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Manuscripts from *all* areas of the discipline of entomology are accepted for consideration. At least one author must be a member of the Florida Entomological Society. Please consult "Instructions to Authors" on the inside back cover.

This issue mailed March 30, 1990

ANNOUNCEMENT 73RD ANNUAL MEETING FLORIDA ENTOMOLOGICAL SOCIETY

The 73rd annual meeting of the Florida Entomological Society will be held August 5-9, 1990 at the Camino Real Hotel in Cancun, Mexico. Travel and hotel arrangements are being handled through Holbrook Travel, 3540 N.W. 13th Street, Gainesville, FL 32609 (Phone 1-800-345-7111), Attn: Ms. Joyce Rickard. Registration forms and additional information will be mailed to members in the Newsletter.

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The deadline for submission of papers and posters for the 73rd annual meeting of the Florida Entomological Society will be May 15, 1990. The meeting format will contain seven symposia so there will be concurrent sessions. Submitted papers will be eight minutes allocated for the oral presentation with two minutes for discussion. A separate Poster Exhibit Session is planned. There will be student paper and poster sessions with awards as in previous years. Students participating in these judged sessions must be members of the Society and registered at the meeting.

For additional information contact:
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FORUM
A New Type of Article for our Authors and Subscribers

We are proud to announce that scientists may submit articles for publication in a *FORUM* section of *Florida Entomologist*. *FORUM* articles (1-2 per issue) will appear at the beginning of each issue in a section marked *FORUM*. If available, the first *FORUM* articles will appear in the June 1990 issue.

Articles for the *FORUM* section must follow the general style guidelines for all other articles submitted to *Florida Entomologist*. *FORUM* articles must be of high scientific quality, demonstrate acceptable experimental design and analysis, and cite appropriate sources to support findings. *FORUM* articles will include "cutting edge" science, scientifically meritorious but controversial subjects, new methodologies (designed and tested), experimentally-based designs and tests of pedagogical methods, and documented challenges to existing entomological techniques, philosophies or experimental paradigms.

Submitted articles should include "Submitted to *Florida Entomologist*: *FORUM*" on the title page. Three or more peer reviews will be acquired by the Associate Editor for *FORUM* publications.

We feel the addition of a *FORUM* section will expand the scope of *Florida Entomologist* and allow readers and publishing scientists an additional creative outlet that will complement our symposia, research articles, and notes.

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____

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All submitted papers should be designed to be 8 minutes long with 2 minutes for discussion; visual materials must be restricted to 2x2 slides or overhead projector transparencies.

Introduction To
ATTACK AND DEFENSE: BEHAVIORAL ECOLOGY OF PREDATORS AND THEIR PREY

ENDEMICS AND EPIDEMICS OF SHIBBOLETHS AND OTHER THINGS CAUSING CHAOS

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> "When I use a word," Humpty Dumpty said, in rather a scornful tone, "it means just what I choose it to mean—neither more nor less."
>
> "The question is," said Alice, "whether you **can** make words mean so many different things."
>
> "The question is," said Humpty Dumpty, "which is to be master—that's all."
>
> Lewis Carroll (1872)

Classical biological control is a set of activities in which non-native predators, parasites, parasitoids, competitors or pathogens, are introduced into an area for the control of pests, especially immigrant pests. The language of classical biological control is that of ecology, which uses words of classical (Greek and Latin) origin because these can be assigned precise meanings. The precision of the meanings allows for conciseness and accuracy of expression, or such is the intention. Unfortunately, the meanings of a group of words describing the origins of predators etc. and pests alike are anything but precise. Their definitions are chaotic in several dictionaries. Therefore we take an etymological voyage to the origins of the words **precinctive**, **autochthonous**, **indigenous**, **epidemic**, **endemic**, **adventive**, **introduced**, and **immigrant** to see how they have been used, and we illustrate this voyage by citations from the literature. Then we show the relationships of the five words that we deem most useful in describing origins, and we redefine the words **adventive**, **immigrant**, and **introduced**.

AN ETYMOLOGICAL VOYAGE

Precinctive (from Latin praecinctus, *present participle of* praecingere, *to gird, encircle)*

David Sharp rose to eminence as a describer of insects, many of them predatory, in the final quarter of the last century. His works include contributions on the faunas of Britain, the Amazon basin, New Zealand, Central America, Japan, and Hawaii. In the last of these works (Sharp 1900: 91), faced with need of a word under which to group organisms restricted in distribution to Hawaii, he chose and defined the word **precinctive**: "I use the word **precinctive** . . . in the sense of 'confined to the area under discussion' . .. '**Precinctive** forms' means therefore forms that are confined to the area specified." The word was adopted by Bequaert (1940: 266) and others: "Of a total of 42 recorded species [of Antillean Tabanidae], 33 (or nearly 80%) are precinctive and 26 (or 60 per cent) are restricted to a single island".

Autochthonous (from Greek autochthon = *sprung from the land itself)*

Browne (1646: 274) "There was never any **Autochthon**, or man arising from the earth but Adam." Gardiner (1804) "If the English have this great predilection for **autoohthonous** bread and butter". Anon. (1860) "Most of them [the Red Indians], of course, believe themselves to be **autochthonous**; but the Chippewas and one or two others retain, or till lately retained, the tradition of a migration from over the sea." Torre-Bueno (1937) **"autochthonous**, native or aboriginal; used for those species which are considered to have arisen as a part of the native or aboriginal fauna or flora, as contrasted with those which are considered to have immigrated from outside regions ([after] Tillyard [1926])." Mackerras (1970: 191) "An **autochthonous** group is one that evolved within the country".

Indigenous (from Latin indigenus = *native)*

Browne (*in* Pseudoxia epidemica 1646: 325) "and although in many parts thereof it be confessed there bee at present swarmes of Negroes serving under the Spaniard, yet were they all transported from Africa, since the discovery of Columbus, and are not indigenous or proper natives of America." Williams (1809: 85) "GINSENG was formerly esteemed a plant **indigenous** only to China and Tartary." Buckle (1857: 118) "Indeed, of those cruel diseases now existing in Europe, scarcely one is **indigenous**; and the worst of them were imported from tropical countries in and after the first century of the Christian era." Lyell (1875: 419) "The insects of Madeira, the Salvages, and the Canaries, unlike the birds, exhibit a large proportion of **indigenous** species".

Epidemic (from Greek epi = *on and* demos = *population, through Late Latin* epidemia *and French* épidémique)

Lodge (1603: B2b) "Popular and **epidemick** have one and the same signification; that is to say, a sicknesse common unto all people, or to the moste part of them." Malthus (1803: 330) "The endemick and **epidemick** diseases in Scotland, fall chiefly, as is usual, on the poor." Southwood & Comins (1976: 963) "The model is used to describe field-data on endemic and **epidemic** populations of aphids and eucalyptus psyllids and to correlate experience in biological control situations." **Epidemic** has a long history of use as a descriptor of populations and is used to describe population explosions, in contrast to the endemic condition.

Endemic (from Greek en = *in and* demos = *population,* through French endémique)

Larousse (1972) lists 2 French synonyms (*chronique, permanent*) and 4 antonyms (*cyclique, épidémique, momentané,* and *passager*) of *endémique,* and defines the French word *endémicité* (endemicity) as the endemic state of a disease. Lodqe (1603: B2) "And such sicknesses as are these, are called **Endemiques**, provintiall or regionall infirmities, yet for all that they are not to be accounted pestilentiall or contagious." Hickeringill (1705: 42) "For which I need not beg credit, since there is no country disease (as at Virginia and Surinam) **endemically** raging throughout the Isle". Malthus (1803, above, under epidemick). Buckle (1857: 118) "For evidence of the extra-European origin of European diseases, some of which, such as the small-pox, have passed from epidemics into **endemics.**" Smith (1869: 77) "Hence famines are periodical or **endemic** in Hindostan." Cameron (1870: 149) "The **endemical** disorder passing rapidly into epidemical." Southwood & Comins (1976) "The predator can reduce all populations below the release point to extinction, so there is no lower equilibrium or **endemic** level." OAD (1980) "Yellow fever was **endemic** in parts of South America. The last American epidemic of this disease occurred in New Orleans in 1905." Price (1984) "When the effect of enemies is disrupted or environmental conditions become particularly favorable for reproduction, the population escapes the stabilizing influence of enemies . . . and increases to epidemic proportions. . . However, shortage of food and disease may lead to massive mortality and low natality causing the population to crash to . . . **endemic** levels." Church (1989) "In a country where problems are **endemic**". **Endemic** has a long history of use as a descriptor of populations and is the antonym of epidemic. It implies nothing about native origin [yellow fever is **endemic** to parts of South America but is believed to be indigenous to Africa].

Second and third meanings of endemic

Darwin (1872: 178) "Although in oceanic islands the species are few in number, the proportion of **endemic** kinds (i.e. those found nowhere else in the world) is often extremely large." Dallas (1872: 311) "**ENDEMIC.**—Peculiar to a given locality". By coincidence, Carroll's "Through the looking-glass. . ." also was published in 1872. Mackerras (1970: 192) "An **endemic** (or **precinctive**) group".

However, Lyell (1875) and Darwin (1876), who were contemporaries and colleagues, used the word **endemic** elsewhere, without definition. Lyell (1875: 413) "General inferences to be deduced from the **endemic**, and other species of animals and plants in the Atlantic Islands." Darwin (1876: 415) "Bees . . . visit many exotic flowers as readily as the **endemic** kinds". These uses of **endemic** apparently were interpreted by some as "Of plants or animals; Having their ordinary habitat in a certain country; opposed to exotic" [= indigenous] (OED 1971), and "belonging or native to a particular region or country" [= indigenous] (Webster 1986), and Ehrlich & Roughgarden (1987: 619) defined **endemic** as "Native to a particular region" [= indigenous].

Only two meanings were defined by Allaby (1977), the ecological meaning, "Of pests or disease-producing species. The normal population level of a species which occurs continuously in a given area", and a biogeographical meaning, "General. Confined to a given region and having originated there."

A fourth meaning of endemic

Wallner (1987) "on the other hand, **endemic** or rare species approximate stable equilibrium. In this review '**endemic**' refers to insects that are either rare or uncommonly abundant and therefore seldom, if ever, occur at densities sufficient for them to be considered pests." The expression **endemic species** is used, but such species are so-named according to their population level, regardless of whether they are indigenous or adventive.

Adventive (from Latin advenire *= to arrive)*

Bacon (1605: 137) "Upon the first of these, the considerations of the origin of the soul, whether it be native or **adventive**". Pemberton (1964: 695) "Since a few hundred more have been added to the endemic [= precinctive] list we can assume that the **adventive** species, including harmful, beneficial and indifferent species number well over 2,000."

A related word, adventitious, is used in biology, especially botany, to describe structures occurring in other than their customary position, e.g., the adventitious roots which arise from branches of some *Ficus* species.

Immigrant (from Latin immigrantem, *present participle of* immigrare, *one who or that which migrates into a country as a settler)*

Belknap (1792: 6) "There is another deviation from the strict letter of the English dictionaries; which is found extremely convenient in our discourses on population . . . the verb IMMIGRATE and the nouns IMMIGRANT and IMMIGRATION are used without scruple in some parts of this volume." Kendall (1809: 252) "*Immigrant* is perhaps the only new word, of which the circumstances of the United States has [sic] in any degree demanded the addition to the English language."

Introduced (species or other taxa introduced deliberately by man)

Sailer (1978) used the expressions **introduced**, exotic and immigrant virtually interchangably, but here we restrict the expression **introduced**, following Zimmerman (1948: 64) "the word introduced should be reserved for those species which have been purposely imported".

A RATIONALIZATION

The words **indigenous** and **autochthonous** are synonyms and mean native. **Indigenous** has been used more widely in biology, so for that reason is preferable to **autochthonous.** We prefer **indigenous** to **native** as a biological term because the latter has subsidiary meanings in English. The third meaning of **endemic** is as a synonym of **indigenous**, but we can find no excuse for this misconception.

Epidemic and **endemic** were employed as antonyms almost 400 years ago and they have retained this sense in epidemiology and ecology to mean outbreak and non-outbreak population levels respectively. The biogeographio meaning of "**endemic**", apparently first employed or at least popularized by Darwin (1872), is unfortunate. Brodie's (1856: 26) words are pertinent: "There are epidemics of opinion as well as of disease, and they prevail at least as much among the well-educated as among the uneducated classes of society." The opinion of persons concerned with distribution of species seems to be to continue Darwin's usage despite existence of a more valid alternative (**precinctive**) and despite prior and continuous usage of **endemic** as an antonym of **epidemic** by persons concerned with populations of organisms. Sharp's (1900) statements are explicit: "I use the word **precinctive** in preference to endemic or peculiar—both of which are in common use—in the sense of 'confined to the area under discussion.' The word endemic has been objected to on the grounds that its definition does not indicate geographical restriction, and that it is actually used in medicine to signify constant, but not necessarily exclusive, presence in a locality." We conceive **precinctive** to be a subclass of **indigenous**, and we prefer not to use **endemic** in this sense.

Wallner's (1987) use of the word **endemic** is a logical extension of the epidemiological/ecological use. We doubt that it will be popularized until Darwin's (1872) sense of **endemic** is replaced widely by **precinctive**.

It is clear that **adventive** has the broadest sense among the words used to denote non-indigenous organisms. Our definitions are: **Adventive** species are those which have arrived in a previously-unoccupied area, whether of their own volition or through the inadvertent or deliberate agency of man. They include the 2 subclasses **immigrant** and **introduced. Immigrant** species are adventive species which arrived without the deliberate agency of man, even though they may have been transported accidentally by man.

The word suggests to us an active movement which is the complement of the passive movement implied by the word **introduced. Introduced** species are adventive species which have been introduced by the deliberate agency of man. Among them are to be included those introduced for biological control purposes, together with those introduced for other purposes (e.g., crop plants, farm animals, and ornamental plants). We exclude those organisms which Sailer (1978) called "accidentally introduced" because we consider them immigrants.

More is known about current and former distributions of *Homo sapiens* L. than about any other species, so we can employ these as examples to demonstrate use of the vocabulary. Man as a species is not indigenous to the Americas, but is adventive and, more specifically, is an immigrant. At an infra-subspecific level, we recognise several waves of immigration. Some immigrants (Amerindians [including Chippewas] and Eskimos) are considered by sociologists to be indigenous to North America because immigration occurred >10,000 yrs BP, whereas no other group is considered indigenous. Eskimos populated Arctic areas of Asia and North America, so were not and are not precinctive to Arctic America. However, Amerindians evolved in and thus became precinctive to the Americas (it is arguable whether they can still be considered precinctive because a few have migrated to other continents). The time frame of these immigrations spans >10,000 years. Descendants of even the earliest European immigrants still are considered immigrants.

Ideally, we should apply the same criteria to all species. The criteria are formulated below as a dichotomous key.

For any species (or other taxon) of organism occurring in a specified area:
1 It achieved its current taxonomic identity elsewhere (it was formerly absent but is now present) .... **adventive** 2
1′ It achieved its current taxonomic status here (and has been present virtually continuously since then) .... **indigenous** 3
For an **adventive** species (or other taxon):
2 It was introduced deliberately by man .... **introduced**
2′ It was not introduced deliberately by man .... **immigrant**
For an **indigenous** species (or other taxon):
3 It is known from no other area .... **precinctive**
3′ It is known from other areas .... **indigenous but not precinctive**

It is reasonably simple to distinguish between alternatives in couplet 2 (**introduced** vs **immigrant**) and in couplet 3 (**precinctive** vs **indigenous but not precinctive**). However, the parenthetic time frame in couplet 1 (**adventive** vs **indigenous**) is uncertain.

The ability to distinguish very recent immigrants is of practical value in economic entomology, because some of these immigrants are, or are likely to become, pests. Whitehead & Wheeler (1990) suggested that **indigenous** species should be distinguished from **immigrant** species through records of former absence and current presence of the putative immigrants in the area of interest (this criterion is placed in parentheses in couplet 1 of the key above) Most records for invertebrates are associated with presence or absence of preserved specimens in museums. For the most part such specimens can at best help us decide whether an organism immigrated or was present continuously during the last few decades of human history.

There are two avenues to extend the record further into the past. The fossil record, although scanty, has demonstrated the presence of some invertebrate species in the distant past though it is better adapted for demonstrating presence rather than absence. Probable immigration can be inferred from cladistic studies.

To take examples from Florida mosquitoes, *Aedes albopictus* (Skuse) is an **immigrant**, and a recent one, with its arrival well-documented. *Aedes aegypti* (L.) likewise is an **immigrant**, believed to have originated in Africa, and probably has been present in Florida for some hundreds of years (at or soon after Spanish settlement), long before humans began to catalog the mosquito fauna. *Toxorhynchites amboinensis* (Doleschall) was **introduced** into Florida for biological control purposes. All 3 species are **adventive.** The two *Wyeomyia* species whose larvae develop in the leaf axils of bromeliads of the genus *Tillandsia* in southern Florida cause more thought. Both occur also in the Greater Antilles (and one in eastern Mexico), so they are not precinctive to Florida (and neither are *Tillandsia utriculata* L. and *Tillandsia fasciculata* Swartz, the 2 plants providing principal habitat for their larvae). It is likely that both *Wyeomyia* were **immigrant** to Florida in prehistoric times, and perhaps immigration by their conspecifics from the Greater Antilles still occurs in hurricane winds. However, their evolutionary biogeography is unstudied, so by default we consider them **indigenous** at least for the present. We do not know of any mosquito species **precinctive** to Florida.

THIS SYMPOSIUM

This tenth Behavioral Ecology Symposium is entitled "Attack and Defense: Behavioral Ecology of Predators and Their Prey." It continues the theme of the ninth symposium, which was entitled "Attack and Defense: Behavioral Ecology of Parasites and Parasitoids and Their Hosts." In our introduction to the ninth symposium (Frank & McCoy 1989), we asked how the contributions fit in with predictions that have been made about the immediate future courses of behavioral ecological research in general (Krebs 1985) and of behavioral ecological research on insects in particular (Burk 1988). The answer clearly was that the contributions fit in well, and it seems approprate to ask the same questions for the contributions to this thematically-similar tenth symposium.

Before we can answer the question, however, we will need to reiterate the predictions. Krebs (1985) predicted five paths of behavioral ecological research: (1) life history and population dynamics in relation to behavioral ecology, (2) mating systems, (3) parasites and sexual selection, (4) learning, and (5) the genetic basis of behavior. Likewise, Burk (1988) predicted five paths for research specifically on insects: (1) sexual selection, (2) resource competition among females, (3) learning, (4) orientation and movement, and (5) communication. The salient difference between the two lists is the emphasis upon studies of orientation, movement, and communication in insects.

It is interesting to note, then, that four of the five contributions to the tenth symposium deal in some manner with orientation, movement, and/or communication. John Linley's contribution details the movements employed by species of *Toxorhynchites* to effect the capture of subsurface prey. His exhaustive analysis reveals an unimagined melange of movements necessary for successful prey capture, rivaling in complexity those documented for many larger, much more visible predators. Jim Lloyd's contribution suggests that the sometimes puzzling "sexual signals" of fireflies may be hard to interpret because they have evolved under constraints beyond simple efficacy of attraction of potential mates. He posits that these signals also reflect strong selection imposed by predation and, therefore, that they are not solely species-isolating mechanisms. Multiplicity of selective pressures also is central to Dave Pearson's contribution. He questions the common assumption that prey have only single anti-predator characters, and presents six theories, based upon his work with tiger beetles, to explain the evolution of multiple anti-predator characters. He shows how various types of movements, orientations, signals, and other mechanisms work in concert to deter predation upon tiger beetles. Finally, Brian Witz catalogues some of the recent literature on predator-prey interactions, and places the studies into categories of taxonomy of participants and type of interaction. Many of the categories of interaction he erects are based upon directed movements of prey species toward predators, or upon some sort of signalling by prey species to predators. He suggests that the frequency with which taxa and types of interactions are studied often is not the same as their proportional representations in nature.

Jon Allen's contribution is quite distinct from the other four. He explores the "phase-locked," "quasiperiodic," and "chaotic" behaviors of predator-prey models in relation to the functional response, and finds unexpected and complex switching among these behaviors. He also finds that some types of functional response produce more complexity than do others. He notes that his models ignore genetics, arrangements of individuals in space, and other real complications, but suggests that inclusion of these complicating factors is not likely to reduce the complexity he has uncovered. Allen discussed some contributions of genetics and arrangement of individuals in space to parasitoid-host models in the ninth Behavioral Ecology Symposium.

ENDNOTES

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THE PREDATORY BEHAVIOR OF *TOXORHYNCHITES AMBOINENSIS* AND *TX. BREVIPALPIS* LARVAE (DIPTERA: CULICIDAE) IN RESPONSE TO SUBSURFACE PREY

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ABSTRACT

Time lapse video recordings and high speed cinematography were used to provide a description and analysis of the predatory behavior of *Toxorhynchites amboinensis* and *Tx. brevipalpis* larvae. Only behavior in response to subsurface prey was examined with emphasis on the bending response, in which larvae turn towards approaching prey, and the strike, which effects prey capture. Bending was a very common response and occurred when prey was positioned in any direction relative to the larva's body. *Toxorhynchites brevipalpis* was more responsive than *Tx. amboinensis; Tx. brevipalpis* larvae bent more rapidly, towards more distant prey, and through angles representing larger proportions of the prey angle. Bend angle increased with increasing prey angle, but as a proportion of prey angle, bend angle increased as prey angle decreased. Bend angle was little affected by prey distance. Movement during being was smooth and continuous. Each bend consisted of a brief accelerative and longer decelerative phase, with average bending rates varying greatly depending on prey angle and distance. Average bending rate increased with decreasing prey distance, the rate of increase being especially rapid as prey approached close to the body. Prey capture during strikes was accomplished in 0.012-0.024 s, and the entire strike completed in 0.060-0.076 s. Only the lateral palatal brushes were used to capture prey. Immediately after capture, prey was seized by the mandibles and released by the palatal brushes, which played no further role in holding or manipulating food.

For descriptive convenience, 3 types of strike were recognized, frontal with head extension, lateral with head extension, and lateral without head extension. These 3 form part of a continuous series. Frontal strikes involved little or no lateral turning towards prey and involved dramatic forward extension of the head, accompanied by opening and closing of the palatal brushes. Head extension was accomplished by sudden increase in the larva's internal pressure resulting from rapid contraction of circular muscles primarily in abdominal segments 1 and 2. Lateral strikes always involved some degree of turning towards prey, and also some degree of head extension when prey was

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RESUMEN

Se usaron grabaciones de video magnetoscópico contínuo y de cinematografía a alta velocidad para proveer una descripción y un análisis del comportamiento depredador de larvas de *Toxorhynchites amboinensis* y *T. brevipalpis.* Solo se examinó el comportamiento como respuesta a la superficie baja de la presa, con las larvas orientándose hacia la presa que se aproxima, y el ataque que efectuó la captura de la presa. Doblarse fue una acción común que ocurrió cuando la presa estaba en cualquier posición relativa al cuerpo de la larva.

La captura de la presa durante el ataque se llevó a cabo en 0.12-0.024 segundos, y todo el ataque se completó en 0.60-0.076 segundos. Solo usaron los cepillos laterales palatales para capturar la presa. Inmediatamente después de la captura, la presa fue sujetada por las mandíbulas y soltada por los cepillos palatales, los cuales no tuvieron mas función en aguantar o manipular la comida.

Por conveniencia descriptiva, se reconocieron 3 tipos de ataque, frontal con extensión de la cabeza, lateral con extensión de la cabeza, y lateral sin extender la cabeza. Estas tres forman parte de una serie contínua. Ataques frontales involucran poco o ningún movimiento lateral hacia la presa y causa una dramática extensión de la cabeza hacia adelante, acompañado del abrir y cerrar de los cepillos palatales. La extensión de la cabeza se llevó a cabo por un aumento repentino de la presión interna de la larva, causada por rápidas contracciones de los músculos circulares, principalmente de los segmentos abdominales 1 y 2. Los ataques laterales siempre involucraron algún grado de orientación hacia la presa, y también un poco de extensión de la cabeza cuando la presa estaba en posición de ángulos pequeños a cualquier lado de la cabeza, pero no cuando la presas estaba en posición de ánglos mayores. Ataques hechos hacia ángulos mayores también estuvieron acompañados por rotación de la cabeza hasta aproximadamente de 90°, y una rotación parcial del tórax. En ataques laterales, el grado del cambio del ángulo durante la orientación fue usualmente mayor entre la cabeza y el tórax, menos en el abdómen, y menor entre el tórax y el abdómen. La velocidad angular y de la cabeza (al margen frontal de la cabeza) durante el ataque varió, en 5 muestras filmadas, de cerca de 5,000°/s a 210mm/seg, a 12,000°/seg y 600 mm/seg. Los ataques se hicieron solo cuandó la presa se aproximó mucho a la cabeza de la larva. Teniendo todo en cuenta, la proporción de ataques exitosos por *Tx. brevipalpis* (71.5%) fue significativamente mayor que por *Tx. amboinensis* (54.7%). En *Tx. amboinensis,* pero no en *Tx. brevipalpis,* la proporción de ataques exitosos y no exitosos fue significativamente con presas localizadas a ángulos pequeños relativos a la cabeza. En ambas especies hubo una relación linear entre el ángulo de la presa y el ángulo de ataque en ataques con éxito y sin éxito, con el ángulo de ataque exitoso promediando de 81% del ángulo de la presa en *Tx. amboinensis* y aproximadamente un 73% en *Tx. brevipalpis.*

The predatory habits of *Toxorhynchites* larvae first attracted attention from entomologists many years ago (Green 1905, Banks 1908, College 1911). Modern studies have enhanced understanding of the behavior, but have generally tended to emphasize the behavior's quantitative impact on both predator and prey populations, rather than description and understanding of the behavior itself. Consequently, much is known about the numbers of prey consumed in the laboratory (Padgett & Focks 1980, Frank et al. 1984), and integrated laboratory and field observations have revealed interactions between predator and prey in nature (Trpis 1973, Lounibos 1979, Frank et al. 1984,Lounibos et al. 1987).

In contrast, accounts of the behavior of *Toxorhynchites* larvae on the approach of prey and during its capture are given only in very general terms (e.g. Breland 1949, Muspratt 1951, Goma 1964, Crans & Slaff 1977, Furumizo & Rudnick 1978), with little or no quantitative information. Some accounts have mentioned that *Toxorhynchites* larvae are capable of detecting potential surface prey from short distances if the water surface is disturbed. Detection is said to be by means of large thoracic setae (Paine 1934, Rubio et al. 1980), and may cause the larva to approach the prey either by inching forward using the siphon as a pivot (Crans & Slaff 1977), or by swimming (Paine 1934, Breland 1949). Neither of these behaviors has been closely studied and Steffan & Evenhuis (1981) concluded from the literature that larvae only rarely swim towards prey. Another easily observed reaction towards approaching prey is that in which larvae bend their bodies to being the head closer to the prospective victim. This behavior, referred to here as bending, has rarely even been mentioned (Russo 1986), despite its probably importance in increasing the success rate during attempted prey capture.

Movements that accompany the final strike, which effects seizure of the prey, are extremely rapid. Consequently, the strike behavior has been described with considerable uncertainty in the literature, especially with regard to the mouthparts involved. Breland (1949) writes that "it has been stated frequently that the larvae use the brushes (the lateral palatal brushes of Harbach & Knight 1980) to seize and hold the prey", but then admits that he did not determine if these statements resulted from observation or conjecture. His own observations, however, led him to conclude that the mandibles and not the palatal brushes were used to capture prey, with the possibility that proper mandibular function was in some way dependent on the brushes. Involvement of the brushes was suggested by the failure of two larvae with damaged brushes to capture prey. Likewise, Furumizo & Rudnick (1978) concluded that the brushes played some role, but at the same time stated that the mandibles primarily were employed to seize and hold prey. Going a step further, Russo (1986) stated that "the mandibles opened as the head reached its maximal extension", a claim one may reasonably question in view of the fact that prey capture requires only 1/50-1/75 s (see results). The fact is that such brief events simply cannot be resolved by unaided stereomicroscopic observation. Reliance on this alone has led not only to incorrect conclusions, because the palatal brushes and not the mandibles are used to seize prey (see results), but has provided no information about the physical actions used to effect prey capture, their timing, or how they are accomplished.

In this paper, I have provided a more complete and quantitative analysis of certain aspects of predatory behavior in *Toxorhynchites* larvae, using *Tx. amboinensis* (Doleschall) and *Tx. brevipalpis* (Theobald) as experimental animals. Emphasis was entirely on behavior connected with response to approaching prey, namely the bending reaction, and with the strike sequence itself. The reaction whereby larvae turn and swim towards the source of surface disturbances (Paine 1934, Breland 1949) is not considered here because it is primarily a response to surface prey, it is probably much more common and important than is suggested by the literature, and is sufficiently complex to warrant separate analysis. When the mosquito larvae used as prey in the present study occasionally broke the water surface with their siphons, the *Toxorhynchites* larvae frequently swam towards the source of disturbance.

MATERIALS AND METHODS

Insects

Tx. amboinensis and *Tx. brevipalpis* larvae were taken from laboratory colonies reared at 27°C under a light regimen of LD 12:12. *Aedes aegypti* L. larvae were provided in excess as prey throughout development. *Toxorhynchites* larvae used for observation were removed from the colony pans on their 2nd day in the 4th instar, placed individually in small wells containing tap water and starved for 72 h at 25-27°C, which was also the temperature at which all subsequent observations were done.

Methods of recording behavior

Video tapes were used for study of some aspects of both bends and strikes; high-speed cinematography were used only for recording movement during strikes. Video records were made as follows. The starved larvae were placed individually in plastic petri dishes, 8.5 cm diameter, 1.4 cm deep, containing tap water about 1 cm deep. Each larva was left undisturbed for 5 min, before addition of a single large 4th instar *Ae . aegypti* larva to serve as prey. Behavior was then recorded for 5 min or until the prey larva was captured. Recording was done with a Panasonic NV 8050 time-lapse video recorder and General Electric TE-44BSA camera fitted with a 7.6 cm (focal length) lens mounted in front of a small extension tube. Individual *Toxorhynchites* larvae were numbered sequentially by means of numerals set close to one side of the dish within the recorded image field. Records were obtained from 112 *Tx. amboinensis* larvae and 130 *Tx. brevipalpis*. Of these, 94 *Tx. amboinensis* and 114 *Tx. brevipalpis* were used for analysis, the remainder being considered superfluous.

For cinematography of strikes, only *Tx. brevipalpis* larvae were used. They were treated exactly as for video records, except that they were placed prior to filming in dishes 3.5 cm in diameter and 0.9 cm deep, filled to about 0.5 cm deep. Smaller dishes allowed greater magnification on film. and the shallower water forced the larva's body to the desired position, almost perpendicular to the optical axis. Larvae were illuminated during filming with 3 lights totalling about 1000 watts, allowing the necessary effective shutter speed of 1/1500 s, using the camera's variable shutter and Kodak 4-X 16 mm reversal film (ASA 320). The camera was a Locam model 51002, capable of filming speeds up to 500 frames/s over a continuously variable range. At the high filming rates used (350 and 500 frames/s,) much film was wasted during "false starts", when the camera was started in anticipation of a strike that eventually did not occur. A few prey larvae were therefore presented by holding them in fine forceps and slowly advancing them towards the predator. On analysis, the initial filming rate of 350 frames/s proved too slow and only 1 strike filmed at this speed, because it illustrated one type of strike particularly well, was used eventually for analysis. In addition, 5 strikes filmed at 500 frames/s were analyzed.

Methods of analysis

Review of the video records showed that where measurements of changes in the angle of the predator's body were needed, only certain bends and strikes could be used. However, the sector (see below) in which prey was positioned was determined for every bend or strike recorded. When bends occurred, the body of the *Toxorhynchites* larva was usually in a straight attitude and all such bends were measured. On those occasions when a bend in one direction was followed immediately by an opposite one (i.e. initiated from a bent position), only the first bend was analyzed. More rarely, when a larva formed a limited angle in response to rather distant prey and then, after a pause, bent further in the same direction as the prey approached more closely, only the initial bend was measured and only one bend was scored. In the case of strikes, which often were initiated from a bent position, all were measured, except in relatively rare instances where surface reflections interfered with the image, or two or three strikes occurred in rapid succession, when only the first was measured.

The video image on the monitor screen was about 2.2x life size. The record for each larva was played back until either a bend or a strike occurred. The video "fields" (each corresponding to 1/60 s) were then reversed at slow speed and stopped at the field immediately preceding that in which motion started. A machinist's caliper was then used to measure the distance of the nearest part of the prey to either (for bends) the middle of the predator's body (middle of the 3rd abdominal segment), or (for strikes), the middle of the head. The angle of the nearest part of the prey to the head (or to the middle of the body for bends) was subsequently measured with a transparent overlay made from polar coordinate graph paper. The overlay was positioned for head measurements with its central point in the middle of the head (or 3rd abdominal segment for bends) and with the 0 line aligned (for strikes) along the mid-line passing through the head to the middle of the thorax and, for bends, along the longitudinal axis of the body. Such measurements were made for plotting the position of prey, but it was also necessary to determine angular change during the bend or strike. To do this, for both bends and strikes, the central point of the overlay was moved to the middle of the thorax, judged to be the approximate pivot point of the body, and the angle to prey measured again. With the overlay kept in position, the video fields were then advanced until the bend or strike motion had reached maximum amplitude, whereupon the angle of displacement was recorded. It was often necessary to re-position the overlay's central point slightly to compensate for small shifts in the position of the thorax, but care was taken to move the overlay without rotation from its original alignment.

A similar method was used to estimate changes in the rate of bending throughout a few selected bends (see results). In this case, points showing the starting alignment of the predator's head, mid-thorax and siphon were marked on a transparent overlay, then the image was advanced uniformly by 4 to 30 field increments, as necessary to resolve movement for different bending rates, and the position of the middle of the head marked at each increment. Angles relative to the starting head/mid-thorax alignment were then measured from enlarged copies of each overlay.

Data on strikes were obtained only from filmed sequences. Each 16 mm image was first re-photographed at 5.7x magnification onto 35 mm Kodak Panatomic-X film using a bellows and Zeiss 63 mm Luminar lens. Resulting negatives were then printed at 6.1x magnification, making the final image of the larva about 80 mm long, or approximately 8x life size. All measurements of head movements and spatial changes in the abdomen (see results) were made from these enlarged prints, using a machinists's caliper, and were then converted to actual distances. To measure changes in angle between head and thorax (Hd-Th), thorax and abdomen (Th-Ab), and within the abdomen (Ab-Ab), high contrast photocopies were first made of these prints. White lines were drawn to mark the longitudinal axes of the head, thorax, and abdominal segments 1 and 2 and 7 and 8 (Fig. 1a), and the required angles (Fig. 1a) measured with a protactor.

In addition to angular changes between body parts, it was necessary for most strikes to determine the actual arc of motion of the head and its speed and angular velocity. For this, each 16 mm frame was projected (magnification about 16x life size) to exact registration on white paper taped to a screen (small background spots in the image

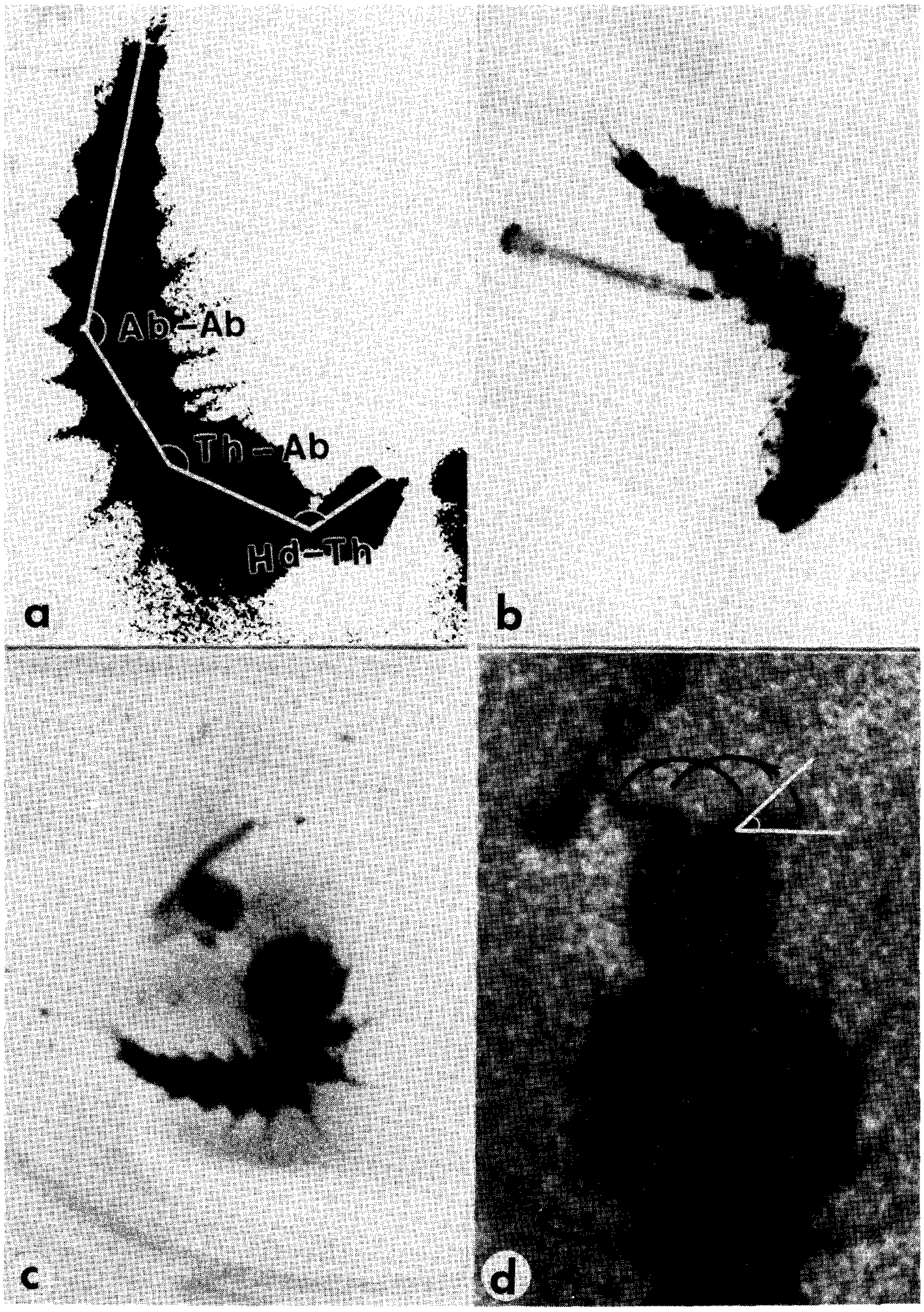


Fig. 1. a, angles measured to record angular changes in body during strike; b, a typical bend towards prey; c, a frontal strike with head extension from bent position; d, closure arc of lateral palatal brushes and angle measured to record brush movement.

served as fiducial markers). The position of a central point on the anterior margin of the head in each frame was then marked and the appropriate angles (relative to mid-thorax) and distance later measured.

Several aspects of the results are presented by data grouped according to which 30° sector of a circle (Table 1) the prey occupied when response occurred. The circle's center was in the middle of the head for strikes and in the middle of the body (abdominal segment 3) for bends.

Scanning electron microscopy

Scanning electron micrographs were made of mouthparts of 4th instar *Tx. amboinensis* and *Tx. brevipalpis* larvae reared in clean water to prevent contamination. The animals were fixed in 30% ethanol, dehydrated in ethanol, and dried finally by the critical point method. Specimens were coated with gold and examined in a Hitachi S-510 scanning electron microscope.

Limitations of the study

The study was limited to movements that were lateral with respect to the larva. Larvae occasionally bent downwards in response to prey passing beneath, but these movements were of small amplitude and were uncommon in the dishes used here. Bending towards surface prey is common, as will be described in a later paper, but the behavior is essentially the same as described here. In the case of strikes, larvae occasionally struck at prey slightly beneath the head, and they will do so at surface prey (Breland 1949). Again, however, the important elements of the behavior are represented by present data.

RESULTS

Confirmation of bending as a subsurface behavior

It was known (unpublished personal observations) that surface prey would elicit the bending response. To be sure that bending occurred in the absence of surface effects, which were sometimes caused by the *Ae. aegypti* larvae, 10 *Tx. amboinensis* and 10 *Tx. brevipalpis* larvae were isolated as usual, but a large 4th instar *Culicoides variipennis* (Coq.) larva was added as prey. The *Culicoides* larvae swam always beneath the surface, but to be certain that surface contacts were not made (that might be undetectable from the video image), the dishes were watched until the midge larva approached closely enough to elicit a bending response. All the *Toxorhynchites* larvae except one *amboinensis*, which did nothing within 5 min, eventually responded without any surface disturbance that could be seen under close scrutiny by reflected light. Subsequently, 2 larvae of each of the predator species, ones that had not captured the midge larva, were placed in a deeper container, in water about 2 cm deep, and induced to dive by gentle probing. A midge larva was again added and, within a few minutes, bending was observed in 3 of the submerged *Toxorhynchites* larvae.

THE BENDING RESPONSE

Frequency and appearance

Of the 94 *Tx. amboinensis* and 114 *Tx. brevipalpis* larvae observed, 87.7% and 93.4%, respectively, bent towards prey. Several animals in each case bent 5 or 6 times as the *Ae. aegypti* larvae moved about them. Of the few larvae that did not bend, most were approached frontally, so that bending did not occur before prey capture. Bending was a very distinct, clear reaction in which the *Toxorhynchites* larva turned towards the prey (Fig. 1b), often when the latter made a sudden, vigorous movement.

Position and distance of prey

In both predators, bends were observed towards prey approaching from or moving in any sector (Fig. 2, Table 1). Fewer bends were recorded for prey located at small

Fig. 2. Spatial distributions of prey (nearest part) when bends initiated.

TABLE 1. PREY DISTRIBUTION (BY SECTOR) AT BEND INITIATION AND MEAN DISTANCES OF PREY FROM MIDDLE OF BODY.

	Tx. amboinensis			*Tx. brevipalpis*		
Sector[1] (°)	No. in sector	%	Mean distance[2] (mm)	No. in sector	%	Mean distance[2] (mm)
0-15	2	1.1	7.0	10	4.6	22.4
16-45	27	14.7	9.9	43	19.6	15.5
46-75	40	21.7	7.8	51	23.3	15.1
76-105	51	27.7	7.4	42	19.2	16.2
106-135	34	18.5	7.6	26	11.9	16.6
136-165	23	12.8	8.1	40	18.3	11.7
166-180	7	3.8	5.8	7	3.1	15.2

[1] Relative to middle of body (abdominal segment 3)

[2] Measured to middle of body

angles to either side of the front of the predator's head, or behind the tail, especially in the case of *Tx. amboinensis* (Fig. 2, Table 1). Bends of very small amplitude sometimes occurred in response to frontally positioned prey, even, in the case of *Tx. brevipalpis*, if the *Ae. aegypti* larvae was some distance away (Fig. 2). Otherwise, the positions of prey were distributed symmetrically about the body, with most (total 67.9% for *Tx. amboinensis*, 54.4% for *Tx. brevipalpis*) in the 3 sectors from 46-135° (Table 1). Prey positions were not clustered with an obvious focus around any particular part of the body, but rather evenly surrounded each predator (Fig. 2), suggesting that the sense organs involved in bending are present along much of the predator's body.

Toxorhynchites brevipalpis larvae were more responsive than *Tx. amboinensis* and bent when prey was considerably further away (Fig. 2). The mean distances at which prey elicited bends were quite uniform between sectors for both species (Table 1), with *Tx. brevipalpis* distances about twice those for *Tx. amboinensis*. The maximum distance recorded for *Tx. brevipalpis* was 49.6 mm, compared to 24.6 mm for *Tx. amboinensis*, while the minimum distances were 1.9 mm and 2.4 mm, respectively. Most prey were distributed in a diffuse belt around the predator (Fig. 2), with density falling off with increasing distance. Since the distributions were similar between sectors, all were combined in each case to reveal the strongly skewed overall patterns (Fig. 3), especially in the case of *Tx. brevipalpis*. The main range of response for both species, with the prey used, was between 3 and 12 mm (Fig. 3), about 1/3 to 1 body length away.

Nature and rate of bending

During bending, most angular change within the body took place between the abdominal segments and less between the abdomen and thorax and thorax and head (Fig. 1b). To examine changes in bending rate, 5 selected bends of different bend angles and prey distances were analyzed for each species (Fig. 4). As seen most clearly in *Tx. amboinensis*, bending consisted of a short accelerative phase and a longer decelerative one (Fig. 4). With one exception, the time increments used were too great in the case of *Tx. brevipalpis* to resolve the brief accelerative phase. In *Tx. amboinensis*, acceleration of the head was complete in from 0.14-0.60s, whereas it was over in less than 0.14s in all the *Tx. brevipalpis* bends except one rather slow one (open circle, Fig. 4). Maximum bending rate varied considerably in both species, from about 30°/s to over 450°/s, with the rates in *Tx. brevipalpis* tending to be somewhat higher. Bends to larger angles were executed at higher bending rates in both species, as measured by calculat-

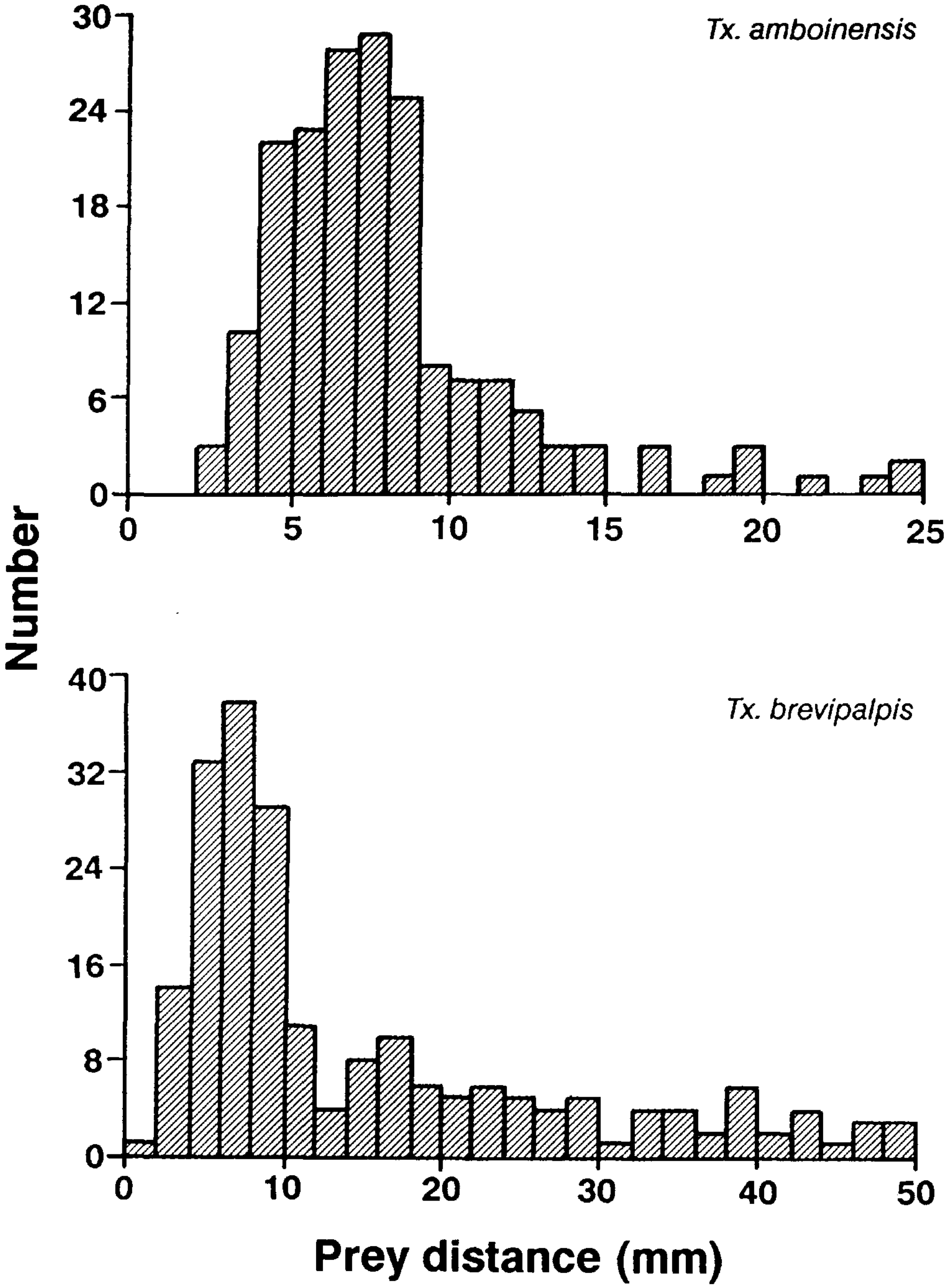


Fig. 3. Distance distributions of prey (all sectors combined) when bends initiated.

ing the regressions of bend rate on bend angle for prey distances of 5-10 mm. Both relationships were linear (not shown), with highly significant regression coefficients (1.044, $P < 0.01$, for *Tx. amboinensis*, 1.468, $P < 0.01$ for *Tx. brevipalpis*), implying, respectively, increases of 10.4 and 14.7°/sec for each 10° increment in the bend angle.

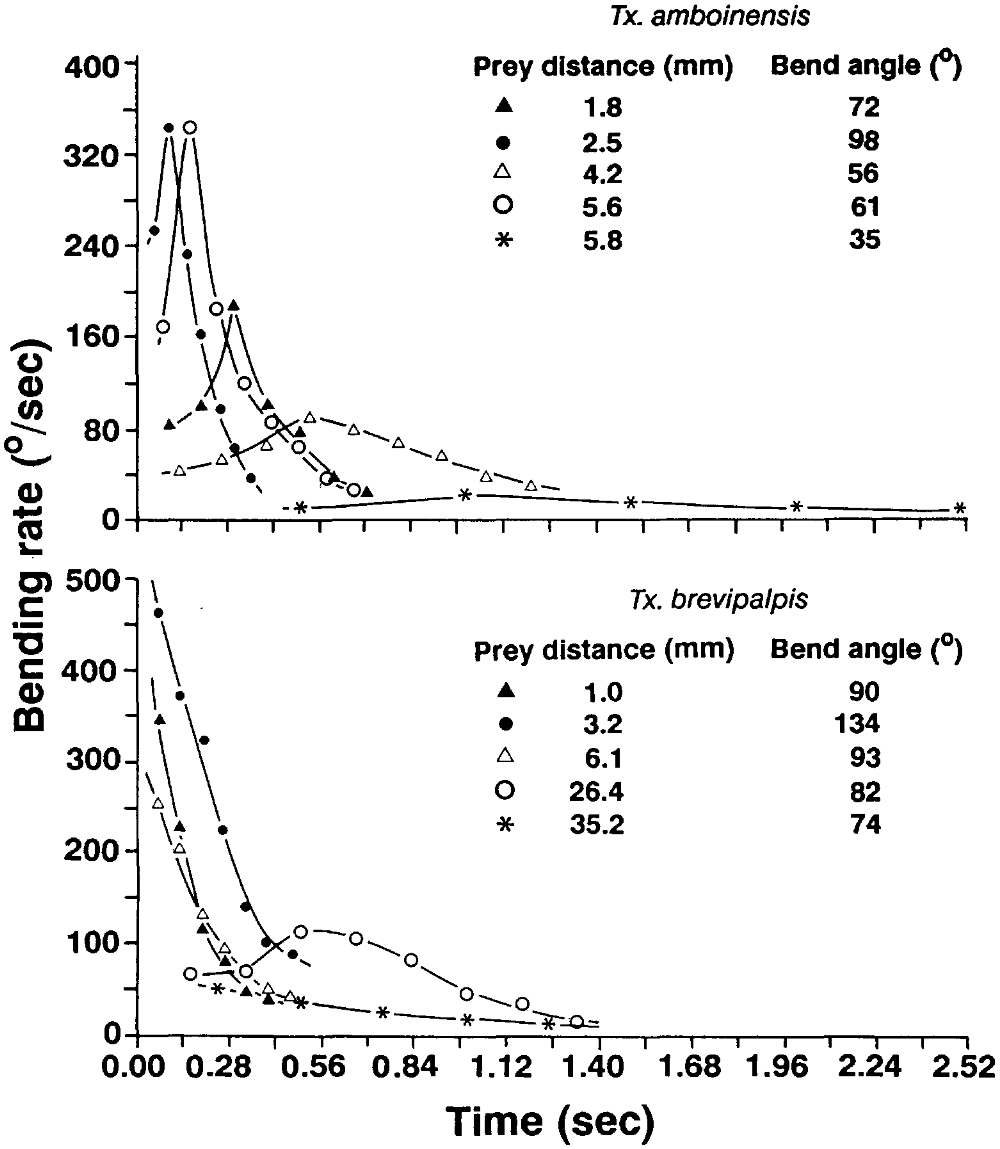


Fig. 4. Bending rates throughout 5 selected bends completed to different bend angles for prey at different distances.

Prey angle, bend angle and prey distance

Both predators showed similar relationships between prey angle and bend angle (Fig. 5). The data could be described empirically in each case by positive exponential regression (Fig. 5), but considerable variation in bend angle was observed for prey in any particular position, and bend angle rarely exceeded prey angle. Variation also increased as prey angle increased. Thus, although the *Toxorhynchites* larvae turned towards prey, the degree of turning was very varible and only rarely was a bend made completely to or beyond the prey angle.

