porter, 1930); the latter species can also transmit, experimentally, intestinal flagellates such as *Giardia* from man to rat (Porter, 1918). Although these examples could be multiplied, it is apparent that, as Bitter and Williams (1949) have stated, tolerance of cockroaches around man's habitations is unwaranted; it may even be dangerous.

There are about 450 genera and more than 3,500 species of cockroaches (Rehn, J. W. H., 1951). Practically nothing is known of the biology of most species. Very little is known of the biologies of the cockroaches associated with man, except for the more common pests such as the German, American, and oriental cockroaches. Yet less than 1 percent of the known species are domiciliary pests (Rehn, J. A. G., 1945). This is a fertile field for future work.

Reproduction, enabling the individual to increase its kind many times, is a vital factor in the biology of an insect species. Only rarely do swarms of insects invade a locality from a distant point; each community usually raises its own insect pests (Metcalf and Flint, 1939). Cockroaches illustrate this principle perfectly. Hence the reproduction of cockroaches is a subject of more than academic interest. Reproduction is a phase of cockroach biology that demonstrates the diversity of behavior that has evolved in this relatively ancient group. In the following pages we shall describe, among several species of cockroaches, these aspects of reproduction: courtship, copulation, reproductive organs and fertilization, parthenogenesis, the oötheca, oviposition and hatching, and egg parasites.

### COURTSHIP

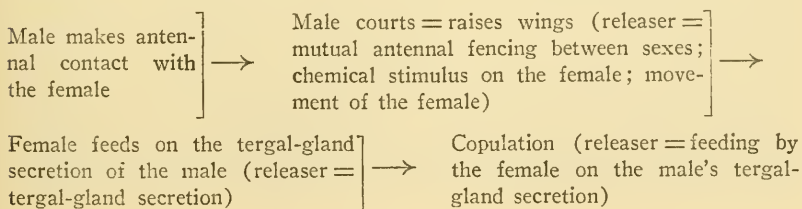
In general the courting behaviors of the species of cockroaches that have been studied appear to be similar in many respects; characteristic differences, however, lend interest to the study of each additional species. The writers (1952) have studied *Blattella germanica*, *Blatta orientalis*, and *Periplaneta americana* and have analyzed the stimuli involved in the courting behavior of the German cockroach. We could not demonstrate distance attraction between males and females of *B. germanica*; yet, when a sexually active male comes in physical contact with the female he responds with a characteristic courting behav-

ior. The male turns around so that his terminal abdominal segments are toward the female, and he raises both front and hind wings to an angle of 45° to 90° (pl. 1, fig. 1). In this way he exposes glandular areas on his abdominal terga which emit a secretion that attracts the female when she is close to him. A responsive female will feed (pl. 1, fig. 2) on the male tergal-gland secretion, and as she does, the male pushes backward and grasps the female genitalia. In *B. germanica* the male must make contact with the female before he will court. Mutual sparring with the antennae between the sexes and movement by the female are important actions in stimulating the male to court. The male courting response (i.e., raising the wings) is the overt expression of male sexual stimulation; it can also be induced by stroking or touching a receptive male's antennae with antennae (pl. 1, fig. 1), legs, abdomen, or wings, which have been removed from a female.

The raising of the male's wings during courtship, or just prior to copulation, apparently is characteristic of those species of cockroaches in which the males have wings. Raising of the wings has been observed in the three domestic species previously mentioned and also in *Leucophaea maderae* (F.) (Sein, 1923); *Blaberus craniifer* Burm. [= *B. fusca* Brunner (Rehn and Hebard, 1927)] (Saupe, 1928; Nutting, 1953); *Supella supellectilium* (Roth, 1952); *Blattella vaga* Heb. and *Nauphoeta cinerea* (Roth and Willis, unpublished data).

Chemical as well as mechanical stimuli are involved in the courting behavior of *Blattella germanica*. This is shown by the fact that a substance that is sexually stimulating to males can be isolated from females. The cuticular surface of the cockroach is covered with a freely exposed grease (Ramsay, 1935; Kramer and Wigglesworth, 1950). Presumably the sex substance is present in the cuticular grease, because this material can easily be rubbed off from females onto males to make the latter sexually stimulating to other males. The available evidence indicates that sex discrimination by the male German cockroach is mainly effected by contact chemoreception.

The sexual behavior of *Blattella germanica*, in terms of stimulus response and releaser mechanisms, may be summarized as follows:





The male receives the female sex stimulus by means of receptors that are present on his antennae and probably on his mouthparts.

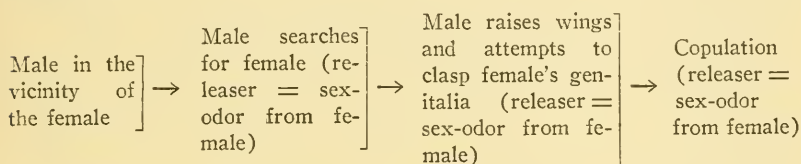
It is highly probable that in those species of cockroaches in which *only* the males have a distinctive, externally visible tergal gland, the function of this gland is to entice the female into a position in which mating can occur. Feeding by the female on the glandular secretion or over the dorsal abdominal surface of the male cockroach has been observed in *Blattella germanica* (Sikora, 1918; Wille, 1920; Roth and Willis, 1952); *Blatta orientalis* (Roth and Willis, 1952); *Ectobius lapponicus* Linnaeus and *Ectobius sylvestris* (Poda) (Konček, 1924); *Supella supellectilium* (Roth, 1952); *Blattella vaga*, *Eurycotis floridana* (Walker), *Nauphoeta cinerea*, and *Leucophaea maderae* (Roth and Willis, unpublished data). The external appearance of the tergal gland may vary considerably between species and genera (cf. pl. 2, figs. 6-8); this structure has considerable taxonomic value (Hebard, 1917; Rehn, J. A. G., 1931; Ramme, 1951). Frequently the glandular area is a depression in one (pl. 2, figs. 7, 8) or sometimes two (pl. 2, fig. 6) of the abdominal tergites and has a mass of secretory cells lying beneath the epidermis. Groups of setae or hairs are often present (pl. 2, fig. 8). In *B. orientalis* the female moves her mouthparts actively over the male's dorsum; yet the source of the male's secretion (if any) is still unknown. Tergal glands are found on the dorsum of the male, female, and nymphs of the oriental cockroach (Minchin, 1888), but they apparently have nothing to do with sex behavior. The contents of these glands have the distinctive odor of the oriental cockroach (Haase, 1889).

In Hawaii, Bridwell (1921), while walking in Palolo Valley at night, saw 50 to 75 *Periplaneta americana* performing their "mating dance" in the middle of the road. In this species the male sexual behavior is released by an odorous material secreted by the female. The source of the sex attractant in the female is unknown, but it is a material that readily rubs off from the female and can be perceived by the male at a considerable distance. By keeping unmated females in containers lined with filter paper, we have collected the attractant on the paper from which the active material was extracted in crude form with petroleum ether. The attractive female odor alone suffices to stimulate the male of *P. americana* to overt sexual activity. Males will even attempt to mate with pieces of paper or glassware that have been in contact with virgin females. Paper taken from jars containing old, nonvirgin females did not stimulate males, indicating that the sex attractant is produced chiefly by unmated females (Roth and Willis,



1952). However, it is possible that a mated female may again become attractive (i.e., secrete the attractant) sometime during her lifetime. Neither we nor Gupta (1947) have observed males of the American cockroach courting the female prior to copulation, as is done by the German and oriental males. The male American cockroach is much more direct in his approach, and the female appears to be relatively passive; movement of the female's mouthparts over the male's dorsum is not a necessary stimulus for the male to attempt to copulate, as in the other two species.

Summarized, the sexual behavior of *Periplaneta americana* is as follows:



In the behavior of *Blattella germanica* there was a succession of releasers that alternately brought forth responses from both partners before culmination of the sexual act. In contrast the sex odor from the female seems to be the only mechanism involved in releasing a chain of responses by the male of *P. americana* that ends in copulation. However, the female of *P. americana* may or may not be receptive to the male's advances. Perhaps there is an as-yet-undetermined releaser that regulates the female's response.

The males of some species of cockroaches perform characteristic body movements during courting behavior. The male of *Leucophaea maderae* stands near the female and rapidly moves his body up and down. According to Sein (1923) the male raises the anterior section of his body and strikes his abdomen against the ground producing a prolonged tapping sound. However, we have seen males of this species move the anterior parts of their bodies up and down rather than their abdomens. The male of *Blaberus craniifer* raises himself on his legs and makes trembling movements with the abdomen (Saupe, 1928); we have observed the male of this species behave in a similar manner and also butt the female with his head or pronotum. The wingless male of *Eurycotis floridana* stands near the female, repeatedly vibrates his body from side to side, and extends his abdomen slightly revealing the light-colored, intersegmental membrane between the sixth and seventh tergites (pl. 1, fig. 3); the female then behaves as described earlier for the other species, applying her mouthparts to the male's dorsum starting near the end of the abdomen (pl. 1, fig. 4) and

working up to the first abdominal tergite (pl. 1, fig. 5), on which is located a small glandular area bearing a patch of setae.

#### COPULATION

The terminal abdominal segments are modified to form the male external genitalia, which consist of genital lobes or phallomeres that are associated with the opening of the ejaculatory duct. These structures are described by Snodgrass (1937) and van Wyk (1952). Certain phallomeres of the adult cockroach form highly complex structures with horny processes or hooks. In the female the external genitalia include the ovipositor and associated sclerites and the openings of the oviduct, accessory glands, and spermathecae (Snodgrass, 1937).

As we mentioned earlier, while the female *Blattella germanica* feeds on the male's glandular secretion, he pushes his abdomen backward so that the female is directly above him. This is the position (pl. 1, fig. 5) just prior to copulation, and it is assumed by most, if not all, species of cockroaches. We have seen this method of initiating copulation, in the female superior pose, in these genera: *Blattella*, *Blatta*, *Periplaneta*, *Eurycotis*, *Nauphoeta*, *Supella*, and *Leucophaea*. Saupe (1928) and Nutting (1953) observed that the female of *Blaberus craniifer* also straddles the abdomen of the male just prior to successful copulation. Because this behavior is so similar among different genera, we are convinced that it is a regular feature in the copulation of *Leucophaea* although we have seen it only once. However, Pessoa and Correa (1928) state that the male of *L. maderae* "draws near [the female] and turns his body in an opposite direction, to that of the female, placing the posterior extremity of his abdomen against [the] posterior extremity of the abdomen of the female." We cannot reconcile their statement with our observations and those of van Wyk (1952) who saw "that the male carries the female on his back at the beginning of copulation with their heads in the same direction and the venter of the female resting on the dorsum of the male and that they later assume an end to end position."

The relationships of the external genitalia during copulation have been studied in *Blattella germanica* (Khalifa, 1950), *Periplaneta americana* (Gupta, 1947), and *Polyzosteria limbata* Burm. (Chopard, 1919). As the male German cockroach pushes backward under the female, he extends his hooked left phallomere. This appendage clasps a large sclerite located near the female's ovipositor. If a hold is secured on the sclerite, the male moves out from under the female, and the couple assume the opposed position in which their heads face in

opposite directions. This is the copulating position (pl. 3, figs. 9-14) assumed by all species of cockroaches in which the act has been observed; we have also seen *Nauphoeta cinerea* in this position, and it has been observed in *Polyzosteria limbata* (Chopard, 1919) and *Parcoblatta pennsylvanica* (Rau, 1940b). Once in the final opposed position, two lateral hooks lying on either side of the anus of the male hold the ovipositor near its base. A small crescentic sclerite, which lies on one side near the right phallomere, grips the ovipositor firmly in a medial position (Khalifa, 1950). In successful matings cockroaches remain in copula in the end-to-end position for at least 30 minutes. Usually copulation lasts more than an hour, and Nutting (1953) noted many pairs of *Blaberus craniifer* that remained joined for 4 hours or more. Statements in the literature to the effect that copulation is rapid, lasting only a few seconds or less, were based on observations of unsuccessful matings.

#### INTERNAL REPRODUCTIVE ORGANS AND FERTILIZATION

The internal genital organs of male cockroaches consist of a pair of testes, genital ducts, accessory genital glands, seminal vesicles, and a phallic gland (Snodgrass, 1937). In *Blattella germanica* each testis consists of four rounded sacs or vesicles which open into a common genital duct. Each vesicle is divided into several zones which contain sex cells in various stages of development; the spermatozoa are contained in the zone nearest the genital duct (Wassilieff, 1907). The testes of *Blatta orientalis* mature at the end of nymphal development and atrophy in the adult; hence the spermatozoa must be stored in the seminal vesicles before the testes degenerate (Snodgrass, 1937). The diploid number of chromosomes (including the X chromosome) has been determined during spermatogenesis for several species of cockroaches; *Loboptera decipiens* Germ. has 34, *Blattella germanica* 24, *Periplaneta americana* 34, *Periplaneta australasiae* (Fabricius) 28, *Blatta orientalis* 48, and *Blaberus fusca* [= *B. craniifer*] 74 (Suomalainen, 1946). All species of cockroaches that have been investigated are XO in the male (White, 1951).

The sperm of cockroaches is transferred to the female by means of a capsule or spermatophore (pl. 4, fig. 17) formed from the secretions of the male accessory sex glands. Spermatophores have been found in males of *Blatta orientalis* (Zabinski, 1933); *Blattella germanica* (Khalifa, 1950; Roth and Willis, 1952); *Periplaneta americana* (Gupta, 1947; Roth and Willis, 1952); *Leucophaea maderae* (van Wyk, 1952); *Eurycotis floridana* and *Nauphoeta cinerea* (Roth

and Willis, unpublished data); and *Blaberus craniifer* (Nutting, 1953). Presumably spermatophores are produced by other blattids as well. Nutting (1953) observed that the spermatophore of *B. craniifer* may be retained in the female's genital pouch for several days, one female carrying her spermatophore intact for 5 days, whereas most of the cockroaches previously noted retain the spermatophore for a shorter period.

The accessory glands ("mushroom-shaped gland") in the oriental cockroach consist of 350 to 450 small, intermediate, and large-sized tubes. Based on their staining reactions, Jurecka (1950) distinguished 6 types of tubes in males of *Blatta orientalis*; their period of most active secretion occurs for several hours following metamorphosis into the adult. This is followed by a resting period from the time secretion ceases until copulation, at which time the secretions and the spermatozoa are ejected and molded into a spermatophore. The spermatophore consists of a number of capsules full of spermatozoa (Qadri, 1938); the female carries it 2 or 3 days then drops it (Zabinski, 1933).

Van Wyk (1952) described the male accessory glands in *Leucophaea maderae*. These are composed of approximately 30 to 40 tubules arranged in three groups. He assumes that each group of glands is responsible for one of the three layers of the spermatophore. The spermatophore of *L. maderae* remains in the genital chamber of the female for about a day before it dries and drops from the female.

If the males of *Blattella germanica* are prevented from mating, the larger accessory gland tubes ("utriculi majores") become so distended with their chalk-white secretion (pl. 4, fig. 15) that they may fill most of the abdominal cavity. After copulation the tubes of the accessory glands are almost emptied of secretion (pl. 4, fig. 16) (Roth and Willis, 1952). The following description of spermatophore formation is taken from Khalifa (1950). The spermatophore in *B. germanica* begins to form in the male as soon as the copulating pair are securely hooked together. In this species the layers of the spermatophore are formed from three protein secretions produced by distinctly different groups of accessory gland tubules. The walls of the tubules consist of a layer of glandular cells surrounded by a muscular layer. The accessory glands open into the ejaculatory duct. The secretions from the various accessory glands pour into the pouch of the ejaculatory duct, and when the spermatophore is completely developed, it distends the pouch. At one point in the formation of the spermatophore, sperm flow from each seminal vesicle into a milky middle layer within the spermatophore; each of the two sperm masses forms



a separate sac. Following formation, the completed spermatophore descends the ejaculatory duct and is pressed by the male's endophallus against three sclerites lying on the left-hand side of the spermathecal groove in the female serve for holding the spermatophore. The tip surround the opening of the common oviduct, and the spermathecal groove in the female serve for holding the spermatophore. The tip of the spermatophore, which contains the openings of the sperm sacs, is inserted into the spermathecal groove so that the two spermathecal pores of the female come in direct contact with the two openings of the sperm sacs. The spermatophore remains in the genital chamber of the female for about 12 hours, during which time the sperm migrate to the spermathecae. In *B. germanica* the sperm have to be chemically activated before they leave the spermatophore; probably the activating chemical originates from a pair of spermathecal glands which are associated with the spermathecae of the female. The empty spermatophore dries and shrinks and is eventually dropped by the female. During her lifetime a female may copulate and receive a spermatophore more than once (Khalifa, 1950), and a male may also copulate and produce a spermatophore more than once (Cros, 1942; Roth and Willis, 1952). The work of the male is now done.

