The Evolution of Genitalia and Mating Behavior in Crickets (Gryllidae) and other Orthoptera

BY

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Erratum, page 21, lines 13-16:

For: "As in the other five genera. . ."

Read: "Unlike the other five genera. . ."

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INTRODUCTION

INSECT GENITALIA have been used extensively in taxonomic studies because they are frequently complicated in structure and useful in distinguishing species, as well as in assessing their relationships. Little attention has been paid, however, to the questions of how genitalic differences arise, in terms of selective action, or when, in regard to the speciation process. The opinion has been expressed that they might frequently function as reproductive isolating mechanisms between newly separated species in the manner of "lock-and-key" devices and undergo accelerated and exaggerated divergence in that context (DuFour, 1844; Dobzhansky, 1951). This hypothesis has never been examined thoroughly, but its attractiveness has been diminished by scattered accounts of successful matings between species with different genitalia (Beheim, 1942; Shull, 1946), discovery that genitalic differences are not nearly universal at the species level, and realization of the inefficiency of an isolating mechanism which can come into play only after a sexually responsive pair has come together and proceeded through courtship and the initial phases of a copulatory act (Dobzhansky, 1951; R. D. Alexander, 1962; Alexander and Moore, 1962; Ehrman, 1964).

An understanding of the behavior of insects during copulation, including how they use their genitalia, is with a few exceptions (e.g., Brinck, 1956, 1957; Spielman, 1964, 1966) almost unbelievably rudimentary. Until a few years ago, the act of insemination had not been described clearly for a single member of any of the several orders of primitively wingless insects. Mating behavior is still totally unknown in Symphyla, Protura, and Zoraptera, and in hundreds of families of insects, some containing thousands of species. As an example, only two or three descriptions of copulation have been published for the entire family Carabidae, containing 25,000 species. Yet many ground beetles are large, conspicuous, commonplace insects, and species descriptions and generic revisions within the family frequently utilize genitalic characters almost exclusively (e.g., Valentine, 1932, 1945; Jeannel, 1941; Krekeler, 1958; Barr, 1965).

In view of the paucity of descriptions and comparisons of copulatory actions among insects, it is not surprising that the functions of the genitalic parts have been neglected. This state of affairs seems almost ludicrous: use of genitalic morphology is sufficiently extensive to warrant publication of a "Taxonomists' glossary of genitalia in insects" (Tuxen, 1956), a highly useful publication, but one which also reveals that morphologists and taxonomists have often shown little hesitation in labelling genitalic parts that they have never seen in action with names that ascribe to them quite specific functions.

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Such one-sidedness in our knowledge has led to some predictable mistakes. Thus, the parameres of ground beetles have been described as pries, but in the species studied so far, they remain outside the female's body and may be wholly sensory in function (Jeannel, 1941; Alexander, 1959). The various parts of orthopteran genitalia have been labelled and homologized as if they were derived from tubular intromittent organs, but there evidently has never been such a device in any of the ancestors of the Orthoptera that do not have it today (Alexander, 1964). Cricket genitalia and mating acts have been described as highly derived in comparison with those of other orthopterans (Walker, 1922; Snodgrass, 1937; Richards, 1927), when in many regards they are actually primitive. The proximal intromittent organ of Odonata has been described as a secondary intromittent device, but from all indications there never was a primary one (Brinck, 1962). Female-above mating positions and the particular kinds of genitalia that go along with them have been explained as derivations from male-above positions with intromittent organs (Richards, 1927), and the reverse or something close to it is evidently true in every case (Alexander, 1964).

The only obvious contexts of evolutionary change in genitalic conformation and copulatory actions are: (1) perfection of intraspecific compatibility and (2) perfection of interspecific incompatibility (reproductive isolation). Genitalia and copulation should evolve, in other words, in much the same manner as any communicative system. But various external influences, such as changes in the physical environment, the activities of predators, and other changes in the habitat or range of a species that cause adjustment in its mode of life might indirectly affect the nature of selective action in either of these two contexts. The kinds of detailed comparative studies of structure and function that would allow us to approach these questions still seem to be entirely lacking.

We have been accumulating descriptions of mating behavior in crickets (Gryllidae) and other Orthoptera for several years (R. D. Alexander, 1961, 1962, 1964), and we have also been studying orthopteran genitalia, both for taxonomic purposes and in attempts to understand some of the observed variations in copulatory position, duration, and activity. We are combining these different kinds of information in an effort to describe some of the probable pathways of evolutionary change in these characteristics and to hypothesize the nature and sequence of selective action in several specific cases. The results appear to carry some significance in the understanding of orthopteran phylogeny and the role of speciation and other events in shaping morphological and behavioral characteristics of crickets and their relatives.

COMPONENTS OF SEXUAL BEHAVIOR

Sexual behavior can be divided into the following general categories: (1) pair formation; (2) courtship; (3) copulation; (4) post-copulatory or inter-copulatory behavior.

The focus of our attention in this paper is on the act of copulation itself, but our goal is not only to correlate evolutionary changes in genitalia with changes in the copulatory act, but also to discover relationships with other changes in any and all aspects of the reproductive sequence. With regard to copulation itself, we have found it necessary to examine variations and correlations in: (1) positions assumed during courtship; (2) actions or movements during courtship; (3) manner of coupling; (4) positions assumed during copulation; (5) actions or movements during copulation; (6) duration of copulation; (7) numbers and rates of repetition of copulatory acts per session or meeting of a pair; (8) positions assumed between copulations; and (9) actions or movements between copulations.

These events vary considerably. When insemination is accomplished with a spermatophore, for example, copulation may terminate either before or after insemination begins. In some arthropods, spermatophores are transferred without coupling, or even with no contact at all between sexual partners (Schaller, 1954; Lipovsky, Byers and Kardos, 1957; A. J. Alexander, 1962). The function of copulation is insemination, but selection can operate in diverse ways to increase the likelihood that females will be inseminated maximally, or that males will inseminate the maximum number of females (or, more specifically, fertilize the most eggs likely to result in reproductively successful individuals). Presumably, changes in any of the nine events listed above could affect the reproductive success of males and females.

THE GENERAL NATURE OF COPULATION IN ARTHROPODS

All terrestrial and secondarily aquatic arthropods have internal fertilization. All apterygote insects transfer spermatophores indirectly without copulatory acts, except for the indirect, "near-coupling" of Thysanura (Stürm, 1952). All pterygote insects except Odonata copulate directly, all Odonata indirectly. Direct copulation refers to apposition of the primary genital openings near the tips of the abdomens; indirect copulation refers to transfer of sperm or spermatophores by male devices, other than appendages developed in the vicinity of the primary genital openings, during some kind of coupling or joining of male and female. Odonata males transfer sperm (or spermatophores) to an apparatus on the second and third abdominal sternites and inseminate the female with this device; some other arthropods use various legs, or perhaps even mouthparts or antennae, to inseminate the female (see references cited by Alexander, 1964).

In most holometabolous insects, insemination of the female is accomplished via an intromittent device (aedeagus) in a copulatory act during which the male mounts the female, placing his venter next to her dorsum. In hemimetabolous insects, spermatophores are more in evidence, intromittent devices are less elaborate, and copulatory positions are generally more variable, frequently involving the female mounting on the male's back or the pair standing side-to-side or end-to-end. In hemimetabolous insects in which the male mounts the female, coupling is more frequently effected by the male placing the dorsal tip of his abdomen next to the ventral tip of the female's abdomen.

COPULATION IN ORTHOPTERA

Evidently, insemination in Orthoptera is always accomplished by means of a spermatophore inserted, attached, or simply held to the female's genital opening by the male. As a consequence, variations of structure and function in the spermatophore must be studied along with variations in genitalia and behavior. In Blattodea, Mantodea, Phasmodea, and some Ensifera (a few Gryllacrididae), as well as Dermaptera, Isoptera, Embioptera, and probably Grylloblattodea, the spermatophore is inserted more or less completely inside the female's body. In all Gryllidae and Tettigoniidae, and some Gryllacrididae, the spermatophore is more elaborate and its ampulla either (1) hangs outside the female's body (even though the tube leading into the female may be quite long, reaching far up the spermathecal tube) or (2) is retained by the male during copulation, its tube being inserted into the female's genital opening and held in place by the male during insemination (some Gryllidae). The studies of Boldyrev (1929) and Gregory (1965) indicate that copulation in Caelifera (grasshoppers) is similar in many ways to that of crickets in the second category above. We shall have more to say about this comparison, and the probable morphological homologies involved.

Even within the Orthoptera there is a general relationship between male-above copulatory positions, presence of a definite intromittent device, and simple (degenerate?) spermatophores (Mantodea, Phasmodea, Caelifera, Embioptera). Likewise, female-above copulatory positions are restricted to species with fairly elaborate spermatophores and little or nothing in the way of intromittent organs (most Ensifera). End-to-end, side-to-side, and combinations of positions are associated with various kinds of spermatophores and intromittent or transfer devices in Ensifera, Blattodea, and Dermaptera. Copulatory behavior is incompletely known in Isoptera and Grylloblattodea.

Spermatophores that function as transfer devices thus seem generally to be primitive in Pterygota, and intromittent devices developed at the tip

of the male's abdomen—even those used merely to insert the long neck of a specialized spermatophore—are probably all derived. The universality of copulation in pterygote insects suggests that direct copulation may have evolved but once, though the Odonata offer an intriguing complication to this picture. At any rate, it would seem that the orthopteroid ancestor must have copulated directly, employed a fairly simple spermatophore, and possessed little or nothing in the way of an intromittent device. This combination of characteristics occurs today only in insects which copulate female-above, side-to-side, or end-to-end, suggesting that one of these positions or some combination of them characterized the orthopteroid ancestor. Further, all orthopteroid side-to-side positions involve the male reaching under the female's abdomen and most end-to-end positions are achieved after starting in a female-above position, suggesting that the common orthopteroid ancestor copulated either with the female on the male's back or with the male backing sideways under the female so that at least the tips of their abdomens were in a "female-above" position (Fig. 11). Alexander and Brown (1963) have suggested that such a copulatory position is primitive for all pterygote insects and that there may be a relationship with the evolution of wing precursors and courtship, since glands and other female-attracting devices are almost universal on the dorsal surfaces of male insects in which the female climbs on the male's back during copulation.

PREVIOUS STUDIES

The studies of Walker (1922), Snodgrass (1937), Quadri (1940), Chopard (1938, 1951b), and Randell (1964) represent the major contributions to understanding of the morphology of orthopteran genitalia. Baumgartner (1911), Gerhardt (1913, 1914), Boldyrev (1915, 1927a, 1927b, 1928a, 1928b, 1929), Turner (1916), Fulton (1915, 1931), Spann (1934), Chopard (1951a), and Gabbutt (1959) added to knowledge of mating behavior and genitalic function in various Saltatoria. Otherwise only scattered papers exist, usually dealing with some aspect of mating behavior or the use of genitalic structure in taxonomy: most are cited by Baumgartner (1911), Spann (1934), R. D. Alexander (1962, 1964), Alexander and Brown (1963), and Randell (1964). Attempts to correlate structure and function and arrive at homologies on a broad scale, either within the Saltatoria or for orthopteroid insects in general, are almost non-existent.

With this general introduction we pass directly to a group-by-group description of the details of copulatory actions and genitalic parts and their functions. Following presentation of these data, and in some cases along with their presentation, we take up the questions of correlated combinations

of characters, evolutionary sequences, phylogenetic relations, and the probable nature of selective action under different circumstances.

GROUPS STUDIED

Following is a list of the species utilized for this study. Species marked with an asterisk were studied by us. Other sources of information are indicated by references in parentheses following indication of the general distribution of the species. In addition, we have utilized all the published information we could find on the courtship and copulation of all other orthopteroid insects; references are cited where this information is considered in the discussions. In particular, Otte has studied mating behavior of numerous species of Caelifera (grasshoppers).

FAMILY GRYLLIDAE

Subfamily Gryllinae
- *Acheta domesticus* (Linnaeus), Asia, now cosmopolitan (Khalifa, 1949, 1950).
- *Gryllus pennsylvanicus* Burmeister, N. America.
- *Gryllus veletis* (Alexander and Bigelow), N. America.
- *Gryllus firmus* Scudder, E. North America.
- *Gryllus bermudiensis* Caudell, Bermuda.
- *Gryllus campestris* Linnaeus, Europe (Huber, 1955, 1962; Hörmann-Heck, 1957).
- *Gryllus bimaculatus* De Geer, Europe, Asia, Africa (Huber, 1955, 1962; Hörmann-Heck, 1957).
- *Gryllus assimilis* Fabricius, Jamaica, Florida.
- *Gryllus rubens* Scudder, E. North America.
- *Gryllus integer* Scudder, S. W. North America.
- *Gryllus vernalis* Blatchley, E. North America.
- *Gryllus fultoni* (Alexander), E. North America.
- *Gryllus personatus* Uhler, W. North America.
- *Gryllus vocalis* Scudder, W. North America.
- *Gryllus armatus* Scudder, W. North America.
- *Gryllodes sigillatus* (Walker), Asia, now cosmopolitan.
- *Modicogryllus conspersus* (Schaum), Hawaii.
- *Teleogryllus commodus* (Walker), Australia.
- *Teleogryllus* sp. 1, South Africa.
- *Teleogryllus* sp. 2, South Africa.
- *Valerifictorus micado* Saussure, Japan? (Studied from Alabama specimens).
- *Miogryllus verticalis* Audinet-Serville, E. North America.
- *Discoptila fragosoi* Bolivar, Europe (Boldyrev, 1928b).
- *Gryllomorpha dalmatina* (Ocskay), Europe (Boldyrev, 1927b).
- *Gryllopsis* sp?, South Africa.

Subfamily Nemobiinae
- *Nemobius allardi* Alexander and Thomas, E. North America (Fulton, 1931, under the name *Nemobius fasciatus* De Geer).
- *Nemobius sylvestris* (Bosc.), Europe (Gabbutt, 1959).

Subfamily Brachytrupinae
- *Anurogryllus muticus* De Geer, E. North America.

Subfamily Gryllotalpinae
- *Gryllotalpa gryllotalpa* Linnaeus, Europe, Africa (Boldyrev, 1913).

*Neocurtilla hexadactyla (Perty), E. North America (Baumgartner, 1905).

Subfamily Eneopterinae

*Hapithus agitator Uhler, E. North America.

Orocharis sp., Florida (R. E. Love, pers. comm.).

Tafalisca lurida Walker, Florida (T. J. Walker, pers. comm.).

Subfamily Phalangopsinae

*Amphiacusta sp., Puerto Rico.

Subfamily Oecanthinae

*Oecanthus argentinus Saussure, E. North America.

*Oecanthus californicus Saussure, California.

*Oecanthus fultoni Walker, E. North America (Fulton, 1915, under the name O. niveus De Geer).

*Oecanthus quadripunctatus Beutenmuller, E. North America.

Oecanthus pellucens (Scopoli), Europe (Chopard, 1938).

Subfamily Trigonidiinae

*Cyrtoxipha columbiana Caudell, E. North America (T. J. Walker, pers. comm.).

*Phyllopalpus pulchellus Uhler, E. North America.

Subfamily Mogoplistinae

*Cycloptilum sp., Florida.

Cycloptilum antillarum (Redtenbacher), Florida (Love, 1966).

FAMILY TETTIGONIIDAE

Subfamily Conocephalinae

*Orchelimum gladiator Bruner, E. North America (K. C. Shaw, pers. comm.).

Subfamily Pseudophyllinae

*Pterophylla camellifolia (Fabricius), E. North America.

Subfamily Phaneropterinae

*Amblycorypha oblongifolia (De Geer), E. North America.

Subfamily Copiphorinae

Belocephalus sp., Florida (J. D. Spooner, pers. comm.).

Subfamily Prophalangopsinae

*Cyphoderris monstrosus Uhler, California.

FAMILY GRYLLACRIDIDAE

Subfamily Rhaphidophorinae

*Ceuthophilus guttulosus Walker, E. North America (Eades, 1964).

*Ceuthophilus latens Scudder, North America (Turner, 1916).

Ceuthophilus meridionalis Scudder, North America (T. E. Moore, pers. comm.).

Ceuthophilus utahensis Thomas, W. North America (C. F. Strohecker, pers. comm.).

Ceuthophilus nodulosus Brunner, W. North America (C. F. Strohecker, pers. comm.).

Pachyramma spp., New Zealand (Richards, 1961).

Pristoceuthophilus pacificus (Thomas), California (R. T. Vinopal, pers. comm.).

Pristoceuthophilus sp., California (R. T. Vinopal, pers. comm.).

Tachycines asynamorus Adelung, Japan (introduced into the U.S.), (R. T. Vinopal, pers. comm.).

*Udeopsylla robusta (Haldemann), North America.

Subfamily Gryllacridinae

Brachybaenus sp., South America (T. H. Hubbell, pers. comm.).

DESCRIPTIONS OF MATING BEHAVIOR AND
GENITALIC STRUCTURE

In this section what is known of the mating behavior and the structure and function of the genitalia is described for a representative species from each genus of crickets, this followed by a discussion of available published information as well as that original to this study, on other species in the genus. We have made our descriptions more detailed when no other published information exists for a particular group. Otte made the dissections and drawings, the latter from specimens or spermatophores preserved in alcohol. Behavioral observations were carried out by both of us, nearly all in the laboratory, with detailed notes tape-recorded and later transcribed.

More work has been done on *Acheta domesticus* (Linnaeus) (European house cricket) and various species of *Gryllus* (field crickets) than on any other crickets, and so we have discussed these two genera first, giving for the house cricket a detailed and comprehensive description that can be used as a basis for the comparisons that will follow. For each genus, or species representing a genus, we have included whatever information is necessary to make an adequate comparison with the preceding genera. The main part of the comparative discussion, however, appears at the end of this series of descriptive accounts.