The relationship between degree of bending and prey angle (Fig. 6), showed that bend angle as a proportion of prey angle was least for the largest prey angles. It then increased with decreasing prey angle relatively slowly, but then progressively much

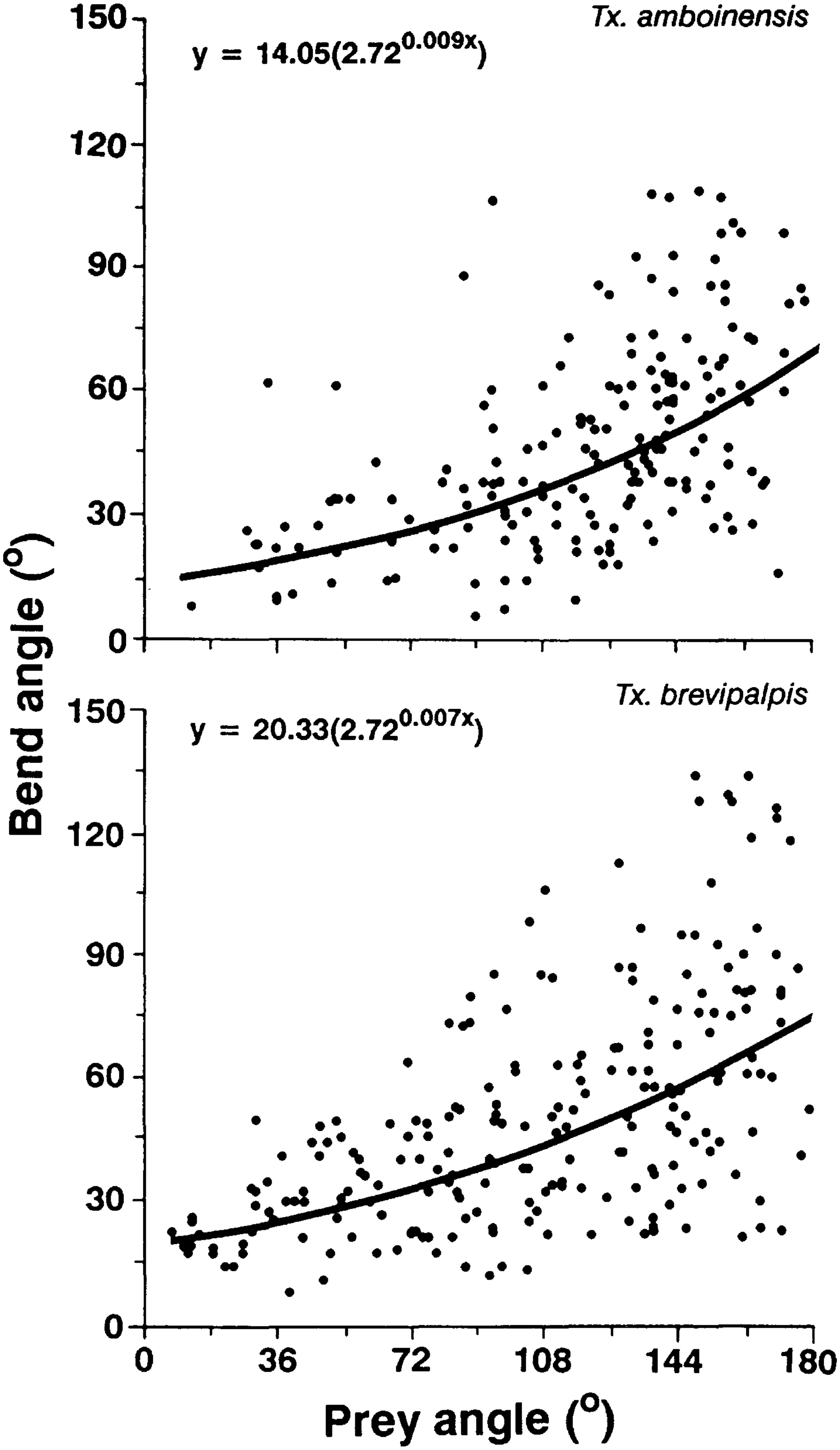


Fig. 5. Relationship between prey angle and bend angle.

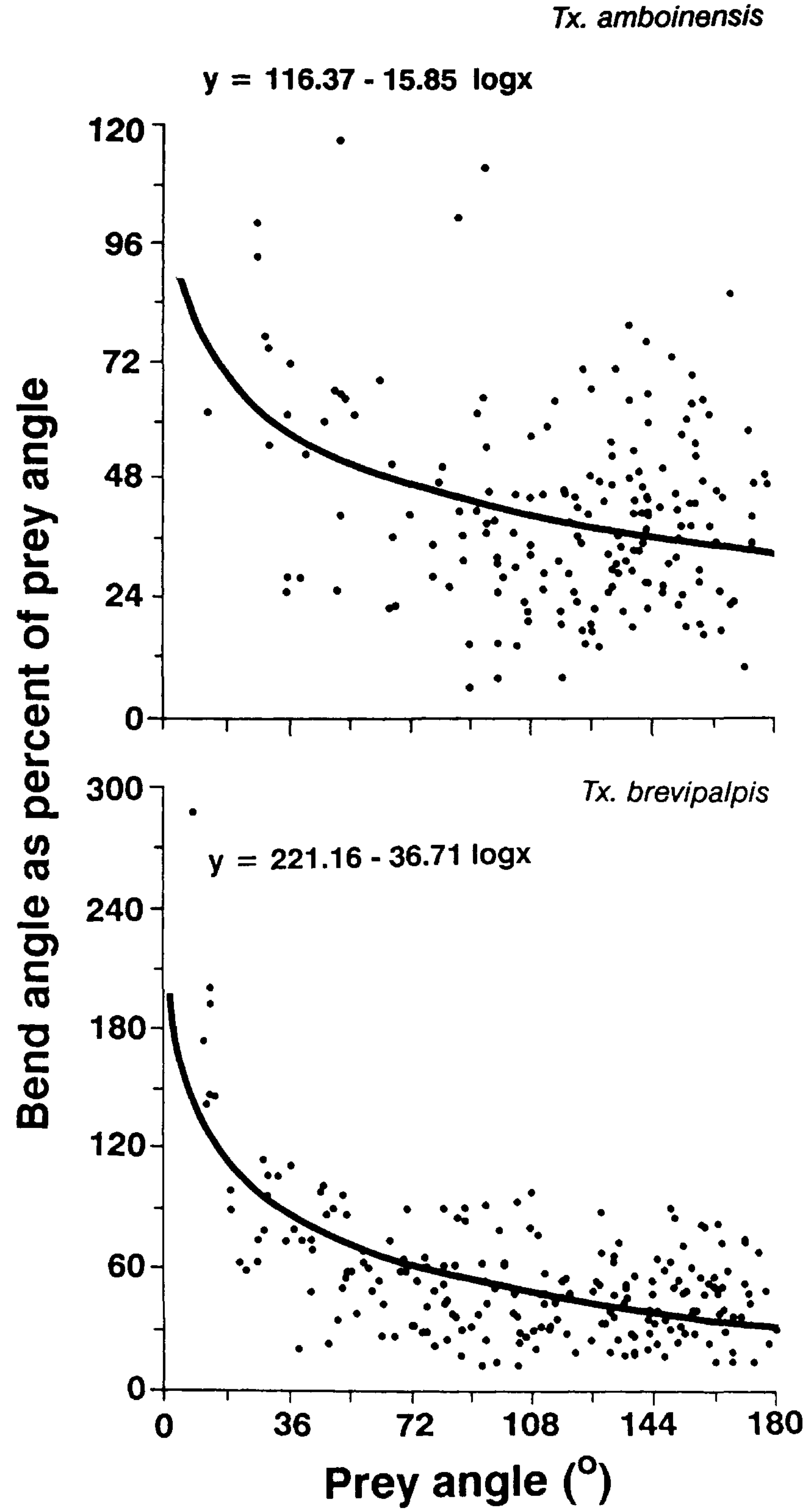


Fig. 6. Relationship between prey angle and bend angle as a percent of prey angle.

more rapidly as prey angle diminished below about 40°. By analysis of variance, the data were best described by negative logarithmic regressions (Fig. 6). From these, it was apparent that bend angle as a percent of prey angle was, for prey angles of 25, 50 to 170°, about 65, 54, and 35% for *Tx. amboinensis* and 103, 78 and 33% for *Tx. brevipalpis*. Again, *Tx. brevipalpis* appeared more responsive, and turned towards the prey by a greater proportion of the prey angle. Additional evidence for this came from a simple comparison of the two species in terms of the average degree of bending, by sector (Table 2).

In contrast to prey angle, the distance of prey affected the degree of bending very little in either species (Fig. 7). For any prey distance there was a great deal of variation in the proportion of the prey angle to which either predator would bend. Calculation of linear regressions (Fig. 7) gave negative coefficients for both species (-0.365 for *Tx. ambionensis*, -0.310 for *Tx. brevipalpis*, but only the value for *Tx. brevipalpis* was significant ($P < 0.02$), because very few values for *Tx. amboinensis* were obtained at longer prey distances (Fig. 7). The very limited effect of prey distance was well illustrated by the data for *Tx. brevipalpis*, where bend angle increased only 3.1% of prey angle for every 10 mm that the prey more closely approached the predator.

Although prey distance had little effect on the degree of bending, its effect on the average bending rate was substantial (Fig. 8), as determined by slow motion timing of complete bends of known angle with a stop watch. Data for the two *Toxorhynchites* species were quite similar and were fitted by negative power regression equations (Fig. 8). Until prey had approached quite closely, bending rate increased only slowly as prey distance decreased. At about 4 mm in *Tx. amboinensis* and 10 mm in *Tx. brevipalpis*, however, the rates began to increase rapidly (Fig. 8), indicating much more rapidly incrementing turning rates as prey moved closer within a narrow range very near the body. Average bending rates did not often exceed 150°/s in either species until prey was closer than 4 or 10 mm, but then a number of bends, particularly in *Tx. brevipalpis*, considerably exceeded 200°/s (Fig. 8).

THE STRIKE

General observations

Execution of the strike movement in *Toxorhynchites* larvae is extremely rapid and its component movements cannot be seen under a stereomicroscope. In this study, only strikes of *Tx. brevipalpis* were recorded by high speed cinematography, but the behavior of *Tx. amboinensis* and other species can be assumed to be very similar.

Basically two movements of the body may be involved during a strike; head extension (and retraction), and lateral turning of the body (contraction and relaxation). These may or may not be combined, depending on prey angle, to produce 3 basic types of strike, (i) frontal with head extension, (ii) lateral with head extension and (iii) lateral without head extension. The distinction between the 3 types is made for descriptive

TABLE 2. MEANS, BY SECTOR, OF BEND ANGLE AS A PERCENT OF PREY ANGLE.

Sector (°)	*Tx. amboinensis* Mean %	*Tx. brevipalpis* Mean %
0-45	64.2	107.2
46-75	49.8	57.3
76-105	39.2	47.7
106-135	35.3	45.5
136-180	41.1	44.3

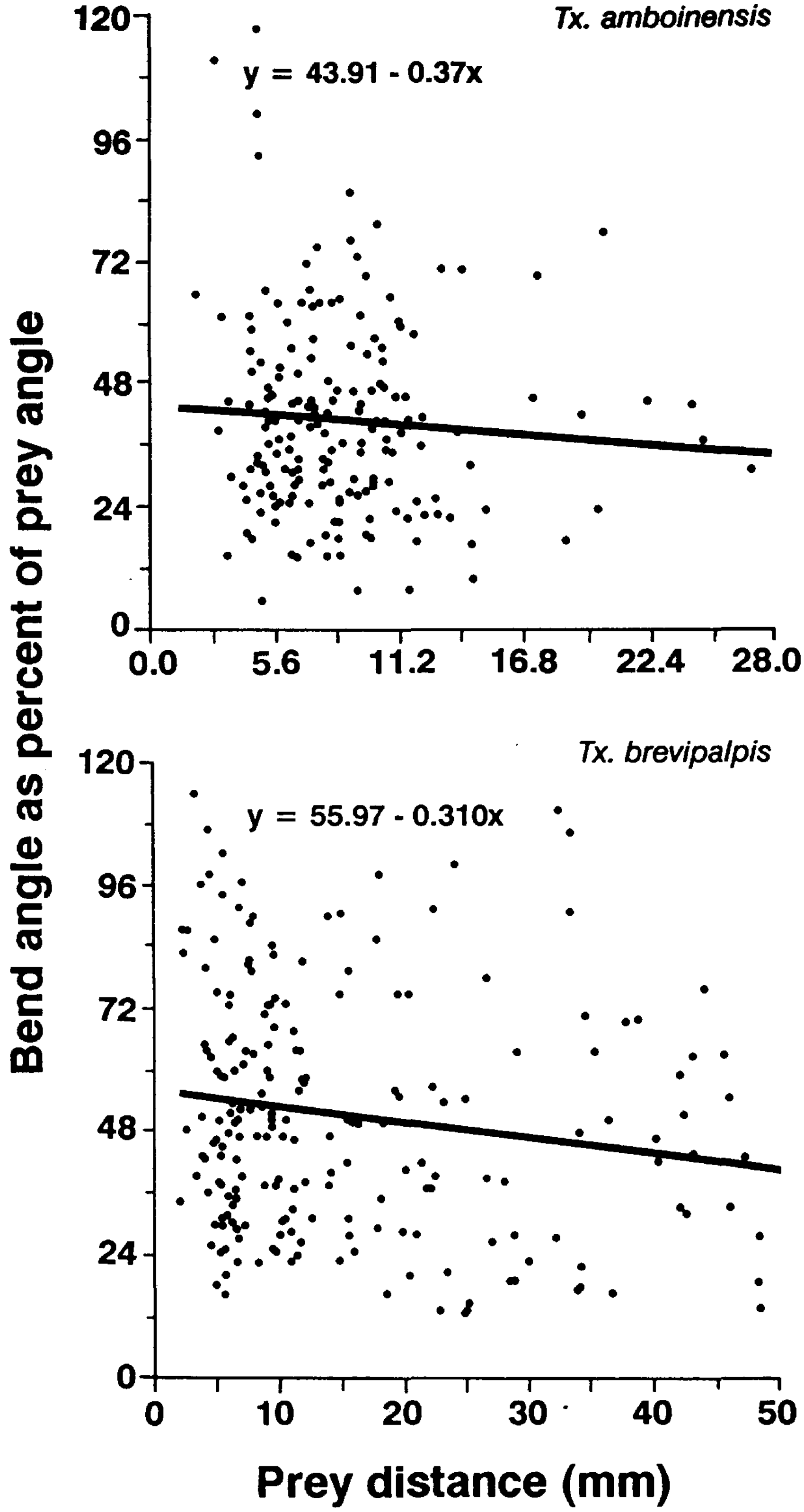


Fig. 7. Relationship between prey distance and bend angle as a percent of prey angle.

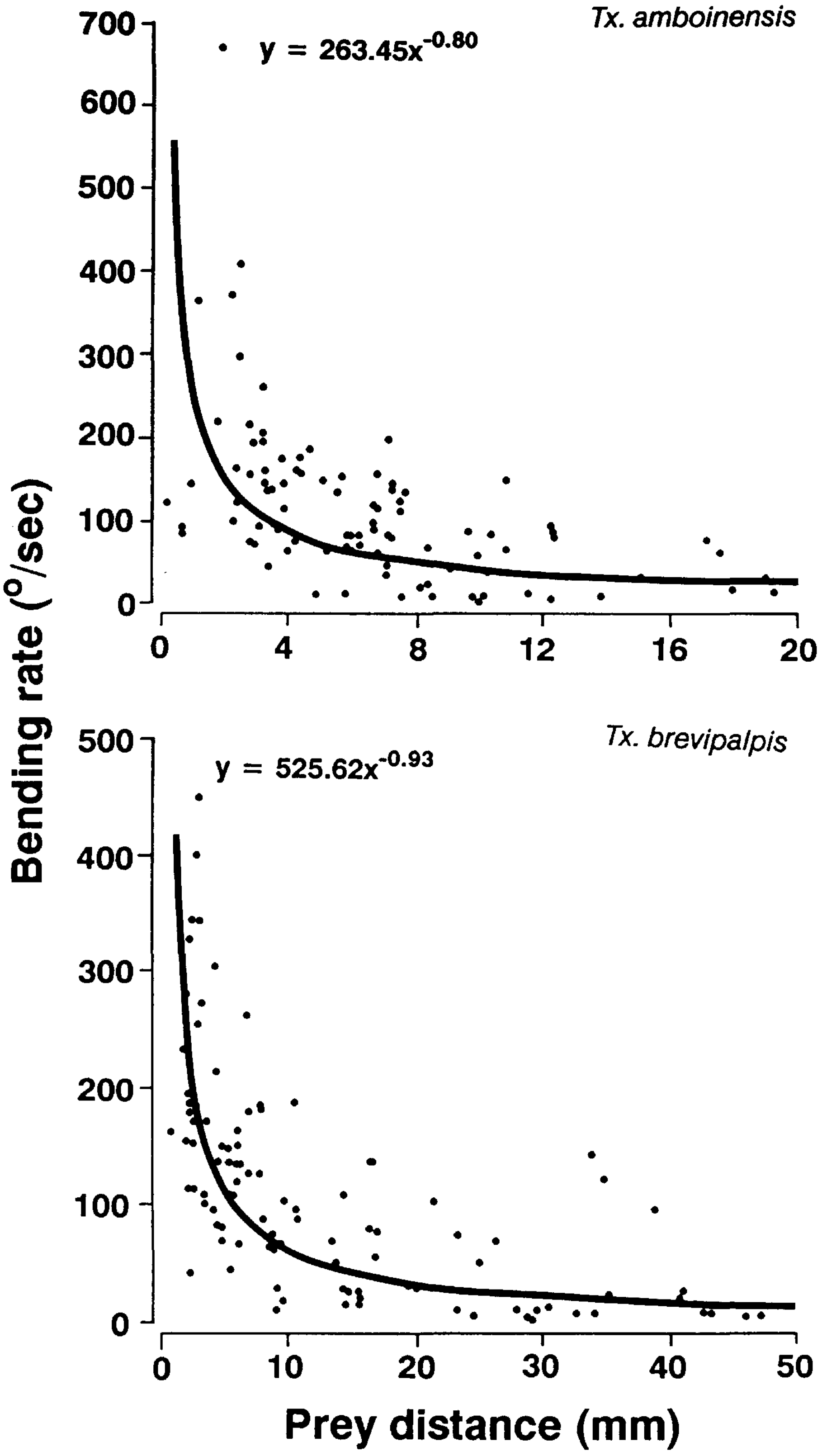


Fig. 8. Relationship between prey distance and bending rate.

convenience only, as it will be shown in due course that the three form part of a continuous series.

Frontal strike with head extension

Strikes of this type occur when the prey is directly in front of the *Toxorhynchites* larva. Head extension and retraction are involved, but very little or no bodily turning, although the larva's body may already be acutely bent when such a strike is made (Fig. 1c). One of the strikes filmed at 350 frames/s showed this type of strike particularly well (Fig. 9).

The remarkable feature of this strike was that it was accompanied by extraordinarily rapid forward extension of the head. The entire strike sequence consisted of extension and retraction phases (Fig. 10a), with extension being about half the duration of retraction. Forward head movement increased progressively at first and then diminished towards the end of the extension phase (Fig. 10a). Thus, the extension phase in expanded time scale (Fig. 10b) revealed that head speed at first accelerated to a maximum of about 145 mm/s, then diminished as the head approached full extension, which was completed in about 0.014 sec (Fig. 10b). About 60% of the head's extension took place in the period from about 0.006 to 0.011 s. Concurrently with movement of the head, the lateral palatal brushes, which clearly were the appendages used to capture prey (Fig. 9), opened and subsequently closed on the victim. Opening of the brushes (arrow, Fig. 9) occurred very rapidly (in < 0.003 s), momentarily after head extension began. As measured by the angle of the brushes (Figure 1d), the rate of closure was then relatively constant (Fig. 10b) at about 10,000°/s. Thus, important events in the action of the palatal brushes took place at the following times after strike initiation; opening, 0.006 sec; first contact with prey (frame 6, Fig. 9), 0.014 s; completion of prey capture (black dot, Fig. 9), 0.02 s.

Front (Fig. 11a) and side views of the head (Fig. 11b) show that when the *Toxorhynchites* larva is at rest the folded palatal brushes are directed ventrally, just inside the protruding antennae. For the brushes to open (Fig. 11c) at strike initiation, they must either lift sideways through 90°, momentarily pushing aside the antennae, or swing forwards and upwards before spreading to the side. However opening is accomplished, the brushes are obviously much better adapted for snaring prey than the mandibles (Fig 11c). They are able to reach further in front of the head, where they close through overlapping arcs, each of approximately 0.46 mm radius (Fig. 1d). Each brush, moreover, is curved inwards apically (Fig. 12a), which prevents escape of prey and pulls it towards the mouth, while terminal hooks on almost all the brush elements (Fig. 12b) provide added security. It is noteworthy that each brush element is distinctly flattened in the plane of the closure arc (Fig. 12b), probably to enhance strength and rigidity and to reduce resistance.

Although the palatal brushes were used to capture prey, all of many *Tx. brevipalpis* larvae examined under a stereomicroscope immediately after prey capture were holding prey with the mandibles. In no instance of many larvae of both species watched throughout the entire consumption of prey, were the palatal brushes used to hold or manipulate food. Prey is captured with the brushes, but is apparently transferred to the mandibles as soon as it is drawn close to the head.

After prey capture, the head retracted back towards the thorax. This phase, plotted in expanded time scale (Fig. 10c) showed rapid acceleration in head speed at first, to a maximum of about 55 mm/s, before speed gradually diminishing as the head returned to its starting position (Fig. 9). The entire strike sequence lasted about 0.05 s (Fig. 10a).

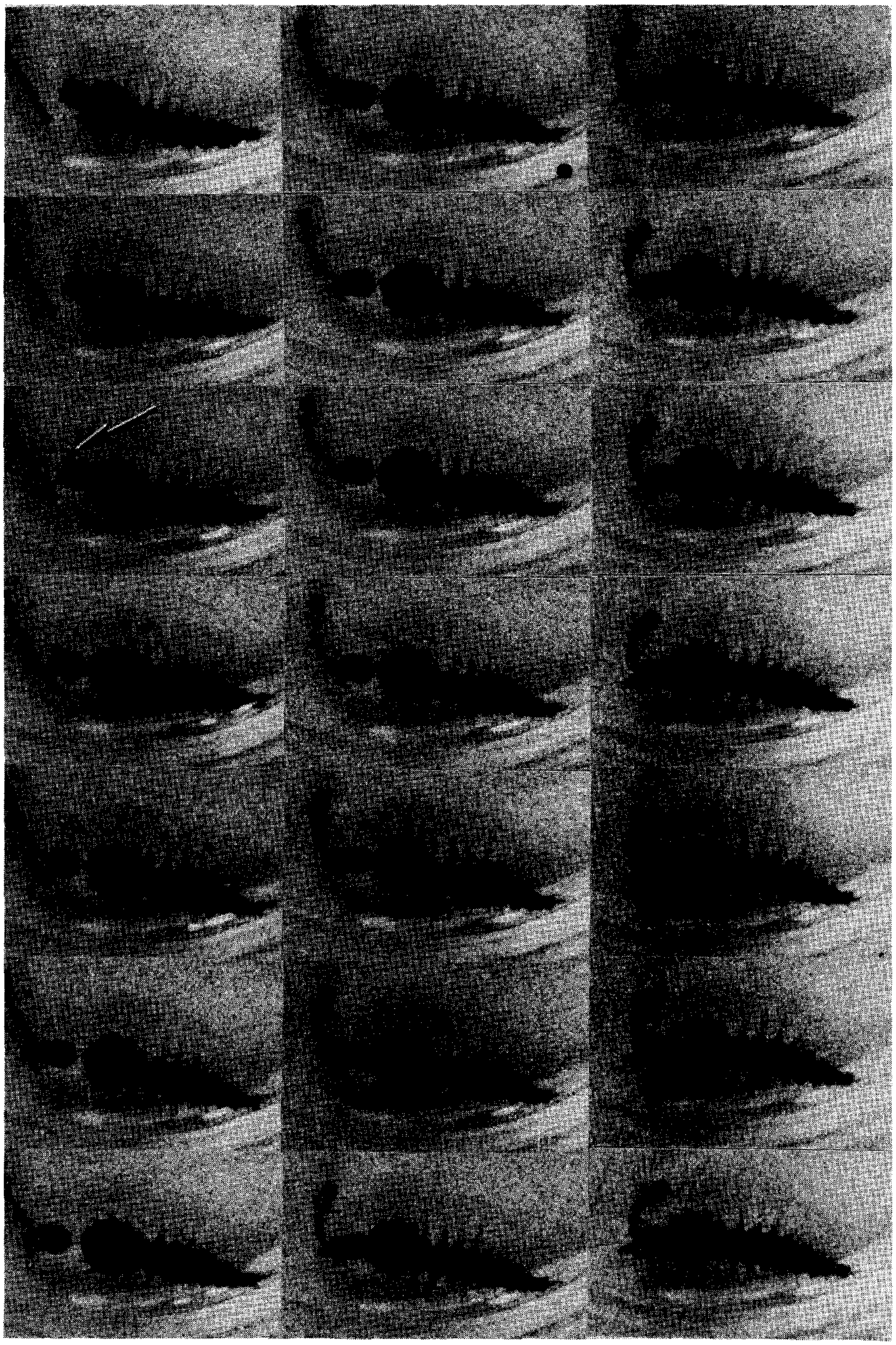


Fig. 9. Frontal strike with head extension (*Tx. brevipalpis*); frames at 1/350 (0.0029) s intervals. Sequence reads top to bottom, left to right. Arrow indicates opening of palatal brushes, dot marks completion of prey capture.

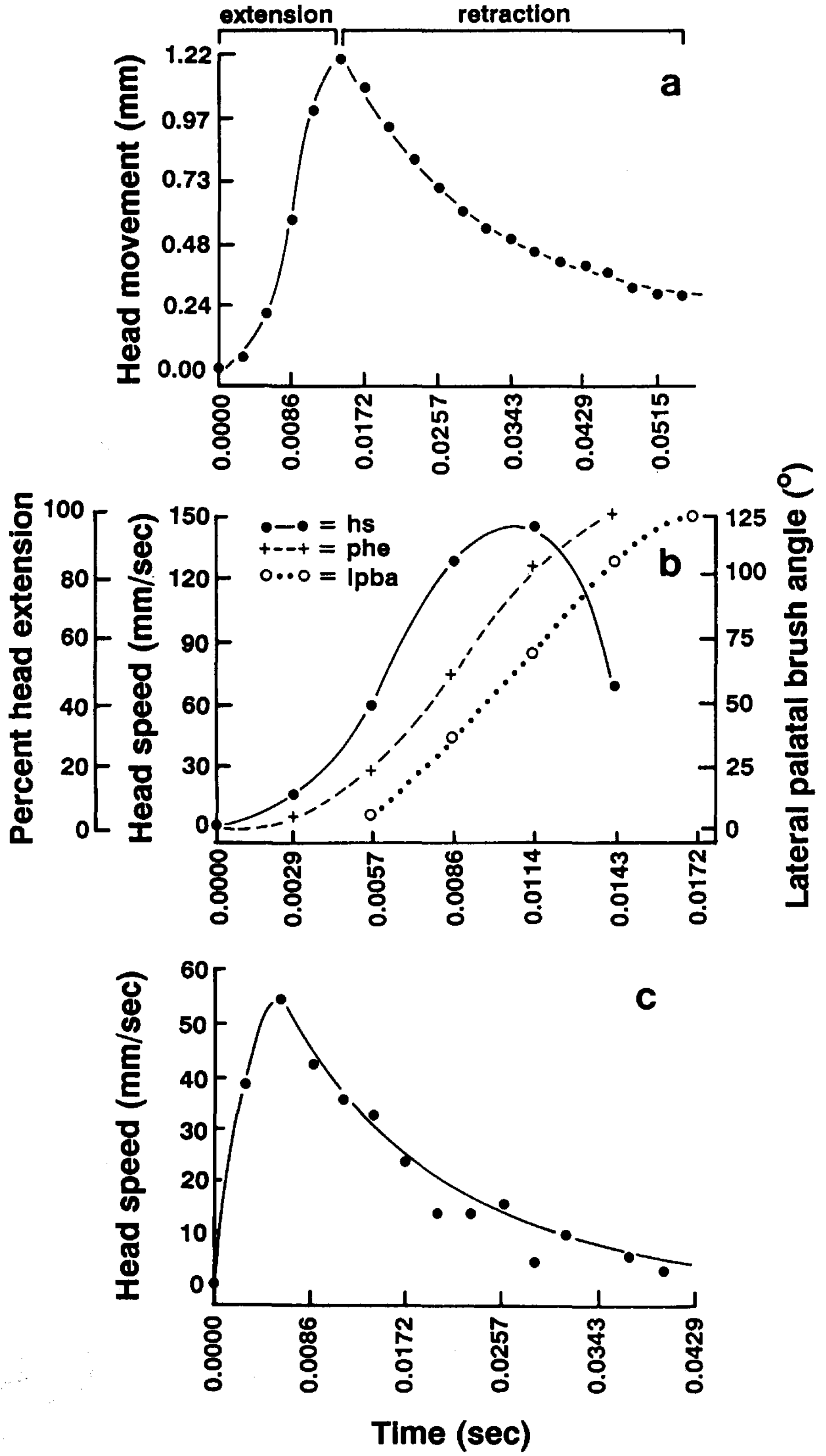
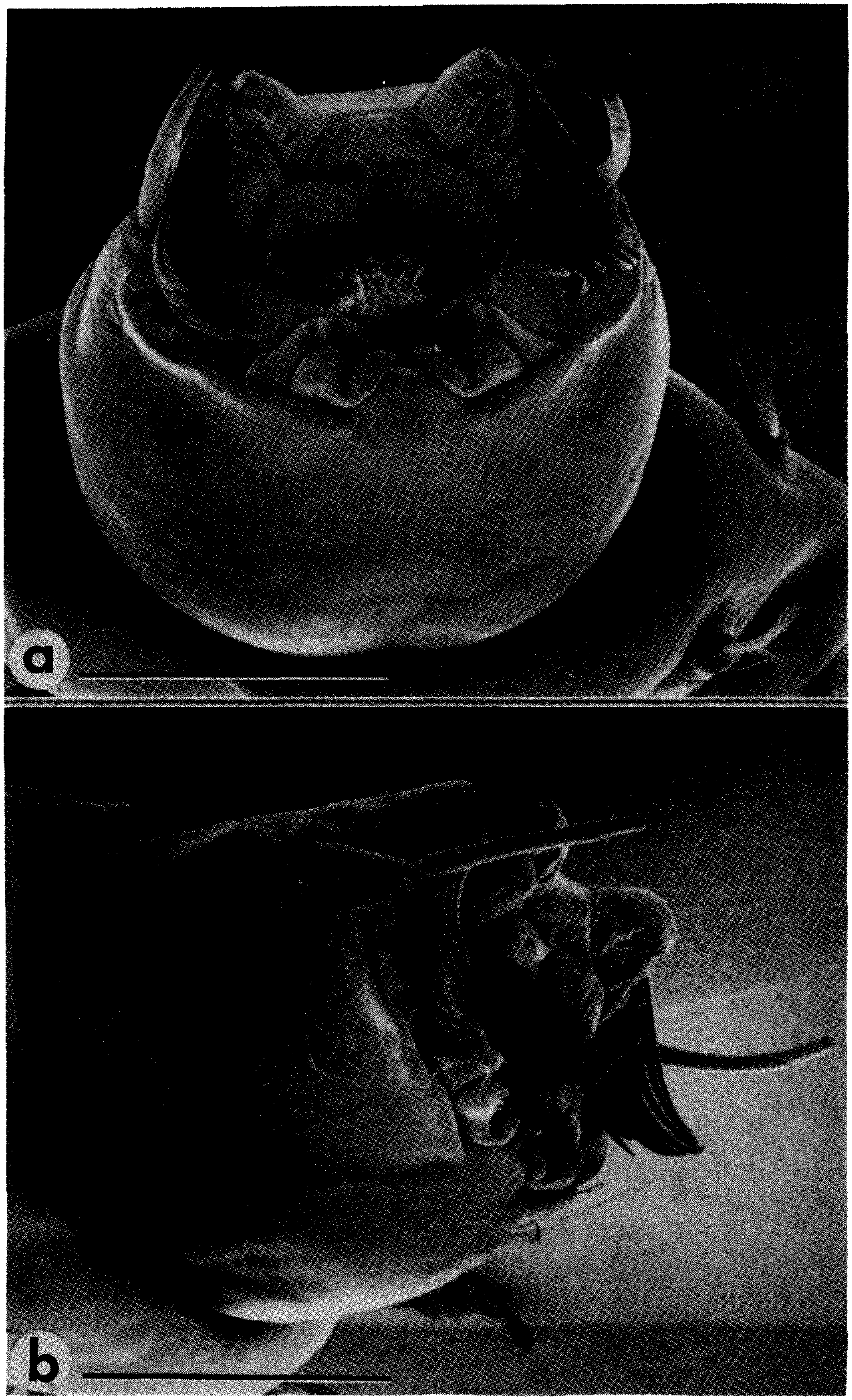


Fig. 10. Analysis of events during a frontal strike with head extension (Fig. 9). a, movement of head during complete strike (extension and retraction); b, head speed, head extension, and palatal brush angle during head extension; c, head speed during retraction.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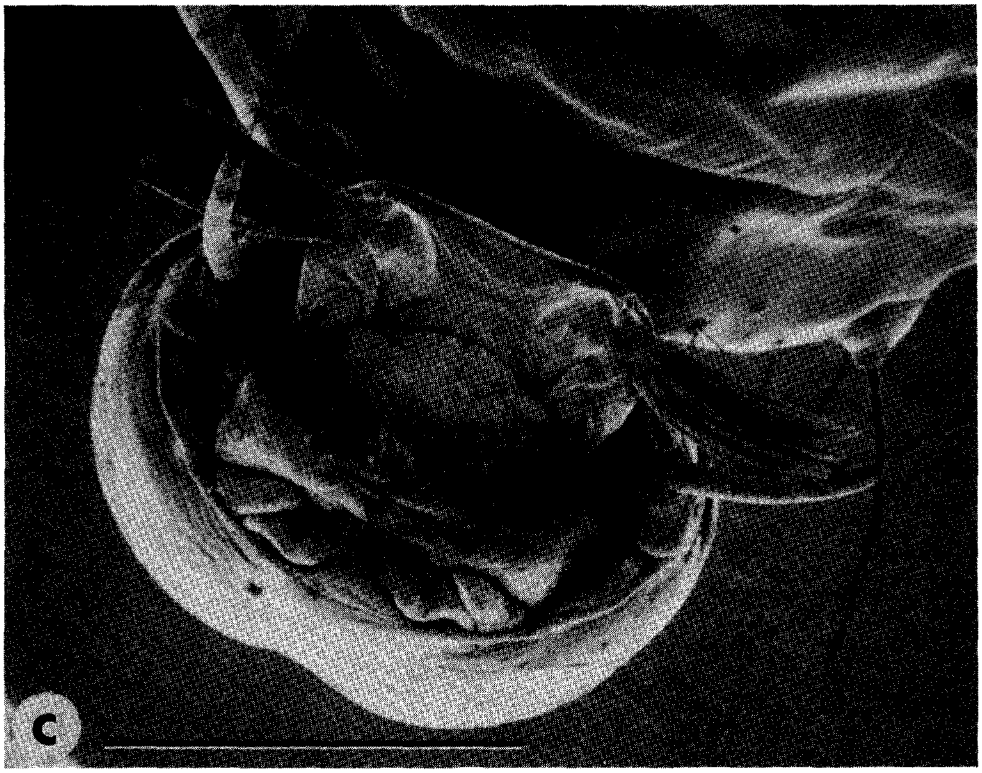

Fig. 11. Scanning electron micrographs showing, a, front view of head (*Tx. amboinensis*), dorsal side uppermost, with palatal brushes at rest position; b, same as (a), partially oblique lateral view; c, front view of head (*Tx. brevipalpis*), with palatal brushes in open position. Scale = 1 mm.

Mechanism of head extension

Toxorhynchites larvae do not possess powerful circular muscles in the neck such as would be necessary to extend the head. In the photographs, however, there were visible changes in the spacing and dimensions of the abdominal segments during the strike (Fig. 9). A machinist's caliper was used to measure the intersegmental diameter between the back of the thorax and abdominal segment 1, and also between successive abdominal segments up to segment 5. The longitudinal distances separating these parts were also recorded.

Over the period of head extension, intersegmental diameter increased between the thorax and abdominal segment 1 and much more so between segments 3-4 and 4-5 (Fig. 13). Especially between segments 1-2 and also between 2-3, however, the diameter decreased very rapidly, as visible in the photographs (Fig. 9). Corresponding changes, but of opposite trend, took place in the distance separating segments (Fig. 14). During retraction, both dimensions returned to the initial state as the head returned to its normal position (Fig. 13, 14).

These measurements indicated that the head was extended by a hydrostatic mechanism powered by very rapid contraction of the abdominal muscles, particularly in the first and second abdominal segments. Contraction produced a sudden increase in internal pressure, forcing the neck to extend rapidly and carry the head forward a distance of somewhat over 1 mm (Fig. 10a).

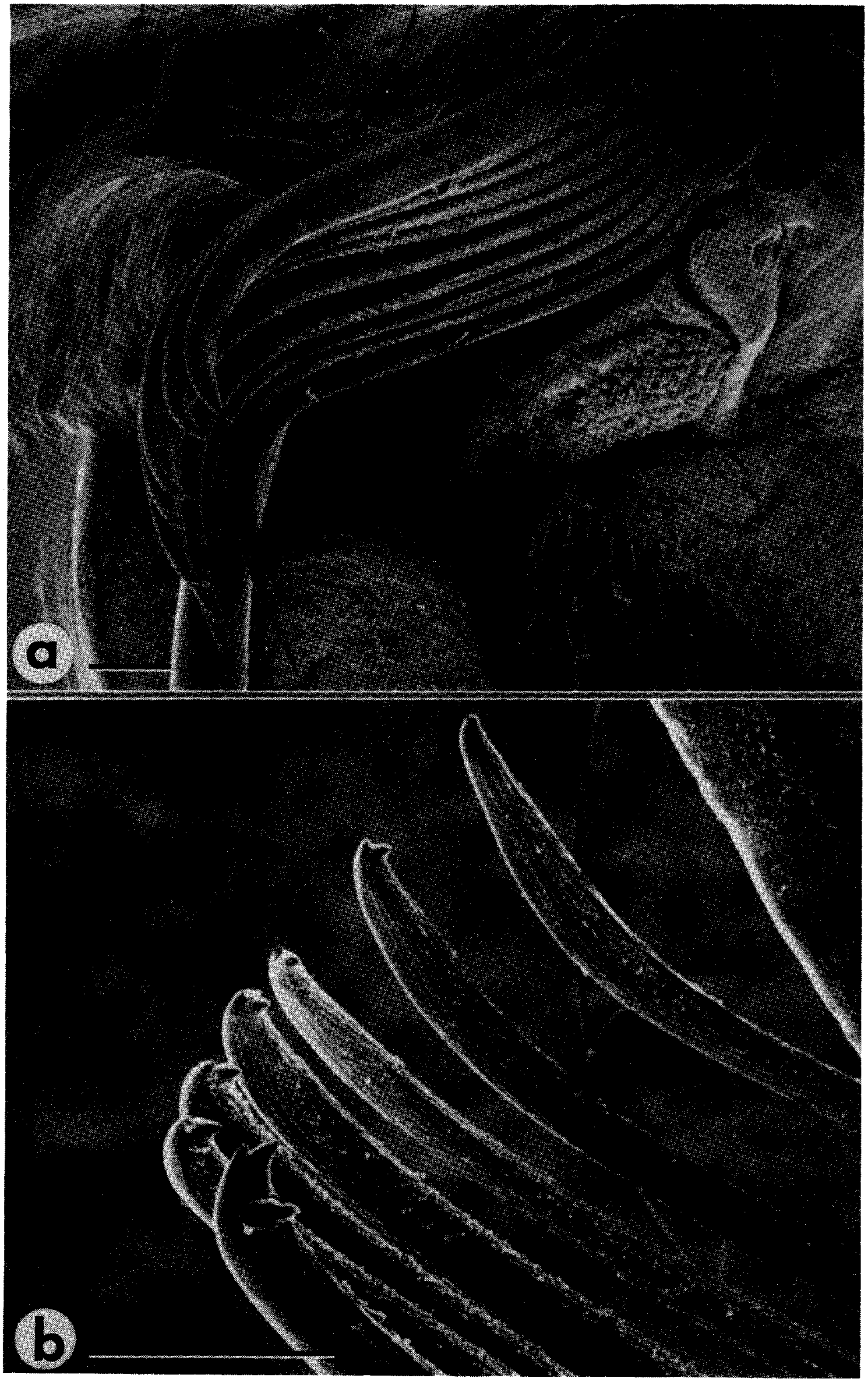

Fig. 12. Scanning electron micrographs (*Tx. brevipalpis*) showing, a, enlarged view of single palatal brush; b, detail of tips of individual brush elements. Scale = 50 μm.

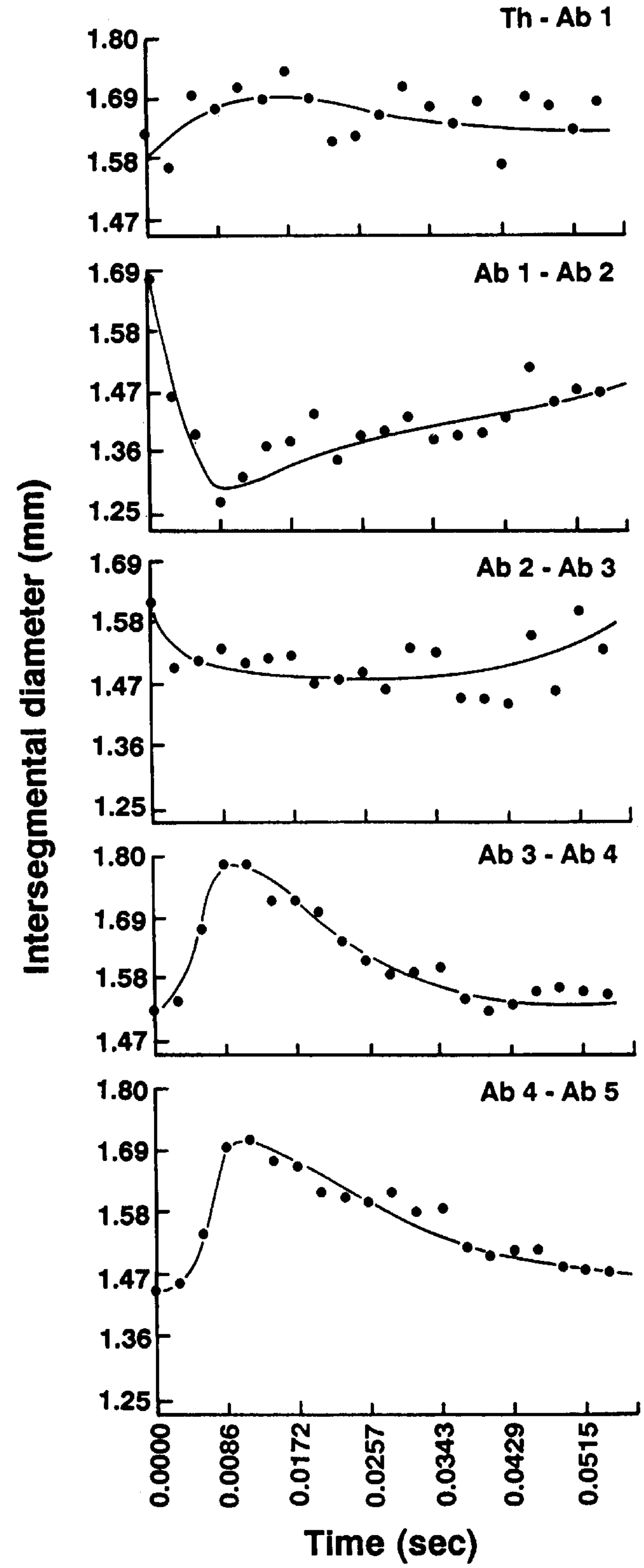

Fig. 13. Intersegmental diameters between indicated body parts during a frontal strike with head extension (Fig. 9).

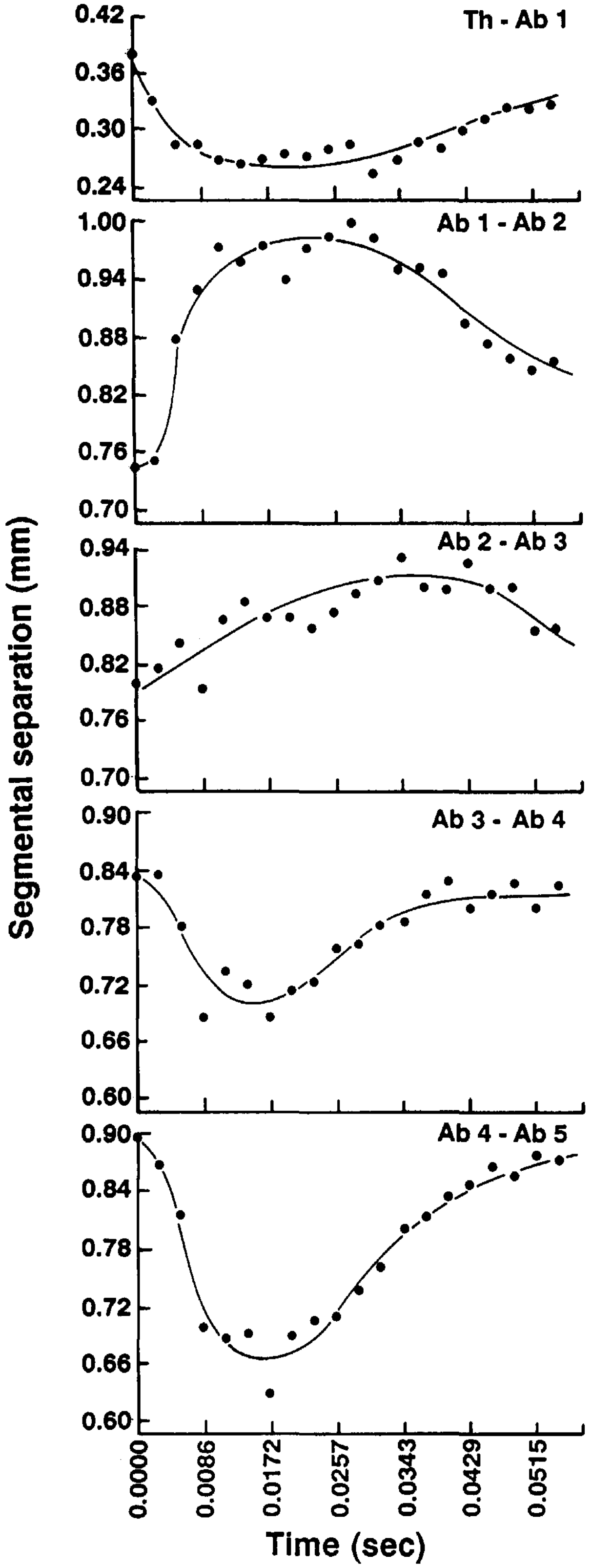

Fig. 14. Segmental separation between indicated body parts during a frontal strike with head extension (Fig. 9).

Lateral strike with head extension

If the prey was slightly to one side of the head, the larva sometimes extended its head during the strike and also turned its body a limited degree (Fig. 15). As illustrated below, however, when the prey angle became too great, the head was not extended, probably because muscular actions necessary to induce extension could not be executed at the same time as those required to turn the body to any appreciable degree. In addition, drag effects would probably make it impossible to have the head extending forward during such rapid turning. The video records were re-examined to determine the approximate maximum limit of turning that still permitted head extension, but it proved impossible to discern whether many strikes had contained an extension component. It was considered unlikely, however, that head extension occurred for prey angles greater than about 30°.

In the example filmed (Fig. 15), head extension was not measured as it seemed generally consistent with the example already described. Also consistent were the actions of the lateral palatal brushes. They opened (arrow, Fig. 15) 0.004 s after the strike was initiated, and completed closure momentarily after full extension of the head, thus effecting prey capture (dot, Fig. 15) in about 0.018 s. Pronounced contraction between abdominal segments 1 and 2 was again visible. For reference, this larva was denoted as larva 1 and its turning movements were analyzed together with those of 4 other larvae that made strikes without head extension (see below).

Lateral strike without head extension

Strikes of this type were made when prey was positioned more to the side of or behind the head. Four examples were filmed (Larvae 2, 3, 4, 5), of which the one that showed the most extreme degree of turning (larva 4) was selected for illustration (Fig. 16). This was an unsuccessful strike at prey held in tweezers, but the strike movements were stereotyped and were not affected by whether prey was ultimately captured.

There were two phases in such strikes, contraction (body turned towards prey with associated movements of mouthparts, head and thorax), and relaxation (body returned to rest position). Several important differences distinguished these strikes from ones incorporating head extension. Firstly, the head clearly was not extended (Fig. 16). Early in the strike, from about 0.004 to 0.008 s (frames 2, 3, 4, Fig. 16), the head began to rotate so that as the body turned to its maximum extent (full contraction), the head was oriented with its dorsal and ventral surfaces in the vertical plane (frames 10-13). Simultaneously, but to a lesser degree, the thorax was rotated (Fig. 16) and was about half turned at full contraction. The palatal brushes did not open as soon in this particular strike as when the head was extended. The head was at least half rotated (about 0.010 s after strike commencement) when the brushes were first discernible (arrow, Fig. 16). Their subsequent closing could not be seen, but was assumed to be complete by the time the body reached full contraction (dot, Fig. 16). Once contraction was completed, relaxation to the rest position took place more slowly (Fig. 16). Summary of the 4 examples filmed (Table 3) showed that opening of the palatal brushes was usually very soon after strike initiation, but was rather slow in larva 4. Head rotation was completed in the first half of the period required to reach full contraction, which also closely approximated the time to prey capture (0.012-0.024 s. Table 3). Relaxation lasted about twice as long as contraction and the entire strike (both phases) was concluded in from 0.058-0.076 s.

Angular change between body parts during the strike (Fig. 17, Table 4) indicated that amplitude of change was usually greatest between the head and thorax, although in larva 4 the angle of change was greatest between the abdominal segments (Fig. 17). Change in angle was usually least between thorax and abdomen (Table 4). As regards timing, angular change during contraction occurred most quickly between head and

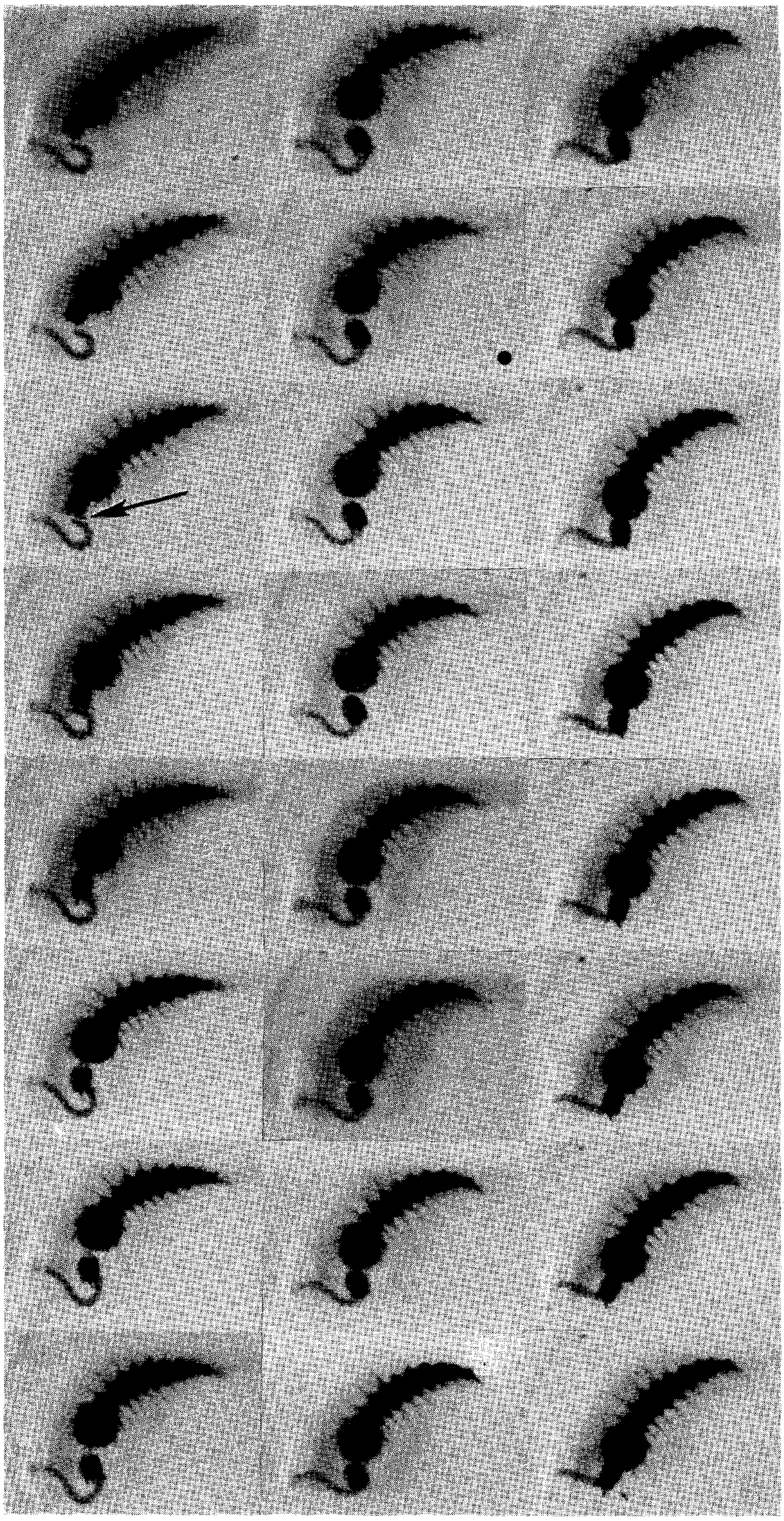

Fig. 15. Lateral strike with head extension (*Tx. brevipalpis*); frames at 1/500 (0.0020) s intervals. Sequence reads top to bottom, left to right. Arrow indicates opening of palatal brushes, dot marks completion of prey capture.