The internal reproductive organs of the female cockroach consist of a pair of ovaries, oviducts, spermathecae, and specialized accessory (colleterial) glands which produce the various secretions that go to make up the oötheca or egg case (Snodgrass, 1937, 1952). In *Periplaneta americana* each ovary usually consists of eight ovarioles. Each ovariole is made up of an elongated egg tube and a short pedicel which connects the basal end of the egg tube to the oviduct. The anterior part of the egg tube consists of a germarium made up of oöcytes or incompletely formed eggs in the early stages of differentiation, and the remainder or vitellarium contains oöcytes in various stages of growth. In the newly emerged adult female all of the oöcytes are relatively small, although a gradation in size is noticeable, the largest being at the base (pl. 4, fig. 18). About 8 days after copulation the basal oöcyte reaches a final size of about 3 mm. in length; it is now encased in a chorion, and is ready for deposition (pl. 4, fig. 19). After oviposition of the basal oöcyte (pl. 4, fig. 20), the next oöcyte in line completes its growth; this cycle results in a succession of mature eggs about every 8 days (Gier, 1936). Actually by the time an oötheca is completely formed and deposited, the basal oöcytes of the ovary are already well developed (pl. 4, fig. 21). Scharrer (1943, 1946) found that the development of the eggs of *Leucophaea maderae*, at least for a certain period of time, is under the hormonal control of the corpora

allata, endocrine glands situated near the brain. Apparently the hormone from these glands is not required for the reproductive activity of the male (Scharrer, 1946).

The external genital structures of the female cockroach lie concealed within a cavity at the end of the abdomen that is closed posteriorly by the apical lobes of the seventh sternum (Snodgrass, 1952). This cavity is divided into a genital chamber, which lies proximal to the base of the ovipositor, and the oöthecal chamber, or vestibulum, which is the posterior part of the cavity. The ovipositor is composed of three pairs of fingerlike valvulae and two pairs of valvifers (Brunet, 1951). The relation of the external genitalia to the formation of the oötheca is discussed below.

Dewitz (1885, 1886) described how sperm enter the eggs of *Blatta orientalis*. The eggs become bent in the oviducts and pass singly into the genital chamber where they approach the spermathecal opening. As the egg passes over the sensory hairs that are found mainly around the spermathecal pore, muscles of the spermatheca contract and force out the sperm. The numerous micropyles, through which the sperm enter, are found at the anterior pole of the egg and come in contact with most of the sperm. The sperm appear to be attracted to the surface of the egg and move clockwise rather than in a straight line. The eggs are fertilized as they pass along the vestibulum.

#### PARTHENOGENESIS

Parthenogenesis is considered to be a rare occurrence among cockroaches. The best-known example of this type of reproduction in blattids is the Surinam cockroach *Pycnoscelus surinamensis*, which in the Indo-Malaysia area is bisexual; but in North America and Europe, where it has been introduced, it is parthenogenetic, producing only females (Mätthey, 1948). It is generally believed by most observers that parthenogenesis does not occur in our domiciliary species or at most is a rare occurrence in the American cockroach. However, only recently we have found that some unfertilized eggs of four species of our common domestic cockroaches may complete their development, and that in two of the species some of the eggs may hatch.

Normally, none of the unfertilized eggs of *Supella supellectilium* or *Blattella germanica* hatch, and only a small number of the eggs in an oötheca sometimes complete development (pl. 6, figs. 36-40). However, we dissected an egg case of *S. supellectilium* and removed a fully developed parthenogenetic embryo; this individual shed its embryonic membrane while we photographed it (pl. 6, figs. 41-45); the nymph

was successfully reared, eventually becoming an adult female. On the other hand, some unfertilized eggs of *Blatta orientalis* and *Periplaneta americana* do hatch normally. In fact in *P. americana*, which has been claimed to be a species in which parthenogenesis is a possible but infrequent phenomenon (Griffiths and Tauber, 1942), we have found that hatching of unfertilized eggs is not uncommon; of 110 unfertilized females, 94 (85 percent) have produced oöthecae from which some eggs hatched (pl. 6, figs. 46-48).

In our experiments, which are still in progress, we have obtained a total of 2,433 undamaged oöthecae from unfertilized *P. americana* females; from these oöthecae at least some of the unfertilized eggs in 1,030 (42 percent) hatched and the nymphs left the oötheca; in 779 (32 percent) some of the embryos developed until their pigmented eyes were visible, or to an older stage, but failed to hatch; and the eggs in 624 oöthecae (26 percent) failed to develop. More than 500 adult females have been reared from parthenogenetically developed eggs; no males have resulted from the unfertilized eggs. These parthenogenetically produced females lay relatively few eggs and these eggs usually fail to hatch. However, if mated, these females frequently produce eggs that hatch. Parthenogenesis in *P. americana* is certainly less important than bisexual reproduction in the preservation of this species in nature. However, parthenogenesis could operate among the wild population, and in a temporary absence of males an unfertilized female could transmit some of her germ plasm beyond the end of her own life span.

## THE OÖTHECA

### FORMATION

Kadyi (1879) and others have described the formation of the oötheca of *Blatta orientalis*. The secretions from the colleterial glands flow out over the inner surface of the vestibulum or oöthecal chamber in a sheet that surrounds and is stretched by the incoming eggs. The vestibulum is closed posteriorly by the apical lobes of the seventh sternum. As the forming oötheca presses against these lobes, a characteristic pattern (pl. 7, fig. 52) is imparted to the distal end of the oötheca (Wheeler, 1889). After a certain number of eggs have entered the vestibulum, the distal end of the oötheca emerges beyond the end of the abdomen. Pryor (1940a) has described the color changes: At first the projecting portion is an opaque white; within 3 or 4 hours it becomes transparent, changes first to pink, and then to reddish chestnut; the oötheca continues to darken after it is laid,



becoming almost black in about 3 weeks. During formation the anterior part of the oötheca remains soft and white, eggs still entering and being pushed to the rear. The similar formation of the oötheca by *Blattella germanica* has been well described by Wheeler (1889).

The organic axis of the egg when it is still within the ovary and oviduct of the female is oriented with the cephalic pole directed toward the head of the mother; the egg then emerges from the oviduct caudal end first and falls into the genital armature caudal end down (Hallez, 1885). Because the oötheca of the viviparous cockroach *Diploptera dytiscoides* Serville lies on its side within the brood sac, with the micropylar ends of the eggs directed toward the left wall of the brood sac, Hagan (1951) stated, "This fact is of considerable historic interest since it causes the embryos to develop with an orientation contrary to the principles of Hallez's law." However, Hallez postulated the orientation of the eggs within the ovarioles and oviducts, en route, so to speak, to the oötheca; hence Hallez's law is not applicable to a secondary orientation of the eggs which depends on any future position of the oötheca. Wheeler (1889) demonstrated this clearly with oöthecae of *Blattella germanica* in which embryos developed normally when the oöthecae were oriented in five different positions; he concluded that gravitation has no perceptible effect on the development of the eggs of this species, and that these eggs have their constituents pre-arranged and completely conform to Hallez's "loi de l'orientation de l'oeuf."

As the eggs move posteriorly, the valvulae of the ovipositor move them into the oöthecal chamber and in some way set them on end with their heads upward (Snodgrass, 1952). The eggs from the right ovary pass into the left side of the oötheca and vice versa (Kadyi, 1879; Wheeler, 1889; Wille, 1920). Gier (1947) found that some of the eggs of *Periplaneta americana* are placed wrong end up in the oötheca, and though development occurs normally, the nymphs cannot emerge from the egg case. We have seen this in *Supella* also. In the completed oötheca, the eggs are placed vertically and, except at the ends of the egg case, arranged in two rows with the axis of each egg in one row opposite the interval between adjacent eggs in the other row (pl. 4, fig. 24; pl. 6, fig. 35). Figures 25 to 34 (pl. 5) show the external appearance of an oötheca of *Eurycotis* as it was being formed.

From what we have seen of oötheca formation in so-called viviparous cockroaches (see pp. 25-28), it is similar to that described above. The eggs of *Pycnoscelus surinamensis*, *Nauphoeta cinerea*, and *Leucophaea maderae* are erected vertically in two rows in the oötheca

which stretches around them (pl. 11, figs. 74, 75; pl. 12, fig. 86) as in the oviparous species. In these three species the wall of the oötheca is relatively thin and membranous. The color varies from pale straw to amber. These oöthecae do not darken and remain quite transparent as does the oötheca of *Blaberus craniifer* (pl. 4, figs. 23, 24; pl. 11, fig. 82; pl. 12, fig. 94). The oötheca of *P. surinamensis* is complete, and although there is no differential keel, such as occurs in the oviparous species, there is a narrow, longitudinal slit between the thickened edges of the wall of the oötheca along its dorsal surface. The oötheca of *N. cinerea* is incomplete, similar to that of *B. craniifer*, and usually does not cover the micropylar ends of the eggs or parts of the sides of the last three eggs deposited. We have seen some egg cases of *N. cinerea* with eggs attached along the outside, apparently rolled back by the walls of the brood sac from the imperfectly covered anterior end of the egg case, as the female retracted the oötheca into the brood sac.

Shelford (1906) found that the oötheca of the viviparous cockroach *Panchlora virescens* is represented by a complete, thin, transparent membrane. However, the membrane forming the oötheca of *B. craniifer* is incomplete; as Saupe (1928) and Nutting (1953) point out, the edges of the oötheca are separated by the micropylar ends of the eggs (pl. 4, fig. 24). In *Diploptera dytiscoides* the oötheca is reduced to a thin membrane that covers no more than half of the egg mass (Hagan, 1951). Riley (1891a) dissected an "egg cluster" of *Panchlora viridis* and reported that the oötheca was only a membranous sheath enclosing about half the length of the eggs. He reported that in some egg cases of this species the eggs were arranged in a double row side by side, with no visible enveloping membrane. This latter condition seems doubtful; the membrane may have been so thin and colorless as to be nearly invisible. Or perhaps this was an abnormal condition; Gould and Deay (1940) and we have seen egg masses of *Periplaneta americana* deposited without an oötheca (pl. 7, fig. 58).

Among cockroaches that do not carry the oötheca internally during embryonic development, the hardened oötheca resembles insect cuticle. Both have been shown to be scleroproteins which are very similar if not identical chemically (Pryor, 1940a, b). However, the oöthecae of *Periplaneta americana* and *Blatta orientalis* contain no chitin (Campbell, 1929; Pryor, 1940a), a compound found in varying amounts in insect cuticles. Most of the materials which go to make up the oötheca are secreted by the colleterial glands (Pryor, 1940a; Brunet, 1952). The left colleterial gland secretes a water-soluble protein (Pryor, 1940a) and an oxidase (Brunet, 1952); the right gland produces a

fluid containing a dihydroxyphenol, specifically protocatechuic acid (3, 4-dihydroxy-benzoic acid) (Pryor et al., 1946). When the secretions from the right and left glands mix, the phenolic substance is oxidized, producing a quinonoid tanning agent; interaction of the tanning agent with the protein gradually hardens and darkens the oötheca (Pryor, 1940a). The oötheca also contains crystals of calcium oxalate (Kadyi, 1879); these crystals occur mixed with protein in the lumen of the left colleterial gland. When the diphenolic substances of the right gland mix with the protein of the left, the calcium oxalate may play a part in maintaining an optimum pH for the oxidation of the phenol (Brunet, 1952).

Certain valvulae of the ovipositor of oviparous species are modified to mold the oötheca, especially the crista or keel. Wigglesworth and Beament (1950) have shown this clearly in *Blattella germanica*. The chorion along the upper pole of each egg is expanded and forms a vacuolated ridge which lies below the crista of the oötheca of this species. In the keel above each egg, overlying the vacuolated ridge of the chorion, is a small, oval, air-filled cavity which has two lateral expansions that pierce the crista and thus connect with the outer air. These cavities are respiratory chambers which, with associated ducts, convey air to the membranes around the eggs. From the roof of the genital chamber of the female, elongated fingerlike genital appendages project downward into the soft part of the forming oötheca and hold the latest egg in place. Near the base of these fingerlike appendages is a pair of thumblike projections directed backward, which serve to mold the upper cavity of the oötheca and to orient the egg within it. At the base of the thumblike lobes is a small median lobe with a tiny sclerotized horn projecting on either side, which has the exact form of the respiratory chambers and is the die on which they are molded. The colleterial glands discharge their secretions at the base of the genital appendages, and the "horned die" molds the material providing a respiratory chamber and respiratory duct for each egg. In *Periplaneta americana* the third valvulae of the ovipositor are modified to form the "horned die" which molds the inner surface of the keel of the oötheca (Brunet, 1951).

These respiratory structures in the oöthecae of oviparous cockroaches, because of their relatively small connections with the outer air, retard loss of water by the eggs. The importance of this function is emphasized when part or all of the keel has been eaten by the cockroaches themselves (pl. 7, figs. 56, 57); the eggs in these damaged oöthecae usually fail to develop at room humidities, or if they do, rarely hatch. Under these conditions death undoubtedly follows ab-

normal loss of water. We have found that the rate of water loss from American cockroach eggs at low humidities is greatly accelerated after removal of the keel. Sometimes abnormal oöthecae are deposited in which the respiratory chambers are not differentiated in the keel (pl. 7, fig. 60).

The oöthecae of different species of cockroaches are quite distinctive as they may vary in size, shape, and the number of enclosed eggs (cf. pl. 4, fig. 23; pl. 6, figs. 36, 39; pl. 7, figs. 49, 59; pl. 12, fig. 87). Lawson (1951, 1952, 1953) has studied the structural features of the oöthecae of several species of oviparous cockroaches. Each egg cell in the oötheca is indicated externally by an evagination (forming half of the respiratory chamber) on each side of the upper part of the keel (Lawson, 1951). Thus the number of respiratory chambers and their corresponding canals (pl. 7, fig. 53), which show clearly in the keels of certain oöthecae (e.g., *Periplaneta americana*, *Blatta orientalis*, pl. 7, figs. 49, 59, and *Eurycotis floridana*), is often a good criterion for the number of eggs in the oötheca. This relationship was recognized by some early workers. For example Sells (1842) described an oötheca of *B. orientalis* with 22 to 24 teeth along the serrated edge, which corresponded with the number of eggs contained within. This is rather a large number of eggs for the oriental cockroach, and Sells may have been dealing with another species. We have found that in abnormally small oöthecae of *P. americana*, usually those containing fewer than eight eggs, the number of respiratory chambers and ducts is frequently not the same as the number of eggs in the oötheca (pl. 7, figs. 54, 55). Wille (1920) also found that the number of egg cells in the oötheca of *Blattella germanica* did not always correspond to the number of teeth in the keel. Occasionally, eggs may be deposited without the formation of a protective oötheca (pl. 7, fig. 58), or an oötheca may be formed which contains no eggs.

