

The Role of Behavioral Study in Cricket Classification

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Introduction

IT IS no longer difficult to secure general agreement among biologists that the best classification of living organisms will eventually take into account a wide range of attributes, functional as well as structural. There is even rather general verbal agreement that taxonomists should make special efforts to accumulate a variety of different kinds of evidence, although it is not always broadly evident in the taxonomic literature that such an attitude has actually become a matter of practice.

The prime questions now are not *whether* to use behavior and physiology and ecology, but *when* and *how* to use them. In terms of animal groups and stages of classification, when are these kinds of information superfluous to classification, when are they merely useful adjuncts, and when is it inadvisable (or inexcusable) to proceed without them?

These are not trivial questions. For one thing, we cannot assume that merely having before us a wide range of characteristics insures that historical relationships will fall inexorably into place without critical and knowledgeable evaluation of the significance of each kind of information in each specific context. And for another, the taxonomist's day is only 24 hours long, and the field is not over-populated; if he is going to find it necessary to go out and gather information on any large scale, then we ought to have some rather sound basis for presuming to suggest how he should go about it.

I have certain rather strong biases concerning these questions, which have developed principally as a result of an admittedly brief and specialized taxo-

nomie experience with three families of insects: Gryllidae (crickets), Tettigoniidae (katydids and long-horned grasshoppers), and Cicadidae (cicadas). I will content myself here with describing a few of these biases, attempting to account for them, and drawing what seem to be appropriate conclusions or generalizations. Crickets will be the principal source of illustration, and behavior will be the principal topic; but I will include other insect groups and other kinds of information when appropriate. I have the feeling that most of my generalizations suffer a significant loss of flavor—for one reason or another—when they are applied to the higher vertebrates. So when I speak generally, my principal interest is the classification of the Arthropoda, where vast problems remain, and where as a result, important information for zoogeography, evolution, and many specific aspects of zoology remains almost completely unavailable. As an example, just the four families of "acoustical" insects—Gryllidae, Tettigoniidae, Acrididae, and Cicadidae—include nearly as many species and world-wide groups as do all the vertebrates combined. Because of the state of their taxonomy, we have very few ideas as to how their various sub-groups came to be where they are—in a sense, we do not know *where* they are because we do not know *what* they are. All too often, we are merely shuffling names.

The State of Cricket Classification

Fossil evidence indicates that the crickets (Gryllidae) became a separate evolutionary line 150-200 million years ago, probably during the Jurassic Period. Their most similar relatives today are

the Tettigoniidae (katydids and long-horned grasshoppers) and the Gryllacrididae (camel and cave "katydids"); the three families are usually grouped together to make up the Tettigonioidea. Presumably the common ancestor of the Tettigonioidea and the Acridoidea (short-horned grasshoppers or locusts) diverged from a cockroach-like ancestor in the late Paleozoic Era (Zeuner, 1939; Ander, 1939).

Linnaeus classified the first crickets in 1758, and since the beginning of the 19th century there have nearly always been three or four contemporary taxonomists in the world describing new cricket species and otherwise adjusting their classification. Today there are about 2000 recognized cricket species, arranged in some 300 genera and 16 subfamilies (or families, depending at this moment upon the classifier's preference); 20-40 new species are still being described every year.

From the species level on up, cricket classification has always been based almost solely on morphological considerations—more precisely on the external morphology of dried, pinned specimens. There are many vexing systematic problems today, at all levels. A good number of them have been explored and re-explored almost exhaustively from the "morphological" angle, which in most cases is an apt description of the methods employed, despite the fact that all available information might have been taken into account. Scarcely any biological information is available today for the vast majority of crickets. Outside Europe (about six species) and eastern North America (about 95 species), significant aspects of behavior, ecology, and life history have probably been published for fewer than 25 species.

There is only one place in the world where the classification of a reasonably large number of cricket species can be said to be approaching stability, and this is in North America. It seems now that

in a few years anyone who wishes will be able to identify for himself any of the stridulating North American crickets, read about how and where it lives, and select appropriate species for particular kinds of experimental investigations. The changes making this prediction possible began on a large scale only a few years ago, and there have been only two or three investigators involved, each engaged in other research as well as cricket taxonomy. But the principal groundwork for a satisfactory classification of North American crickets was laid between 1915 and 1956, by the late Bentley B. Fulton's straightforward analyses of cricket behavior and its significance in taxonomic contexts. Fulton's work not only directly stimulated all four of the present North American cricket biologists (Richard Davenport, Robert Bigelow, Thomas Walker, and the present writer), but it also gave them most of the clues that have accelerated progress toward a reasonable classification.

Changes in the classification of North American crickets since 1957 have indeed been striking. Apart from nomenclatural problems, which have often been oppressive, the number of recognized species has already increased by 14 (Alexander, 1957a; Thomas and Alexander, 1957; Alexander and Thomas, 1959; Walker, in press), and 28 additional species have been discovered which are either completely new to science or else were represented by names synonymized 50 or 100 years ago (T. J. Walker and R. D. Alexander, unpubl. information). The result will be almost a doubling of the number of recognized species. Few species have distributions closely resembling those previously presumed for them, and practically all of the species that would be termed "sibling" by most definitions have been clarified for the first time. These changes are important for many reasons, but here I am concerned with the fact that the synthesis is being effected across a period of a few years by a few people,

following a half century during which fewer than ten species were described, and during which scarcely any other changes in the classification of the group were accomplished. I think it is principally the basis for such an acceleration that interests taxonomists in general, and I will concentrate upon possible extrapolations from the techniques employed.

The Nature of Cricket Behavior

Behaviorally speaking, crickets are unusually versatile invertebrates. They utilize all of the major classes of sensory perception—sight, sound, taste, smell, and touch—in their communicative interactions, and they exhibit specialized aggressive behavior, hierarchical behavior, and a degree of territoriality not yet demonstrated in any other nonsocial invertebrate. Many of them show behavioral and morphological “phase” changes which correspond to variations in population density and may actually be brought about by behavioral interactions. With regard to sexual behavior, crickets represent the highest order of specialization along an evolutionary line leading to elaboration of an externally attached spermatophore and the means of maneuvering the female into the proper position for its attachment. They are among the very few invertebrates that literally “fight over” food, mates, and territory (Alexander, 1961).

A cricket's behavioral gadgetry is impressive. He can walk, leap, fly, climb, burrow, and swim. He manipulates food, substrate, and other crickets in different ways with two sets of finger-like palpi, and with mandibles and maxillae, as well as with all six of his legs at different times and in different situations (Alexander, 1961). He characteristically has three sets of auditory organs (Wever and Vernon, 1959); one species apparently has four sets (Chopard, 1926). He has two sets of long tactile organs, one at each end of his body; and a variety of

shorter-range tactile devices, among them his four palpi. He has two compound eyes and usually three simple eyes or ocelli. He has special moisture-, chemical-, and heat-detecting devices in various arrangements on his antennae, cerci, palpi, and tarsi (Herter, 1923; Dethier and Chadwick, 1948). The usual male cricket has the only stridulatory device known which produces a “pure” frequency—a sound reproduced as a sine wave on an oscillograph and sometimes exceeding 100 decibels at its source. He may have elaborate female-attracting glands on his metanotum, either single or paired (Boldyrev, 1928; Fulton, 1915); or on his dorsal abdomen (Alexander, unpubl.), hind legs (Fulton, 1931), or forewings (Gabbutt, 1954). Occasional crickets have anal glands with which they can eject a stream of sticky substance several inches out behind them (Griffith, 1937).