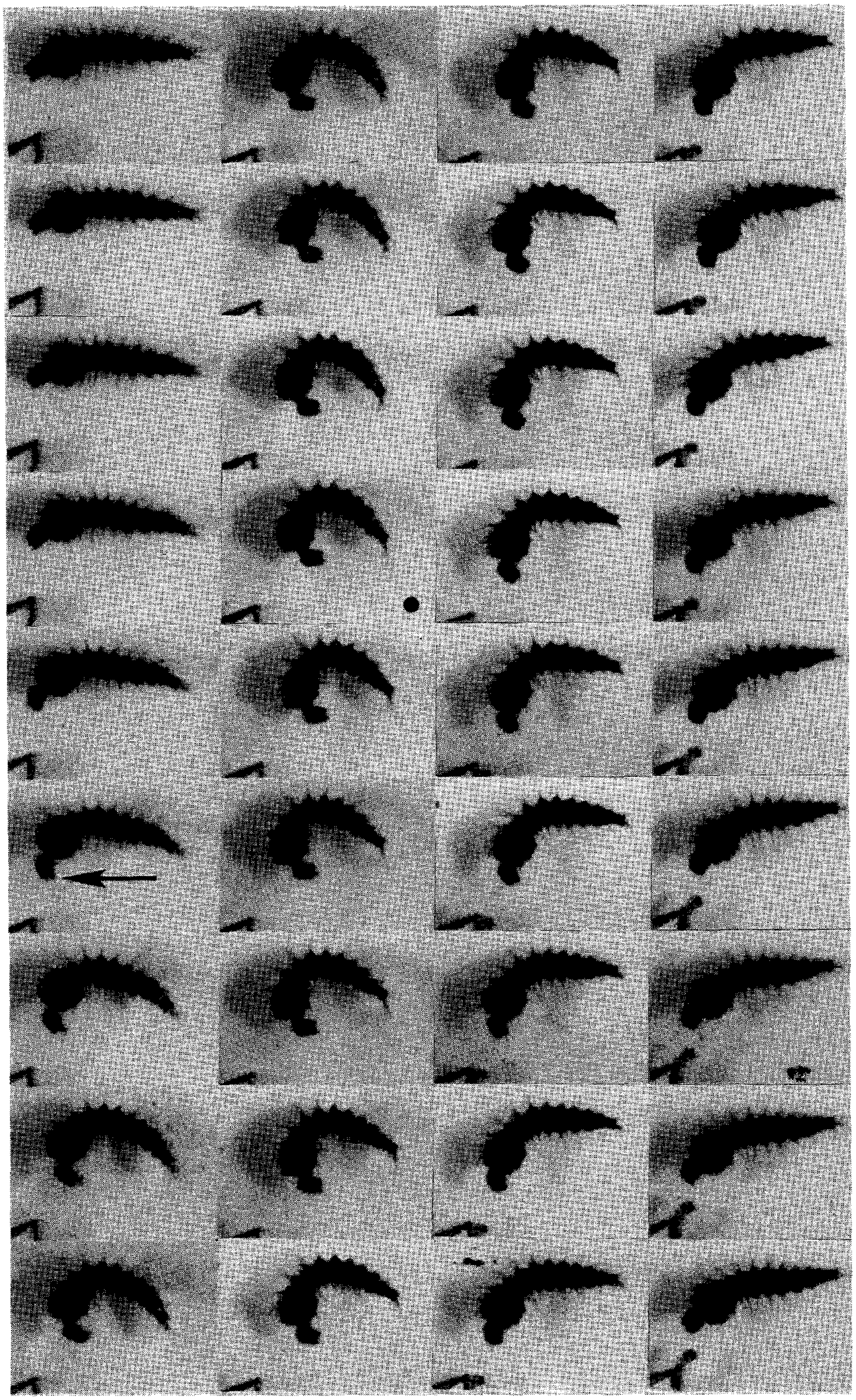

Fig. 16. Lateral strike without head extension (*Tx. brevipalpis*); frames at 1/500 (0.0020) s intervals. Sequence reads top to bottom, left to right. Arrow indicates opening of palatal brushes, dot marks completion of prey capture.

TABLE 3. TIMING OF EVENTS IN LATERAL STRIKES WITHOUT HEAD EXTENSION IN 4 *TX. BREVIPALPIS* LARVAE.

Larva No.	Time (s) from strike initiation to Opening of palatal brushes	Complete rotation of head	Completion of contraction phase	Completion of entire strike
2	0.002	0.012	0.020	0.058
2	0.004	0.012	0.022	0.064
4	0.010	0.012	0.024	0.076
5	0.004	0.008	0.012	0.076

thorax (Fig. 17). Thus, in the initial stages of the strike, the head led in amplitude the degree of turning towards prey. An exception was larva 4, in which turning between all body parts occurred at approximately the same time. During relaxation, because contraction between head and thorax was usually greatest, the rate of return to the rest position was usually higher between these parts than for the other body parts in the early stages of relaxation (Fig. 17). The rates were quite similar in the later stages, however.

Combining all the angle changes (Fig. 18) gave a clearer impression of the entire strike as a coordinated action of the body and showed the uniformity of the movement despite differences in the total angle of change. For reasons given below, it was evident also that the total angular change undergone overall was considerably greater than achieved by the head relative to the prey.

The small time increments during filmed strikes did not effectively convey how rapid the body movements were and the extraordinarily high angular velocities achieved, particularly during contraction. Larvae 4 and 5 serve to illustrate this point (Fig. 19). Plotted separately for purposes of clarity, the data showed a peak head-thorax angular velocity of about 3,800°/s for larva 4, and a remarkable level of almost 11,000°/s for larva 5 (Fig. 19). A very high velocity was attained also within the abdomen in larva 4, as expected from the large angle of change that occurred in this individual (Table 4). Somewhat lower peak velocities (4,000-5,000°/s), recorded for changes between thorax and abdomen, reflected the smaller angles of change between these parts (Table 4).

Although the measurements discussed above provided information about angle changes between body parts, they did not describe the actual arc or rate of movement of the striking head. This was because for a *Toxorhynchites* larva suspended freely in water, only a portion of the turning angle generated between body parts is transferred to the head. The position of the body at full contraction (dotted outline, Fig. 20) com-

TABLE 4. TOTAL ANGULAR CHANGE WITHIN ENTIRE BODY, AND MAXIMUM ANGULAR CHANGE BETWEEN BODY PARTS OF 5 *TX. BREVIPALPIS* LARVAE MEASURED AT REST AND THEN AT FULL CONTRACTION IN STRIKE.

Larva No.	Total angular change (°)	Maximum angular change between body parts (°) Hd-Th	%	Th-Ab	%	Ab-Ab	%
1	102	42	41.2	20	19.6	41	39.2
2	147	73	49.7	32	21.8	42	28.5
3	133	50	37.6	41	30.8	42	31.6
4	199	62	31.2	53	26.6	84	42.2
5	133	69	51.9	42	31.6	22	16.5

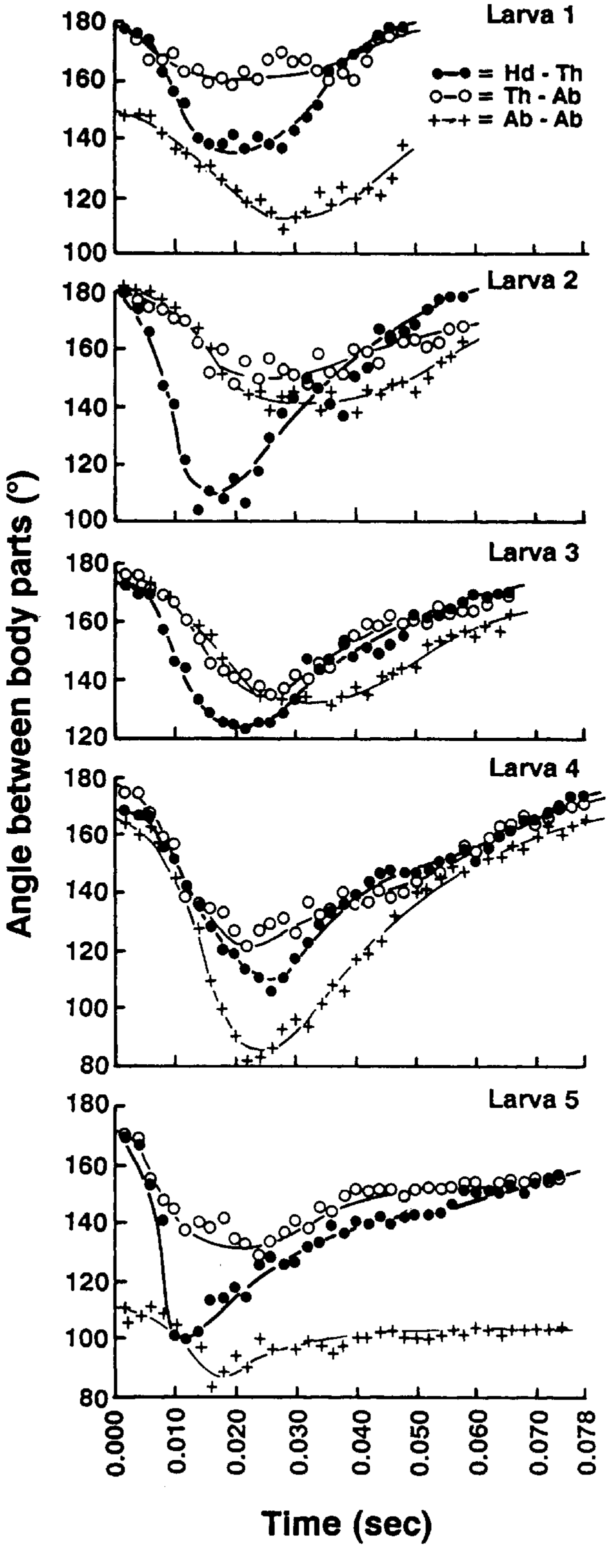

Fig. 17. Angles between body parts during complete strike sequences of 5 *Tx. brevipalpis* larvae filmed at 500 frames/s. Larva 1 is depicted in Fig. 9, larva 4 in Fig. 16.

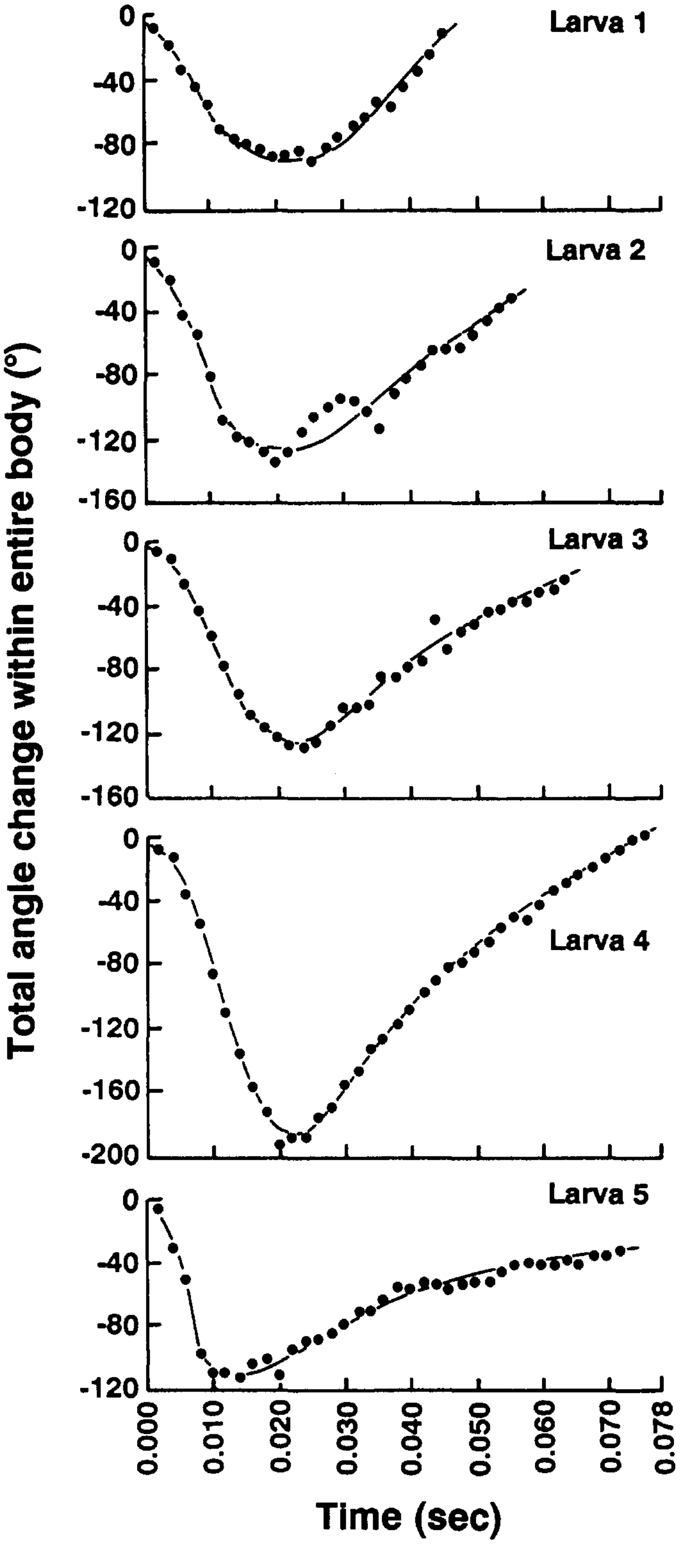

Fig. 18. Total angle change within entire body during complete strike sequences of 5 *Tx. brevipalpis* larvae filmed at 500 frames/s. Larva 1 is depicted in Fig. 9, larva 4 in Fig. 16.

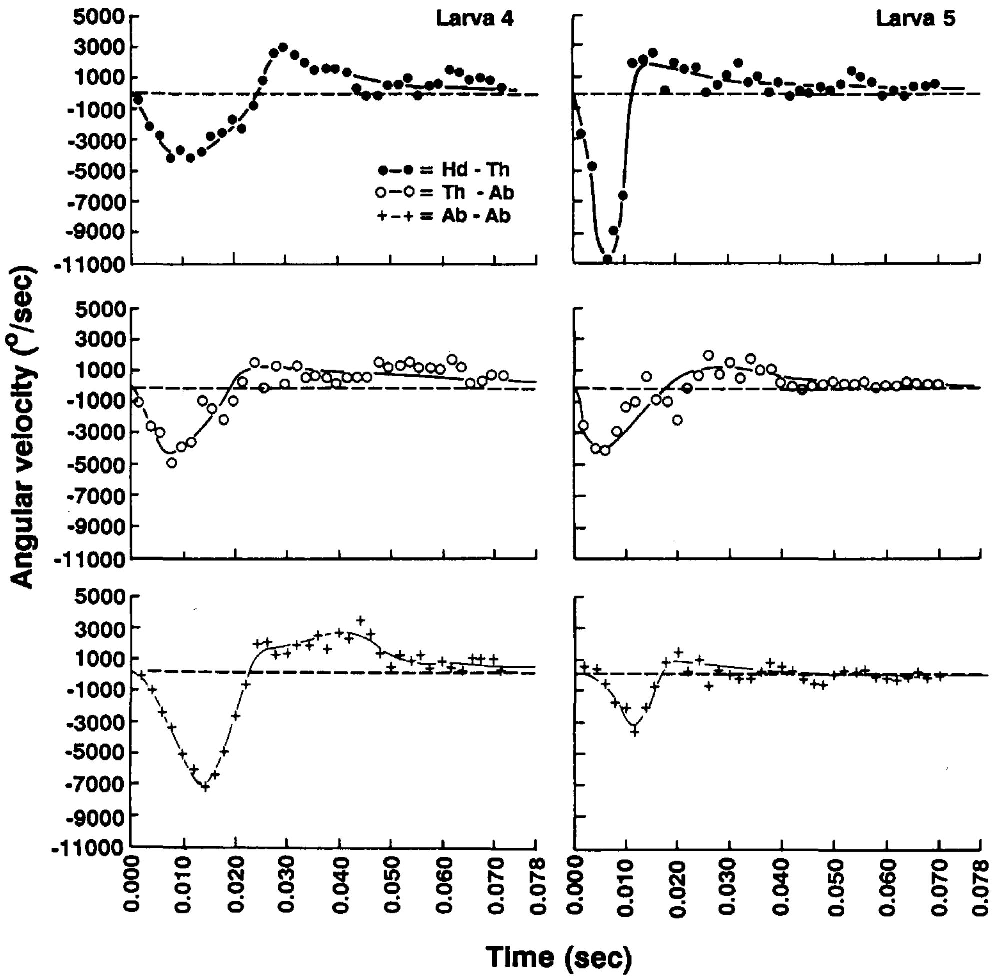

Fig. 19. Angular velocities between body parts during complete strike sequences of 2 *Tx. brevipalpis* larvae. Larva 4 is depicted in Fig. 16.

pared to the starting position (continuous outline), showed that most of the anterior portion of the abdomen was displaced away from the direction of the strike, while the tail was pulled towards it. The pivot point varied somewhat from strike to strike, but was usually near the middle of the thorax (Fig. 20). Consequently, the striking head travelled through an arc of only limited radius, with prey accessible within small lateral distances.

Enlarged plots of the actual arcs (points at 0.002 s increments) showed the paths followed by a central point on the head's front margin (Fig. 20). There was an apparent difference between the paths for 2 strikes of more limited angle (larvae 1 and 2) compared to larger angle strikes (larvae 3, 4, and 5). Forward movement of the head was expected in larva 1 (Fig. 15), but the head of larva 2 also moved (Fig. 20). This movement occurred early in the contractive phase (Fig. 20), suggesting that it resulted from the usual hydrostatic mechanism. It is probable, therefore, that muscular actions effecting head extension are initiated in every strike, but that their effects are offset in strikes involving appreciable turning by other changes in body position that affect internal pressure. The three types of strike probably form parts of a continuous series in which the degree of head extension diminishes with increasing lateral turning.

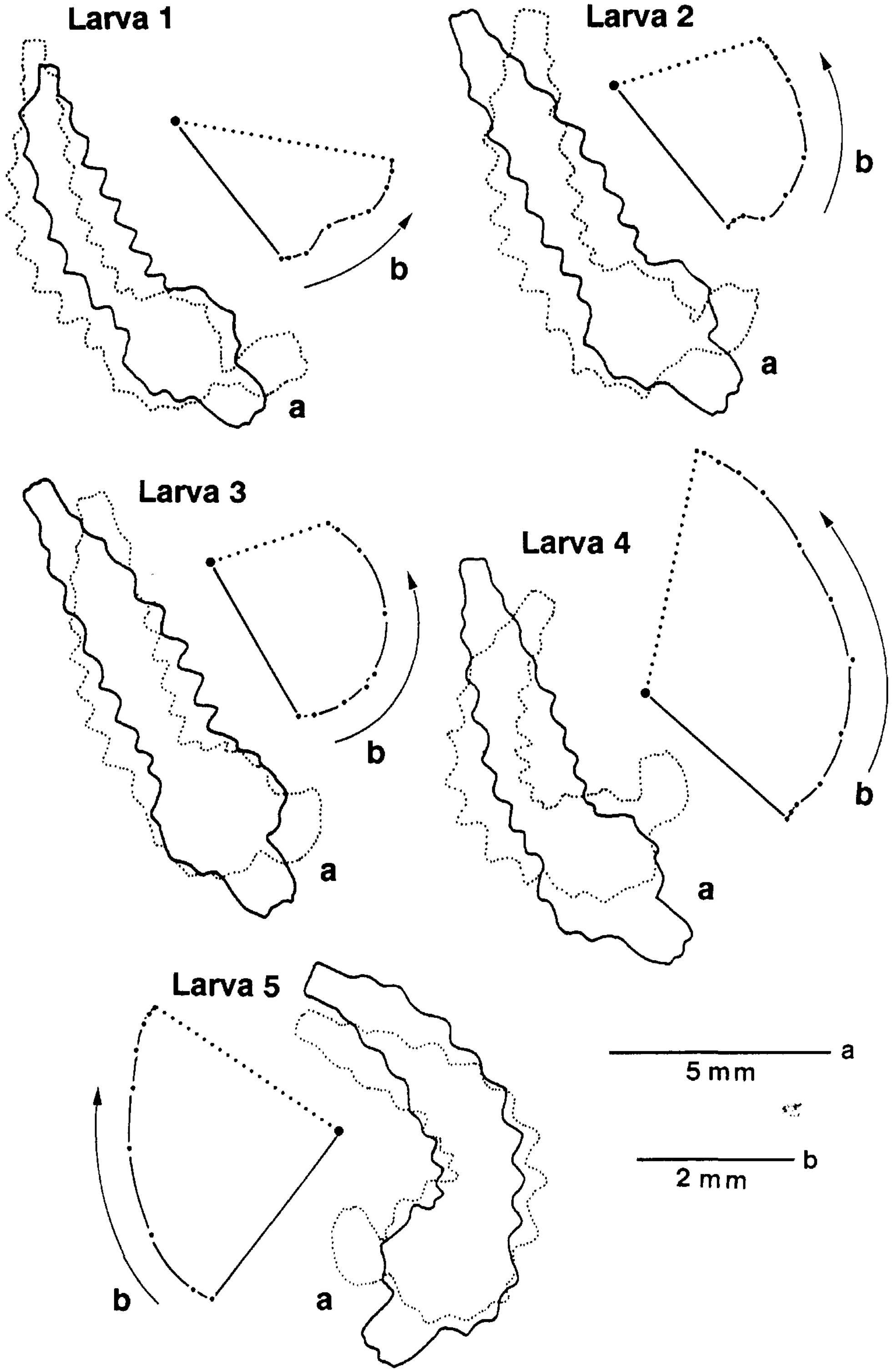

Fig. 20. a, Relative body position at initiation of strike (continuous line) and at fully contracted position (dotted line) for 5 *Tx. brevipalpis* larvae; b, enlarged plots of each true strike arc, relative to the middle of the thorax, of a point on the mid-front margin of the head (points at 0.0020 s intervals). Larva 1 is depicted in Fig. 9, larva 4 in Fig. 16.

From measurements of head position and angle in the strike arcs (Fig. 20), it was possible to estimate the actual head speeds and angular velocities relative to the middle of the thorax (Fig. 21). Generally, despite variation between individuals, increase and decrease in head speed and angular velocity were fairly equally distributed in time within the contraction phase. Head extension affected the rates in larvae 1 and 2 (Fig. 21) and in larva 5 the accelerative stage was of shorter duration than the decelerative. Angular velocities and speeds attained by the head (measured at the middle of the anterior margin) were remarkably high. Even in larva 1, which extended its head (Fig. 15), angular velocity reached nearly 5,000°/s and the head speed almost 30 cm/s, while the fastest rates observed, in larva 5, were 12,000°/s and 70 cm/s.

Spatial distribution of prey

Points were plotted to show, at the instant of strike initiation, the closest part of the prey's body in relation to the predator. Separate plots differentiated successful and unsuccessful strikes (Fig. 22, 23). The distributions of these points with respect to distance from the head (within each sector) were skewed, but could be rectified by logarithmic transformation, allowing the mean prey distance and 95 percent confidence regions to be superimposed (Fig. 22, 23).

With the capability of capturing prey only within a limited distance of the head, it was not surprising to find that larvae initiated strikes only when prey approached very closely. Even for unsuccessful strikes, the outer limit of the 95 percent confidence region was no more than about a body length away from the head in every sector (Fig. 22, 23). Larvae of both species occasionally initiated strikes at more distant prey, as shown by the few outlying points, one of which, in the case of *Tx. brevipalpis*, was 31.4 mm away (Fig. 23). Rather obviously (Fig. 22, 23), mean prey distance from the head increased with increasing sector angle for all strike categories (Table 5), and was considerably greater for unsuccessful strikes compared to successful. The confidence regions showed that both species were successful in capturing prey only within limited cresent-shaped regions centered on the head, and extending some distance along each side of the abdomen (Fig. 23, 23). The region was more limited in *Tx. brevipalpis* (Fig. 23) and extended posteriorly only to about the level of abdominal segment 1. *Toxorhynchites brevipalpis'* capture area was particularly small, probably because this species tended to reduce the prey angle by bending proportionately further towards its inteded victims.

On the basis of all strikes made (Table 6), rather than just those that were measured and plotted, the two species did not quite differ significantly with respect to the proportions of strikes made in each sector ($\chi^2 = 9.424$, d.f. = 5, $P << 0.1$). Nonetheless, data for the first three sectors (0-75°) combined and compared to the last three (76-180°) showed that a smaller portion (135:176 = 40.2%) of the *Tx. amboinensis* strikes was to prey at the lower angles, as compared to *Tx. brevipalpis* (107:100 = 51.7%). This difference was not unexpected in view of *Tx. brevipalpis'* tendency to bend more towards prey, and it is probably important even though the difference did not quite attain the 5 percent level of significance, because the two species did differ with respect to the proportion of successful strikes in each sector. In *Tx. amboinensis*, the proportions of successful as opposed to unsuccessful strikes (Table 6) were significantly different between sectors ($\chi^2 = 12.597$, d.f. = 5, $P < 0.05$), with higher success percentages in the three lower angle sectors, whereas the proportions were not significantly different in *Tx. brevipalpis* ($\chi^2 = 3.277$, d.f. = 5, n.s.). However, the success levels for *Tx. brevipalpis* were distinctly higher than for *Tx. amboinensis* in all sectors except one (Table 6) and, on the basis of the data for all strikes combined, *Tx. brevipalpis* was significantly more successful ($\chi^2 = 15.132$, d.f. = 1, $P < 0.001$). Of *Tx. brevipalpis'* strikes, 148/207 (71.5%) resulted in prey capture as compared to 170/311 (54.7%) in *Tx. amboinensis*.

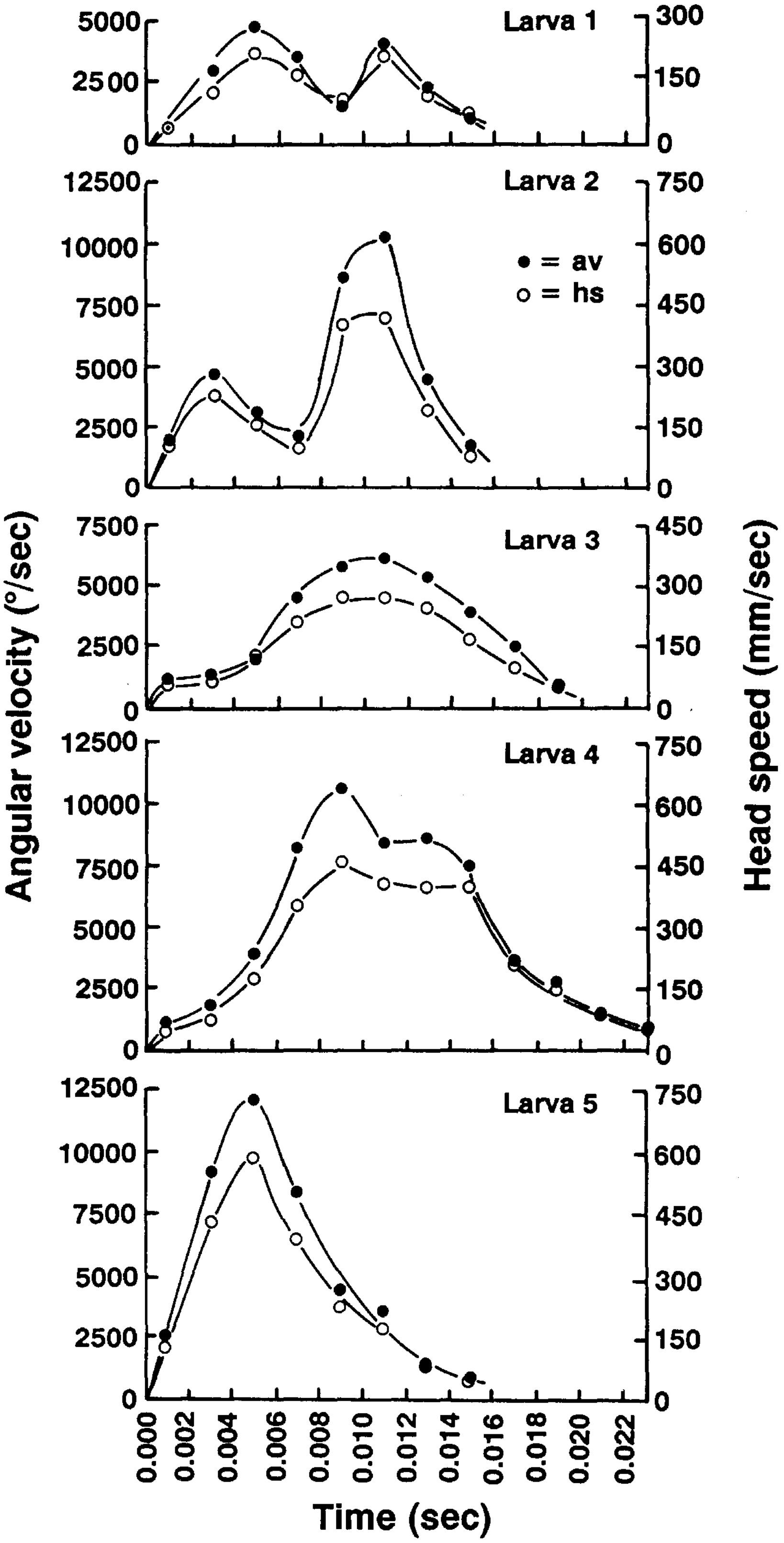

Fig. 21. Angular velocity and head speed during the true strike arc (see Fig. 20) of 5 *Tx. brevipalpis* larvae. Larva 1 is depicted in Fig. 9, larva 4 in Fig. 16.

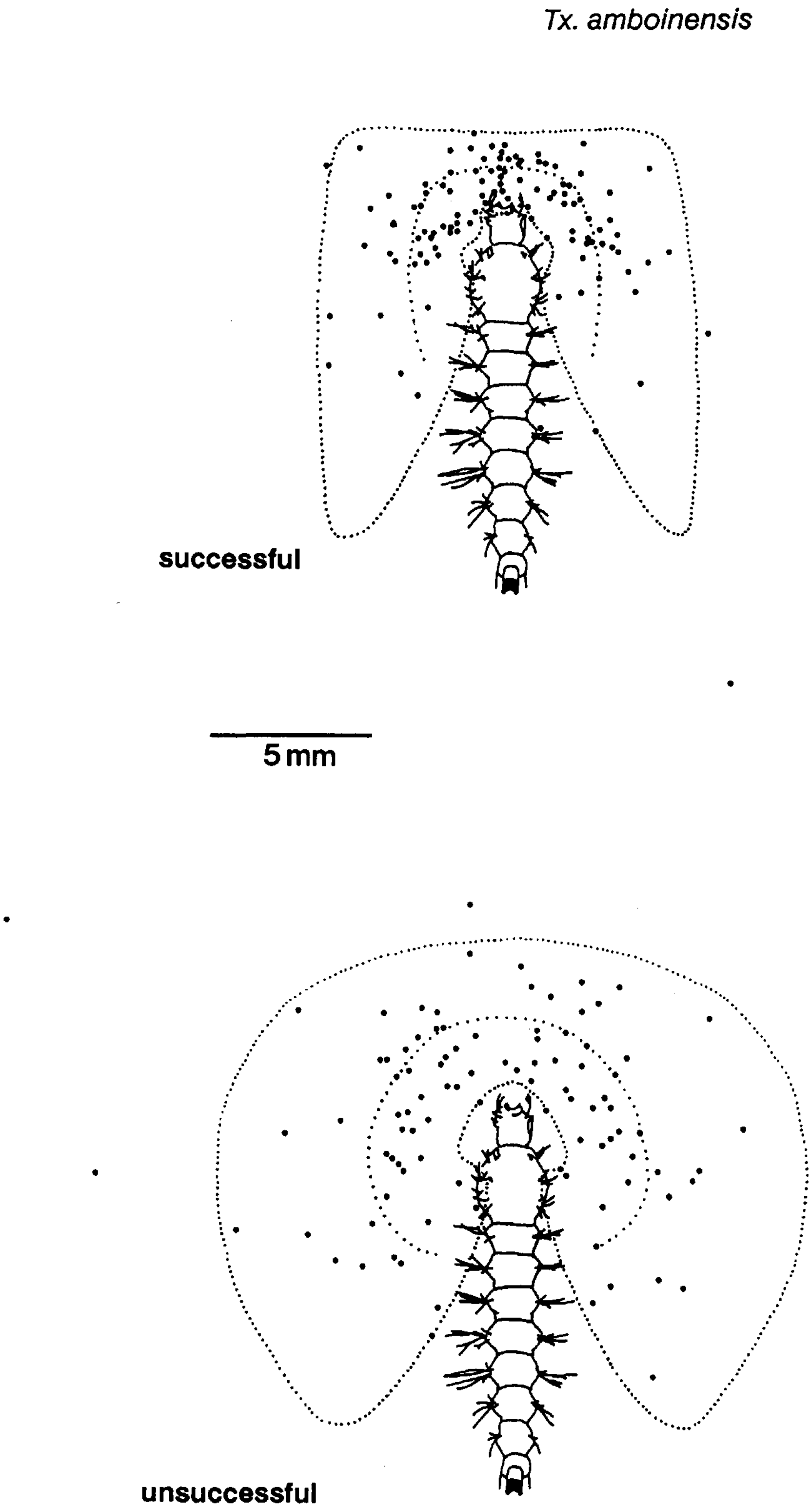

Fig. 22. Spatial distributions of prey (nearest part), mean prey distance (line with dots widely spaced), and 95% confidence regions (line with dots closely spaced), for successful and unsuccessful strikes of *Tx. amboinensis*.

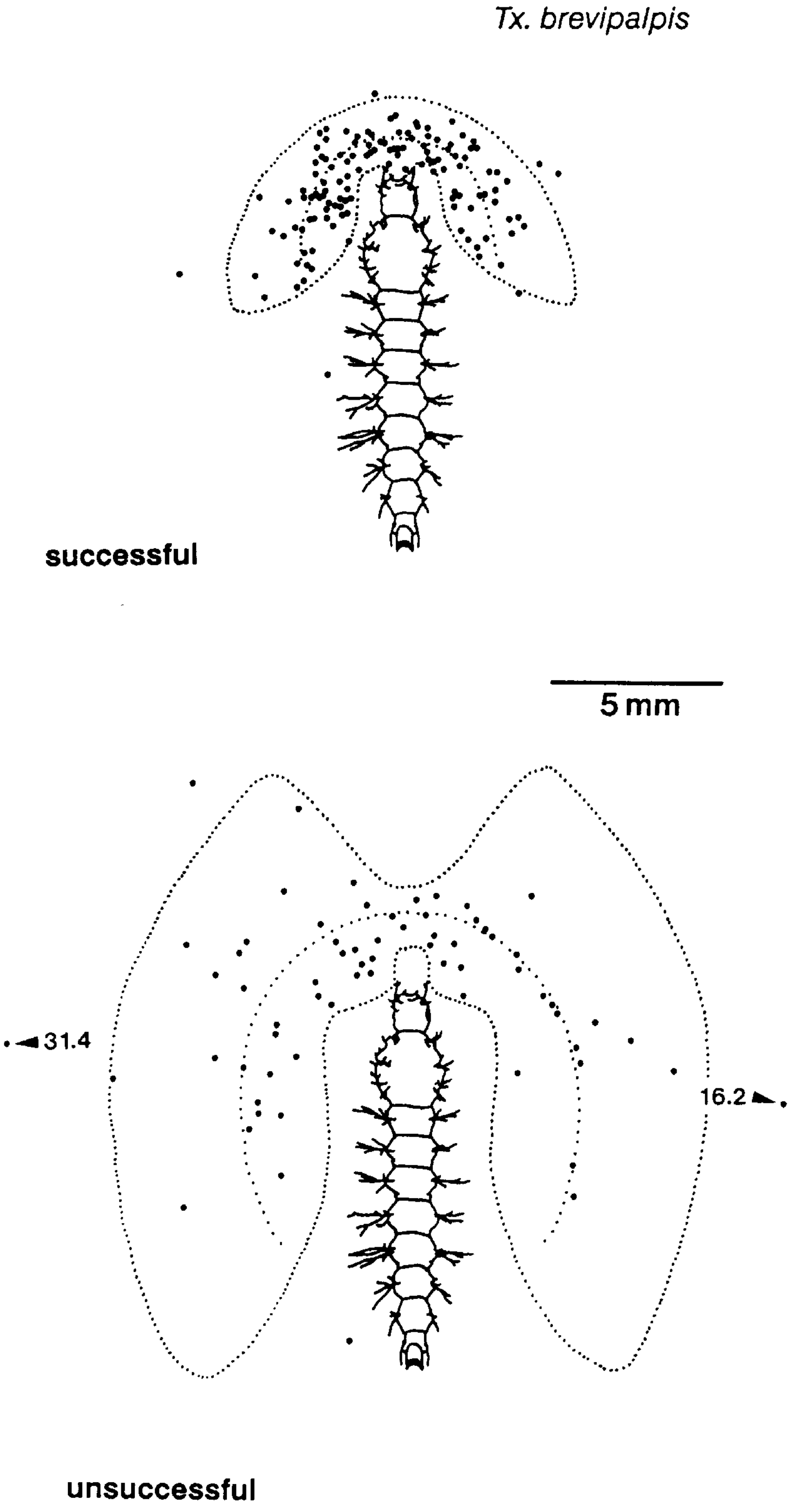

Fig. 23. Spatial distributions of prey (nearest part), mean prey distance (line with dots widely spaced), and 95% confidence regions (line with dots closely spaced), for successful and unsuccessful strikes of *Tx. brevipalpis*.

TABLE 5. MEAN DISTANCES OF PREY FROM HEAD, BY SECTOR, FOR SUCCESSFUL (S) AND UNSUCCESSFUL (U) STRIKES, AND ALL STRIKES (A) COMBINED.

Sector	*Tx. amboinensis* Mean distance (mm)			*Tx. breviopalpis* Mean distance (mm)		
(°)	s	u	A	s	u	A
0-15	1.36	2.71	1.75	1.49	2.38	1.72
16-45	1.63	3.57	2.68	1.64	2.94	2.07
46-75	2.29	3.10	2.70	1.90	2.87	2.26
76-105	2.19	3.65	2.84	2.11	4.06	2.64
106-135	3.10	4.19	3.63	2.84	4.74	3.51
136-180[1]	4.38	4.18	4.26	-[2]	6.50	6.08

[1] Sectors 136-165° and 165-180° combined
[2] One observation only

Prey angle and strike angle

Regressions of prey angle on strike angle for successful strikes were linear (Fig. 24), indicating that both predators pivoted through strike angles that were a fairly constant proportion of prey angle for all prey angles. Strikes were not made at proportionately greater angles as prey angle diminished. The proportions are given by the regression coefficients, so that *Tx. amboinensis* pivoted about 81% and *Tx. brevipalpis* about 73% of the prey angle. The regression coefficients did not different significantly.

These results indicated that the *Toxorhynchites* larvae were able to estimate prey angle with considerable accuracy and match the strike angle accordingly. Some degree of error was implied in the scatter of points about the regression line in each case. However, the coefficients of determination (r^2) showed that prey angle accounted for 74.4% of the variation in strike angle for *Tx. amboinensis*, and 70.7% for *Tx. brevipalpis*. Moreover, the prey angle/strike angle relationships for unsuccessful strikes were very similar (Fig. 25), suggesting that accuracy with respect to angle was not due to curtailment of the strike arc when the predators's head or mouthparts made sensory contact with the prey. Some contact may have occurred in unsuccessful strikes, but probably not in a large portion. The regression coefficients were lower in both cases (but not significantly so) and the scatter of points somewhat greater (Fig. 25), with r^2 values of 62.7% for *Tx. amboinensis* and 51.9% for *Tx. brevipalpis*. Underexecution and inaccuracy in the strike angle may have reduced success in capturing prey to a limited extent.

TABLE 6. NUMBERS OF SUCCESSFUL (S) AND UNSUCCESSFUL (U) STRIKES, TOTAL (T) STRIKES, AND PERCENT SUCCESSFUL STRIKES (%S) IN EACH SECTOR.

Sector	*Tx. amboinensis*				*Tx. brevipalpis*			
(°)	s	u	T	%s	s	u	T	%s
0-15	39	17	56	69.6	24	11	35	68.6
16-45	20	18	38	52.6	34	8	42	81.0
46-75	38	13	41	68.3	22	8	30	73.3
76-205	36	38	74	48.6	29	16	45	64.4
106-135	31	37	68	45.6	21	9	30	70.0
136-180	16	18	34	47.1	18	7	25	72.0

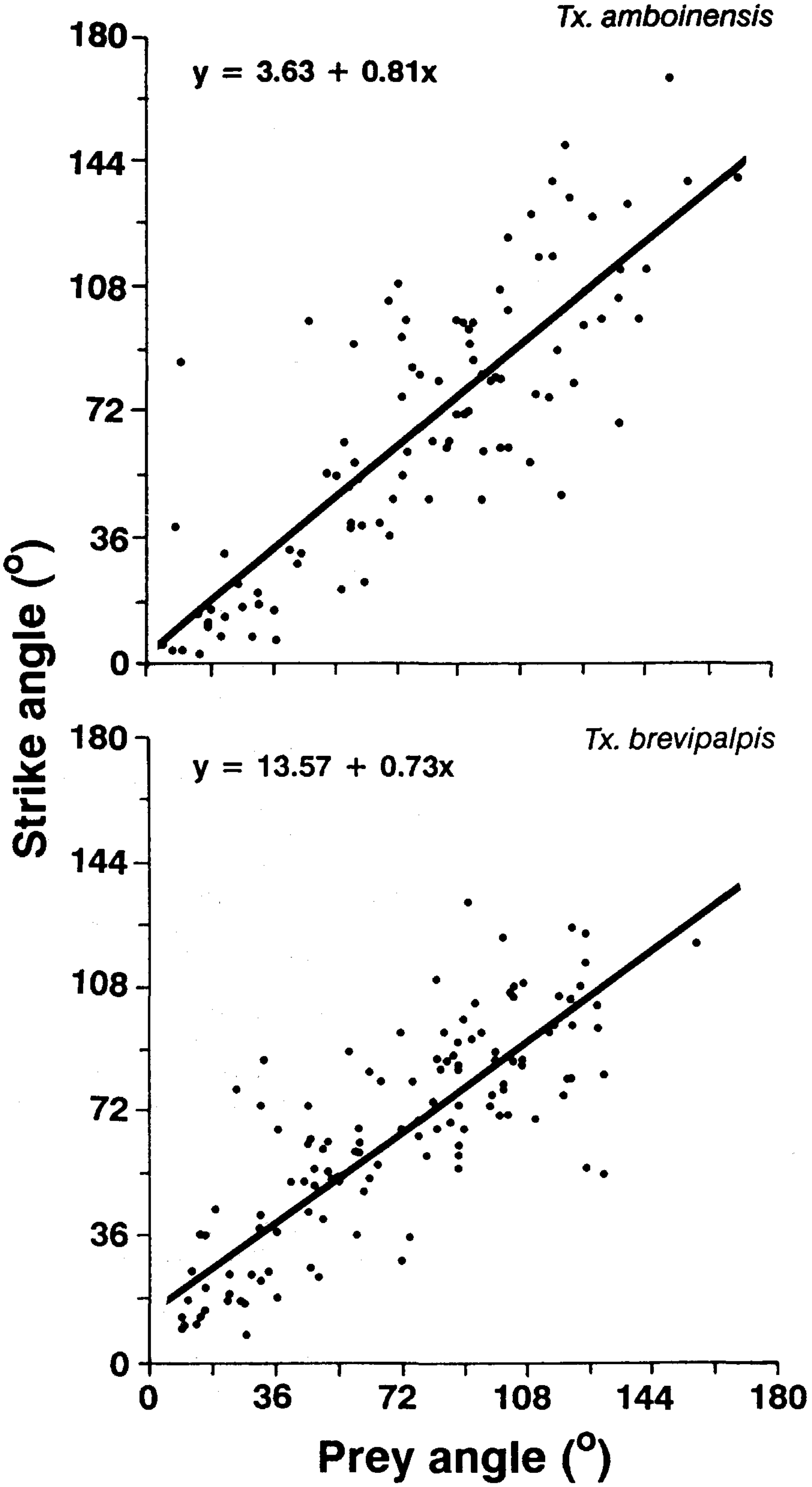

Fig. 24. Relationship between prey angle and strike angle for successful strikes.

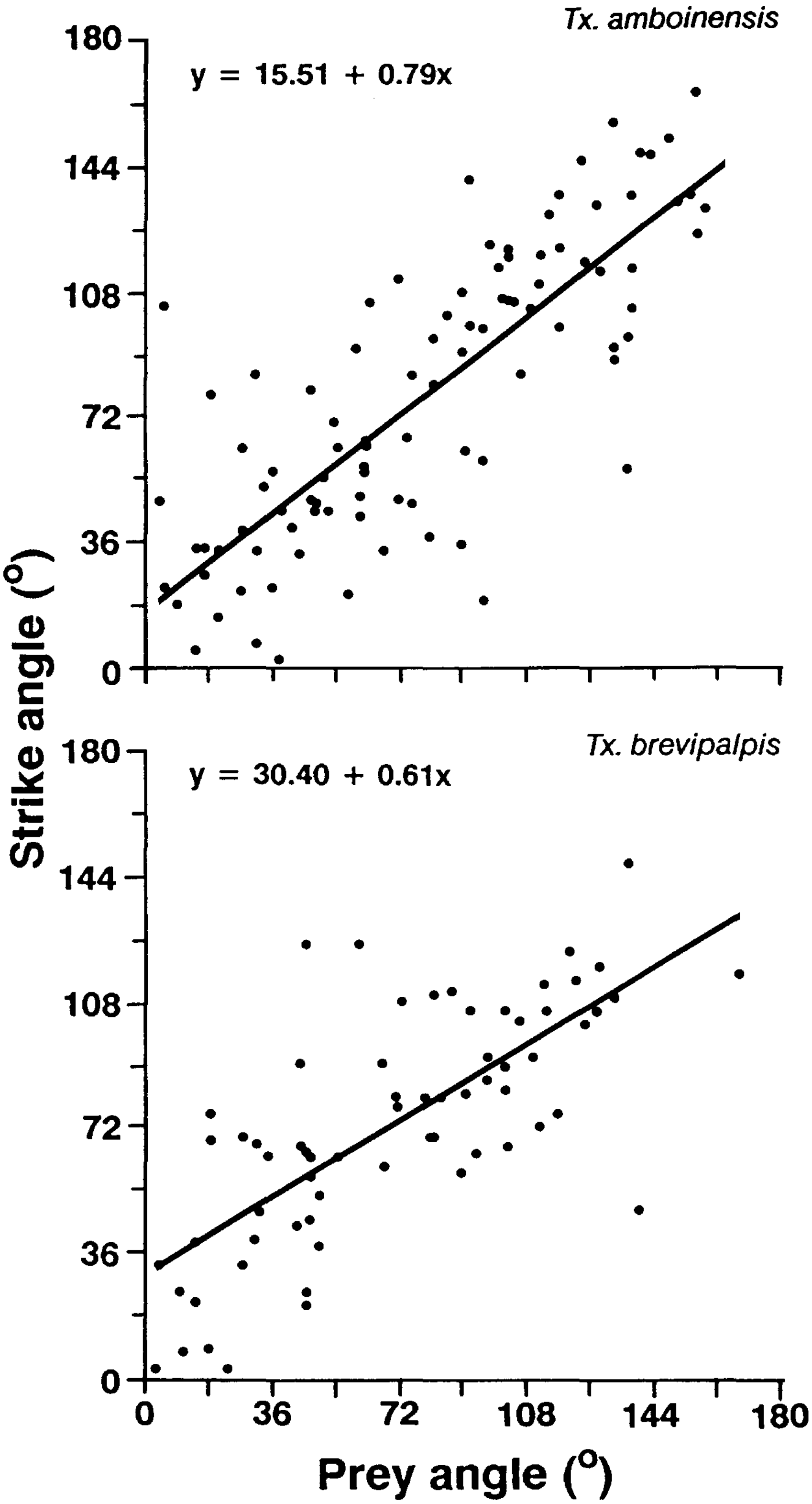

Fig. 25. Relationship between prey angle and strike angle for unsuccessful strikes.

DISCUSSION

It has been stated many times in the literature (e.g. Rubio et al. 1983, Steffan & Evenhuis 1981, Russo 1986) that *Toxorhynchites* larvae are passive ambush predators that wait for prey rather than actively seek it. This characterization is only partially accurate. The larvae certainly do not move constantly through their habitat seeking prey, but the degree to which larvae actively respond to prey depends on sensory cues indicating the prey's location, whether beneath or on the surface. In container habitats, favored by these insects, potential prey organisms also living in the water are usually few in number and occupy the same relatively limited volume. These are prey that probably will remain in the container for some time and,. because of their own activity, will probably encounter the *yToxorhynchites* larvae. For such prey it is apparently more energy efficient for the *Toxorhynchites* to remain inactice until the prey approaches closely, and then respond so as to optimize the chance of capture. Logic supports this tactic because a container of water provides a 3-dimensional universe in which considerable search energy would be required for each prey encounter, especially when prey are active and limited in number. Even with sensory mechanisms capable of fixing the position of prey, considerable probability of error remains because the prey can move or escape in any direction. When potential prey is on the surface, however, the situation is different in two important ways. Firstly, the prey may have fallen onto the surface and may soon escape, or it may be there temporarily for its own purposes. This food, therefore, is much less likely to move itself within range by chance, and it will lprobably be lost unless the predator acts. Secondly, surface prey is moving in a 2-dimensional sense, where sensory mechanisms for localizing the prey's position and locomotory ones for approaching it must deal with reduced potential for erro. Thus, as reported by Paine (1934) and Breland (1949), and as I shall describe quantitatively in a later paper, hungry *Toxorhynchites* larvae will almost always turn and swim towards surface prey, provided the latter creates surface disturbances. The fact that *Toxorhynchites* larvae in the laboratory have been maintained and studied almost exclusively using other mosquito larvae as food, has overemphasized the perception of them as sessil, almost totally inactive predators.

Given that the *Toxorhynchites* larva must rely on the movement of subsurface prey and chance to bring a potential victim close enough to attack, then it is very important to optimize the probability of successful capture, especially with such a limited strike range. Bending towards prey is a device for increasing the probability that the prey will enter the capture arc. It may immediately cause prey to come within strike range. If not, it at least reduces the distance of the head from the prey, which in turn causes the angle subtended at the prey by the strike arc to be increased, so that the prey is less likely to pass outside capture range. A less obvious factor that leads to the same result involves the shapes of the capture regions (Fig. 22, 23), which are such that more of each region is presented to the prey when a bend is executed. For *Tx. amboinensis*, bending also is important for increasing the likelihood that the prey will enter the strike arc at a relatively small angle, where more of the strikes are successful. This consideration presumably would not be important for *Tx. brevipalpis*, which, on the basis of the present data, showed no difference in the proportion of successful strikes between sectors. However, the overall level of success in *Tx. brevipalpis* was significantly higher than in *Tx. amboinensis* (71.5% c.f. 54.7%) and, although the difference was not quite significant, *Tx. brevipalpis* made proportionately more strikes to lower angles (0-75°) than *Tx. amboinensis* (51.7% c.f. 40.2%). In view of the evidence that *Tx. brevipalpis* bends towards prey to a greater degree, as well as more rapidly, it seems by this activity to have improved its overall success rate for strikes and eliminated differences in proportional success rate between sectors.

While there are advantages to bending, there are also possible disadvantages. One involves the generation of disturbances in the water that might precipitate avoidance reactions by prey. It is perhaps for this reason that bending takes place, particularly in *Tx. brevipalpis*, before prey approaches extremely closely, and is executed smoothly and slowly, rather than suddenly. Bending may also be important in bringing sense organs involved in strike initiation, which probably include mechanoreceptors on the antennae (Jez & McIver 1980), to a more frontal position, from which the prey's position may be estimated more accurately.

Confusion in the past over which appendages are used to seize prey has arisen for two reasons. Firstly, the extreme rapidity of the strike sequence (prey is seized in about 0.02 s) renders it impossible to resolve events with the naked eye or under a stereomicroscope. Secondly, and perhaps the factor that has contributed most of the confusion, the appendages used to handle prey are switched as soon as prey is captured. The palatal brushes are certainly the capture instruments, but prey is then immediately engaged by the mandibles. The palatal brushes release their hold and return to their resting position, and are never seen holding or manipulating food as it is consumed.