#### REPRODUCTIVE POTENTIAL

The maximum number of eggs deposited at one time by a cockroach is largely dependent on the number of ovarioles comprising the ovaries. The number of eggs per oötheca varies with the species. In the oriental cockroach, a species which normally has 8 ovarioles per ovary, the normal number of eggs per oötheca has been stated to be 16 (Seiss, 1896; Rau, 1924; Gould and Deay, 1940). Because there are usually 8 ovarioles in each ovary, it is often stated that *Periplaneta americana* normally deposits 16 eggs. However, the oöthecae of this species frequently contain fewer than 16 eggs. Disease or some ab-



normality of one or more of the ovarioles will reduce the number of eggs produced in an oötheca (Gier, 1947). We have records of one female American cockroach which consistently deposited six to eight fertile eggs per oötheca; dissection revealed that she had one normal ovary, whereas the other had degenerated; several eggs had been liberated into her body cavity. The number of eggs per oötheca that have been reported for various species of cockroaches are given in table 1. However, because this information is not available for many species, we have included some data on the number of nymphs hatching per oötheca. Counts of nymphs are usually smaller than egg counts because the undeveloped eggs or unhatched eggs left in the oötheca are not included.

Among the domiciliary oviparous cockroaches at least, the number of egg cases produced by a female during her lifetime is even more variable than the number of eggs per egg case. There is comparatively little information about the egg-laying potential of other cockroaches. Table 2 summarizes the more comprehensive data. Certain unique values have been included because they extend the range of observations.

Temperature, fecundation, and age of the female influence the rhythm of egg and oötheca production of *Blatta orientalis* (Ricci, 1950); the rhythm accelerates with an increase in temperature, resulting in more oöthecae in a given period of time. Diet may also affect the reproductive ability of blattids. Chauvin (1949) found that the fecundity of *Blattella germanica* decreased considerably on a diet deficient in sterols, and the reproductive ability of these insects disappeared almost entirely after two or three generations had been reared on the experimental diet. Noland et al. (1949) also found that the oöthecae produced by German cockroaches reared on certain synthetic diets were often small, deformed, or shriveled, and only a small proportion of the eggs hatched. This nutritional effect on reproduction could not be traced to any known deficiency in the diet, and these workers suggested that a "reproduction factor" was lacking from the diets. In *Periplaneta americana* specific diets such as peptone or dextrose reduced the frequency of oötheca production as well as the number of eggs in the oötheca (Gier, 1947). However, female adults of *Blatta orientalis* maintained on a diet containing only 2.5 percent protein deposit normal oöthecae (Lafon, 1951). The lack of vitamin E in the diet for periods of 4 to 8 months does not influence the vitality of mature sperm of *B. orientalis* (Kudrjaschow and Petrowskaja, 1937).

TABLE I.—Number of eggs per oötheca, or nymphs hatched per oötheca, of various species of cockroaches

SPECIES	NUMBER OF EGGS OR NYMPHS PER OÖTHECA			Stage	SOURCE
	Mean	Minimum	Maximum		
<i>Blaberus craniifer</i> Burmeister.....	23.3	11	38	Nymphs	Saupe, 1928
Do .....	36.4	23	45	Eggs	Nutting, 1953
<i>Blatta orientalis</i> Linnaeus.....	16 <sup>a</sup>	..	..	Eggs	Rau, 1924
Do .....	13.8 <sup>b,e</sup>	5	15	Nymphs	Gould and Deay, 1940
Do .....	..	8	16	Eggs	Cros, 1942
Do .....	14	1	18	Eggs	Roth and Willis, unpublished data
<i>Blattella germanica</i> (Linnaeus).....	40	28	58	Eggs	Wheeler, 1889
Do .....	41	34	48	Eggs	Girault, 1911
Do .....	37	18	50	Eggs	Ross, 1929
<i>Blattella humbertiana</i> (Saussure).....	..	..	40	Eggs	Takahashi, 1940
<i>Blattella vaga</i> Hebard.....	31	15	39	Eggs	Roth and Willis, unpublished data
<i>Ectobius panseri</i> Stephens.....	12 <sup>b</sup>	9	13	Eggs	Brown, 1952
<i>Epilampra wheeleri</i> Rehn.....	..	35	50	Nymphs	Sein, 1923
<i>Eurycotis floridana</i> (Walker).....	23	15	25	Eggs	Roth and Willis, 1954a
<i>Iscnoptera deropeltiformis</i> (Brunner) ...	39 <sup>b</sup>	38	40	Nymphs	Rau, 1947
<i>Leucophaea maderae</i> (Fabricius).....	..	30	35	Nymphs	Scharrer, 1951
Do .....	40 <sup>a</sup>	..	..	Eggs	van Wyk, 1952
<i>Nauphocta cinerea</i> (Olivier).....	32.4	26	40	Eggs	Roth and Willis, unpublished data
<i>Parcoblatta pensylvanica</i> (Degeer).....	32 <sup>a</sup>	..	..	Eggs	Gould and Deay, 1940
Do .....	24.6 <sup>b</sup>	18	30	Nymphs	Rau, 1940b
<i>Periplaneta americana</i> (Linnaeus).....	16	12	18	Eggs	Lefroy, 1909

(continued)

TABLE I.—*Concluded*

SPECIES	NUMBER OF EGGS OR NYMPHS PER OÖTHECA			Stage	SOURCE
	Mean	Minimum	Maximum		
<i>Periplaneta americana</i> (Linnaeus).....	16 <sup>a</sup>	..	24 <sup>d</sup>	100+	Gould and Deay, 1940
Do .....	11.9 <sup>b</sup>	6	16	40	Rau, 1940a
<i>Periplaneta australasiae</i> (Fabricius).....	26	22	28	20	Girault, 1914
<i>Periplaneta fuliginosa</i> (Serville).....	24 <sup>a</sup>	..	..	..	Gould and Deay, 1940
Do .....	24 <sup>b</sup>	22	26	4	Rau, 1945
<i>Pycnoscelus surinamensis</i> (Linnaeus).....	24	14	42	..	Zappe, 1918
Do .....	..	..	48	1	Caudell, 1925
Do .....	23.8 <sup>b</sup>	11	32	6	Saupe, 1928
Do .....	18.2 <sup>b</sup>	3	34	36	Roeser, 1940
Do .....	..	30	36	..	Schwabe, 1949
Do .....	25.8	17	34	20	Roth and Willis, unpublished data
<i>Supella supellectilium</i> (Serville).....	12	..	..	..	Cottam, 1922
Do .....	13.7	..	..	224	Gould and Deay, 1940
Do .....	16	11	18	27	Roth and Willis, unpublished data
<i>Symploce hospes</i> (Perkins).....	19.5 <sup>b</sup>	18	20	4	Illingworth, 1915

<sup>a</sup> Stated to be the normal or usual number, or number in a perfect capsule.

<sup>b</sup> Calculated from source data.

<sup>c</sup> Gould and Deay (1940) give a mean of 14.4 nymphs hatched from all (number not stated) fertile capsules in their experiment.

<sup>d</sup> Maximum based on one capsule only. Rosenfeld (1910) gives an average of 24 eggs per oötheca (10 capsules) with a range from 10 to 28; this high value may have resulted from a misidentification of *P. fuliginosa* as *P. americana*.



TABLE 2.—*Production of oöthecae by various species of cockroaches*

SPECIES	NUMBER OF OÖTHECAE PER FEMALE					Temp. °C.	SOURCE
	Mean	Minimum	Maximum	No. ♀♀			
<i>Blattella germanica</i> (Linnaeus)	2.5 <sup>a</sup>	1	4	55	..	Rau, 1924	
Do	9 <sup>a</sup>	1	18	5	Room	Gould and Deay, 1940	
Do	6 <sup>a</sup>	4	9	3	28 <sup>ob</sup>	do.	
Do	..	..	22°	1	22-24°	Ricci, 1950	
Do	11.5	0	27	30	29-37°	Roth and Willis, unpublished data	
Do	..	..	4	..	22°	Wille, 1920	
Do	1.7 <sup>a</sup>	1	2	16	35°	Ross, 1929	
Do	..	4	8	6	Room	Gould and Deay, 1940	
Do	5.5 <sup>a</sup>	2	12	26	..	Morriset, 1946	
Do	7.3	2	9	14	21-30 <sup>ob</sup>	Gerber, 1950	
Do	5.1 <sup>a</sup>	3	7	58 <sup>a</sup>	29-37°	Roth and Willis, unpublished data	
Do	4.5	0	11	5	..	Rau, 1940b	
Do	7.8	4	22°	1	Room	Gould and Deay, 1940	
Do	..	..	46	10	..	Klein, 1933	
<i>Periplaneta americana</i> (Linnaeus)	21.5	5	90	16	Room	Gould and Deay, 1940	
Do	55.8 <sup>a</sup>	16	76	5	28 <sup>ob</sup>	do.	
Do	50.8 <sup>a</sup>	13	52	20 <sup>f</sup>	17-28°	Griffiths and Tauber, 1942	
Do	28.9	10	21	15 <sup>g</sup>	17-28°	do.	
Do	10.6	3	17 <sup>h</sup>	11	..	Spencer, 1943	
<i>Periplaneta australasiae</i> (Fabricius)	..	..	..	4	Room	Gould and Deay, 1940	
Do	17	..	..	26	..	Roeser, 1940	
<i>Periplaneta fuliginosa</i> (Serville)	1.4 <sup>a</sup>	1	3	4	..	Cottam, 1922	
<i>Pycnoscelus surinamensis</i> (Linnaeus)	7.5 <sup>a</sup>	5	9	4	..	Gould and Deay, 1940	
<i>Supella supellecillum</i> (Serville)	13.7	6	22	7	Room	do.	
Do	11.5	1	27	8	Constant	do.	
<i>Symphloe loeopes</i> (Perkins)	..	..	38 <sup>i</sup>	1	..	Illingworth, 1915	

<sup>a</sup> Calculated from source data.

<sup>b</sup> Source data, given as ° F., converted to nearest ° C.

<sup>c</sup> During a period of 202 days, not the entire adult life of female.

<sup>d</sup> Virgin females which produced infertile eggs.

<sup>e</sup> During a period of 150 days, not the entire adult life of female.

<sup>f</sup> Females kept in 1,000 cc. containers.

<sup>g</sup> Females kept in 250 cc. containers.

<sup>h</sup> During a period of 100 days, not the entire adult life of female.

<sup>i</sup> Unfertilized.

<sup>j</sup> During a period of 210 days, not the entire adult life of female.

## OVIPOSITION AND HATCHING

As we shall show below, cockroaches exhibit, or have exhibited at some time during their phylogeny, a variety of ovipositional behaviors from single-egg oviparity through multiple-egg oviparity and ovoviviparity to viviparity. Unfortunately these descriptive terms have been used so diversely in the literature that their use creates confusion (see Hagan, 1951). We shall make no attempt to redefine these terms, but shall point out their limitations with respect to cockroaches, as they appear to us.

Birth in insects is characterized as *oviparous*, in which the birth product is an egg covered by a chorion or shell, or *viviparous*, in which the egg hatches within the mother and the birth product is an embryo devoid of a chorion (Hagan, 1951). Viviparity may be further divided, with respect to cockroaches, into *ovoviviparity*, in which the egg contains enough yolk to nourish the embryo until hatching, and *pseudoplacental viviparity*, in which the embryo possibly derives a part of its nutriment from the mother by means of a pseudoplacenta (Hagan, 1951).

## THE OVI PAROUS COCKROACHES

In marked contrast to the viviparous species, which carry the oötheca internally, the oviparous species of cockroaches always carry the oötheca externally (pl. 5, figs. 32-34; pl. 8, figs. 63, 64). The period during which the oviparous female carries the oötheca before dropping it depends on the habits of the genus and external factors such as temperature, etc. Most genera, the ovipositional habits of which are known, deposit the oötheca on the substratum shortly after its formation, within a few days or less. Genera in which this habit has been observed are *Periplaneta* (Sein, 1923); *Blatta* (Miall and Denny, 1886; Moore, 1900); *Supella*, *Parcoblatta*, *Cariblatta*, *Eurycotis* (Roth and Willis, unpublished data); and others. Many species carry the oötheca with the keel upward, as it was formed, until deposition. This condition may be observed in *Blatta orientalis*, *Periplaneta americana*, *P. australasiae*, *P. fuliginosa*, *Supella supellectilium*, *Cariblatta lutea minima* Hebard, *Eurycotis floridana*, and undoubtedly others.

On the other hand, certain genera of cockroaches rotate the oötheca 90° to the left or right and carry it until, or shortly before, the eggs hatch. This habit has been described in *Blattella germanica* (Wheeler, 1889; Wille, 1920; Ross, 1929; Woodruff, 1938; Gould and Deay, 1940; Pettit, 1944; Rau, 1944). It has also been observed in other

species of this genus: *B. lituricollis* (Walker) (Zimmerman, 1948); *B. humbertiana* Saussure (Takahashi, 1940); *B. vaga* (we have observed the young hatching from an oötheca that was still being carried by the female; see pl. 8, fig. 65). The direction of rotation of the egg case of *B. germanica* has been reported to be toward the right (Wheeler, 1889; Wille, 1920; Ross, 1929) or toward the left (Gould and Deay, 1940). Possibly the direction of rotation is of genetic origin and is relatively constant within a particular laboratory colony. The oötheca seems to be held in position by pressure of the encircling genital armature (Ross, 1929). Rarely *B. germanica* may form a new oötheca before the empty one is discarded, and the empty oötheca remains attached to the fresh one (pl. 7, fig. 62). We have also seen instances of *Periplaneta americana* depositing two oöthecae attached to each other by their ends; formation of the second was started before the first was dropped, and the soft end of the new oötheca curved around the hard end of the old one.

The oviposition behavior of *Ectobius panzeri* Stephens combines aspects of both the *Blatta* and *Blattella* types just described. Brown (1952) reported that *E. panzeri* usually rotates the oötheca through 90° and most often to the left. Some females carry the egg case for as long as 16 days, but the majority deposit it in less than 10 days. This species winters in the egg, and the nymphs hatch out the next spring (Brown, 1952). Lucas (1928) found a female of *Ectobius lapponicus* Linnaeus that carried her egg case at least 12 days. In this species the egg case is deposited in the summer and the eggs hatch quite soon.

Some of the species that deposit the oötheca shortly after it is formed frequently conceal it and cement it to the substrate. The female may cover the oötheca with bits of debris which she chews from the substrate (Latreille, [1803/1804]; Sampson, *in* Shelford, 1912) and mixes with saliva (Haber, 1920). The habit of concealing the oötheca, or covering it with debris, is practiced by *Periplaneta americana* (Haber, 1920; Adair, 1923; Rau, 1943); *P. australasiae* (Girault, 1915; Spencer, 1943); *Blatta orientalis* (Qadri, 1938; Rau, 1943); *Loboptera decipiens* (Berland, 1924); *Supella supellectilium* (Flock, 1941); *Cryptocercus punctulatus* Scudder (Cleveland et al., 1934); and *Eurycotis floridana* (Roth and Willis, 1954a). The habit of covering the oötheca with debris is not equally developed in all the domiciliary species. In the laboratory, the eggs of *P. americana* are covered most frequently; those of *B. orientalis* are usually dropped free, uncovered and not cemented to the substrate (Gould and Deay, 1940; and our own observations); those of *Supella* are usually ce-

mented to the substrate but are only sometimes partly covered with bits of feces or other debris which is cemented to the oötheca. These females show no further care for the oötheca after it has been deposited, leaving the eggs to hatch, which often requires several weeks.

As mentioned earlier, with few exceptions the embryos are arranged in the oötheca with their heads directed toward the keel (pl. 9, fig. 66) or dorsal side of the oötheca. Generally at hatching the two halves of the keel separate, and most of the young of *Periplaneta americana* emerge almost simultaneously in less than 10 minutes (Gould and Deay, 1938) or at the most within the hour (Klein, 1933). Goeze (1782) stated that the hatching cockroaches produce a material which softens the cement between the halves of the serrated crista enabling the young nymphs to escape from the egg case. This view has been repeated in many publications, but there seems to be no experimental evidence for the statement. Internal pressure exerted by the fully developed nymphs causes the oötheca to split along the keel (Wheeler, 1889; Gould and Deay, 1938; Gier, 1947). If some of the young are late in hatching, they cannot escape from the capsule (which tends to snap shut after the young have emerged), or they may be trapped between the two lips of the keel (Fischer, 1928) (pl. 6, figs. 46-48). Pettit (1944) found that the oötheca of *Blattella germanica* splits apart more readily as the development of the embryo nears completion. As soon as the crista opens, the young cockroaches swallow air bubbles at the rate of two or three a second. These unite to form a large bubble in the alimentary canal that almost doubles the volume of the insect. By squirming and waving the upper parts of their bodies, the young cockroaches worm their way out. We have also observed the hatching nymphs of *Periplaneta americana* swallow air. The emerging insects are covered by thin, transparent embryonic membranes which are quickly shed, usually during emergence (pl. 6, figs. 44, 47), and often eaten. Sometimes in *P. americana* these membranes remain caught between the lips of the keel. In *Ectobius panzeri*, the oöthecae of which are buried in sand, this first nymphal skin is shed after the nymphs reach the surface (Brown, 1952). Brown did not observe these exuviae to be eaten.

