UNFINISHED BUSINESS AND BECKONING PROBLEMS

THEODORE H. HUBBELL*

When I was inveigled into agreeing to take part in this symposium I chose a title that left me plenty of room to decide later what to talk about and one that might encourage speculation. I shall disappoint any of you who may expect me to philosophize about the importance of behavioral studies for systematics, or utter other words of wisdom. Actually, I don’t belong here. I do not myself work on insect behavior, but I am interested in it and greatly impressed by the research you behaviorists are doing. And I must tell you that although the insects I study neither sing nor flash lights, almost every one of my projects has revealed problems or situations that can only be explained in terms of behavior. Many other so-called old-fashioned taxonomists, among whom I class myself, would doubtless say the same.

When I began my studies of the Orthoptera only a few men of insight such as H. K. Poulton were using behavior as a systematic tool and an indicator of relationship; the rest of us were quite oblivious of its possibilities. We based our classifications on “characters” (morphological, of course), and assessed degree of relationship according to closeness of resemblance in those which we considered “good”—that is, distinctive and dependable. Distribution and ecology were also taken into account. Most of us still have to operate under those rules.

Much of my early work on Orthoptera was done in Florida, and my “unfinished business” relates mostly to Florida and adjoining states. As background, I am going to describe briefly what it was like to be a biologist at the University of Florida in the 20’s and 30’s—before most of you were born. I had gone in 1922 to study under W. M. Wheeler at Harvard, whence I was plucked the next year, degreeless, by the offer of a position as instructor in the Department of Biology and Geology at the University of Florida. (Such things happened in those days). The offer came from J. Speed Rogers, a professor at Grinnell College, Iowa, who had just been appointed head of the department at Gainesville. We had first met at Michigan, and had done field work together. It was his job to build a staff from scratch, and with complete disregard for procedures now routine, he picked the men he wanted from among his former fellow graduate students, and thus assembled what came to be known as the University of Michigan Department of Biology, Florida Branch. In spite of its faults this procedure can, with judgement and good luck, make a small department strong in a limited field at the cost of breadth and variety.

So it happened at Florida. Speed (crane flies), a mammalogist, a botanist and I (Orthoptera) made up the original staff, plus an economic entomologist who soon went over to Agriculture. Each of us was interested in a group of organisms and the problems it posed rather than in some biological phenomenon as such. Only the botanist had a doctoral degree, but in those

*Theodore H. Hubbell is Emeritus Professor of Zoology at the University of Michigan and former Director of the Museum of Zoology of that institution. He was on the faculty of the University of Florida from 1922 to 1946, and was President of the Florida Entomological Society in 1942-43. He is a student of the Orthoptera and in particular of the camel-crickets (Rhaphidophoridae). Address: Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109.
days a degree was not too important. The administration was satisfied if we gave our courses acceptably. I taught Geology, Physical Geography, general Zoology, and occasionally Entomology. The M.S. was then the highest degree given in biology at Florida, and we tended to make it a little Ph.D., complete with committee, research problem and thesis. When, some years later, the doctoral program was added we professors took turns in going off and getting properly appointed. Research by the teaching staff was regarded as commendable and not in any way discouraged. For example, the dean would overlook an occasional few days’ absence from campus of a professor and group of students, ostensibly for a course exercise but often little more than a camouflaged collecting trip. The 5000 students were all male, and the faculty was so small that most of us knew one another. All in all it was an easy-going place. One great difference from now was the lack of pressure to publish, which fostered a relaxed attitude towards one’s own research. In fact, almost the only incentives for doing research were curiosity about nature and the desire for recognition by one’s colleagues elsewhere.