Collectively, the crickets live practically everywhere on the earth except in the Arctic and the Antarctic. Among the nine vegetation-inhabiting subfamilies, there are species that live on nearly every kind of tree, bush, and herb; some (such as the tamarack tree cricket) are limited to a single host, and others (such as the snowy tree cricket) live on about any kind of plant suitable for oviposition. Seven subfamilies live principally on the ground or beneath it. One of these (Phalangopsinae) has many obligate cave inhabitants among its members; another (Gryllinae) includes at least two species that are almost entirely limited to occurrence in and around human habitations and refuse heaps. The Myrmecophilinae occur only in ant nests, and one species of Eneopterinae is apparently termitophilous. Two other subfamilies, Brachytrupinae and Gryllotalpinae, are almost entirely subterranean, and both have developed sub-social life. There are crickets in almost every kind of terrestrial habitat from the driest deserts to the wettest marshes; one species of Trigonidiinae apparently spends most of its time walking

and leaping about on the water's surface, and Gryllotalpinae often extend their burrows below the water level. Most crickets approach omnivory, but a few are specific feeders. Some characteristically attack living, healthy insects; and some cut, carry, and accumulate food in specific locations usually inside a burrow.

Using Cricket Behavior in Cricket Classification

Cricket behavior has been used extensively to solve taxonomic problems only in North America; in Europe, the only other region where cricket biology has been studied, there are few species and taxonomic problems have been minor. Most use of cricket behavior in classification—except for the use of calling songs to separate species—is still unpublished. Although it is tempting in a compilation of this sort to include a good deal concerning how cricket behavior *might* be used in classification or *could* be used in classification, I am going to restrict myself largely to ways that behavior has actually been used in classification. These arrange under seven different headings.

1. The long-range calling songs of male crickets have been extensively used for many years to initially distinguish species that are sexually active in the same places at the same times.

2. The calling song has been extensively used to determine ecological and geographic limits, and to analyze geographic variation and hybridization.

3. Comparisons of entire acoustical repertoires have been used to relate the members of species groups and to clarify relationships between species that have never lived together.

4. Courtship song, copulatory position, duration of copulation, and movements during and after copulation have been used to distinguish and relate genera and species groups.

5. Differences in various behavioral characteristics, such as song structure and

copulatory act, have been used to determine the significance of structural differences in the forewings, genitalia, and spermatophores of crickets not yet studied behaviorally.

6. Behavioral observation is indispensable in determining the significance of failure of interspecific pairings to produce hybrids in the laboratory.

7. Grooming similarities and differences have been used only slightly, but show some promise in relating families, subfamilies, and perhaps even higher categories of Orthoptera.

Calling Songs and Species Recognition. The long-range calling songs of male crickets, katydids, long-horned grasshoppers, locusts, and cicadas have attracted some attention in recent years because they stand out in their reliability for initial recognition of species that are sexually active in the same places at the same times. Actually, the only new aspect of this technique has been the advent of electronic recording and analyzing equipment which allows us to put song differences down on paper in a highly communicative fashion. In North America, such field biologists as H. A. Allard, W. S. Blatchley, W. T. Davis, B. B. Fulton, E. S. Thomas, and many others have been using songs to separate species of Orthoptera and Cicadidae for nearly 100 years. Some of them, such as Davis, Blatchley, and Fulton, followed up their initial recognition by song and looked for morphological characteristics on the specimens they had distinguished by this method. When they found differences, they described new species; and often the fact that song was their initial clue was barely mentioned or entirely omitted. When they did not find structural differences, or sometimes when they found only overlapping differences or what they thought to be "slight" differences, they either described subspecies or else discussed their finds without the aid of formal nomenclature. In either case, their data were largely ignored by the taxonomists of the

day, leaving today's workers in the position of describing or re-elevating to formal taxonomic status species that the amateurs and field biologists had clearly differentiated long ago (cf. Alexander and Bigelow, 1960; Alexander and Moore, in press).

Fulton was the only one of the early workers to concentrate intensively on the questions of how and why calling songs should differ among species that live together. Although he had no recording or analyzing devices, and so had to rely solely upon his ears and upon word descriptions to transmit his information to others, it is still a fact that an interested neophyte can identify most of the species Fulton discussed more easily, quickly, and confidently by his song descriptions than by all the keys, pictures, and structural descriptions available in the literature. If one eventual goal of systematists is to make all species everybody's property, then this is a significant commentary.

But Fulton accomplished several important things in addition to describing calling songs:

1. He showed that most acoustical insects have a repertoire of several different sounds, each one characteristic of a particular behavioral situation.
2. He analyzed and took into account the effects of environmental variables, such as light and temperature.
3. He proved that some male orthopterans hear and respond to neighboring males.
4. He crossed species with different songs, analyzed the songs of hybrids, back-crossed and analyzed the songs of the F_2 generation, and established that some song differences are as clearly genetic in their origin as the kinds of structural differences that we usually discuss in this regard (song differences that now appear to be based on central nervous system structure, cf. Huber, 1960).
5. He showed that song patterns can be arranged in hierarchies, corresponding to

taxonomic hierarchies and suggesting genetic similarities and differences.

6. He used song extensively to determine species distributional limits and to search for field hybridization.

7. He constructed biological keys by which all of the different species in his groups that lived in particular regions could be easily separated without the aid of a microscope or complicated and obscure morphological criteria.

Approximately 300 insect species with long-range calling songs have now been tape-recorded from various parts of the world, including every continent and many islands, and there is as yet no exception to the rule that acoustical behavior is always clearly different among species that are sexually active in the same places at the same times. No other characteristic or group of characteristics approaches this kind of reliability, and we cannot get by with describing insect calling songs as "just another tool." Here is a case where it would indeed be inexcusable to proceed without utilizing behavioral characteristics.

But why should calling songs be so infallible, and do they have counterparts in non-acoustical groups? Or are you justified in turning away from this discussion with the comment that I have heard so often: "That's all very nice, but, unfortunately, my animals don't have songs!" Let us take a look at the calling song of a cricket and see how it fits into the mating sequence, which does happen to be a characteristic of at least all sexually reproducing animals.

The mating sequence of crickets can be divided into three parts: coming-together, copulating, and staying-together. Coming-together is mediated to varying degrees by the calling song. At the one extreme, there are species in which it is doubtful that sexually responsive males and females ever come together in any other fashion; we recognize such species by the fact that the males are spaced in the field and are highly residential and

territorial; their songs are loud and clear; and such a male will not travel more than a few steps from his residence to chase a passing female. At the other extreme, there are crickets in which the males have no calling song at all, having lost it; in these species, there are always localized colonies of adults—I know of a colony of *Hapithus agitator* Uhler only a few yards in diameter which has not moved in seven years. When a male of these crickets locates a female, he stays with her for hours, or even days—following her about wherever she goes and courting whenever she stops for a moment.