Numerous writers have repeated the statement that the female German cockroach assists her young to hatch by slitting the oötheca along the seam with her mandibles. This belief originated with a statement by Hummel (1821); he misinterpreted the behavior of a female which apparently was only "exploring," with her antennae and palpi, a recently dropped oötheca when the nymphs coincidentally began to emerge. This egg case, incidentally, had been dropped by another fe-



male, and the female in question was still carrying her own oötheca. Wheeler (1889), Ross (1929), and Pettit (1944) have thoroughly discredited this midwifery.

Although the usual method of emergence among oviparous cockroaches is to split the keel of the oötheca, Terry (1910) states that the young of *Euthyrrhapha pacifica* (Coquebert) gnaw an exit hole through the capsule; a similar method for emergence of the young is said to occur in *Nyctibora lutsi* Rehn and Hebard (Wolcott, 1950).

#### THE VIVIPAROUS COCKROACHES

For our use viviparity as defined by Hagan (1951; see above) may be too restrictive, in that different individuals of the same cockroach species (e.g., *Pycnoscelus surinamensis*) may give birth either to nymphs, which emerge as such from the mother, or to eggs, still enclosed in the oötheca, which hatch immediately or shortly after the egg case has been dropped. Hence the species may be considered ovoviviparous or oviparous depending upon the behavior of the individual insect. Snodgrass's (1935) broader definition would include both types of behavior in viviparity, as in both, the eggs complete development within the body of the female. By accepting a broader definition of viviparity we avoid the anomaly of having oviparous behavior, by definition, in species that logically would be considered ovoviviparous. Such facultative oviparity, in typically ovoviviparous species, differs greatly from the obligate oviparity of the common domiciliary cockroaches, certainly much more than it differs from viviparity.

Viviparity among the so-called ovoviviparous cockroaches, as we shall show below, differs fundamentally from viviparity in other insects. Among the insects considered by Hagan (1951), viviparity is the birth of embryos from eggs retained in the mother's genital tract. The ovoviviparous cockroaches, however, oviposit into an oötheca, and the eggs actually pass out of the female's body. This fact has only recently been elucidated (Chopard, 1950; Nutting, 1953; and original observations below) and perhaps is not generally known. Oviposition among the ovoviviparous cockroaches is very similar to that of oviparous forms, except that the completed oötheca is retracted by the ovoviviparous female and deposited in her brood sac instead of on the substrate. Viviparity among ovoviviparous cockroaches is, therefore, a secondary condition. The birth product is first an egg enclosed in a chorion, and as such satisfies the criteria for oviparity. After the female retracts the oötheca into her brood sac, the eggs may hatch

within her body and the secondary birth product is an embryo devoid of a chorion, thus satisfying the criteria for viviparity. However, eschewing all theological implications, can an individual once born be born again? If not, the so-called ovoviviparous cockroaches of which we have the greatest knowledge are, strictly speaking, oviparous. Yet it is a decided convenience to use the term viviparous for those species of cockroaches which incubate the eggs in the brood sac, as opposed to oviparous species which do not incubate the eggs within the body.

Viviparity has been reported for several cockroach genera and species (Chopard, 1938). It has been assumed by some observers that a species is viviparous when, upon dissection, embryos are found developing in a brood sac, even though hatching was not observed (e.g., *Panesthia javanica*, Wood-Mason, 1878; *Eustegaster micans* Sausure, and *Oxyhaloa saussurei* Borgmeier, Holmgren, 1903-1904). Recently emerged nymphs found associated with a female, with no evidence of an oötheca, have also been cited as evidence of viviparity (e.g., *Panchlora*, Scudder, 1890; Davis, 1930). Newly hatched nymphs of viviparous cockroaches frequently eat the oötheca (Nutting, 1953; our own observations), so its absence is not surprising.

A number of workers have observed that the females of apparently viviparous species produce oöthecae that protrude externally. This event may occur as the oötheca is formed (see below) or later on when the oötheca is expelled either prior to or at the time of hatching. Frequently, expulsion of the oötheca does not coincide with completion of embryonic development. If the female deposits the oötheca prematurely, the eggs usually fail to hatch. This has been reported for *Blaberus craniifer* (Nutting, 1953), *Pycnoscelus surinamensis* (Saupe, 1928; Roeser, 1940), *Nauphoeta cinerea* (Illingworth, 1942), *Gromphadorhina laevigata* (Chopard, 1950), and *Leucophaea maderae* (Scharrer, personal communication). Karny (1924) described a female of *Pseudophoraspis nebulosa* Burmeister carrying a weakly "chitinized," pale-yellow oötheca which contracted on drying; this description together with the fact that this species has a brood sac, and has been found with young clinging to the underside of the abdomen (Shelford, 1906), would lead us to believe Karny was dealing with a species similar in oviposition behavior to the above viviparous forms.

The observations of Chopard (1950) first served to explain the carrying of oöthecae by the above cockroaches. He found that *Gromphadorhina laevigata* extrudes an oötheca which after several hours extends about 25 mm. beyond the end of the abdomen. Then when the oötheca is held only by its end, it is slowly drawn back into a large brood sac that extends into the metathorax. In the gravid female the

ovipositor is completely inverted; Chopard states that the inversion probably occurs at the moment the oötheca penetrates the brood sac. Snodgrass (1952) thinks that the ovipositor of *Gromphadorhina* probably inserts the fully formed oötheca into the brood sac. The eggs are incubated within this pouch for about 70 days at the end of which time the young are born. Nutting (1953) observed a similar behavior in *Blaberus craniifer*. Gurney (1953) suggested that this method of transference of the oötheca into the brood sac may occur in other viviparous genera which have been seen with protruding oöthecae.

We have observed the extrusion of the oötheca during its formation and its subsequent retraction into the brood sac in *Pycnoscelus surinamensis*, *Nauphoeta cinerea*, and *Leucophaea maderae*; it is apparent that the formation and retraction of the oötheca in these species is quite similar to that of *Gromphadorhina* and *Blaberus*. The oviposition behavior of the three former species is described below:

*Pycnoscelus surinamensis*.—Ten females have been observed during various stages of extruding and retracting their oöthecae (pl. 11, figs. 74-79). One female completed the entire process in 2 hours and 15 minutes from the time the first eggs were extruded to the time they disappeared back into her abdomen. She took 1 hour and 25 minutes to extrude the oötheca to its fullest extent; the oötheca then remained more or less unchanged in this position for 40 minutes, and then the female began to retract the oötheca into the brood sac. Retraction time took only 10 minutes. The retraction time for the oöthecae of two other females was also about 10 minutes. When the egg case is extruded (pl. 11, figs. 74, 75), the abdomen of the female is much contracted, the segments being tightly telescoped. The axes of the eggs are vertical at this time and remain so until the egg case is fully extruded. As the female begins to retract the oötheca, the axes of the eggs incline more and more to the left (pl. 11, figs. 76, 77), so that as the last eggs disappear from view they are horizontal. When the oötheca is finally retracted, the abdominal segments return to the normal position. Saupe (1928) was incorrect in his assumption that the oötheca was formed and rotates 90° *inside* the brood sac.

Nymphs hatched from the eggs of three of the observed females 31, 33, and 35 days after formation of their oöthecae. We did not observe the hatching process. One of these females which we dissected after the young had hatched had ovaries in which none of the eggs were well developed. A female dissected 37 days after she had formed an oötheca had no egg case in her brood sac; but her ovaries contained well-developed eggs which were apparently ready to be deposited in an oötheca. It is likely that this female had expelled and eaten the



oötheca which we had seen her retract. Another female dissected 36 days after forming an oötheca had a recently formed egg case containing undeveloped eggs in her brood sac. Apparently this female had also expelled and eaten the egg case we had seen formed, and then formed a new one unobserved. Obviously in determining the time required for the embryonic development of cockroaches which are incubated in a brood sac, one must be certain that the oötheca which is seen being retracted is not subsequently dropped, eaten, and replaced by a new one without the knowledge of the observer.

*Nauphoeta cinerea*.—More than 20 females have been observed with oöthecae in various stages of extrusion and retraction (pl. 12, figs. 86-90). Complete extrusion of the eggs takes about  $1\frac{1}{2}$  hours or less. As the eggs are extruded, the female invests them with a thin, straw-colored oötheca. During the early stages of formation the oötheca frequently projects upward at a slight angle. Usually by the time the oötheca is half formed it bends slightly downward, and when completely extruded it assumes a curve of rather short radius (pl. 12, fig. 87). Except for the first egg, which lies with its axis on an angle to the others, the eggs are extruded with their axes vertical; they remain in this position until the oötheca has been completed. The female then rotates the egg case to the left rather rapidly so that within about 5 to 10 minutes the axes of the eggs are horizontal; the female then retracts the oötheca, in about 1 to 2 hours or sometimes much longer. One female carried her egg case with about three eggs exposed for 22 hours before complete retraction occurred. Sometimes retraction is incomplete and several eggs remain protruding from the end of the abdomen. These exposed eggs dry up and shrivel. One female which had failed to retract her oötheca completely (about 15 eggs had remained exposed) gave birth to 12 nymphs 34 days later. Inasmuch as the genital opening is blocked when dead eggs protrude from the abdomen, the female must drop the oötheca or extrude it at least partially to allow the developed nymphs to hatch. Hatching of the eggs of four females occurred from 33.5 to 41 days after they formed their oöthecae. The oötheca in the brood sac fills almost the whole abdominal cavity (pl. 12, figs. 91-94).

*Leucophaea maderae*.—Two females were observed as they extruded and retracted their egg cases. As a result of an accident, the egg case of the first female broke incompletely into two halves which were held together by a thin portion of the delicate membrane forming the oötheca. This female could not retract all the eggs into her abdomen. The eggs that protruded became dry and shrunken after 3

days' exposure, but remained attached to the female. She died on the fourth day; the eggs within the brood sac appeared normal.

When the second female was first observed, four eggs were already visible beyond the end of her abdomen. As more eggs were extruded, their axes, which were originally vertical, began to tilt toward the left side of the female. After 3 hours and 20 minutes the oötheca was fully extruded; it contained about 38 eggs and extended three-quarters of an inch or more beyond the posterior end of her abdomen. After another 10 minutes the axes of the eggs were horizontal, and the female began to maneuver the oötheca into the brood sac. When fully extruded, the oötheca was curved so that the terminal eggs farthest from the body were far to the left of the midline of the body of the female. While being retracted, the oötheca stuck out straight behind the female. After 45 minutes only one egg (the first laid) was visible. But this egg projected for 1 hour and 25 minutes more before it disappeared. Total retraction time was 2 hours and 10 minutes, and the whole process took more than 5½ hours.

In all species of viviparous cockroaches in which oviposition has been observed, including *Leucophaea maderae*, the last eggs deposited in the oötheca are the first to enter the brood sac as the oötheca is retracted. This action places the most recently laid eggs in the anterior end of the brood sac and the oldest eggs in the posterior end of the brood sac. Yet van Wyk (1952) stated that in *Leucophaea maderae* "The oötheca is contained in the vestibulum<sup>2</sup> and the latter extends cephalad as the former increases in size. The oldest eggs are therefore situated at the anterior end of the vestibulum." Obviously this description was not based on direct observation of the transfer of the oötheca into the brood sac.

Though the formation of the oötheca is very similar in the above three species, certain differences should be noted. In *Pycnoscelus* the axes of the eggs remain vertical until the oötheca is fully extruded and then they gradually incline toward the left as the egg case is retracted into the brood sac; retraction itself is very rapid requiring only about 10 minutes. In *Nauphoeta* the axes of the eggs are also vertical until the oötheca is fully extruded. However, unlike *Pycnoscelus*, the oötheca is completely rotated in about 5 or 10 minutes and is then retracted in about an hour or more. In *Leucophaea*, as in *Nauphoeta*, the axes of the eggs are horizontal when the retraction process begins.

<sup>2</sup> The vestibulum or oöthecal chamber is the portion of the genital cavity lying above the 7th sternum (Snodgrass, 1937, 1952). Van Wyk (1952) considers the brood sac to be an anterior expansion of the vestibulum.

The time required for the formation and retraction of the oötheca is quite variable; we may have induced some variation by disturbing the females. However, the complete formation and extrusion of the oötheca (not including retraction) by the above species occurs more rapidly than among species in which the oöthecae remain exposed after they are formed. For example, *Eurycotis floridana* (Walker) forms its egg case in about 6 hours (Roth and Willis, 1954a), and *P. americana*, *B. orientalis*, *B. vaga*, and *B. germanica* require about the same length of time or longer for oötheca formation; Wille (1920) reported 16 to 24 hours for complete oötheca formation in *B. germanica*. Brown (1952) reported 6 hours for oötheca formation by *Ectobius panzeri*. The longer period taken by oviparous cockroaches to form their oöthecae may be related to the fact that in these species the toothed keel of the oötheca is a complicated structure containing respiratory chambers and ducts. Obviously a certain amount of time is necessary to form each of the respiratory chambers; the protein substance of the oötheca must harden around the "horned die" before the next chamber is formed. The oöthecae of *Pycnoscelus*, *Nauphoeta*, and *Leucophaea* have no respiratory chambers in a specialized crista; this may account for the comparative rapidity with which these species form their egg cases.

It is very difficult to ascertain just how birth occurs in the cockroaches that retain their eggs within a brood sac; the young may hatch as the oötheca is extruded from the brood sac into the vestibulum or oöthecal chamber, and the nymphs then issue from the body of the female; they may hatch as the oötheca is extruded beyond the oöthecal chamber; or the oötheca may be dropped completely, the young hatching shortly afterward. Only direct observation can determine the method, and inasmuch as it is practically impossible to tell the exact moment when birth will occur, the insects have to be watched closely and at times continuously.

Actual observations of the hatching of viviparous cockroaches are few in number. Hatching has been observed in *Panchlora viridis* (Riley, 1890, 1891a, b); *Pycnoscelus surinamensis* (Thomas, 1949; Schwabe, 1949); *Diploptera dytiscoides* (Hagan, 1939); *Blaberus craniifer* (Nutting, 1953); *Gromphadorhina laevigata* (Chopard, 1950); *Leucophaea maderae* (Scharrer, 1951; van Wyk, 1952); and *Nauphoeta cinerea* (Roth and Willis, unpublished data).

We have observed birth twice in *Nauphoeta cinerea*. The first time, we saw a female extrude an oötheca containing fully developed embryos; while it was still attached to the female, two other cockroaches seized the egg case, and one, managing to free the oötheca from the

mother, carried it off. We retrieved this oötheca; four eggs hatched immediately, and the nymphs commenced feeding on the oötheca. About 23 well-developed embryos failed to hatch. The second time we observed birth, most of the nymphs had hatched before we noticed the event. The young cockroaches, still invested with their embryonic membranes, dropped from the female's oöthecal cavity as she extruded the oötheca. When we isolated the female in a vial, she seized and ate two nymphs immediately after they had dropped free and before they shed their embryonic membranes. The remainder of the oötheca, which had been extruded as far backward as the oöthecal cavity, was removed from this female when further hatching ceased. There were six live embryos in this fragment of oötheca; these did not hatch.