Subfamily Gryllinae
genus *Acheta*

Acheta domesticus (Linnaeus).—Although the house cricket is most commonly found in buildings, compost heaps, garbage, trash, and the like, it also lives "wild" in arid sub-tropical or tropical regions such as southern California, where its burrows and crevices under stones are much like those of some field crickets. Males apparently are able to recognize females upon antennal contact, either by the usual immobility reaction of the female to antennation or, possibly, by some additional chemotactual stimulus received through the antennae. The formation of sexually responsive pairs, as in most crickets, occurs either by accidental contact or by the male calling the female to his burrow, crevice, or perch. Almost immediately upon contact, the males change from the intense chirps of the calling or aggressive sound (produced with the tegmina held at a 30–45° angle above the abdomen, cf. Figs. 6a–d, 7a–c, 9b–e) to a mixture of the pulses from these sounds and the soft, rustling pulses of the courtship sound (produced with the tegmina held just above the abdomen and tilted roof-like, Figs. 6d, 7a). If the female remains immobile, the male slowly turns his body away, continuing to stridulate, and begins to rock gently from side to side as he turns. After turning away, he continually reaches back toward the female with his hind legs and antennae and backs toward her. Upon contact be-

tween his cerci and any part of her body or appendages, he deletes the calling and aggressive kinds of pulses from his stridulations, holds the tegmina only in the lowered courtship position, and produces only the softened courtship pulses, interspersed with a regular, louder "tick." Much of the shuffling noise produced between ticks seems to be caused by the sides of the tegmina striking the sides of the abdomen. Only species of *Acheta, Gryllus, Gryllodes,* and possibly *Modicogryllus,* among those observed, possess this peculiar kind of courtship stridulation.

When the female antennates and palpates the rear extremities of a courting male, he stops stridulating, flattens the tegmina and his body, and backs and extends his abdomen under her, continually whipping his antennae back over his body and against the female as he does so. The female moves forward, in effect mounting upon the flattened male's body (Figs. 1e, 8a–c), and the male inserts the tip of his median epiphallus between the base of her ovipositor and the subgenital plate. She then everts the papilla that surrounds the opening of the spermathecal duct into the genital cavity, and the male grasps this protuberance with his phallic complex (epiphallus and ectoparameres) (Fig. 1d). For this reason we have named this structure the "copulatory papilla."

Up to this time, the spermatophore can be seen lying in the spermatophore mold of the male, just below his epiphallus. Now the spermatophore is lifted slightly and manipulated as the male evidently "threads" its long tube into the spermathecal tube of the female. The structure that some authors have termed the "virga" is used in this process, and we have referred to it here as the "guiding rod." This threading process seems to be completed about 30 seconds later, at which time both individuals become motionless. Within a few seconds the female dismounts and the male turns almost immediately and antennates her. Following copulation the male is aggressive toward male crickets, and maintains contact with the female, regaining it by a rapid searching behavior if it is lost. He may initiate post-copulatory behavior with other females accidentally touched, but cannot maintain it because such females will be unresponsive. During this post-copulatory (or "inter-copulatory") staying-together, the female remains immobile most of the time, especially when she is antennated by the male. While the pair is staying together, the male forms another spermatophore and, shortly after it becomes visible in the spermatophore mold, turns about and begins courtship again. In 20 copulations, Khalifa (1950) found the time from copulation to formation of a new spermatophore by the male to vary between 15 and 65 minutes. Sometime after the male begins courtship again, the female either rubs off the old spermatophore by dragging her abdomen on the ground or bends her body sharply, lowers her head, and chews it off with her mandibles. The interval between copulations is apparently deter-

mined by the male rather than the female, as indicated by more rapid successions of mating by individual females (observed by us in *Gryllus, Miogryllus,* and an African species of *Teleogryllus*) when two males are available.

Alexander (1961) described the various sounds made by *A. domesticus* (and other cricket species) and included audiospectrographs; Khalifa (1949) described many details of its sexual behavior.

The reproductive apparatus of the male house cricket (Fig. 1b) includes two testes, two vasa deferentia leading posteriorly from them, and accessory glands at the junction of the vasa deferentia. From the junction a sperm duct leads posteriorly to two pouch-like folds constituting the mold for the ampulla of the spermatophore (ampulla mold, Fig. 1b). Anterior and dorsal to the ampulla mold is a large compressed cavity (dorsal cavity) which contains the molds for the attachment plate and tube of the spermatophore. These two cavities of the spermatophore mold are separated by a partition, the shape and direction of which correlates with the flexure at the base of the spermatophore neck. The sclerotized guiding rod originates on the dorsal wall of the cavity, is attached to the lateral walls, and extends posteriorly to the epiphallus or beyond it. The groove in the wall of the dorsal cavity, which is the mold for the spermatophore tube, is continuous with a ventral groove in the guiding rod. The median epiphallus and two lateral ectoparameres (phallic complex) are the only sclerotized portions of the male genitalia easily visible on living or undissected specimens.

The spermatophore of the house cricket (Fig. 1c) consists of a bulb-like ampulla, a narrow connecting neck, a flattened attachment plate with variously sculptured wings and hook, and a long whip-like tube or duct. A capsule containing the spermatozoa is located within the ampulla. A duct leads from the capsule through the neck and attachment plate region into the tube, and presumably opens at the end of the tube. Attachment plates are usually symmetrical with respect to the duct. While the spermatophore is still held by the male, its ampulla lies partially enclosed by the ampulla mold; its neck extends across the partition into the dorsal cavity; the plate lies along the ventral, posterior wall of the cavity; and its tube extends along the groove of the dorsal cavity and the guiding rod.

In females, the ovaries filled with eggs occupy most of the abdominal cavity. Lateral oviducts descend from each ovary and join beneath the subgenital plate. The common oviduct opens into the genital chamber near the spermathecal aperture (Fig. 1a). The bases of the two ventral rods of the ovipositor make up the soft lateral walls of the genital chamber. The chamber is enclosed ventrally by the subgenital plate. The papilla of the spermathecal aperture, the "copulatory papilla," is partially sclerotized, and is essentially the only hard structure in the female's genitalia.

During copulation, while the everted copulatory papilla is held by the male's phallic complex, the guiding rod containing the spermatophore tube is inserted into the spermathecal aperture and passes an unknown distance up the spermathecal duct. The anterior hollowed end of the attachment plate and the tapered end of the spermathecal papilla are brought together, and in some matings, though not all, the wings of the attachment plate extend upward on either side of the soft base of the ovipositor and are held firmly in place there by the subgenital plate. The peculiar conformation of the spermatophore tube and attachment plate are thus closely matched, not only by the cavities of the male in which they are formed, but also by the structures of the female into and against which they are fitted during copulation.

In *Acheta domesticus,* as in all species examined during this study, the spermatophore tube does not appear to be long enough to reach the spermatheca. After entering the spermathecal tube the sperm probably migrate. Khalifa (1949) says: "Once the sperm reach the tip of the spermatophore tube they become very active, stimulated most probably by the spermathecal fluid, and carry on the remaining part of the way to the spermatheca apparently by their own movements."

Their movement up the spermathecal tube may be aided by forcible expulsion from the spermatophore tube.

The mechanism whereby sperm are expelled from the spermatophore in Orthoptera has been studied only in the house cricket (Khalifa, 1949). Khalifa states that the ampulla is composed mainly or entirely of protein material. Its layers are (1) a thin, membranous outer layer, (2) a thick, firm, inner layer, (3) an evacuating fluid layer between the outer and inner layers, and (4) an inner membrane which lines the central cavity. The posterior end of the ampulla bears a protuberance, the papilla, which contains the greater part of the evacuating fluid, and also a small "sperm sac," completely isolated from the cavity of the ampulla (visible in Fig. 3d). At the posterior end of the central cavity, there are two pressure bodies, separated from the anterior sperm-containing sector of the chamber by the inner membrane. According to Khalifa, the spermatophore is emptied by an osmotic mechanism in the following manner: The strong inner layer of the ampulla acts as a semipermeable membrane separating two fluids of different osmotic pressure—the evacuating fluid and that of the pressure bodies. When the closure of the tip of the tube is removed (experimentally by, for example, cutting the tube, and in the female evidently by dissolution in the spermathecal duct), and the pressure bodies swell, pressure is exerted on the seminal fluid.

The use of the spermatophore as a transfer device in insemination, and the ease with which spermatophores can be obtained by plucking them

directly from the spermatophore molds of male crickets, caused us to wonder if artificial insemination might not be a useful and easy technique in studies involving hybridization. But the precision and complexity of the inseminating and fertilizing processes have so far thwarted our attempts. We have tried, without success, both insertion of the spermatophore tube into the genital chamber and spreading the contents of a spermatophore on eggs removed from the ovaries. Wigglesworth (1950) notes that in many insects the eggs are so oriented as they pass the spermathecal aperture that the micropyle comes to lie exactly opposite the mouth of the spermathecal aperture, and this seems likely in crickets, for the descending eggs would obviously have to be closely apposed to the spermathecal aperture as they enter the genital chamber. In one *Miogryllus* female dissected during this study, an egg was found halfway protruding into the genital chamber from the common oviduct. In this location it was pressed firmly against the ventral side of the copulatory papilla, and therefore against the opening of the spermathecal tube. Eggs or sperm may also require some sort of activation, in addition to correct positioning of the micropyle, if fertilization is to take place.

Oviposition does not usually occur until after copulation. Distention of the spermatheca may be the stimulus for initiation of oviposition, just as pressure of the spermatophore in the spermatophore mold is evidently a stimulus to the males of some crickets to call and court (Huber, 1955). Roth and Stay (1961) found that in a cockroach, *Diploptera punctata* (Eschscholtz), oöcytes of females that are less than one day adult (the usual mating age in this case) begin development as a direct result of mating and fail to develop if the pair is separated before spermatophore transfer or if the spermatophore is removed sooner than five hours following copulation. These findings emphasize some striking differences between cockroaches and crickets. Cricket females mate only after being adult several days, remove the spermatophore usually a few minutes after copulation, and begin to oviposit within a few minutes after copulation.

INFORMATION ON OTHER SPECIES OF *Acheta.*—Apart from the information presented above and cited from other investigations, all that is known of genitalia and mating behavior in the genus *Acheta* concerns the structure of the male genitalia, principally the hard parts described from specimens for taxonomic purposes. Chopard (1951*b*), in his division of the old genus *Gryllus* into nine genera, utilized male genitalic characters almost exclusively. He placed seven species in the genus *Acheta: domesticus* Linnaeus (type), *chudeaui* Chopard, *hispanicus* Rambur, *canariensis* Chopard, *confalonierii* Capra, *rufopicta* Uvarov, and *pachycephalus* Karsch. He also believed that *Gryllus gossypii* Costa probably belongs in *Acheta*.

With the exception of *domesticus,* now cosmopolitan, all of these species

are African or South European. Ghouri (1961), however, discovered that close relatives of *domesticus*—perhaps even its siblings—occur in Pakistan and India, and that several species of *Acheta* remain to be described there.

The genitalia of all of Chopard's species of *Acheta* (with the possible exception of *gossypii,* which was not pictured) are similar to those of *domesticus* in having at least the semblance of a "half-tubular" epiphallus. The ectoparameres are also similar. This suggests that the male genitalia are used in approximately the same way, grasping the copulatory papilla of the female, as in *domesticus.* Only *hispanicus* deviates significantly, having prominent U-shaped notches in the epiphallus that give this structure the appearance of a three-pronged device, not too dissimilar from that of *Gryllus,* except that the ectoparameres are large as in *domesticus* and other *Acheta.* It is likely that all of these crickets copulate in essentially the same fashion, and there does not seem to be any basis for disagreeing with Chopard's including these species in the genus *Acheta.*

GENUS *Gryllus*

Genitalia and mating behavior are quite similar in all studied members of this widely distributed genus. Compared with *Acheta,* the genitalia of both sexes are small, and the male epiphallus, instead of being a half-tube, is a three-pronged structure. The ectoparameres are also small. The shallow notches on either side of the median part of the epiphallus in *Acheta,* and the deep notches in *A. hispanicus,* seem to correspond to the deep, U-shaped notches which give the *Gryllus* epiphallus its three-pronged appearance.

The guiding rod in *Gryllus* is shorter and straighter than that of *Acheta,* and the dorsal cavity is much smaller (Fig. 2b).

Spermatophores of the species illustrated (Fig. 2c; an unnamed or possibly merely unidentified Mexican species), as well as those of *campestris* (Lespes, 1855) and other species, do not have the extreme flexure between ampulla and attachment plate that occurs in *Acheta,* and the tube is much shorter: these differences could be predicted from the angle of the partition in the spermatophore mold and the size of the dorsal cavity. The attachment plate of the *Gryllus* spermatophore also has several hook-like projections that are absent from the *Acheta* spermatophore. The copulatory papilla is considerably smaller in *Gryllus* (Fig. 2a) than in *Acheta,* corresponding to the smaller male apparatus, and somewhat differently shaped. Otherwise the females of these two genera are quite similar.

Mating seems to be identical in the two genera, beginning and ending in the female-above position, usually lasting about 30 seconds, and repeated as frequently as every 15 minutes (Spann, 1934; Khalifa, 1950; Alexander, 1961). Evidently, the structural differences in the genitalia of these two genera constitute a mechanical barrier to copulation between them. We

have watched numerous attempted copulations between males of *G. penn-sylvanicus* and females of *A. domesticus,* and on one occasion, the reciprocal, a male house cricket with a female field cricket. None succeeded, evidently because repeated attempts failed to connect the genitalic parts.

OTHER SPECIES OF *Gryllus.*—Cousin (1938) provided a good description and illustration of the male and female genitalia of the type species *(G. campestris)* in this genus. Chopard (1951*b*) greatly restricted the old genus *Gryllus,* listing seven species from Europe, Africa, and Asia, and including all of the North and South American species. He suggested that four others belong to this genus. He pictured the genitalia of three American species and six of the seven other species he included. Randell (1964) listed 42 names under this genus, including all of those listed by Chopard. He pictured the male genitalia of *campestris,* and indicated that he had dissected the male genitalia of 15 additional species. Randell did not describe his methods of identifying species, and, if the North American fauna is any indication, the status of many of the specific names listed by Chopard and Randell must remain doubtful until additional biological information is available (Alexander, 1957). But there seems to be no doubt that the specimens examined by these authors are all appropriately included in the genus *Gryllus.*

GENUS *Gryllodes*

The genitalia of the decorated cricket, *Gryllodes sigillatus,* are more similar to those of *A. domesticus* than to those of *Gryllus,* except in size (Fig. 3d-f). The dorsal cavity is large, the partition of the spermatophore mold is nearly vertical, and the guiding rod is intermediate in length, though curved as in *Acheta.* The spermatophore is long, as in *Acheta,* and the flexure of the neck is similar. The spermatophore of *G. sigillatus* has a large fibrous mass (spermatophylax) attached to the ampulla. The phallic complex of *Gryllodes* resembles that of *Acheta,* the basic difference being a "cup-like" effect caused by the shape and position of the ectoparameres.

Female genitalia in *Gryllodes* are similar in size to those of *Gryllus,* although the copulatory papilla is more slender and has a deeper transverse depression ventrally. Mating in *G. sigillatus* is similar to that in *Gryllus* and *Acheta,* except that it lasts from 2 to 3 minutes (7 copulations), and the male does not pull the female's ovipositor sharply downward upon engagement of the genitalia, as in *Gryllus* and *Acheta.* Evidently, the latter difference is correlated with the different shape of the epiphallic complex in *Gryllodes.*

Upon termination of copulation, the female *Gryllodes* turns immediately, removes the spermatophylax with her mouthparts, and eats it. Movements toward spermatophore biting in females of *Gryllus* and *Acheta* immediately following copulation are prevented by the male's antennation. *Gryllodes*

males are definitely less intense in their post-copulatory interaction with the female, suggesting that the spermatophylax carries much of the function of this interaction. This emphasizes the importance of post-copulatory behavior in preventing the female from destroying the spermatophore prior to complete insemination, as contrasted with the effect of keeping the female available for subsequent inseminations. Perhaps the added time of *Gryllodes* in copula, compared with *Gryllus* and *Acheta,* is in some way related to the variation in post-copulatory behavior.

Evidently, neither sexual behavior nor genitalia has been described for any other member of this genus.

GENUS *Modicogryllus*

This genus was studied from a group of specimens collected in Honolulu, Hawaii, and mailed to us alive by Dr. Henry Townes. They evidently belong to *conspersus,* the only species of this genus recorded from Hawaii. No drawings or dissections were made, but one copulation was observed. The courtship stridulation seemed to resemble that of *Acheta, Gryllus,* and *Gryllodes,* the wings being lowered and tilted, and the sound a soft rustling. Copulation lasted three minutes, with the spermatophore evidently attached within one minute. Post-copulatory behavior was similar to that of *Acheta,* and the female made the first motions to dislodge the spermatophore six minutes after copulation, finally removing it 32 minutes after copulation; she began to eat it six minutes later. The male formed another spermatophore 24 minutes after copulation, but copulation was not repeated during 40 more minutes of observation. Nothing else is known of mating behavior in this genus.

GENUS *Teleogryllus*

Males of *Teleogryllus commodus* have an extraordinarily long guiding rod and a correspondingly long spermatophore tube (Fig. 3b, d). The anterior portion of the dorsal cavity, compared with that of *Acheta* and *Gryllus,* seems enlarged dorsally and rotated so that the base of the guiding rod is directed dorsally and then curves ventrally and posteriorly. The epiphallus and ectoparameres are not easily distinguishable. Females of this genus (Fig. 3a) do not differ greatly from those of *Gryllus* and *Gryllodes,* though, as might be expected, the spermathecal tube is unusually long.