In both cases, a pair of crickets which has proved its compatibility by one successful mating stays together through repeated copulations until the female is maximally inseminated—maximally from a behavioral point of view, because she will not mate again until she has oviposited.

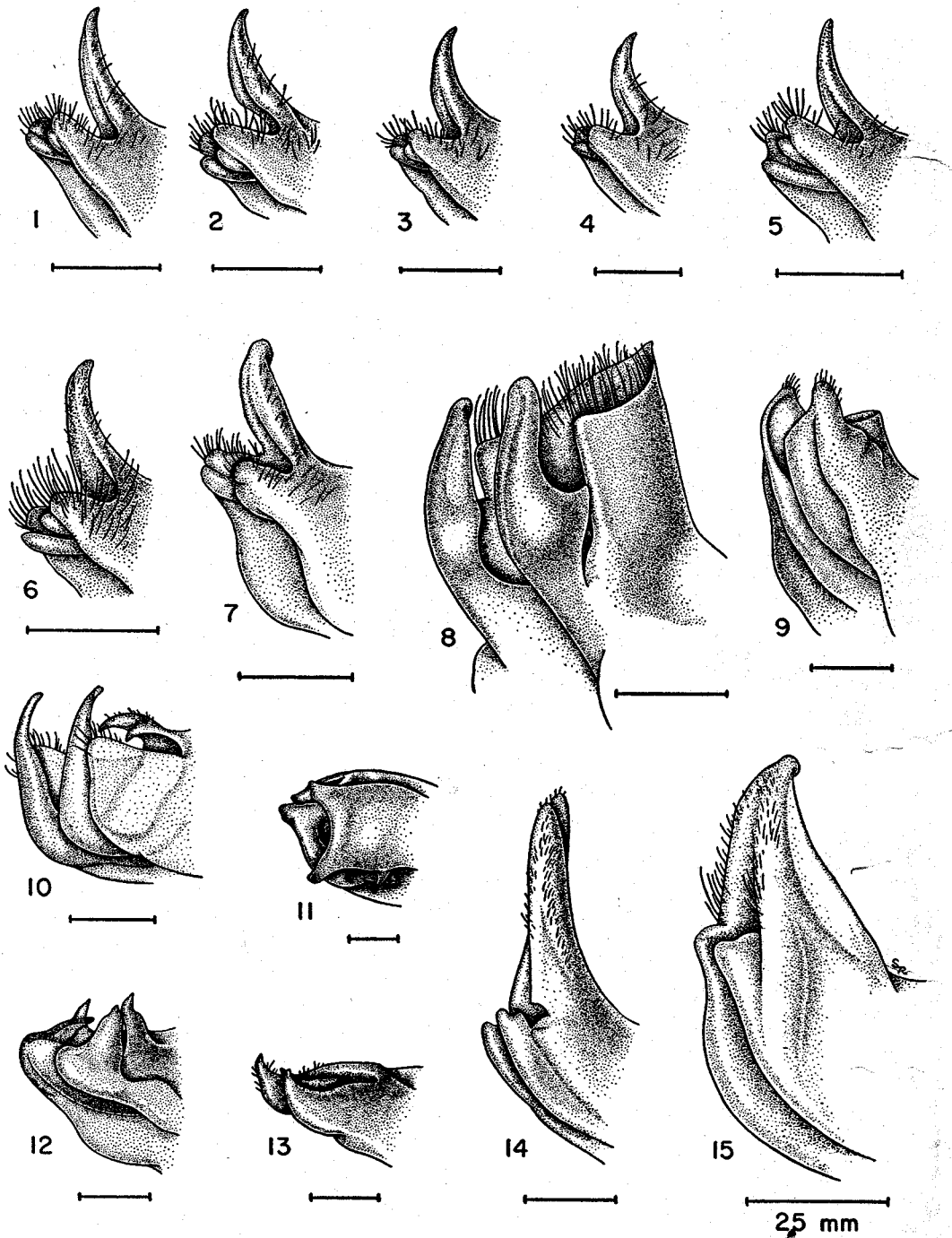
Staying-together—under these circumstances—has no business being species-specific, and it is not. We can find differences among species groups in the nature of post-copulatory behavior, and of course differences among higher categories (Table 1). But they do not consistently occur at the species level. Staying-together in crickets—the so-called post-copulatory behavior—probably originated in connection with keeping the female from removing the externally attached spermatophore before it is emptied of sperm. There are other clear adaptations in this regard, such as caps and covers of gelatinous material on the spermatophore which distract the female, and the male's behavior during the staying-together also specifically keeps the female from manipulating the spermatophore. But we should not ignore the additional obvious advantage of keeping compatible males and females together for maximal insemination. Actually, special "staying-together" mechanisms seem to have evolved in a wide variety of arthropods, such as dragonflies, termites, web-spinners, cock-

roaches, earwigs, and perhaps even in some of those arthropods in which there is long-term interlocking of the genitalia. The lesson for the taxonomist is simply that it is an expensive procedure to bring together sexually responsive, compatible males and females, and the mechanisms involved should be highly specific and efficient.

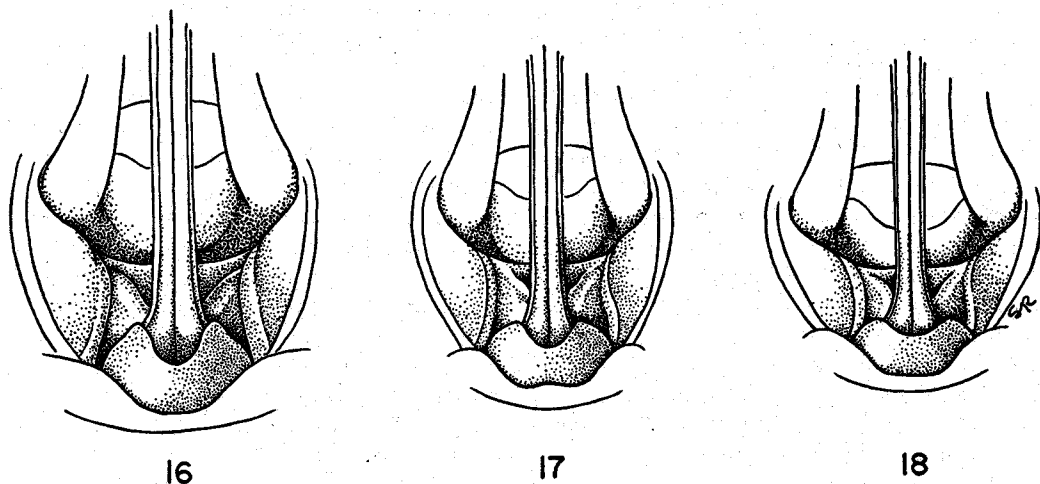
But let us go back for a moment to the mating act itself. After a pair of sexually responsive crickets has come together—into range of senses other than auditory—there is a period of courtship lasting from a few seconds to a few minutes, depending upon the receptiveness of both partners, the kind of cricket in some instances, and perhaps whether or not either or both has previously copulated. This courtship may involve acoustical, tactile, chemical, or visual stimuli; usually it involves some combination of all four parameters. Then, in all crickets, the female mounts the male. Attachment of the spermatophore may require 20-40 seconds, 3-4 minutes, 7-10 minutes, or 15-30 minutes; it may or may not require 180° turning of the body after engagement of the genitalia; and it may or may not involve special kinds of body movement or cercal vibration on the part of the male (Table 1). These various behavioral characteristics involving courtship and copulation are consistently invariable within species and consistently variable among species groups, genera, and subfamilies; they are not species-specific within any genus. They are associated with genitalic differences in both male and female, and with differences in the structure of the spermatophore, which also begin to be clear at the level of species groups and genera (Figs. 1-18). And despite wide-scale laboratory crossing experiments among field crickets in North America, Europe, and Asia (Bigelow, 1958, 1960; Cousin 1961; Alexander, 1957a), not a single case of complete behavioral or morphological incompatibility or combined behavioral and morphological incompatibility has been