Some reports about hatching in viviparous cockroaches are conflicting. For example, Scharrer (1951) states that the young of *Leucophaea maderae* hatch from their eggs the moment they leave the mother. Van Wyk (1952) says the eggs of this species "hatch in pairs in the oötheca while it is still in the vestibulum<sup>3</sup> and the young immediately leave the mother. . . . The remains of the oötheca and the chorion of each egg are thrown out by the mother after all the eggs have hatched." Yet Pessoa and Correa (1928) state that this species deposited the egg case, and the young hatched from the capsule 20 days after laying.

Saupe (1928) argued that the oötheca of *Blaberus craniifer* fills the brood sac so completely that the nymphs have no room to hatch within the sac. Although he did not observe the act, Saupe believed that hatching occurred in *B. craniifer* as the oötheca was extruded or shortly after it had been dropped. Nutting (1953) also believes that it is impossible for the young to hatch in the brood sac of *B. craniifer*; he observed the hatching of nymphs from an oötheca that was being extruded by the female and also from recently dropped oöthecae of this species. In *Pycnoscelus surinamensis* the oötheca completely fills the brood sac which is stretched tightly against the egg case. Thomas (1949) observed that in this species the nymphs were delivered alive and individually. Schwabe (1949) stated that the nymphs of *P. surinamensis* hatch within the body of the female. Even in *P. surinamensis*, however, the female may expel the oötheca, and then the

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<sup>3</sup> As van Wyk (1952) considers the vestibulum to include the brood sac, we do not know from his description whether or not hatching occurred within the brood sac proper or within the posterior part of the vestibulum. After the oötheca has been released from the brood sac, hatching most probably occurs as the oötheca is extruded beyond the vestibulum.



young hatch outside the female; we have observed this several times. According to Zappe (1918) hatching of *P. surinamensis* may occur within the mother, or the oöthecae containing well-developed embryos are laid in the soil, the young hatching within 24 hours. Later Zappe (Hagan, 1951) claimed that in Connecticut this species is oviparous. The two females of *Nauphoeta cinerea* that we observed giving birth expelled their oöthecae, at least partially, before the eggs started to hatch.

The site in which the eggs of viviparous cockroaches hatch would seem to depend upon the rapidity with which the embryos respond to a stimulus to hatch. The site might be anywhere from the vestibulum to a position outside of the body of the female. Presumably hatching does not occur within the tightly investing brood sac because of spatial limitations and the pressure exerted by the wall of the brood sac. This pressure undoubtedly increases between the time the oötheca is retracted and the time of hatching, as the eggs of viviparous cockroaches increase in size during embryonic development (Hagan, 1951; Nutting, 1953), thereby stretching the brood sac even more. Nutting (1953) believes that pressure exerted by the female on the oötheca during extrusion may supply the necessary hatching stimulus. His evidence is not convincing: he secured hatching from oöthecae, that had been extruded 2 to 6 days earlier, after manipulating the oötheca with his fingers. Yet these same oöthecae had been subjected to whatever pressure the female might apply prior to and during extrusion, and the eggs had not hatched. These oöthecae might have been dropped prematurely before the embryos were ready to hatch. On the other hand, the release of the oötheca from the tightly stretched brood sac during extrusion might be a hatching stimulus—at least this seems to be true in *Pycnoscelus surinamensis* (see below).

*Pycnoscelus* will drop its oötheca when exposed to temperatures above 35° C. or below 5° C., and after being poisoned, injured, or decapitated (Roeser, 1940). Roeser observed that seldom is an oötheca found inside a dead female; shortly before or after death due to natural causes the female expels the oötheca from the brood sac. We decapitated five females 33 to 35 days after they had retracted their oöthecae. Each female extruded her oötheca, and nymphs began hatching as soon as the egg case was released from the brood sac (pl. 11, figs. 80-85). The nymphs swallowed air, swelled up, and emerged from the oötheca, shedding the embryonic membranes which had surrounded them (pl. 11, figs. 83, 85, arrows). Some of these eggs were obviously ready to hatch before the females were killed, and release

from the pressure of the brood sac was followed by immediate hatching. Just what the stimulus is for the female to extrude the oötheca at the end of the gestation period is unknown. Some eggs were completely undeveloped and others not far enough developed to hatch; these remained in the oötheca. Apparently some of the eggs may develop at different rates. Schwabe (1949) recorded one instance in which 36 hours elapsed between the birth of the first and last nymphs of the brood. The oötheca is sufficiently developed to prevent hatching if only a few individuals in the egg case have reached the hatching stage and the egg case is dropped prematurely. Yet we noticed two nymphs which hatched from one dropped egg case in which only five embryos had developed; two of the others were only able to free part of their heads from the oötheca.

Injury or death causes the extrusion of the oötheca by females of other species of viviparous cockroaches. From the number of genera in which this reaction has been observed, we think that the phenomenon is probably general among cockroaches that carry their oöthecae in brood sacs. Beebe (1925) saw a giant "woodroach," which was being eaten by a spider, give birth to 51 young which "had burst from their mother." Shelford (1906) recorded a specimen of *Epilampra burmeisteri* Guerin from Brazil that was preserved with two nymphs (still partly surrounded by their embryonic membranes) emerging from the tip of the female's abdomen; these nymphs may have been expelled by the female as she died. Gissler (Riley, 1891b) observed 24 young emerge from the genital orifice of a female *Panchlora viridis* which had died. Stewart (1925) killed a female of *Blaber cubensis* [= *Blaberus discoidalis* Serville (Rehn and Hebard, 1927)] in a cyanide bottle; during the few seconds the female survived she partly extruded an oötheca containing 44 eggs. Heal (personal communication) observed *Leucophaea maderae* females with creamy-white, fragile egg cases protruding from the ends of their abdomens; these females had been killed either with cyanide or pyrethrum during disinfestation of buildings. We have seen *Blaberus craniifer* partially expel an oötheca after decapitation prior to dissection (pl. 4, fig. 22); a pin placed against the posterior end of this oötheca prevented further extrusion. We have also seen a female of *Nauphoeta cinerea* expel its oötheca on being dropped into boiling water. Insecticidal sprays may cause the German cockroach female to drop its oötheca prematurely (Woodbury, 1938; Parker and Campbell, 1940). A similar occurrence of oviposition by injured or dying mosquitoes, *Aedes sollicitans* (Walker), and the phenomenon of "death stress" have been studied by DeCoursey and Webster (1952).

Hagan (1939, 1941, 1951) has worked extensively with the viviparous cockroach *Diploptera dytiscoides*. He has described evanescent embryonic structures, the pleuropodia, to which, tentatively, he ascribes nutritional or respiratory functions, or both. The pleuropodia arise as a part of the swelling of the first abdominal segment. With embryological development they increase greatly in length, becoming thin-walled tubes which end near the micropyle. They are bound to the inner surface of the chorion by the yellow serosal cuticle. Because of this modification Hagan cites *D. dytiscoides* as the one example of pseudoplacental viviparity among cockroaches.

Hagan (1951) described oviposition in *Diploptera dytiscoides*: On reaching the lower end of the common oviduct the eggs "are directed by the ovipositor from the genital chamber ventrally into the open end of the uterus." The implication here, which has subsequently been confirmed by Hagan (personal communication), is that the first-laid eggs are the first to enter the brood sac and the last-laid eggs are the most posterior in the brood sac. A pronounced central dome in the roof of the genital pouch is presumed to facilitate "tilting of the eggs as they pass into the uterus" (Hagan, 1941). This method of oviposition contrasts markedly with what has been observed in other viviparous cockroaches, as Snodgrass (1952) has noted. For this reason we are re-evaluating oviposition in *D. dytiscoides* in the light of what is now known of oviposition in other viviparous cockroaches.

Hagan (personal communication) had not observed protrusion of the oötheca by *Diploptera dytiscoides*, in the field or in rearing cages. Other entomologists in Hawaii whom he questioned had not observed this species with the oötheca extruded. Apparently Hagan based his account of oviposition in *D. dytiscoides* on an interpretation of the anatomical relationships in dissected specimens. *D. dytiscoides* is a small insect three-quarters inch in length (Hagan, 1941); the eggs it produces are also small, being 1.20 mm. long and 0.43 mm. in the greatest dorsoventral dimension (Hagan, 1951). As only 12 oöcytes are usually matured at one time, the oötheca is very short, with a computed length of about 3 mm. Possibly the posterior end of the forming oötheca does not protrude far enough from the oöthecal cavity to be easily seen. As the complete process of formation and retraction can be very rapid with much larger oöthecae containing many more eggs (e.g., *Pycnoscelus surinamensis*, *Nauphoeta cinerea*, above), the transfer of the egg case by *D. dytiscoides* into the brood sac might pass unnoticed by anyone not specifically looking for it.

It is difficult for us to visualize the formation of the oötheca of *D. dytiscoides* during a direct passage of the eggs from the oviducts



into the brood sac. The oötheca of this species is apparently comparable to those of *Pycnoscelus surinamensis*, *Blaberus craniifer*, *Nauphoeta cinerea*, and *Leucophaea maderae*, except that it may possibly be less extensive than those of the first two species. The delicate oötheca of *D. dytiscoides* encloses the lower ends and sides of the eggs, the micropylar ends remaining free (Hagan, 1951). This is very similar to the condition that we have found in *N. cinerea*, in which, at times, the oötheca seems to be merely a thin film of varnish applied over the sides of the eggs. There are other close similarities between the oötheca of *D. dytiscoides* and the oöthecae of other viviparous cockroaches. For example, the eggs are disposed in the oötheca in two parallel rows, the eggs of one row fitting opposite the intervals in the other row; the ventral surfaces of the eggs in one row face the venters of the eggs in the opposite row; and at the ends of the oötheca the first and last eggs lie in the midline (Hagan, 1951). These features of the oötheca of *D. dytiscoides* apply to blattid oöthecae in general; hence we would expect the mode of formation of the oötheca in this species to be similar to what has been found in other viviparous cockroaches.

Probably the oötheca of *Diploptera dytiscoides* is formed around the eggs as they are aligned in a double row in the oöthecal cavity with their axes vertical, as has been observed in other species of cockroaches. Then, after the last egg is deposited, the female presumably rotates the oötheca and retracts it into her brood sac with the last-laid eggs coming to lie in the anterior end of the brood sac. This procedure would place the oötheca in the brood sac with the axes of the eggs rotated 90° to the left as Hagan (1951) found in his specimens. Until direct observation proves the above interpretation to be wrong, it seems logical to identify oviposition in *D. dytiscoides* with that in other viviparous cockroaches.

#### VARIATION IN OVIPOSITION

Wood-Mason (1878) suggested that the habit of certain species of blattids of carrying the oötheca for a week or more before deposition represents the retention of a vestige of a lost viviparity. However, Shelford (1909, 1912) believed that the method of depositing eggs in an oötheca onto a substrate is probably a more primitive behavior than incubating the eggs in a brood sac. Not only have fossil oöthecae been found, but also fossil cockroaches which possessed elongated ovipositors, indicating that during the Permo-Carboniferous period there were two categories of cockroaches; the more primitive had a

long external ovipositor and laid eggs not united in an oötheca; the other had a much reduced internal ovipositor and made oöthecae like recent blattids (Laurentiaux, 1951).

Various adaptations of oviposition behavior and oöthecal structure serve to some extent to protect the cockroach eggs. Two general methods of protection have evolved; the eggs are either retained within the mother as long as possible, or the eggs are surrounded by a hard cover (Shelford, 1912). The method of incubating the eggs in a brood sac within the mother possibly affords greater protection to the species than does the deposition of a hardened oötheca; certainly the danger from insect parasites of the eggs would be largely eliminated in this way. Sells (1842) reported that an oötheca of *Blaberus maderae* [= *Leucophaea maderae*], which he received from Jamaica, contained 96 specimens of a small chalcid wasp; some oöthecae had a round hole through the side of the capsule from which the wasps had emerged. His statement that the oötheca had a keel with 16 dentations indicates that he was dealing with an oviparous species rather than a specimen of *L. maderae*. Bordage (1896) was undoubtedly incorrect in stating that *Blatta maderae* [= *L. maderae*] was a host of the egg parasite *Evania desjardinsii* [= *E. appendigaster*], because the oötheca is protected from the parasite within the body of the cockroach.

However, the egg-laying rate is decreased among viviparous species because the female cannot produce more egg cases during the gestation period, which usually takes more than a month. During embryonic development the offspring of viviparous species are subject to the vicissitudes that beset the mother. As we have shown, premature death of the mother may release the embryos from her brood sac. However, if the female were killed before the embryos had developed sufficiently to maintain themselves without the protection of the brood sac, the eggs would die with her.

The admitted success of the common oviparous cockroaches, in establishing themselves in practically every man-made niche, may in part stem from the ability of the embryo to develop independently of the female. Coupled with this are an increased egg-laying rate and the ease with which egg cases may accidentally be transported far beyond the territory occupied by the mother. These factors may offset any apparent advantage gained by viviparous cockroaches through internal incubation of their eggs.

Shelford (1906) grouped several genera and species of cockroaches according to whether the oöthecal membrane is complete or incomplete. Hagan (1951) has suggested that an almost complete series of

cockroaches is available to illustrate a tendency toward the elimination of the blattid oötheca: "The list could start with species dropping the oötheca early, followed by species retaining a protruded oötheca until shortly before hatching occurs. Then there are species with internally retained oötheca [sic] with varying degrees of fragility to *Diploptera* whose oötheca is most delicate and imperfect, and finally ending with species which are said to secrete none at all" (Imms, 1925).

We have arranged the types of oviposition behavior found in cockroaches in a similar series to show a progressive tendency toward retention of the eggs within the body of the female until hatching. We, like Hagan, do not imply that this is an evolutionary series, but it serves to summarize what is known about blattid oviposition.

Ancestral types:

- (1) Cockroaches with long ovipositors that presumably deposited single (?) eggs not enclosed in an oötheca.
- (2) Cockroaches that deposited eggs enclosed in an oötheca.

Present-day cockroaches:

- (1) Oötheca extruded, not rotated, carried by female for only a short time, then deposited and abandoned. (*Priplaneta americana*, *Blatta orientalis*, *Eurycotis floridana*, *Supella supellectilium*.)
- (2) Oötheca extruded, rotated, carried by female for a longer period than in first category, but eventually deposited a long time before hatching. (*Ectobius panzeri*.)
- (3) Oötheca extruded, rotated, carried by female until, or shortly before, hatching. (*Blattella germanica*, *Blattella vaga*, *Blattella humbertiana*.)
- (4) Oötheca extruded, rotated, and retracted into the brood sac where the embryos develop until, or shortly before, hatching. (*Nauphoeta cinerea*, *Pycnoscelus surinamensis*, *Leucophaea maderae*, *Blaberus craniifer*, *Gromphadorhina laevigata*.)
- (5) Oötheca possibly not extruded (see p. 33); eggs possibly directed from oviduct into brood sac where they remain until hatching (*Diploptera dytisoides*.)

Coincident with the retention of the eggs within the body of the female is a reduction in the hardness, thickness, and extent of the walls of the oötheca. In *Blattella germanica* the walls of the oötheca are relatively thin, and premature dropping of the egg case may be detrimental to hatching, undoubtedly because of desiccation. Parker and Campbell (1940) found that, although there may be a reduction in hatching, some eggs in shriveled oöthecae that had been removed from the female did hatch. One such egg case hatched 24 days after removal from the female. These workers found 36 percent complete and 29 percent partial hatching of detached oöthecae, kept under

laboratory conditions, compared to 70 percent complete and 3 percent partial hatching in the controls.

On the other hand, the eggs of ovoviviparous cockroaches apparently never hatch if the oötheca is expelled from the brood sac before the embryos are well developed. The oöthecae of these species are less well developed than in *Blattella germanica*. Not only is the wall of the oötheca thinner, but in several genera the oötheca is incomplete, being absent along the anterior ends of the eggs. We have found that at a very low humidity the eggs (in the oötheca) of *Pycnoscelus surinamensis* and *Nauphoeta cinerea* lost water much more rapidly than the eggs of *B. germanica*, which in turn lost water more rapidly than the eggs of *Periplaneta americana*.