Actually we worked hard. We were young and enthusiastic, in love with Florida, and passionately fond of field work. We were fired by the belief that we had a unique opportunity and mission—to make known the fauna of Florida by our own efforts and those of our students. Each student was encouraged to work on a different group, or, as an alternative, to study the biota and ecology of some characteristic Floridian environment. With this as the department’s program we hoped that its faculty and students would become a cooperative, self-renewing body of field oriented biologists with interests focussed on Florida. And do you know, after we got going this
plan worked pretty well for quite a while. It produced a crop of students each of whom soon knew far more about his chosen group than did his major professor, a series of theses on various Florida taxa and environments, and eventually a number of distinguished biologists, some of whose names are certainly familiar to you. It also fostered a relationship among faculty and students that in my estimate was well-nigh unique in the respect and high regard we had for one another. How much this depended on one man—James Speed Rogers—is hard to say; everyone contributed. But it is perhaps no coincidence that departmental solidarity and elan suffered after his eventual departure to Michigan.

It was about the time we were assembling that Thomas Barbour, Director of the Museum of Comparative Zoology of Harvard University, pub-
lished his book, "That Vanishing Eden," in which he deplored the rape and devastation of the state he had known for so long. But for us late-comers Florida was virgin country—wonderful in its diversity of life and environment—fresh and new and strange. We threw ourselves into the study of our chosen groups, spending every possible moment in the field. Exploring and collecting. We wanted to know what occurred, and where. Accomplishment was to find the right place, locate the species, collect specimens and bring them home to study—dead, but accompanied by meticulous field notes. We did not, of course, spend all our time and energy on Florida. Most summers we dispersed, to do field work in more northerly climes, study in museums, or even, rarely, to take vacations. (And please note: we ourselves paid for our field trips and expeditions, sometimes with a little help from a museum for which we collected. There was no such thing as a grant-in-aid. Those expenses were not great in terms of dollars, but they were not small in relation to our resources; my salary as instructor at Florida in 1923 was $1800, and 12 years later, as professor, I was making $3200).

Fig. 3. T. H. Hubbell, Rock Bluff Landing, 4 April 1927 (photo by J. Speed Rogers).
Most of our Florida field work was done in the vicinity of Gainesville. Only once in a long time did we get as far south as Royal Palm Park or the Keys, but forays to central peninsular Florida or the panhandle were more frequent. It took us two or even three days to get to the Apalachicola ravines over the unpaved roads, hand-pushing the cars when they got stuck in the deep sand and sleeping in the woods. We generally camped beside a ravine south of the present park, a site which became known as Old Camp Torreya and is the type locality of many insect species. On some of our visits we were accompanied by out-of-state visitors, among them, on one such occasion, Cy Crosby and James G. Needham from Cornell and W. M. Barrows from Ohio State, and on another A. P. Morse, W. T. Davis and W. S. Blatchley. The accompanying photos were taken on such trips. (Figs. 1-4).

To a biologist one of the fascinating things about Florida is the variety and distinctness of its habitats, and the often sharp boundaries between them. Detailed county soil maps were available even in the '20s, and having been produced largely by mapping vegetation types they proved useful in our field work. Sand scrub is one of the most distinctive Floridian environments, developed on the little altered dune and beach sands that constitute the St. Lucie and Lakewood soils (Fig. 5). It is very dry, and supports a thin forest of sand pine and scrub oaks, with shrubs such as Xolisma and Ceratiola, sparse grass and herbage, and much exposed sandy soil. The scrub is widespread in central and northern Florida, occurring as a few large and a multitude of small island-like patches isolated sometimes by streams but mostly by intervening swamps, flatwoods, hammocks, or ‘high pine’ ridges—that is, pine oak forests on loamy uplande. As is now well known, prolific speciation has occurred in this scrub archipelago among animals that share the following characteristics: they are generally small but not minute, flightless or at least sedentary, not normally subject to passive dispersal, and for one reason or another closely associated with the scrub environment. Among such animals we observe (1) the existence of
Fig. 5. The archipelago of "scrub islands" in central Florida (black); the largest is that located in Ocala National Forest.

numerous morphologically distinct, allopatric or parapatric populations, often with very small ranges separated by what appear to be trivial barriers; (2) the absence from many isolated scrub patches of any member of the group; and (3) a tendency for the taxa of these microspeciating groups to share a common distributional pattern.