TABLE 1.—SOME CHARACTERISTICS OF THE MATING ACT IN 15 VARIOUSLY RELATED CRICKET GENERA REPRESENTING SEVEN SUBFAMILIES. COURTSHIP SONG PATTERN DESIGNATIONS TAKEN FROM CLASSIFICATION AND EXPLANATION BY ALEXANDER (IN PRESS).

GENERA (AND NO. SPECIES OBSERVED)	COURTSHIP		DURATION		TERMINAL		SPECIAL		REPEAT		POST-COPULATION	
	SONG TYPE	GLANDS	(MIN.)	POSITION	CHARACTERISTICS		TIME	POSITION	STIMULI	POST-COPULATION		
					CHARACTERISTICS	POSITION				STIMULI		
GRYLLINAE												
<i>Gryllus</i> (15-20)	G ₁₋₅	none	½	♀/♂	♂ cerci vibrate; ♀ ovipositor pulled down	15 min.	♂ → ♀	antennation				
<i>Acheta</i> (1)	G ₃	none	½	♀/♂	same as above	15 min.	♂ → ♀	antennation				
<i>Gryllodes</i> (1)	G ₃	none	3-4	♀/♂	♂ cerci don't vibrate; ♀ ovipositor not pulled down	hours?	♂ → ♀ (weak)	antennation, spermatophore cap				
<i>Gryllomorpha</i> (1) (Boldyrev, 1928)	?	none	3-4	♀/♂	same as above	hours?	♂ → ♀ (weak)	antennation, spermatophore cap				
<i>Discoptila</i> (1) (Boldyrev, 1927)	none	2 metanotal	15-90	♀/♂	♂ keeps spermatophore	12-84 hrs.	?	?				
"Acheta" (Australia) (1)	A ₁	none	7-10	♀/♂	♂ jerks body	1 hour	♂ → ♀	antennation				
<i>Scapsipedus</i> (1)	E ₃	none	3-4?	♀/♂	♂, ♀ reverse bodies just before separation	?	← ♂ ♀ →	cercal contact?				
"Acheta" (Hawaii) (1)	G ₁ ?	none	3-4	♀/♂	similar to <i>Gryllus</i>	hours?	♂ → ♀ (weak)	antennation				
<i>Miogryllus</i> (2)	B ₁	none	3-4	← ♀ ♂ →	♂ jerks body	1 hour	← ♂ ♀ →	song, cercal contact				
BRACHYTRUPINAE												
<i>Anurogryllus</i> (1)	E ₃	none	7-10?	← ♀ ♂ →	occurs in burrows	♀ never ♂?	← ♂ ♀ →	song, cercal contact				
NEMOBINAE												
<i>Nemobius</i> (2+)	A ₂ , B ₁ , E ₄ E ₃ , F	tibial	15-30	♀/♂	♂ holds hind leg up and forward	hours?	♀/♂	tibial gland				
OECANTHINAE												
<i>Oecanthus</i> (2+)	A ₁	1 metanotal	15-30	♀/♂	♂ wings at approx. 90°	hours?	♀/♂	metanotal gland				
TRIGONIDINAE												
<i>Cyrtorhiza</i> (1) (T. J. Walker, unpubl.)	none	none	few sec.	♀/♂	♂ dashes back under ♀	?	?	?				
ENOPTERINAE												
<i>Hapithus</i> (1)	none	none	?	♀/♂	no calling song; ♂ wings at 60-70°	?	♀/♂	♀ eats ♂ wings				
GRYLLOTALPINAE												
<i>Gryllotalpa</i> (2)	E ₃	none	?	← ♀ ♂ →	takes place in burrow	?	?	?				



FIGS. 1-15. Male genitalia in various crickets, showing relative differences at various taxonomic levels (all drawn to same scale, lines = body lengths). 1, *Gryllus assimilis* Fabricius; 2, *G. bermudiensis* Caudell; 3, *G. veletis* (Alexander and Bigelow); 4, *G. pennsylvanicus* Burmeister; 5, *G. rubens* Scudder; 6, *G. campestris*, Linnaeus; 7, *G. bimaculatus* (De Geer); 8, *Acheta domesticus* (Linnaeus); 9, *Gryllodes sigillatus* (Walker); 10, *Scapsipedus micado* Saussure; 11, *Nemobius fasciatus* (De Geer); 12, "*Acheta*" *conspersus* (Walker) (Hawaii); 13, *Miogryllus verticalis* (Serville); 14, *Anurogryllus muticus* (De Geer); 15, "*Acheta*" *commodus* (Walker) (Australia). 1-10, 12, 13, 15, Gryllinae; 11, Nemobiinae; 14, Brachytrupinae; 3-4, sibling *Gryllus* species; 1, 2, 5, represent other *Gryllus* species groups from North America; 6, 7, represent another *Gryllus* species group from Europe.



FIGS. 16-18. Posterior ends of female field and house crickets, showing a difference related to a generic morphological barrier to copulation (see text). 16, *Gryllus campestris* Linnaeus; 17, *Gryllus pennsylvanicus* Burmeister; 18, *Acheta domestica* (Linnaeus).

discovered between species in the same genus. In other words, once the male calling song is by-passed, there are no absolute barriers to inter-specific copulation. This is particularly important, because with one special exception that I will discuss later, we expect—as investigators studying widely different animals are beginning to expect—that species in the same genus will be able to hybridize in the laboratory, even when we are dealing with four or five species that live individually intermingled in the field and give no evidence of ever hybridizing there.

In these days it is in vogue to speak of series or chains or combinations of partial isolating mechanisms which operate together to keep species from interbreeding. This is always an easy “out”, and it would be here, because males and females of different species almost invariably copulate less frequently in laboratory crosses than do males and females of the same species, apparently because of tactile-chemical differences (Hörmann-Heck, 1957; Alexander, 1961). But isolating mechanisms are not “potential” things; they are by definition *functional*, and we should not obscure the fact that calling songs represent one probable area

of occasional complete discordance among sympatric, synchronic species of stridulating crickets. They do not operate as interspecific repellents; it is just that whenever sexually responsive males and females locate one another solely through the calling song, there simply is no reasonable chance for males and females of different species to meet at a time when both are sexually responsive.