We have noticed that in the laboratory *Cariblatta lutea minima* invariably deposited its oöthecae on the cotton stoppers of water vials. The only eggs that hatched were from oöthecae left on the moist cotton; eggs in oöthecae removed from the cotton and placed in dry vials did not hatch.

#### EGG PARASITES

This, then, is reproduction in cockroaches; with the oviparous forms sexual behavior of the female culminates with the deposition of the oöthecae. But her entire effort to perpetuate the species may have been in vain, for in spite of a hard oötheca which presumably protects the eggs, the eggs may be destroyed by various parasites. The Diptera parasitic on cockroach eggs are *Coenosia basalis* Stein and *Megaselia* sp. Edmunds (1952) reared these flies from two different oöthecae of *Parcoblatta* species.

In searching the literature we have found about 25 species, in about 15 genera, of hymenopterous parasites of cockroach eggs. For example, *Tetrastichus hagenowii* (Ratz.) is a parasitic wasp which has been reared from the oöthecae of several species of cockroaches. This small wasp pierces the oötheca with her ovipositor (pl. 9, fig. 67) and deposits her eggs in the eggs of the cockroach. The wasp deposits over half her eggs during the first 2 days after emergence (Roth and Willis, 1954b). Development (pl. 9, fig. 68) is completed in from 23 to 57 days at about 30° C. or higher. Developmental time is a function of the size of the parasite brood. The smaller the brood the longer the wasps take to complete development. If sufficiently numerous, the wasp larvae destroy all the cockroach eggs (pl. 9, fig. 71). With an average of 48 wasps per oötheca all the cockroach eggs are eaten. With an average of 18 wasps per oötheca not all the cockroach eggs are



eaten, but the uneaten eggs fail to hatch. When there is an average of only eight wasps per oötheca, about eight cockroaches complete development and hatch. Eventually the larvae pupate (pl. 9, fig. 69), metamorphose into adults, and emerge from a hole chewed through the side of the egg case (pl. 9, fig. 70). The wasps mate immediately and the females soon seek out other oöthecae and parasitize the eggs.

The evaniids or "ensign flies" are another group of parasites that destroy cockroach eggs; however, in contrast to other cockroach-egg parasites, only one evaniid develops within each oötheca, the single parasite larva destroying all the eggs. These wasps (pl. 10, figs. 72, 73) are frequently seen at windows, indicators of otherwise well-hidden cockroach infestations (Edmunds, 1953).

#### SUMMARY

The reproductive behavior of most of the more than 3,500 species of cockroaches is still unknown. Less than half a dozen species have been studied intensively, and it is from these, the species most closely associated with man, that most of our knowledge of the behavior of the group comes. Enough additional information now exists, on some of the less common forms, to enable us to summarize the reproduction of cockroaches of quite dissimilar habits.

*Courtship.*—Male cockroaches prior to copulation engage in several kinds of activity or display. In *Periplaneta americana* this is a response to an odor from the female; in *Blattella germanica* it is a response to a chemical substance on the body of the female which the male detects by antennal contact. Among species in which the males are alate, the male raises his wings, still folded and crossed, exposing the dorsal surface of his abdomen. This activity is probably general throughout the group; it has been seen in several genera: *Blatta*, *Blattella*, *Periplaneta*, *Supella*, *Blaberus*, *Leucophaea*, and *Nauphoeta*. Males of certain species perform characteristic body movements during courtship. In *Leucophaea maderae* the male moves his body rapidly up and down against the substrate producing a tapping sound. The male of *Blaberus craniifer* butts the female with his head and his abdomen trembles. The male of *Eurycotis floridana* vibrates his body from side to side and extends it posteriorly.

In response to the male's display the females of many species apply their mouthparts to the male's dorsum; starting near the anal end of his abdomen the female gradually works forward, apparently feeding on a secretion on the surface of the abdomen, until she is astride the male. This activity has been observed in these genera: *Blatta*, *Blat-*



tella, *Blaberus*, *Ectobius*, *Supella*, *Eurycotis*, and *Nauphoeta*. The males of many genera have specialized tergal glands which secrete the substance attractive to the female.

*Copulation*.—When the female is astride the male, he pushes his abdomen farther backward until he can make genital contact with her. The male grasps the female with the aid of the hooked left phallomere and moves out from under her. The cockroaches complete copulation in the opposed position with their heads in opposite directions. This final act of copulation has been seen in *Blatta*, *Blattella*, *Parcoblatta*, *Periplaneta*, *Eurycotis*, *Leucophaea*, *Nauphoeta*, *Polyzosteria*, *Supella*, and *Blaberus*.

*Fertilization*.—Sperm transfer from male to female is accomplished by means of a spermatophore which is elaborated by the male accessory glands. The spermatophore is only formed during copulation, and after it is transferred to the female the sperm migrate from the spermatophore into the spermathecae of the female. Within a day or longer the dry, shrunken, empty spermatophore drops from the female's genital cavity. Spermatophore formation has been seen in *Blatta*, *Blattella*, *Periplaneta*, *Nauphoeta*, *Leucophaea*, *Eurycotis*, and *Blaberus*.

As each egg passes out of the oviduct into the genital chamber of the female, sperm are forced out of the spermatheca against the micropylar end of the egg. The eggs are fertilized as they pass along the vestibulum.

*Parthenogenesis*.—Parthenogenesis can occur among several species of cockroaches. It occurs regularly in *Pycnoscelus surinamensis* in North America and Europe. We have found some parthenogenesis in *Supella*, *Blattella*, *Periplaneta*, and *Blatta*. Unfertilized eggs of only *Blatta orientalis* and *Periplaneta americana* hatched normally.

*The oötheca*.—The eggs of all cockroaches, so far as we know, are invested with a covering, the oötheca. This may be hard and protective as in *Periplaneta*, *Blatta*, *Eurycotis*, *Blattella*, *Parcoblatta*, *Cariblattella*, *Ectobius*, *Supella*, and others, or the oötheca may be reduced in thickness and/or enclose only part of the eggs as in *Blaberus*, *Leucophaea*, *Nauphoeta*, *Pycnoscelus*, *Diploptera*, and others. Reduction of the oötheca is associated with viviparity; hard protective oöthecae are characteristic of oviparous forms.

The oötheca of *Blatta orientalis*, and presumably of other species, is formed from a protein, a phenol, and an oxidase secreted by the colleterial glands. This material stretches around the eggs as they are erected in a double row in the forming oötheca. In oviparous species the dorsal edge of the oötheca is modified into a series of respiratory

chambers, usually one per egg, which admit air to the developing embryo.

*Oviposition and hatching.*—The oöthecae of some oviparous forms are not rotated but are carried for a few days or less until the female drops them (e.g., *Blatta*, *Periplaneta*, *Eurycotis*, *Cariblatta*, *Supella*). Some of these cockroaches cement the oötheca to the substrate and cover it with debris. Other oviparous cockroaches rotate the completed oötheca and retain the proximal end between the plates of the genital chamber for some time before deposition (e.g., *Ectobius panzeri*), or retain the egg case until or shortly before the eggs hatch (e.g., *Blattella*).

Nymphs hatch from the eggs of oviparous cockroaches by a concerted swallowing of air, thereby increasing their bulk which spreads apart the dorsal seam of the oötheca. At hatching each nymph is invested with a membrane which it sheds while emerging from, or when free of, the oötheca.

Viviparous cockroaches, which incubate their eggs in a brood sac within the mother's body, extrude the oötheca as it is formed around the eggs. However, in contrast to the oviparous forms, the viviparous cockroaches retract the completely formed egg case into a brood sac, where it remains until, or shortly before, hatching (e.g., *Pycnoscelus*, *Nauphoeta*, *Leucophaea*, *Gromphadorhina*, *Blaberus*). Hatching of the eggs of viviparous cockroaches apparently may occur either within the vestibulum, while the oötheca is being extruded, or shortly after the oötheca is dropped by the female.

The types of oviposition among cockroaches may be arranged in a series showing a tendency toward retention of the oötheca within the body of the female until hatching: Shortly after extrusion the oötheca may be dropped, sometimes buried or covered, and then abandoned; the egg case may be carried, extending from the female's body, for various periods up to and including hatching; the oötheca may be retracted into a brood sac until or shortly before hatching.

*Egg parasites.*—Although the oötheca of oviparous cockroaches protects the eggs from desiccation, it does not prevent destruction of the eggs by parasites, particularly Hymenoptera. The wasp egg parasites insert their ovipositors through the wall of the oötheca and deposit their eggs in or on the eggs of the cockroach. Frequently the wasp larvae destroy all the cockroach eggs. The eggs of viviparous cockroaches, being protected within the brood sac, are apparently not subject to attack by these parasites.

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PLATES

PLATE I

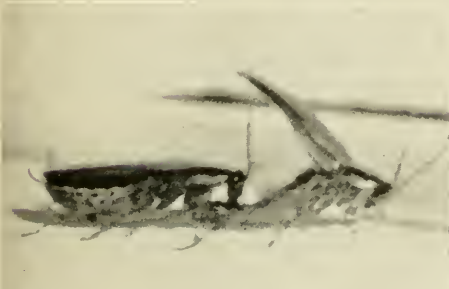
Fig. 1. The male of *Blattella germanica* in a courting position (induced by touching his antennae with the isolated antennae of a female).  $\times 1.8$ .

Fig. 2. The female of *Blattella germanica* feeding on the male's tergal-gland secretion.  $\times 1.8$ .

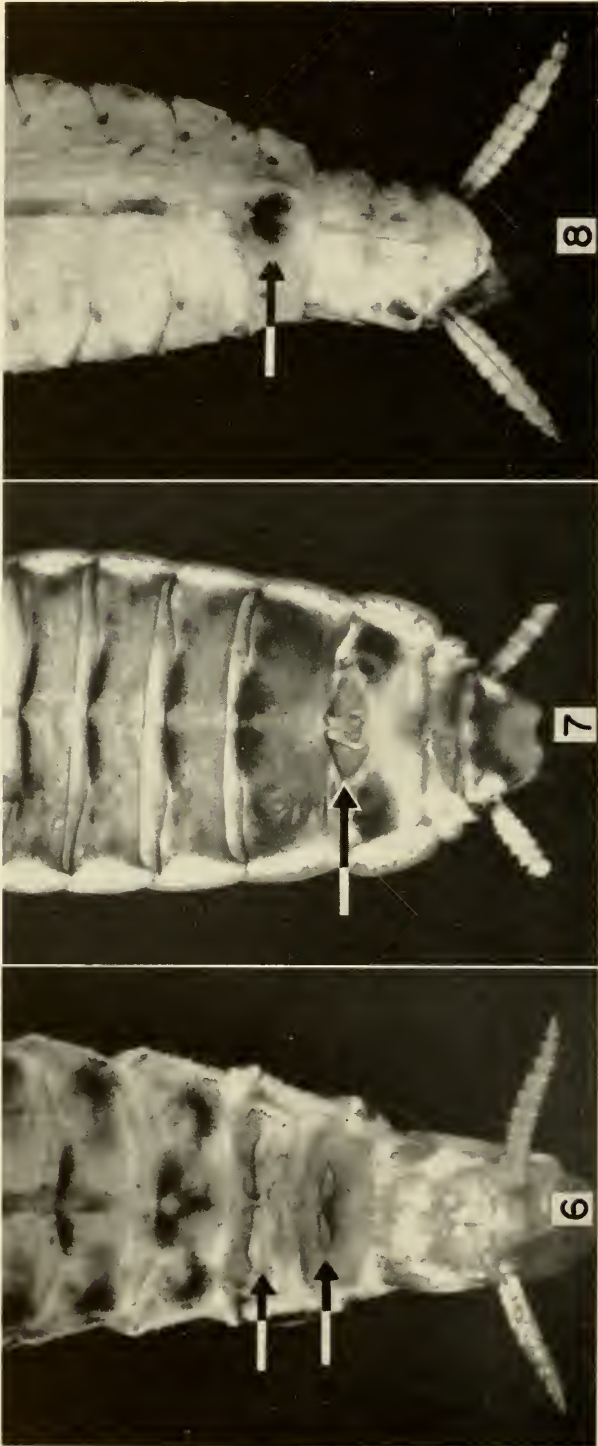
Figs. 3-5. Courting behavior of *Eurycotis floridana*. 3, The male (top) vibrating his body while standing near the female and exposing the intersegmental membrane between his sixth and seventh tergites. 4, The female has commenced feeding on the dorsal surface of the male. 5, The female in working her mouthparts over male's dorsum has nearly placed herself in a position from which male can initiate copulation.  $\times 1.1$ .

(Figures 1 and 2 from Roth and Willis, 1952.)

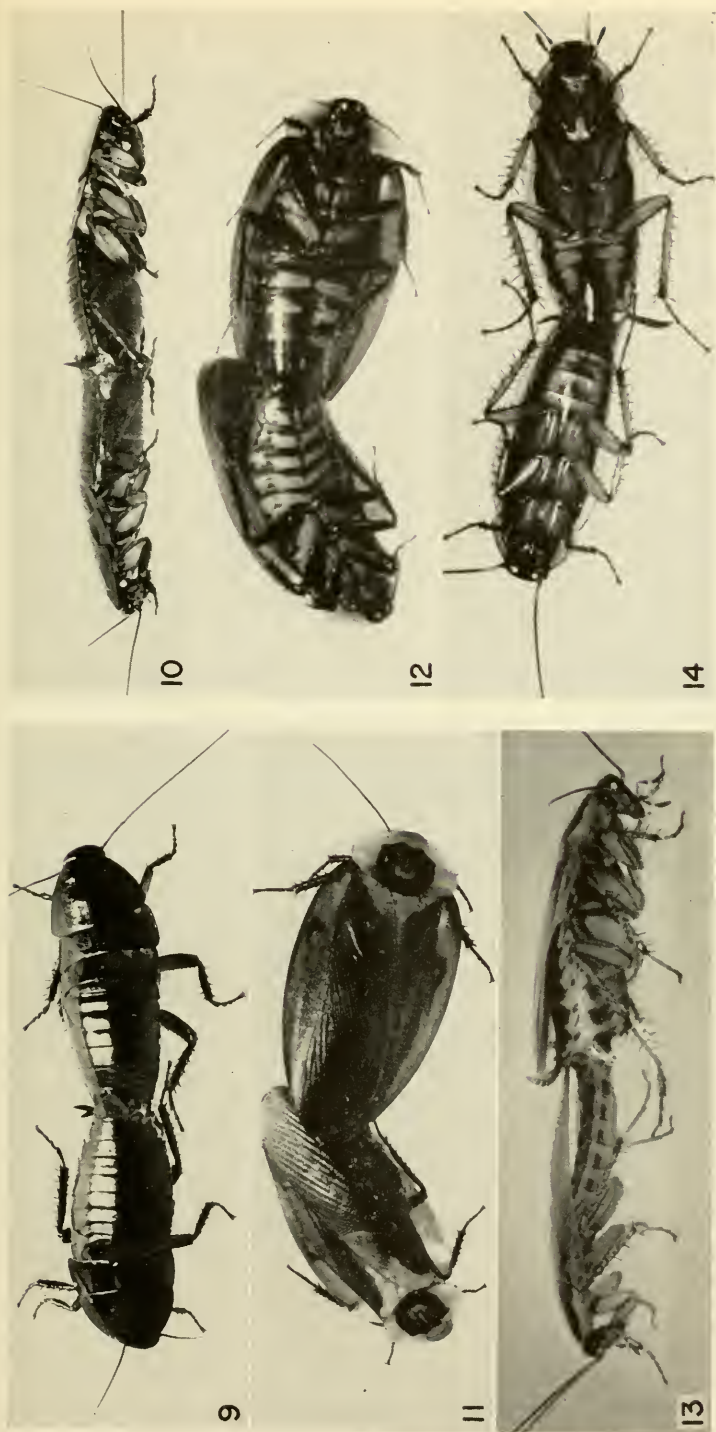




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Figs. 6-8. Dorsal views of portions of the abdomens of three species of male cockroaches showing the characteristic tergal glands (arrows). 6, *Blattella germanica*. 7, *Blattella vaga*. 8, *Supella stipellitium*; notice the brush-like groups of setae. About  $\times 12$ .