Mating behavior in *Teleogryllus* differs from that of *Gryllus, Acheta,* and *Gryllodes.* Copulation in *T. commodus* lasts 8–10 minutes (2 copulations), during which obvious jerking motions are made by the male, evidently in association with threading of the long spermatophore tube. The pair is much more firmly attached during copulation. Often, the female falls off the male sideways or turns her body as much as 30° sideways off the male without causing separation of the genitalia (Fig. 10c).

Copulation, male genitalia, and spermatophores were similar in two African species belonging to this genus and collected by Otte on the Umfolozi Game Reserve in South Africa. Three copulations observed lasted 240–275 seconds; the genitalia were firmly attached, with the female sometimes falling sideways or twisting at an angle as in *T. commodus*. During one copulation, the female remained perched on the male's back for several minutes after separation of the genitalia. This behavior was also seen in *T. commodus*. The males of the South African species also carried out upward, thrusting movements of the tips of their abdomens during copulation. An important difference between these species and *T. commodus* is that the spermatophore of both of the African crickets bears a spermatophylax, and as in *Gryllodes* the female turns after copulation, removes the spermatophylax and eats it. One pair of copulations by the same male and female occurred about 15 minutes apart.

Apparently, mating behavior has not been described for any of the other 28 African and Asian species assigned to this genus by Chopard (1951b). Chopard's drawings of the male genitalia of ten species indicate considerable variation.

GENUS *Valerifictorus*

Males of *Valerifictorus micado*[1], like those of *Gryllus,* have a relatively small dorsal cavity, a short guiding rod, and a short spermatophore tube (Fig. 2g–i). But the ectoparameres are large, and the shape of the dorsal wall of the dorsal cavity and attachment of the guiding rod seem to resemble more closely those of *Acheta* and *Gryllodes.* The partition of the spermatophore mold is nearly horizontal. The epiphallus has lateral projections, as in *Gryllodes,* but the median portion is shallowly bifid, unlike the other genera described. So far, the spermatophore seems most similar to that of *Teleogryllus.* The copulatory papilla of the female is flattened dorsoventrally, unlike the four genera discussed so far.

Only two copulations have been seen by us. On the basis of one observation, R. D. Alexander (1962) recorded a duration of 3–4 minutes. A copulation observed by Otte lasted approximately 30 seconds, but the pair separated when touched by another male. Alexander noticed a turning of the pair at almost the moment of separation to an end-to-end position. Otte, however, did not see such turning and a copulation watched by Robert Love at the University of Florida (pers. comm.) did not terminate in this

[1] Specimens for this study were collected from the colony at Huntsville, Alabama, believed to be Asiatic in origin (Alexander and Walker, 1962). Randell (1964) named this genus on the basis of a hood constructed over the burrow entrance by a male excavating in damp clay (Alexander, 1961). Randell's specimens (from the U.S. National Museum) were collected in China, and no indication of comparison with the Alabama material is given. The genitalia, however, seem alike.

fashion. These observations are not necessarily incompatible, for the pair watched by Alexander may have remained together in the manner of *Teleogryllus* after functional separation of the genitalia, and the peculiar turning may have been correlated with this behavior. Otte observed a new spermatophore on the male 40–55 minutes after copulation. Post-copulatory behavior has not been watched carefully, though the pair watched by Alexander remained close together in an end-to-end position for a while.

Sexual behavior has not been described for any of the other six species included by Randell (1964) in this genus, nor for any member of the similar genus *Scapsipedus.*

<h3 style="text-align:center">GENUS *Miogryllus*</h3>

This genus introduces the first major variation in both mating behavior and genitalia. As in the other five genera of Gryllinae discussed so far, and *Gryllomorpha* (Boldyrev, 1927*b*) and *Discoptila* (Boldyrev, 1928*b*), copulation always terminates in an end-to-end position (Fig. 9e), after beginning in the usual female-above position (Fig. 9a). The only other cricket known to copulate in this fashion is *Anurogryllus muticus,* although *Neocurtilla hexadactyla* both begins and ends copulation in an end-to-end position.

The partition in the spermatophore mold of *Miogryllus verticalis* is vertical, even directed slightly forward in contrast to the other genera discussed so far, and the spermatophore is correspondingly sharply flexed at the neck (Fig. 2f). The phallic complex of *Miogryllus* most closely resembles those of *Modicogryllus* and *Valerifictorus,* among the previously considered genera. The epiphallus differs strikingly from those of *Acheta, Gryllus, Gryllodes,* and *Teleogryllus;* instead of being a median projection, it is bifid, with a deep U-shaped cleft containing two small, sharp structures, which may be projections of the ectoparameres. The male illustrated (Fig. 2e), as with the examples for *Valerifictorus* and *Amphiacusta,* was carrying a spermatophore when killed.

As in *Valerifictorus* (and *Anurogryllus*), the copulatory papilla of the female *Miogryllus* is flattened dorsoventrally (Fig. 2d); this characteristic is evidently correlated with the bifid nature of the male phallic complex.

The copulatory act in *Miogryllus* lasts approximately four minutes (2 complete copulations); in one case it was repeated after post-copulatory behavior lasting an hour. The courtship sound, as with *Valerifictorus* and *Teleogryllus,* does not resemble that of *Gryllus, Acheta,* and *Gryllodes* (Alexander, 1961), but involves only a slight lowering of the wings from the calling sound (Fig. 9e). The female-above position is maintained for only a few seconds, and then the male turns out from under the female. During the end-to-end phase, the male carried out bursts of jerking motions, 4–6 jerks per burst, at a rate of 5–10 jerks per second, with bursts occurring at intervals of about $1\frac{1}{2}$ seconds.

Immediately following copulation, the male begins a more or less steady chirping (Fig. 9d) that seems indistinguishable from calling. The end-to-end position (Fig. 9e) is generally maintained, apparently with the cerci in contact, and re-assumed after disturbances. When the male has produced another spermatophore, he begins to change to courtship chirps without changing his position with regard to the female. She turns eventually and mounts him again.

Evidently, the jerking motions of the male are related to threading of the spermatophore tube, as in *Teleogryllus,* which makes the end-to-end position doubly interesting.

How can the male of *Miogryllus* turn end-to-end after attaching the genitalia, and what are the consequences with regard to position of the genitalia? Either the male's phallic complex is twisted, the copulatory papilla of the female is twisted, or the phallic complex rotates on the copulatory papilla. The appearance of the male and female genitalia suggests that they cannot twist the necessary amount. The bifid nature of the male epiphallus also supports the third alternative, that rotation of the phallic complex on the copulatory papilla occurs either during or after the turning of the male to the end-to-end position.

Turning end-to-end seems to have been added to the old female-above copulatory position by which the *Miogryllus* act still begins. This kind of change is not limited to Gryllidae; it occurs in Tettigoniidae (Fig. 10f), Blattodea, and Caelifera as well (though seeming to be more or less accidental in Caelifera), and probably appeared several times independently within the crickets. Why should such a change occur?

Compared with that of *Acheta* and *Gryllus,* copulation in *Miogryllus* is a prolonged affair. The significance of this prolongation is not clear; it may, in some cases, be related to longer spermatophore tubes that require more time for threading. *Teleogryllus,* for example, has a longer spermatophore tube and a longer copulatory act than either *Gryllus* or *Acheta.* In other cases, the copulatory act may have been prolonged into the inseminating period, part of the "post-copulatory" function being accomplished during coupling itself.

A longer copulatory act, whatever its advantages, could change selection in several ways—for example, by giving a stronger advantage to more elaborate female-attracting dorsal glands or smaller similar stimuli, or to a greater ability of the male to grasp and hold the female. Firmer attachment between the pair has the additional possible advantage that slight disturbances might be less likely to disrupt copulation. Males and females of *Teleogryllus,* for example, are more firmly coupled than copulating pairs of *Gryllus* or *Acheta,* and, as already noted, a pair can walk several steps or be turned as much as 30° with regard to one another without separating.

Relative to effects of disturbances, a cricket such as *Teleogryllus* can derive advantage from firmer coupling only if it is able to continue copulation after being turned as a result of disturbance. Initially, such a cricket might be able to thread the spermatophore only in the original female-above position: such species could derive benefits only if turning happened after spermatophore threading. But if turning occurred frequently enough before the spermatophore tube had been threaded, then it would be advantageous to be able to thread the tube in the new (end-to-end) position as well. If at any stage in these changes incompatibility developed between threading the spermatophore tube in the old position, and threading it in the new position, greater likelihood of the new position occurring before spermatophore threading would give advantage to males that perfected ability to thread the spermatophore tube in the new position, and in fact to males that assumed this position as soon as coupling had occurred.

These hypothetical steps seem to represent a reasonable series of changes by which a cricket that copulates as *Miogryllus* does could evolve from one that copulates as *Acheta* or *Gryllus* does.

GENERA *Discoptila* AND *Gryllomorpha*

Boldyrev (1927*b*, 1928*b*) observed the copulation of *Gryllomorpha dalmatina* and *Discoptila fragosoi*. Both copulate in the female-above position. The male *Gryllomorpha* attaches the spermatophore within three minutes, and the pairs watched by Boldyrev remained together motionless for an additional 2–9 minutes. The spermatophore of *Gryllomorpha* bears a spermatophylax which the female removes about one minute after separation from the male and chews for as long as two hours before removing the spermatophore.

The male *Discoptila* retains the spermatophore, holding it in place during a copulatory act that lasts 15–90 minutes (4 copulations observed by Boldyrev). The male's tiny, pad-like tegmina are lifted and tilted forward over the pronotum. Boldyrev says that a glandular secretion keeps the female's attention; he illustrates two metanotal glands which he says produce a viscous, dark, translucent secretion that the female removes from the undersurface of the raised tegmina just before and during copulation.

GENUS *Gryllopsis*

An unidentified species, probably belonging to this genus, was collected by Otte on the Umfolozi Game Reserve in South Africa and observed subsequently in the laboratory. Both sexes are wingless, and burrow extensively. Copulation is most like that of *Gryllus* and *Acheta*. The courting male jerks and vibrates near the female, and the responsive female mounts and seems to clutch the male, while standing motionless over him. The male first

exposed the spermatophore when the female seemed to direct her mouth-parts precisely to his genitalia during courtship. He attached the genitalia by an upward, forward thrust, and copulation lasted less than three minutes (not timed exactly). Two matings were seen on separate occasions.

SUBFAMILY NEMOBIINAE
GENUS *Nemobius*

Fulton (1931) and Gabbutt (1959) have published descriptions of copulation in American and British species currently placed in the genus *Nemobius*, and we have observed copulation in *Nemobius allardi* (Eastern United States) and *Nemobius sylvestris* (Czechoslovakia). Fulton did not indicate the species he was discussing; Gabbutt discussed *N. sylvestris*. The two descriptions differ in several regards. Both kinds of crickets copulate in the female-above position with the male's tegmina lowered, but the male of the American species has a long glandular spine at the base of the hind tibia, and holds his hind legs in an unusual position during copulation, which enables the female to reach the spine with her mouthparts. The male of *N. sylvestris* has no tibial gland, but evidently possesses a glandular area at the base of the tegmen which holds the female's attention during copulation.

Fulton says the spermatophore is formed shortly before copulation, which lasts 15–25 minutes. He does not mention post-copulatory behavior or repeat time. The female eats the spermatophore.

Gabbutt says that males of *N. sylvestris* form spermatophores independent of the presence of females. These spermatophores, the first transferred during a copulatory bout, are very small compared with those transferred during the subsequent copulations (averaging 0.303 mm in diameter vs. 0.946), and may serve principally to set up the post-copulatory (or inter-copulatory) interaction during which the male can form the larger spermatophores, evidently containing many more sperm. Copulations last only a few seconds (2–3 seconds in two copulations watched in our laboratory in Czechoslovakian crickets mailed to us alive by V. Novak, Prague). The copulation of *N. sylvestris* is particularly interesting because it suggests the general importance of the post-copulatory behavior in keeping pairs together until (presumably) maximal insemination of the female has been accomplished. When *Gryllus* males carry spermatophores for a long time without mating, the spermatophore ampulla darkens. Such spermatophores evidently can no longer be used in copulation, for they are removed by the male, either in the complete absence of females or following unsuccessful attempts to attach them to a female. The photographs of *Miogryllus* show both a white spermatophore early in copulation (Fig. 9a) and dark spermatophores late in copulation (Figs. 9d,e).

Snodgrass (1937) described the male genitalia of *Nemobius fasciatus* in

detail. The most striking peculiarity seems to be that the guiding rod is represented only by "an elongate plate on the floor of the dorsal cavity" which "tapers distally into a groove between the halves of a soft, globular, median lobe." The spermatophore tube is relatively short, and the male phallic complex is somewhat bifid.

<div align="center">

SUBFAMILY BRACHYTRUPINAE

GENUS *Anurogryllus*
</div>

Copulation in *Anurogryllus muticus* occurs either inside or outside burrows. Following is a description of a copulation observed in the laboratory. The female excavated a shallow burrow. When the male was introduced into the cage, he immediately entered the female's burrow, and she ran out. The male then turned head-out at the entrance of the burrow and began to produce short chirps while pushing his body back and forth, (as in Fig. 6b), in and out of the entrance of the burrow. The female stayed near the entrance, turning toward it, and finally re-entered the burrow, running over the male's back as she did so. When this happened, the male lowered his wings and began to reach upward with the tip of his abdomen and extrude his epiphallus. The female ran back and forth across his back three or four times, and on the last run the genitalia became attached. The pair stayed in a female-above position for ten minutes with only slight movements of mouthparts, antennae, and legs, mostly near the end of this period. The spermatophore was easily visible during this time, but it was low on the male, and appeared not to be attached to the female. At the end of ten minutes, the female started climbing out of the burrow, turning in the process so that the bodies of the two crickets were at about a 45° angle with regard to one another. They remained in this position for 14 minutes and 45 seconds, then the female vibrated her antennae up the burrow. Six minutes later, the pair rather abruptly turned into an end-to-end position. The female's abdomen was a little higher than the male's; her cerci were above the male's cerci; her abdomen was twisted a little; the ampulla of the spermatophore was visible between the male's subgenital plate and his cerci. Twelve minutes and 15 seconds later, the spermatophore was noticed to be turning slightly brownish. Three minutes and 35 seconds later, the male turned around and raced forward, and the female dashed out of the burrow and stopped. Then the female turned around and antennated the male, still in the burrow. The female then came back into the burrow and the male dashed out. The female came back to the burrow entrance and shook her body. Three minutes later the female began pushing sand in the bottom of the burrow. The male showed no inclination to return to the burrow.

This copulatory act resembles that of *Miogryllus* in that it terminates end-to-end. The turning, however, is quite different, and the male seems to

keep the spermatophore during copulation (a conclusion supported by observations made by Thomas J. Walker at the University of Florida, pers. comm.). Insemination is finished when the pair separates, and threading of the spermatophore tube may occur during the initial female-above position. This act, then, seems to resemble that of *Miogryllus* only in a superficial way, and the end-to-end terminal position may well be independently evolved in the two cases. It is probably significant, though, that both genera, as well as *Modicogryllus,* are extensive burrowers.

The spermatophore of *Anurogryllus* (Fig. 4f) differs strikingly from those of the other crickets examined so far. Its tube is short and thick. It is difficult to understand precisely how the spermatophore is inserted into the female during copulation, unless the tube of the preserved spermatophore illustrated is somewhat distorted. Sketches made during the copulation described above place the ampulla of the spermatophore beneath the tip of the female's abdomen.

The male's guiding rod is very thick and rigid (Fig. 4e), and the female's copulatory papilla is greatly flattened (Fig. 4d), with the dorsal portion protruding "canopy-like" over the opening to the spermathecal tube. The spermathecal tube is short and thick compared with the other genera described so far.

The male epiphallus of *Anurogryllus,* like that of *Miogryllus,* is bifid. The ectoparameres, however, are much larger, the guiding rod is quite different, and the epiphallus has a ventral notch not found in *Miogryllus.* Furthermore, the spermatophore molds are quite different, particularly in the shape of the dorsal cavity and the position and nature of the partition between the dorsal and ventral cavities.

The many genitalic differences between these genera make it questionable that the bifid nature of their epiphalli, the flattened copulatory papilla, and the superficial similarities in mating behavior are the result of common ancestry.

The above interaction between the male and female of *Anurogryllus* is of particular interest because the female in this species is sub-social, sealing herself into her burrow, piling food, eggs, and fecal pellets in different parts of the burrow, and interacting with her young (West and Alexander, 1963). The female evidently copulates several times with a male, but only if the "bout" of copulations is uninterrupted. In the laboratory, two females that had copulated several times in succession with single males, and one that copulated only one time and was then separated from males for a while, did not copulate again, but reacted hyper-aggressively to the presence of a male or any other cricket. These females were capable of expelling any other individual from their burrows. In such species a female attracted to a male that has excavated a burrow and is calling at its entrance may expel

the male and take over his burrow. The male in this case would be expected to behave in such a way as to maximize his chances of locating and mating with another female—to leave his pre-empted burrow and call elsewhere, perhaps digging another burrow. But a curious alternative exists. If a male's chance of finding a second mate are sufficiently reduced, for example, by an abundance of males and a sufficient lengthening of the minimal time involved in all successful sexual interactions, then it is possible that a male's own reproductive success would be most enhanced by his contributing to the probability of reproductive success by the female with which he has already mated. This could be accomplished, for example, by the male expending more of his time and energy in developing an adequate burrow for the female or cooperating with her after copulation in further excavation of the burrow or accumulation of food in the burrow. At the extreme, it could be accomplished by the male allowing the female to kill and eat him after the pair has copulated. This suggestion is not as far-fetched as it might sound. Food is undoubtedly at a premium in the burrow, for specialized behavior has evolved that results in its accumulation (West and Alexander, 1963). The female of *Anurogryllus* probably always dies in her burrow and is consumed by her offspring, and this rather large supply of food could be of enormous importance to her brood. Emerson (1961) pointed out that in parental animals, "post-reproductive" is often a difficult term to define, and that there can be selective action not only on how and where and when a parent dies, but even on the manner in which it decays. All of these kinds of selective action could have acted on sub-social, burrowing crickets.