T. E. Moore and I have been working for several years on the 17-year and 13-year cicadas of eastern North America. These are also acoustical insects, and the songs of the different species that live together are strikingly different. No bona-fide instance of interspecific copulation—male and female locked together in the usual manner of a copulating pair—has ever been reported among the thousands of mating pairs collected, even though the adults live together by the millions. Yet in a simple breeding test involving cheesecloth cages over small trees, we obtained every possible kind of interspecific mating within a few hours. All interspecific matings were delayed, and frequently a pair was not locked together as thoroughly as in the usual conspecific matings. There are morphological differ-

ences in genitalia, and females approached by males of other species seem to fly more frequently than when approached by male of their own species. But neither of these incompatibilities can prevent copulation. It would be tempting to emphasize the genitalic differences here, and ignore or play down the behavioral differences. But the fact is that there is no chance now for selection toward morphological incompatibility because males and females of different species do not ever *start* to copulate. We must deal with the behavior here, as it seems we must in every case if we are to utilize the kinds of differences between siblings that are most exaggerated because they are the prime factors responsible for keeping species from interacting. Insect calls, frog calls, firefly flashing rhythms, moth odors, fly and ant mating swarms, dragon-fly territorial flights—all of these signals represent the initial unit in the interaction sequence associated with mating. Because of their location in the mating sequence, they have to be relatively more efficient than any other factor in the sequence. Regardless of selective action on later-acting factors such as courtship, or genitalic, or even physiological and genetic differences, selection should ordinarily continue to diverge the early-operating characteristics. But as early-operating differences increase in effectiveness, potential isolating mechanisms which follow them are reduced to divergence through chance, or through linkage with some other characteristic. Late-operating factors, therefore, may reflect discordance in situations we construct, not because they *sometimes* isolate but because they *once* isolated.

The practicality of using early-operating behavioral isolating differences to initially distinguish species depends of course upon how observable and useful they are in the field, coupled with how practical it is to move parts of the population into the laboratory for study. As examples, odors are at the present time more difficult to analyze and compare than

sounds; and flying insects that require sunlight for sexual activity are difficult to study in the laboratory. But there are many alternative techniques. One can always use the animals themselves, both for producing the signals and for studying response differentiation, and field studies are not always difficult to arrange. At any rate, the generalization seems clear. Whether we deal with male signals, female signals, specific responses to host animals or plants, or simply extra-ordinarily short periods of highly synchronized mating activity—those factors which are responsible for interspecific incompatibility in the earliest stages of the mating sequence represent by far the most profitable sampling aids the taxonomist can hope to find in his search for characters to initially distinguish congeneric species in any given region. And in nearly every case, these early-operating isolating factors must involve behavioral characteristics in one way or another.

Calling Songs, Species Distribution, Geographic Variation, and Field Hybridization. When a behavioral characteristic that is highly reliable in distinguishing species is also easily discerned in the field, it presents unusual opportunities for the study of ecological and geographic distribution. Most of the calling songs of the 250-odd species of acoustical Orthoptera and Cicadidae of eastern North America can be recognized while one is either driving in an automobile or stopped briefly along the highway. Dr. Edward S. Thomas of The Ohio State Museum has used this technique to study the distributional limits of these groups in Ohio for more than 30 years, and he has ecological notes and township distribution maps of the entire state for nearly every species. His records must be among the most complete ever compiled for any similar group of insects across a region of comparable size; Ohio is the only region that I have worked with the tape recorder and audio-spectrograph where I did not find a single species that had not already been noted

somewhere in another worker's files. T. E. Moore and I now use mimeographed "listening" sheets which include date, time of day, locality, and a complete list of the singing Orthoptera and Cicadidae of eastern North America, and it is quite clear that the distributional information one can amass by this method in one or two seasons of intensive work can far surpass in accuracy and completeness that available from all literature records and museum specimens combined.

Listening records also have considerable value in the study of geographic variation and field hybridization. I consider it extremely significant that in my field work I have encountered but one apparent hybrid among the seven field cricket species in eastern North America (Alexander, 1957a). The size of the sample resulting from seven years of listening across all parts of eastern North America is enormous; and the song distinctiveness of the laboratory hybrids that have been produced substantiate the value of negative listening records. K. C. Shaw and I (in prep.) have used song intergradation combined with male genitalic variation to study an Appalachian zone of hybridization between the true katyids in the genus *Pterophylla*. In less than two weeks, working only at night, we were able to trace the precise width and nature of this zone from the Susquehanna River in eastern Pennsylvania nearly to the Gulf Coast in Alabama and northern Florida. The insects involved are flightless, treetop-inhabiting night-singers that are seldom seen alive, even by entomologists; and there are only a few hundred specimens in all collections combined. Yet we estimate our tape recording and listening samples to number in the hundreds of thousands of individuals from the area of hybridization alone.

In another case, geographic variation in the southern wood cricket, *Gryllus fultoni* (Alexander), has been studied across all of the southeastern states, using calling song changes as the principal evidence

and sampling technique (Alexander, in prep.). Associated with the song changes, which involve chirp rate, length, and regularity, there are differences in body size and coloration, a very surprising and localized tendency for singing males to climb trees, and changes in ecological distribution. All of these changes except the structural ones have been traced principally by song records, and specimens for morphological examination have also been sampled and collected principally by song. Prior to 1957, this species was represented by about a dozen specimens in all collections combined, excepting B. B. Fulton's private collection.

Calling Songs and Species That Do Not Live Together. If calling songs diverge principally because of disadvantageous interaction among species that live together, we should expect them to differ less consistently among species that do not live together. We are just beginning to acquire evidence that this is the case. In three instances of species pairs or groups that are now either geographically or seasonally isolated, and to all appearances have never lived together, the siblings have not only identical calling songs, but identical (or nearly identical) repertoires of three or four signals. One of these species groups involves the European field cricket, *Gryllus campestris* L., the Bermuda field cricket, *G. bermudiensis* Caudell, and the North American sand cricket, *G. firmus* Scudder. *G. campestris* has likely been isolated from the other two species for at least tens of thousands of years; it differs strikingly from them in such characteristics as head size, body shape, and the size and length of the legs. The fact that it lives essentially alone in its habitat in Europe and has not diverged in acoustical behavior suggests that under the right conditions acoustical behavior can be an exceedingly slow characteristic to change. This is what we would expect for a communicative system involving specific signals and responses, and vital to the reproductive success of the species.

The two other species pairs are made up of very similar siblings which diapause in different stages and have different seasonal life histories (Alexander and Bigelow, 1960; Masaki, 1961). These seasonally separated species are the only sympatric species known to have identical acoustical repertoires. In neither case does it appear that the seasonal separation occurred after hybridization had become disadvantageous; rather, Alexander and Bigelow (1960) suggest that accidental differences in times of maturation and overwintering stages, and later the cementing of diapause differences, may actually have been responsible for speciation. It is interesting that the two North American species involved—*Gryllus veletis* (Alexander and Bigelow) and *G. pennsylvanicus* Burmeister—in spite of their striking similarity in all other regards appear to be genetically incompatible. Comparison of results obtained by Cousin (1958, 1961) and Bigelow (1958, 1960) indicate that in the genus *Gryllus* most non-diapausing species can hybridize (with one degree of success or another) with most egg- or nymph-diapausing species, regardless of geographic origin or degree of relationship suggested by other characteristics, while egg- and nymph-diapausing species cannot hybridize with one another. Apparently there is a definite incompatibility associated with diapause in the two different stages, making selection for diapause difference the quickest route to genetic isolation apparent in this genus, and an unusually quick route to speciation.