Striking at prey is a vigorous action and for its brief duration is undoubtedly energy expensive. Furthermore, individual prey may only rarely come within reach. These factors exert strong selective pressure in favor of strike behavior that optimizes high success/failure ratio. Ensuring success is one reason why strikes are initiated only when prey approaches very closely, almost always within the region where capture probability is high. For *Tx. amboinensis*, for example, 85.5% of all strikes were at prey within the 95% confidence zone for successful strikes, with a comparable figure of 77.8% for *Tx. brevipalpis*. The confidence zones are themselves limited because prey can only be reached at small distances and captured only within the overlapping closure arcs of the palatal brushes as they move through the strike arc of the head. In addition to any direct energy consequences of failed strikes, the sudden movements they involve almost certainly have the effect of warning some prey organisms of the predator's presence and precipitating escape reactions.

The need to offset escape reflexes in the prey is undoubtedly the major reason why the strike is so fast. Very rapid movement in water, however, because of friction and drag, imposes limitations that doubtless have been important in shaping the strike appendages and behavior in *Toxorhynchites* larvae. A feature of the palatal brushes that seems initially surprising is that they are so small. Longer brushes spread to a greater angle would seem more effective for securing prey. Such brushes, however, would probably cause excessive drag, especially during large angle lateral strikes, where head speed may reach 70 cm/s. Even with the brushes in their observed form, frictional forces on them and on the head itself have probably influenced behavior. During lateral strikes, for example, rotation of the head takes place very early in the strike, within 0.012 sec, and probably permits the head to bend to a more acute angle relative to the thorax and, since the head's frontal aspect now leads along the path of the strike arc, offer less resistance. Also, it is in the rotated head position that the narrower aspect of each element of the palatal brushes is aligned in the plane of the strike arc.

Although the majority of strikes are successful, some are missed, probably for the following reasons. In many instances, strikes are made before the prey is close enough and the larva simply cannot reach its intended victim. There is some evidence that unsuccessful strikes are executed to a somewhat smaller portion of prey angle than successful ones. Thus, "understriking" may be a factor, as well as greater inaccuracy in matching strike angle to prey angle. It is important to remember, also, that the palatal brushes can capture only if part of the prey intersects the arc and plane of the brushes as they close. Capture is much more likely if the prey, or part of it, is aligned at right angles to the closure plane of the brushes. It is quite often observed that when a larva misses a strike, it will immediately strike again if the prey is still close, sometimes several times. Repeat strikes are often successful and function as a behavioral means of compensating for the limitations of the capture system.

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FIREFLY SEMIOSYSTEMATICS AND PREDATION: A HISTORY[1]

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ABSTRACT

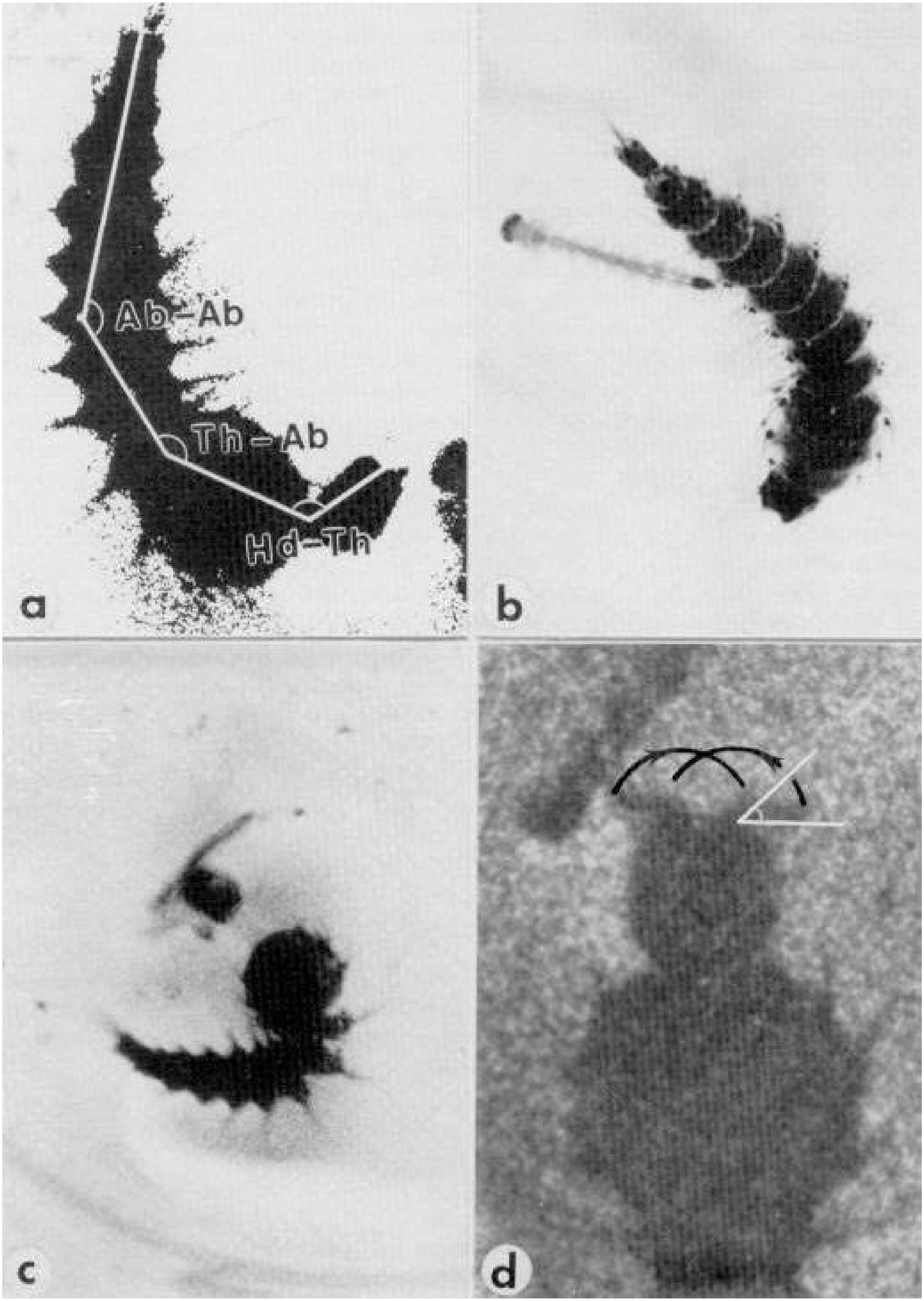
Modern firefly systematics began when it was realized that the luminescent patterns emitted by flying, mate-seeking males provided an invaluable clue for recognizing species in nature. An approach in systematics giving special attention to these signals ("semios") could be called *semiosystematics*, the focus thus being on the coded patterns that the insects are using for "interbreeding" (gene flow), and/or non-interbreeding (isolation).

In North America, *Photuris* spp. females prey upon signaling males of other species by mimicking the mating signals of their preys' females, and by directing aerial attacks toward the males' signals. Countermeasures against these attacks that have evolved in the signals of prey species, and aspects of the signals of the predator species that have evolved as a result of the mimicry predation, may be dominant features in the signaling of many of these fireflies. The flash signals that firefly systematists have used, and in particular those that have given difficulty for decades, may often be (or historically have been) closely connected with this strong ecological force, predation.

RESUMEN

La sistemática moderna de las luciérnagas comenzó cuando se dieron cuenta que los patrones luminiscentes emitidos por machos en vuelo en busca de la hembra, dan una pista valiosa de cómo reconocer las especies en la naturaleza. Un aproche en sistemática dándole una atención especial a estas señales ("semios") se pudiera llamar *semiosistemático*, el foco siendo entonces el código de patrones que los insectos usan para "intercruzarse" (flujo de genes), y o el no-intercruze (aislamiento).

En Norteamérica, hembras de *Photuris* spp. depredan los machos de otras especies que hacen señas, imitando la señal de las hembras presas, y dirigiendo ataques aéreos contra la señal de los machos. Contramedidas contra esos ataques que han evolucionado en la señal de la especie depredada, y los aspectos de las señales de la especie depredadora que ha evolucionado como el resultado de la mímica de depradción, pudieran ser razgos dominantes en las señales de muchas de estas luciérnagas. Las señales de destello que los sistemáticos han usado, y en particular aquellas que han dado dificultad por décadas, pudieran haber sido (o historicamente lo han sido) cercamente asociadas con esta poderosa fuerza ecológica, la depredación.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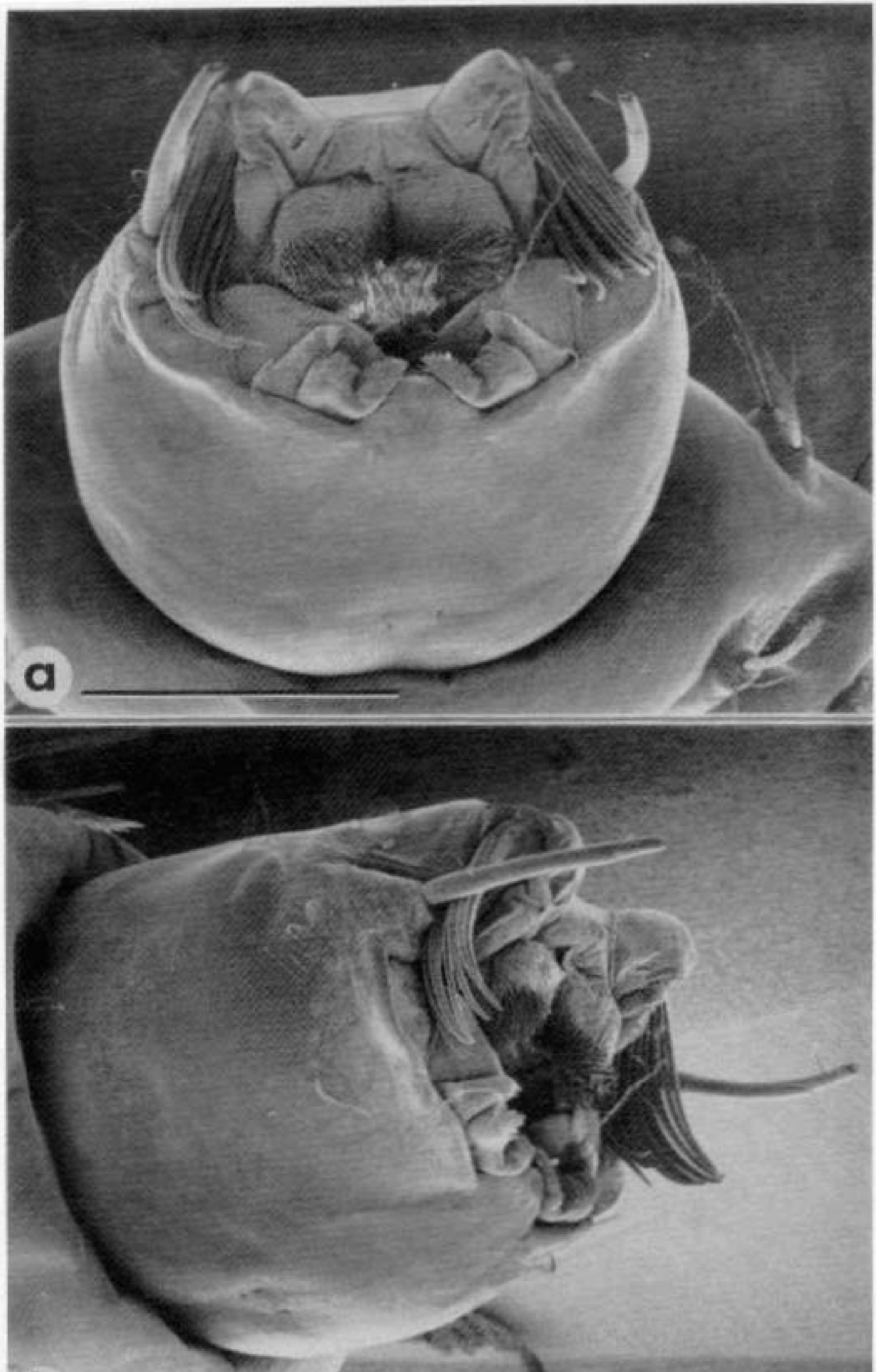
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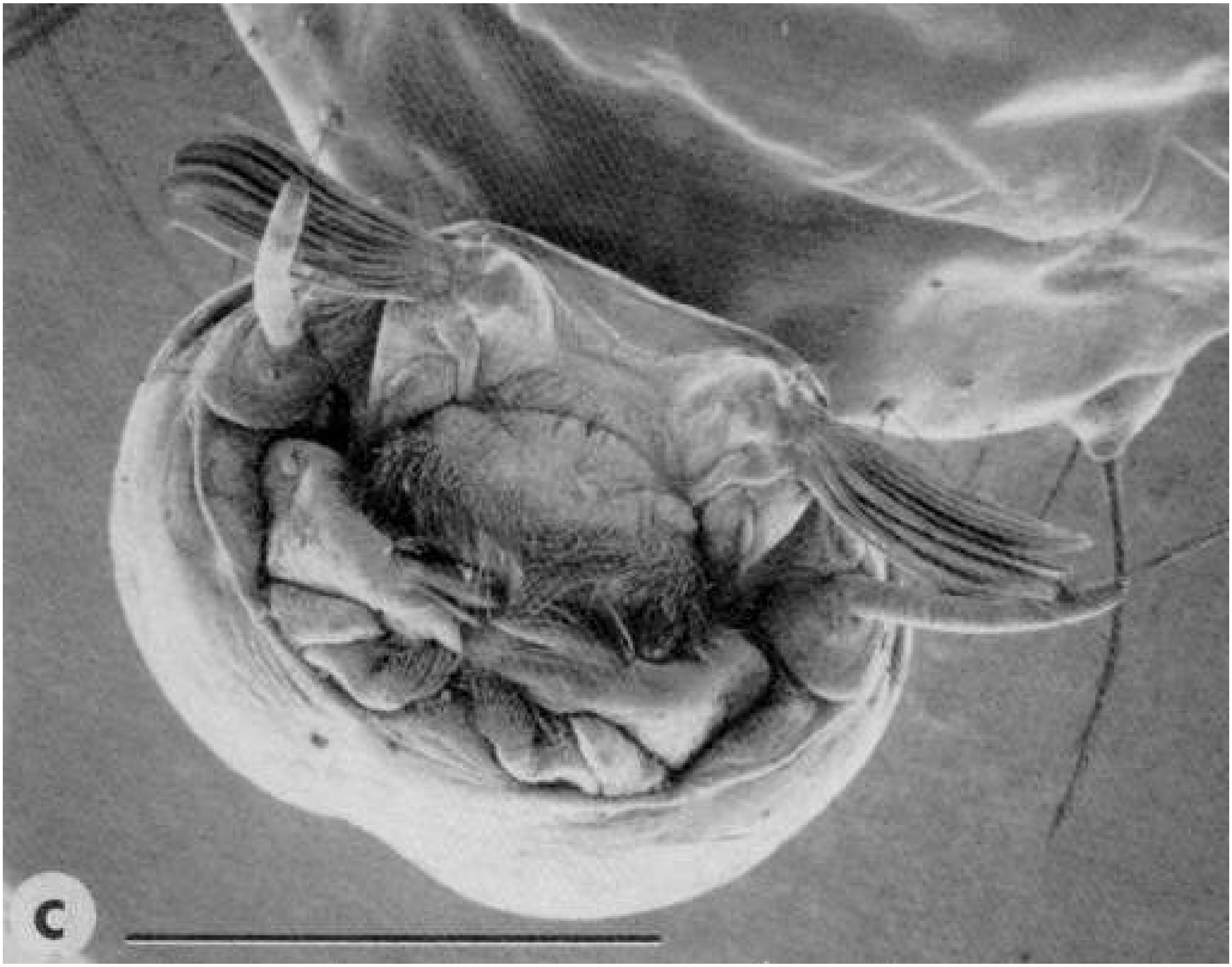
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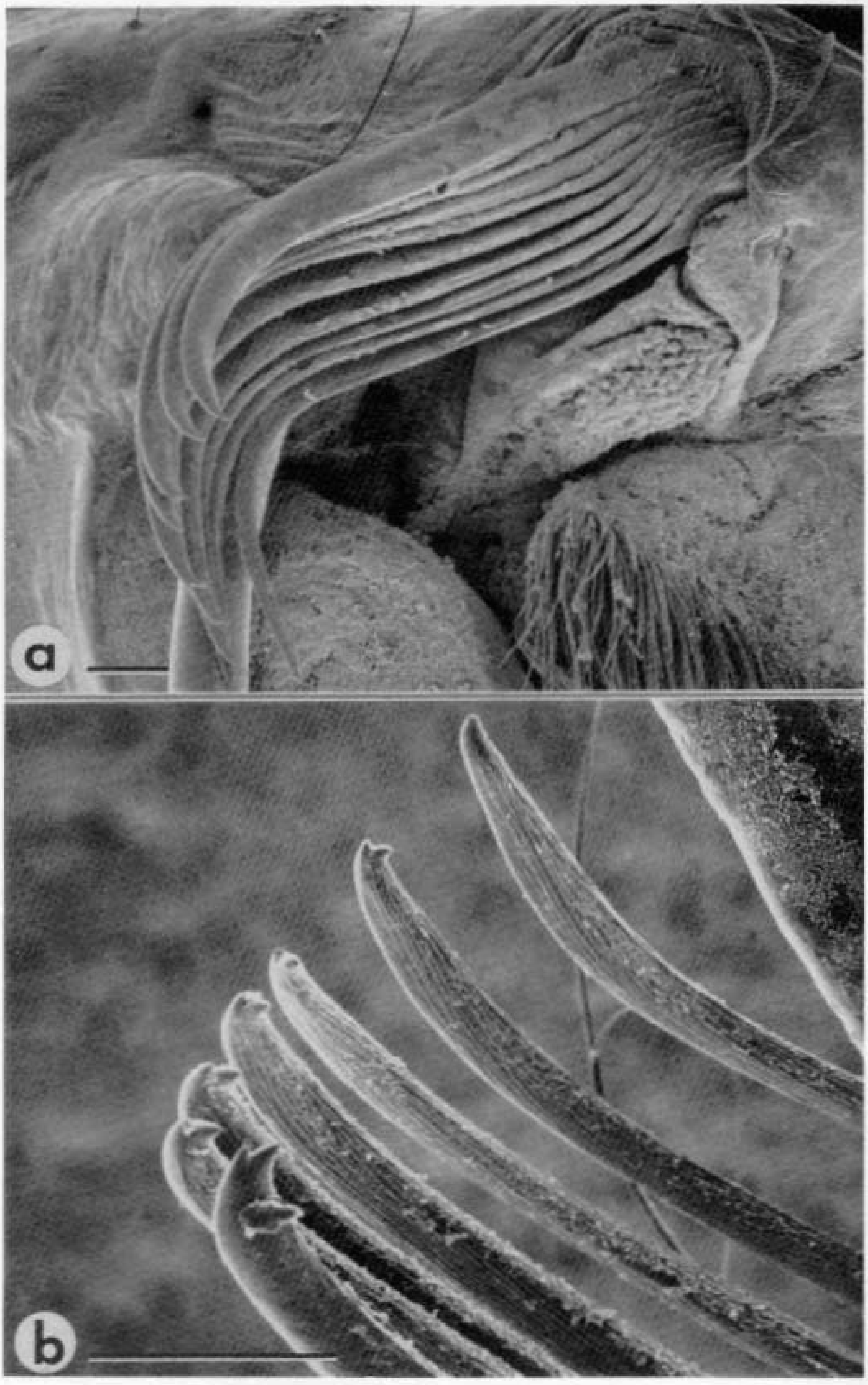
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An insect systematist or naturalist functioning as one, who has worked on a group of organisms for a while, after first inheriting and learning the standard techniques, procedures, and conceptual beliefs for the group begins to modify and develop them, and discover some new ones. With luck he (= he or she) may discover or identify some key technique or ecological element that seems at the heart of taxonomic resolution or a new understanding of the taxon. If luckier, he may be correct. I cannot imagine a cricket taxonomist worth a chirp being without a taperecorder and audiospectrograph since about 1950 (I have heard that a group of Michigan orthopterists once discussed the possibility — each jocularly encouraging the next to a higher level of seeming impracticality — that each cricket specimen should have its song preserved with it, perhaps in a tiny case on the insect pin below the corpse, maybe with a string that could be pulled to hear the song the insect sang in life, and certainly this should be required for all Holotype specimens). With time, perhaps decades, a systematist may even develop new and idiosyncratic notions of speciation and species concepts for "his" animals.

In my long hunt of North American fireflies, I inherited, improved, and added some techniques, and developed a feeling for the continuity and epigenesis of discovery and contribution in the field. I think I have identified a key factor for understanding the systematics of these insects, one that has been responsible for much confusion.

Firefly Semiosystematics: Beginning and Theory

Modern study of firefly systematics began with Frank A. McDermott, a nonprofessional (i.e., unpaid) lampyridologist who spent most of his working life as a chemist. He published his first observations on firefly flashing behavior in 1910. Among his last works, i.e., published in the mid-1960s, were a catalogue of the nearly 2,000 described species of Lampyridae of the world (the notes for which fill a large carton of fileboxes), and the *Taxonomy of the Lampyridae* (1964), which have a worldwide taxonomic synopsis and overview of the family.

In the 1910s McDermott reported and urged that if you watched fireflies closely you would see that the flashes were sexual signals. He found how the basic signal system works in flashing American fireflies, and in particular in the common *Photinus pyralis* (L.). The fact that Osten-Sacken (1861) had observed and connected mating and flashing in *P. pyralis* decades earlier, or that the significance of luminescence in sexual interactions in European glowworm species had been appreciated centuries earlier (early 1600s?), cannot diminish the significance of McDermott's independent discovery; he rediscovered the sexuality of *pyralis*' luminescent signals, but only started there. He found that the student could locate and identify male fireflies of different species in the field by the species-specific flashing patterns they emitted as they flew about their habitat seeking mates (Fig. 1). He found that he could simulate the flashes of male and female fireflies with matches and electric lights and experimentally determine significant elements. And, he discussed how different patterns and timings could prevent the intermixing of species.

McDermott's firefly taxonomy work thus began with locating, recognizing, discriminating and experimenting with mating signals, and he thought about species and "reproductive isolating mechanisms." He put his conclusions into practical application by making what appears to be the first formal taxonomic decision based on mating signals; he took *Photinus castus* LeConte out of synonomy because he believed that its mating signals were different from those of the species it had been lumped with (McDermott 1912). (Though *castus* is now again synonomized, the biological significance of the *castus* "morph" is yet to be understood; see Green 1956: 575). When you read McDermott's 1912 paper you realize that he had a feeling for what amounted to biological species and sibling species, long before biology at large did, though another solitary

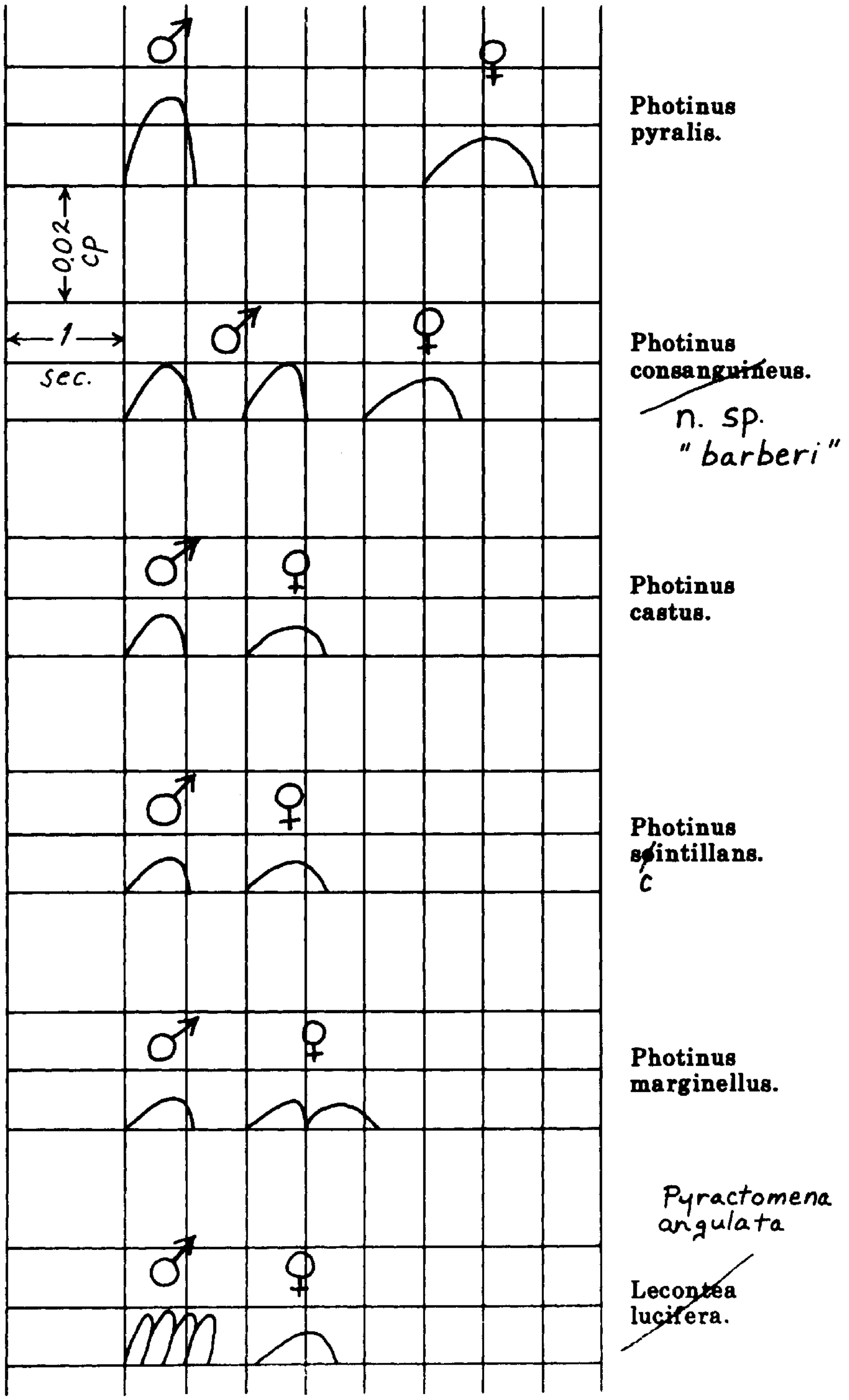

Fig. 1. First known firefly flash pattern chart, from McDermott (1914). Nomenclatural changes in keeping with current understanding (Green 1956, 1957; Lloyd unpub.) are indicated. Horizontal axis is time, as indicated; vertical axis, intensity.

entomologist, Benjamin Dann Walsh, had tracked this swampy ground nearly 50 years earlier (1864); and, Samuel Scudder had carefully listened to and scored (musically speaking) the songs of several Orthoptera species [e.g., 1874; note also B. B. Fulton in Alexander (1964), and the latter's discussion of the use of cricket songs in their classification].

Such a point of departure and orientation in the literal and figurative pursuit of firefly species, in nature and thought, and the tendency to be more than attentive to and even favor the evidence of mating signals when it conflicts with that from morphology, is what I mean by **semiosystematics** (semio from the Greek word for sign or signal). It is not *the* last word, but *a* first word; a tentative and hypothetical word; a cautionary word and watch word, in a study of firefly species. At the end of the successful chase, its etymology and entomology will be understood, or so a semiosystematist hopes. The rationale for such an approach is obvious, recalling that mating signals "actuate" identification, copulation, and insemination, hence flowing of genes and defining of biological species: which definition may not be preferred or best, but elements and the error of it must be part of finding a satisfactory understanding of what firefly "species" are in nature.

To summarize, McDermott showed that one pursues and watches firefly flashes to pursue and understand species. At night in the dark, as an avocation, with primitive technology (including transportation to study sites), with many yet unknown and mostly poorly or inadequately described, nominate species, McDermott saw through a confusion of flashing patterns in the field, and put together the working foundation for semiosystematics.

Photuris Semiosystematics: Application and Technique

McDermott recognized that different *Photinus* and *Pyractomena* species emit different flash patterns, and applied this in an example case of conflicting evidence, but he never acted on his theory in the case of *Photuris pennsylvanica* (DeGeer). For many decades it had been assumed that the genus *Photuris* had limited representation in the North American fauna. America's Dean of Coleoptera John L. LeConte (1881:37, 1883:208) had concluded that except for *Photuris frontalis* LeConte and another from the Near West, all of the *Photuris* fireflies in the United States and Canada were *P. pennsylvanica*.[3] McDermott observed that the presumptive Pennsylvania Firefly emitted distinctively different flash patterns, but he left it without further comment. It should be noted that a little earlier Henry W. Wentzel (1896) of Philadelphia, "One of the best collectors of Coleoptera in the country" (Smith 1899:730), had made the generalization that each firefly species has a different way of flashing (:294), and had distinguished two species of *Photuris frontalis (sic)* on the basis of unspecified flashing differences (:296).

In the 1920s Herbert S. Barber, a beetle taxonomist at the National Museum, and long-time correspondent of McDermott, chased fireflies seriously as a (job-related) hobby. He used the semiosystematic approach on LeConte's ubiquitous *P. pennsylvanica*, and recognized several unnamed species (Barber, in Barber and McDermott 1951). His chart of firefly flash patterns has since been often used to illustrate how a study of mating signals can disclose the presence of sibling (=cryptic) species (Fig. 2)[4]. From his experience with *Photuris*, Barber particularly stressed the importance of repeating observations on flashing patterns, and the preservation of flash (pattern)-voucher specimens. He found that with carefully collected series of such vouchers, specimens that had emitted various discrete and distinctive patterns could be distinguished morphologically — of course this was not critical, but it was what was needed for building confidence in such an approach. Barber gave some of his species scientific

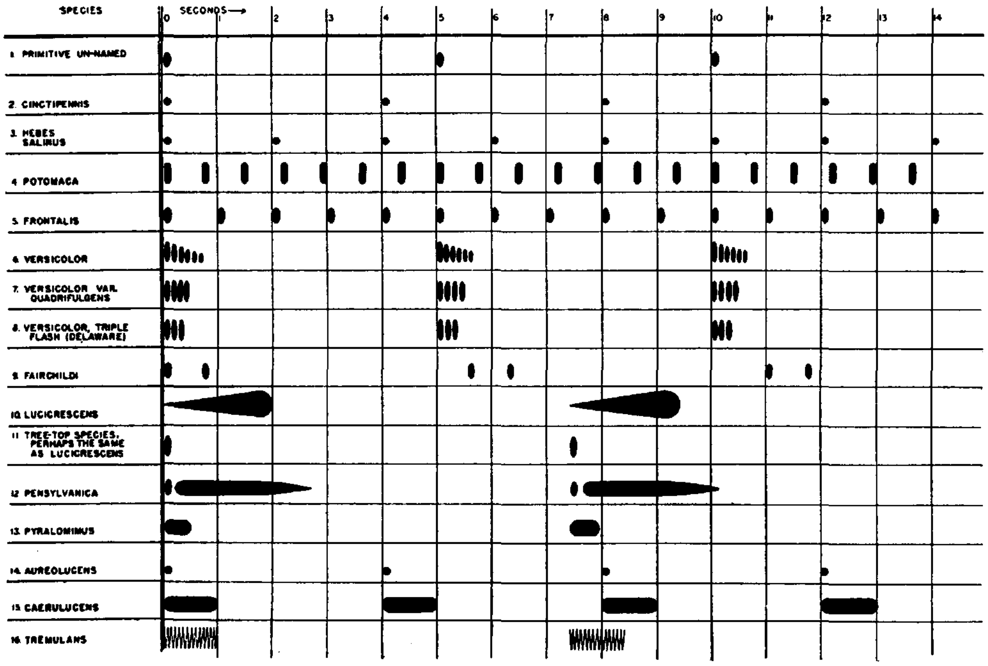

Fig. 2. Flash pattern chart from Barber's (1951) classic, often- cited study. As in Figure 1, axes indicate time and intensity.

names descriptive of their distinctive flash patterns: *Photuris tremulans, P. lucicrescens*.

Thus, Barber began to pick at and understand the *Photuris* species problem that LeConte could not see in dead specimens, and apparently had not looked for on his several trips and expeditions, and that McDermott had observed but silently put aside. Barber began to understand, and to "split up" *P. pennsylvanica* as his mentor and fellow coleopterist E. A. Schwarz (Fig. 3) much earlier had predicted someone would do (McDermott, in B. and M. 1951: iv). His work was certainly more exciting and better empirical documentation and application of what McDermott The Theorist had thought about. When it was ultimately published, posthumously and nearly three decades after his major field work was done, it was current, but not prescient as it could have been, for the New Synthesis in evolutionary and systematic biology was in full charge by that time (Mayr 1982).

Of equal importance, a *posteriori*, because it led to the next step in the development and understanding of *Photuris* systematics, was Barber's observation that males of some *Photuris* species actually do emit more than one flash pattern (Fig. 2, nos. 10 & 11; Barber, in B. and M. 1951: 6-8). This must have been of as much concern to Barber as apparent multiple patterns in *P. pennsylvanica* may have been to McDermott, but neither appears to have left us his inner suspicions or thoughts on the matter, at least to my knowledge none was published except for Barber's brief "concerned, rhetorical musings" on the legitimacy of using the flashing patterns to distinguish species (Barber, in B. and M. 1951: 8).

Photuris flash pattern changing was and is a significant problem. Aye, now there's a rub, for if species-specific flash patterns are "only reproductive isolating mechanisms" as was believed for a long time, insuring that their uncomplicated, small-brained possessors get mates of the same species, what could be the utility of switching among multiple, distinctive patterns? Why should a species need more than one pattern? It was here

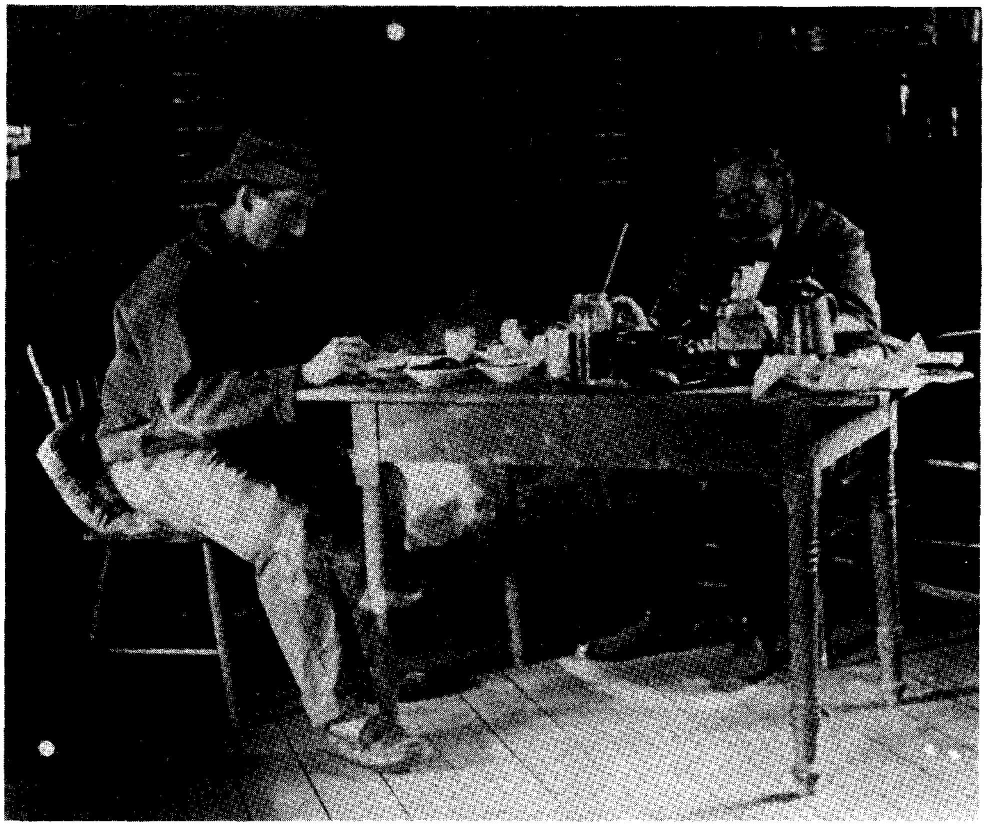

Fig. 3. H. S. Barber (left) and his mentor E. A. Schwarz in early 1900s, dining while on a collection trip to Plummer's Island in the Potomac River, at Washington, D.C. Photo from the USNM Archives, courtesy of T. Spilman. Barber was a photographer and may have taken the photo; there does not appear to be a third place-setting, and Barber's pose suggests that he may have tripped the shutter timer, rushed to his chair and "froze."

that the Father and Great Uncle of firefly semiosystematics left the problem to future lightningbug chasers.

Predation By *Photuris*

Fireflies Barber passed along a critical anecdote on the phenomenon that I am suggesting may be the key to understanding the signaling behavior of American fireflies. He observed female *Photuris* fireflies flashing correct "sexual" answers to the flash patterns of males of other species (Barber, in B. and M. 1951: 9-10). Since he and others had found female *Photuris* eating males (only) of other luminous species (Fig. 4), Barber was cautiously suspicious that the females preyed on the males by luring them via signal mimicry [see Lloyd (1984a) for review, including early history of observations of *Photuris* predation, and references, analysis, and tabulation of observations of aggressive mimicry]. Predation by *Photuris* females is an insidious affront to those who wish to see beauty and serenity in the silent, twilight sparkling of these gentle, leather-winged beetles. It is aimed at the signals that the fireflies would use for mate finding, mate recognizing, and gene flow: the signals that a naive semiosystematist believes will enable him to resolve firefly species problems "simply."

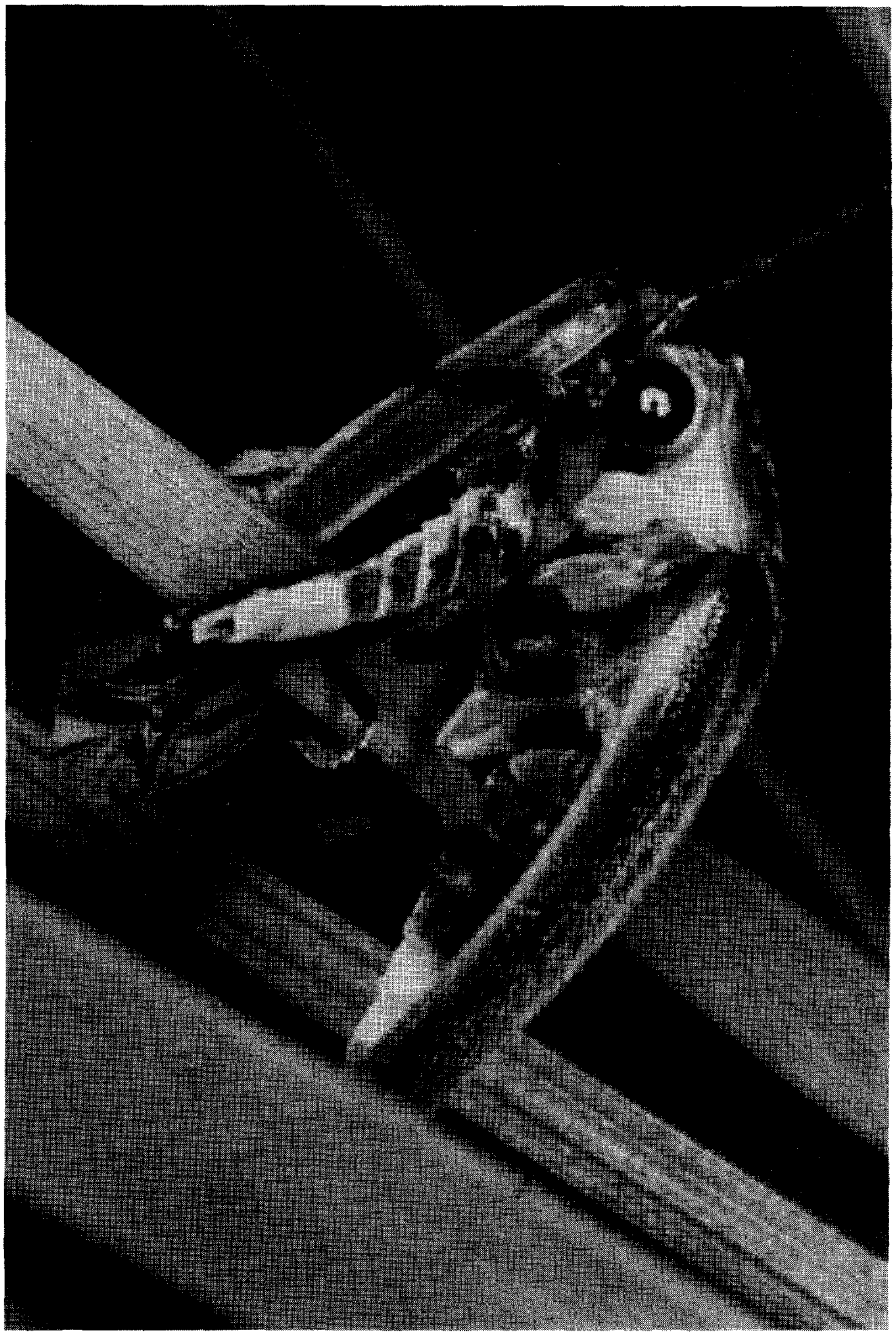

Fig. 4. *Photuris* species "B" female eating a male of *Pyractomena angulata*, on campus of U. of Florida, Gainesville. Her males mimic the flash pattern of male *P. angulata* (Lloyd 1980).

The *Photuris* female, again collectively speaking, though it is technically improper to use a generic name in such fashion (Blackwelder 1968: 51), attacks signaling males in two main ways. In Barber's tactic, she pretends to be a female of the targeted male's species and with false signals lures him to where she is perched (McDermott was also long suspicious that this occurred, pers. comm. ca. 1965, see also McDermott 1917:60). In this predation the predators have gotten inside the coded signal programs of their prey, and must cause eternal pressure for arms races as they track changes that prey species must evolve in their signaling behavior to avoid them.

In the second tactic, which the females sometimes use in conjunction with their aggressive mimicry, they launch aerial, hawking attacks, guided by the light-emissions of flying males (Figs. 5-7; Lloyd & Wing 1983). Obviously, flashed signal patterns that let males transmit their message and then hide in the dark should be safer than long patterns that offer easy targets, and allow attackers to approach from a distance. How could luminescent signals not be affected by the actions of these females, or at least, how could a semiosystematist not theorize that they were?

On Technique: Predation by semiosystematists. The physical pursuit of firefly species by semiosystematists is predation, and because it is fundamental to semiosystematic practice it is worth mentioning. The semiosystematist scouts, locates, identifies, and tracks; lures, nets, traps, and trolls for his quarry in ways dependent upon precise and detailed knowledge of the most intimate sexual habits and entreaties of his prey. While in the dark, he quantifies the behavior (see Barber, in B. & M. 1951: 10 for early technology), even borrows techniques of the stalking sportsman with gun (photo-multiplier) and fishing rod (with light-emitting diode lures),for the pursuit of individually observed and significant trophies called behavior- or semiosystematic-voucher specimens. (When in restricted areas such as National Parks, having not planned ahead for collecting permits, it is possible that he circumspectly poaches.) Vouchers are carefully curated with genitalia extruded, colorfully labelled, identified and displayed in "voucher cabinets": their behavior and capture are described in detail in field-journals which, with recordings and specimens, are cross-referenced and indexed.

Consequences Of Predation For Firefly Systematics

Given: 1) that firefly signals are easily simulated by "foreigners" with light organs (and LED's), and 2) that most luminescent fireflies in the dark have little information for decision-making other than light flashes, THEN, their luminescent behavior must be expected to have changed, as they evolved escapes. Through comparative studies there should be little difficulty in finding illustrative examples, and in experimentally demonstrating their feasibility. Tests with LED's on fishpoles, proved the "obvious," that continuous glows make better targets than intermittent, short flashes, and that complete darkness is safest (Lloyd & Wing 1983, see Figs. 4-6)[5].

Here are some possible predation-systematic connections, keeping in mind that the interests of systematists range from the location, identification and capture of specimens mentioned above, through the understanding of the evolution of higher taxonomic categories, to the natures and evidences of evolutionary tempo and mode (with driving mechanisms).

* * *

Species of North American *Photinus* for the most part fit comfortably into apparent phylogenetic groups, each of which is defined by a characteristic male genitalic form [Green (1956: 561-562); note that beetle taxonomy in McDermott's early time did not know of this character, and without it many nearctic *Photinus* and *Pyractomena* are sibling species[4]]. Characters in addition to genitalia are often useful, but many are

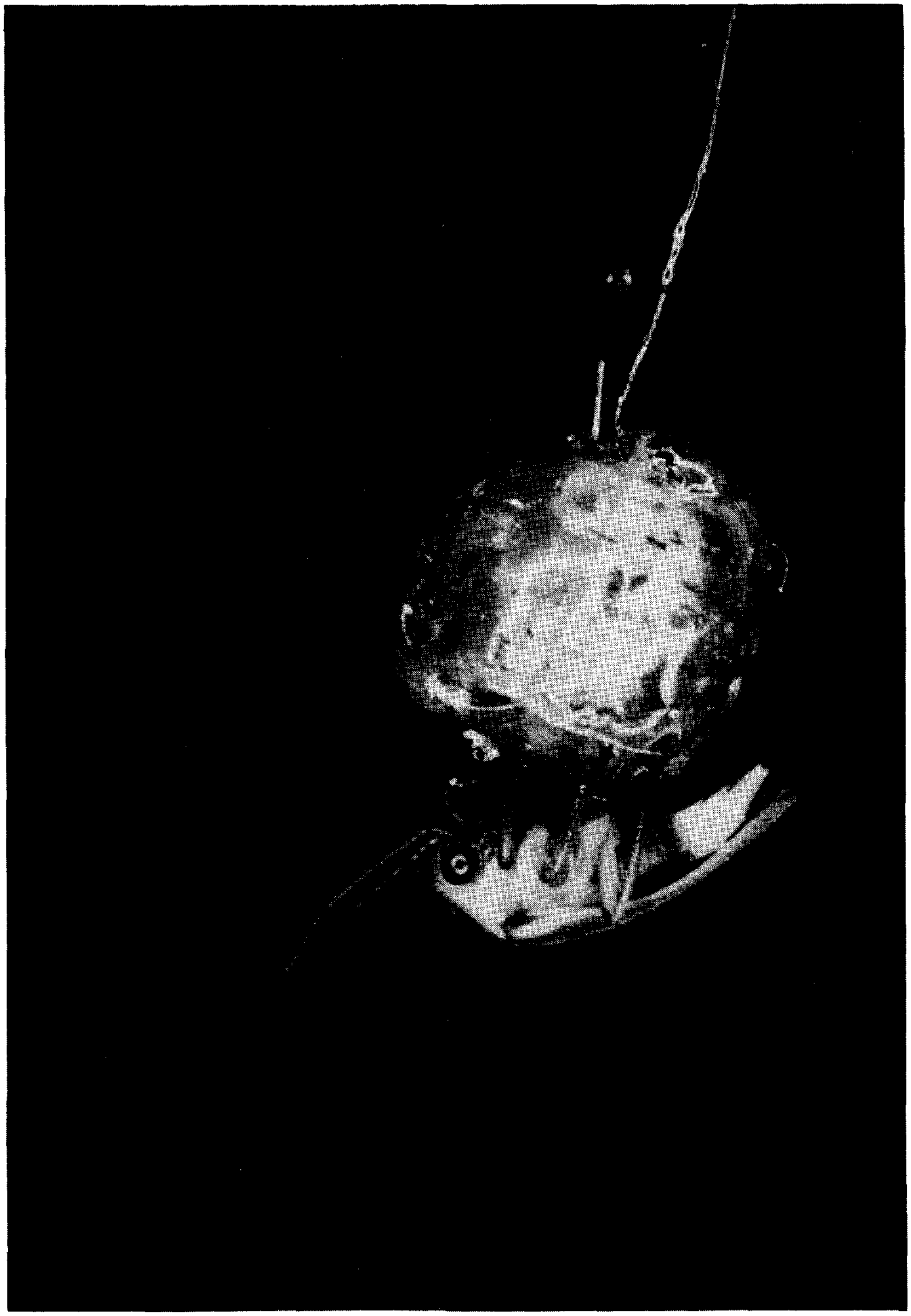

Fig. 5. *Photuris* species "D" female, with feet stuck on decoy (light-emitting bead) she has attacked. Wires to fishpole and electronic controls are above.

subtle and require initial separation by genitalia for appreciation. Today an experienced *Photinus* pin-pusher and connoisseur is not likely to misidentify this taxon even as it is now, somewhat broadly constituted. Flash patterns within *Photinus* (genitalic) groups also show relationship (Green 1956: 563; Lloyd 1966: 77, 1984b).

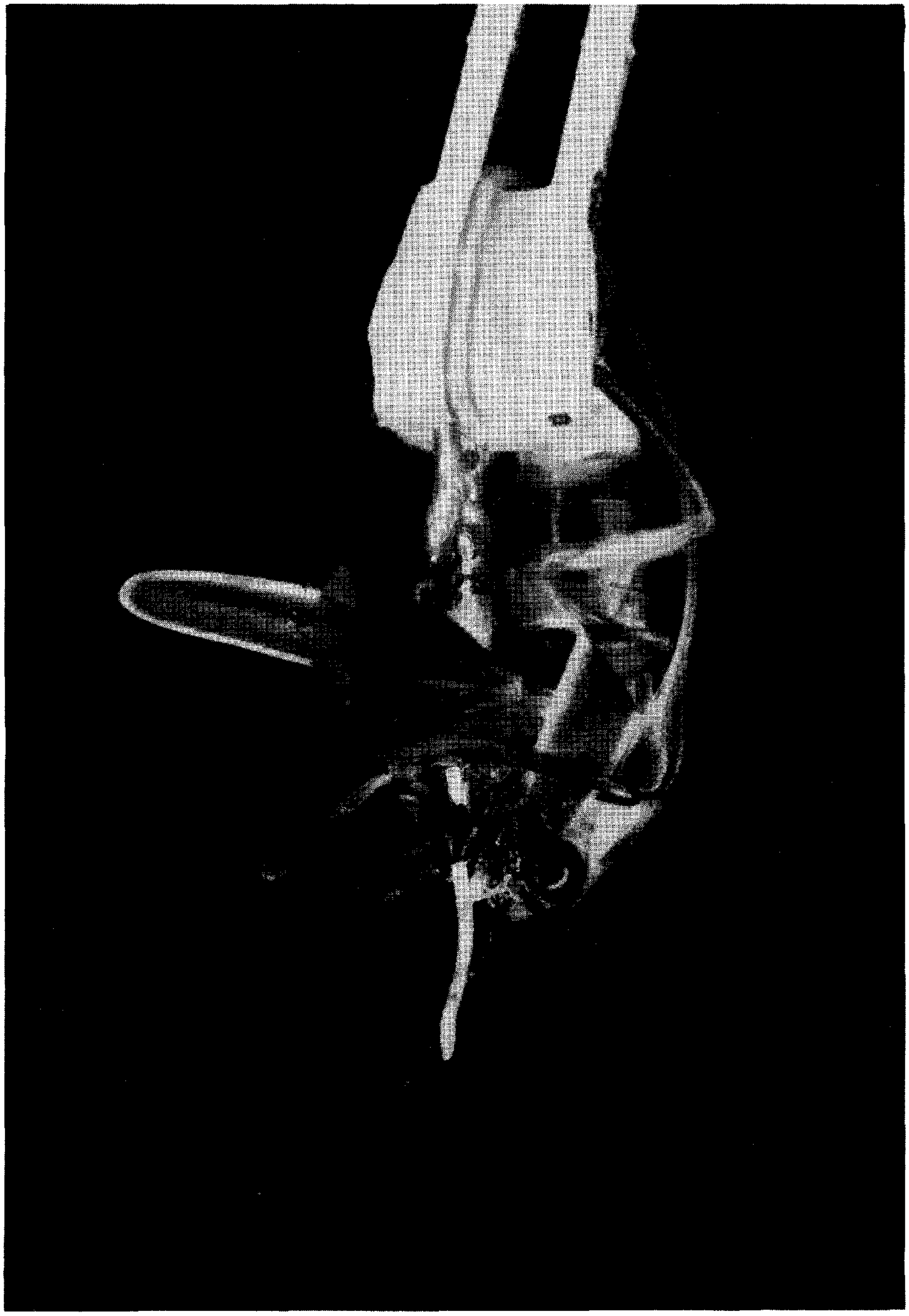

Fig. 6. *Photuris* "D" female eating a prey male that had been attached to an LED target, indicating that females that are attracted to "flying" LEDs are in predacious mode (or switch to it after striking the light).