Observations on a burrowing *Gryllus*-like cricket from South Africa provide interesting information in this connection. In this case we attempted to set up a mating interaction by introducing an adult male into the burrow of an adult female of unknown history. The female only reacted aggressively. Her burrow had been sealed off from the surface, as in *Anurogryllus*, but we opened the entrance and forced the male into the burrow. He managed to get past the female so that she was between him and the entrance. She patched the entrance and then encountered the male as she moved back into the recesses of her burrow. Instantly she attacked him, but the aggression was unlike that of the ordinary fight between two male crickets in that with each contact she attacked so fiercely that she either tore off an appendage or bit a hole in the male's abdomen. After several encounters we removed the male, who by this time had lost both hind legs, parts of other legs, and had at least one large hole in the side of his abdomen. To our surprise, the male did not at any time show the usual kinds of aggression toward the female, though he snapped his mandibles together audibly, and continued to do this in our hands when we removed him from the burrow.

The female ate the appendages the male left behind, as did a female of *Anurogryllus* when we conducted a similar experiment with that species (West and Alexander, 1963). It seems possible that circumstances might arise in species of this sort when selection would cause males that had copulated to re-enter the burrow, or remain in it, and, slowly or rapidly, be killed and consumed by the female.

Females of *Anurogryllus* differ from those of field or house crickets in two regards: they possess a very short ovipositor (eggs are dropped on the burrow floor, not injected into the soil), and the papilla of the spermathecal aperture is funnel-shaped, or perhaps dish-shaped, with the aperture to the spermathecal duct ventral and at the anterior end.

Miogryllus and *Anurogryllus* are distinctive in that the male stridulates directly following copulation, while standing in the end-to-end position. Otherwise, only Oecanthinae and Phalangopsinae are known to stridulate soon after copulation, before another spermatophore is formed. *Oecanthus* males stridulate with the female still mounted, and *Amphiacusta* males begin to stridulate when they locate and start to eat the dropped spermatophore after separating from the female.

Sexual behavior has not been described in any other member of the Brachytrupinae.

The identity of Brachytrupinae as a unit distinct from Gryllinae has repeatedly been questioned, most recently by Randell (1964), who believes on the basis of male genitalia that *Anurogryllus* and *Brachytrupes* are distantly related genera. However, a constellation of characters enables one immediately to distinguish from other Gryllinae these two genera and some others. These characters are not always easy to identify, but they include (1) a nearly linear arrangement of three ocelli, when three are present, as contrasted with a more triangular arrangement in most Gryllinae; (2) a waxy, glossy appearance of the entire body and wings; (3) the general shape of the head and pronotum; (4) short hind tibiae, as compared with the length of the hind femora; (5) more prominent spines on the hind tibiae; (6) short ovipositor; and (7) a general tendency to subterranean life and parental attention to eggs and young juveniles. None of these characteristics is impressive when considered alone, but together they comprise a unit unlikely to have evolved independently so as to produce the distribution of genera and species here included in the Brachytrupinae. We suggest that the Brachytrupinae, even if all the generic relationships are not correctly designated, do comprise a monophyletic group with the above characteristics, and that at least *Brachytrupes, Anurogryllus,* and *Urogryllus* are members of this unit. The genitalic differences between *Brachytrupes* and *Anurogryllus* do not necessarily conflict with this suggestion.

Subfamily Gryllotalpinae
Genera *Neocurtilla* and *Gryllotalpa*

Neither the mating behavior nor the genitalic structures of mole crickets resemble those of other crickets. The male genitalia differ to such a degree that it is difficult to homologize their features with those of other genera (Fig. 4a–c). No dorsal cavity is distinguishable, and there is no guiding rod. The male of *N. hexadactyla* has two epiphallic processes, or what are presumed to be epiphallic processes, a dorsal one which overlaps a ventral one at the distal ends. These structures are more internal than in other crickets. They may be derivatives of the epiphallus and the ectoparameres; Snodgrass (1937) refers to the dorsal structure simply as a "distal process of the dorsal wall of phallic cavity." The male of *Neocurtilla* also possesses a "phallic gland" which opens just dorsal and posterior to the dorsal phallic process.

The spermatophore examined shows only a shortened tube. Boldyrev (1915) reports a long tube for the spermatophore of *Gryllotalpa gryllotalpa;* the spermatophore of that species is in other regards quite similar to that of *N. hexadactyla.* Unlike the previously described spermatophores, the duct leading from the sperm capsule does not follow a more or less direct route to the attachment plate region but makes a loop first. How the spermatophore lies within the male is not yet known.

Female genitalia, too, are significantly different from the generalized pattern. The copulatory papilla, which terminates in two processes, is ventral to the spermathecal aperture, and the aperture does not terminate on the protuberance itself, as it does in all other crickets studied. There is a darkly sclerotized wall at one point along the spermathecal duct, the function of which is unknown. Exactly how the male and female genitalia are used in transfer of the spermatophore is not yet known, but the dorsal and ventral phallic processes are probably used as a clamp to hold the female's sclerotized papilla during insertion of the spermatophore tube.

Two kinds of mating have been described for mole crickets. Boldyrev (1915) stated that in *G. gryllotalpa* the female mounts the male and transfer of the spermatophore takes place in this position; Baumgartner (1905) and R. D. Alexander (1962) described copulation in *N. hexadactyla* inside a burrow as follows: the male and female make contact while facing 180° away from one another, while the male lies on his back or on his side with his abdomen sharply twisted, so that the tips of the two abdomens are end-to-end with the female venter down and the male venter up. This position can be derived from that described by Boldyrev simply by having the animals rotate through 180° in a vertical plane. It seems possible that both kinds of mating occur in both species, depending on whether mating occurs in a

burrow or above ground. Boldyrev's description was apparently from above-ground observation, while both Baumgartner's and Alexander's observations were on pairs mating in burrows. Fulton (1924) described a variation in the copulatory position of the European earwig, *Forficula auricularia* L., depending upon the conformation of the mating site: "After [the male] has located a female with his antennae, he turns around and tries to slip the forceps under the tip of the female's abdomen. At this time the two are facing in opposite directions. It is then necessary for him to twist [his] body around so that the two ventral surfaces are together, the ends of the abdomens touching. . . . In [the corners of cages] the male usually stood on one side of the corner and the female on the other. This required the male to twist his body only ninety degrees instead of a half revolution . . . in . . . narrow crevices . . . a number of pairs were observed in coitus, but always with the male clinging to one surface and the female to the other so that no twisting of the body was necessary."

Mole crickets, like *Anurogryllus,* are sub-social (Hayslip, 1943; Hahn, 1958). We have not observed their behavior sufficiently, however, to know whether or not there are similar restrictions in the mating of the females.

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SUBFAMILY ENEOPTERINAE

GENUS *Hapithus*

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We have discussed the mating behavior of *Hapithus agitator* in another paper (Alexander and Otte, 1967). The following account from that paper is based on observation of seven complete copulations.

"A male following a female . . . moves in front of her with lifted forewings if she pauses. . . . If she remains more or less motionless during this behavior, the male eventually produces a spermatophore, then turns about in front of the female and begins to back toward her head. . . . The female, if responsive, finally begins to palpate the male's cerci, spermatophore, and dorsum, moving slowly up on his back. . . . Eventually the female moves so far forward that her head is hidden beneath the male's wings at their base . . . , and at this time the male makes upward and forward hooking motions with the tip of his abdomen, which is turned upward against the venter of the tip of the female's abdomen. Evidently at just the moment that he engages the genitalia and pulls the female's abdomen and her ovipositor downward, the female starts to raise her head slowly until her mouthparts are near the tips of his raised tegmina, which she then begins to eat. . . . The condition of the male's tegmina following one copulation is shown. . . .

"Time between appearance of a spermatophore on the courting male and initiation of copulation varied in our observations from 67 seconds to 12 minutes; time from initiation of copulatory actions to female starting to

eat the wings varied from 25 to 42 seconds; time from female beginning to eat the wings until the pair separated varied from six minutes 50 seconds to 12 minutes. One male produced another spermatophore 12 minutes after copulating, and once a female initiated copulation with a second male 12 minutes 30 seconds after copulating. After separating, in two instances the female found the spermatophore on the ground a few seconds after it had dropped from her abdomen or was rubbed off by her, and ate it. . . . In one case another male found the spermatophore and started to eat it, dropping it eventually; the female found and ate the remaining portion. In another case the female found and ate the spermatophore several minutes after copulation had terminated. After copulation the male and female in all cases stayed together, and the male was aggressive toward other individuals that approached, as in most other crickets."

The epiphallus of *Hapithus* is bifid, the guiding rod is short and stout, and the partition between the ampullar mold and the dorsal cavity is somewhat obscure (Fig. 5d–f). The spermathecal tube of the female is short, corresponding to the short neck of the spermatophore.

No obvious relationships of other than a general nature exist between this genus and any of the others studied.

Genera *Orocharis* and *Tafalisca*

Mating has not been described for any other member of the Eneopterinae. Dr. Thomas J. Walker and Mr. Robert Love of the University of Florida, however, have watched courtship and copulation in two species of *Orocharis* and in *Tafalisca lurida,* and transmitted the following notes to us:

Orocharis: ". . . the male passed 8 spermatophores in about 30 minutes. The first spermatophore was immediately stuck to the substrate by the female and picked up with her mouthparts. She then climbed back on the male and the male passed the second while she ate the first. When she finished the first she transferred the second from genital opening to substrate to mouthparts, climbed back on, and received the third while eating the second, etc. . . . the same sort of procedure [was observed] in a pair of *Orocharis*. In both species the male made an audible drumming sound, evidently with the maxillary palps, at times when the female was not in position to receive the next spermatophore."

Tafalisca: "The female mounts the male, who has his tegmina raised, and mouths the dorsum of his abdomen and the metanotum. The male exudes a spermatophore and engages the female genitalia with her aid. With genitalia engaged, the female reaches around and grabs the spermatophore with her mouth, then rotates so she is end-to-end with the male. With genitalia still engaged (but not twisted) they stand there with the female munching on the spermatophore. We saw this sequence three times." Walker and

Love observed this sequence three times but believe that they may have caused the end-to-end pair to separate prematurely. It is not known if the female was inseminated.

SUBFAMILY PHALANGOPSINAE
GENUS *Amphiacusta*

Copulation was observed in a species of *Amphiacusta* (Fig. 8e) collected in Puerto Rico and mailed to us alive by Dr. Jose A. Ramos. About seven mating sequences were observed. Male and female remain in a head-to-head position prior to copulation, during which time the male chirps fairly regularly, occasionally jerking his body up and down. His tegmina are held at a near vertical position between chirps. After the spermatophore has been formed, or, more precisely, at about the time it becomes visible, the male lowers his tegmina, turns around, and lifts his tegmina again into the vertical position. He may chirp in this position if the female does not mount immediately after his turn. On one occasion the female walked forward and onto the male without the male backing up. On another occasion the female remained stationary until the male backed up to her, whereupon she mounted. The placing of either the palpi or the tarsi on the male's back stimulates him to extend and lift the terminal portion of his abdomen under that of the female who at the same instant moves forward onto him. This tactual sensitivity of the courting male's tergum can be demonstrated by touching it with a hair brush. When the posterior segments are touched, the male lifts and extends the tip of his abdomen and extrudes his genitalia.

The male attaches his genitalia as the female mounts and usually performs several upward thrusts of his abdomen before becoming motionless. In the copulatory position the male holds his wings a bit forward from vertical, and the female's head is held motionless behind the wings. Both the male's and the female's antennae are held in an almost vertical position; the female's ovipositor is slightly lower than horizontal and the male's cerci are in a horizontal position, not in contact with the female.

On six occasions, with four different pairs, copulation lasted almost exactly seven minutes; on one occasion the mating broke up after 65 seconds. The behavior of this pair and the manner in which they separated, however, indicated that this was an abortive mating. At the end of the copulation, the female suddenly steps off the male. The male retains the spermatophore, and immediately following copulation removes it by dragging the end of his abdomen on the substrate. He then backs over it, palpating the substrate before he reaches the spermatophore. When he finds it he picks it up and begins to eat it, and at the same instance begins to stridulate.

The female remains stationary nearby. After eating the spermatophore (perhaps while eating it), the male re-establishes antennal contact with the

female, and continues to stridulate. A new spermatophore was on one occasion formed five minutes after mating had ended. However, mating was not attempted until 24 minutes had elapsed. If male and female become separated after mating, the female will move toward a chirping male. When the spermatophore that a male had just removed was taken away before he was able to find and eat it, he continued to go through the motions of removing the spermatophore and searching for it. In one such case, the male did not chirp or re-establish contact with the female.

Aggression has been observed several times between males near females; the males in each case had both been stridulating before the encounter. The two males stood almost upright, leaning against one another with only the hind legs touching the substrate. There was no stridulation during such encounters. No physical damage was apparent.

The genitalia were more or less everted in the male illustrated (Fig. 5b). The epiphallus and ectoparameres are difficult to indentify. There is no partition separating the ampullar mold from the dorsal cavity; instead, there is a single chamber or cavity with the sperm duct opening at the anterior end of this cavity. The guiding rod is a short, stout structure hidden within the phallic complex. The spermatophore (Fig. 5c) is almost teapot-like in shape, with a shorter tube than in any other species studied. Hubbell (1938) illustrated the spermatophore of *A. yucatana* Hubbell with a somewhat longer tube, still shorter than any others seen in this study.

The female genitalia in this species are similar in arrangement to those found in Gryllinae (Fig. 5a). The tip of the spermathecal papilla, however, is sharply curved, evidently conforming to the curved structure of the male guiding rod. The illustration is not a medial sagittal section, but, as with *Hapithus,* is slightly to the left of the median.

As already mentioned, the male retains the spermatophore; all insemination occurs during copulation. The spermatophore tube has a large diameter, perhaps facilitating a rapid evacuation of sperm, although the mechanism is unknown. Boldyrev (1929) indicated that the male grasshopper, which also holds the spermatophore during insemination, may squeeze the ampulla. *Amphiacusta* males may do likewise, but the rigidity of the ampulla of the spermatophore makes this a doubtful possibility.

Sexual behavior has not been described for any other member of the Phalangopsinae.

SUBFAMILY OECANTHINAE
GENUS *Oecanthus*

Lespes (1855) described the mating of the European tree cricket, *Oecanthus pellucens,* and Fulton (1915) gave an excellent description of the

spermatophore and the male and female reproductive organs for a tree cricket, probably the snowy tree cricket, *Oecanthus fultoni* (but under the name *O. niveus* De Geer). Fulton's description (p. 13) is so clear and useful to this study that we quote extensively from it:

"The male calls vigorously until a female comes near him, in which case he sidles toward her, without any cessation in his singing and keeping his head in an opposed direction. If he succeeds in attracting her attention she climbs over his body and begins to feed on the secretion of a glandular cavity on the metanotum, which is described by Hancock as an 'alluring gland.' The male stands with legs spread wide apart and the tegmina are held at an angle of about 45 degrees above the abdomen. . . . His body sways and twitches considerably and the hind wings, which lie folded along the back have a peculiar jerky movement whenever the female bites at the gland. The antennae are waved about wildly and are often thrown back so as to cross and rub against those of the female. After about half an hour [may have been the second copulation in a series], the male reaches back with his abdomen and the female bends her abdomen downward. This enables him to slip a pair of small, laterally compressed blades into the notch at the tip of the female's subgenital plate. . . . At this time the barbed capillary tube of a spermatophore is pushed into the vagina and when the tip of the abdomen is withdrawn the bulb of the spermatophore is drawn out of its pocket in the male and remains fastened to the female. The latter does not leave immediately but continues to partake of the secretion of the gland for a half hour or more [Figs. 7d, 8d]. She finally crawls away to some secluded spot and arches up her back, bringing the tip of the abdomen forward beneath and pulls off the spermatophore with her mouth. She straightens out again and proceeds to eat the capsule in a leisurely way, after which she doubles up again and works at the ovipositor with her mouth, as if endeavoring to clean it.

"In fastening the spermatophore to the female, the male places his cerci on opposite sides of the ovipositor, and they appear to guide him in striking the proper opening. A male from which both cerci had been removed at the base, was observed trying to copulate. When he succeeded in striking the base of the ovipositor, the female turned the tip of the abdomen down as usual. The male then passed the pair of chitinous blades up and down the ovipositor but was unable to strike the opening at the base and after several attempts the pair became separated. . . .

"The exact function of the gland on the metanotum of the male has been a matter of doubt. Hancock first described it as an 'alluring gland,' claiming that it served to attract and hold the attention of the female until copulation could take place. Boldyrev and Engelhardt of Moscow, Russia, have concluded from observations on the European species, *OE. pellucens* Scop.,

that its chief function is to hold the attention of the female after the spermatophore has been attached, and thus prevent her from devouring it before the sperms have had time to pass into the seminal receptacle. These two theories are not diametrically opposed, and from my own observations it seems that the gland may serve both purposes equally well. In no instance did the male transfer the spermatophore before the pair had been together less than a quarter or half an hour. During both periods, before and after passing the spermatophore, the female would occasionally start to crawl away. At such times the male would begin to sing and follow after her, placing himself in front of her and taking such a position as to expose the alluring gland. Usually the female would return, but sometimes she would leave to stay, even before the spermatophore had been fastened to her. Considering the length of time for the first part of the mating process, and the willingness with which the female departs from the male, it seems doubtful if the male, without the help of the gland, could hold the attention of the female long enough to place the spermatophore in the genital opening. On the other hand, the female devours the spermatophore very soon after leaving the male, and if the insects separated immediately after the spermatophore was given over, only a small part of the sperms would have time to flow into the seminal receptacle.