At this point, a common misconception regarding calling song differences needs to be clarified, and this is that song differences between sibling species do not necessarily involve the external sound-producing apparatus itself, but are usually a matter of rhythm differences. Likewise, response differences are not known to involve the external auditory apparatus. In both cases, the differences appear to reside principally or solely in the central

nervous system (Huber, 1960), and so they cannot be directly correlated with external structural differences. It is true that in the Tettigoniidae and Gryllidae, certain structural changes in the stridulatory apparatus seem to follow song rhythm changes: for example, faster pulse rates are frequently related to shorter wing strokes and to shorter files with fewer teeth (Walker, in press). But such differences cannot be expected to occur in every case, or perhaps even in most cases. On the other hand, I should also emphasize that there is only one case, involving two katydids (*Amblycorypha rotundifolia* Scudder and an unnamed sibling—cf. Alexander, 1960), where two species initially distinguished by song differences have not yet been distinguished by non-overlapping morphological differences in at least one sex.

Genetic incompatibility should be considered in another regard here, with respect to behavioral information and classification. Cousin (1961) and Bigelow (1960) have discussed degrees of "genetic" incompatibility, for example, in ranking species taxonomically. But, as has apparently been the case in many kinds of animals where genetic incompatibility has been discussed, complete failure to hybridize has been treated as a single category, even though it is due in some cases to behavioral or structural inability to copulate or inseminate and in other cases to inability to fertilize or to some other physiological or genetic incompatibility. Obviously, if one is going to utilize genetic incompatibility in arranging taxonomic hierarchies, he cannot avoid studying behavior, for he must in the end understand which failures are due to inability to copulate and which are due to failure of gametes to combine or zygotes to develop.

Before leaving genetic incompatibility and pre-mating incompatibilities, a further question seems pertinent. Blair (in press) and I have both noted that with certain exceptions we *expect* genetic compatibility among congeneric species, whether

they live together or not. We also expect pre-mating behavioral incompatibilities among those which live together, and it seems therefore that these must be elaborated principally or solely as a result of disadvantageous hybridization. I think it is an interesting question to ask what percentage of species pass through a stage during which they hybridize disadvantageously for a time with another incipient species. The genetic compatibility evident among long-separated and strikingly different species—such as American and European *Gryllus* species—suggests that a high percentage of speciation might involve such a stage. If so, the evolutionary role of hybridization that is associated with the eventual *prevention* or *disappearance* of particular genotypes may deserve an increased emphasis as compared with the role of hybridization in *producing* unusual genotypes. We are reminded by this how much of the nature of species—their particular directions of evolutionary change—must be determined at the time of speciation, by the particular events of speciation and immediately following speciation.

In view of the great similarity between some siblings, especially in insects, the probability of wide-scale genetic compatibility and active divergence in pre-mating discordances among sympatric species casts doubt on our manner of determining the taxonomic status of allopatric populations. Most approaches include evaluation of either degrees of difference or degrees of genetic incompatibility. Some include the state of difference between characteristics known to effect isolation in sympatric siblings. But acknowledgment of widespread genetic compatibility within genera and drastic retardation in the divergence of just the sorts of characteristics by which we recognize sympatric siblings (as evidenced by the identities in acoustical behavior between extrinsically isolated species mentioned earlier) indicates the arbitrariness of these procedures. If most sympatric siblings have passed

through a stage in which they hybridized disadvantageously, and if complete behavioral and other pre-mating incompatibility accounts for the general condition of incomplete genetic incompatibility, then if we wish to approach a description of minimal irreversible evolutionary divergence—which is what I think we are eventually aiming at with the species concept—we must ask instead concerning allopatric populations: how different are they in the kinds of characteristics which differ between similar sympatric species but do not in any way relate to reproductive isolation? In effect, we must ask: would these species hybridize disadvantageously if they became sympatric? And because we obviously know so little about what it has been that has caused the disadvantage in hybridizing among the vast numbers of siblings that appear to have passed through such a stage, we cannot yet answer the question satisfactorily. This brings up the proposition that it might be practical to consider as species, allopatric or allochronic populations that one can clearly distinguish, regardless of *how* different they are, and especially if it appears that the extrinsic barrier between them is a permanent one. At first it may seem that this would result in taxonomic chaos, but I think that just the opposite is the case. In the animals that I deal with, it would eliminate many problems and make rather clearcut the task of assigning taxonomic status to most allopatric populations. And it would neither add greatly to the number of Latin names, nor greatly shift their meaning. The kind of divergence that under conditions of sympatry would prove to be irreversible does not ordinarily take place overnight, even though we sometimes derive this impression. For example, Ghouri and McFarlane (1957) thought that they had discovered reproductive isolation between North American Pakistani house crickets, probably isolated only a few hundred years at most. But later Ghouri (personal communication) dis-

covered that *two* "house" crickets occur in Pakistan, one of them interfertile with and identical to the North American population. Nevertheless, when American house crickets do become distinguishable from those in Asia and Europe, as they are bound to with the present restrictions on transport, which kinds of biologists will not need to separate them? And what would be gained by the use of trinomials? North America and Europe are not going to connect in the foreseeable future, and if they support recognizably separate evolutionary lines, why should we delay so treating them?

As another case in point, T. E. Moore and I are faced with the question of how to treat the three pairs of sibling cicadas which have different life cycles of 13-years and 17-years but otherwise differ only in an overlapping geographic distribution. These populations are now almost completely isolated extrinsically, both because of their different geographic ranges and because of their different times of maturation. Could we suppose that even if the apparently permanent extrinsic barriers were removed, the three pairs of populations would be able to hybridize without severe disadvantage? The intrinsic life cycle differences make this very doubtful. Similarly, our information concerning hybridization in the genus *Gryllus* would have told us that *G. veletis* and *G. pennsylvanicus* with their different diapause stages are already distinct evolutionary lines, even without direct evidence of genetic incompatibility, and in spite of their striking similarities in other regards.

Behavioral Information and the Significance of Structural Characteristics. It is sometimes remarked that our classification of living organisms must always be based essentially upon structural characteristics because we will never have more than a few structural fragments of the vast majority of extinct and prehistoric species. I have never heard anyone argue with this contention, and it would be silly to do so. But there is an emphasis

in it which ignores the fact that the structural fragments of extinct animals will have precious little significance except in the light of what we know about the *functions* of comparable structural parts in living animals. It is also interesting that papers are now being published, however sketchy, on such subjects as the natural history of trilobites (Whittington, 1961) and the behavior of dinosaurs (Colbert, 1958), and I have wondered—not always with tongue in cheek—if some taxonomists are not already running the risk that their animals are more poorly understood functionally than some extinct groups. But even the realization that these kinds of correlations must be funnelled through the channel of structural comparisons does not permit the taxonomist to ignore function. I can illustrate this with a brief anecdote.