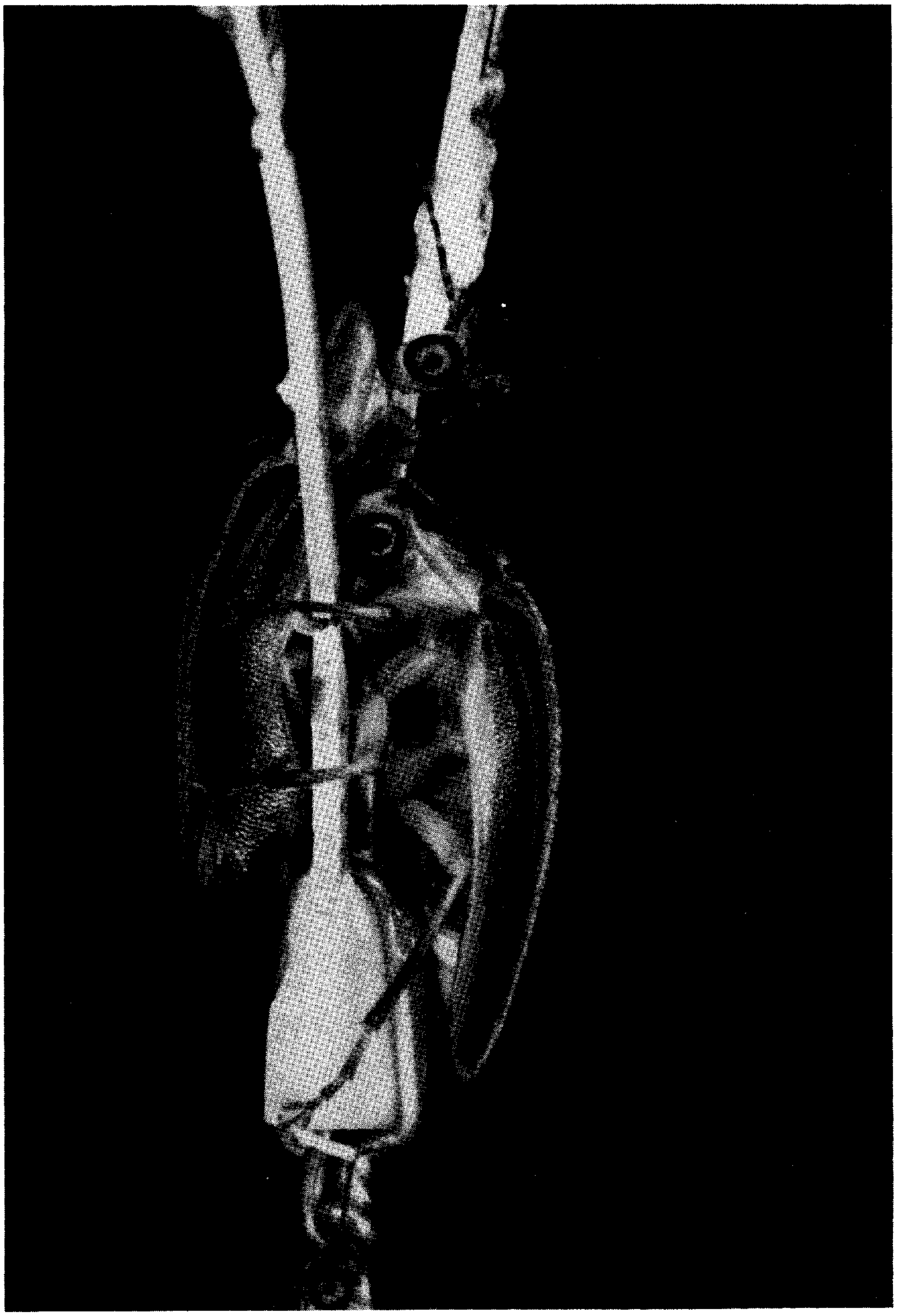

Fig. 7. Two *Photuris* "D" females simultaneously attacked the target LED with impaled male. One attacker has nearly severed the head from the other (above). The head of the impaled prey male is seen below.

Species in the *Photinus consanguineus* group (Fig. 8, n=6+) are most interesting: *P. indictus* shares the group characters, except that it has no light organ. The eyes of males are smaller than typical, and *indictus* uses pheromones for sexual communication (Lloyd 1973. LeConte (1881) described and named *indictus* (before the value of using genitalia had been discovered), and placed it in a genus with unrelated, nonluminescent fireflies, noting that (p. 33): "This insect has a deceptive resemblance to *Photinus consanguineus* and other species of that genus." LeConte thus set aside the unmistakable resemblance of habitus detail and gave absolute weight to a character that "merely" revealed a somewhat recent change in the mode of sexual **signaling**. Some-day, -millennium, descendent species of *indictus* may comprise/warrant a different genus; maybe this is what happened to modern genera with diurnal adults, such as *Pyropyga*, *Lucidota*, and *Ellychnia*, which account for 18 species in North America—the species of two of these genera were considered congeneric with *indictus* by LeConte.

Why would *indictus* give up flashing? What better hypothesis than predation by *Photuris*? Might not some prey species, now flash-signaling in the dark with no other information available, use chemical clues to distinguish predacious from conspecific respondents? —a hitherto unsuspected bridge for the presumptive gap between the luminous ancestors of *indictus* and total reliance upon pheromones. We cannot criticize LeConte as an erring semiosystematist, since there is no indication that he knew why fireflies flashed. Nonetheless, his taxonomy may well have been influenced by an unappreciated predation connection.

Certain other species in this group have 2-flash patterns, with differences among species being in the interval between the (homologous) two flashes (see Lloyd 1984b for illustrations). In one species the interval is often 2 sec or more, depending upon temperature, allowing plenty of time for an attacker to fly toward the first flash and be in position to strike the second. Three other species in this group could have evolved their shorter, species-specific intervals, and a fourth dropped the second flash of its pattern, because of this. Could such signal changes coupled with geographic isolation lead to rapid speciation? Notably, the 2-sec species (*P. macdermotti*) has an extensive geographic range, and the ranges of the others are peripherally sympatric. There are other predator-related explanations for the noted changes in flash patterns in this species group (Lloyd 1984c).

Not only could the flash patterns have been influenced by predator action, but so also the space in which sexual activity takes place, and whether 3-dimensional, dark airspace must be used for hiding between flashes. It is doubtful that sedentary flashing systems as known from Asia and New Guinea could occur with *Photuris* present. Cicero (1984) studied an Arizona member of the *consanguineus* group, *P. knulli*, outside the range of *Photuris*, and found that it has a sedentary signaling system! One could venture that this species is not likely to extend its range into eastern North America without changing its sexual manners!

In a predator vacuum new and quite different evolutionary pathways must open up, as Cicero's firefly suggests. Implications for taxonomy?: In the swarming Asian and New Guinea species mentioned, where high density has resulted in keen male sexual competition, males have evolved clamps to hold their females (see especially Wing et al. 1984, Lloyd & Wing 1982, Lloyd et al. 1989). This has apparently happened independently two or more times (L. Ballantyne, pers. comm.). The bent elytral tip, forming the upper jaw of the clamp was the primary character that taxonomists used to separate these species from *Luciola*, and put them in their own genus *Pteroptyx* (which because of the aforementioned convergence is to be divided).

I will now summarily blame historical and present confusions of *Photuris* taxonomy on the predations by females, and leave the details for later. *Photuris* genitalia are largely the same throughout the genus and so far offer little help; nor are there any

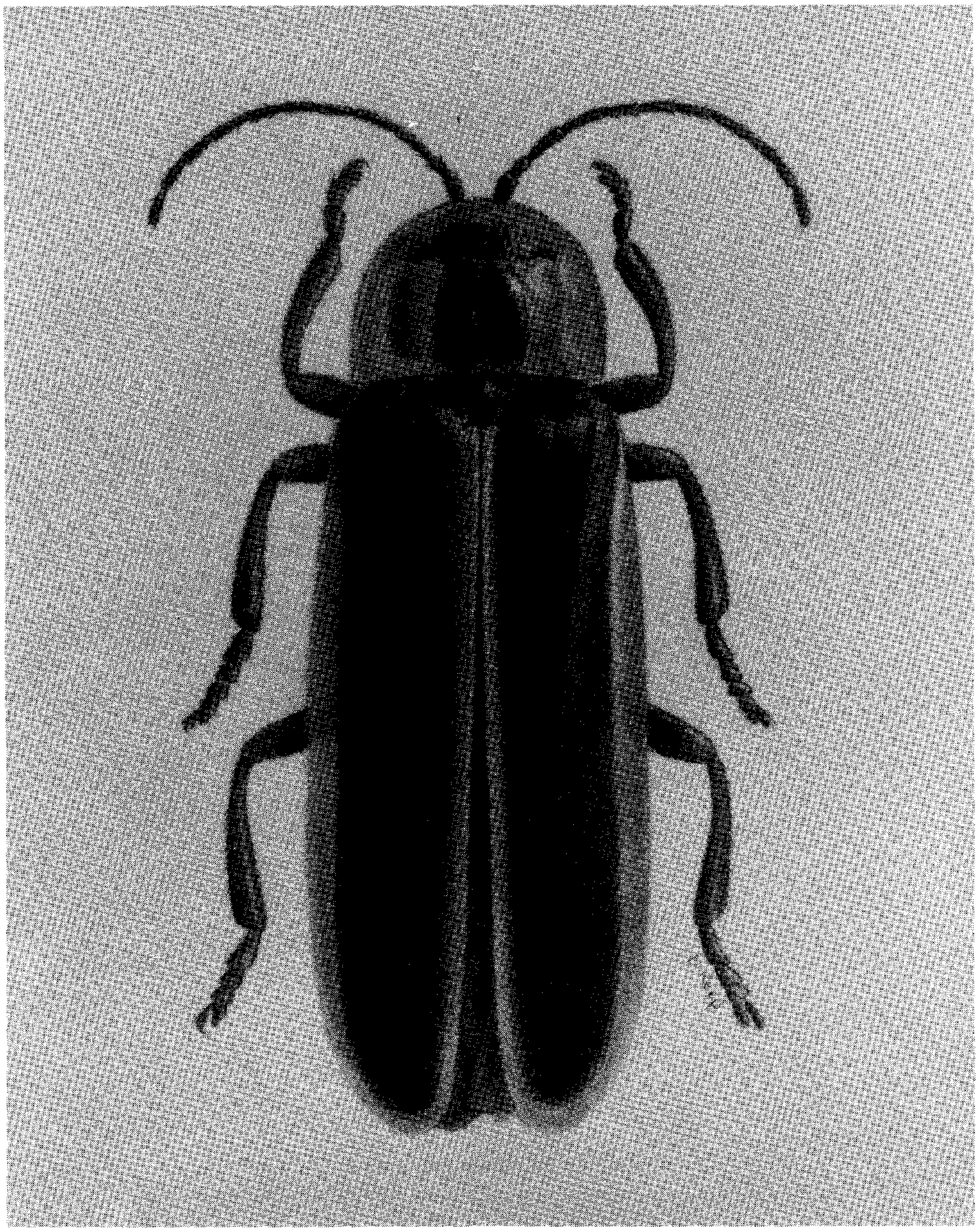

Fig. 8. Habitus of *Photinus macdermotti* Lloyd. Without observing the male flash pattern in the field, identification of this species is very difficult or impossible. From the dorsal view this could as well be the nonluminescent *P. indictus* (LeConte). (Carbon dust by L. Reep.)

apparent morphological characters to permit a satisfactory separation into species, the hundreds of drab specimens now in museum trays. Hence the century-long existence of "*Photuris pennsylvanica.*" In the field *Photuris* males often emit flash patterns that to be distinguished require electronic analysis. Males of several presumptive species switch from one discrete pattern to another (Fig. 9), and some patterns they switch among are copies of the patterns of species flying with them. To demonstrate this with

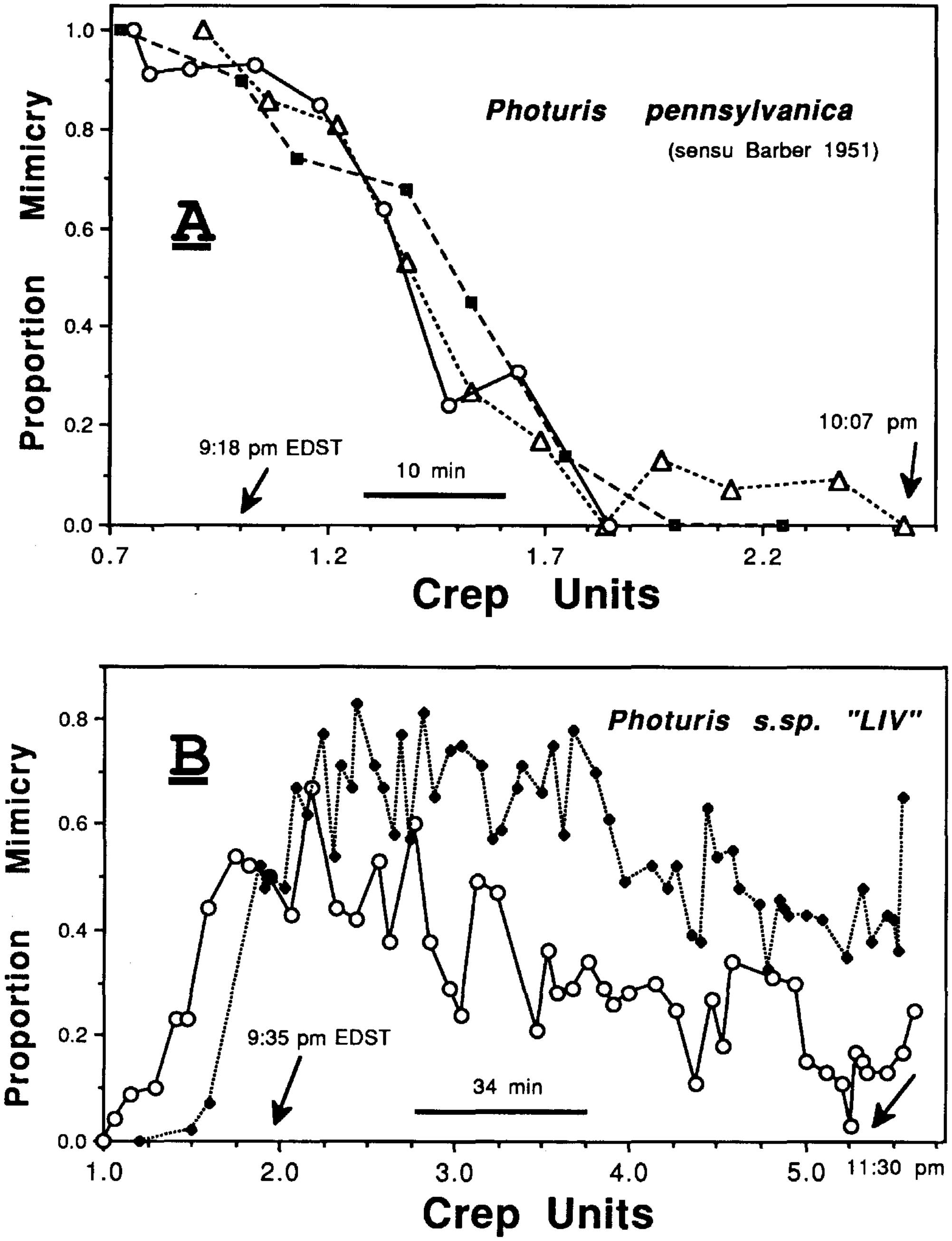

Fig. 9. Barber (1951) noted that both *P. lucicrescens* and *P. tremulans* emitted two different flash patterns: the former varying usage among sites, the latter spontaneously switching back and forth with apparent "contagion." The switching of two species from northern U.S. shows temporal consistency. (9A) During early evening males of *P. pennsylvanica (sensu* Barber 1951) emit a single flash, an apparent copy of those emitted by twilight *Photinus* spp. (1980), but gradually all switch to the species' "own" pattern (Fig. 2, pattern 12). The 3 samples shown are from the same site in two different months and years (4 July 1984; 15, 16 June 1987), the only samples that were made.

Fig. (9B) On two consecutive nights the proportion of *Photuris* "LIV males emitting the mimicry pattern (a *Pyractomena angulata-* like flicker, see Lloyd 1980) rapidly increased to more than 60% and then gradually fell off [with an at-the-time unnoted confidence requires electronic analysis of patterns AND careful immediate collection of PM-recorded specimens.

In many cases the flash patterns that *Photuris* males mimic are those of known prey of their own firefly-hunting females. Thus, there is reason to suspect that problems relating to multiple patterns are connected to female predation (Lloyd 1980). Male pattern mimicry is recognized because models belong to other genera. But, *Photuris* females also hunt *Photuris*; if *Photuris* males of one species mimic the pattern of males of another and look-alike *Photuris*. . . .

The individual patterns used by males of a species are potential sources of reproductive isolation should members of isolated demes "lock onto" one, excluding others from their repertoires[6], because, say, of local predation ecology. For example, males using one of the species' patterns might be less subject to aerial or mimicry predation from other (or their own?) *Photuris* females. There are many models possible.

These facts, 1) prey and predator species vary in their geographic and seasonal distributions and densities, 2) some *Photuris* may (through predation) dominate others under certain circumstances, and 3) *Photuris* have multiple prey and probably switch among them depending upon a variety of ecological circumstances, suggest that local conditions must be extremely variable for prey and predator.

In the past thousands of years glaciers have closed out, opened up, and isolated habitats and ranges, and shuffled species combinations and isolations considerably. With a kaleidoscopic historical and environmental background, with shifting mosaic distributions, ecologies, and strong and sharply-focused predation, and given *Photuris*' certain intrinsic potentials such as signal (neural) "plasticity," I temporarily feel comfortable suggesting that recent (current) and rapid speciation is a common phenomenon in *Photuris*, and invoke it as the blame for the cabinet taxonomic problems that the genus has given. It is time to add technical developments such as electrophoresis to the semiosystematic backpack. Surely there must be a knowable explanation for it all.

ENDNOTES

1. Extracted and abstracted from a monograph in preparation, "Fireflies of North America."
2. I thank the editors of this symposium for inviting me to participate; Jon Allen, Paul Choate, Howard Frank, and Tom Walker for helpful comments on the manuscript; Jack Schuster for translating the "Resumen"; Steve Lasley for technical assistance in computer analysis of data in Fig. 9; and Barbara Hollien for preparing the manuscript. Florida Agric. Exp. Sta. J. Series No. R-00410.
3. Author of this species Karl DeGeer originally spelled the epithet with one "n," an apparent, obvious misspelling of Pennsylvania (territory), and though both spellings are seen (see Fig. 2, pattern 12), I believe "pennsylvanica" is a legitimate emendation.
4. The term "sibling species" is used here for species that were not distinguished by previously used methods, and does not necessarily imply relatedness or evolutionary affinity.
5. Such studies are easily within the reach of student and class field-trip, given a little instruction and familiarity with local species, and can integrate insect natural history, basic electronics and computer driven and analyzed experimental protocols (see Lloyd & Wing 1983).

←

sharp rise at the last observation(?)]. Two other samples made at a different site had much smaller percentages of mimicking males, and the (a) profile (curve) is not apparent. (Vertical axis, proportion of males emitting mimicry pattern; horizontal axis, time, measured in Civil Twilight durations (creps) for geographic locality and date.)

6. Some evidence suggests that the possibility of polymorphism or other complex mechanisms should not be overlooked (Lloyd 1983: 152).

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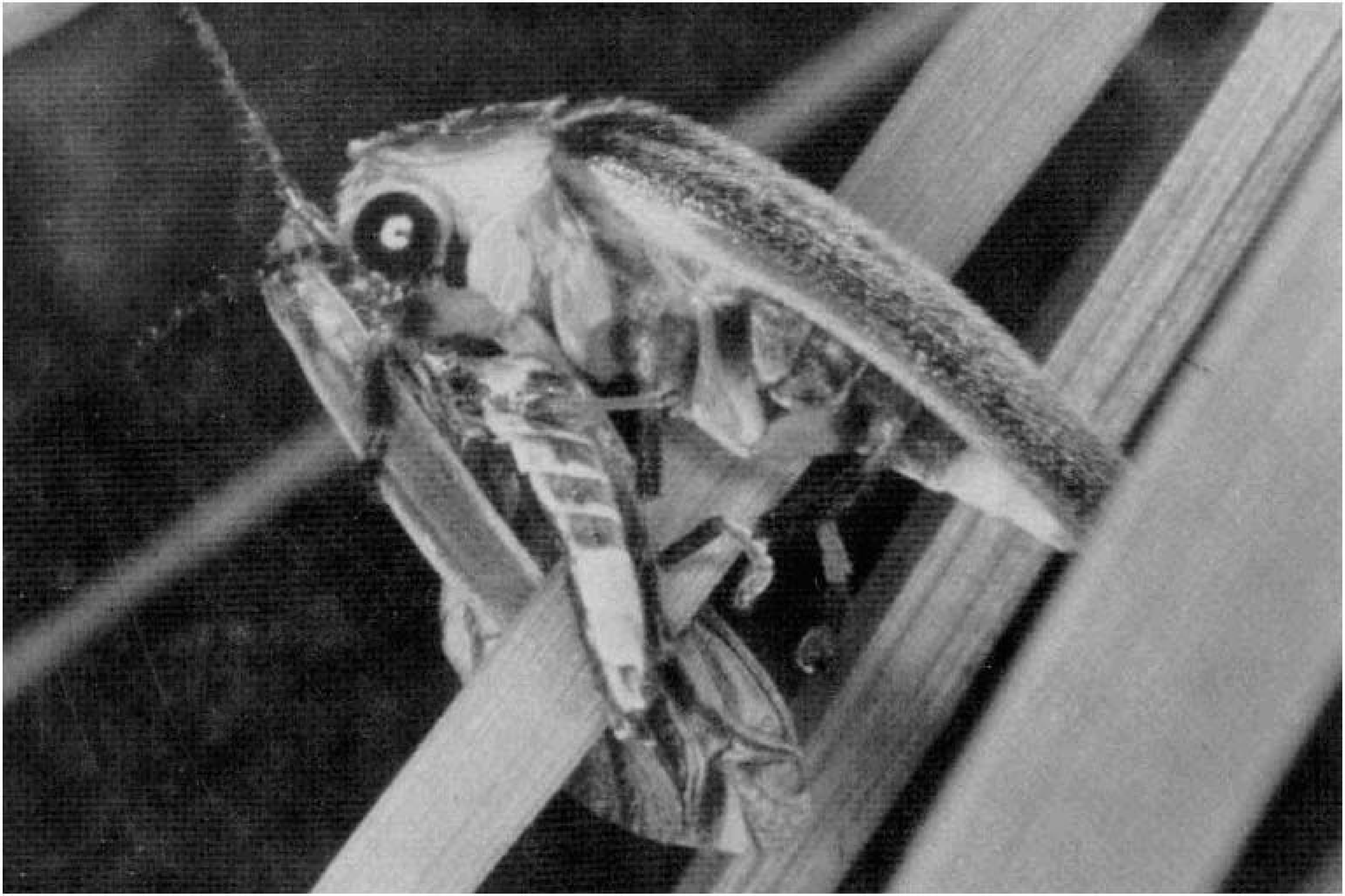

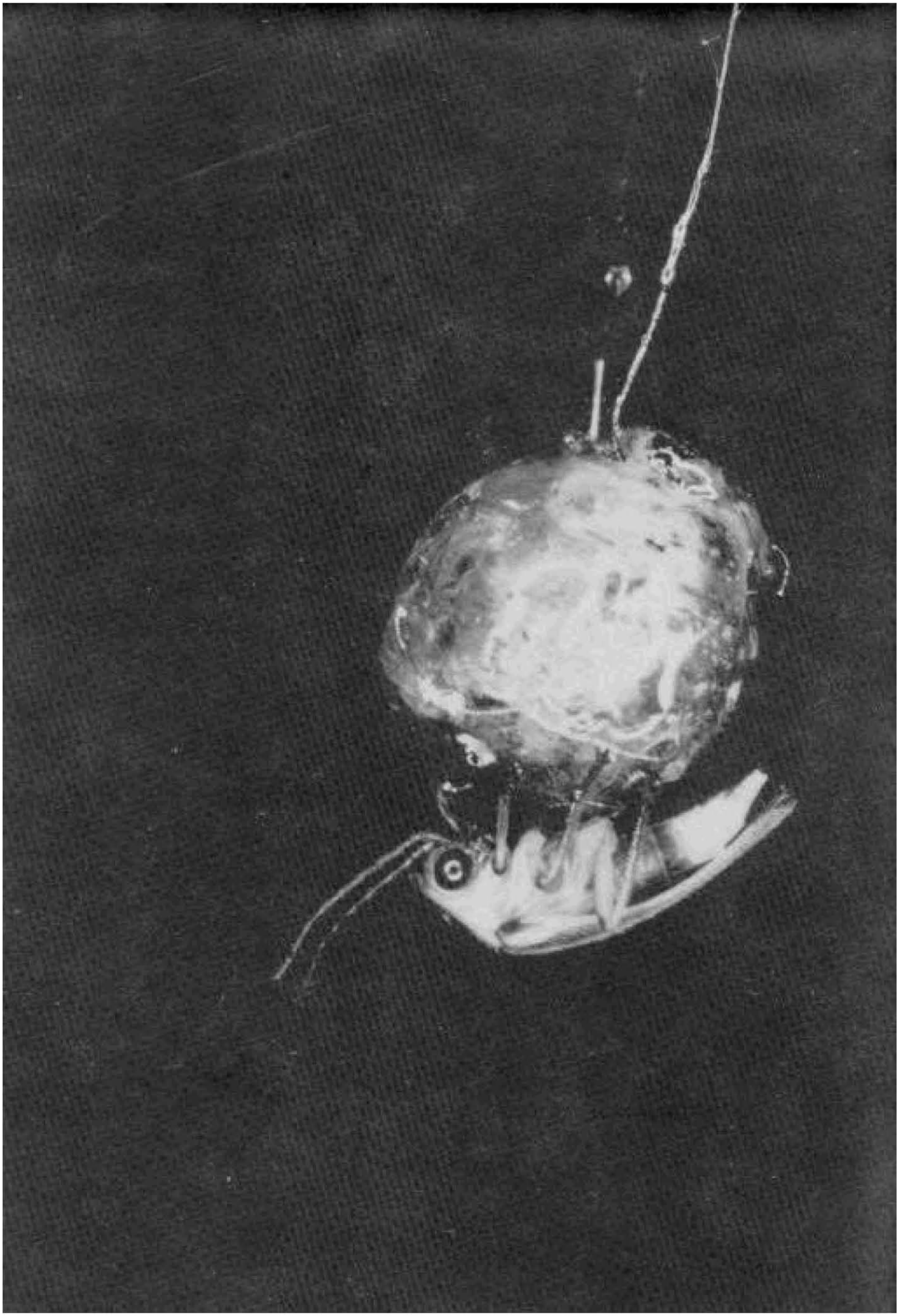

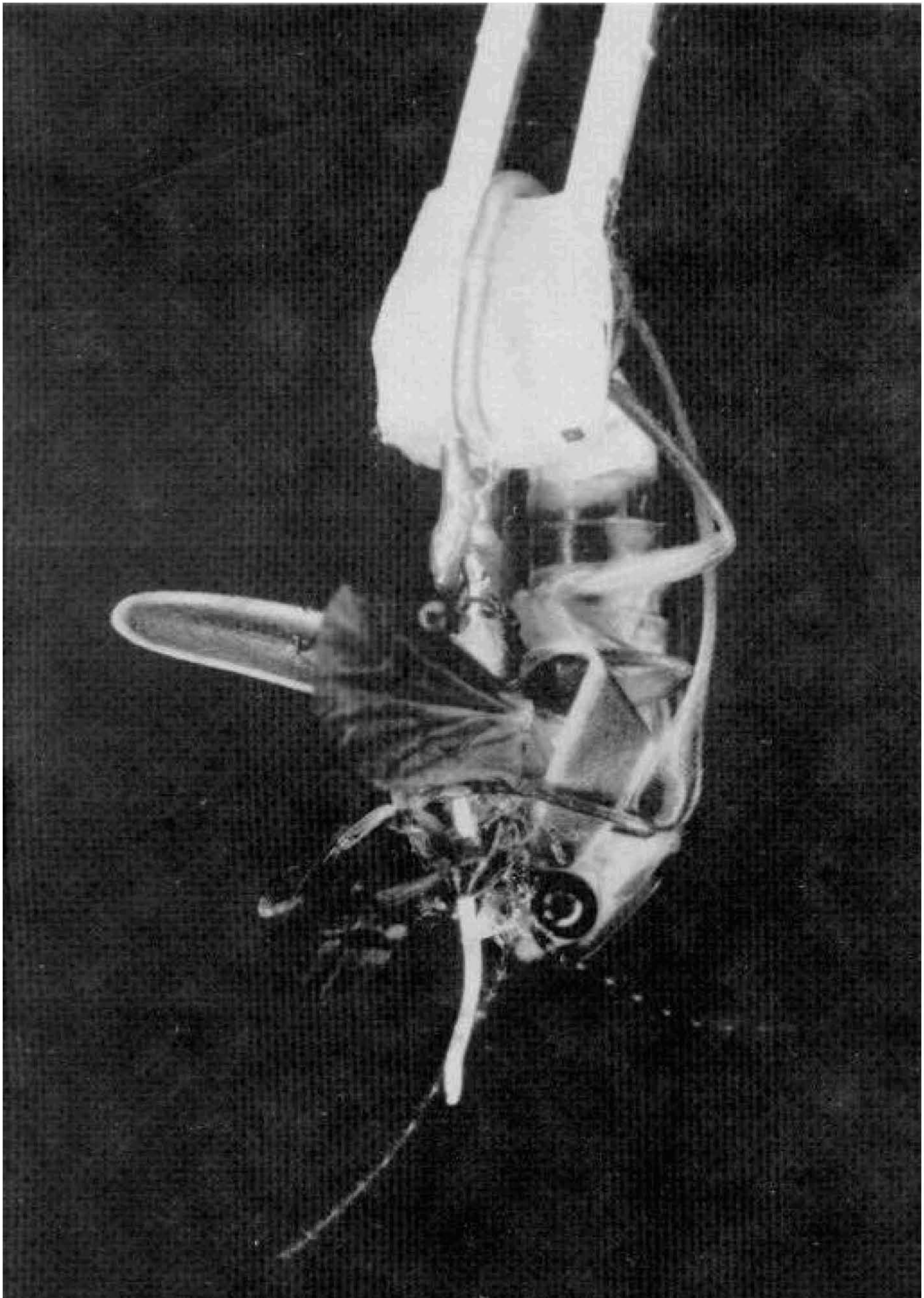

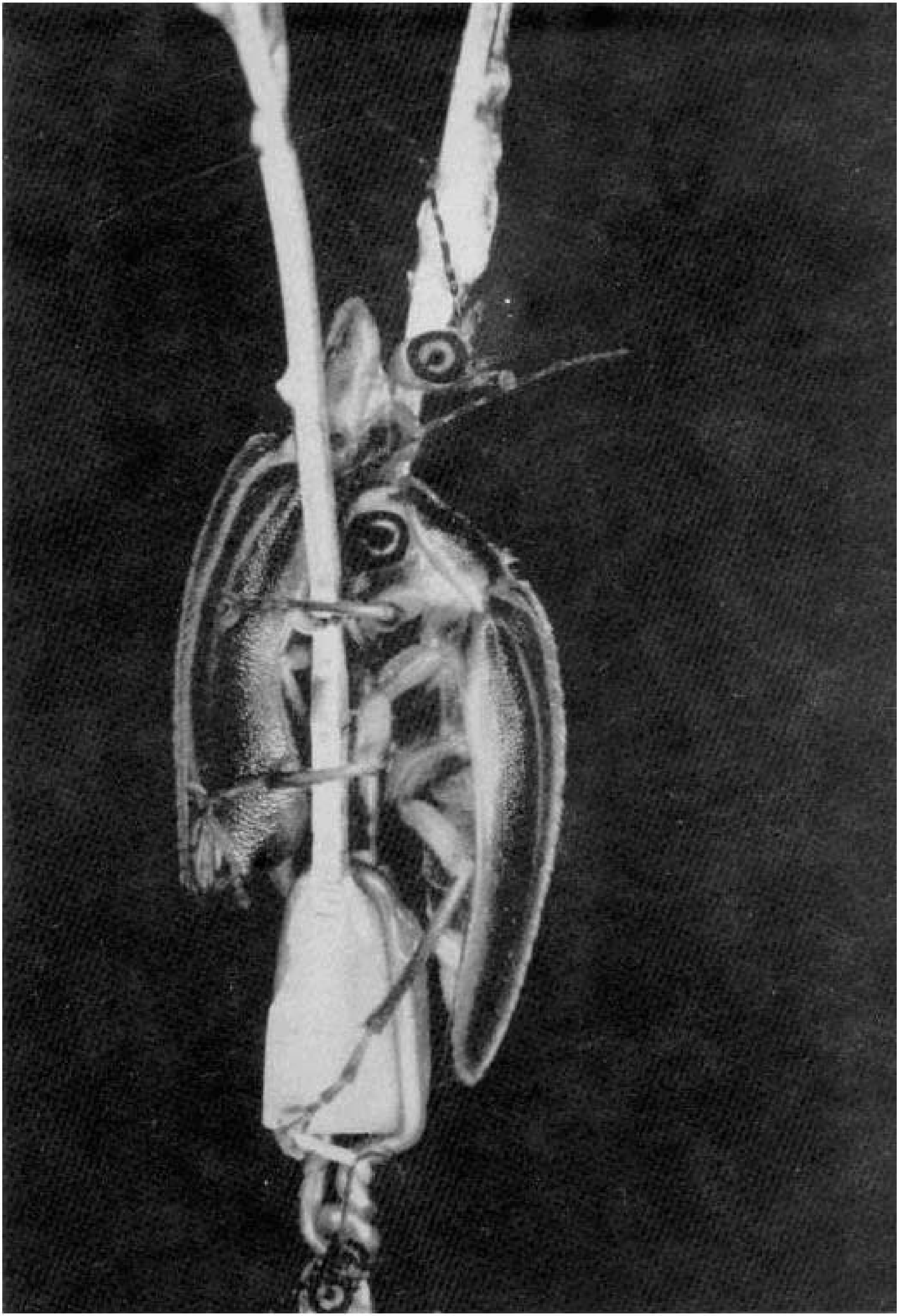

THE EVOLUTION OF MULTI ANTI-PREDATOR CHARACTERISTICS AS ILLUSTRATED BY TIGER BEETLES (COLEOPTERA: CICINDELIDAE)

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ABSTRACT

Tiger beetles as a family show a broad spectrum of morphological, behavioral and physiological mechanisms by which their enemies are deterred. This phenomenon of multiple anti-predator mechanisms is also evident within species and individuals. Although multiple anti-predator mechanisms have been widely recognized among most if not all insects groups, general models and broad theoretical studies of predator-prey interactions have largely ignored this confounding pattern. Based on experiments and observations of tiger beetles, six theories are presented that explain the evolution of multiple anti-predator characters: 1) several characters must operate in concert to minimize predation, 2) each anti-predator character is largely or uniquely targeted against one of several distinct foraging phases used by the predator, 3) increasingly potent lines of defense may be used as a predator overcomes the primary ones, 4) separate anti-predator characters are directed at each of several different types of predator, 5) an individual prey is the result of a phylogenetic or ontogenetic accumulation of anti-predator characters, and 6) competing or counterselective forces may override or supplement the effectiveness of some anti-predator characters.

RESUMEN

Las cicindelas, como familia, demuestran amplios espectros morfológicos, de comportamiento y de mecanismos fisiológicos por los cuales sus enemigos son disuadidos. Este fenómeno de mecanismo múltiples anti-depredador, también es evidente entre las especies y entre individuos. Aunque mecanismos múltiples anti-depredadores han sido reconocidos ampliamente entre la mayoría si no de todos los grupos de insectos, modelos generales y amplios estudios teoréticos sobre la interacción entre depredadores y su presa, han practicamente ignorado estos patrones desconcertantes. Basado en experimentos y observaciones de cincindelas, se presentan seis teorías que explican la evolución de caracteres múltiples anti-depredadores: 1) varios caracteres deben de operar al mismo tiempo para disminuir depredación, 2) cada carácter anti-depredador es mayormente, o es el blanco único, contra una de las distintas fases forageras usadas por el depredador, 3) aumentando la potencia de las lineas de defensa pudieran ser usadas a medida que el depredador sobrelleva las primarias, 4) caracteres separados anti-depredadores son divigidos hacia cada uno de los diferentes tipos de depredadoves, 5) una presa individual es el resultado de una acomulación filogenética o ontogenética de caracteres anti-depredadores, y 6) fuerzas competitivas o contra-selectivas pudieran sobrellevar o suplementar la efectividad de algunos caracteres anti-depredadores.

It is likely that the vast majority of prey species exhibit multiple anti-predator characters (Pearson 1985, Endler 1988). However, most general models and mathematical theories of predator-prey interactions assume, at least implicitly, that prey have only single anti-predator characters. This single character assumption has great potential for misleading and invalid results.

At least six theories predict the evolution of multiple anti-predator characteristics within a single individual prey: 1) *Some characters may function in concert to minimize predation.* For instance, aposematic coloration and distasteful compounds are frequently associated. A complication with this category is that each of these characters may not effectively deter predation by itself, and if they only or usually function in combination, they may technically be considered one character. Tiger beetles use body size, brightly-colored abdomens exposed in flight, and defense chemicals against robber fly predators. The per cent deterrence by these characters is greatest for larger beetles with bright orange abdomens and benzaldehyde released from their defense glands (Pearson 1985). As each of these characters is eliminated from models presented to wild robber flies, the deterrent effect is reduced. Some characters such as large body size are more important by themselves than other single characters, but the greatest protection is derived from a combination of all three together. Tropical forest tiger beetles use nocturnal communal roosts that apparently rely on gregariousness to enhance defense compound potency (Pearson and Anderson 1985).

2) *Some anti-predator characters may be largely or uniquely targeted against each of the distinct foraging phases of a predator (Endler 1986).* Predator behavior can be divided into distinct stages such as search, pursuit, capture and processing (Holling 1966). Among tiger beetles anti-predator characters like crypsis (Willis 1967) are primarily effective against the searching phase, rapid flight against the pursuit phase (Pearson 1985), chemical defense such as benzoyl cyanide (Pearson et al. 1988) against the capture phase, and sharp mandibles together with enzymes in extradigestive juices against the processing phase. Most individual tiger beetles have all these characters, and together they provide protection from either a single predator or several different predators through all these foraging phases.

3) *Increasingly potent lines of defense may be used as a predator overcomes the initial ones.* The primary lines of defense function regardless of whether the predator has been perceived by the prey, and they are likely to be energetically cheap (crypsis). The secondary lines are initiated by an encounter with a predator and are generally more energetically expensive (chemicals) (Robinson 1969, Rotheray 1986). Tiger beetle colors that may serve as camouflage (Schultz 1986) or in mimicry of stinging hymenopterans (Acorn 1988) are always present and take no extra energy to protect the beetle. Flight and pygidial chemicals are only used when the primary defenses have been breached.

4) *Prey encountering several different types of predators may need a separate anti-predator character targeted at each predator (Downes 1987).* This phenomenon compounds problems interpreting results from over-simplified experimental design as well as makes models of frequency-dependent predation extremely complex (Endler 1988). Tiger beetle adults use flight as an important mechanism to escape predation from insectivorous lizards. However the instant they fly up from the ground, they become susceptible to predation by robber flies, most of which can only take flying prey items (Lavigne 1972. Pearson 1985). Specific defense chemicals like benzaldehyde are targeted at robber flies. In addition, tiger beetles are the only beetles known to possess tympana, and many species are thus apparently able to hear and respond to ultrasounds produced by the wings of attacking robber flies (Spangler 1988). Tiger beetles respond to these sounds with an instant contraction of abdominal muscles that in flight disrupts aerodynamics and causes the beetle to fall to the ground where it is again susceptible to the reptilian ground predators.

Tiger beetle body size is also related to reduction of predation from various predator types. Small tiger beetles (<8 mm are more readily taken by insectivorous lizards and spiders than are larger beetles. Large tiger beetles (>15 mm), however, are more likely to be taken by insectivorous birds. Intermediate size tiger beetles are taken by robber flies (Pearson 1985). As with flight, body size that provides protection against one type of predator automatically makes the prey more susceptible to another type of predator.

5) *Selective forces on one stage of the life cycle or direct ancestors can be carried over into other stages or descendants (Endler 1986, Downes 1987), and the resultant individual may be a composite of anti-predator characters derived from predators on all life cycle stages and ancestors.* Larval tiger beetles have several highly specialized parasitoid enemies (Pearson 1988). Large sized larvae need considerably more time than do smaller congeners to sequester sufficient food to advance through their three instars and pupal stage (Pearson & Knisley 1985). They are thus exposed longer to mortality from parasitoids than are small larvae and are at an adaptive disadvantage. However, selection for large size in the larval stage is probably at least partially the result of adaptive advantages for large individuals as adults (Pearson & Knisley 1985).

Closely associated with this theory of an ontogenetic composite of multiple anti-predator characters is a theory that explains a composite individual based on historical factors (see Edwards & Reddy 1986), evolutionary lag times, and differential genetic lability of various characters. Among tiger beetle species, it is apparent that body color for camouflage and mimicry can evolve relatively quickly (Schultz 1986). Chemical defenses, however, evidently are extremely conservative and evolve very slowly (Pearson et al. 1988). These differential evolutionary rates could result in an accumulation of slowly evolving characters adapted for different predators over time. Some of these characters may have served as pre-adaptations against subsequent predator(s), and others may have taken on other functions such as in thermoregulation, competition or courtship.

6) *Additional factors may supplement selection for anti-predator characters or even be counter-selective (Pearson 1988).* This multiplicative or synergistic potential tremendously complicates a simple understanding of the function and evolution of multiple anti-predator characters and this complicating factor can impinge on all the preceding theories. Thermoregulation, competition, courtship and a host of additional factors can supplement the function of anti-predator characters or be counter selective (Endler 1987, Kingsolver & Wiernasz 1987). Among larval tiger beetles, for instance, the longer it takes to capture sufficient food to molt into the subsequent instars and finally imagoes, the greater the probability of mortality to parasitoids (Pearson & Knisley 1985).

Body size among endothermic and ectothermic insects can have a significant effect on heating and cooling rates (May 1976, Heinrich 1981). Body size may also help minimize interspecific competition (Pearson & Mury 1979, Pearson and Stemberger 1980, Pearson 1980, Pearson & Lederhouse 1987). If small body size to maximize thermoregulation and minimize competition overrides the disadvantages accrued by susceptibility to predation, small body size is likely to be selected regardless of the increased costs to predation. The ambiguities of character function involving several types of adaptation besides predation is likely a common phenomenon.

Considerations for investigating the role of multiple anti-predator characters:

1) *Determine all the potential predators and the relative risks to lifetime fitness by each predator (Endler 1988).*
2) *Identify the rate of susceptibility and mortality in all life cycle stages.*
3) *Validate the target of each anti-predator character or suite of characters.*
4) *Establish the reduction of successful predation produced by each character.*
5) *Determine alternative functions of the anti-predator characters such as courtship, thermoregulation, competition, etc.*

ENDNOTES

John S. Edwards and John A. Endler critically reviewed early drafts of this article. Thomás Zoebisch provided the Spanish translation of the abstract.

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ANTIPREDATOR MECHANISMS IN ARTHROPODS: A TWENTY YEAR LITERATURE SURVEY

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ABSTRACT

Sixteen ecological and entomological journals were surveyed from 1969-1989 for articles concerning defensive mechanisms in arthropods. Predators and prey are listed taxonomically by family, and grouped according to the specific defensive mechanism employed by the prey. A dichotomous categorization scheme is proposed which primarily reflects the hypothesized energetic costs of various antipredator mechanisms.

In total, 354 papers were examined involving 555 potential or real predator/prey interactions. It is concluded that certain defensive mechanisms are prevalent in particular taxonomic groups as indicated by the literature. Several predator/prey pairs occur together in interactions more frequently than would be expected by chance (up to 39 times in one case). Most pairs (71 percent) occur together ten or fewer times. Thirty-four pairs (nine percent) occurred only once. It is questionable whether this phenomenon is an accurate representation of the natural distribution of defensive mechanisms in arthropods because of the potential and real bias involved in the investigative process.

Many studies assume but do not demonstrate the efficacy of the alleged defensive mechanism. Of 555 real or potential interactions, a defensive function was demonstrated 354 times (64 percent). No defensive function was demonstrated 201 times (36 percent). It is suggested that whenever possible, future investigations incorporate tests of the hypothesized defensive function against sympatric, and therefore ecologically relevant predators.

RESUMEN

Se hizo una encuesta de 16 jornales ecológicos y entomológicos publicados entre 1969-1989 sobre artículos tratando con mecanismos de defensa de artrópodos. Se listan taxonomicamente y por familia, depredadores y presa de acuerdo a los mecanismos específicos de defensa empleados por la presa. Se propone una categorización dicótoma que primariamente refleja la hipótesis de los costos energéticos de los varios mecanismos antidepredadores.

Se examinaron 354 artículos en total, involucrando la interacción de 555 depredadors/ presa real o potencial. Se concluye que ciertos mecanismos de defensa son prevalentes en grupos taxonómicos particulares como es indicado por la literatura. La interacción de varias parejas de depredadores/presa ocurren más frequentemente que se pudiera esperar al azar (hasta 39 veces en un caso). La mayoría de las parejas (71%) ocurren juntas diez o menos veces. Treinta y cuatro parejas (9%) ocurrieron solo una vez. Es dudoso que este fenómeno sea una representación precisa de la distribución natural de mecanismo de defensa en artrópodos por el potencial verdadero o posible de prejuicios envueltos en el proceso investigativo.

Muchos estudios presumen pero no demuestran, la eficacia de los alegados mecanismos defensivos. De 555 interacciones reales o potenciales, se demostró una función defensiva 354 veces (64%). No se demostró ninguna función defensiva 201 veces (36%). Se sugiere que cuando sea posible, las investigaciones futuras incorporen pruebas sobre la hipótesis de la función defensiva contra simpátricos, y de aquí, contra los depredadores ecologicamente relevantes.

As biologists, and as scientists in general, we accumulate voluminous quantities of information via the inductive process in an attempt to explain natural phenomena. Inductive observation is the first step in the investigative process which enables us to deductively generate testable hypotheses. It occasionally is necessary to summarize and examine the accumulated data for patterns and formulate testable hypotheses which guide research toward understanding any underlying causal mechanisms. In addition, it often is useful to have ready access to review articles of a particular discipline as they can alleviate, at least in part, the time consuming (and sometimes expensive) task of exhaustive literature searches.

It has long been recognized that many organisms defend themselves against their natural enemies. It also is abundantly clear that not all organisms defend themselves in the same fashion (see Robinson 1969, Eisner 1970, Blum 1981, Matthews 1982, Herman 1984 for reviews on defensive mechanisms in certain arthropod taxa). More recently, it has been noted that even within a particular individual or a particular species, multiple defensive mechanisms are used (Pearson 1989).

In studying these defensive mechanisms, there is a tendency to focus on those which are either unique, particularly interesting to the investigator, or readily studied, perhaps because of logistical ease. This real or potential bias in the investigative process may either conceal or artificially create patterns. The task in the present paper was to examine some of the major ecological and entomological journals over the past twenty years in an attempt to detect such bias. It is hoped that the exposition of these imbalances will redirect future research into those areas where minimal information exists, to aid in evaluating the phylogeny of arthropod antipredator mechanisms. In addition, the number of papers which actually demonstrated a defensive function for a given mechanism was quantified.

MATERIALS AND METHODS

Sixteen ecological and entomological journals were examined for articles concerning antipredator mechanisms in arthropods (Table 1). Although this is a relatively small sample of the literature, these journals were selected because their format frequently includes articles on defensive mechanisms. The original intention was to focus primarily on insects, hence crustacean and arachnid journals were excluded. Articles appearing in less taxonomically specialized journals, dealing with non-insectan arthropods, were included as discovered. English articles were surveyed almost exclusively because of time constraints imposed by translation. The journal volumes from 1969-1989 were surveyed according to their availability at the University of South Florida library. The years prior to 1969 were excluded as several reviews from this time period already exist in the literature (see Blum 1981, Eisner 1970, Hermann 1984, Matthews 1982, Rettenmeyer 1970, Robinson 1969). Short communications, letters to the editor, and scientific notes were excluded as many of these articles did not include detailed descriptions of the defensive mechanism or its function. Only feature articles were surveyed. The article titles were examined in each journal's annual table of contents, whenever available, for one or more of the following key words: defensive mechanism; antipredator mechanism; predator-prey interaction; mimicry; crypsis; chemical defense; defensive secretion; aposematic coloration; escape behavior; biting; stinging; defensive posture; dilution; predator satiation; tending behavior; predation; mobbing; feigning death; avoidance; and repellent. In addition, titles of suspected antipredator studies were noted. Abstracts then were scanned to confirm the subject matter of the article, identify the prey, predator(s), and the specific defensive mechanism(s) employed by the prey. If the abstract failed to provide this information, the remainder of the article was read. A "general" predator category was devised for articles which neither demonstrated nor hypothesized the defensive efficacy of the investigated mechanism against a specific predator taxon.

Only articles dealing with classic predator/prey interactions were included. Interactions of this sort typically are characterized by 1) the predator actually or potentially killing and consuming the prey, 2) the predator being large relative to the prey, and 3)

TABLE 1. JOURNALS SURVEYED FOR ANTIPREDATOR MECHANISMS.

Journal Title	Years and Volumes
American Naturalist	1969-1989: 103-133
Animal Behaviour	1969-1989: 17-38(2)
Annals of the Entomological Society of America	1969-1989: 62-82
Annual Review of Entomology	1969-1989: 14-34
Behavioral Ecology and Sociobiology	1976-1989: 1-25(1)
Canadian Entomologist	1969-1989: 101-121(8)
Ecological Entomology	1976-1989: 1-14(3)
Ecology	1969-1989: 50-70(4)
Ethology	1986-1989: 71-81
Florida Entomologist	1969-1989: 52-72(2)
Journal of Animal Ecology	1969-1989: 38-58(2)
Journal of Chemical Ecology	1975-1989: 1-15(9)
Oecologia	1969-1989: 2-8(2)
Oikos	1969-1989: 20-55(3)
Psyche	1976-1988: 83-95
Zeitschrift fur Tierpsychologie	1974-1985: 34-70

the predator consuming all or most of the prey individual. The following types of articles were excluded from the study: grazing/partial predation; food site defense/territoriality; predatory behavior if prey behavior was excluded; intraspecific interactions; predator/prey interactions with simulated prey; applied entomology using predators as biological control agents; methodological articles; general organismal biology unless the title included mention of predator/prey interactions; phylogenetic articles unless antipredator characteristics were used in the phylogenetic analysis; defensive mechanisms against parasites; alarm pheromone articles that did not demonstrate a defensive function of the chemical, and theoretical/modeling articles.

The following information was recorded for each article whenever provided: 1) scientific name of predator and prey species; 2) the defensive mechanism(s) employed by the prey: 3) the taxonomic position of the predator and prey. This includes class, order, family, genus, and species, whenever available; 4) the journal name, year, volume, page numbers, author(s), and title.

In general, the taxonomy presented in the current paper is that supplied by the author(s) in each article. It often was necessary, however, to use other sources because the author(s) neglected to include taxonomic information in the article. For arthropods, Borror, DeLong, and Triplehorn (1976) was the primary reference, supplemented with Borror & White 1970, Levi & Levi (1987), Barnes (1974), Schultz (1969), and Edmondson (1959). Burt & Grossenheider (1976) was used for mammals; Robbins et al. (1983) for birds; Conant (1975) for reptiles and amphibians, and Wainwright (1976), Moyle & Cech (1988), and Robbins & Ray (1986) for fish. It occasionally was necessary to use a taxonomic synonym for the author's nomenclature to prevent redundant categories. For example, several British authors use the ordinal name Heteroptera which was replaced with Hemiptera. Although other taxonomic schemes may be more current and perhaps more accurate, these references were chosen for logistic reasons. It was not the intent of this paper to dispute the phylogenetic validity of any taxon.

After the list of articles was compiled, the following information was quantified: 1) number of citations occurring in each defensive mechanism category; 2) the taxonomic distribution of prey within each defensive category at the ordinal level. This reflects the percent contribution of a given order to the number of articles dealing with a specific defensive mechanism; 3) the frequency of occurrence of specific predator/prey pairs. This was an attempt to determine if a given prey taxon consistently defends itself against a certain predator taxon, as indicated by the literature; and 4) if a defensive function actually was demonstrated, and if so, the taxonomic position of the predator against which it was effective.

The following defensive categories were recognized, most of which are well established in the literature: 1) chemical (e.g. Blum 1981, Eisner 1970, Hermann 1984); this includes a broad diversity of both specialized exocrine gland secretions and other "systemic" defenses such as reflexive bleeding, sequestration of toxic or noxious chemicals, etc. 2) crypsis (e.g. Bishop 1972, Erichsen et al. 1980, Heinrich 1979, Lees & Creed 1975, Robinson 1969)—this includes cryptic coloration, mimicking some portion of the environment, and behavioral crypsis whereby the organism remains in a concealed region of the habitat; 3) mimicry (e.g. Brower 1988, Doyen 1974, Hetz & Slobodchikoff 1988, Pough 1988, RettenmeYer 1970)—both Batesian and Mullerian; 4) escape (e.g. Krasne & Woodsmall 1969, Nentwig 1982, Roitberg et al. 1979)—this involves detection of the predator by the prey and usually rapid movement away from the predator; 5) biting (e.g. Hermann 1984); 6) stinging (e.g. Hermann 1984); 7) mobbing (e.g. Wittmann 1985)—this involves physical contact or intimidation displays by a group of prey; 8) fighting—this includes all other physical contact with the predator such as kicking, wing beating, shoving, pinching, entangling (e.g. Bildstein et al. 1989, Mills & Partida 1976, Nutting & Spangler 1969), etc. Although this category is not well established in the literature, it was devised to include an array of defensive mechanisms which may have similar energetic requirements (see discussion below); 9) posture/size (e.g. Jakobsen & Johnsen 1988, Kevan et al. 1983)—this involves predator avoidance of prey because of behavioral posturing (including phragmosis, e.g. Wheeler and Holldobler 1985) or large size; 10) dilution/satiation (e.g. Gillett et al. 1979, Heller & Milinski 1979, Milinski 1979, 1984)—the predator is either confused or satiated by large numbers of individual prey, thereby reducing the probability that any one individual is eaten (safety in numbers); 11) flash/warning coloration (e.g. Coppinger 1970, Malcolm 1986)—the predator is either confused, startled, or conditioned to avoid prey because of bright coloration or patterns; 12) misdirected attack (e.g. Robinson 1969)—the predator is confused by the morphology of the prey and attacks less vulnerable regions of the body; 13) acoustic (e.g. Bauer 1976, Buchler et al. 1981, Sandow & Bailey 1978)—the prey produces a loud noise such as stridulation which startles the predator; 14) feigning death (thanatosis) (e.g. Capinera 1976, Howard et al. 1982, Otto & Sjostrom 1983); 15) mutualism (e.g. Bristow 1984, Burns 1973, Cushman & Whitham 1989, Fritz 1984)—this involves defense of prey by a mutualistic symbiont; and 16) armor (e.g. Klein & Burkholder 1983, Otto & Sjostrom 1983, Pecarsky 1987, Silgerglied & Aiello 1976)—including all anatomical weaponry such as spines, thick cuticle, horns, etc. It should be noted that certain categories are not always mutually exclusive. Stinging and biting are usually accompanied by venom injection, aposematic coloration often is coupled with noxious or toxic chemicals, flash coloration with crypsis, and armor is sometimes associated with fighting. Hence a single interaction may appear in multiple defensive categories. Biting, stinging, mobbing, and fighting were grouped together for statistical analyses as they are all mechanical defenses (at least in part) which involve active physical contact with the predator and approach by the prey.