"In this connection it is of interest to note that a female nymph of the fifth instar was at one time observed eagerly feeding on the gland of a mature male [According to L. M. Roth, pers. comm., juvenile cockroaches feed on the dorsal secretions of courting male cockroaches]. This behavior of the nymph would indicate that the mature females probably have a taste for the secretion of the metanotal gland independent of the act of copulation with the male.

"The exact process of spermatophore formation is as yet only a matter of conjecture. It seems very probable, however, that a mass of sperms which have collected in the enlarged portion of the vas deferens move out into the mold and are later surrounded by a quantity of secretion from the glandular tubules which hardens around them and in some way forms the spermatophore. The tube is probably formed in the groove, but why it develops as a tube and not as a solid rod is a mystery.

"A new spermatophore is usually formed soon after the last one is removed. In mating it was observed that in about ten minutes after the spermatophore is passed to the female and while the latter is still feeding at the metanotal gland, the collapsed mold begins to swell out and in another minute or so is fully distended and remains so. In one case a male was examined about half an hour after the mold became distended. The mold contained a white, globular mass of sperms with a long attenuated thread at one end. It appeared to be enclosed in a delicate membrane al-

though this could not be distinguished. It was surrounded by a clear viscid liquid about the consistency of egg albumen. I removed the sperm mass with forceps and the liquid began to congeal. A small drop on the point of a needle could be pulled out into a very fine thread which would harden very quickly. The hardening continued even after the mass was placed under the water and resulted in a hard substance like the wall of the spermatophore.

"Another male which had disposed of a spermatophore was examined in an hour and three-quarters after the mold had become distended and it was found to contain a fully formed and hardened spermatophore.

"In order to follow the course of the sperms after the deposition of the spermatophore it is necessary to understand a little of the anatomy of the female reproductive system. The ovaries occupy a large portion of the central part of the abdominal cavity. They are made up of a large number of separate egg tubes, each of which contains several ovarian follicles in various stages of development. . . . The tubes all converge into the broad, thin-walled oviduct . . . and these unite to form the vagina . . . which continues as a straight tube to the ovipositor. A single tubular accessory gland . . . opens above the vagina at the base of two short rods which are between and hidden by the four large rods of the ovipositor. The gland probably furnishes the mucilaginous substance exuded at the time of oviposition. The notch at the end of the subgenital plate opens into the ventral side of the vagina. . . . Just anterior to this on the dorsal wall of the vagina is a hard plate, which is slightly hollow on the inner side and bears a small hole in the center. This hole passes through and opens on the dorsal side into a small convoluted duct which leads to an ovoid seminal receptacle lying just anterior to the junction of the two oviducts. . . .

"A female bearing a spermatophore was killed and dissected. The tube was inserted in the notch at the end of the subgenital plate, and the point was directed into the hole in the plate at the dorsal wall of the vagina. It would appear that the sperms discharging through the tube would thus be directed into the duct of the seminal receptacle."

We have watched and photographed the copulation of *Oecanthus californicus* and find that it does not deviate noticeably from Fulton's description. Walker and Gurney (in press) report that postcopulatory feeding at the metanotal gland may last 65 minutes (*O. pini*), and that a second spermatophore may be transferred within 70 minutes of the first (*O. argentinus*). They found that variations in the structure of the metanotal gland are useful in grouping species but usually not in distinguishing species. They speculate, however, that the secretions may be "specifically distinct and account for the usual failure of females to respond to the courtship of heterospecific males. . . ."

SUBFAMILY TRIGONIDIINAE
GENERA *Crytoxipha* AND *Phyllopalpus*

Dr. Thomas J. Walker (personal communication) observed two copulations of *Crytoxipha columbiana* in Florida. The male lowered his forewings and dashed back under the female, attached the spermatophore and dashed out in a total time of about one second. We have watched males of *Phyllopalpus pulchellus* trill while backing toward females with their genitalia extruded and spermatophores in evidence, but we have seen no copulations. Evidently there are no other published observations on the mating behavior of members of this subfamily.

Fulton (1956) found that the male genitalia of several North American species of *Anaxipha* vary, in some cases sufficiently to allow species identification.

SUBFAMILY MOGOPLISTINAE
GENUS *Cycloptilum*

Two species of *Cycloptilum* were observed in the laboratory. In both cases the male backed under the female after stridulating near her and producing a spermatophore. In one case the pair separated within a few seconds, and the male retained the spermatophore; evidently this was an incomplete mating, even though the female mouthed her genital region following separation. In the other case the two individuals remained motionless for about 20 seconds, and no spermatophore was seen on the male afterward. The female mouthed her genital region, as in the other case, but no spermatophore was seen.

Love (1966) described a copulation in *Cycloptilum antillarum* (Redtenbacher) as occurring in the female-above position. The female retained the spermatophore and the male showed vigorous post-copulatory behavior. No timings were given. The female eventually kicked off the spermatophore and ate it.

OTHER SUBFAMILIES

Evidently there are no records of mating behavior in the remaining five subfamilies of crickets: Myrmecophilinae, Cachoplistinae, Pteroplistinae, Scleropterinae, and Pentacentrinae. Males of some wingless, cavernicolous Pentacentrinae in the University of Michigan Museum of Zoology, however, have large dorsal abdominal glands, suggesting that they at least begin mating in a female-above position.

SUMMARY AND CONCLUSIONS

SUMMARY OF BEHAVIORAL VARIATIONS

Returning to the nine behavioral events mentioned in the introduction, we are concerned now with their relationship to four variables:

1. The structure of the genitalia and the spermatophore.
2. The kind of environmental situations in which mating occurs.
3. The phylogenetic relationships of the groups involved.
4. Species interactions, particularly reproductive isolation, among closely related or newly sympatric species.

POSITIONS ASSUMED DURING COURTSHIP.—All male crickets turn their rear ends toward the females during courtship. In most species the male's cerci are thereby directed toward the female's head, though they may also (apparently accidentally) be directed at some other part of her body; in all such crickets copulation begins with the female mounting the male or the male backing under the female. But in *Neocurtilla* and *Udeopsylla* (Gryllacrididae), the male backs up to the female's rear end and copulation begins end-to-end. The difference in courtship position seems owing to the males of *Neocurtilla* and *Udeopsylla* responding to the rear end of the female, perhaps her cerci or genitalia, rather than to her antennae as the stimulus for turning and starting courtship. How this change may have occurred, we will leave for the moment.

ACTIONS OR MOVEMENTS DURING COURTSHIP.—All of the crickets we studied lift their tegmina at least slightly and vibrate them during courtship, and all sway, jerk, or vibrate their bodies and whip their antennae while backing slowly toward the female. The wingless species of *Gryllopsis* and some individuals of *Hapithus agitator* (with tegmina but an ineffective vestigial stridulatory apparatus) are silent during courtship; all others produce some sound, either greatly differentiated from other stridulatory signals (as in *Gryllus, Acheta,* and *Gryllodes*) or weakly differentiated (as in *Oecanthus*). The female in most or all cases works her palpi across the male's rear appendages (legs, cerci) and abdomen before she mounts and as she mounts.

An obvious variable in courtship activity involves the height to which the male's tegmina are lifted during courtship. In Oecanthinae, Eneopterinae, and Trigonidiinae, they are held nearly vertical. In the first two subfamilies, the female mounts so that her head is eventually positioned behind or beneath the male's tegmina, as in many Blattodea and Tettigoniidae, including *Cyphoderris* (Prophalangopsinae). This is likely a primitive condition in crickets, associated with dorsal secretions of the male. In Nemobiinae, Brachytrupinae, Mogoplistinae, and some Gryllinae *(Miogryllus),* the tegmina are lowered only slightly during courtship and flattened upon the

start of mounting. In Gryllotalpinae and the rest of the Gryllinae *(Gryllus, Acheta, Gryllodes, Modicogryllus,* and *Teleogryllus*), the tegmina are lowered considerably during courtship and flattened as the female mounts. In two species of Trigonidiinae (T. J. Walker, pers. comm.), the tegmina are vertical during courtship but flattened against the male's back during copulation.

MANNER OF COUPLING.—In all orthopteran mating acts beginning with the female above, it seems that the dorsal surface of the male's abdomen is applied to the ventral surface of the female's. In all matings beginning end-to-end, including Gryllidae, Gryllacrididae, Tettigoniidae, Blattodea, and Dermaptera, the ventral tips of the abdomens are apposed, the male being primarily or entirely responsible for this positioning. He approaches the female either with his abdomen twisted strongly *(Udeopsylla)* or upside-down in a burrow *(Neocurtilla)* or on the opposite side of a plant stem *(Orchelimum).*

POSITIONS ASSUMED DURING COPULATION.—With regard to body positions, orthopteran copulatory acts are of three kinds: (1) female-above, (2) end-to-end, and (3) female-above followed by end-to-end. The third kind of act may be subdivided into (a) lateral turning of the male from under the female *(Miogryllus)* and (b) dropping of the male, or vertical turning under the female *(Pterophylla).* Vertical turning leads to a venter-to-venter positioning of the abdomens, as occurs in all known acts beginning end-to-end. We can find no evidence from which it can be determined whether or not the history of the *Neocurtilla* act or other venter-to-venter, end-to-end acts involved sideways turning of the male during copulation. However, vertical turning during copulation is, in the Orthoptera examined, restricted to vegetation-inhabiting forms. *Cyphoderris,* living on low vegetation and on the soil surface, copulates for about seven minutes (two copulations); after engagement of the genitalia the male turns sideways out from under the female, and through a series of struggling movements finishes copulation turned more or less on his side at an angle to the female, his back toward her and his abdomen somewhat twisted.

There are three somewhat different ways that end-to-end mating can evolve from female-above mating (Fig. 12): (1) vertical turning after an initial engagement of the genitalia or hooking together of the abdomens, (2) lateral turning after hooking together of the abdomens, and (3) gradual shifting of the initial position during evolution with little specific turning during the act. The first two methods are indicated by our observations on Gryllidae and Tettigoniidae.

Lateral turning, as indicated, could involve either genitalic rotation or abdominal rotation. There are 2 possible kinds of rotation: (1) rotation of female or male genitalia on the abdomen and (2) rotation of the male

genitalia on the female genitalia. The twisting of the male abdomen in *Udeopsylla, Cyphoderris,* Blattodea, and Dermaptera, and the upside-down position of the *Neocurtilla* male, suggest that Orthoptera that mate end-to-end retain the ancestral positioning of the genitalia—the position evident today in crickets that mate in the female-above position.

ACTIONS OR MOVEMENTS DURING COPULATION.—Aside from turning of the bodies of the partners, discussed above, the most obvious and variable actions during copulation are thrusting and pumping movements by the male. Some of these, early in copulation, are evidently involved in proper positioning and engagement of the genitalic parts. But rhythmical pumping motions sometimes occur later, particularly in copulatory acts of long duration. We do not know the function of these movements, but they seem likely associated directly with insemination, since the chief difference between long and short acts is that in the former insemination occurs before the partners disconnect, in the latter after they disconnect. There is a corresponding delay following short acts before the female is permitted to remove the spermatophore. Fulton (1915) found that a spermatophore of *Gryllus pennsylvanicus* emptied in about 15 minutes, which approximates the minimal time between copulations in this genus.

DURATION OF COPULATION.—Copulatory acts in crickets vary in length from one second or less (Trigonidiinae:*Cyrtoxipha*) to 15–90 minutes, (Gryllinae:*Discoptila*). Insemination occurs chiefly or entirely *during* long copulations, chiefly or entirely *following* short copulations. Long acts are prevalent in groups in which dorsal secretions are mouthed by the female during copulation *(Hapithus, Amphiacusta, Discoptila)* and in groups in which coupling is firm *(Neocurtilla).* Short acts seem to be universal in groups without evident dorsal secretions or other attractants to the copulating female and seeming to use only tactual and acoustical signals during inter-copulatory behavior. On the other hand, at least one group (Oecanthinae) has dorsal secretions and acoustical signals available to the female in the copulatory position, yet disengages the genitalia during insemination.

REPETITION OF COPULATION.—Apparently no crickets have evolved a spermatophore large enough to inseminate a female fully; all species studied copulate repeatedly if uninterrupted. Intervals between successive copulations, as already indicated, seem related to (1) the male's rate of spermatophore construction and (2) whether insemination occurs during copulation or between copulations.

POSITIONS BETWEEN COPULATIONS.—Two general post- or inter-copulatory positions occur in crickets: (1) the male facing toward the female, generally at an angle toward her forebody (most genera), and (2) the pair facing away from one another, more or less end-to-end *(Miogryllus, Neocurtilla, Anurogryllus).* The latter is restricted to copulatory acts finishing end-to-end.

Alexander (1964) speculated that end-to-end copulation may sometimes have been initiated first as the second act in a series in which the pair begins female-above, terminates end-to-end, and stands end-to-end between copulations.

ACTIONS OR MOVEMENTS BETWEEN COPULATIONS.—In all cases the pair is more or less motionless between copulations, except for *Gryllodes,* in which the female seizes and chews the spermatophylax, and *Amphiacusta,* in which the male and female locate the empty spermatophore kept and dropped by the male and eat it. If a pair is accidentally separated, the female tends to wander but the male actually "searches" the immediate locality, moving swiftly and turning frequently with his antennae actively sweeping in front of him. Otherwise activity occurs only if the female moves, whereupon the male jerks forward and antennates her until she again becomes motionless. The male in all cases seems to touch some part of the female with his antennae before resuming courtship, and the female usually lacks opportunity to remove or eat the spermatophore (except in *Amphiacusta* and *Gryllodes*) until the male again begins to court.

BEHAVIOR, GENITALIC STRUCTURE, AND HABITAT

Many kinds of changes in the mode of life of a species could affect selective action on genitalia and mating behavior. The best clues concerning particular cases are parallel changes in distantly related species, such as the appearance of end-to-end copulation in burrowing Gryllidae and Gryllacrididae (Fig. 10) and in crevice-dwelling Dermaptera (Fulton, 1924) and Blattodea (Roth and Willis, 1958; Willis, 1966). Evidently the only other situation in which end-to-end mating has evolved in Orthoptera is among species living on small stems of vegetation, such as meadow grasshoppers (for example, *Orchelimum*). To some degree, a small grass stem or leaf causes restrictions in movement similar to those caused by burrowing life: to an orthoperan, a grass stem may in some ways be like a burrow turned inside-out.

Other evolutionary changes related directly to habitat or mode of life are not obvious to us. Indirect effects, however, could be unexpectedly important. Thus, changes in habitat or mode of life may affect genitalia ultimately because changes in courtship position are brought about. This would affect selective action on the initial position assumed during copulation, and in turn would change the effectiveness of certain features of the genitalia. It seems probable that genitalic evolution cannot be understood without understanding positions and behavior during courtship. If this is true, then genera or subfamilies which live in a single kind of habitat ought to show little variation in copulatory position and general

genitalic conformation; most of the genitalic variation among species in such groups should be related to reproductive isolation.

BEHAVIOR, GENITALIC STRUCTURE, AND PHYLOGENY

Which characteristics, and which combinations of characteristics, were primitive in orthopteroid insects? The following characteristics show wide ranges of variation in the fashions indicated:

1. Spermatophore tube (and spermathecal tube)	Short	Long
2. Spermatophore ampulla	External	Internal
3. Copulatory act	Short	Long
4. Dorsal secretions	Present	Absent
5. Tegminal position during copulation	Raised	Lowered
6. Coupling	Weak	Firm
7. Copulatory position	Female-above	Other

Characteristics on the left can be assumed from a parsimonious view to be primitive in Orthoptera. Unfortunately, this does not eliminate the problem of which variations of the other characteristics were combined with them during any particular primitive state. Thus, Caelifera have prolonged acts in which the male holds the spermatophore and coupling is firm; but the male mounts the female in an evidently derived position (Fig. 9f). Most cockroaches, on the other hand, mate in a probably primitive position and couple firmly; the spermatophore is more or less completely inserted and the act is prolonged (Roth and Willis, 1952; Stay and Roth, 1958). Males of *Udeopsylla* completely insert a miniature spermatophore during brief, rapidly repeated copulations.

Grasshoppers, cockroaches, and mole crickets have evolved along pathways favoring prolongation of the mating act by increasingly effective coupling devices; *Discoptila,* on the other hand, has accomplished essentially the same thing by elaborating female-attracting glands that function during copulation. The male holds the spermatophore ampulla during copulation.

At what time in orthopteran history was any particular combination of these characteristics present? The first pterygote copulatory act, derived from some form of indirect spermatophore transfer, must have been brief, and it seems most likely that insemination occurred following disconnection of the genitalia. Coupling must have been weak, and the copulatory position must have been female-above and female-side, with the male reaching beneath the tip of the female's abdomen (Fig. 11).

We can speculate upon a beginning, then, involving a short, female-above copulatory act, short spermatophore tube and spermathecal tube, probably an external ampulla, weak coupling, and some dorsal, female-attracting

secretions. If orthopteroids evolved from an insect that picked up the spermatophore from the ground or from a stalk, the spermatophore must have been large; if they evolved from one that transferred sperm via threads, as do various thysanurans, then the spermatophore must have been small.

According to Boldyrev (1929), and various information summarized by Uvarov (1966), caeliferans have both short and long spermatophore tubes and spermathecas; the spermatophore is formed shortly after coupling, and (at least in *Locusta*) part of the empty spermatophore is retained by the male and part by the female. In spite of the male-above position, caeliferan mating is quite like that of Ensifera and Blattodea. The male's genitalia protrude dorsally, and he must reach beneath the female's abdomen to engage them. There is little doubt that the Caelifera are derived from an ancestor that behaved as did the ensiferan and blattodean ancestor postulated above.

One cockroach, *Pycnoscelus surinamensis* (Linnaeus), starts copulation with the male on the female's back, reaching the tip of his abdomen under that of the female as in Caelifera, and terminates in the usual blattodean end-to-end position (Roth and Willis, 1958).