When we began our studies none of this was known, and most of the taxa involved were undescribed. I became particularly interested in the flightless scrub grasshoppers of the genera *Melanoplus* and *Aptenopedes* and the burrowing scarabs of the genus *Myctinus*. In 1932 I published a revision of the Puer Group of *Melanoplus*, in which the scrub species were distinguished largely by their concealed male genitalia. Surprisingly, this was the first time those protean and easily observable structures had been
used in the taxonomy of New World grasshoppers. I concluded that most of
the species do not intergrade even when their territories are only narrowly
separated. A single one, however, *Melanoplus puer*, has an extensive north-
south range in the sandy areas along the east coast and their inland exten-
sion in central Florida north of Lake Okeechobee. Its populations show broad
regional or subspecific differences and also many localized morphotypes. It
seems probable that in the central part of its range a complex zone of
hybridization exists, with differences in the amount and content of gene
exchange between populations.

In my revision I suggested that the scrub areas where the microspecies
now occur might once have been real islands at times of high sea level during
the Pleistocene (shades of vicariance biogeography!). This hypothesis I
later elaborated in a study of *Mycotrupes* (1954). It needs reexamination,
particularly with regard to the timing of postulated events, in the light of
more recent interpretations of the terraces of the southeastern coastal plain.
The Puer study also demonstrated that much more field work was needed,
and in the summer of 1938 a graduate student and I investigated numerous
previously unvisited areas. I even persuaded my dentist, an amateur pilot,
to fly me over much of the territory north of the Oklawaha River in search
of any scrub we might have missed. We turned up three more species of the
Puer group, one in west and one in northeast Florida and another con-
finned to the Ocala Forest (all still undescribed). The Ocala species proved
to be separated from its nearest neighbor to the south only by Alexander
Spring Creek and its narrow bordering swamp.

And there this particular problem sits. Events conspired to prevent me
from pursuing it, and there has been no followup. It would be interesting
to determine how far individuals of the parapatric species wander in a life
time and whether they can and do penetrate the insignificant-seeming
barriers between colonies, and to try cross-mating the scrub microspecies
and also the local forms of *puer* among themselves to see if any behavioral
barriers exist and whether the genitalic differences cause mechanical iso-
lation. Chromosomal and electrophoretic studies might also provide data
indicative of degrees of relationship and relative ages of the scrub forms.

Just as there is a pattern for xerophiles in this region, so is there a
reverse one for hygrophiles, among which belong the grasshoppers of the
Furcatus Group of *Melanoplus*. The three species of this group, clypeatus,
*furcatus* and *symmetricus*, inhabit the shrub zone on seepage slopes border-
ing the edges of swampland. The first two face each other across the Al-
tamaha River along a large part of its course, as shown by many paired
collections. In west Florida *furcatus* and *symmetricus* are separated only by
a two-mile wide sand ridge. The middle species, *furcatus*, includes several
populations that differ in male cercal form and genitalia; all but one of
these are known to intergrade with their neighbor or neighbors, and that
one is suspected of doing so. Two of these subspecies, if one may call them
so, are separated by a narrow ridge at the east edge of the Okefenokee
Swamp but intergrade around its south end. How or why these parapatric
colonies are kept separate across such an insignificant distance (insignifi-
cant to a medium-sized grasshopper, that is) remains a tantalizing question—
just one more instance of unfinished business.