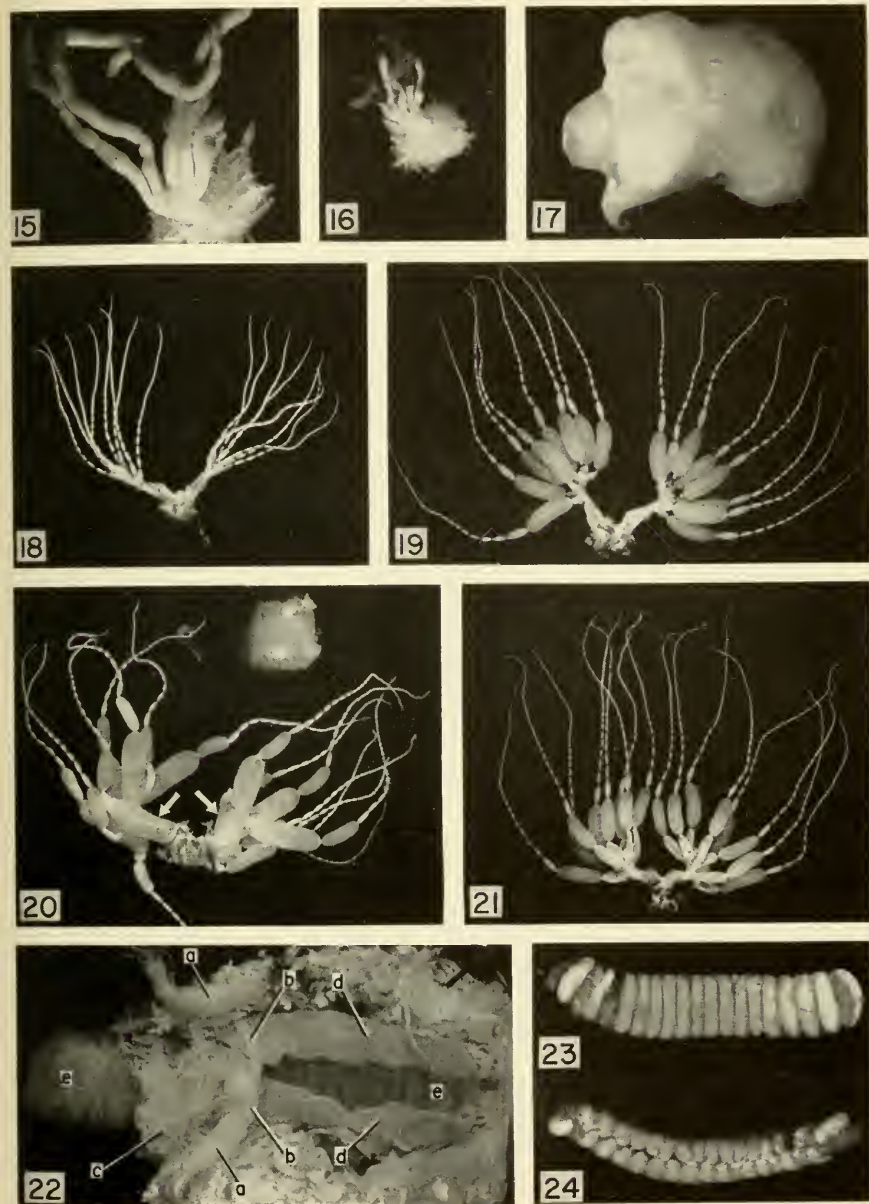


Figs. 9-14. Cockroaches in copula. The male is on the right in figures 9 and 10 but on the left in figures 11-14. 9-10, *Eurycotis floridana*: 9, Dorsal view; 10, lateral view.  $\times 0.9$ . 11-12, *Blaberus crantifer*: 11, Dorsal view; 12, ventral view.  $\times 0.7$ . 13-14, *Blattella vaga*: 13, Lateral view; 14, ventral view.  $\times 3.3$ .

PLATE 4

- Figs. 15-16. Accessory sex glands of male *Blattella germanica*. 15, From a virgin male 37 days old. 16, From a male that copulated 3 hours prior to dissection.  $\times 6.8$ . (From Roth and Willis, 1952.)
- Fig. 17. Spermatophore of *Eurycotis floridana* which was removed from the female just after copulation and kept for 18 hours on moist paper before being photographed.  $\times 3.6$ .
- Figs. 18-21. Ovaries of *Periplaneta americana*. 18, From a newly emerged adult. 19, Shortly before oviposition. 20, During oviposition; eggs are in the oviducts (arrows); the partially formed oötheca (top) was removed during the dissection. 21, Just after formation of an oötheca.  $\times 2.2$ .
- Figs. 22-24. Oötheca of *Blaberus craniifer*. 22, Abdomen of a female dissected to show the large brood sac or uterus which was cut open to reveal the enclosed oötheca; the oötheca was partially extruded by involuntary contractions of the female while she was being dissected: *a*=ovary; *b*=oviduct; *c*=colleterial glands; *d*=uterus or incubation pouch; *e*=oötheca.  $\times 2.1$ . 23-24, Two views of an oötheca removed from the brood sac; the embryos are visible through the thin transparent membrane which forms the oötheca.  $\times 1.2$ .



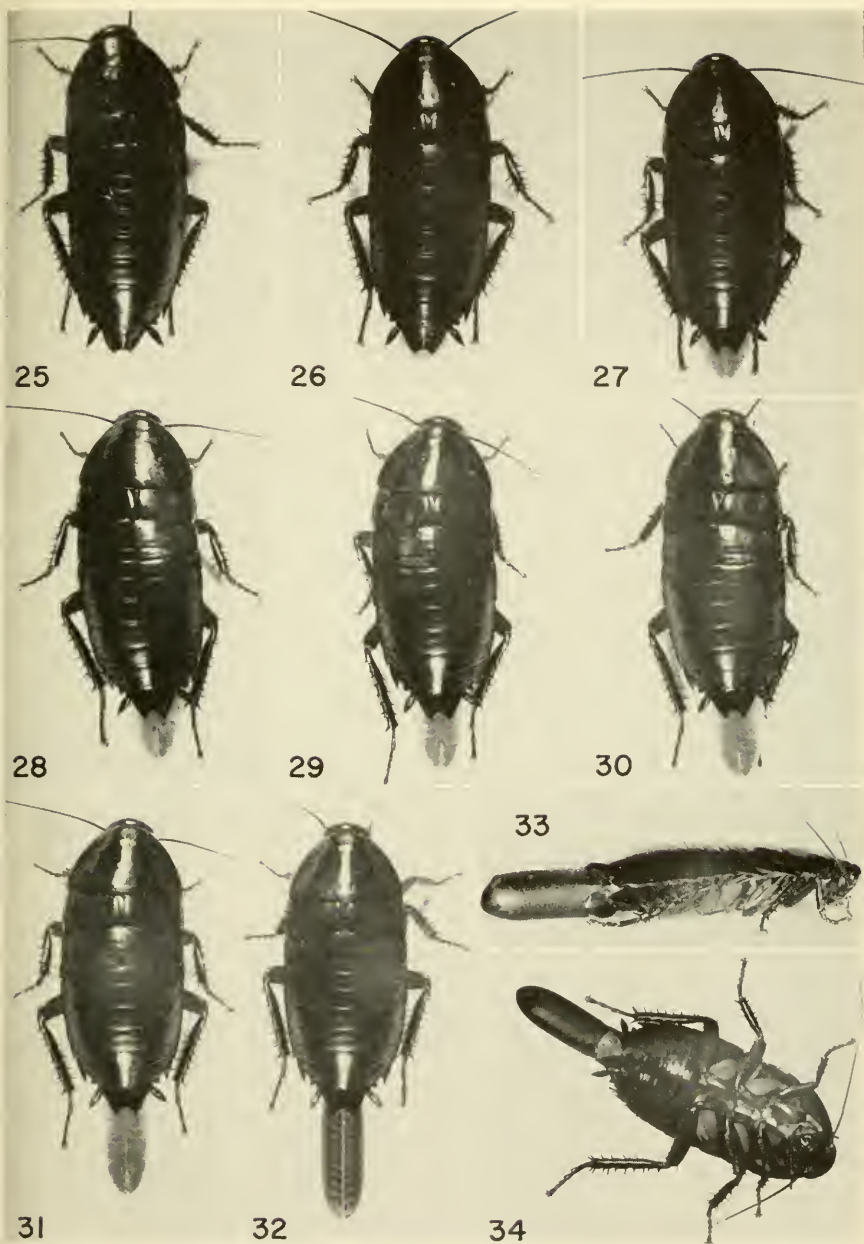


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PLATE 5

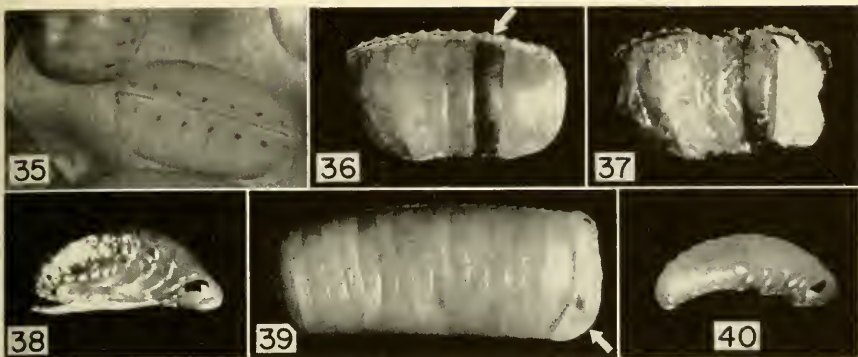
Figs. 25-34. A female of *Eurycotis floridana* in the process of forming an oötheca. Elapsed time during oötheca formation is given in hours (hrs.) and minutes (min.). 25, 0 hrs. (oötheca just beginning to form; the remaining values are taken from this as the starting point.) 26, 1 hr. 30 min. 27, 2 hrs. 20 min. 28, 3 hrs. 5 min. 29, 3 hrs. 40 min. 30, 4 hrs. 10 min. 31, 5 hrs. 10 min. 32, 20 hrs. 22 min. 33-34, 21 hrs. 5 min. (25-32, Dorsal views; 33, lateral view; 34, ventral view). Natural size.



(See opposite page for legend.)

PLATE 6

- Figs. 35-38. *Supella supellectilium*. 35, Normal oötheca (top view) containing well-developed embryos; the black eyes of the embryos show through the walls of the egg case.  $\times 6.1$ . 36, Oötheca containing unfertilized eggs; one (arrow) has developed but, failing to hatch, died and turned dark.  $\times 6.1$ . 37, Oötheca shown in figure 36 with one wall removed to reveal the well-developed embryo.  $\times 6.1$ . 38, Embryo shown in previous two figures removed from the oötheca.  $\times 9$ .
- Figs. 39-40. *Blattella germanica*. 39, Oötheca containing unfertilized eggs one of which has developed (arrow).  $\times 6.1$ . 40, Developed embryo removed from the oötheca.  $\times 9$ .
- Figs. 41-45. A parthenogenetically developed embryo of *Supella supellectilium* which, when dissected out of the oötheca (41), succeeded in shedding (42-45) its embryonic membrane (44, arrow). This individual later developed into an adult female.  $\times 9$ .
- Figs. 46-48. Hatching of a parthenogenetically developed egg of *Periplaneta americana*. The embryonic membrane (47, arrow) was left behind attached to the oötheca. Two embryos were caught between the lips of the keel and failed to hatch.  $\times 7.7$ .

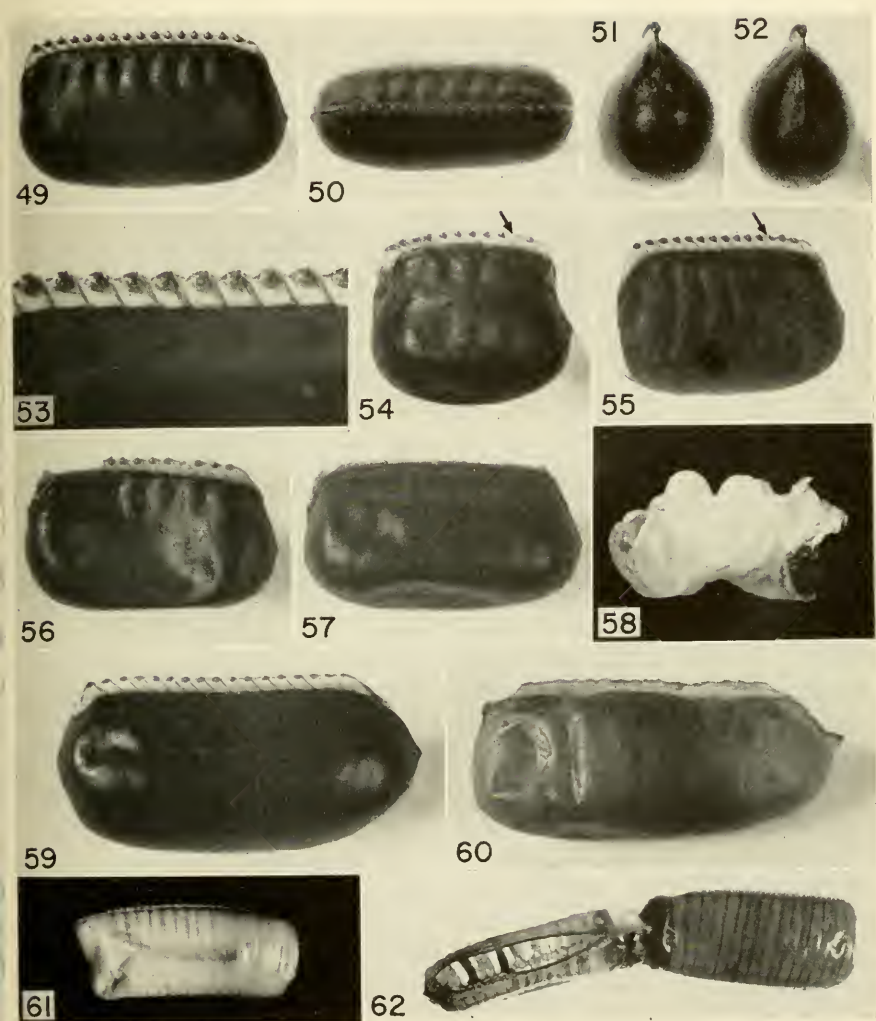


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PLATE 7

- Figs. 49-58. *Periplaneta americana*. 49, Oötheca containing 16 eggs; there are 16 respiratory chambers and ducts in the keel. 50, Dorsal aspect of oötheca. 51, Anterior end of oötheca (portion held in the oöthecal chamber after the egg case is formed). 52, Posterior end of oötheca showing pattern impressed by apical lobes of female's genitalia. 53, Portion of the keel showing some of the ducts and evaginated respiratory chambers ( $\times 11.3$ ). 54, Oötheca which contained seven eggs; there are 10 "teeth" or evaginations in the keel and 11 ducts; the tooth (arrow) of one of the ducts is missing. 55, Oötheca which contained 13 eggs; there are only 13 teeth but 14 ducts, one of the teeth (arrow) being missing. 56-57, Oöthecae in which the keels have been partly (56) and completely (57) eaten by cockroaches. 58, Eggs which were deposited without the formation of an oötheca. All figures except 53 are  $\times 4.5$ .
- Figs. 59-60. *Blatta orientalis*. 59, Normal oötheca. 60, Abnormal egg case which did not harden or develop normal pigmentation; respiratory chambers and ducts were not molded in the keel.
- Figs. 61-62. *Blattella germanica*. 61, Newly formed oötheca that partially collapsed 2 days after it had been removed from the female. 62, Two attached oöthecae; eggs from the egg case on the left have hatched. Notice that the first oötheca rotated to the right; the keel of the second is upward.  $\times 4.5$ .





(See opposite page for legend.)