RESULTS

A total of 354 articles was recorded with 555 real or potential interactions (Appendix 1). The number of interactions exceeds the number of articles because 1) several articles dealt with more than one predator/prey interaction and 2) some articles investigated multiple antipredator mechanisms in a given prey. Because of space limitation, the species list of predator and prey is not presented here. This list is available upon request to the author, and is arranged in an alphabetized order of journals with articles listed in chronological sequence within journals. Appendix 1 lists the predator and prey of each interaction according to family (when available) in each of the defensive categories delineated above.

Many articles appear in more than one defensive category. Combining all categories results in 452 articles dealing with specific antipredator mechanisms. Chemical defense was by far the most prevalent (208 or 46 percent of all cases), exceeding other mechanisms by at least a factor of five (Fig. 1). This is attributed at least in part to the Journal of Chemical Ecology dealing exclusively with chemical defense (109 citations). Coleopterans, followed by hymenopterans and lepidopterans, are the most prevalent taxa in the chemical defense category (Fig. 2), exceeding all other arthropod orders by at least a factor of two.

Fighting (via biting, stinging, and all other modes) is the second most abundant mechanism. Hymenopterans dominate this category, exceeding all others by at least a factor of four (Fig. 2). Lepidopterans dominate the third most abundant category, crypsis. The fourth category, escape, is more evenly distributed among the orders, with hymenopterans, homopterans, and coleopterans dominating. Mimicry and flash/warning coloration are nearly equally represented in the literature and constitute the fifth and sixth most abundant categories respectively (Fig. 3). The taxonomic distribution of the remaining six categories is presented in Fig. 3 and 4.

The most prevalent predator/prey interaction at the ordinal level is between hymenopteran predators and hymenopteran prey, representing 39 out of 364 predator/prey pairs (11 percent). Lepidopteran prey are paired with passeriform predators 24 times (7 percent). The third most prevalent interaction is between coleopteran prey and hymenopteran predators, comprising 18 interactions (5 percent). All other predator/prey pairs occur together less than 15 times, with 34 interactions represented only once (Table 2). This distribution of occurrences of predator/prey order-pairs differs significantly from a Poisson distribution (χ^2, 14 df = 180.25; $p<0.005$), indicating that pairs are non-randomly represented in the literature. Certain pairs occur together more frequently than expected by chance, while others are under represented.

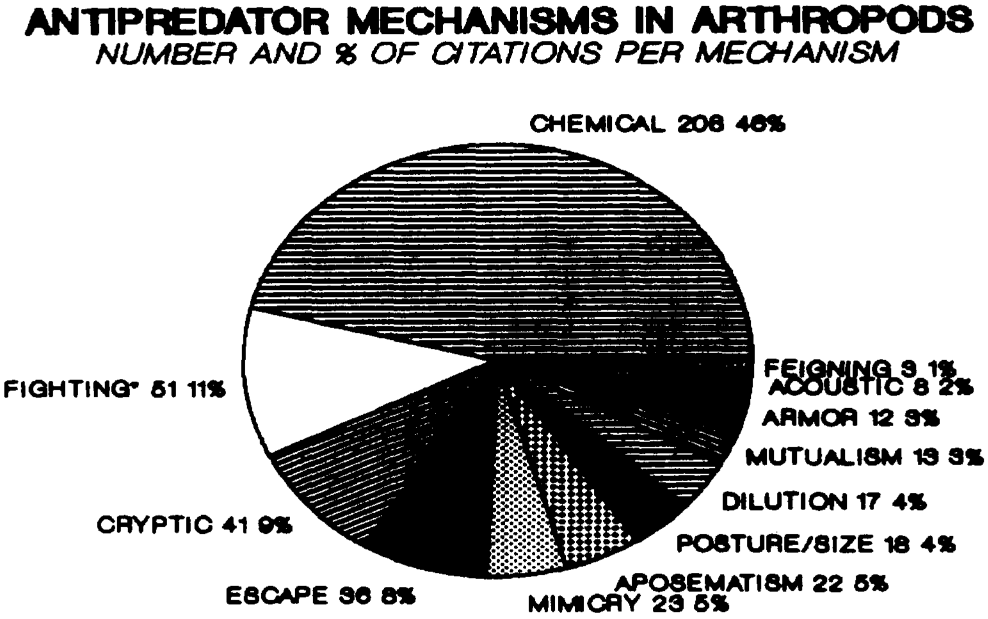
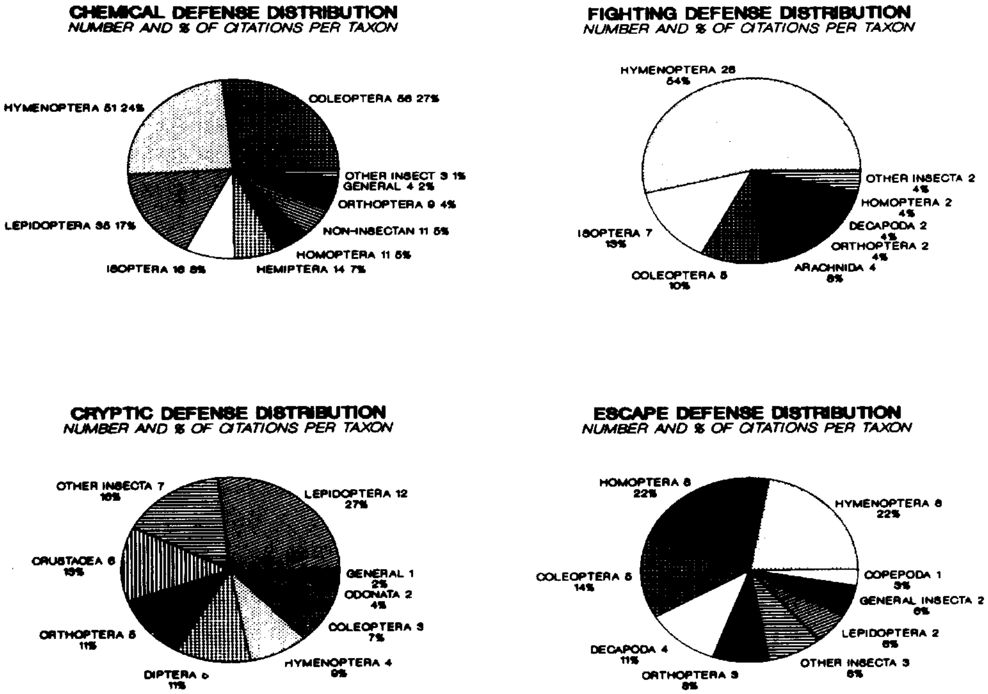


Fig. 1. Distribution of references concerning antipredator mechanisms in arthropods. * Fighting is a combination of stinging, biting, and all other modes of physical contact e.g. kicking, wing beating, pinching, etc.



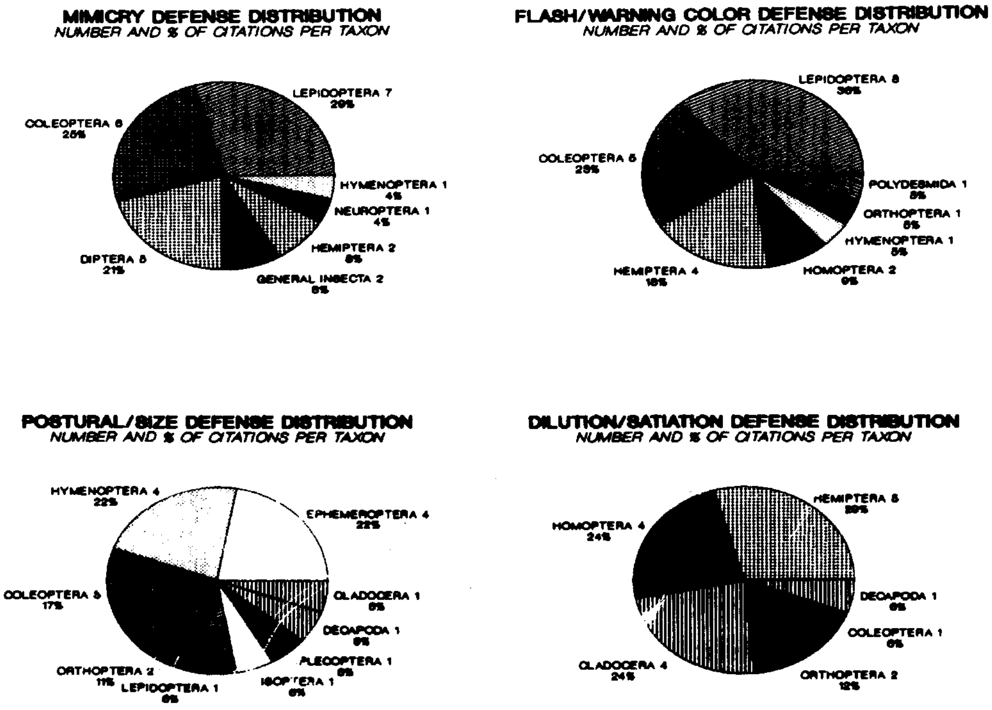
CHEMICAL DEFENSE DISTRIBUTION
NUMBER AND % OF CITATIONS PER TAXON

FIGHTING DEFENSE DISTRIBUTION
NUMBER AND % OF CITATIONS PER TAXON

CRYPTIC DEFENSE DISTRIBUTION
NUMBER AND % OF CITATIONS PER TAXON

ESCAPE DEFENSE DISTRIBUTION
NUMBER AND % OF CITATIONS PER TAXON

Fig. 2. Distribution of chemical, fighting, cryptic, and escape defensive mechanisms among arthropod orders.



MIMICRY DEFENSE DISTRIBUTION
NUMBER AND % OF CITATIONS PER TAXON

FLASH/WARNING COLOR DEFENSE DISTRIBUTION
NUMBER AND % OF CITATIONS PER TAXON

POSTURAL/SIZE DEFENSE DISTRIBUTION
NUMBER AND % OF CITATIONS PER TAXON

DILUTION/SATIATION DEFENSE DISTRIBUTION
NUMBER AND % OF CITATIONS PER TAXON

Fig. 3. Distribution of mimicry, flash/warning coloration, postural/size, and dilution/satiation defensive mechanisms among arthropod orders.

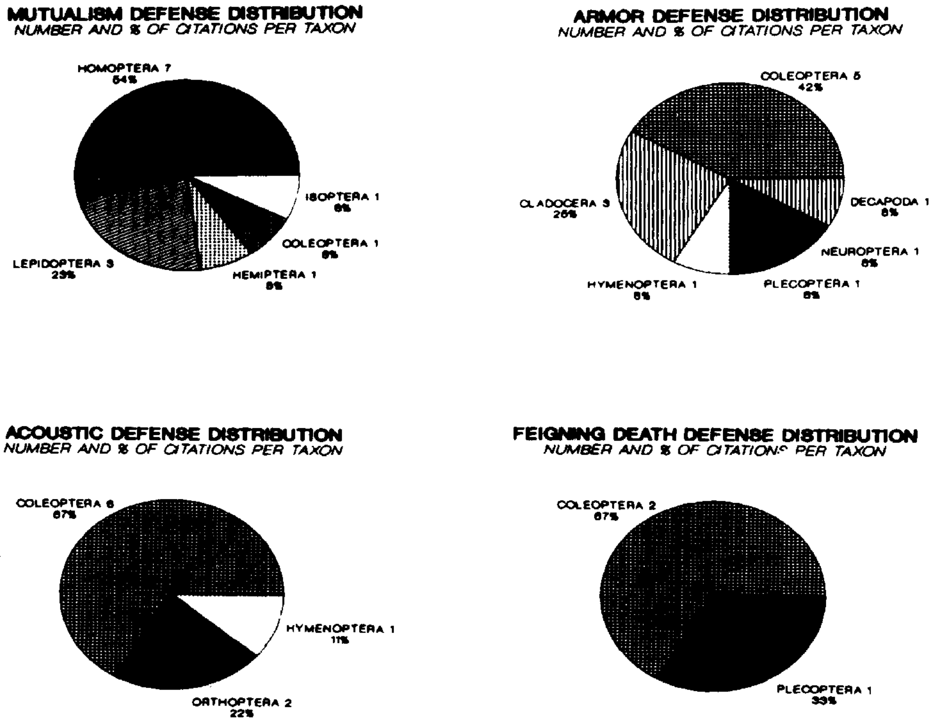


Fig. 4. Distribution of mutualism, armor, acoustic, and feigning death defensive mechanisms among arthropod orders.

A defensive function of the alleged antipredator mechanism was demonstrated in 364 cases (66 percent). In most articles it was not possible to determine if the predator was sympatric with the prey (and therefore ecologically relevant) (see Witz & Mushinsky 1989). The efficacy of the alleged defensive mechanism was not demonstrated in 191 cases (34 percent). Of this 34 percent, the effectiveness of the mechanism against specific predator taxa was hypothesized, but not demonstrated in 81 cases (15 percent); the defensive function was neither demonstrated nor hypothesized to be effective against specific predator groups in 120 cases (21 percent).

DISCUSSION

Although the prevalence of chemical defense in the literature is biased by the predominance of such articles in the Journal of Chemical Ecology (109 citations), this category constitutes the majority of antipredator mechanisms investigated, even with that journal removed from the analysis (99 citations). Several prolific authors further contribute to this imbalance, publishing multiple papers on chemical defensive mechanisms. Two authors combined were involved in 20 percent of the chemi.cal defense articles. Many papers dealt almost exclusively with analytical chemistry.

It would be interesting to attempt to control for multiple authorship and journal imbalance statistically. Comparing this corrected literature representation of antipredator mechanisms with an estimated, geographically-corrected number of species per order may reveal a more accurate picture of the true distribution of defensive mechanism categories among arthropods. It is questionable however, whether sampling the literature will ever truly reflect the natural distribution of a particular phenomenon. This is perhaps particularly true of arthropod defensive mechanisms, given the high diversity of the phylum, the myriad antipredator categories, and the often cryptic na-

TABLE 2. ORDERS PAIRED IN PREDATOR/PREY INTERACTIONS.

# Occurrences	# Pairs	# Interactions
1	34	34 (09%)
2	17	34 (09%)
3	10	30 (08%)
4	11	44 (12%)
5	6	30 (08%)
6	7	42 (12%)
7	1	7 (02%)
9	3	27 (07%)
10	1	10 (03%)
11	1	11 (03%)
14	1	14 (04%)
18	1	18 (05%)
24	1	24 (07%)
39	1	39 (11%)

ture of certain species. I believe that summarizing the literature, at the very least, can reveal areas where a paucity of information exists and perhaps stimulate subsequent investigation.

The fact that 34 percent of the studies examined in the present review did not demonstrate a defensive function may be attributed to several factors: 1) it is not always logistically feasible to do so; 2) it is possible that the defensive function was demonstrated in previous studies which were not discussed in the text; 3) some authors may choose to postpone demonstration of the defensive function for future publications; 4) the natural history of sympatric predators may be unknown or unfamiliar to the authors; 5) because previous work on similar species demonstrated the defensive efficacy of a particular mechanism, the authors assume a similar function in the species which they are investigating. There are, no doubt, other reasons which have been overlooked. It is difficult to determine which, if any, of these reasons are prevalent. Of the above reasons, I believe number 5) to be the most critical. Reason 1) and 4) are perhaps the most difficult to circumvent. It is suggested, however, that reasons 2) and 3) often can be avoided by a brief mention of previous or expected investigations which demonstrated or will demonstrate the defensive function of the mechanism under investigation. Finally, reason 5) can be avoided by refusing to assume defensive efficacy and endeavoring to incorporate tests of the alleged antipredator mechanism against ecologically relevant predators.

It is suggested that the energetic requirements of the aforementioned defensive categories may differ. It would be interesting to measure the energy required for a prey to defend itself on a per predation event basis. Chemically defended prey for example, often need to replenish their chemical arsenal following an attempted predation event. Conversely, cryptic coloration is a permanent, non-depletable mechanism which may require energy only to find the appropriate habitat. The following dichotomous categorization for antipredator mechanisms is therefore proposed: passive defenses are those relatively energetically inexpensive mechanisms that reduce the probability of an encounter between prey and predator. Included in this category are cryptic, dilution/satiation, flash/warning coloration, and mimicry antipredator mechanisms; active defenses are those energetically expensive mechanisms which increase the probability of surviving a predator attack. Included in this category are chemical, fighting, acoustic, escape, armor, and postural/size antipredator mechanisms. It is suggested that when possible, future investigations might incorporate estimates of the energetics involved in defensive mechanisms to aid in understanding the relative importance of predation pressure in the evolution of antipredator mechanisms.

APPENDIX

CHEMICAL DEFENSIVE MECHANISMS

REF.NO.	PREY	PREDATOR
296.	TENEBRIONIDAE	RODENTIA
351.	ACRIDIDAE	VERTEBRATA: GENERAL
338.	CHRYSOMELIDAE	FORMICIDAE
144.	FORMICIDAE	MAMMALIA: GENERAL
344.	CARABIDAE	MURIDAE
327.	TENEBRIONIDAE	MAMMALIA: GENERAL
339.	CHRYSOMELIDAE	FORMICIDAE
14.	GYRINIDAE	SALMONIDAE, CENTRARCHIDAE
179.	STAPHYLINIDAE	TERMITIDAE
15.	PTERONARCIDAE PELTOPERLIDAE	FORMICIDAE
217.	DYTISCIDAE	CYPRINIDAE
172.	REDUVIIDAE	GENERAL
366.	TERMITIDAE	FORMICIDAE
326.	TENEBRIONIDAE	GENERAL
4.	COREIDAE	GENERAL
17.	ACRIDIDAE	HOMINIDAE
363.	MEMBRACIDAE	COCCINELLIDAE REDUVIIDAE SYRPHIDAE
145.	FORMICIDAE	GENERAL
364.	MEMBRACIDAE	IGUANIDAE
345.	APIDAE	FORMICIDAE
223.	APHIDIDAE	INSECTA: 41 SPP.
63.	APIDAE	HOMINIDAE
355.	APHIDIDAE	GENERAL
230.	GYRINIDAE	GENERAL
187.	FORMICIDAE	FORMICIDAE
62.	APIDAE	GENERAL
295.	HETERONEMIIDAE	CRICETIDAE FORMICIDAE CORVIDAE
65.	APIDAE	GENERAL: SIMULATED
349.	NOTODONTIDAE	BRACONIDAE
180.	CUCUJIDAE	ANTHOCORIDAE CUCUJIDAE
146.	FORMICIDAE	HOMINIDAE
352.	ACRIDIDAE	CRICETIDAE
303.	HYMENOPTERA: GENERAL	VERTEBRATA: GENERAL
155.	TENEBRIONIDAE	GENERAL
194.	PENTATOMIDAE	FORMICIDAE GENERAL
190.	CHRYSOPIDAE	FORMICIDAE
188.	HYMENOPTERA: GENERAL	FORMICIDAE VESPIDAE HALICTIDAE APIDAE
304.	HYMENOPTERA: GENERAL	VERTEBRATA: GENERAL
348.	ELMIDAE	OSTEICTHYES: 10 SPP., TRIONYCHIDAE
266.	RHOPALIDAE	BUFONIDAE CORVIDAE
141.	VESPIDAE	FORMICIDAE
22.	APIDAE FORMICIDAE TERMITIDAE	GENERAL
1.	VESPIDAE	HOMINIDAE GENERAL
156.	FORMICIDAE TENEBRIONIDAE	GENERAL
285.	INSECTA: GENERAL	GENERAL
238.	ARTHROPODA: GENERAL	GENERAL
259.	TERMITIDAE	GENERAL
82.	COLEOPTERA: GENERAL	GENERAL
24.	ARTHROPODA: GENERAL	GENERAL
301.	ARCTIIDAE NOCTUIDAE	AVES: GENERAL
242.	CICINDELIDAE	GENERAL
3.	HEMIPTERA: GENERAL	GENERAL
100.	TERMITIDAE	FORMICIDAE
358.	FORMICIDAE	FORMICIDAE
332.	THERIDIIDAE	CRICETIDAE
209.	FORMICIDAE	FORMICIDAE
163.	VESPIDAE	HOMINIDAE, SIMULATED
70.	TENEBRIONIDAE	CRICETIDAE FORMICIDAE
201.	APHIDIDAE	ARANEIDAE PARIDAE
73.	SATURNIIDAE	GENERAL: SIMULATED
320.	NEODIPRIONIDAE	PENTATOMIDAE
341.	POLYDESMIDA	GENERAL
87.	TENEBRIONIDAE	GENERAL
362.	MEMBRACIDAE	IGUANIDAE
117.	APIDAE	APIDAE
281.	CTENUCHIDAE	AVES (6 SPP) LACERTIDAE
29.	NYMPHALIDAE	CORVIDAE
331.	DANAIDAE	ARANEIDAE
135.	INSECTA 22 SPP.	FORMICIDAE
241.	CICINDELIDAE	ASILIDAE LANIIDAE ACCIPITRIDAE TEIIDAE IGUANIDAE
77.	PAPILIONIDAE	FORMICIDAE SALTICIDAE
340.	FORMICIDAE	COLUBRIDAE
175.	COPEPODA: GENERAL CLADOCERA: GENERAL	SALMONIDAE CENTRARCHIDAE PERCIDAE
139.	LEPIDOPTERA: GENERAL	PARIDAE
290.	CULICIDAE	NOTONECTIDAE
249.	LASIOCAMPIDAE	FORMICIDAE
284.	COREIDAE PYRRHOCORIDAE PENTATOMIDAE	EMBERIZIDAE
224.	VESPIDAE APIDAE	GENERAL: SIMULATED
92.	FORMICIDAE	GENERAL
219.	GYRINIDAE	AMPHIBIA: GENERAL AVES: GENERAL OSTEICTHYES: GENERAL
283.	STAPHYLINIDAE	GENERAL
218.	DYTISCIDAE GYRINIDAE	CYPRINIDAE
169.	GEOPHILIDAE	FORMICIDAE
90.	XYSTODESMIDAE	FORMICIDAE
346.	FORMICIDAE	GENERAL
101.	COSMETIDAE GONYLEPTIDAE	FORMICIDAE: GENERAL
233.	APHIDIDAE	GENERAL
182.	STAPHYLINIDAE	FORMICIDAE: GENERAL HEMIPTERA: GENERAL ARANEAE: GENERAL
260.	TERMITIDAE	FORMICIDAE
158.	LYGAEIDAE	CORVIDAE
91.	LIMNEPHILIDAE	FORMICIDAE
25.	CHRYSOMELIDAE	FORMICIDAE
207.	BLATTIDAE	HOMINIDAE
76.	CHRYSOMELIDAE	AVES: GENERAL
342.	NOTODONTIDAE	GENERAL
258.	ISOPTERA: GENERAL	GENERAL
314.	CHRYSOMELIDAE	FORMICIDAE
231.	DYTISCIDAE	AMPHIBIA: GENERAL OSTEICTHYES: GENERAL
80.	CARABIDAE	GENERAL, SIMULATED
299.	PHASMATIDAE	GENERAL
137.	ANTHOPHORIDAE	FORMICIDAE DERMAPTERA: GENERAL
208.	SCOLOPENDRIDAE	GENERAL
315.	CHRYSOMELIDAE	GENERAL
250.	APHIDIDAE	GENERAL
267.	COSMETIDAE GONYLEPTIDAE	GENERAL
110.	MUTILLIDAE	FORMICIDAE
9.	TERMITIDAE	FORMICIDAE DASYOPIDAE MYRMECOPHAGIDAE
8.	TERMITIDAE	FORMICIDAE MYRMECOPHAGIDAE
261.	TERMITIDAE	GENERAL
128.	STAPHYLINIDAE	GENERAL
93.	STYGNOMMATIDAE	FORMICIDAE IGUANIDAE
129.	TENEBRIONIDAE	GENERAL
321.	FORMICIDAE	FORMICIDAE
152.	PAPILIONIDAE	VESPIDAE: GENERAL FORMICIDAE: GENERAL ARANEAE: GENERAL AVES: GENERAL
102.	CANTHARIDAE	SALTICIDAE
81.	CHRYSOMELIDAE	GENERAL
262.	TERMITIDAE	GENERAL
170.	FORMICIDAE	GENERAL
154.	CHRYSOMELIDAE	FORMICIDAE
64.	APIDAE	GENERAL: SIMULATED
35.	DANAIDAE	CORVIDAE
248.	STAPHYLINIDAE	GENERAL
165.	APIDAE	REDUVIIDAE
83.	STAPHYLINIDAE	GENERAL
164.	STAPHYLINIDAE	FORMICIDAE
58.	TERMITIDAE	FORMICIDAE
61.	ARCTIIDAE	CHIROPTERA: GENERAL
41.	FORMICIDAE	GENERAL
282.	TERMITIDAE	FORMICIDAE
113.	DYTISCIDAE	OSTEICTHYES: GENERAL AMPHIBIA: GENERAL
298.	APIDAE	GENERAL: SIMULATED
51.	ANTHOPHORIDAE	FORMICIDAE
54.	GLOMERIDAE	ARANEAE: GENERAL INSECTA: GENERAL VERTEBRATA: GENERAL

REF.NO.	PREY	PREDATOR
322.	TERMITIDAE	FORMICIDAE
37.	DANAIDAE	CORVIDAE
184.	LYGAEDAE	GENERAL
131.	TERMITIDAE	GENERAL
31.	TERMITIDAE	GENERAL
255.	VESPIDAE	VESPIDAE
239.	CHRYSOMELIDAE	TENTHREDINIDAE
256.	VESPIDAE	FORMICIDAE
36.	DANAIDAE	GENERAL
60.	DANAIDAE NYMPHALIDAE	GENERAL
112.	CHRYSOMELIDAE	MANTIDAE
66.	APIDAE	GENERAL: SIMULATED
132.	SCUTELLERIDAE	FORMICIDAE
166.	APIDAE	GENERAL
130.	TENEBRIONIDAE	GENERAL
12.	FORMICIDAE	FORMICIDAE VERTEBRATA: GENERAL
221.	LYGAEIDAE	GENERAL
84.	STAPHYLINIDAE	DROSOPHILIDAE FORMICIDAE
26.	TENTHREDINIDAE	FORMICIDAE PARIDAE
150.	TENEBRIONIDAE	GENERAL
45.	PAPILIONIDAE	FORMICIDAE
133.	SCUTELLERIDAE	GENERAL
59.	TERMITIDAE	GENERAL
55.	OEDEMERIDAE	HOMINIDAE
167.	ACRIDIDAE	FORMICIDAE
288.	DANAIDAE	CORVIDAE RODENTIA: GENERAL
287.	LYGAEIDAE	MANTIDAE
276.	CHRYSOMELIDAE	FORMICIDAE: GENERAL
50.	APIDAE	FORMICIDAE REDUVIIDAE ASILIDAE AGELENIDAE ARANEIDAE
104.	SILPHIDAE	FORMICIDAE
213.	SILPHIDAE	SALTICIDAE
197.	DANAIDAE	CORVIDAE
228.	ZYGAENIDAE	VERTEBRATA: GENERAL
319.	FORMICIDAE	FORMICIDAE
168.	ACRIDIDAE	FORMICIDAE
275.	APIDAE	HOMINIDAE VERTEBRATA: GENERAL
157.	TENEBRIONIDAE	GENERAL
354.	LEPIDOPTERA: GENERAL	GENERAL
205.	DANAIDAE	AVES: GENERAL RODENTIA: GENERAL
40.	CANTHARIDAE	GENERAL
308.	GEOMETRIDAE	CORVIDAE
214.	FORMICIDAE	GENERAL
171.	TENTHREDINIDAE	ARANEAE: GENERAL FORMICIDAE: GENERAL
119.	YPONOMEUTIDAE	GENERAL
121.	NYMPHLAIDAE	VERTEBRATA: GENERAL
6.	FORMICIDAE	FORMICIDAE
203.	DANAIDAE	CORVIDAE
361.	CARABIDAE	SCINCIDAE

REF.NO.	PREY	PREDATOR
30.	LYCAENIDAE	GENERAL
240.	FORMICIDAE	FORMICIDAE
79.	CARABIDAE	HOMINIDAE
202.	APHIDIDAE	ARANEIDAE
67.	APIDAE	GENERAL: SIMULATED
232.	APHIDIDAE	COCCINELLIDAE
264.	ACRAEINAE	GENERAL
142.	ARTHROPODA: GENERAL	CICHLIDAE
206.	FORMICIDAE	FORMICIDAE: GENERAL
226.	PERGIDAE	FORMICIDAE REDUVIIDAE MUSCICAPIDAE CRICETIDAE
138.	NOTODONTIDAE DANAIDAE LASIOCAMPIDAE NYMPHALIDAE NOCTUIDAE LYPARIDAE	PASSERIFORMES: 5 SPP.
178.	PIERIDAE	CORVIDAE
148.	TENEBRIONIDAE	VESPERTILIONIDAE MUSTELIDAE BASSARISCIDAE
18.	LEPIDOPTERA: GENERAL	FORMICIDAE
236.	DANAIDAE	AVES: GENERAL
237.	DANAIDAE ACRAEIDAE	GENERAL
195.	FORMICIDAE	FORMICIDAE
162.	PAPILIONIDAE	PARIDAE
292.	LYGAEIDAE	PARIDAE
212.	MIRIDAE LYGAEIDAE	IGUANIDAE
109.	LYGAEIDAE	PHASIANIDAE
153.	ARANEIDAE	CORVIDAE
307.	ACRIDIDAE	SPHECIDAE
103.	SILPHIDAE	GENERAL
69.	CARABIDAE	MYRMELEONTIDAE
11.	CARABIDAE	SCOLOPACIDAE
34.	FORMICIDAE	FORMICIDAE BUFONIDAE ALAUDIDAE PERMELIDAE MURIDAE
191.	TENEBRIONIDAE	CRICETIDAE

CRYPTIC DEFENSIVE MECHANISMS

REF.NO.	PREY	PREDATOR
280.	NOCTUIDAE	AVES: GENERAL
2.	ACRIDIDAE	AVES: GENERAL
125.	ACRIDIDAE	HOMINIDAE SQUAMATA CRACIDAE
127.	ACRIDIDAE	AVES: 5 SPP.
94.	PAGURIDAE	HOMINIDAE
111.	PERILIDAE	SALMONIDAE
13.	CULICIDAE	GENERAL
120.	ACRIDIDAE PIERIDAE	GENERAL
310.	GEOMETRIDAE	GENERAL HOMINIDAE
254.	PSOCIDAE	AVES: GENERAL
124.	ORTHOPTERA	AVES: GENERAL SAURIA: GENERAL
134.	PAPILIONIDAE	AVES: GENERAL
200.	ENNOMINAE	MUSCICAPIDAE TROGLODYTIDAE STURNIDAE
135.	INSECTA: 22 SPP.	FORMICIDAE
350.	FORMICIDAE	IGUANIDAE
48.	COPEPODA:	SALMONIDAE
139.	LEPIDOPTERA: GENERAL,	PARIDAE
118.	COPEPODA	ATHERINIDAE
290.	CULICIDAE	NOTONECTIDAE
78.	PYRALIDAE	FORMICIDAE GENERAL ARANEAE: GENERAL
199.	HIPPOLYTIDAE	SPARIDAE
183.	PALAEMONIDAE	CYPRINODONTIDAE
20.	GEOMETRIDAE	AVES: GENERAL
192.	GEOMETRIDAE	TROGLODYTIDAE MUSCICAPIDAE PARIDAE PASSERIDAE
311.	GEOMETRIDAE	AVES: GENERAL HOMINIDAE
107.	TENEBRIONIDAE	PARIDAE
81.	CHRYSOMELIDAE	GENERAL
26.	TENTHREDINIDAE	FORMICIDAE PARIDAE
138.	NOTODONTIDAE DANAIDAE LASIOCAMPIDAE NYMPHALIDAE NOCTUIDAE LYPARIDAE	PASSERIFORMES: 5 SPP.
185.	CYMOTHOIDAE	LABRIDAE
71.	NOTONECTIDAE	CENTRARCHIDAE
343.	LIBELLULIDAE	CENTRARCHIDAE
251.	LIBELLULIDAE	CENTRARCHIDAE
300.	EPHEMERELLIDAE	PERLIDAE
353.	CERCOPIDAE	AVES: GENERAL
356.	LIMNEPHILIDAE	GENERAL
273.	CHRYSOMELIDAE	PENTATOMIDAE NABIDAE COCCINELLIDAE
147.	VESPIDAE	GENERAL
347.	FORMICIDAE	GENERAL
105.	CHRYSOPIDAE	GENERAL
204.	GEOMETRIDAE	MELLPHAGIDAE EMBERIZIDAE

MIMICRY DEFENSE MECHANISMS

REF.NO.	PREY	PREDATOR
296.	CERAMBYCIDAE	RODENTIA
265.	INSECTA: GENERAL	GENERAL
39.	NYMPHALIDAE	GENERAL
87.	TENEBRIONIDAE	GENERAL
313.	BRASSOLIDAE	AVES: GENERAL IGUANIDAE
281.	ZYGAENIDAE	AVES: 6 SPP. LACERTIDAE
136.	SYRPHIDAE	PASSERIFORMES: GENERAL
29.	NYMPHALIDAE	CORVIDAE
274.	INSECTA: GENERAL	GENERAL
337.	DIPTERA: 21. SPP.	AVES: GENERAL
336.	SYRPHIDAE CONOPIDAE TACHINIDAE ASILIDAE MANTISPIDAE	PASSERIDAE, MIMIDAE, EMBERIZIDAE, CORVIDAE
160.	REDUVIIDAE	GENERAL
81.	CHRYSOMELIDAE	GENERAL
308.	GEOMETRIDAE	CORVIDAE
148.	TENEBRIONIDAE	VESPERTILIONIDAE MUSTELIDAE BASSARISCIDAE
236.	ACRAEIDAE	AVES: GENERAL
237.	NYMPHALIDAE SATYRIDAE PAPILIONIDAE LYCAENIDAE	GENERAL
212.	MIRIDAE LYGAEIDAE	IGUANIDAE
291.	CERAMBYCIDAE	GENERAL, HOMINIDAE
99.	TEPHRITIDAE	GENERAL
85.	MORDELLIDAE MELOIDAE	GENERAL
108.	SYRPHIDAE	EMBERIZIDAE
333.	FORMICIDAE	IGUANIDAE

ESCAPE DEFENSE MECHANISMS

REF.NO.	PREY	PREDATOR
186.	HOMARIDAE	MAMMALIA: GENERAL
294.	BLATTIDAE	VERTEBRATA: GENERAL
189.	FORMICIDAE	FORMICIDAE
89.	FORMICIDAE	FORMICIDAE
53.	CALLIPHORIDAE	LANIIDAE
367.	PORTUNIDAE	OSTEICTHYES: GENERAL AVES: GENERAL CRUSTACEA: GENERAL
196.	FORMICIDAE	MYRMELEONTIDAE
52.	CHRYSOMELIDAE	CORVIDAE PARIDAE
301.	NOCTUIDAE ARCTIIDAE	CHIROPTERA: GENERAL
242.	CICINDELIDAE	GENERAL
88.	FORMICIDAE	FORMICIDAE
73.	SATURNIIDAE	GENERAL: SIMULATED
225.	APIDAE	GENERAL
272.	APHIDIDAE	COCCINELLIDAE
368.	APHIDIDAE CICADELLIDAE	COCCINELLIDAE
159.	CICADIDAE	FORMICIDAE
135.	INSECTA: 22 SPP.	FORMICIDAE
241.	CICINDELIDAE	ASILIDAE LANIIDAE ACCIPITRIDAE TEIIDAE IGUANIDAE
122.	FORMICIDAE	HOMINIDAE
306.	PALAEMONIDAE	CENTRARCHIDAE
305.	PALAEMONIDAE	CENTRARCHIDAE
350.	FORMICIDAE	IGUANIDAE
244.	HEPTAGENIIDAE BAETIDAE	PERLIDAE, PERLODIDAE PTERONARCIDAE
289.	NOTONECTIDAE	HEMIPTERA
74.	COPEPODA: GENERAL	BLENIIDAE
272.	APHIDIDAE	COCCINELLIDAE
177.	APHIDIDAE	SYRPHIDAE
233.	APHIDIDAE	GENERAL
81.	CHRYSOMELIDAE	GENERAL
154.	CHRYSOMELIDAE	FORMICIDAE
229.	INSECTA: 10 ORDERS	ARANEIDAE
312.	CICADIDAE	EMBERIZIDAE
277.	APHIDIDAE	ANTHOCORIDAE
56.	VESPIDAE	FORMICIDAE
307.	ACRIDIDAE	SPHECIDAE
191.	ACRIDIDAE	CRICETIDAE

FIGHTING DEFENSE MECHANISMS (STINGING)

REF.NO.	PREY	PREDATOR
49.	FORMICIDAE	FORMICIDAE: GENERAL
97.	APIDAE	PYRALIDAE
65.	APIDAE	GENERAL: SIMULATED
146.	FORMICIDAE	HOMINIDAE
303.	HYMENOPTERA: GENERAL	VERTEBRATA: GENERAL
188.	FORMICIDAE VESPIDAE HALICTIDAE APIDAE	VERTEBRATA: GENERAL
304.	HYMENOPTERA: GENERAL	VERTEBRATA: GENERAL
1.	VESPIDAE	HOMINIDAE
163.	VESPIDAE	HOMINIDAE, GENERAL: SIMULATED
225.	APIDAE	GENERAL
137.	ANTHOPHORIDAE	FORMICIDAE DERMAPTERA: GENERAL
64.	APIDAE	GENERAL: SIMULATED
214.	FORMICIDAE	GENERAL
67.	APIDAE	GENERAL: SIMULATED
191.	VAEJOVIDAE	CRICETIDAE
108.	APIDAE	EMBERIZIDAE
333.	FORMICIDAE	IGUANIDAE

FIGHTING DEFENSE MECHANISMS (BITING)

REF.NO.	PREY	PREDATOR
49.	FORMICIDAE	FORMICIDAE
144.	FORMICIDAE	MAMMALIA: GENERAL
259.	TERMITIDAE	GENERAL
100.	TERMITIDAE	FORMICIDAE
360.	APIDAE	APIDAE
260.	TERMITIDAE	FORMICIDAE
370.	RHINOTERMITIDAE	FORMICIDAE
321.	FORMICIDAE	FORMICIDAE
298.	APIDAE	GENERAL: SIMULATED
322.	TERMITIDAE	FORMICIDAE
166.	APIDAE	MAMMALIA: GENERAL
275.	APIDAE	HOMINIDAE VERTEBRATA: GENERAL
79.	CARABIDAE	HOMINIDAE
307.	ACRIDIDAE	SPHECIDAE

FIGHTING DEFENSE MECHANISMS (MOBBING)

REF.NO.	PREY	PREDATOR
57.	THERIDIIDAE	SPHECIDAE

FIGHTING DEFENSE MECHANISMS (OTHER)

REF.NO.	PREY	PREDATOR
106.	PAGURIDAE	GENERAL
115.	OXYOPIDAE	FORMICIDAE: GENERAL
19.	OXYPODIDAE	THRESKIORNITHIDAE
234.	DERMESTIDAE	INSECTA: GENERAL VERTEBRATA: GENERAL ARACHNIDA: GENERAL
220.	DERMESTIDAE	TENEBRIONIDAE
363.	MEMBRACIDAE	COCCINELLIDAE REDUVIIDAE SYRPHIDAE
198.	DERMESTIDAE	CHELONETHIDA HYMENOPTERA
209.	FORMICIDAE	FORMICIDAE
316.	TINGIDAE	COCCINELLIDAE: SIMULATED
88.	FORMICIDAE	FORMICIDAE
278.	TETRANYCHIDAE	PHYTOSEIIDAE
73.	SATURNIIDAE	GENERAL: SIMULATED
320.	NEODIPRIONIDAE	PENTATOMIDAE
181.	SCARABEIDAE	SCARABEIDAE
137.	ANTHOPHORIDAE	FORMICIDAE DERMAPTERA: GENERAL
277.	APHIDIDAE	ANTHOCORIDAE
307.	ACRIDIDAE	SPHECIDAE
147.	VESPIDAE	GENERAL

POSTURAL/SIZE DEFENSE MECHANISMS

REF.NO.	PREY	PREDATOR
326.	TENEBRIONIDAE	GENERAL
259.	TERMITIDAE	GENERAL
176.	ACRIDIDAE	HOMINIDAE
241.	CICINDELIDAE	ASILIDAE LANIIDAE ACCIPITRIDAE TEIIDAE IGUANIDAE
306.	PALAEMONIDAE	CENTRARCHIDAE
318.	LASIOCAMPIDAE	FORMICIDAE
245.	EPHEMERELLIDAE	PERLIDAE PERLODIDAE PTERONARCIDAE
86.	DAPHINIDAE	TEMORIDAE
370.	RHINOTERMITIDAE	FORMICIDAE
154.	CHRYSOMELIDAE	FORMICIDAE
50.	APIDAE	REDUVIIDAE ASILIDAE AGELENIDAE ARANEIDAE
171.	TENTHREDINIDAE	ARANEAE: GENERAL FORMICIDAE: GENERAL
235.	TAENIOPTERYGIDAE	SALMONIDAE PERLIDAE
245.	EPHEMERELLIDAE BAETIDAE	PERLODIDAE PTERONARCIDAE PERLIDAE
246.	EPHEMERELLIDAE	PERLODIDAE
247.	EPHEMERELLIDAE	PERLODIDAE
307.	ACRIDIDAE	SPHECIDAE
147.	VESPIDAE	GENERAL
347.	FORMICIDAE	GENERAL

FLASH/WARNING COLORATION

REF.NO.	PREY	PREDATOR
242.	CICINDELIDAE	GENERAL
201.	APHIDIDAE	ARANEIDAE PARIDAE
341.	POLYDESMIDA	GENERAL
87.	TENEBRIONIDAE	GENERAL
362.	MEMBRACIDAE	IGUANIDAE
313.	BRASSOLIDAE	AVES: GENERAL IGUANIDAE
241.	CICINDELIDAE	ASILIDAE LANIIDAE ACCIPITRIDAE TEIIDAE IGUANIDAE
284.	COREIDAE PYRRHOCORIDAE PENTATOMIDAE	EMBERIZIDAE
81.	CHRYSOMELIDAE	GENERAL
154.	CHRYSOMELIDAE	FORMICIDAE
61.	ARCTIIDAE	CHIROPTERA: GENERAL
26.	TENTHREDINIDAE	FORMICIDAE PARIDAE
287.	LYGAEIDAE	MANTIDAE
228.	ZYGAENIDAE	VERTEBRATA: GENERAL
308.	GEOMETRIDAE	CORVIDAE
202.	APHIDIDAE	ARANEIDAE
369.	MORPHOIDAE	TYRANNIDAE GALBULIDAE
178.	PIERIDAE	CORVIDAE
162.	PAPILIONIDAE	PARIDAE
292.	LYGAEIDAE	PARIDAE
212.	MIRIDAE LYGAEIDAE	IGUANIDAE
307.	ACRIDIDAE	SPHECIDAE

DILUTION/SATIATION EFFECT

REF.NO.	PREY	PREDATOR
309.	MAJIDAE	AVES: GENERAL
125.	ACRIDIDAE	HOMINIDAE SQUAMATA CRACIDAE
126.	ACRIDIDAE	HOMINIDAE LACERTIDAE
140.	DAPHINIDAE	GASTEROSTEIDAE
215.	DAPHINIDAE	GASTEROSTEIDAE
323.	GERRIDAE	AVES: SIMULATED
324.	GERRIDAE	AVES: SIMULATED
325.	GERRIDAE	CLUPEIDAE MUGILIDAE
216.	DAPHINIDAE	GASTEROSTEIDAE
161.	BOSMINIDAE	GASTEROSTEIDAE
201.	APHIDIDAE	ARANEIDAE PARIDAE
159.	CICADIDAE	FORMICIDAE
241.	CICINDELIDAE	ASILIDAE LANIIDAE ACCIPITRIDAE TEIIDAE IGUANIDAE
173.	CICADIDAE	STURNIDAE MUSCICAPIDAE CORVIDAE EMBERIZIDAE
328.	APHIDIDAE	COCCINELLIDAE
7.	NOTONECTIDAE	SIMULATED
312.	CICADIDAE	EMBERIZIDAE

MUTUALISM DEFENSE MECHANISMS

REF.NO.	PREY	PREDATOR
365.	MEMBRACIDAE	GENERAL
253.	LYCAENIDAE	THERIDIIDAE SPARASSIDAE THOMISIDAE CLUBIONIDAE ARANEIDAE FORMICIDAE VESPIDAE
32.	COCCIDAE	COCCINELLIDAE
46.	COCCIDAE	COCCINELLIDAE PYRALIDAE
317.	APHIDIDAE	COCCINELLIDAE MIRIDAE SPHECIDAE LINYPHIIDAE
116.	CHRYSOMELIDAE	FORMICIDAE
74.	MEMBRACIDAE	SALTICIDAE
33.	APHIDIDAE MEMBRACIDAE	COCCINELLIDAE CRYSOPIDAE
151.	COCCIDAE	COCCINELLIDAE
43.	MEMBRACIDAE	GENERAL
114.	LYCAENIDAE	GENERAL
297.	LYCAENIDAE	GENERAL
149.	TERMITIDAE	FORMICIDAE

ARMOR DEFENSE MECHANISMS

REF.NO.	PREY	PREDATOR
70.	TENEBRIONIDAE	FORMICIDAE
371.	DAPHINIDAE	ATHERINIDAE
330.	PAGURIDAE	CANCRIDAE
174.	BOSMINIDAE	TEMONIDAE CYCLOPIDAE
86.	DAPHINIDAE	TEMORIDAE
96.	FORMICIDAE	SALTICIDAE
81.	CHRYSOMELIDAE	GENERAL
79.	CARABIDAE	HOMINIDAE
235.	TAENIOPTERYGIDAE PERLIDAE	SALMONIDAE
291.	CERAMBYCIDAE	GENERAL HOMINIDAE
273.	CHRYSOMELIDAE	PENTATOMIDAE NABIDAE COCCINELLIDAE
105.	CHRYSOPIDAE	GENERAL

ACOUSTIC

REF.NO.	PREY	PREDATOR
279.	TETTIGONIDAE	SCINCIDAE
42.	PASSALIDAE	CORVIDAE
52.	CHRYSOMELIDAE	CORVIDAE PARIDAE
242.	CICINDELIDAE	GENERAL
211.	MUTILLIDAE HYDROPHILIDAE CARABIDAE	LYCOSIDAE CRICETIDAE
81.	CHRYSOMELIDAE	GENERAL
21.	ACRIDIDAE	GEKKONIDAE
11.	CARABIDAE	SCOLOPACIDAE

FEIGNING DEATH

REF.NO.	PREY	PREDATOR
52.	CHRYSOMELIDAE	CORVIDAE PARIDAE
154.	CHRYSOMELIDAE	FORMICIDAE
235.	TAENIOPTERYGIDAE PERLIDAE	SALMONIDAE

MISDIRECTED ATTACK

REF.NO.	PREY	PREDATOR
291.	CERAMBYCIDAE	GENERAL HOMINIDAE

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CHAOS AND PHASE-LOCKING IN PREDATOR-PREY MODELS IN RELATION TO THE FUNCTIONAL RESPONSE

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ABSTRACT

The dynamics of a simple predator-prey model:

$$\begin{aligned} \dot{x} &= \phi x(1\text{-}x) - \gamma g(x)z && \text{(prey)} \\ \dot{y} &= (x\text{-}y)/\tau && \text{(lagged prey)} \\ \dot{z} &= \gamma g(y)z - \nu z && \text{(predator)} \end{aligned}$$

with periodic forcing (ϕ) on the prey's reproductive rate and a functional response, g(x), is investigated in relation to parameters and the functional response. The system is sampled at the forcing period and plotted against a parameter for each of four functional responses: Linear, Type 1, Type 2 and Type 3. Sampling at the forcing period allows one to see when the system is phase-locked in some ratio with the forcing cycle. The analysis reveals very complicated and unexpected switching between different phase-locking ratios alternating with regions of quasiperiodic and chaotic behavior within each functional response as a parameter is varied. Of the four functional responses tested, the Type 2 response produces the most complex behavior.

RESUMEN

Se investigó la dinámica de un modelo simple de depredador/presa:

$$\begin{aligned} \dot{x} &= \phi x(1\text{-}x) - \gamma g(x)z && \text{(presa)} \\ \dot{y} &= (x\text{-}y)/\tau && \text{(presa rezagada)} \\ \dot{z} &= \gamma g(y)z - \nu z && \text{(depredador)} \end{aligned}$$

forzando periodicamente la tasa de reproducción de la presa y su respuesta funcional en relación a los parámetros y la reacción funcional. Se muestra el sistema durante el período forzado, y conjurado contra un parámetro para cada una de cuatro reacciones funcionales: Linear, Tipo 1, Tipo 2 y Tipo 3. Muestrear en el período forzado le permite a uno ver cuándo el sistema está en la fase cerrada en alguna proporción al ciclo forzado. El análisis revela unos cambios muy complicados e inesperados entre varios niveles de fase cerrada que alternan con regiones de comportamiento casi-periodos y caóticos dentro de cada respuesta funcional cuando un parámetro se varía. De las cuatro reacciones probradas, el Tipo 2 produjo el comportamiento más complejo.

The discovery of deterministic chaos in simple nonlinear models of weather (Lorenz 1963), ecological systems (May 1974, 1976) and chemical reactions (Rossler 1976) has added a new dimension to scientific inquiry. In ecology the possibility of such behavior in simple models raises the question of its existence in real highly complex natural systems and whether such a system could survive. It is quite a simple matter to write down predator-prey models which are chaotic (Gilpin 1979, Inoue & Kamifukumoto 1984, Allen 1989a). The primary ingredients for chaos in these models are the naturally arising nonlinear functions combined with time lags and periodic forcing from the environment (e.g., prey reproductive rate becoming a periodic function) (Allen in press).

At the heart of the nonlinear interaction between attacker and victim is the so called functional response of the predator to prey density. This function describes the per predator attack rate as a function of prey density (Holling 1959a,b, 1965).

Four types of functions have been commonly used for the functional response: 1) linear (an "insatiable" predator whose attack rate never saturates at any prey density), 2) a linear rise to a saturation plateau (Type 1), 3) a convex rise to a saturation plateau (Type 2) and 4) a sigmoid rise to a saturation plateau (Type 3). The form of the functional response is largely a reflection of the predator's behavior in response to the prey density and/or distribution in space. The Type 3 response is unique in its ability to produce attracting point ("stable") behavior in what would otherwise be an attracting cycle system, and this type of response has been generally associated with predators capable of learning (Holling 1959a,b, 1965, Murdoch & Oaten 1975). More recently, however, it has been shown that a Type 3 response can also result from more intense searching of high density prey patches (Murdoch & Oaten 1975, Oaten & Murdoch 1975, Van Lenteren & Bakker 1976, 1978, Hassell et al. 1977, Luck et al. 1979, Walde & Murdoch 1988). If the predator simply concentrates on patches without regard to density within the patch, however, then the interaction is not stabilizing (Allen 1989a).

While chaos has been shown to exist in simple predator-prey models, these have typically involved only a linear functional response (Gilpin 1979, Kot et al. 1988, Allen 1989a) or a Type 2 response (Inoue & Kamifukumoto 1984, Schaffer 1989). Little has been done on comparing the effect of the functional responses in a potentially chaotic system, and this is made a bit more interesting by the possibility of spatial density dependence producing a Type 3 response. In this paper I will examine the effect of the different types of functional responses on the dynamic behavior of a predator-prey model which is capable of chaotic dynamics.