In 1957 I was collecting at night in southern Ohio when I heard a noise in the leaf litter beside me. I turned my light on the spot and saw two large ground beetles (Carabidae) running almost in tandem. Eventually the rear beetle, which turned out to be a male, caught the other, which turned out to be a female, seized her with his mandibles, flipped her on her back, extruded his genitalia, and tapped with the parameres at the tip of her abdomen until she opened the genital aperture. Then he inserted the aedeagus, and the pair copulated and separated (cf. Alexander, 1958).

I took careful notes of this event, but thought little of it until some time later when I learned that the parameres of beetles had frequently been interpreted as pries. So I went to the literature to compare this copulatory act with those known in other ground beetles. There are more than 25,000 recognized species of ground beetles, and taxonomists have been utilizing beetle genitalia in taxonomy for a very long time, but I have still to find the first published description of copulation in any ground beetle!

Most people have at one time or another

seen one of the common, large, "narrow-waisted" ground beetles (Fig. 19). Most entomologists are aware that in such beetles, the males have considerably longer mandibles than the females. But how many know that the two characters are related—that the male uses his long mandibles to seize the female around the slender "waist" between pronotum and mesonotum and thereby to put her into the appropriate mating position?

Most entomologists also know that in beetles there are accessory structures alongside the male aedeagus (or penis) which have been termed "parameres" (cf. Figs. 1, 2, Alexander, 1958). Jeannel (1941) even emphasized the fact that one of the principal differences between sibling species in ground beetles (oddly enough) is in the number and arrange-

ment of the bristles near the end of the parameres. In dealing with allopatric cave beetles, Valentine (1945) considered that such slight differences were not enough to distinguish species, and so used trinomials for such "slightly different" allopatric populations. But paramere bristle differences suddenly take on new significance when one understands how the parameres work—it is even possible that significant differences in bristle numbers and arrangement sometimes follow (in an evolutionary sense) changes in the manner of tapping.

A final point can be made in this connection by comparing structural differences in the external genitalia of some crickets. Figs. 16-18 show the rear ends of the females of three cricket species. The two on the left are in the genus *Gryl-*

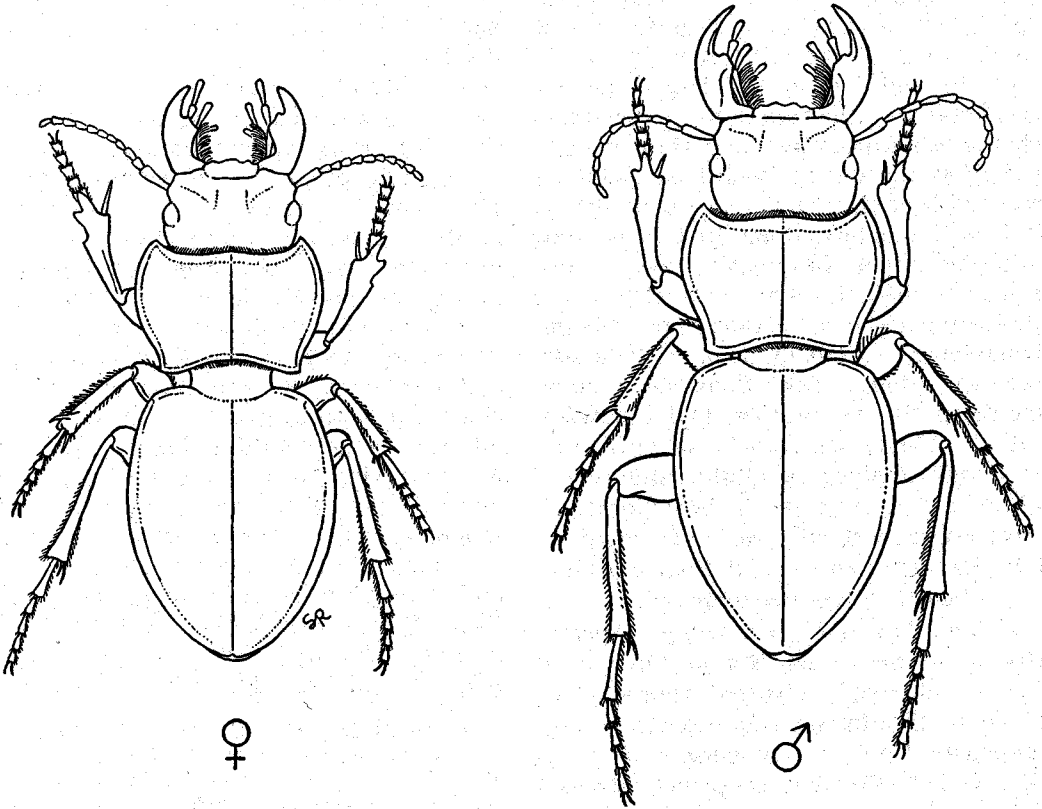


FIG. 19. Male and female of *Pasimachus punctulatus* (Haldemann) (Coleoptera: Carabidae), showing difference in mandible size associated with the mating act.

lus Linnaeus, the one on the right is in the genus *Acheta* Fabricius. The principal difference is in the curvature of the subgenital plate, and it is a relatively slight difference that would scarcely be the sort one would ordinarily use to distinguish genera. But it is related to differences that prevent the males of *Gryllus* species from mating with *Acheta* females and the males of *Acheta* species from mating with *Gryllus* females. The secret is that *Acheta* males grasp the female with two slotted guides on a broad cylinder (Fig. 8), while *Gryllus* males grasp her with a single upturned hook (Figs. 1-7). There is only one way to discover such morphological incompatibility, and that is by temporarily becoming a behaviorist.

Genitalic differences are one of the most important characters used at the specific and generic levels in the classification of insects, but in how many cases do we have a clear idea of the functional significance of the differences that we see? In addition to the importance of understanding the functions of structural characteristics that are important in classification, there is the additional point, as true with cricket and beetle genitalia as it is with song rhythms, that behavioral differences are frequently much more elaborate than the structures with which they are performed. A case in point is the behavior of various kinds of crickets during copulation: gross differences in movements, position, duration, and repetition rate (Table 1) are associated with some seemingly minor genitalic differences (Figs. 1-15). As a result, behavioral differences are not only easier to compare, but they are more useful than morphology when they can be compared.

Using Behavior to Arrange Species Groups, Genera, and Higher Categories. I have obviously stressed reproductive behavior throughout this discussion, and emphasized only a few aspects of reproductive behavior that are principally useful at the specific and intraspecific levels. But several aspects of cricket behavior

have become involved in classification of species groups, genera, and higher categories as well. I will describe only a few of these.