PLATE 8

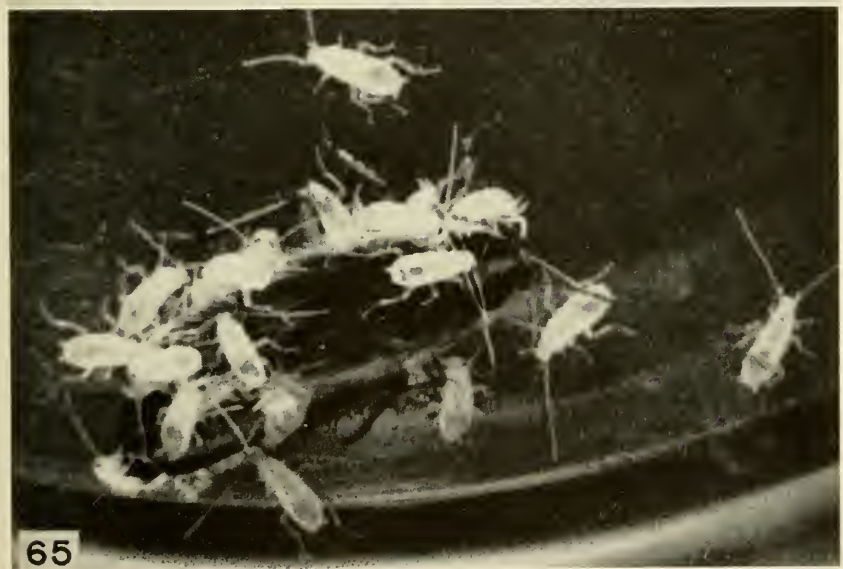
Figs. 63-65. *Blattella vaga*. Dorsal (63) and ventral (64) views of a female carrying an oötheca. The keel is turned toward the female's right.  $\times 5.8$ .  
65. Newly hatched nymphs clustering around and climbing over the female. This female was still carrying the oötheca (keel to the right) at hatching, but dropped it soon after this photograph was taken. The nymphs crawled all over the mother and seemingly fed on the greasy material covering the surface of her body; the female raised her wings and some of the nymphs crawled under them on the dorsal surface of her abdomen.  $\times 5.8$ .



63



64



65

(See opposite page for legend.)

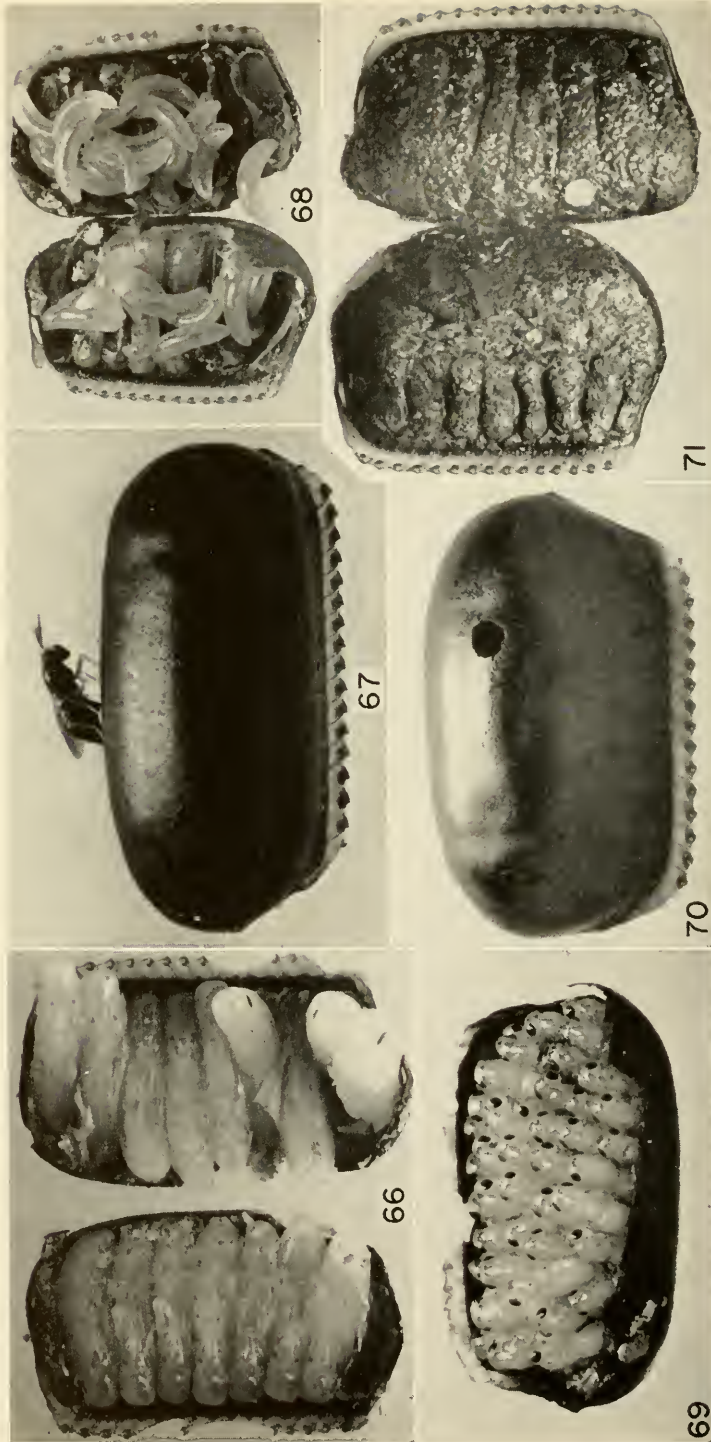
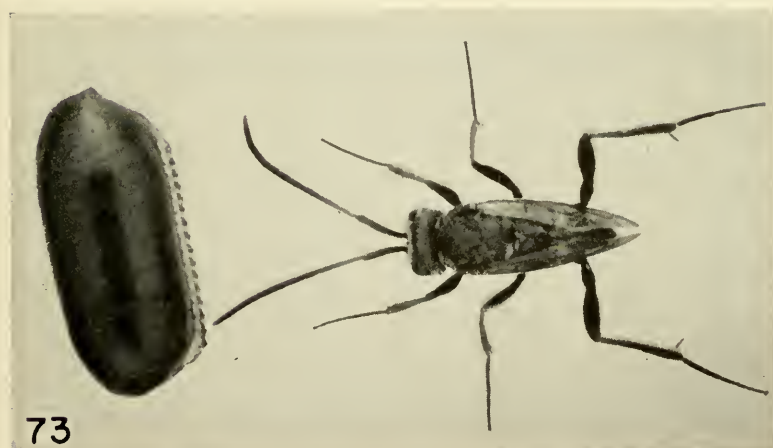


Fig. 66. Oötheca of *Periplaneta americana* cut open to show two rows of well-developed embryos. The respiratory ducts open into the oötheca above the head of each embryo.  $\times 5.8$ . Figs. 67-71. Oöthecae of the American cockroach parasitized by the wasp *Tetrastichus lugenrovi*. 67, Female wasp ovipositing.  $\times 6.9$ . 68-69, Oötheca opened to show wasp larvae (68,  $\times 4.5$ .) and pupae (69,  $\times 6.9$ ). 70, Oötheca showing hole made by the adult wasps in emerging.  $\times 6.9$ . 71, Oötheca (in fig. 70) opened to show complete destruction of the cockroach eggs by the wasps.  $\times 5.8$ .



Figs. 72-73. The evaniid *Prosevania punctata* (Brullé) which parasitizes the eggs of the American and oriental cockroaches. 72, Male with an oötheca of *Periplancta americana*.  $\times 4$ . 73, Female with an oötheca of *Blatta orientalis*.  $\times 3.3$ . Notice the size of these wasps in relation to the oöthecae and compare with figure 67.

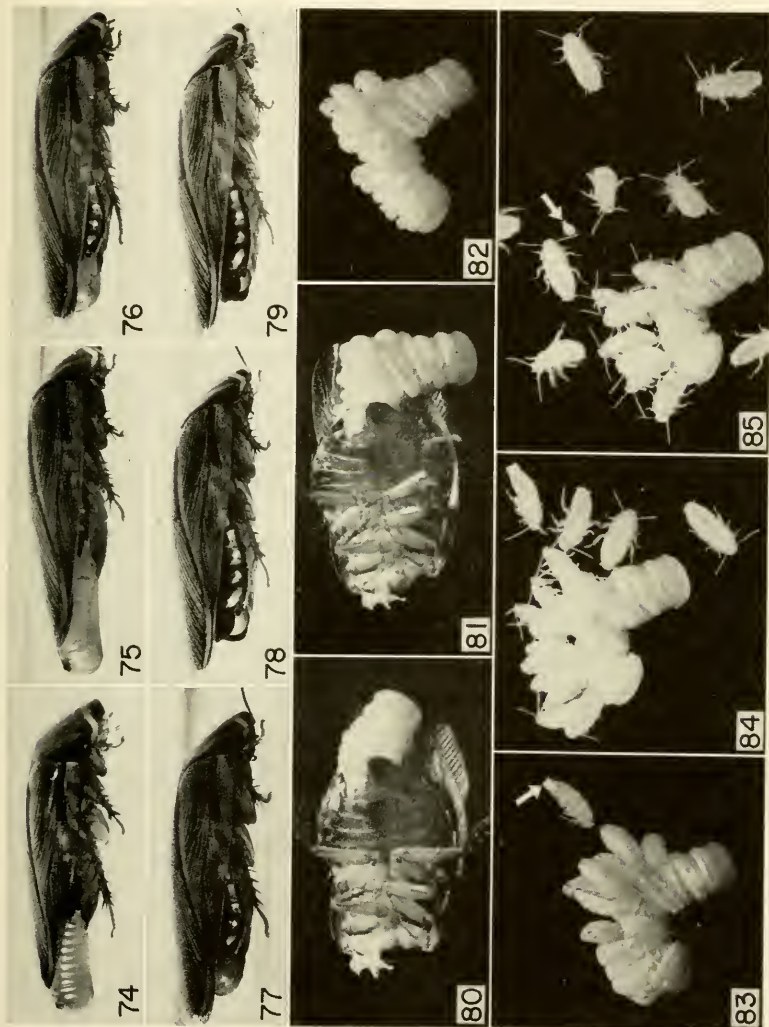


PLATE II

Figs. 74-79. *Pycnoscelus surinamensis* forming and retracting an egg case, August 18, 1953. Notice position of her head with the frons ventrad. 74, 9:30 a.m. The female is forming and simultaneously extruding the egg case; the seam of the egg case is dorsad. 75, 9:45 a.m. Maximum extent to which the female extruded her egg case; about 24 eggs protrude beyond the end of the abdomen. The axes of the eggs are still vertical. 76, 9:55 a. m. Within a period of 10 minutes the female rotated the egg case, seam to her left, and retracted most of it into her brood sac. 77, 10:00 a.m. 78, 10:01 a.m. 79, 10:01+ a.m. The egg case was completely retracted by 10:01.5 a.m., at which time the female raised her head and scurried off. The female was decapitated September 21, 1953, at which time she expelled this egg case. Five nymphs, of 21 that developed, hatched, and there were 11 undeveloped eggs.

Figs. 80-85. Premature expulsion of an egg case by a decapitated female of *Pycnoscelus surinamensis* with concurrent hatching of the eggs. Series of photographs taken within a 5-minute period. 80, In the few seconds that elapsed between decapitating the insect and placing it beneath the camera, the egg case was ejected about half its length. 81, Nymphs began to emerge through the suture along the dorsal edge of the egg case before it had been completely expelled. 82-85, Sequence of hatching of 15 nymphs from the dropped egg case. A few other eggs had developed but the nymphs failed to hatch. The embryonic membrane shed by one of the nymphs is indicated by arrows.

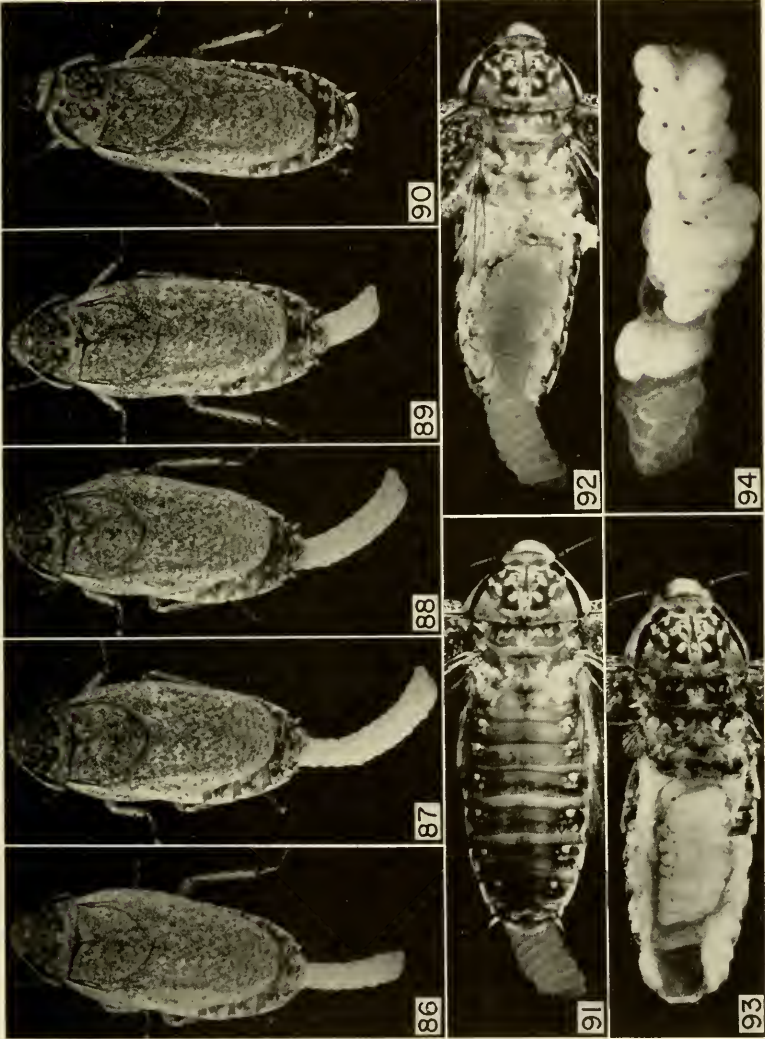
All figures  $\times 1.9$ .



(See opposite page for legend.)

PLATE 12

- Figs. 86-90. *Nauphocta cinerica* forming and retracting an egg case, August 18 and 19, 1953. 86, 1:30 p.m., August 18. The female is forming and extruding the egg case. The cephalic ends of the eggs are dorsad at this time. 87, 2:30 p.m. Maximum extent to which the female extruded her egg case; about 30 eggs are visible beyond end of her abdomen. The egg case curves strongly ventrad, and its distal end twists to the side from contact with the substrate. The axes of the eggs in the proximal end of the oötheca have been tilted slightly to the female's left. 88, 2:45 p.m. The female has retracted part of the egg case. The axes of the eggs now lie in a horizontal plane. 89, 4:40 p.m. Extent of retraction while the insect was under direct observation. 90, 7:25 a.m., August 19. The female had completely retracted the egg case into the brood sac during the night. The female carried this oötheca until September 11, 1953, when she expelled it. Only 10 embryos had developed; about 15 eggs did not develop.  $\times 1.4$ .
- Fig. 91. Female of *Nauphocta cinerica* killed 30 minutes after she had begun to retract the oötheca into her brood sac.  $\times 1.9$ .
- Fig. 92. Dissection of female in figure 91 showing anterior end of oötheca lying in the brood sac which has been cut open.  $\times 1.9$ .
- Fig. 93. Female of *Nauphocta cinerica* dissected 27 days after she had formed an oötheca. The oötheca fills nearly the entire body cavity. Notice the well-developed embryos with dark eyes and mandibles which show through the transparent wall of the oötheca.  $\times 1.9$ .
- Fig. 94. The oötheca in figure 93 removed from the female's brood sac. Notice the two groups of undeveloped eggs at the left.  $\times 3.6$ .



(See opposite page for legend.)