A SIMPLE PREDATOR-PREY MODEL

The model used here is a Lotka-Volterra type of system with the slight complication of periodic forcing of the prey reproductive rate and a one-stage lag in the predator's numerical response. These changes seem realistic and can greatly complicate the dynamic behavior even in the case of a linear functional response (Allen 1989a). The starting equations are

$$\begin{aligned} dx_o/dt_o &= \phi r x_o(1-x_o/k) - ag(x_o)z_o &&\text{(prey)}\\ dy_o/dt_o &= (x_o-y_o)/b &&\text{(lagged prey)}\\ dz_o/dt_o &= \epsilon a g(y_o) - c z_o &&\text{(predator)} \end{aligned}$$

where $\phi = (1+\delta\cos(2\pi t_o/T_o))$ is the periodic forcing with mean = 1, period T_o and amplitude δ $(0<\delta<1)$. $g(\cdot)$ represents the functional response (note that the numerical response in the predator equation is a function of "lagged" prey). These equations can be simplified to dimensionless form by letting $x_o = xk$, $y_o = yk$, $z_o = z\epsilon k$, and $t_o = t/r$. We then have

$$\begin{aligned} \dot{x} &= \phi x(1-x) - \gamma g(x)z &&\text{(1a)}\\ \dot{y} &= (x-y)/\tau &&\text{(1b)}\\ \dot{z} &= \gamma g(y)z - \upsilon z &&\text{(1c)} \end{aligned}$$

where $\gamma = \epsilon a/r$, $\tau = br$ (mean time lag in the numerical response), $\upsilon = c/r$, $T = rT_o$ and $t = rt_o$. ($\dot{x} = dx/dt$).

The four functional responses, $g(x)$, are as follows:

$$g(x) = x \qquad \text{(Linear)}$$

$$g(x) = \begin{cases} x, & x < x_m \\ x_m, & x \geq x_m \end{cases} \qquad \text{(Type 1)}$$

$$g(x) = x_m \frac{x}{(x_m/2) + x} \qquad \text{(Type 2)}$$

$$g(x) = x_m \frac{x^2}{(x_m/2)^2 + x^2} \qquad \text{(Type 3)}$$

These are compared graphically in Figure 1. All of the saturation curves (Types 1, 2 and 3) share the same saturation prey density (x_m) and same midpoint ($x_m/2$) so as to keep them as similar as possible. These four attack functions give rise to four separate models whose dynamics we wish to investigate. From these models we first need to extract equilibria (fixed points) and determine conditions on the parameters for these points to be positive real numbers (since they represent population densities). This will help to limit the parameter space in which dynamic behavior is to be investigated.

In the absence of periodic forcing ($\delta = 0$), eqs. (1) have fixed points ($\overset{*}{x},\overset{*}{y},\overset{*}{z}$) for the different functional responses as follows:

$$\text{(Linear \& Type 1)} \quad \overset{*}{x} = \overset{*}{y} = \upsilon/\gamma, \quad \overset{*}{z} = (1-\overset{*}{x})/\gamma \qquad \text{(2a)}$$

$$\text{(Type 2)} \quad \overset{*}{x} = \overset{*}{y} = \frac{\upsilon x_m}{2(\gamma x_m - \upsilon)}, \quad \overset{*}{z} = \overset{*}{x}(1-\overset{*}{x})/\upsilon \qquad \text{(2b)}$$

$$\text{(Type 3)} \quad \overset{*}{x} = \overset{*}{y} = (x_m/2)\sqrt{\upsilon/(\gamma x_m - \upsilon)}, \quad \overset{*}{z} = \overset{*}{x}(1-\overset{*}{x})/\upsilon \qquad \text{(2c)}$$

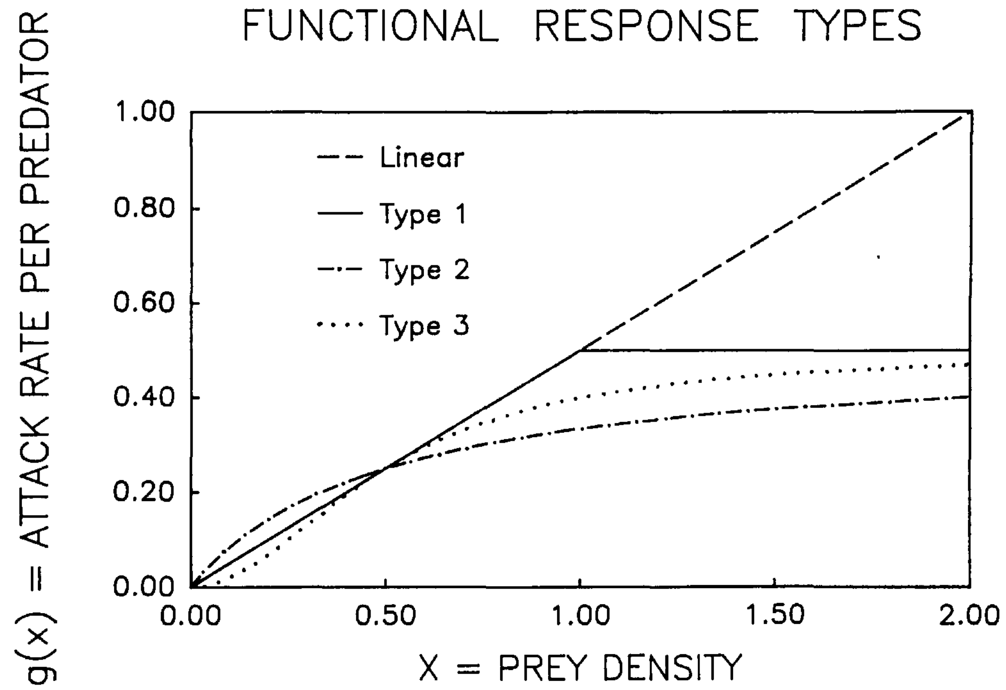

Fig. 1. The 4 most commonly used functional response curves, g(x), (See formulas following the model, eqs. (1)). All of the saturation curves have the same saturation attack rate: $g(x) = 0.5 = \gamma x_m$. γ (= 0.5) is the slope of the linear response and x_m (= 1.0 is the prey density which causes predator saturation. All curves share the same "half-saturation" prey density (= $x_m/2$ = 0.5).

From eq. (2a) (Linear functional response) we must have ($\overset{*}{x} < 1$) for a positive predator fixed point ($\overset{*}{z}$) which implies

$$\gamma > \upsilon, \text{ or } \gamma/\upsilon > 1 \qquad (3a)$$

i.e., the predator's attack rate (γ) must be greater than its mortality rate (υ) if it is to survive (which makes intuitive sense). From eq. (2b) (Type 2 functional response) we must also have a positive predator fixed point which leads in this case to

$$x_m > 1/((\gamma/\upsilon) - (1/2)) \qquad (3b)$$

From eq. (2c) Type 3 functional response) similar argument leads to the relation

$$2(\gamma/\upsilon - \sqrt{(\gamma/\upsilon)^2 - 1}) < x_m < 2(\gamma/\upsilon + \sqrt{(\gamma/\upsilon)^2 - 1}) \qquad (3c).$$

These requirements (eqs.(3)) are summarized graphically in Figure 2 where the γ/υ ratio is plotted against x_m showing the parameter region for positive, real fixed points. The simulations reported in this paper use parameter values from the lower righthand region of Fig. (2b), i.e., a predator with relatively high attack and low mortality rates which satiates (or saturates) quickly.

MODEL SIMULATION AND ANALYSIS OF DYNAMIC BEHAVIOR

Solution of the differential equations (eqs. (1)) was carried out by 4th-order Runge-Kutta integration with a variable timestep using the programs from Press et al. (1986) written in Pascal. This software was run on an IBM-AT microcomputer, and when more computational speed was needed, a VAX-6320. Models like eqs. (1) have cycles within cycles: i.e. periodic cycles arise from the model itself and also from the independent forcing cycle. These cycles can interact in a very complex way to produce periodic, quasiperiodic or chaotic dynamics depending on parameters, initial conditions and (in our case) the functional response. One way of seeing the behavior of the model in response to changes is to simulate the system and use a plotting or sampling interval equal to the forcing period. This is a bit like flashing a strobe light on a rotating fan blade. When the fan (or model) appears to be standing still, it is "phase-locked" with the sampling interval, indicating a truly periodic oscillation. Otherwise the motion is quasiperiodic ("almost" periodic) or chaotic (having no repeating pattern). More detailed definitions of these dynamic behaviors can be found in Parker & Chua (1987) and Allen (1989a,b).

If the dynamics are such that one cycle of the model occurs during one forcing cycle, then sampling the system at the forcing period produces a single point, and we say that the model has 1:1 phase-locking with the forcing cycle. If the model completes its cycle on every other forcing cycle, then sampling at the forcing period produces two points, and we say that the model has 2:1 phase locking with the forcing cycle. If sampling at the forcing period produces no repeating points, then the model is either quasiperiodic or chaotic. These phenomena can be exploited graphically to map the model behavior as a function of the parameters.

Graphing the behavior as a functicn of a parameter is a rather simple but computationally intensive procedure. First, a parameter range is selected, and this range is evenly divided among the screen pixels along the horizontal axis on the computer screen. (That is, the x-axis represents the parameter.) Then the model is run for a long enough time for transient behavior to die down and attracting behavior to establish itself. (How long is long enough? In general, we don't know, but it can be very long indeed (Allen 1989a). When in doubt, it is best to be conservative. In the graphs to follow, 10000

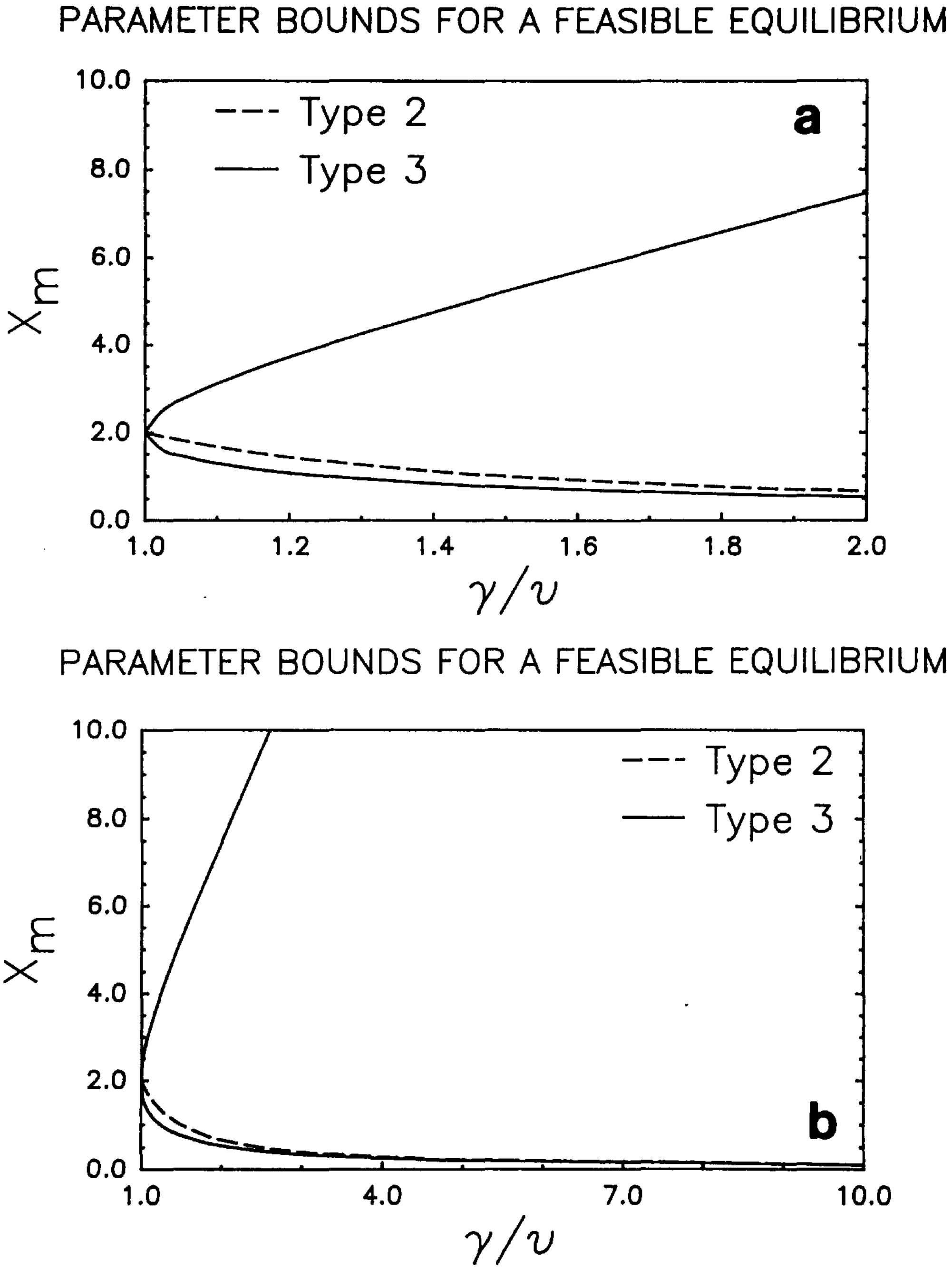

Fig. 2. Relationship between x_m and the γ/υ ratio for the existence of a positive, real predator and prey fixed point in the absence of periodic environmental forcing. γ/υ must always be > 1. In addition, parameters must lie above the dashed line for a Type 2 response and between the solid lines for a Type 3 response.

transient points were discarded before the graph was started.) After transient behavior has been discarded, many points are plotted at intervals of the forcing period at the parameter value on the x-axis. If all the points fall in the same place, then the system is phase-locked 1:1 with the forcing cycle for this parameter value. If (say) five points appear, then the system is phase-locked 5:1 with the forcing cycle. The result of doing this over a range of parameter values is a flowing pattern of lines whose number represents the phase-locking ratio which can be seen to change in response to the changing parameter.

What if the system does not phase-lock, i.e., lines fail to appear, and one sees only a smear of points over some bounded vertical range? This indicates either quasiperiodic or chaotic dynamics at the parameter value being observed. Distinguishing further between quasiperiodicity and chaos is not as simple as the phase-locking case. One tell-tale sign of chaos is the well-known "period-doubling" route to chaos. Thus if one sees phase-locking lines each of which divides again and again (period-doubling) to give rise to a vertical smear of points as a parameter changes, it is likely that the smear of points represents a chaotic region for the parameter. Abrupt changes from phase-locking lines to irregular points may represent either quasiperiodic or chaotic dynamics.

Results and Discussion

The predator's mortality rate (υ), the attack rate (γ) and the satiation level (x_m) were varied at each of the four functional responses to illustrate the dynamical behavior typical of this model and how it is influenced by the functional response. In all simulations, the forcing cycle was held at $\delta = 0.5$ and $T = 10$ and mean lag in the numerical response was $\tau = 4$. These choices are somewhat arbitrary, and no attempt has been made to cover the whole parameter space. The effect of varying the predator's mortality rate (υ) from 0.05 to 0.1 is shown in Figure 3. At the start of each graph, initial (x,y,z) conditions were (0.5,0.5,0.5) and 10000 initial time periods were discarded before any plotting began. At each parameter increment along the x-axis, 300 initial forcing periods (3000 time points) were discarded and the next 50 were plotted. The mortality rate was

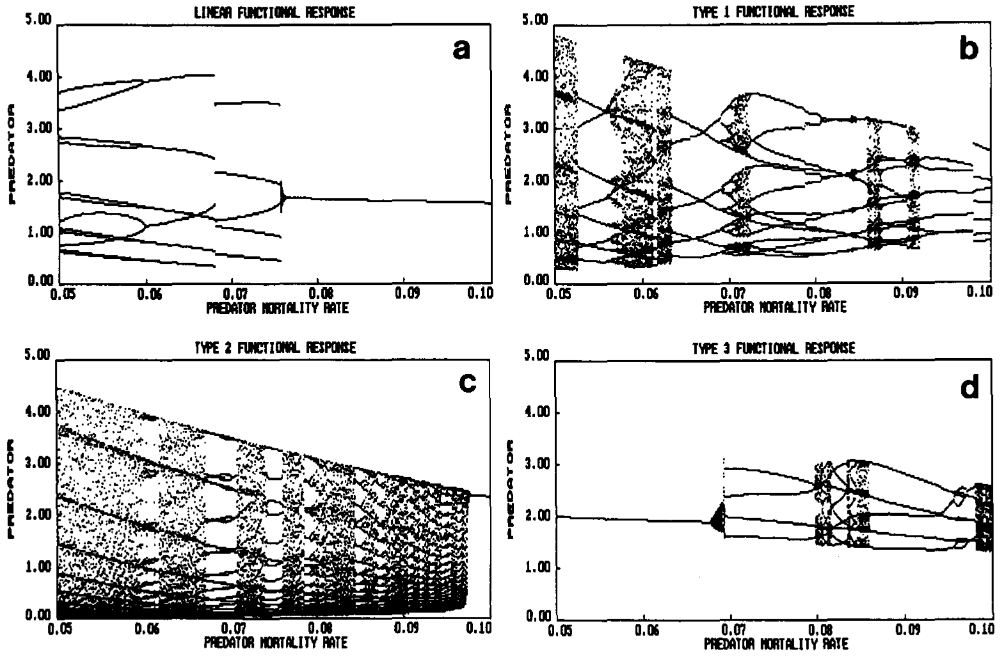

Fig. 3. The effect of varying the predator's mortality rate (υ) on the model dynamics (the predator) for each of the four functional responses. The other parameters are $\delta = 0.5$, $T = 10$, $\tau = 4$, $x_m = 0.25$, $\gamma = 0.5$.

then incremented, and the procedure was repeated using the final (x,y,z) values of the previous increment as starting values. Since we are solving differential equations, this procedure requires considerable computational effort, and the calculations were done on a VAX-6320 where typical run times were on the order of one hour per graph.

The effect of varying the predator's attack rate (γ on the model dynamics is shown in Figure 4, and the effect of the satiation level of prey (x_m) is shown in Figure 5. In all of the simulations, Figures 3-5, one is struck with the intricate switching of phase-locking from one ratio to another in a complex, seemingly arbitrary manner often alternating with bands of quasiperiodicity and chaos (indicated by period-doubling cascades). This degree of dynamical complexity is a bit surprising and would bewilder an observer using only standard simulation techniques. In fact the complex dynamical changes are confusing enough even when they are exposed in these graphs.

Some overall messages are apparent from the graphs. First, the Type 2 functional response is much less apt to phase-lock with the forcing cycle, being more prone to quasiperiodicity and chaotic dynamics and exhibits an extremely complicated sequence of switching between phase-locking and chaos. Both linear and Type 3 functional responses appear to phase-lock a bit more than Type 1 and certainly more than Type 2. The idea that the Type 3 response is more stabilizing than the Type 2 seems to be true here, although the Type 3 response does go through some complicated changes. In addition, the effect of changing the forcing cycle (δ and T) and the lag in the numerical response (τ) have not been studied here.

As a quick check on the credibility of the graphs we can examine a test case to see if the actual dynamics agrees with that predicted by the diagrams. Consider the expanded version of the interesting section of Figure 5b between $x_m = 0.30$ to 0.34 in Figure 6. For this range of saturation prey densities, there are alternating intervals of phase-locking, period-doubling cascades and apparently chaotic bands. Choosing x_m =

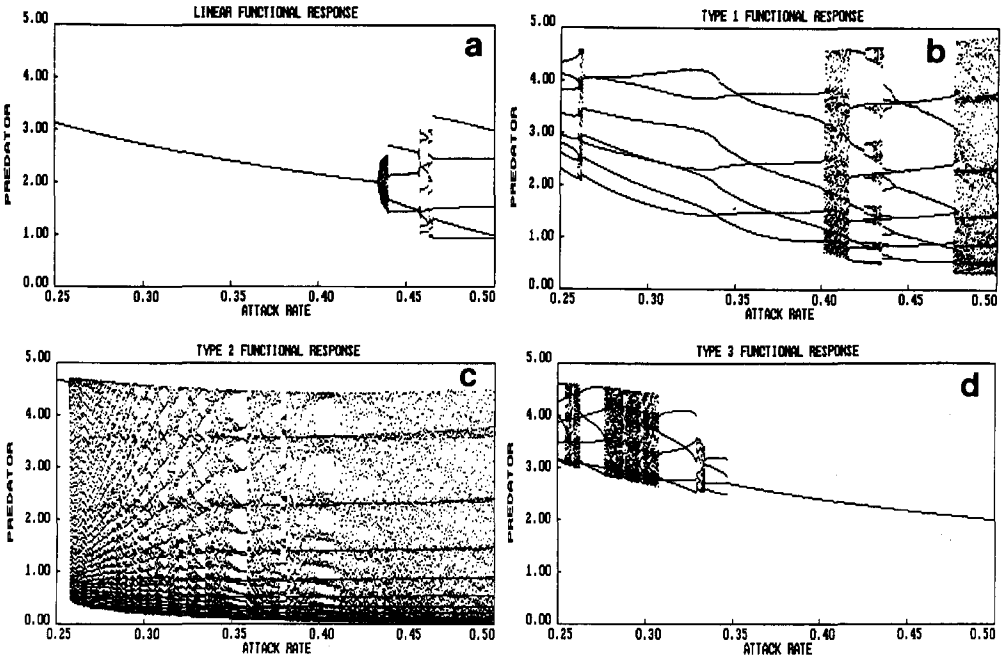

Fig. 4. The effect of varying the predator's attack rate (γ) on the model dynamics (the predator) for each of the four functional responses. The other parameters are: δ = 0.5, T = 10, τ = 4, x_m = 0.25, υ = 0.05.

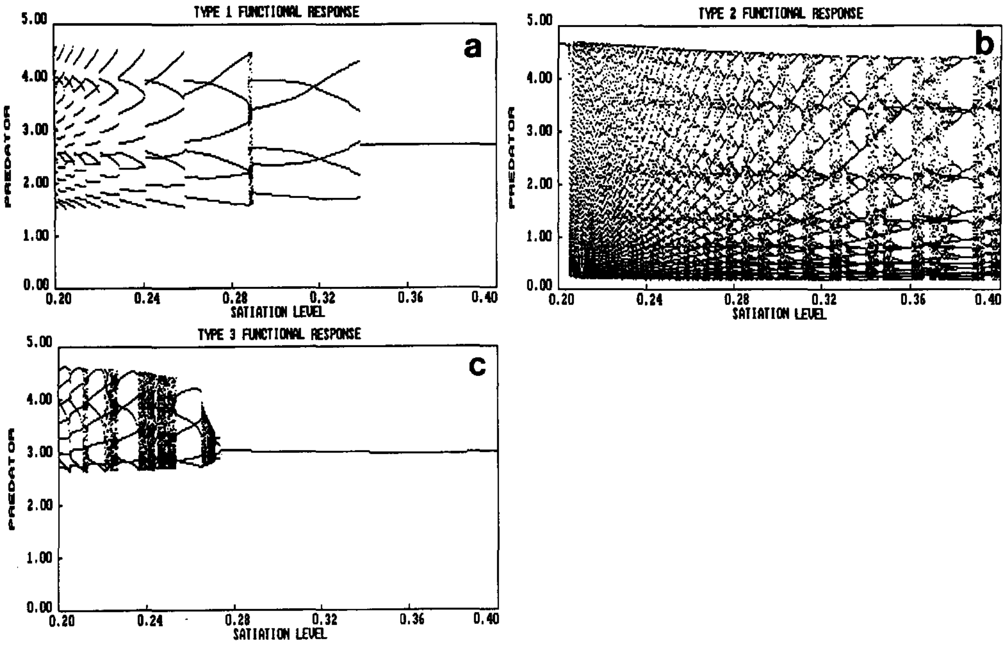

Fig. 5. The effect of the satiation level of prey density on the model dynamics (the predator) for the three "saturating" types of functional response. (Linear does not saturate.) The other parameters are: $\delta = 0.5$, $T = 10$, $\tau = 4$, $\upsilon = 0.1$, $\gamma = 0.5$. Note the period-doubling cascades suggesting chaotic dynamics in (b). (An expanded part of (5b) is shown in Fig. 6.)

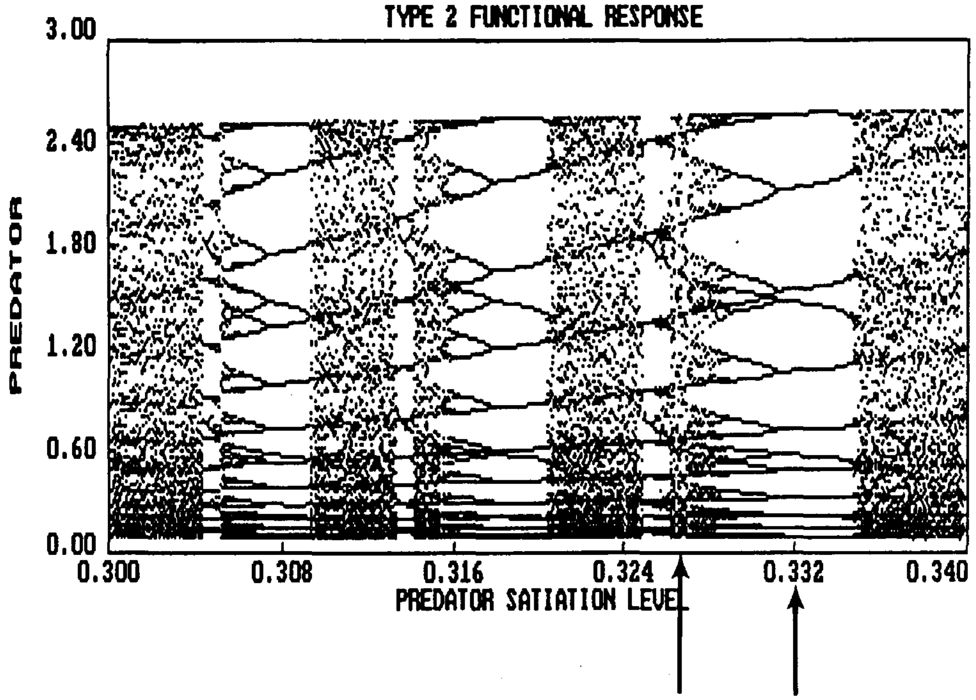

Fig. 6. An expanded part of Fig. 5b. from $x_m = 0.30$ to 0.34. The period-doubling is more apparent. Simulation for $x_m = 0.332$ (periodic) and $x_m = 0.327$ (probably chaotic) are shown in Fig. 7.

0.332 in a phase-locked region, we simulate the system (eqs.(1)) with all other parameters as in Figure 5. The first 10000 transient time intervals are discarded and the next 10000 are plotted (with lines between points) in (x,y,z) phase space in Figure 7a, and we see a periodic cycle as expected. We now choose $x_m = 0.327$ in an apparently chaotic region nearby and repeat the procedure above, plotting the result in Figure 7b. As predicted, we now see a swirling mass of flow lines which is either quasiperiodic or more likely chaotic. Another phase-space view is shown in Figure 7c and a time plot in Figure 7d. The small change of 0.05 in x_m has produced a dramatic change in the kind of dynamics that we see.

SUMMARY, CONCLUSIONS AND A DISCLAIMER

It has been shown that a simple type of periodically forced predator-prey model can have very complicated and unexpected transitions in dynamic behavior as parameters vary and that these transitions are greatly influenced by the type of functional response exhibited by the predator. The Type 3 functional response appears to be somewhat more likely to phase-lock with the forcing cycle than the Type 2 response although there is complicated behavior from all responses. These results do not change the basic notion that the Type 3 response is somewhat more stabilizing than the Type 2, but they do add another dimension to the problem. If the behavior of the predator determines the

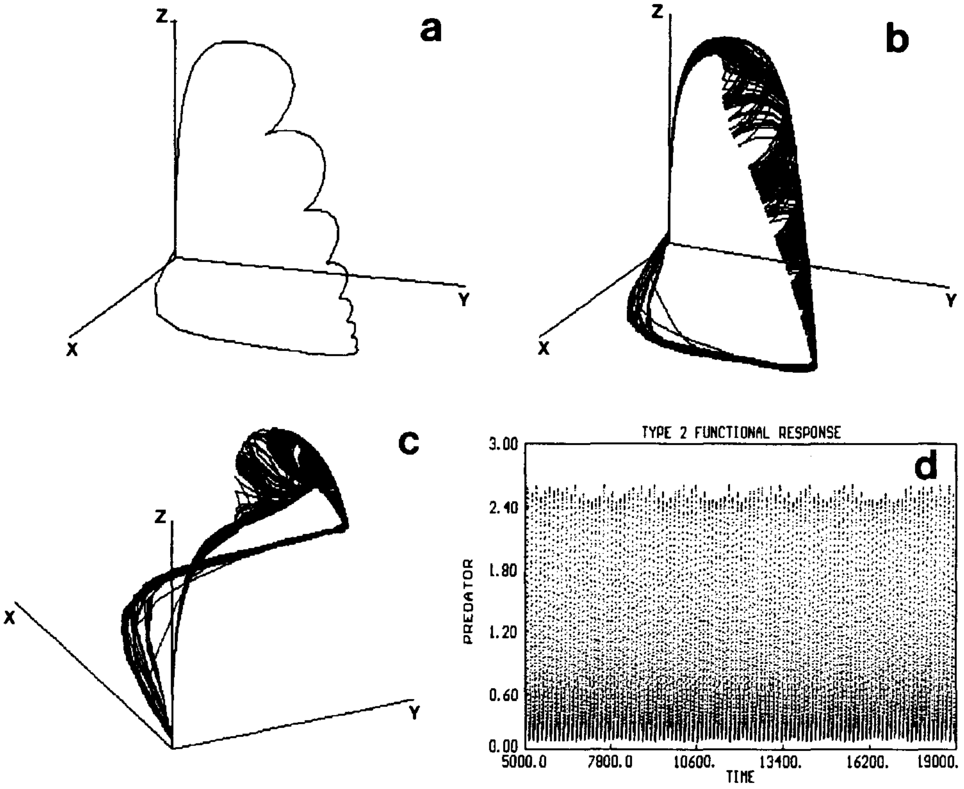

Fig. 7. (a). Simulation of the point $x_m = 0.332$ from Fig. 6. Periodic, phase-locked dynamics. (b). Simulation of the point $x_m = 0.327$ from Fig. 6. Probably chaotic dynamics. (In all plots the other parameters are as in Fig. 5.) (c). Another view of (b). (d). Time plot of (b) and (c)—5000 points discarded 14000 plotted. No repeating pattern develops.

functional response, then within that behavior there also exists the possibility of sudden and unexpected shifts in the attracting dynamics due to small and seemingly inconsequential changes in behavior or environment.

While these results are interesting and important, it should be noted that there are several things "wrong" with the model (eqs. (1)) as given. Among the most glaring of these is that there is no genetics, there is no explicit spatial component and the predator's mortality is not effected by a scarcity of prey. Inclusion of any of these factors will certainly have a profound effect on the dynamics. It is not immediately obvious whether the inclusion of such factors would greatly simplify the dynamics, but we would hope that the main results are fairly robust to such changes. That is, that there is a surprising degree of complexity both within and between the functional responses in such models and that without detailed analyses such as this we can never hope to understand them.

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RESISTANCE TO FALL ARMYWORM IN CONVERTED SORGHUMS

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ABSTRACT

Field experiments were conducted in 1988 to evaluate newly converted sorghum, *Sorghum bicolor* (L.) Moench, germplasm for both whorl and panicle resistance to feeding by larvae of the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith). In the whorl-stage resistance study, over 20 and 30 of the entries were significantly more resistant to FAW feeding than the resistant check at 7 and 14 days after infestation, respectively. Significant differences also were found among the entries for the number of FAW larvae that established per panicle 4 days after infestation.

RESUMEN

En 1988 se hicieron experimentos en el campo para evaluar la resistencia del verticilo y de la panícula de nuevos germoplasmas de sorgo, *Sorghum bicolor* (L.) Moench, hacia larvas del gusano cogollero *Spodoptera frugiperda* (J. E. Smith). En el estudio de resistencia del verticilo, más del 20 y 30 de los sorgos fueron significativamente más resistente al gusano cogollero que el patrón resistente, a los 7 y 14 días respectivamente después de la infestación. Se encontraron diferencias significativas entre los sorgos en el número de larvas del gusano cogollero establecidas por panículas, 4 días después de infestadas.

Grain sorghum, *Sorghum bicolor* (L.) Moench, is one of the world's most important food, feed, and fiber crops. The value of sorghum has steadily increased in the United States especially in the southeast over the past two decades (Wiseman & Morrison 1981). The management of insect pests, however, remains a great concern in agricultural systems. Annual loss estimates due to the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), exceed $300 million in the US (Mitchell 1979). Sparks (1979) reported that farmers in the southeastern United States annually lose between $30 to 60 million due to the FAW.

One of the best alternatives for controlling insect pests of agricultural crops is to grow insect-resistant cultivars. Painter (1951) defined plant resistance as "the relative amount of heritable qualities possessed by the plant which influences the ultimate degree of damage done by the insect". The concept of host plant resistance is based on the natural defense mechanisms developed by plant species during their evolution with various herbivorous enemies. The development of resistant germplasm is an important factor for the success of the overall scheme of integrated pest management.

We report here the evaluation of sorghum germplasm for resistance to FAW in the whorl-stage and in the panicle-stage of plant development. The genotypes used in this study were plant introductions that had been converted to day-length-sensitive types (Stephens et al. 1967). Characterization of the potential of new germplasm as sources of pest resistance should be useful for breeding programs.

MATERIALS AND METHODS

The FAW larvae used in this research were reared at the USDA Insect Biology and Population Management Research Laboratory at Tifton, Georgia using the procedures described by Perkins (1979). The sorghum genotypes are originally from different parts of the world including Ethiopia, India, Mexico, Nigeria, Pakistan, Sudan, South America, South Africa, Tanzania, USA, Yemen, and Zimbabwe. The sorghum entries were obtained from the Texas Agricultural Experiment Station at Lubbock after they had been converted to day-length-sensitive types for subtropical use (Stephens et al. 1967). Separate field experiments to determine whorl- and panicle-stage resistance in the converted sorghums to FAW were conducted in 1988 at the Coastal Plain Experiment Station Research Farm at Tifton, Georgia.

Whorl-Stage Resistance Test. The study was conducted on a sandy loam soil (pH ca. 6.4) to which 448 kg ha^{-1} of 5-10-15 (N-P-K) fertilizer was incorporated prior to sorghum planting. Conventional tillage procedures were employed and plots were irrigated as needed. On May 13, 1988, 340 newly converted sorghums were planted in single rows of 3 m x 76.2 cm. A randomized complete block design with two replications was used. Seeding rate was 5-6 seeds/30.5 cm row. Plants were thinned to a density of 15 to 20 plants per row. A seedling-stage resistant [1821 (CIMMYT)] and susceptible [Huerin] cultivars (Wiseman & Lovell 1988) were used as checks. The sorghums were infested with 2 applications of 25 FAW neonates/plant into the whorl using a mechanical larval dispenser (Wiseman et al. 1980). Applications were made 38 and 39 days after planting. Most of the sorghum lines were in the growth stage (GS) 3 or early GS 4 at time of infestation; but a few were in the GS 5 (Vanderlip & Reeves 1972). Visual insect damage ratings were taken (average of two independent ratings) at 7 and 14 days after infestation (DAI). A 0-9 scale permitted a separation of relative differences in resistance into resistant (0-3), intermediately resistant (4-6), and susceptible (7-9) categories (F. M. Davis, USDA, Mississippi State, MS, personal communication).

Panicle-Stage Resistance Test. A separate planting of the converted sorghum entries for evaluating panicle-stage resistance to feeding by FAW larvae was made on May 16, 1988 using the same procedures as described above. Panicle-stage resistant (Northrup King Savanna 5) and susceptible (Funk H-5245) cultivars (Wiseman et al. 1986) also were included. Prior to the initiation of flowering (between GS 5 and GS 6), the panicle of each plant was infested with ca. 50 FAW neonates using the mechanical larval dispenser. Larvae were maintained on the plant at time of infestation by tihtly securing a paper shoot-bag around the base of the panicle just prior to infesting (Wiseman 1989). Establishment/panicle by FAW was determined at 4 DAI. Since germination was not uniform for the different germplasm, counts of larvae were made on 5-15 panicles/entry/replication. Size of the larvae in each panicle was also visually scored as small (<5 mg), medium (6-15 mg), or large (>15 mg) based on weights of several field samples.

Statistical Analysis. Data were subjected to analysis of variance (SAS 1985) and means were separated at the 5% level using the Waller-Duncan multiple range test (Waller & Duncan 1969). The larval establishment data were transformed to $\log_{10}$ for analysis of variance.

TABLE 1. FALL ARMYWORM LEAF-FEEDING DAMAGE TO CONVERTED SORGHUMS AT 7 AND 14 DAYS AFTER ARTIFICIAL INFESTIONS (DAI), TIFT CO., GA, 1988[1].

Entry	Country of origin	$\bar{x}$ injury rating[2]	
		7 DAI	14 DAI
1821 cm (Res. check)	Sudan	5.0 abc	7.0 ab
IS 7565C	Nigeria	6.5 a	5.0 cdef
IS 7757C	Nigeria	6.0 ab	5.0 cdef
IS 3169C	South Africa	5.0 abc	5.0 cdef
IS 12678C	Nigeria	4.5 bc	5.0 cdef
IS 7715C	Nigeria	4.5 bc	4.0 efgh
IS 628C	South America	4.0 c	5.0 cdef
IS 2401C	USA	4.0 c	4.5 defg
IS 7382C	Nigeria	4.0 c	4.5 defg
IS 7438C	Nigeria	4.0 c	4.0 efgh
IS 1333C	Tanzania	4.0 c	4.0 efgh
IS 3612C	Nigeria	4.0 c	4.0 efgh
IS 2246C	India	3.5 cdef	4.5 defg
IS 7367C	Nigeria	3.5 cdef	4.5 defg
IS 3598C	Sudan	3.5 cdef	4.0 efgh
IS 1056C	India	3.5 cdef	4.0 efgh
IS 7498C	Nigeria	3.5 cdef	3.5 fgh
IS 1151C	India	3.0 defg	4.0 efgh
IS 6964C	Sudan	3.0 defg	5.5 bc
IS 3552C	Sudan	3.0 defg	6.5 bc
IS 12679C	Nigeria	3.0 defg	6.5 bc
IS 4023C	India	3.0 defg	7.0 ab
IS 7947C	Nigeria	3.0 defg	3.5 fgh
IS 7399C	Nigeria	3.0 defg	6.0 bc
IS 2177C	India	3.0 defg	8.0 a
IS 7695C	Nigeria	3.0 defg	3.0 gh
IS 7301C	Nigeria	2.5 efgh	3.0 gh
IS 7794C	Nigeria	2.5 efgh	5.5 bc
IS 6962C	Sudan	2.5 efgh	4.5 def
IS 7273C	Nigeria	2.5 efgh	4.0 efgh
IS 7724C	Nigeria	2.0 fgh	3.0 gh
IS 2541C	Sudan	2.0 fgh	5.0 c
IS 12680C	India	2.0 fgh	3.5 fgh
IS 7013C	Sudan	1.5 gh	2.5 h
IS 12633C	Ethiopia	1.5 gh	2.5 h
IS 7444C	Nigeria	1.5 gh	4.0 efgh
IS 12573C	Sudan	1.0 h	4.5 def
IS 6984C	Sudan	1.0 h	3.0 gh
IS 7668C	Nigeria	1.0 h	5.5 bc

[1] Ratings followed by the same letter within a column are not significantly different ($P>0.05$; Waller and Duncan's [1969] multiple range test).

[2] Based on a visual rating scale of 0-9: for rating 7 DAI, 0 = no damage and 9 = many elongated lesions on whorl and furl leaves plus elongated or irreular portions of the furl leaves eaten including basal membrane; for rating 14 DAI, 0 = no damage and 9 = plants almost totally destroyed (F. M. Oavis. USDA, Mississippi State, Miss., personal communication). Visual ratings were made 7 and 14 days after infestation on a plot basis of ca. 15-20 plants/entry with 2 replications.

RESULTS AND DISCUSSION

More than 20 sorghum entries had significantly lower damage ratings than the resistant check at 7 DAI and over 30 entries had significantly less damage than the resistant check at 14 DAI (Table 1). The distribution of the converted sorghum entries based on the leaf-feeding damage for ratings at 7 DAI and 14 DAI is reported in Table 2. Thirty-five entries were rated resistant (<4 rating) to FAW feeding 7 DAI, but only 10 entries maintained that rating 14 DAI. Damage by leaf-feeding did not increase after 7 days on these lines.

More of the sorghum entries were rated susceptible or highly susceptible to FAW leaf-feeding at 14 DAI than at 7 DAI and, thus, a higher frequency of susceptibility was observed at 14 DAI than at 7 DAI (Table 2). However, several damaged entries exhibited tolerance and produced panicles. Also, the early maturing entries grew rapidly through the whorl-stage and FAW larvae did not feed beyond initial establishment as indicated by only pin-hole feeding at 14 DAI.

Significant differences were found among the entries for the number of FAW larvae that established/panicle 4 DAI. However, none of the sorghum introductions had significantly lower larval establishment than the resistant check, and only 3 entries had establishment levels significantly lower than those of the susceptible check (Table 3). Approximately 6 and 15 larvae were counted/panicle on the resistant and susceptible check, respectively. Fourteen entries had establishment levels of <5 larvae/panicle (Tables 3 and 4), while 97 entries had levels of FAW larval establishment of 5-10 per panicle (Table 4). The entries with a larval establishment count between 10 to 15 had the highest frequency. More than 25 larvae/panicle were observed for only 8 entries.

Fewer medium to large larvae were found on panicles of sorghums in which resistance to FAW was a result of non-establishment. In such germplasm as the resistant

TABLE 2. DISTRIBUTION OF DAMAGE RATINGS OF FALL ARMYWORM ON LEAVES OF CONVERTED SORGHUMS AT 7 AND 14 DAYS AFTER ARTIFICIAL INFESTATIONS (DAI), TIFT CO. GA, 1988.

Damage Ratings Class		Distribution of Damage Ratings[1]			
		No. of entries in Class		Frequency of class	
		Rating 7 DAI	Rating 14 DAI	Rating 7 DAI	Rating 14 DAI
0-2		6	0	0.018	0
2-3		7	2	0.021	0.006
3-4		22	8	0.065	0.024
4-5[2]		79	15	0.232	0.044
5-6		126	28	0.371	0.082
6-7[3]		83	57	0.244	0.168
7-8		17	110	0.050	0.324
8-9		0	120	0	0.353
	C.V.	18	13		
	Total	340			

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[1] Based on a visual rating scale of 0-9: for rating 7 DAI, 0 = no damage and 9 = many elongated lesions on whorl and furl leaves plus elongated or irregular portions of the furl leaves eaten including basal membrane; for rating 14 DAI, 0 = no damage and 9 = plants almost totally destroyed (F. M. Davis, USDA, Mississippi State, Miss., personal communication). Ratings were made 7 and 14 days after infestation, respectively, on a plot basis of ca. 15-20 plants/entry with 2 replications.

[2] Class of the resistant check [1821 (CIMMYT)] for rating 7 DAI.

[3] Class of the resistant check [1821 (CIMMYT)] for rating 14 DAI.

TABLE 3. FALL ARMYWORM LARVAE ESTABLISHMENT/PANICLE OF CONVERTED SORGHUMS AT 4 DAYS AFTER ARTIFICIAL INFESTATIONS, TIFT CO., GA, 1988[1].

Entry	Country of origin	x̄ no. of larvae/ panicle[2]
Funk H-5245 (Suscep. check)	USA[3]	15.0 ab
NK Savanna 5 (Res. check)	USA[3]	6.0 abcd
IS 7668C	Nigeria	8.5 abcd
IS 7498C	Nigeria	7.0 abcd
IS 1477C	India	4.5 abcd
IS 7595C	Nigeria	4.5 abcd
IS 2549C	Ethiopia	4.5 abcd
IS 6404C	India	4.0 abcd
IS 7518C	Nigeria	4.0 abcd
IS 2508C	Sudan	3.5 abcd
IS 2740C	Uganda	3.5 abcd
IS 2478C	Ethiopia	3.5 abcd
IS 12543C	Ethiopia	3.5 abcd
IS 6411C	India	3.0 abcd
IS 1387C	India	2.5 bcd
IS 530C	Nigeria	2.0 cd
IS 3072C	Sudan	2.0 cd
SC 972C	Sudan	2.0 d

[1] Means followed by the same letter are not significantly different (P>0.05; Waller & Duncan's [1969] multiple range test).

[2] Transormed back to actual numbers from log transformations used for analysis of variance. FAW larvae establishment/panicle was counted 4 DAI. Counts were based on 5-15 panicles/entry with 2 replications.

[3] Commercial industry USA.

TABLE 4. DISTRIBUTION OF FALL ARMYWORM LARVAE ON DEVELOPING PANICLES OF CONVERTED SORGHUMS AT 4 DAYS AFTER ARTIFICIAL INFESTATIONS, TIFT CO., GA, 1988.

No. of larvae/panicle class[1]		No. of entries in class	Frequency of class
0-5		14	0.042
5-10[2]		97	0.289
10-15		118	0.351
15-20[3]		70	0.208
20-25		29	0.086
25-30		3	0.009
30-35		2	0.006
35-40		1	0.003
40-45		1	0.003
45-50		1	0.003
	CV	21	
	Total	336	

[1] FAW larvae establishment/panicle was counted 4 days after infestation. Counts were based on 5-15 panicles/entry with 2 replications.

[2] Class of the resistant check, NK Savanna 5.

[3] Class of the susceptible check, Funk H-5245.

TABLE 5. DISTRIBUTION OF FALL ARMYWORM LARVAL SIZE ON DEVELOPING PANICLES OF CONVERTED SORGHUMS AT 4 DAYS AFTER ARTIFICIAL INFESTATIONS, TIFT CO., GA, 1988.

Larva size/panicle class[1]	No. of entries in class	Frequency of class
Small[2]	34	0.101
Medium	70	0.208
Large	66	0.196
Small/Medium	55	0.164
Small/Large	19	0.057
Medium/Large[3]	77	0.229
Small/Medium/Large	15	0.045
Total	336	

[1] FAW larva size for each panicle was determined 4 days after infestation. Classes were defined as follows: Small = <5 mg, Medium = 6-15 mg, Large = >15 mg.

[2] Class of the resistant check, NK Savanna 5.

[3] Class of the susceptible check, Funk H-5245.

check (NK Savanna 5), where antibiosis has been reported as the major cause of resistance (Wiseman et al. 1986), the larvae observed/panicle were usually small though sometimes numerous (Tables 4 and 5). Entries such as the susceptible check (Funk H-5245) had a relatively high number of medium to large size larvae/panicle. 'International sorghum (IS) 7498 converted (C)', and 'IS 7668C' showed some degree of both whorl- (ratings of 3.5 and 1.0, respectively) and panicle-stage (7.0 and 8.5 larvae/panicle) resistance.

Visual ratings of whorl damage and counts of the number of FAW larvae that established/panicle provide an indication of both whorl- and panicle-stage resistance in the converted sorghum introductions. However, the more promising entries need to be re-evaluated and the mechanism(s) of resistance need to be investigated in more detail.

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SEASONAL CHANGES IN BAIT PREFERENCE BY RED IMPORTED FIRE ANT, *SOLENOPSIS INVICTA* (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

Bait stations were established in four different vegetational habitats near Houston, Texas, to attract *Solenopsis invicta* Buren, the red imported fire ant (RIFA). Bait preferences were compared in each habitat for each monthly 24-h sampling period. Foragers located both the high carbohydrate and high protein baits, but greater numbers were recruited to the carbohydrate bait during the sampling periods of the year registering lower temperatures (mean = 17°C). In contrast, when the seasonal temperatures were greater (mean = 25°C), RIFA's were collected in higher numbers on the proteinaceous bait. These findings must be considered when planning a field research project to collect RIFA's.

RESUMEN

Para atraer a la hormiga de fuego roja importada, *Solenopsis invicta* Buren, se establecieron estaciones con cebos en cuatro diferentes habitats vegetacionales en los alrededores de Houston, Texas. Se compararon las preferencias por los cebos en cada habitat para cada período de muestreo (mensual-24 horas). Las forrajeras localizaron tanto los cebos ricos en proteinas como los ricos en carbohidratos, pero mayores números fueron atraidos hacia los cebos de carbohidratos durante los períodos de muestro que registraron temperaturas más bajas (media = 17°C). En contraste, cuando las temperaturas estacionales fueron más alta (media = 25°C), se colectaron mayores números

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de hormigas en los cebos proteicos. Estos resultados deben ser considerados al planear colectar *S. invicta* en proyectos de investigación en campo.

The red imported fire ant (RIFA), *Solenopsis invicta* Buren, was introduced into the United States in the 1940's from South America (Lofgren et al. 1975). The range of the RIFA now encompasses ca. 93-101 million ha of the southern United States, including most of eastern and central Texas (Lofgren 1986a, D. P. Wojcik, personal communication). RIFA colonies are characterized by large mounds and the mass recruitment of worker ants to food sources (Lofgren et al. 1975, Wilson 1962).

Food collection is the major objective of RIFA foraging activity. RIFA's are opportunistic omnivores (Lofgren et al. 1975, Lofgren 1986b) that feed on alive and dead insects and other animal material (Hays & Hays 1959, Wilson & Oliver 1969), tend Homoptera for honeydew (Nielsson et al. 1971, Adams 1986, Wojcik 1986), and feed on various plants (reviewed by Adams 1986, Lofgren 1986b). RIFA's have been called an "oil-loving" species (Hays & Arant 1960, Lofgren et al. 1961, 1964), and oils have been incorporated in baits used for chemical control (Banks et al. 1978).

Fats, proteins, and carbohydrates attract RIFA foragers in the laboratory. However, foraging RIFA's exhibit little attraction to dry foods, or to foods that contain a minimum amount of liquid (Lofgren et al. 1961). Glunn et al. (1981) reported that sugar (0.1 M sucrose) was preferred over both 1:10 casein hydrolysate and soy oil, and feeding rates for aqueous solutions (sucrose and casein hydrolysate) were 7 to 10 times greater than for soy oil.

Field RIFA colonies in Florida showed great variation in their preference for carbohydrate, protein, and lipid foods (1.0 M sucrose, rat serum, and unrefined soybean oil, respectively) (Glunn et al. 1981). Seven different food preference hierarchies occurred among 10 colonies in April and May. In general, all colonies had a mean preference for oil, serum, and sucrose in decreasing order. However, greater time spent at the oil bait may not have reflected the volume of food consumed or returned to the colony.

In a June field study in Louisiana (Ali & Reagan 1986), molasses was more attractive than peanut oil to RIFA foragers when exposed over short exposure periods (30 min). However, peanut oil was more attractive and resulted in more ant recruitment when baits were exposed for a longer duration (120 min). The study also indicated that foragers were nonselective and searched for both carbohydrate and protein sources during June.

Food preference changes with time, long-term feeding history, stage and presence of brood, colony age, caste composition, and weather. For example, foragers gathered more protein for the colony when brood was present (Sorensen et al. 1983b) and fed it directly to larvae (Sorensen et al. 1983a). After a rainfall when RIFA's were rebuilding their mounds, a high rate of foraging for sucrose was observed by Glunn et al. (1981). Increased work output may have required more "adult food." Also, the materials upon which colonies had previously fed and food availability altered colony food preferences.

Tissue protein, lipid, and glycogen contents of field colony workers change during different periods of the year (Ricks & Vinson 1972). During early summer when brood production was greatest, worker tissue protein and lipid content decreased as these materials were distributed to the developing brood. Worker tissue protein content peaked in the fall and was correlated with cessation of colony brood production. A fall buildup of tissue lipid may have been important as an overwintering energy source. Glycogen content increased slightly during the summer months and was used probably as a food reserve during the cooler months (Ricks & Vinson 1972).

The major objectives of this research were to determine if foraging RIFA's prefer a high carbohydrate or a high protein bait, and if preferences change during a 12-month study in selected habitats.

MATERIALS AND METHODS

The study was conducted at the Sienna Plantation near the town of Arcola in Fort Bend Co., Texas. The Sienna Plantation is ca. 20 km southwest of Houston and is in the Gulf Prairie and Marshes vegetational region of Texas (Correll & Johnston 1970). Research plots were established in four habitats with designations based on major plant associations. Each habitat site was two to three km distant from other habitats.

The first habitat was designated as dense forest. Sugarberry (*Celtis laevigata* Willd.), cedar elm (*Ulmus crassifolia* Nutt.), and pecan [*Carya illinoensis* (Wangenh.) K. Koch] were the dominant tree species, and the understory consisted of mixed grasses and broadleaved plants. The second habitat was designated as lowland pasture and consisted mainly of several genera of broadleaved plants dominated by snow-on-the-prairie (*Euphorbia bicolor* Engelm. & Gray). The lowland pasture site was less than 1 km from the Brazos River. The third habitat was designated as forest-with-pasture. The forest section was similar in species composition to the dense forest; the pasture section was dominated by blackberries (*Rubus* spp.) and bermuda grass [*Cynodon dactylon* (L.) Pers.]. The fourth habitat was designated as upland pasture, and common carpetgrasses (*Axonopus* spp.) and paspalum grasses (*Paspalum* spp.) were the dominant species (P. Grissom, personal communication). The pastures were mowed once or twice a year, and all sites were grazed by cattle.

Within each habitat, three rectangular bait attraction plots were established >30 m apart. Each 45 x 75 m plot consisted of 24 bait stations spaced on 15 m centers from each other. Each bait station consisted of two 36-ml plastic bait cups spaced 30 cm apart.

TABLE 1, NUMBERS OF RED IMPORTED FIRE ANT WORKERS, *SOLENOPSIS INVICTA* BUREN, COLLECTED IN FOUR HABITATS IN FORT BEND COUNTY, TEXAS, JULY 1985 THROUGH JUNE 1986.