Photographs by Roth and Willis, showing the male lying on his back end-to-end with the female after engaging the genitalia and before standing in the end-to-end position, suggest that the male engages the genitalia by curling the tip of his abdomen under the tip of the female's abdomen so that his venter is apposed to her dorsum. In other words, this male-above position may be derived from an end-to-end terminal position (Fig. 12d) rather than from a female-above starting position.

The question is unanswered whether the ampulla of the spermatophore of the common orthopteran ancestor remained outside the female's body, as in all modern Gryllidae, Tettigoniidae, Acrididae, and most Gryllacrididae, or was inserted as in Blattodea and a few Gryllacrididae. However, the ampulla that is external by virtue of being held by the males of Caelifera and a few Gryllidae ought not to be confused with the ampullae that simply hang externally from the female's genital opening in most Ensifera. Without further evidence it seems impossible to compare these variations in regard to degree of departure from a primitive orthopteroid ancestor.

Gupta (1947) described in some detail the spermatophore of a cockroach, *Periplaneta americana* (Linnaeus), and its formation. This spermatophore is a three-layered capsule with no tube, resembling in its entirety the ampulla of a *Gryllus* spermatophore. The inner layer is secreted by large peripheral accessory glands during the second, third, and fourth days of adulthood, the middle layer by the epithelium of the ejaculatory duct during the fifth and sixth days of adulthood, the outer layer by the phallic gland outside the ejaculatory duct while the spermatophore is being attached to the spermathecal papilla of the female. Insemination in cockroaches occurs chiefly

following the copulatory act. According to Stay and Roth (1958), copulations in *Diploptera punctata* (Eschscholtz) lasted 24–63 minutes, averaging 38 minutes. Males that had been adults less than 10 days spent longer periods in copula than males adult 15 days or longer. Females rejected males after one mating, but males would copulate again if another female were provided. Such males stayed in copula longer and produced smaller spermatophores. Duration of the act apparently depends on the time required to construct and transfer the spermatophore, which does not begin to form until after the pair has coupled. One male mated 17 minutes after transferring a 1.7-mm spermatophore during a 30-minute copulation, and in this second act remained coupled 25 hours and produced a 1.0-mm spermatophore.

Behavior, Genitalic Structure, and Speciation

Although our data are broadly comparative within only a few genera (particularly *Gryllus*), together with intergeneric comparisons they indicate that neither the activities nor the structures associated with copulation and post-copulatory behavior are very often species-specific. If this information is combined with the evidence that pair-forming mechanisms may *always* be species-specific among sympatric, synchronic species (R. D. Alexander, 1962; Ehrman, 1964; Lloyd, 1966), and the evidence that differences in courtship stimuli usually exist at the species level (mostly from reduced matings in interspecific pairings in hybridization experiments), then strong support is provided for the frequently expressed idea that early portions of the sexual sequence are reinforced in the context of reproductive isolation, almost to the exclusion of later portions. Genitalia and copulatory behavior, then, are either rarely or not at all changed directly in the context of reproductive isolation, and do not usually undergo change in direct association with the speciation process. At least in crickets and their close relatives, this leaves the general context of intraspecific compatibility to account for the initiation of most evolutionary changes in genitalia and copulatory behavior, interspecific incompatibility to account for most changes in pair formation and courtship. The only exceptions obvious in this study are the direct and indirect consequences of drastic shifts in mode of life, such as result in mating in burrows or on small stems of plants. Ultimately, however, changes in any aspect of mating behavior can shift selective action on other aspects of the mating sequence and result in additional changes that are equally evident, or, even, that seem more striking.

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LITERATURE CITED

ALEXANDER, A. J.
  1962 Biology and behavior of *Damon variegatus* Perty of South Africa and *Admetus barbadensis* Pocock of Trinidad, W.I. Zoologica, 47:25–37.
ALEXANDER, R. D.
  1957 The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: *Acheta*). Ann. Ent. Soc. Amer., 50:584–602.
  1959 The courtship and copulation of *Pasimachus punctulatus* Haldeman (Coleoptera:Carabidae). Ann. Ent. Soc. Amer., 52:485.
  1961 Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). Behaviour, 17:130–223.
  1962 The role of behavioral study in cricket classification. Syst. Zool., 11:53–72.
  1964 The evolution of mating behavior in arthropods. *In:* Insect reproduction, K. C. Highman, Ed., Symp. No. 2, Royal Ent. Soc., London, 78–94.
ALEXANDER, R. D., AND W. L. BROWN, JR.
  1963 Mating behavior and the origin of insect wings. Occ. Papers Mus. Zool. Univ. Mich., 628:1–19.
ALEXANDER, R. D., AND T. E. MOORE
  1962 The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). Miscl. Publ. Mus. Zool., Univ. Mich., 121:1–59.
ALEXANDER, R. D., AND D. OTTE
  1967 Cannibalism during copulation in the brown bush cricket, *Hapithus agitator* (Gryllidae). Fla. Ent., 50:79–87.
ALEXANDER, R. D., AND T. J. WALKER
  1962 Two introduced field crickets new to eastern United States (Orthoptera:Gryllidae). Ann. Ent. Soc. Amer., 55:90–94.

BARR, T. C.
    1965 The *Pseudanopthalmus* of the Appalachian Valley (Coleoptera:Carabidae). Amer. Midl. Nat., 73:31–72.

BAUMGARTNER, W. J.
    1905 Observations on some peculiar habits of the mole crickets. Science N.S., 21:855.
    1911 Observations on the Gryllidae: IV. Copulation. Kans. Univ. Sci. Bull., 5:323–345.

BEHEIM, D.
    1942 Über den taxonomischen und isolierenden Wert der Forcepsvariationen einiger Caraboidea. Z. Morphol. u. Ökol. Tiere, 39:21–46.

BOLDYREV, B. TH.
    1913 Die Begattung und Spermatophoren bei der Maulwurfsgrille. Zool. Anz., Leipzig, 42:592–605.
    1915 Contributions a l'etude de la structure des spermatophores et des particularities de la copulation chez Locustodea et Gryllodea. Horae Soc. Ent. Rossicae, Petrograd 1914(1915), 41:1–245.
    1927*a* Einige Daten über die Spermatophoren-Befruchtung bei den Insekten. Rev. Russ. d'Ent., Leningrad, 21:133–136.
    1927*b* Copulation and spermatophores of *Gryllomorpha dalmatina* (Osck.) (Orthoptera:Gryllidae). Eos, Madrid, 3:279–288.
    1928*a* Biological studies on *Bradyporus multituberculatus* F. W. Eos, 4:13–56.
    1928*b* Einige Episoden aus dem Geschlechtsleben von *Discoptila fragosoi Bol.* (Orthoptera,Gryllidae). Rev. Russe Ent., 22:137–147.
    1929 Spermatophore fertilization in the migratory locust (*Locusta migratoria* L.). Repts. Appl. Ent., Leningrad, 4:189–218.

BRINCK, P.
    1956 Reproductive system and mating in Plecoptera. Opusc. Ent., 21:57–96.
    1957 Reproductive system and mating in Ephemeroptera. *Ibid.*, 22:1–37.
    1962 Die Entwicklung der Spermaübertragung der Odonaten. Int. Congr. Ent., Vienna, 11:715–718.

CHOPARD, L.
    1938 La biologie des Orthoptères. Vol. XX of Série A. Encyclopédie Ent. P. Lechevalier, Paris, 541 pp.
    1951*a* Faune de France, 56:Orthopteroides. P. Lechevalier, Paris:359 pp.
    1951*b* Les divisions du genre *Gryllus* basees sur l'etude de l'appareil copulateur (Orthoptera, Gryllidae). Eos, 37:267–287.

COUSIN, G.
    1938 La néoténie chez *Gryllus campestris* et ses hybrids. Bull. Biol. de la France et de la Belgique, 72:79–118.

DOBZHANSKY, TH.
    1951 Genetics and the origin of species. Columbia Univ. Press, New York, 364 pp.

DUFOUR, L.
    1844 Anatomie général de Diptères. Ann. Sci. Nat., 1:244–246.

EADES, D. C.
    1964 General biology and geographic variation of *Ceuthophilus guttulosus* Walker (Orthoptera:Gryllacrididae:Rhaphidophorinae). Trans. Amer. Ent. Soc., 90:73–110.

EHRMAN, L.
    1964 Courtship and mating behavior as a reproductive isolating mechanism in *Drosophila*. Amer. Zoologist, 4:147–153.

EMERSON, A. E.
    1961   Vestigial characters of termites and processes of regressive evolution. Evolution, 15:115–131.
FULTON, B. B.
    1915   The tree crickets of New York: life history and bionomics. N. Y. Agric. Exp. Sta. Tech. Bull., 42:3–47.
    1924   Some habits of earwigs. Ann. Ent. Soc. Amer. 17:357–367.
    1931   A study of the genus *Nemobius* (Orthoptera:Gryllidae). *Ibid.,* 24:205–237.
    1956   The genus *Anaxipha* in the United States (Orthoptera:Gryllidae). Jour. Elisha Mitchell Sci. Soc. 72:222–243.
GABBUTT, P. D.
    1959   The bionomics of the wood cricket, *Nemobius sylvestris* (Orthoptera:Gryllidae). Jour. Animal Ecol., 28:15–42.
GERHARDT, U.
    1913   Kopulation und spermatophoren von Grylliden und Locustiden. Teil 1. Zool. Jahrb. Jena., 35:415–530.
    1914   Copulation und spermatophoren von Grylliden und Locustiden. II. *Ibid.,* 37:1–64.
GHOURI, A. S. K.
    1961   Home and distribution of the house cricket *Acheta domesticus* L. Nature, 192:1000.
GREGORY, G. E.
    1965   The formation and fate of the spermatophore in the African migratory locust, *Locusta migratoria migratorioides* Reiche and Fairmaire. Jour. Exp. Biol., 42:423–435.
GUPTA, P. D.
    1947   On the structure and formation of spermatophore in the cockroach, *Periplaneta americana* (Linn.). Indian Jour. Ent. New Delhi, 8:79–84.
HAHN, E.
    1958   Untersuchungen über die Lebensweise und Entwicklung der Maulwurfsgrille (*Gryllotalpa vulgaris* Latr.) im Lande Brandenburg. Beiträge Ent., 8:334–365.
HAYSLIP, N. C.
    1943   Notes on biological studies of mole crickets at Plant City, Florida. Florida Ent., 26:33–46.
HÖRMANN-HECK, S. VON
    1957   Untersuchungen über den Erbgang einiger Verhaltensweisen bei Grillenbastarden (*Gryllus campestris* L., *Gryllus bimaculatus* De Geer). Z. Tierpsychol., 14:137–183.
HUBBELL, T. H.
    1938   New cave-crickets from Yucatan with a review of the Pentocentrinae, and studies on the genus *Amphiacusta* (Orthoptera:Gryllidae). Article XVI, Pp. 191–233. *In:* Pearce, A. S. *et al.,* Fauna of the caves of Yucatan. Carnegie Inst. Wash. Publ. No. 491, iv + 304 pp.
HUBER, F.
    1955   Sitz und Bedeutung nervösen Zentren für Instinkthandlungen beim Männchen von *Gryllus campestris* L. Z. Tierpsychol., 12:12–48.
    1962   Central nervous control of sound production in crickets and some speculations on its evolution. Evolution, 16:429–442.
JEANNEL, R.
    1941   L'isolement, facteur de l'evolution. Rev. Franc. Ent., 8:101–110.

KHALIFA, A.

  1949   The mechanism of insemination and the mode of action of the spermatophore in *Gryllus domesticus*. Quart. Jour. Micr. Science, 90:281–292.

  1950   Sexual behavior in *Gryllus domesticus* L. Behaviour, 2:264–274.

KREKELER, C. H.

  1958   Speciation in cave beetles of the genus *Pseudanopthalmus* (Coleoptera, Carabidae). Amer. Midl. Nat., 59:167–189.

LESPES, C.

  1855   Memoir sur les spermatophores des Grillons. Ann. Sci. Nat. Paris, France, 3:366–377.

LIPOVSKY, L. J., G. W. BYERS, AND E. H. KARDOS

  1957   Spermatophores—the mode of insemination of chiggers (Acarina:Trombiculidae). Jour. Parasit., 43:256–261.

LLOYD, J. E.

  1966   Studies on the flash communication system in *Photinus* fireflies. Miscl. Publ. Mus. Zool., Univ. Mich., 130:1–95.

LOVE, R. E.

  1966   A revision of the Mogoplistinae (Orthoptera:Gryllidae) of the United States. Master's thesis, University of Florida, vii + 114 pp.

QUADRI, M. A. H.

  1940   On the development of the genitalia and their ducts of orthopteroid insects. Trans. Roy. Ent. Soc. London, 90:121–175.

RANDELL, R. L.

  1964   The male genitalia in Gryllinae (Orthoptera:Gryllidae) and a tribal revision. Canad. Ent., 96:1565–1607.

RICHARDS, A. M.

  1961   The life history of some species of Rhaphidophoridae (Orthoptera). Trans. Roy. Soc. New Zealand, Zool., 1:121–137.

RICHARDS, O. W.

  1927   Sexual selection and allied problems in the insects. Biol. Rev., 2:298–364.

ROTH, L. M., AND B. STAY

  1961   Oöcyte development in *Diploptera punctata* (Eschscholtz) (Blattaria). Jour. Insect Physiol., 7:186–202.

ROTH, L. M., AND E. R. WILLIS

  1952   A study of cockroach behavior. Amer. Midl. Nat., 47:66–129.

  1958   The biology of *Panchlora nivea* with observations on the eggs of other Blattaria. Trans. Amer. Ent. Soc., 83:195–207.

SCHALLER, F.

  1954   Die indirekte Spermatophoren-überträgung und ihre Probleme. Forsch. Fortschr. deutsch. Wiss., 28:321–326.

SHULL, A. F.

  1946   Inheritance in lady beetles. IV. The form of the chitinous male genitalia in crosses of the species *Hippodamia quinquesignata* and *H. convergens*. Genetics, 31:291–303.

SNODGRASS, R. E.

  1937   The male genitalia of orthopteroid insects. Smithson. Inst. Miscl. Publ., 96:1–107.

SPANN, L.

  1934   Studies on the reproductive systems of *Gryllus assimilis* Fabr. Trans. Kansas Acad. Sci., Manhattan, 37:299–340.

SPIELMAN, A.

    1964   The mechanics of copulation in *Aedes aegypti*. Biol. Bull., 127:324–344.

    1966   The functional anatomy of the copulatory apparatus of male *Culex pipiens* (Diptera:Culicidae). Ann. Ent. Soc. Amer., 59:309–314.

STAY, B., AND L. M. ROTH

    1958   The reproductive behavior of *Diploptera punctata* (Blattaria:Diplopteridae). Proc. 10th Internatl. Congr. Ent., 2:547–552.

STÜRM, H.

    1952   Die Paarung bei *Machilis* (Felsenspringer). Naturwissenschf., 39:308.

TURNER, C. L.

    1915   Breeding habits of *Ceuthophilus latens*, the camel cricket. Bull. Wisc. Nat. Hist. Soc. (N. Ser.), 13:32–41.

    1916   Breeding habits of the Orthoptera. Ann. Ent. Soc. Amer., 9:117–135.

TUXEN, S. L. (ED.)

    1956   Taxonomists' glossary of genitalia in insects. Ejnar Munksgaard, Copenhagen. 284 pp.

UVAROV, B. P.

    1966   Grasshoppers and locusts. A handbook of general acridology. Cambridge Univ. Press, Cambridge, England., xi + 481 pp.

VALENTINE, J. M.

    1932   A classification of the genus *Pseudanophthalmus* Jeannel (Fam. Carabidae) with descriptions of a new species and notes on distribution. Jour. Elisha Mitchell Sci. Soc., 47:261–280.

    1945   Speciation and raciation in *Pseudanophthalmus* (cavernicolous Carabidae). Trans. Conn. Acad. Arts Sci., 36:631–672.

WALKER, E. M.

    1922   The terminal structures of Orthopteroid insects: a phylogenetic study (Part II). Ann. Ent. Soc. Amer., 15:1–76.

WALKER, T. J., AND A. B. GURNEY

    (in press)   The metanotal gland as a taxonomic character in *Oecanthus* (Orthoptera, Gryllidae) of the United States. Proc. Ent. Soc. Wash.

WEST, M. J., AND R. D. ALEXANDER

    1963   Sub-social behavior in a burrowing cricket *Anurogryllus muticus* (De Geer) (Orthoptera:Gryllidae). Ohio Jour. Sci., 63:19–24.

WIGGLESWORTH, V. B.

    1950   The principles of insect physiology. Methuen & Co., Ltd., London. viii + 544 pp.

WILLIS, E. R.