I shall end by describing two problems among the camel-crickets (the
Fig. 6. Pronotal form in males of *Ceuthophilus seclusus*: (a) unmodified pronotal form of minor males inhabiting peripheral part of range of species; (b) modified pronotal form of major males inhabiting core part of range centered on the Ozarks (the arrow points to the adventitious cleft separating the fore and hind parts of the protuberance).

group Theodore Cohn and I are currently studying)—problems that can only be solved by behavioral studies. Both of them involve the presence in single species of two kinds of males—major and minor—that differ strikingly in bodily conformation but not at all in gonitalic structure. The first case, that of *Ceuthophilus seclusus*, I described in 1986. In every collection from a sizeable area centering on the Ozarks every male is a major, with a pronotum that is strongly elevated and deformed (Fig. 6); such a modification occurs in no other species of the genus. Outside that area, forming a complete ring around it and extending into Arkansas, westernmost Indiana, Illinois, Iowa, eastern Nebraska, Kansas and Oklahoma, is a zone in which the male pronotum is entirely ordinary. Only in a few specimens from the northern part of that zone does a hint of the modification occur. Furthermore the constricted neck of the pronotal elevation has been traumatically destroyed in a high percentage of the major males seen—almost surely by the jaws of the female during or prior to mating. Can it be that there is an abrupt behavioral change at the edge of the area where only major males occur? How could there be a behavioral cline when the structure involved is either present or absent? Is the major morphotype so successful that where it is present only majors can secure mates, and is it consequently spreading into peripheral territory at the expense of minors? And how do provincial females acquire their taste for the pronotal juices or pheromones or whatever it is that the sophisticated major males provide? Questions such as these can only be answered by observation, but I find behavioral observations frustrating. Last year I watched a female and major male *seclusus* in
Fig. 7. Differences in the abdomens (upper, dorsal views; lower, lateral views) of three supposed species of *Pristocentrophilus: cercalis* (Sc.) (left; minor), *gaigei* Hub. (center; major), and *sargentae* Gurney (right; major); see text.

dim light for several hours, and then suddenly it was all over; they were in copula, apparently with no more preliminaries than a nudge or two by the male, and the female did not even give him a nibble.

The other beckoning problem that I shall briefly mention is that posed by three “species” of *Pristocentrophilus* that occur in the northwestern United States and adjacent Canada—*cercalis, gaigei* (one that I described), and *sargentae*. They differ enormously in the ornamental nodules, processes or bosses on the dorsum of the abdomen of the males: *cercalis* has either a
smooth back or a large number of tiny low tubercles; *gaigei* has a very peculiar enlarged structure in the middle of the abdomen accompanied by long finger-like lateral projections, and *sargentae* has, in addition to "fingers," an enormous median organ as tall and as wide as or wider than the abdomen (Fig. 7).

For a long time we were certain that we were dealing with at least two species. It was not until we plotted the distributions of *cercaulis* and *gaigei* that we noticed that their ranges are absolutely coextensive, that in practically every large collection made anywhere from Idaho to British Columbia to Oregon both are present, and that they are synchronic. Later we found that the distinctive male genitalia are completely alike in all three forms. We have been forced to conclude that we are dealing with a remarkable instance of male dimorphism, with *cercaulis* based on the minor male phase and *gaigei* and *sargentae* representing extremes of the major phase. Majors and minors occur in more or less equal numbers, at least in many places, and are of the same general size; we therefore presume that they are equally successful in obtaining mates, from which it seems logical to suppose that this is accomplished by different tactics. The central organ of the majors may disperse pheromones; but what can be the role of the "fingers," unless to enable the female to discriminate among the males by tactile stimuli? Having exposed this problem by old-fashioned means, we would give a great deal to learn the answers to some of these questions of function and behavior.

The "natural history" approach to systematics that has pervaded my talk may seem naive and old-fashioned to you, who are applying new tools and new concepts to the study of systematic and evolutionary problems. But are the concepts really so new? Is it not true that, by whatever means, we are all simply engaged in filling in the details of Darwin's great vision in ways he never dreamed of? Since by some magic he is expected to attend this meeting, I wonder what he will think of the studies to be described here today. I think he will find them fascinating; perhaps he may even ask some penetrating questions.

**Literature Cited**