Table 1 compares some copulatory actions in 15 cricket genera. Three of these genera, *Gryllus*, *Acheta*, and Australian "Acheta," are very much alike morphologically, and they have not previously been clearly distinguished. Australian field crickets have been placed in both *Acheta* and *Gryllus* by various authors. But only a few minutes of watching these crickets alive reveals that either classification is misleading: courtship singing and copulatory movements and duration in Australian crickets are quite different from those in *Acheta* and *Gryllus*, genera which are alike in both respects. This finding is confirmed by male genitalic differences (compare Figs. 1-7, 8, and 15) which had escaped emphasis previously, apparently because their functional significance was not known.¹

Several other surprises are apparent from the information in Table 1. Although they are among the diverse crickets usually placed in the genus *Acheta*, Hawaiian field crickets very closely resemble American *Miogryllus*. But they differ strikingly from *Miogryllus* in copulatory and postcopulatory behavior, and they have a courtship song which may be homologous with those of *Gryllus*, *Acheta*, and *Gryllodes*. This particular kind of courtship singing is quite different from all other cricket stridulation, involving a different wing position and motion (Alexander, in press); it seems to have evolved independently of the calling song for a very long time. As already noted, *Gryllus* and *Acheta* are alike in many ways, but *Gryllodes* is rather distinctive, both structurally and functionally (compare Figs. 1-7, 8, 9, and Table 1). It is surprising to

¹Chopard has recently (Eos, 37:267-288) described seven new genera for crickets formerly placed in *Gryllus* and *Achaeta*, on the basis of male genitalia; Australian and Hawaiian *Acheta* are thereby placed in *Teleogryllus* and *Modicogryllus*, respectively.

find that this special kind of courtship is so ancient.

A further puzzle is provided by the two apparently unrelated genera, *Miogryllus* (Gryllinae) and *Anurogryllus* (Brachytrupinae). Both have developed distinctive postcopulatory songs, apparently from the calling song in each case; both finish copulation end-to-end; and both have copulatory acts lasting 7-10 minutes. Among the crickets studied, there are no others which possess all these characteristics, and whether this represents convergence or failure to diverge, it poses some interesting questions.

In another comparison between subfamilies, *Miogryllus verticalis* (Serville) shows great similarity to *Nemobius fasciatus* (De Geer) in all phases of its acoustical behavior (Alexander and Thomas, 1959; Alexander, 1961, and unpubl.). *N. fasciatus*, in turn, differs greatly in acoustical behavior from the two species, *N. allardi* Alexander and Thomas and *N. tinnulus* Fulton, with which it had been confused until recently (Alexander and Thomas, 1959). Fulton (1933, 1937) showed that the last two species can hybridize in the laboratory, while *N. fasciatus* is not able to hybridize with either. Morphological differences, although relatively slight by most standards, bear out these findings in the degrees to which they differ among the three species. *N. tinnulus* and *N. allardi* are in turn extremely similar in all aspects of acoustical behavior to a supposed subspecies of *N. fasciatus*—*N. griseus* Walker (Alexander, unpubl.). The logical conclusion is that *N. allardi*, *N. tinnulus*, and *N. griseus* belong in one species group, while *N. fasciatus* and *N. maculatus* Blatchley make up two other distinctive units within the same subgenus. This classification is confirmed by Davenport's finding (1960) that these are the only North American *Nemobius* species with 15 chromosomes (*griseus* not tested).

Erratic similarities and differences in behavior have sometimes given unex-

pected clues as to possible relationships. For example, the males of two related American field crickets, *Gryllus integer* Scudder and *G. rubens* Scudder, and an apparently unrelated European field cricket, *G. campestris* L., wobble their heads in a similarly elaborate fashion during courtship (Huber, 1955; Alexander, 1961). This appears to be an outgrowth of the antennal lashing of the male. But has it been elaborated independently in the two cases, or is this characteristic traceable to a common ancestor? The other European field cricket, *G. bimaculatus* De Geer does not wobble its head during courtship, and Hörmann-Heck (1957) has shown that hybrids between the two European species are intermediate in this regard.

In another species group, *N. confusus* Blatchley, *N. carolinus* Scudder and *N. melodius* Thomas and Alexander were shown to be related through both courtship songs and morphology after the great differences in the calling songs of the last two species—which had been used to initially separate them in the field—had suggested that they might even belong in different subfamilies (Alexander, 1957b; Thomas and Alexander, 1957). Again, Davenport's finding that these three species are the only North American *Nemobius* with seven chromosomes confirms this classification.

Finally, crickets possess an elaborate and consistent array of grooming patterns. More than 30 different, predictable actions are involved in the cleaning of different body parts. These actions are similar or identical among different species, genera, and in some cases even subfamilies; they appear to diverge only following gross changes in morphology. While behavior associated with food-getting and defense—the other two obvious functional categories of behavior—seem in crickets at least to be erratic and unpredictable in regard to rates and directions of evolutionary change, grooming and reproductive behavior are both

consistent and predictable, and they are in some senses at opposite ends of a spectrum with regard to rates of evolutionary change. As a result, grooming actions can be of significance in determining such things as whether or not long, slender antennae evolved more than once in the orthopteroid insects. Because some doubt is still attached to the relationships presumed for certain groups—for example, Caelifera, Phasmatoidea, Mantodea, and Blattodea—either identity or differences in the manner of cleaning long, slender antennae wherever they occur in these groups has to have some taxonomic significance.

Concluding Remarks

I have been particularly glad to discuss the use of behavior in classification for two reasons. First, there is no doubt that the use of behavioral information in crickets is greatly accelerating progress in classification at all levels; and there seem to be some extrapolative possibilities. And second, anyone with more than a passing curiosity about the study of animal behavior soon acquires the feeling that it has been neglected too frequently in many aspects of zoology, but especially among the systematists, who have almost a priority on the comparative attitude. This seems to me especially unfortunate, because any way that I examine it, I am brought back to the feeling that the evolution of animals is typified by nothing quite so clearly as it is by the elaboration and combination of behavioral characteristics. Behavioral attributes are too often the limiting factors in ecological and geographic distribution, too often the principal and most elaborate evidence of isolation between sibling species, too often at the core of diverse problems in animal evolution to allow us to get by with the vague feeling that structure and physiology can be compared but behavior cannot—that a structural description is important information but a behavioral description is a useless anecdote. Of

course there are some special pitfalls in being careless about a behavioral observation, but the proof of the pudding is in the eating, and constructive criticism probes at the basis of confidence and works at perfecting its communication—particularly when the contenders prove to be right over and over again, as the field biologists and amateurs have certainly proved to be with respect to the classification of the groups I study. We should not be confused into forgetting that it is one thing to attempt to analyze the entire complex of factors responsible for the whole development of a behavior pattern (or for the whole development of a structural or physiological pattern for that matter), but quite another to describe, compare, and account for differences and similarities in particular behavioral units between different animals. These things need to be emphasized to the systematists, for they are probably the only people to whom we can turn for the accumulation of behavioral information on a large scale. And my particular taxonomic experience with crickets and other acoustical insects has caused me to become strongly biased that the old shoulder-shrug about “getting on with the business of describing and classifying species” really has to mean “getting on with the business of understanding how species live,” *regardless of the present state of taxonomic knowledge in the group*. To paraphrase an old adage, it is not what one *has* that counts in evolution, it is what one *does* with what one has—and what one *does* is not always entirely clear from what one *apparently has*.

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