    1966   Biology and behavior of *Panchlora irrorata*, a cockroach adventive on bananas (Blattaria:Blaberidae). Ann. Ent. Soc. Amer. 59:514–516.
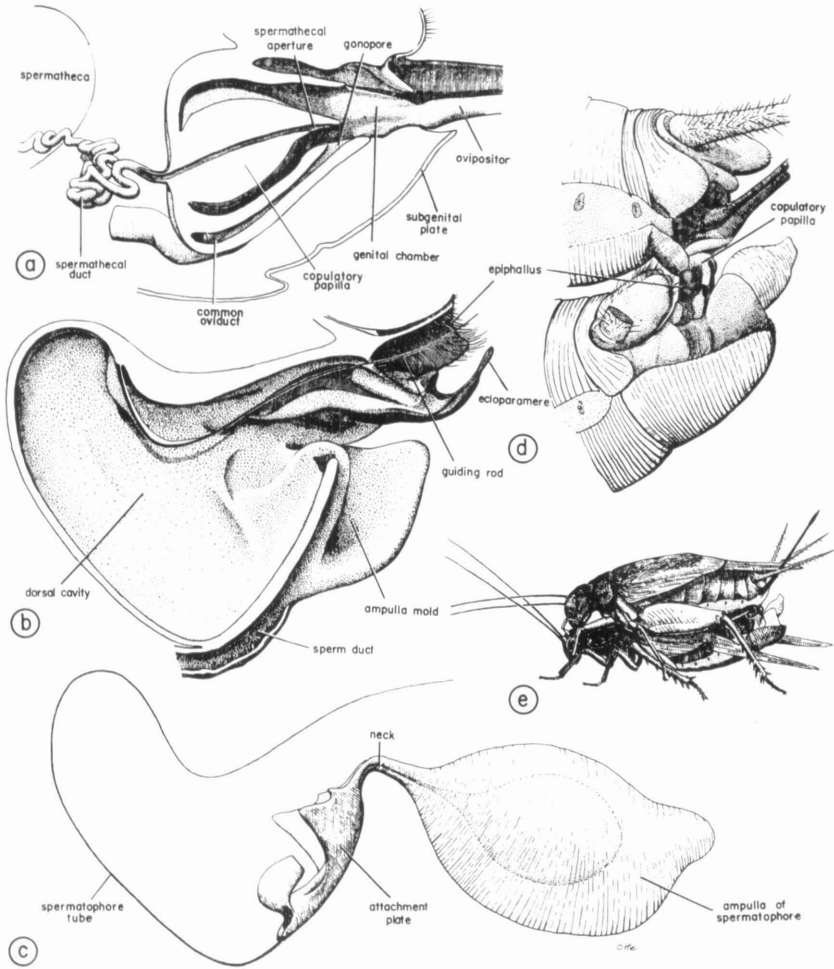
FIG. 1. Genitalia and copulation of the house cricket, *Acheta domesticus*: (a) sagittal section of female; (b) sagittal section of male with spermatophore removed; (c) spermatophore; (d) male and female terminalia in the copulatory position (female-above); (e) copulating pair (female-above). All drawings from the left side.
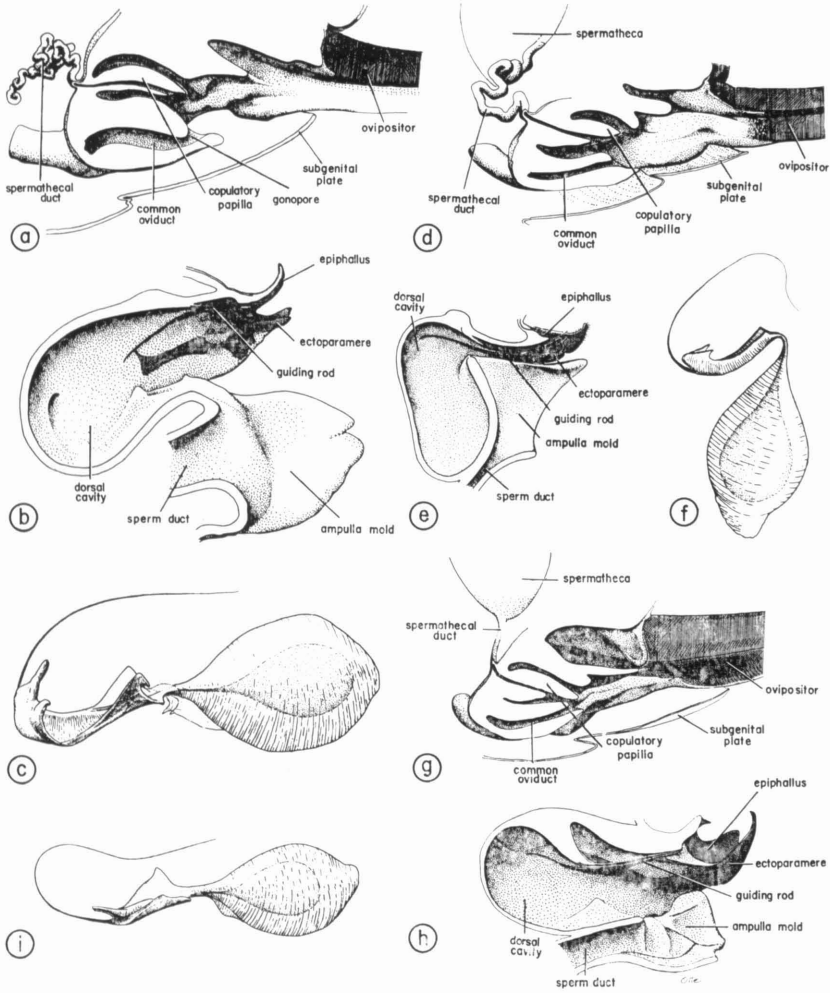
FIG. 2. Female genitalia, male genitalia, and spermatophores of *Gryllus* sp. (Mexico): (a–c), *Miogryllus verticalis* (d–f), and *Valerifictorus micado* (g–i). All drawings from left; genitalia in sagittal section.
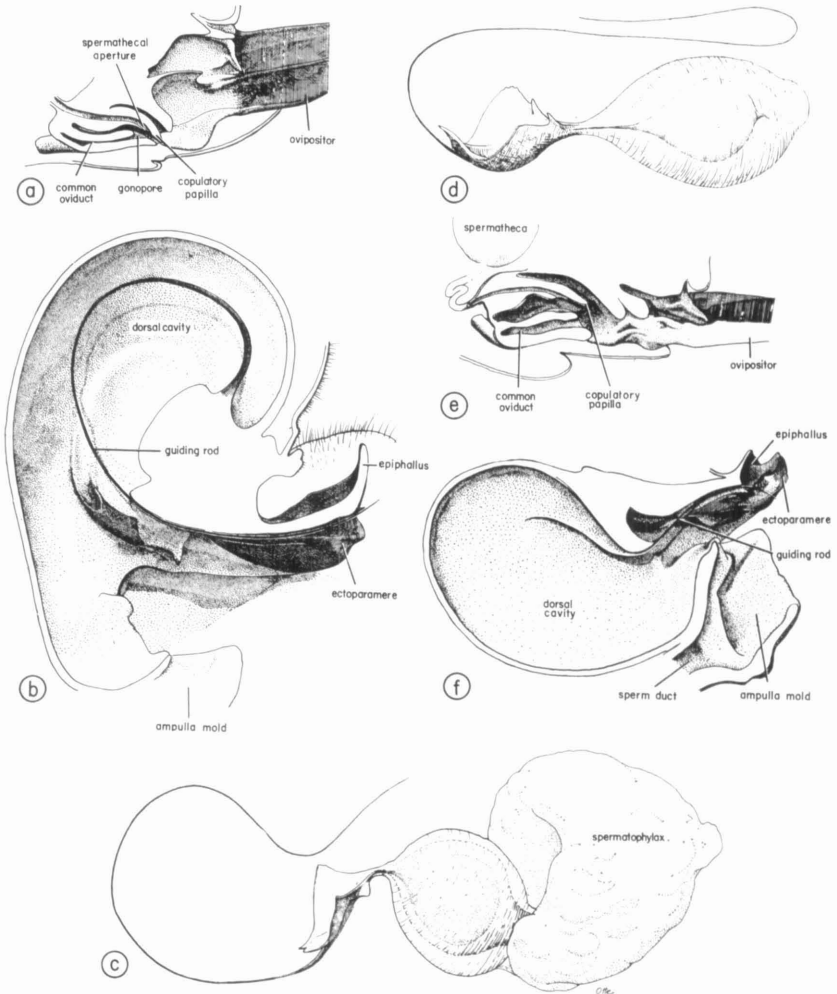
FIG. 3. Female genitalia, male genitalia, and spermatophores of *Teleogryllus commodus* (a, b, d) and *Gryllodes sigillatus* (e, f, c). All drawings from left; genitalia in sagittal section.
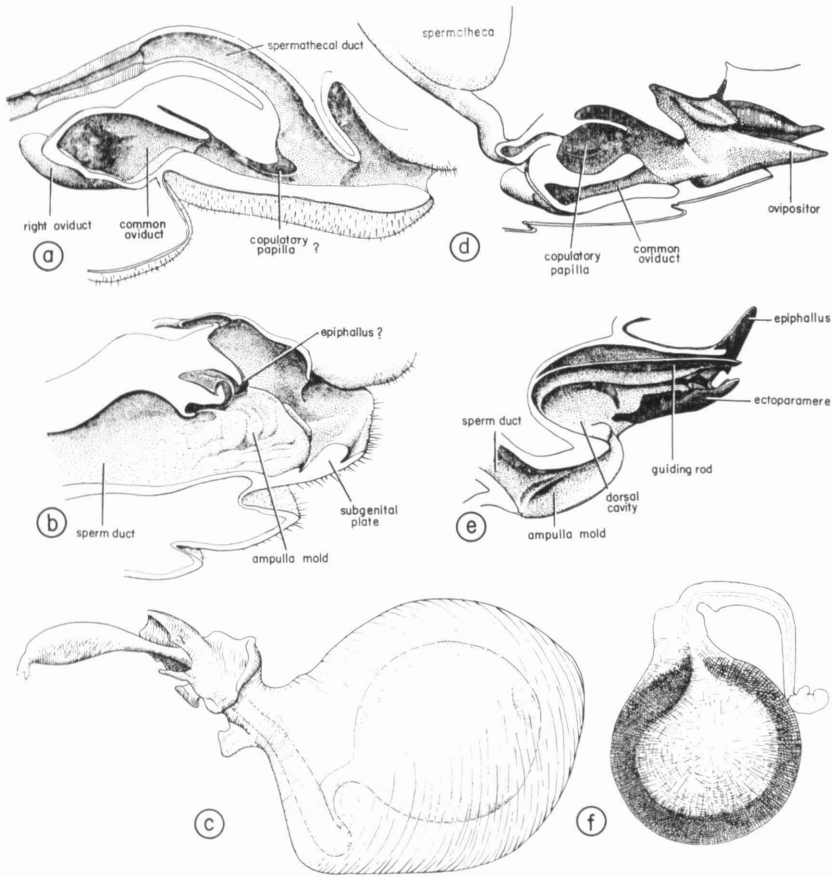
FIG. 4. Female genitalia, male genitalia, and spermatophores of the subterranean cricket, *Neocurtilla hexadactyla* (a–c) and *Anurogryllus muticus* (d–f). All drawings from left; genitalia in sagittal section.
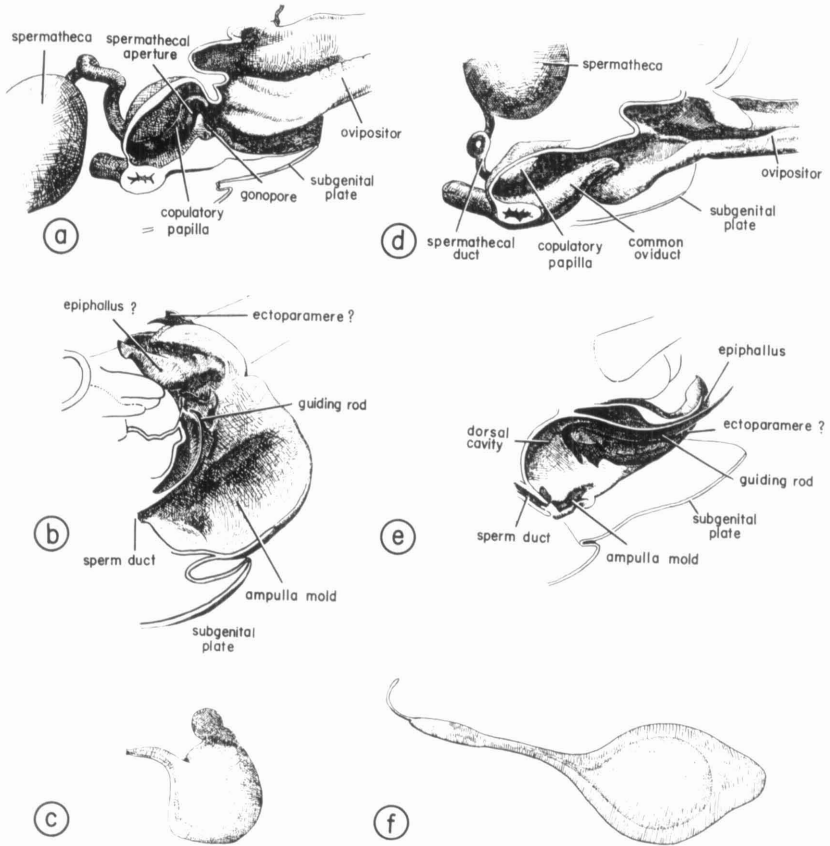
FIG. 5. Female genitalia, male genitalia, and spermatophores of *Amphiacusta* sp. (Puerto Rico) (a–c) and *Hapithus agitator* (d–f). All drawings from left; genitalia in sagittal section.
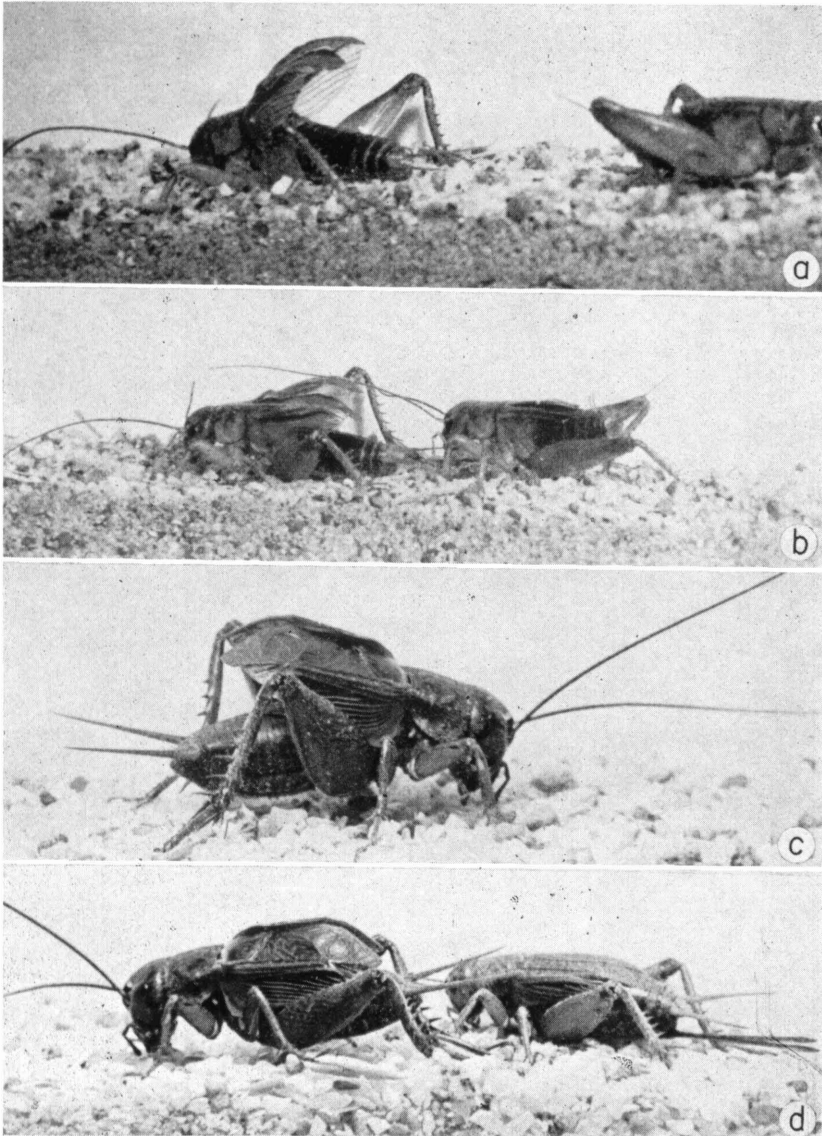
FIG. 6. Pre-mating and aggressive behavior in *Anurogryllus muticus* and *Gryllus firmus;* (a) aggressive stridulation in *Anurogryllus;* (b) courtship of *Anurogryllus* (male in front); (c) calling in *Gryllus;* (d) courtship in *Gryllus* (male in front). During aggression, the tegmina are slightly raised from the calling position in both genera.
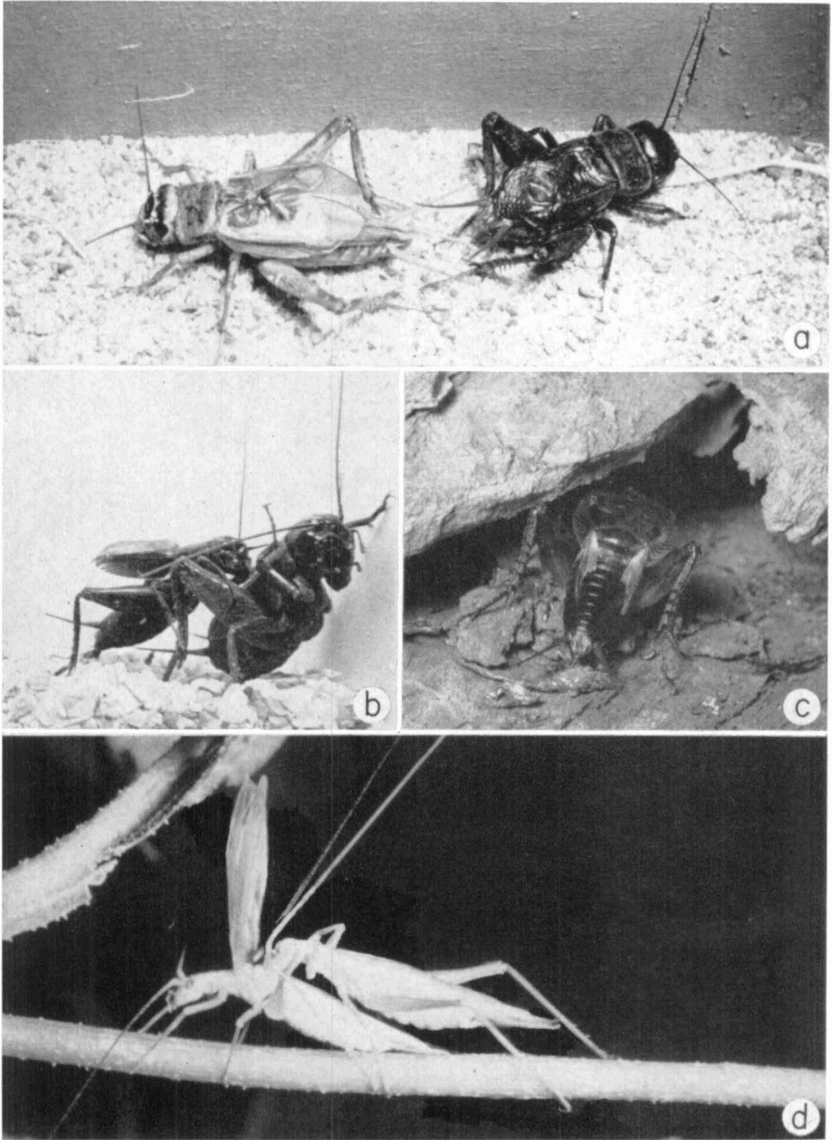
FIG. 7. Pre-mating, post-mating, and aggressive behavior in various crickets: (a) male of *Acheta domesticus* (left) courting a male of *Gryllus veletis* (right); (b) male of *Gryllus firmus* attacking a much larger male after copulation and, after a prolonged fight, causing his retreat; (c) micropterous male of *G. veletis* calling from his lair under the bark of an old stump; (d) a pair of tree crickets (*Oecanthus* sp.) following copulation, the female feeding on secretions of the male's metanotal gland.
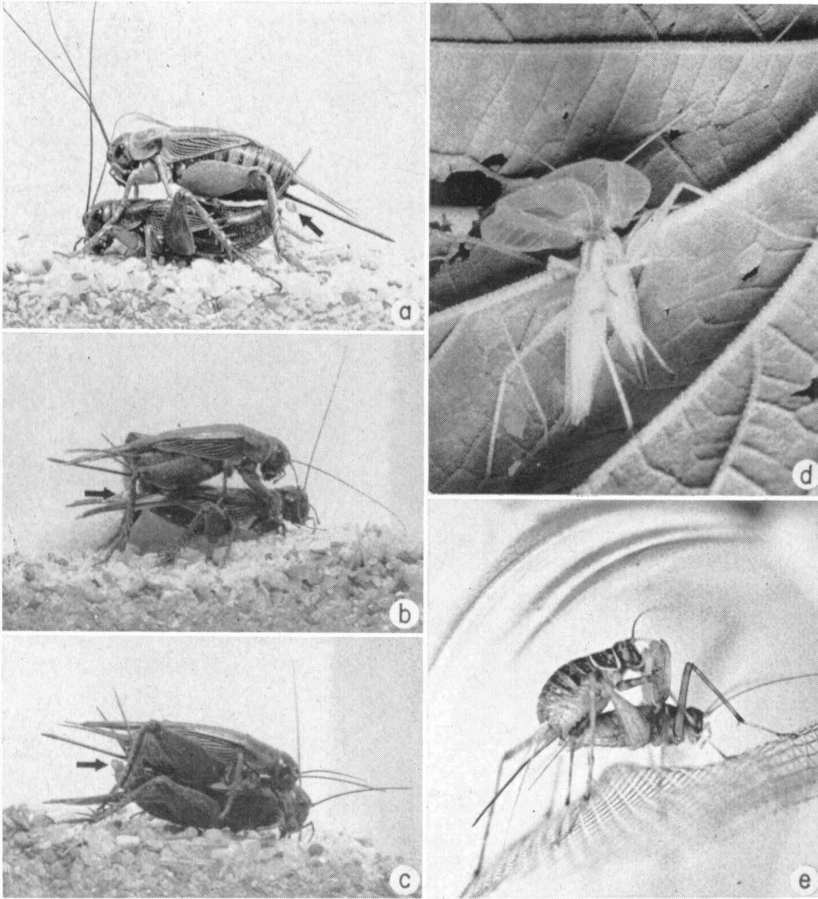
Fig. 8. Mating behavior in several crickets (female-above in all cases): (a) a pair of *Gryllus firmus* immediately following attachment of the spermatophore; (b, c) pairs of *Teleogryllus commodus* just prior to attachment of the spermatophore; (d) a pair of tree crickets (*Oecanthus* sp.) just prior to copulation; (e) a copulating pair of *Amphiacusta* sp. Arrows indicate spermatophores.
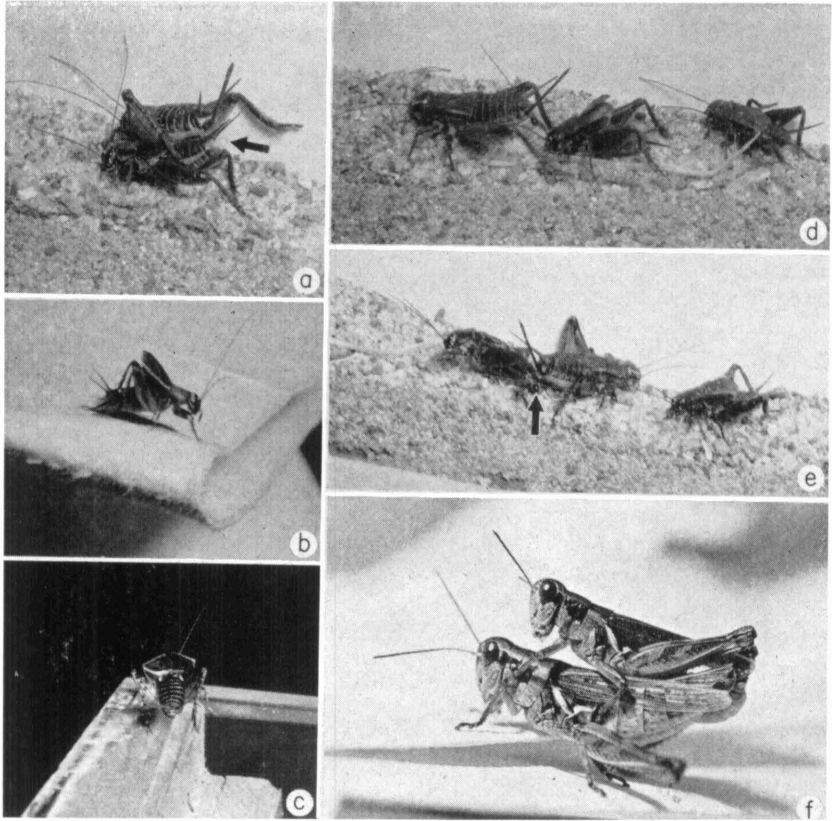
FIG. 9. Calling, courtship, and copulation in crickets and grasshoppers: (a) a pair of *Miogryllus verticalis* in the initial position assumed during copulation (female-above); (b, c) a calling male of *Nemobius maculatus*, side view and rear; (d) male of *Miogryllus verticalis* (center) chirping during his post-copulatory interaction with a female (left); (e) male of *M. verticalis* (right) courting near a pair already in copula and in the terminal (end-to-end) position; (f) a copulating pair of the crytacanthacridine grasshopper, *Melanoplus confusus* Scudder (male-above). Arrows indicate spermatophores.
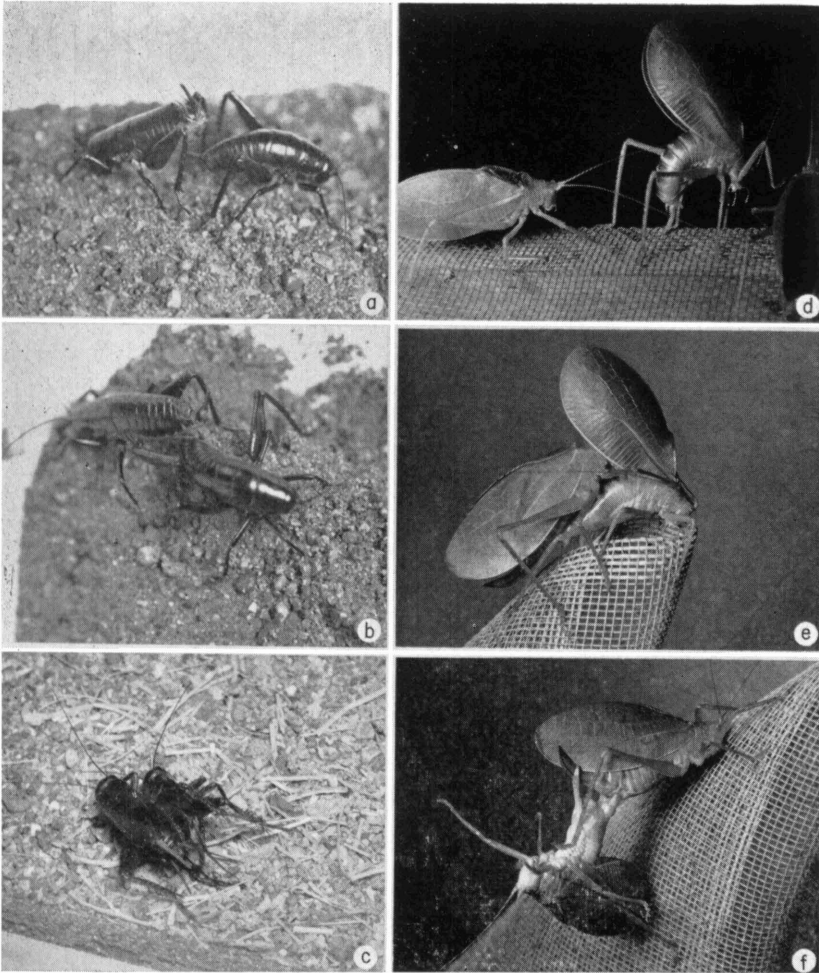
Fig. 10. Courtship and copulation in various Ensifera: (a) the end-to-end approach to copulation of the subterranean gryllacridid, *Udeopsylla robusta;* (b) copulation in *U. robusta;* (c) a copulating pair of *Teleogryllus commodus* falling sideways without separating; (d) courtship by a male of *Pterophylla camellifolia* (right) upon his being touched by the antennae of another male (left); (e) mounting by a female of *P. camellifolia* approaching a courting male from behind; (f) the end-to-end position assumed by the pair following engagement of the genitalia by the male (left). Note the placement of the male's subgenital plate with its slot against the female's ovipositor. This was not a successful copulation; it terminated at this point. Evidently the female was unresponsive, even though she repeatedly mounted the courting male (responding to dorsal secretions?) when placed behind him.

BLATTODEA

MANTODEA

PHASMODEA

CAELIFERA

GRYLLIDAE

TETTIGONIIDAE

GRYLLACRIDIDAE

ENSIFERA

TRIASSIC

PALEOZOIC
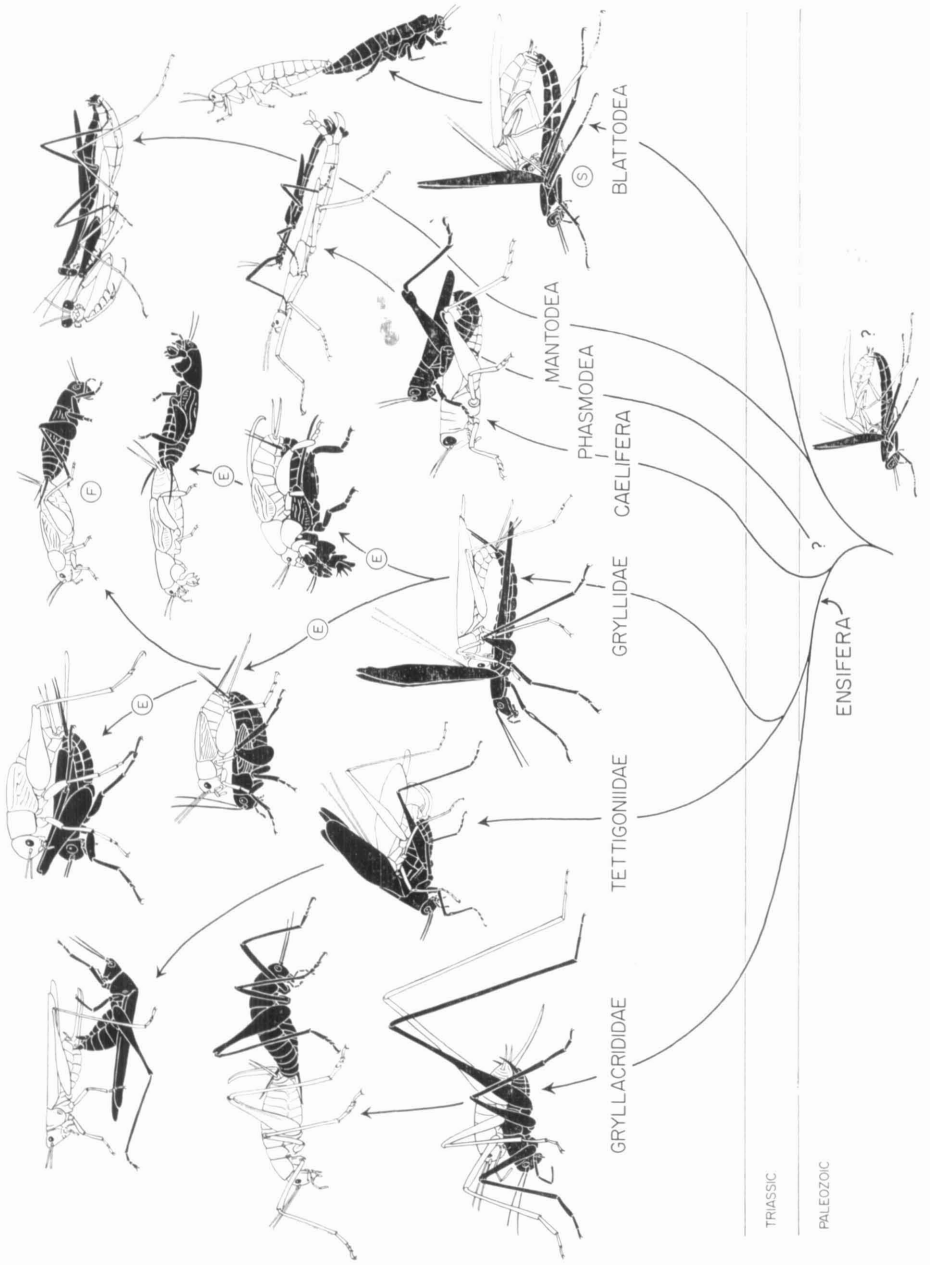
FIG. 11. Diagram of the probable relationships of major groups of Orthoptera and positions assumed during copulation. Males black, females white. Some species start and finish in each position shown, except those labelled (S) (start only) or (F) (finish only). Arrows marked (E) designate position differences not known to occur as changes during the copulation of any single species. Otherwise arrows between different positions within taxonomic groups indicate both that some species change from one position to the other during copulation and, except for (F) and (S) positions, that some species differ from one another in the same regard. Drawing at bottom of chart represents probable copulatory position of the postulated cockroach-like orthopteroid ancestor. At least one blattodean begins male-above (see Fig. 12) and some Caelifera turn end-to-end (more or less accidentally) during copulation.
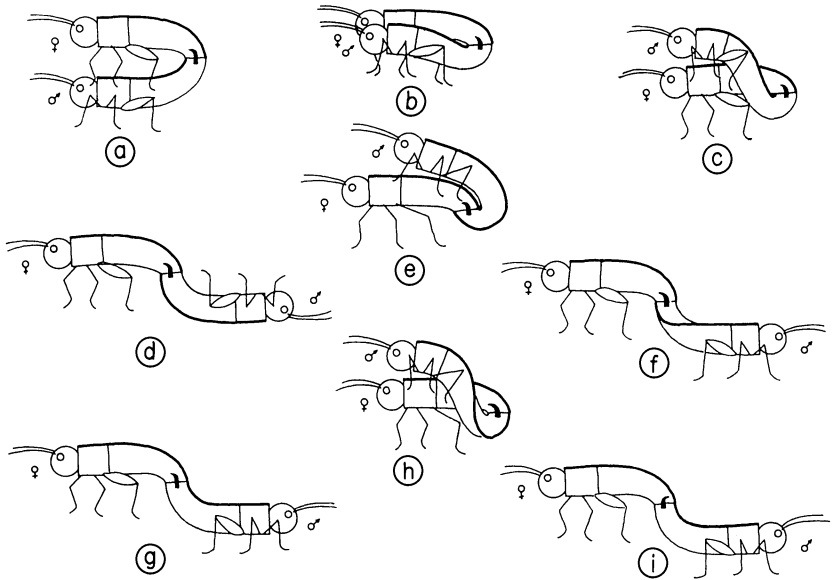
FIG. 12. Diagrammatic representation of probable evolutionary changes in positioning of the bodies and genitalia of male and female Orthoptera during mating: (a) prevalent, and probably primitive, female-above position, (b) closely similar male-side position, (c) male-above position evidently derived from female-above or male-side, (d) end-to-end position evidently derived from female-above by vertical turning of male, (e) male-above position (known only in one cockroach genus) probably derived from (d), (f) end-to-end position probably derived from (d) by male twisting upright, (g) end-to-end position in which male and female genitalia (or both) rotate inside possessor, (h) hypothetical male-above position derivable from (g), (i) end-to-end position in which male and female genitalia rotate in some way upon one another. These various positions are known to occur among major orthopteran groups as follows: Mantodea (c); Phasmodea (c); Blattodea (f), (a–b–f), (e–d–f); Caelifera (c), (c–b–f), (b–c); Ensifera:Gryllacrididae (a) (a–b–f), (f); Ensifera:Tettigoniidae (a), (d), (f), (a–d), (a–d–f); Ensifera:Gryllidae (a), (d), (a–d–g), (a–b–i).