		Habitat[1]				
	Month	Dense Forest	Lowland Pasture	Forest with Pasture	Upland Pasture	TOTAL
1985	July	5474 abc	23 310 ab	36 079 a	32 007 b	96 870
	Aug.	9377 a	28 186 a	33 411 a	40 745 a	111 719
	Sept.	6192 ab	22 053 b	23 707 b	25 260 c	77 212
	Oct.	2942 bcd	1807 de	5408 c	2118 f	12 275
	Nov.	1698 cd	1975 de	408 c	1758 f	5839
	Dec.	1 d	2 e	0 c	102 f	105
1986	Jan.	55 d	2664 de	510 c	3247 f	6476
	Feb.	58 d	2444 de	785 c	1767 f	5054
	Mar.	78 d	3026 de	1144 c	4392 ef	8640
	Apr.	12 d	6514 d	5076 c	12 762 d	24 364
	May	3255 bcd	18 053 bc	19 701 b	25 124 c	66 133
	June	2473 bcd	13 181 c	17 041 b	10 291 de	42 986
TOTAL		31 615	123 215	143 270	159 573	457 673

[1] Numbers followed by the same letter within habitats are not significantly different. ANOVA, LSD (P>0.05).

One cup contained a mixture of agar and grape jelly (Welch's; 1.25 cm cube), and the other cup contained 7.5 ml of tuna fish cat food (Topco brand). The first bait consisted mainly of carbohydrates (> 50%; Welch's, Concord, MA 01742, personal communication). The tuna cat food bait was packed in water and contained no added oil (Topco Assoc., Skokie, IL. 60076, personal communication). Tuna canned in water contains ca. 70% water, 28% protein, and 1% fat by weight (Leveille et al. 1983).

Bait cups were placed at three randomly designated bait stations within each plot and, after a 3-h interval, were collected, and newly baited cups were placed at three other randomly designated bait stations. Arthropods within cups were collected by quickly placing a tight-fitting lid on each cup. This procedure continued for a 24-h cycle and was repeated in all three plots in each habitat at approximately the same time. Before each collection, soil surface temperatures were measured by a thermometer at each habitat, and general climatic conditions and precipitation were recorded. The arthropods in cups were frozen for later identification and enumeration. Cups from which all bait was removed or missing and cups that were gnawed by scavenging vertebrates were omitted from the analysis. Sampling procedures were repeated each month from July 1985 through June 1986.

The total number of RIFA's collected from each habitat each month was tabulated, and monthly data within habitats were compared by ANOVA and LSD ($P=0.05$). The percentages of RIFA's collected in each bait type for each 24-h period were analyzed by chi-square ($P=0.05$) to test the hypothesis of equal bait preferences during each monthly sample within each habitat.

RESULTS AND DISCUSSION

A total of 457,673 RIFA's was collected during the study (Table 1). The greatest number was collected in the upland pasture habitat, and the least collected in the dense forest habitat. As expected, the greatest number was collected during the warmest sample period (August; mean = 30.8°C), and the least in December (mean = 11.6°C), the coolest sample period. The same trend was evident within each habitat.

Significant RIFA bait preferences ($P < 0.05$) were detected in each monthly sample period, except in December and May, in the dense forest habitat (Table 2). Bait preference could not be measured in December because of the sample size which violated Cochran's (1954) rule. Grape agar bait was preferred by RIFA's from October through February and in April in the dense forest habitat when the mean soil surface temperature during the 24-h sampling periods ranged between 12.5 and 25.0°C. Greater numbers of RIFA's were collected on tuna cat food during the months when the mean soil surface temperature during the 24-h sampling periods ranged between 27.0 and 29.0°C.

Significant RIFA bait preferences ($P < 0.05$) were detected in each month except November and December in the lowland pasture habitat (Table 2). The grape jelly agar bait was preferred during the January and February sampling periods when the mean soil surface temperature was 16.0 and 17.0°C, respectively. During the March through October sampling periods, when the mean soil surface temperature ranged between 12.0 and 31.0°C, the tuna cat food bait was preferred.

Significant bait preferences ($P < 0.05$) were detected each month in the forest-with-pasture habitat (Table 2) except in December, when no RIFA's were collected. The grape jelly agar bait was preferred during the January and February sampling periods (mean soil surface temperature equaled 15.0 and 17.0°C, respectively). During the March through November sampling periods when the mean soil surface temperature ranged between 11.0 and 30.0°C, the tuna cat food was preferred.

Grape jelly agar was preferred ($P < 0.05$) by RIFA's during the October through February sampling periods in the upland pasture habitat (Table 2) when the mean soil

TABLE 2. PERCENT OF TOTAL RED IMPORTED FIRE ANT WORKERS, *SOLENOPSIS INVICTA*, COLLECTED IN GRAPE JELLY AGAR AND TUNA CAT FOOD BAITS DURING EACH MONTHLY SAMPLING PERIOD IN EACH HABITAT IN FORT BEND COUNTY, TEXAS, JULY 1985 THROUGH JUNE 1986.

		Habitat[1] and Bait Type							
		Dense Forest		Lowland Pasture		Forest with Pasture[2]		Upland Pasture	
	Month	jelly	tuna	jelly	tuna	jelly	tuna	jelly	tuna
1985	July	22	78	1	99	4	96	1	99
	Aug.	33	67	1	99	10	90	21	79
	Sept.	23	78	1	99	4	96	1	99
	Oct.	98	2	2	98	11	89	72	28
	Nov.	100	0	58	42§	0	100	99	1
	Dec.	100	0§	50	50§	—	—	100	0
1986	Jan.	100	0	98	2	100	0	100	0
	Feb.	100	0	98	2	97	3	100	0
	Mar.	3	97	0	100	2	98	6	94
	April	100	0	1	99	6	94	1	99
	May	50	50§	1	99	6	94	1	99
	June	19	81	1	99	2	98	2	98

[1] Percents followed by § within a month and habitat are not significantly different (Chi-square; $P > 0.05$).
[2] No RIFA's were collected in December.

surface temperature ranged between 11.0 and 24.0°C. During the March through September sampling periods, the tuna cat food was the preferred bait. Mean soil surface temperature ranged between 15.0 and 33.0°C during the period.

In general, more RIFA's were attracted to and recruited in greater numbers to the grape jelly agar bait during periods of lower soil surface temperatures (mean = 17°C). Perhaps carbohydrates were needed by colonies for maintenance during periods of colder temperatures, and few natural sources of sugars were available. In contrast, when the mean soil surface temperatures were warmer (mean = 25.4°C), RIFA's were collected in higher numbers in the tuna cat food bait. Because most colony growth occurs during the warmer parts of the year (Markin et al. 1973) and during this time proteinaceous food collected is given preferentially to the developing brood (Sorensen et al. 1981, Vinson 1968), the present research supports the hypothesis of greater recruitment to protein food sources during periods of colony brood production.

These conclusions must be considered when planning a research program. A sampling study during a warm season may be more successful if a proteinaceous bait type is used; whereas, a carbohydrate bait may collect more RIFA's during the cooler months of the year.

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COLORED SPHERICAL TRAPS FOR CAPTURE OF CARIBBEAN FRUIT FLY, *ANASTREPHA SUSPENSA*

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ABSTRACT

Colored spheres of five different sizes (6.3, 8.9, 14.0, 16.5, 20.0 cm diam) and five colors (orange, black, yellow, green, white) were coated with a trapping compound and presented to field-caged flies (males, virgin females, mated females). The most females were captured on the 20 cm orange, green, and white balls and the 8.9 cm yellow ball. There was no statistically significant preference on the part of males for any particular size or color. When the four most attractive spheres were presented simultaneously to mated and virgin females they were most likely to be captured on 20.0 cm orange and green spheres. More males were caught on the 20.0 cm orange ball. When data were summed, 20.0 cm orange balls were statistically superior overall. In a field release test, 20.0 cm orange balls, 20.0 cm orange balls with a protein hydrolysate bait, 20.0 cm diam orange balls with caged live males, and 10 cm yellow balls with food bait were compared to McPhail traps baited with protein hydrolysate. The orange sphere with males was superior to all the other traps.

RESUMEN

Esferas de cinco tamaños diferentes (6.3, 8.9, 14.0, 16.5, y 20.0 cm de diam.), y de cinco colores (naranja, negro, amarillo, verde, y blanco), se cubrieron con una substancia atrayente y ofrecida a moscas en jaulas en el campo (machos, hembras vírgenes, y hembras fertilizadas). Se capturaron más hembras en las esferas color naranja, verdes y blancas de 20 cm, y la amarilla de 8.9 cm. Estadísticamente no hubo ninguna diferencia significante en preferencia por parte de los machos hacia ningún tamaño o color en particular. Cuando las cuatro esferas más atractivas se les ofreció simultaneamente a hembras fertilizadas y vírgenes, fue mas probable que se capturaron en esferas de color naranja y verdes de 20.0 cm. Se capturaron más machos en la esfera color naranja de 20.0 cm. Cuando se sumaron las cifras, las esferas color naranja de 20.0 cm fueron generalmente estadísticamente superior. En una prueba de liberación en el campo, las esferas color naranja de 20.0 cm, esferas color naranja de 20.0 cm con un cebo de proteina hidrolisada, esferas color naranja de 20.0 con machos vivos enjaulados, y esferas amarillas de 10.0 cm con cebos de comida, se compararon a trampas de McPhail cebadas con proteina hidrolisada. La esfera color naranja con machos fue superior a todas las otras trampas.

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Esferas de cinco tamaños diferentes (6.3, 8.9, 14.0, 16.5, y 20.0 cm de diam.), y de cinco colores (naranja, negro, amarillo, verde, y blanco), se cubrieron con una substancia atrayente y ofrecida a moscas en jaulas en el campo (machos, hembras vírgenes, y hembras fertilizadas). Se capturaron más hembras en las esferas color naranja, verdes y blancas de 20 cm, y la amarilla de 8.9 cm. Estadísticamente no hubo ninguna diferencia significante en preferencia por parte de los machos hacia ningún tamaño o color en particular. Cuando las cuatro esferas más atractivas se les ofreció simultaneamente a hembras fertilizadas y vírgenes, fue mas probable que se capturaron en esferas de color naranja y verdes de 20.0 cm. Se capturaron más machos en la esfera color naranja de 20.0 cm. Cuando se sumaron las cifras, las esferas color naranja de 20.0 cm fueron generalmente estadísticamente superior. En una prueba de liberación en el campo, las esferas color naranja de 20.0 cm, esferas color naranja de 20.0 cm con un cebo de proteina hidrolisada, esferas color naranja de 20.0 con machos vivos enjaulados, y esferas amarillas de 10.0 cm con cebos de comida, se compararon a trampas de McPhail cebadas con proteina hidrolisada. La esfera color naranja con machos fue superior a todas las otras trampas.

Colored spheres attract tephritid fruit flies of several genera (*Rhagoletis*, Prokopy [1975]; *Ceratitis*, Nakagawa et al., [1978]; *Anastrepha*, Cytrynowicz et al. [1982]; *Toxotrypana.*, Landolt et al. [1988]). So strong is the reaction of some species to particular sizes and hues that, once coated with a trapping compound, colored spheres alone can serve as a sufficient means of control (Prokopy 1975). When combined with chemical attractants, either host cues, parapheromones, or pheromones, the ability of spheres to attract fruit flies is often enhanced (Swift 1982, Nakagawa et al. 1978, Landolt et al. 1988).

The standard means of monitoring the distribution of the Caribbean fruit fly, *Anastrepha suspensa* (Loew), is the McPhail trap, an invaginated glass bottle containing a solution of protein hydrolysate in water. Entomologists experienced in tephritid studies consider the McPhail trap baited with a food lure to be relatively less efficient than parapheromone baited traps developed for the capture of other species of fruit flies (C. O. Calkins, personal communication, see Sivinski & Calkins 1986). The following study describes sphere sizes and colors that were effective in trapping field-caged Caribbean fruit flies. In a field-release test, several alternative sphere traps were compared to the McPhail trap.

METHODS AND RESULTS

The search for a Caribbean fruit fly sphere trap was undertaken in three stages: 1) to discover if different size spheres of a certain color are more attractive than others to flies in field cages; 2) to simultaneously compare in field cages the most attractive colored spheres discovered in experiment 1; and 3) to compare the attractive spheres by themselves and in conjunction with food lures and pheromone-producing males to the food-baited McPhail trap using released flies in the field.

Experiment 1. Relationship Between Size and Color.

Experiments were conducted at the USDA/ARS Insect Attractants, Behavior, and Basic Biology Research Laboratory at Gainesville, Florida, during the months of March-August. Flies were obtained from a colony maintained at the Laboratory for more than 10 years. Mated females (i.e. >12 days old and held since eclosion with males) and >12-day-old males were placed in 2.9 m X 2 m screen-mesh field cages erected in a shady woods on the laboratory grounds. The insects had been sterilized by exposure to 5 kR of radiation 24-28 h before eclosion. This is more than sufficient dosage for sterilization (Calkins et al. 1988; for details of irradiation see Webb et al. 1987), and was done to prevent infestations of local fruit by escapees. Due to equipment and space constraints, virgin females (>12 days old and separated from males at eclosion) were released into a 2.3 X 2.4 m field cage inside a greenhouse. In all instances, 100 insects were put into the cages at 0900 H and the traps and uncaught flies were removed at 1600 h.

At any one time, males and mated females were presented with five styrofoam balls (6.3 cm diam, 8.9 cm diam, 14 cm diam, 16.5 cm diam, 20.0 cm diam) of one of the following colors, orange (glowing sunset by Krylon, Columbus, OH), saturn yellow (Day Glo, Cleveland, OH), gloss black (Ace, Oak Brook, IL), gloss white (Ace), and signal green (Day Glo). Colors were chosen on the basis of previous tephritid work. *Anastrepha fraterculus* (Wied.) and the Mediterranean fruit fly, *Ceratitis capitata* (Wied.), are known to be attracted to black and yellow spheres (Nakagawa et al. 1978). The papaya fruit fly, *Toxotrypana curvicauda* Gerstäcker, comes to green spheres (Landolt et al. 1988), and *A. suspensa* is attracted to flat surfaces colored orange (Greany et al. 1977). Painted spheres were coated with the sticky trapping component, Tack Trap (Animal Repellents, Inc., Griffin, GA). Balls were spaced equidistantly, 25 cm from the margin of the cage. Five replicates of each color were presented and the position of the balls rotated each replicate so that each ball occupied each location once.

Because a different sized field cage was used to hold virgin females, they were exposed to a different regime of ball presentation. The colors were identical to the above, but only three size categories at a time were hung in the cage. The two sets of balls consisted of 8.9, 14.0, 16.5 cm diam spheres, followed by 14, 16.5, 20 cm diam balls. Thus, the 8.9 and 20 cm diam balls were presented three times, and the 14 and 16.5 cm diam balls six times; 6.3 cm balls were not presented. Statistical analysis was performed by two factor analysis of variance (SAS Institute 1982). Because a strong interaction was discovered between size and color, each combination of color and size was considered a separate factor of the variable color/size. Means were separated by Duncan's multiple range test (SAS Institute 1982).

Results:

There was no significant relationship between male capture and ball color ($p = .08$) or size ($p = 10$; Table 1). However, there were highly significant differences in female captures (color, virgin $p = .0003$, mated $p = .001$; size, virgin $p = .001$, mated $p = .0003$ (Table 1)). There were highly significant interactions between color and size (virgin $p = .0001$; mated $p = .006$). For instance, orange on large balls had the highest numerical values for both female types but other colors (e.g. yellow) had higher mean captures on smaller spheres. The highest captures of virgin females were on 20.0 cm orange, green, and white balls. More mated females were taken on 20.0 cm orange and green balls and 9.0 cm yellow balls.

TABLE 1. THE MEAN NUMBER (STANDARD ERROR) OF FLIES TRAPPED ON VARIOUS SIZES AND COLORS OF SPHERES.

	Sphere diam (cm)				
Color	6.3	8.9	14	16.5	20
			Males		
Orange	12.6(3.4)	17.6(5.5)	17.2(4.4)	18.0(5.0)	23.6(10.2)
Green	17.4(2.3)	19.6(5.7)	11.8(0.4)	14.2(4.3)	21.0(10.8)
Yellow	6.4(1.2)	5.6(2.0)	9.6(1.5)	16.6(3.1)	22.8(4.0)
Black	9.6(4.5)	11.8(4.0)	14.2(7.0)	14.8(5.1)	9.2(3.2)
White	5.6(2.7)	3.4(1.6)	13.2(5.1)	17.2(6.4)	12.6(10.1)
			Virgin Females		
Orange	—	10.7(0.9)	17.7(2.3)	37.3(6.6)	59.3(2.7)a[1]
Green	—	8.8(2.5)	7.3(1.0)	24.0(5)	50.0(1.2)a
Yellow	—	10.3(1.3)	21.3(5.9)	21.0(4.2)	22.3(4.9)
Black	—	15.3(2.4)	13.5(6.5)	31.0(4.2)	33.3(7.8)
White	—	10.0(3.1)	4.3(1.5)	15.8(3.9)	51.7(5.3)a
			Mated females		
Orange	11.5(2.5)	5.8(1.4)	10.4(2.2)	12.4(1.2)	23.4(7.7)a
Green	7.2(1.7)	6.0(3.4)	5.4(2.2)	8.8(1.8)	19.4(4.0)a
Yellow	12.3(3.7)	20.0(2.6)	18.6(2.4)a	8.8(2.6)	13.6(4.0)
Black	6.2(1.0)	10.4(1.3)	8.2(1.8)	8.2(1.5)	5.4(1.3)
White	2.4(0.9)	0.0(0.0)	0.6(4.0)	1.8(1.1)	7.2(1.3)

[1] Means marked with an 'a' are statistically identical yet significantly greater than other means in the same sexual category.

Experiment 2: Comparison of Most Effective Colors/Sizes.

Since the various colors were presented separately in experiment 1, it was considered prudent to simultaneously compare the most effective size and color combinations. The most effective colors and combination size for the capture of females were the 9.0 cm yellow and the 20 cm orange, green and white spheres, (male preference was not significant in regards to size and color in experiment 1). These were placed in an outdoor field cage in a manner similar to that previously described for males and mated females. Initial trap placement was random and spheres were rotated for each replicate. There were eight replicates each of males, virgin females, and mated females. Males were included to see if a statistically clear preference emerged in this different format. Statistical analysis was by analysis of variance and means were separated by Duncan's multiple range test (SAS Institute 1982).

Results:

The efficiency of the various traps was similar for virgin and mated female flies (Table 2). The 20.0 cm orange and green balls captured statistically more females than white and yellow balls. Orange balls were statistically more attractive than any other color for the capture of males and were also more attractive when results from males and females were combined.

Experiment 3: Comparison of Spheres and McPhail Traps.

Field comparisons of various traps were performed in mixed citrus groves on the USDA-ARS, A. H. Whitmore Foundation Farm in Lake County, Florida. Flies were sterilized by exposure to 5 kR of radiation 24 h before eclosion and were 10-18 days old at the time of release (see Webb et al. 1987, Calkins et al. 1988). Of a random sample of 292 flies taken from those to be released, 47% were males and 77% (10 of 13) of the females contained sperm in spermathecae. In addition to McPhail traps baited with protein hydrolysate and water solution (ca. 6.0 g/liter), the following spheres were presented: 20 cm orange with ca. 0.5 liter of the above mentioned protein hydrolysate solution suspended in an open jar 5.0 cm beneath, a 20.0 cm orange with a screen wire cage (7.5 X 6.9 cm) containing 12 mature (10 day old) males suspended beneath it, and a 10.0 cm yellow ball baited with 20 ml of protein hydrolysate solution. The yellow-sphere trap consisted of a plastic ball perforated by numerous large holes. The bait-containing vial was placed inside the sphere. Large orange spheres were chosen because of their overall higher capture rate in Experiment 2 and the neurological evidence that *A. suspensa's* eyes are most sensitive to orange light (Greany et al. 1977). The smaller yellow sphere was included because of its success in Experiment 1 and because if it competed well in this field format it might be

TABLE 2. THE MEAN NUMBER (STANDARD ERROR) OF FLIES TRAPPED ON SPHERES WITH THE MOST SUCCESSFUL SIZE AND COLOR COMBINATION.

	Virgin females	Mated females	Summed females	Males	Summed flies
20 cm Orange	18.3 (.71)a[1]	20.6 (.74)a	19.4 (.35)a	17.4 (1.9)a	18.8 (1.2)a
20 cm Green	17.0 (.82)a	15.6 (.57)a	16.3 (.35)a	11.5 (1.5)b	14.7 (1.1)b
20 cm White	8.3 (.32)b	9 (.57)b	8.5 (.23)b	5.4 (0.8)c	7.5 (0.7)c
8.5 cm Yellow	8.1 (.71)b	8.6 (.64)b	8.4 (.33)b	6.9 (1.2)c	7.9 (0.9)c

[1] Numbers in columns sharing the same letters are not significantly different; Duncan's multiple range test.

cheaper and easier to use on a large scale than 20 cm orange balls. One of each of the above was hung in trees in a pentagon pattern with ca. 11.5 m between different traps. Initial trap placement was random. Four pentagons, each 60 m or more apart, were set up.

Approximately 300 flies were released at ca. 1200 h in the center of each pentagon. On the following day (1130 h), flies were counted and removed from traps, the traps were then rotated and another 300 flies released. There were five replicates, sufficient for each trap to be placed in each location within a pentagon. Data were analyzed with Freidman's random block analysis of variance and the Newman-Keuls procedure (Zar 1974). The sex ratios of captured flies in various traps were compared through analysis of variance (SAS Institute, 1982).

Results:

About 4% of the released flies were captured by traps. There was no statistical difference between any of the traps with the exception of the orange sphere and adult male combinations that caught more flies of both sexes than any of the other traps (Table 3). There was no difference in the sex ratios of flies caught on the traps ($P>0.05$).

DISCUSSION

There are similarities between the responses of *A. suspensa* to colored spheres and those of other tropical tephritids. In *C. capitata* and *A. fraterculus*, as well as *A. suspensa*, the size of a sphere influences the effectiveness of a particular color as an attractant (Cytrynowicz et al. 1982, Nakagawa et al. 1978). For instance, orange was more effective in capturing virgin females on 20.0 cm balls, but among 9.0 cm balls yellow was a more attractive color. A novel quality of *A. suspensa* is its sensitivity to and response to orange in addition to the black and yellow preferred by the other species (see Greany et al. 1977).

The superiority of the 20 cm orange sphere and adult male combination over the McPhail trap suggests that a sphere-pheromone combination might be an improvement over traditional food-bait trap designs. Male-emitted pheromones in the Tephritidae often have broad attractiveness to virgin females and (to some extent) mated females seeking insemination, and to males apparently searching for signaling positions within male mating aggregations (Perdomo 1974, Sivinski & Heath 1988). However, it is not clear to what extent the sphere itself contributes to the success of the sphere-male trap. Males in conjunction with simple sticky cardboard traps also are more attractive than McPhail traps (Perdomo et al. 1976). The question of sphere efficacy might be more profitably posed when and if synthetic *A. suspensa* pheromones are available. It should be kept in mind that the test releases did not include sexually immature flies that might be common in the field and perhaps more likely to respond to a food cue than a pheromone.

TABLE 3. THE MEAN NUMBER (STANDARD ERROR) OF FLIES TRAPPED IN THE FIELD ON VARIOUS TRAP DESIGNS.[1]

	O	O_b	O_m	Y	M
Total	2.1 (2.9) b	0.8 (1.1) b	5.8 (6.3) a	1.2 (1.9) b	2.5 (5.8) b
Males	0.8 (0.9) b	0.4 (0.7) b	2.7 (2.6) a	0.9 (1.7) b	0.7 (1.4) b
Females	1.4 (2.3) b	0.4 (0.9) b	3.7 (4.2) a	0.5 (0.7) b	1.9 (4.5) b

[1] O = 20.3 cm diam orange sphere, O_b = 20.3 cm diam orange sphere with food bait, O_m = 20.3 cm diam orange sphere with mature males, Y = 10 cm yellow sphere with food bait, M = McPhail trap with food bait. Numbers in a row sharing letters are not significantly different.

ENDNOTE

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This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or the recommendation for its use by USDA.

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WATER-ABSORBENT STARCH POLYMER: SURVIVAL AID TO NEMATODES FOR CONTROL OF *DIAPREPES ABBREVIATUS* (COLEOPTERA: CURCULIONIDAE) IN CITRUS

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ABSTRACT

A water absorbent starch polymer apparently increased survival of the entomogenous nematode *Steinernema carpocapsae* (Weiser) applied for control of a root weevil, *Diaprepes abbreviatus* (L.). on roots of *Citrus* sp. Increased mortality of wax moth, *Galleria mellonella* (L.), larvae exposed to soil from the starch polymer/nematode treated area occurred compared with water/nematode treatment alone. Mortality of *D. abbreviatus* larvae buried in the soil on the side of the tree receiving the starch/nematode treatment was 52% compared with 42% for the water/nematode and 0% for the control treatments. Enhanced infection of *G. mellonella* larvae by entomogenous nematodes was apparent for more than 2 months under field conditions.

RESUMEN

Un polímero de fécula absorbente de agua, aparentemente aumentó la sobrevivencia del nemátodo entomógeno *Steinernema carpocapsae* (Weiser) que es usado para el control de la vaquita *Diaprepes abbreviatus* (L.), en *Citrus* sp. Un aumento en la mortalidad de las larvas de la polilla de cera *Galleria mellonella* (L.), expuestas a tierra del área tratada con polímero de fécula/nemátodo occurió comparado con el tratamiento de agua/nemátodo solo. La mortalidad de *D. abbreviatus* enterrado en la tierra al lado del árbol recibiendo el tratamiento de fécula/nemátodo fue 52% comparado con 42% para el tratamiento de agua/nemátodo y 0% para los tratamientos de control. La acrecentada infección de las larvas de *G. mellonella* fue evidente por más de dos meses bajo condiciones de campo.

Diaprepes abbreviatus (L.) or the "vaquita" is a common weevil pest of sugarcane citrus and other agricultural crops in the West Indies (Ballow 1912). The weevil, first reported in the United States in 1964 in Florida, has since become a serious problem in citrus (Woodruff 1964, Schroeder & Beavers 1977). Under natural conditions, the adult oviposits between leaves of various plants. First instars drop to the ground, burrow into soil, feed on roots, pupate, and emerge as adults (approximately one year) (Wolcott 1936). Larval feeding on the roots of citrus trees leads to tree decline and mortality (Schroeder & Sutton 1977). Currently, control is limited to the application of insecticides to reduce adult populations. The short residual action, expense, environmental contamination, and human hazard involved with chemical control greatly restrict this approach in the management of *D. abbreviatus*.

Entomogenous nematodes are promising biological control agents for a broad range of soil inhabiting insect species (Poinar 1971). Beavers et al. (1983) conducted a survey of Florida citrus grove and ornamental nursery soils and found native strains of *Steinernema carpocapsae* (Weiser) and *Heterorhabditis heliothidis* (Khan et al.) that were infectious to *D. abbreviatus* larvae. Entomogenous nematodes were subsequently evaluated in greenhouse and field tests and found to have potential as biological control agents for larvae of *D. abbreviatus* (Beavers 1984, Schroeder 1987).

Soil moisture is a limiting factor in the survival of entomogenous nematodes under field conditions (Poinar 1971). Evaporative retardants, water thickeners, and gels have been evaluated to enhance nematode efficacy (Webster & Bronskill 1968, Kaya & Reardon 1982, MacVean et al. 1982, Kaya & Nelson 1985). A water-absorbent poymer was used as an aid in the infestation of field sites with the root-knot nematode, *Meloidogyne* spp. (Fortnum et al. 1987). Hence, field tests were conducted to determine if a water retention agent could be used as an adjutant when the entomogenous nematode *S. carpocapsae* was applied for control of *D. abbreviatus* larvae.

MATERIALS AND METHODS

The nematode *S. carpocapsae* (All strain) was obtained from Biosys (Palo Alto, California, and maintained on water-soaked sponges at 10°C. Nematodes were checked for mobility by microscopic examination before application. Wax moth, *Galleria mellonella* (L.), larvae were obtained from Northern Bait (Chetek, Wisconsin) and *D. abbreviatus* larvae (3 months old, 602 ± 7 mg SEM) were reared on an artificial medium (Beavers 1983).

The citrus grove was located near Lake Gem, FL, and planted on a Lakeland sandy soil (thermic, coated typic quartzipsamments, 95% sand, less than 5% clay silt). There are 173 trees per ha. (7.6 m between trees and rows). The 10-year-old grove was managed by a private grove service, and the average tree height was 3.0 m.

One hundred soil samples were taken in April 1987 from the Lake Gem grove to determine levels of indigenous populations of steinernematid or heterorhabditid nematodes. A sample consisted of a 100 x 15 mm petri dish of soil at 12% field moisture. Five wax moth larvae were added to each dish and examined for entomogenous nematodes after 7 days (Bedding & Akhurst 1975). For comparison, 100 soil samples were taken from a grove that had an apparent endemic population of entomogenous nematodes (Beavers et al. 1983).

The tank mix contained 2.5 million nematodes per liter. The water-absorbent starch polymer (Ag Sorbent Flakes, Super Absorbent Co., Lumberton, North Carolina) was added to half the tank mix at 5 g per liter. One liter of the tank mix with and without the starch polymer was placed in a 10 cm deep by 20-cm circular depressin on the east (E) and west (W) of 10 trees each month for 3 months (September, October, and November) for a total of 30 trees.

To determine the effect of the starch polymer when nematodes were applied directly to the soil surface, an application was made on the E-W side of 10 trees with and without the starch polymer in November. The soil surface covered by one liter with the polymer was 30 cm in diam. and the area without the polymer was 40 cm in diam. and irregular.

Five soil samples of 100 g each, 0 to 10 cm deep were taken from treated sides of each tree 2, 4, and 8 weeks after treatment and 5 wax moth larvae were placed in each sample and maintained at 27°C for 1 week. Dead larvae were dissected to determine the presence or absence of nematodes.

D. abbreviatus larvae were buried individually in 10 x 10 x 4 cm screen cages. Each cage held 150 ml of soil and was buried 10 cm belw the surface on the E-W side of trees in treated zones. There were 8 trees, 20 cages per tree. Four trees (80 weevils) were treated with the starch polymer and 4 (80 weevils) with no polymer in the tank mix. Nematodes were applied to the soil surface at the rate of 25 nematodes per cm^2 in one liter of water per tree. Forty larvae in cages were buried adjacent to 2 untreated trees as checks. The cages were recovered 21 days later and larvae dissected to determine nematode infection.

RESULTS AND DISCUSSION

None of the 500 wax moth larvae added to the 100 soil samples taken from the Lake Gem grove became infected with entomogenous nematodes. Conversely, we recovered 160 nematode-infected larvae from the grove with a known endemic population. Because of the apparent lack of this biocontrol agent in the test grove, larval mortality caused by nematodes was attributed to introductions and not to an endemic population.

Addition of the starch polymer to the tank mix increased mortality of wax moth larvae (Table 1). The introduced nematodes persisted for more than 2 months. Surface application of the nematodes with starch in the tank mix was significantly better than water only. This method of application could be used during periods of high rainfall or with grove irrigation.

Fifty-two ± 5% (SEM) of larvae recovered from cages placed in the polymer treated soil were dead, compared to 42 ± 3% f larvae treated with water only (significantly different by *t* test, t = 2.83: df = 6; $P<0.05$). None of the 40 larvae placed in untreated soil died in the 3-week period. The total effect of nematodes would probably have been greater if larvae had been exposed for more than a month. Identification of nematode infected larvae, pupation, and lack of food limited the exposure period. Additional field trials with adult ground emergence traps are required to assess the use of nematodes as a biological control agent for larvae of *D. abbreviatus* feeding on citrus under Florida conditions.

This study has demonstrated that use of a water retention agent in the tank mix increased mortality of insect larvae by entomogenous nematodes. This was probably due to nematode survival in the moist soil.

ENDNOTE

This paper reports the results of research only. Mention of a proprietary product does not constitute an endorsement of a recommendation for its use by USDA.

TABLE 1. PERCENTAGE MORTALITY OF *GALLERIA MELLONELLA* LARVAE DUE TO *STEINERNEMA CARPOCAPSAE* IN SOIL TREATED WITH A STARCH POLYMER AND NEMATODES COMPARED WITH NEMATODES IN WATER ONLY.

Date	Application method	% mortality in a soil sample weeks post treatment			% Total mortality
		2	4	8	
Sept.	Starch	91**	72	44	69
	Water	76	64	44	61
Oct.	Starch	100	93	38*	77
	Water	100	88	28	72
Nov.	Starch	100	48**	59**	69**
	Water	100	39	12	50
Nov.	Starch (surface app.)	92*	56	38*	62**
	Water	70	45	20	45

[1] *significant at the 0.05 level; **significant at the 0.01 level (paired *t* test).

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ESTIMATING TOTAL LOSSES FROM PARASITOIDS FOR A FIELD POPULATION OF A CONTINUOUSLY BREEDING INSECT, CASSAVA MEALYBUG, *PHENACOCCUS HERRENI*, (HOMOPTERA: PSEUDOCOCCIDAE) IN COLOMBIA, S.A.

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ABSTRACT

A *Phenaccocus herreni* Cox & Williams population studied in Colombia, S.A., across a complete cassava crop cycle did not exceed 81 mealybugs/plant. *P. herreni* densities in Colombia were highest in the dry season, as were levels of parasitism by the encyrtids *Acerophagus coccois* Smith and *Epidinocarsis diversicornis* (Howard). Mealybug densities declined sharply during the dry season prior to the onset of rains. Stage survival among female mealybug nymphs was lowest in the third instar. Nine percent of all female first instar mealybugs survived to enter the adult stage. The combined action of the parasitoid species present caused 54.9% mortality to the host population as estimated by a new analytical method (Bellows et al. 1989).

RESUMEN

Una población de *Phenacoccus herreni* Cox & Williams estudiada en Colombia, S.A. durante un ciclo completo del cultivo del casave, no excedió 81 escamas harinosas por planta. En Colombia, la densidad de *P. herreni* fue mayor en la estación seca, así como el nivel de parasitismo de *Acerophagus coccois* Smith y de *Epidinocarsis diversicornis* (Howard). La densidad de escamas harinosas declinó bruscamente durante la temporada de seca antes del comienzo de las lluvias. La sobrevivencia entre las etapas de las ninfas hembreas de escamas harinosas fue más baja en el tercer estadio. El nueve porciento de todas las hembras en el primer estadio sobrevivieron para entrar a la etapa adulta. La acción combinada de las especies presentes de parasitoides causaron una mortandad de 54.9% en la población hospedera cuando se estimó por un nuevo método analítico (Bellows et al. 1989).

Phenacoccus herreni Cox & Williams infests cassava (*Manihot exculenta* Crantz) in Colombia and other tropical areas in South America (Varela & Bellotti 1981, Bellotti et al. 1983). *P. herreni* in Colombia is parasitized by a number of species, the most important of which are the encyrtids *Acerophagus coccois* Smith and *Epidinocarsis diversicornis* (Howard) (Bellotti et al. 1983, Van Driesche et al. 1987a). Quantifying the impact these parasitoids have on *P. herreni* populations is of interest to management of cassava pests in Colombia where *P. herreni* is a sporadic pest. In addition, understanding the role of parasitoids as mortality factors in *P. herreni* populations is of interest for comparison to the impact that the parasitoid *Epidinocarsis lopezi* (De Santis) has had on the closely related cassava pest *Phenacoccus manihoti* Matile-Ferrero in tropical Africa, where both pest and parasitoid are recent introductions from South America.

We report here an analysis of stage survival and parasitism levels for one population of *P. herreni* over a complete cassava crop cycle (11 months) in the Cauca Valley in Colombia, covering the equivalent of 5 to 6 mealybug generations. Mealybug generations, however, overlapped due to continuous breeding by this species. Results of this study, while limited to a single site, are the first detailed quantification of the effect of parasitism on *P. herreni*'s population dynamics. Furthermore, this report illustrates the use of a recently developed technique for quantification of parasitism applicable to a variety of continuously breeding insects. Specifically, the methods of analysis employed were, for stage survival, a non-graphical use of the method of Southwood & Jepson (1962) (to estimate numbers entering mealybug life stages) and, for total losses due to parasitism, a recent extension of Southwood & Jepson (1962) explicitly developed for this purpose by Bellows et al. (1989). The Southwood & Jepson (1962) technique has previously been applied, with modification, to the problem of estimating total losses from parasitism (Gargiullo & Berisford 1983, Kolodny-Hirsch et al. 1988, Schneider et al. 1988). Bellows et al. (1989) have recently analyzed the biases inherent in several possible methods of using the Southwood & Jepson technique for estimating losses from parasitism. We employ here one of the modifications of the Southwood & Jepson technique as developed by Bellows et al. (1989). The objective of our study was to provide an improved quantification of the total amount of mortality due to parasitism in the *P. herreni* population studied. We contrast estimates obtained from the Bellows et al. (1989) method to values of percentage parasitism seen in pooled sets of field samples, an approach currently in common use for assessing parasitism of insects such as mealybugs and aphids.

METHODS

Description of Field Site

A cassava field was established 1 May 1984 by planting 20 cm "stakes" of variety "MC-22" with 1 m between rows and between plants within rows. Six rows of 6 plants constituted a plot and two meter aisles were left between plots. Forty two plots were arranged in a rectangle 18 rows wide and 84 plants long, for a total of 1,512 plants in the field. The field was established on clay-loam soil at the Cali, Colombia research station of CIAT, weeded by hand as needed to maintain clean culture and irrigated once in August to stimulate growth. Because the 1984 dry season was cooler and wetter than average, *P. herreni* populations throughout the station were low and artificial infestation was used to initiate a population in the plot. Every third plant (504 total) was infested with one ovisac or an adult female mealybug on 17 July. A release of the parasitoid *E. diversicornis* was made on 5 August 1984, by placing eight plants bearing parasitized mealybugs in the field. Release of small numbers this species was done to ensure its occurrence in the study plot since it had only recently been imported into the region. No releases of A. coccois were made because this species was native to the Cauca Valley and known to be widely distributed. No pesticide applications of any type were made to the crop or to adjoining plots.

Sampling for Mealybug Density and Percentage Parasitism

Each week 50 plants were randomly selected and all leaves and terminals counted and classified as infested by *P. herreni* or not. One hundred infested leaves and 15 infested terminals were randomly selected from sample plants for further examination by taking the first infested leaves (up to 3 per plant) or infested terminals encountered until the total number desired was obtained. To avoid taking mealybugs only from the upper portions of plants, the order in which leaves were examined (bottom to top and vice versa) was reversed after each plant. Leaves and terminals were placed individually in plastic bags and returned to the laboratory where mealybugs were counted and classified to life stage. One hundred mealybugs, excluding first instars (which were too small to dissect), were randomly selected from each sample and dissected to determine the proportion parasitized. Mealybugs in samples which were mummified due to parasitism at the time of collection (hereafter referred to as mummies) were counted. Dissection of live mealybugs was done under alcohol using a stereomicroscope. The number of parasitoid eggs and larvae in each host were recorded. Since parasitoid larvae of the two principal species could not be distinguished, the relative proportions of the two parasitoids were determined by rearing the mummies present in the samples. Mummies were placed in petri dishes and held at 25°C, 70% r.h., 12L:12D photoperiod until parasitoid emergence. Parasitoids that emerged were classified into three groups: *E. diversicornis*, *A. coccois*, and all others combined. Mummies from which no parasitoids emerged were not dissected. Sample percentage parasitism was calculated using equation 1. This estimate includes both (1) the proportion of live mealybugs found by dissection to be parasitized and (2) the appropriate fraction of mummies counted in the sample prior to dissection.

$$\%\ \text{parasitism} = \frac{\begin{array}{c}\text{No. parasitized mealybugs}\\\text{found in dissection}\end{array} + \begin{array}{c}\text{mummies}\\\text{in full}\\\text{sample}\end{array}\left(\dfrac{\begin{array}{c}\text{No. live mealybugs}\\\text{dissected}\end{array}}{\begin{array}{c}\text{No. live mealybugs}\\\text{in full sample}\end{array}}\right)}{\begin{array}{c}\text{No. mealybugs}\\\text{dissected}\end{array} + \begin{array}{c}\text{mummies}\\\text{in full}\\\text{sample}\end{array}\left(\dfrac{\begin{array}{c}\text{No. live mealybugs}\\\text{dissected}\end{array}}{\begin{array}{c}\text{No. live mealybugs}\\\text{in full sample}\end{array}}\right)}$$

Total mealybug densities per plant on sample dates were calculated by multiplying the number of infested leaves per plant by the number of mealybugs per infested leaf and adding this figure to the corresponding value for terminals. Sampling commenced on 25 August 1984 (approximately one host generation after infestation of field plants) and ended 24 April 1985 when the crop was harvested. The sampling period covered a dry, wet, and dry season in that order.

Analysis of Data

Numbers of mealybugs entering each successive life stage during specific periods were calculated from stage frequency counts per plant using a non-graphical version of the method of Southwood & Jepson (1962). Data were grouped into three periods (26 August-17 October, 18 October-2 January, and 3 January-24 April), corresponding to dry, wet, and dry seasons, as well as being analyzed together for th entire crop cycle. Non-linear temperature-dependent growth curves for *P. herreni* and the two parasitoids (Herrera et al. 1989) were used to calculate the number of "stage-lifetimes" completed between each pair of successive sample dates. Computations were made as follows. On each day, the average temperature ($\frac{\text{max.} + \text{min.}}{2}$) observed in the field was noted and for each given mealybug or parasitoid life stage the portion of that stage which would be completed at that temperature in one day was estimated, using developmental rate data of Herrera et al. (1989). This estimate was then multiplied by the observed density per plant of the mealybug life stage on that day to determine the number of stage-lifetimes completed. Stage densities for each day were determined as the average values of the two samples bounding the day. In this manner for all days in the experiment the number of stage-lifetimes completed by each mealybug or parasitoid life stage on each day was computed. These numbers were then summed within stages and periods for analysis.

Total parasitism was calculated using the method of Southwood & Jepson (1962) as modified by Bellows et al. (1988). This was done using counts of "subsequent host and parasitoid stages" (i.e., those stages that are next in development after the host stage bearing immature parasitoids and the immature parasitoid stage associated with the host). This approach has fewer inherent biases than analysis of the host stages actually parasitized because transferrence of individuals from the non-parasitized host category to the immature parasitoid category (= parasitized hosts) is a major bias affecting computation of stage mortality from parasitism (Bellows et al. 1988). The parasitoid mummy stage is well suited for use as a "subsequent stage". Adult female cassava mealybugs and male cocoons are less well suited because these stages are still subject to possible new parasitism. Average percentages of parasitism of adult female mealybugs and male cocoons in field density samples were used to lower estimates of numbers entering these stages, so as to better estimate numbers of non-parasitized insects entering these stages. It should be noted that in "subsequent stage" analysis, the developmental time of the stage is part of the analytical method and hence differential "residence times" of host and parasitoid stages is not a source of bias. Total numbers of mealybugs that became parasitized (P) were estimated as the number of parasitoids reaching the mummy stage. Numbers of mealybugs that escaped parasitism (N) were estimated by application of the Southwood and Jepson method to the numbers of unparasitized mealybugs in their final observed stages (for males, the cocoon and for females, the adult) minus the proportion of these stages observed in pooled density samples to be parasitized. Data used in these calculations were densities of these stages per plant in field samples over the course of the experiment, field temperature records, data on developmental rates of the stages to be quantified (Herrera et al. 1988) and estimates of parasitism from dissections of field-collected mealybugs taken once per week. The proportion of hosts parasitized is found as $P/P+N$. The analytical technique assumes that stage survivals of the stages used to estimate insects escaping parasitism (here, male cocoons and adult females) and insects being parasitized (here, mummies) are similar but need not be equal (Bellows et al. 1989). Because mealybug densities were recorded for leaves and terminals separately, analyses were performed on both a whole plant and a leaves-only basis. To obtain estimates of total mortality caused by parasitoids, the estimates of parasitism (sensu stricto) obtained from the Bellows et al. (1988) method were multiplied by 1.13 to account for additional losses due to ovipositor piercing and host feeding, known sources of mortality caused in *P. herreni* by the parasitoids under study (Van Driesche et al. 1987b).

Stage-specific survival rates for five mealybug life stages (1st instar mixed sexes, 2nd instar ♀, 2nd instar ♂, 3rd instar ♀ and adult ♀) and one parasitoid stage (egg plus larva) were estimated as the ratio of estimates of numbers entering successive stages in the insects' life histories.

Meteorological Data Collection

Air temperatures were recorded within the crop canopy using a hygrothermograph in a wooden shelter at ground level. Rainfall was measured with a rain gauge at the edge of the field.

RESULTS

Mealybug densities per plant showed two peaks, one of 69 per plant on 11 September 1984 and the second of 81 per plant on 5 February 1985 (Fig. 1). Early mealybug instars dominated samples throughout the sampling period, with numbers decreasing from younger to older life stages (Fig. 2). The same pattern occurred in Southwood & Jepson's estimates of numbers entering successive life stages (Table 1). Stage-specific survival for female mealybugs was lowest in the third nymphal instar for all time periods and survival from the beginning of the first nymphal instar to the beginning of the adult stage for females was 9% (Table 2).

E. diversicornis was initially more abundant than *A. coccois*, but in October and thereafter A. coccois was the principal species recovered from collections of mummified mealybugs (Table 3). Sample percent parasitism, for the two species combined based on occurrences of mummies and dissection of mealybugs found on leaves, showed little seasonality with a relatively constant level of 10-25% prior to the commencement of the 1985 dry season and a steady rise thereafter to 35-45% during that period (Fig. 3). Percentage parasitism obtained from pooling estimates from samples within each seasonal period were 16.5%, 13.5%, and 30.8% for the 26 August-17 October, 18 October-2 January, and 3 January-24 April periods respectively. These values become 18.6%, 15.3%, and 34.8% after adjustment for host feeding and mutilation—other types of parasitoid-caused mortality which are estimated using laboratory data. Using the modification of Southwood & Jepson (1962) developed by Bellows et al. (1989) we estimated losses due to parasitism on leaves to be 33.7% for the entire crop cycle. Losses were highest in the driest period (Table 4). During the 3 January-24 April dry season, parasitism levels were higher on whole plants than on leaves due to higher levels of parasitism of mealybugs on terminals. On whole plants, parasitoids caused an estimated 54.9% mortality to the *P. herreni* population (Table 4).

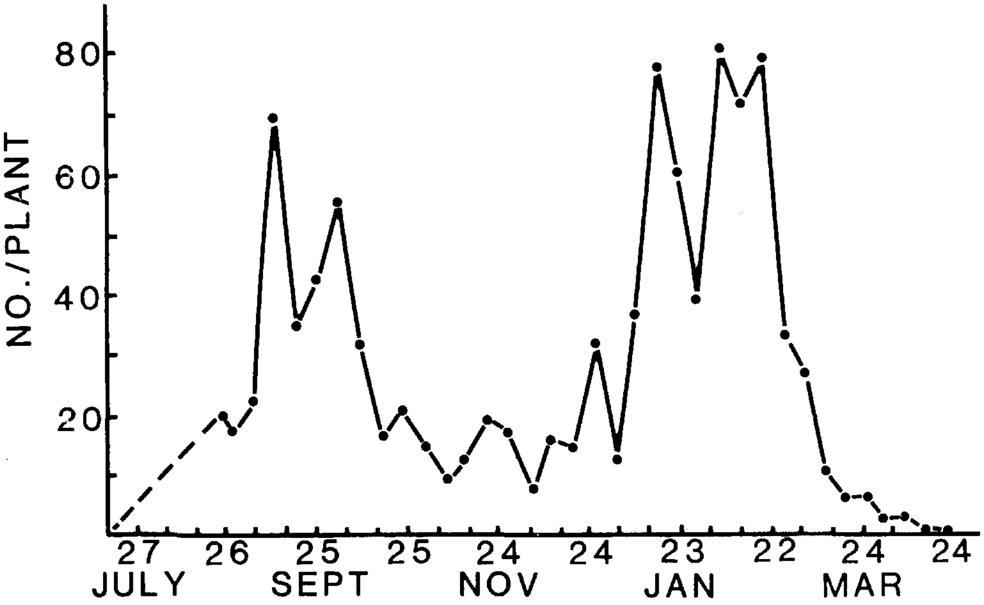

Fig. 1. Numbers of *Phenacoccus herreni* mealybugs (all stages combined except the egg and adult male) per plant in a cassava field at Cali, Colombia in 1984-85.

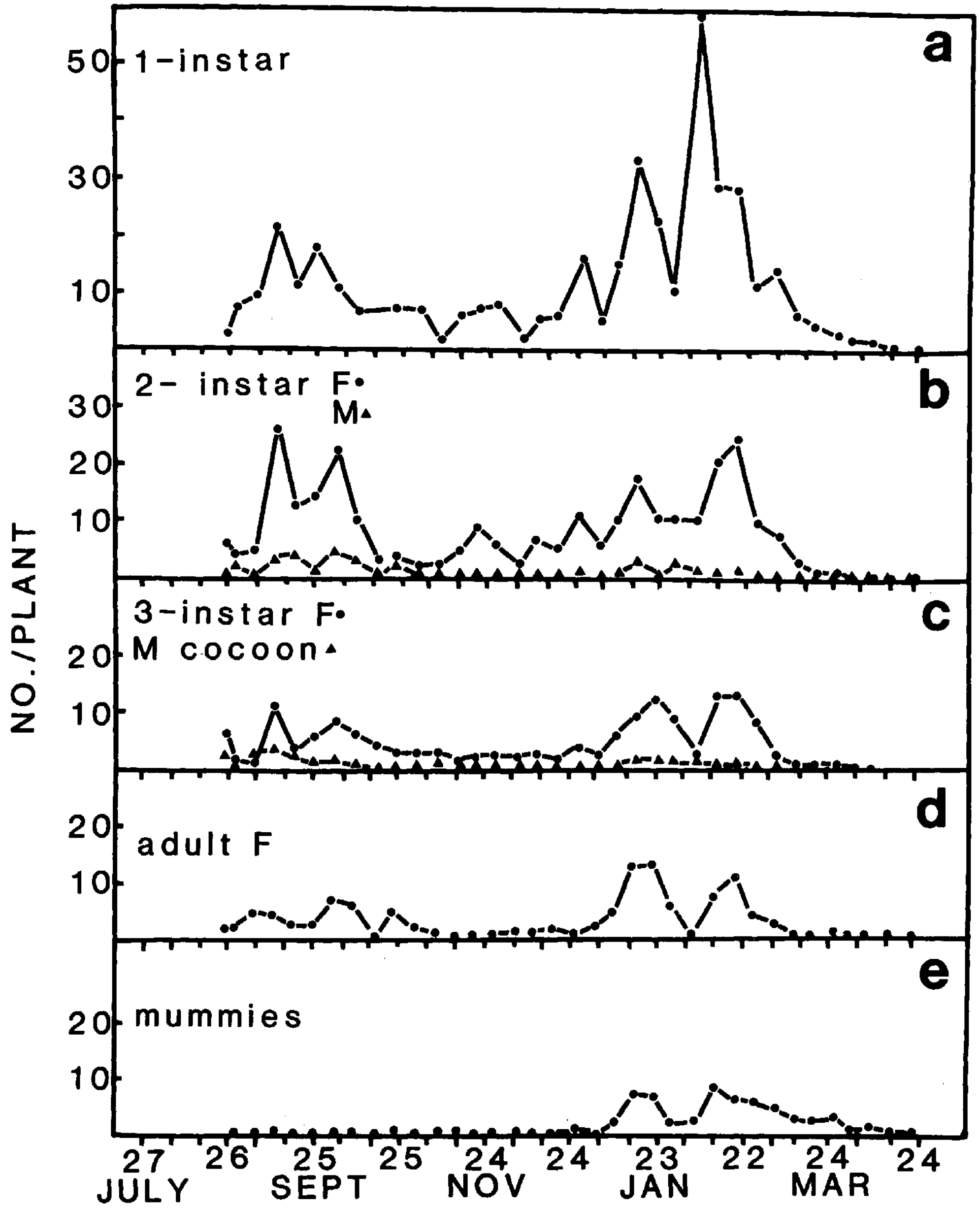

Fig. 2. Numbers of *P. herreni* per plant (a-d) divided by instar and sex (M = male; F = female), and numbers of parasitoid mummies (e) (*Acerophaous coccois* and *Epidinocarsis diversicornis* combined), in a cassava field at Cali, Colombia in 1984-85.

DISCUSSION

The Southwood and Jepson estimates of numbers of mealybugs entering the successive stages in the mealybug and parasitoid life histories (Table 1) should be viewed as indexes of the true numbers entering these stages as it is well known that such estimates are universally too low due to the effect of mortality within the stage. In addition, if stages differ in the efficiency with which they can be sampled, this also will affect estimates of numbers in stages. Our estimates of first and second stage mealybugs, for

TABLE 1. NUMBERS OF *PHENACOCCUS HERRENI* AND ITS PARASITOIDS *EPIDINOCARSIS DIVERSICORNIS* AND *ACEROPHAGUS COCCOIS* ON CASSAVA AT CALI, COLOMBIA, 1984-85.

	Numbers per plant entering various life stages						
	26 August-17 October	18 October-2 January		3 January-24 April		whole season 26 August-24 April	
Life Stage	leaves only[1]	whole plant	leaves only	whole plant	leaves only	whole plant	leaves only
Mealybug							
1st instar (mixed sexes)	114.2	90.3	88.3	355.1	270.3	559.6	472.8
2nd instar ♀	139.6	84.6	79.9	194.7	152.7	418.9	372.2
2nd instar ♂	22.9	9.6	9.6	17.4	16.1	49.9	48.6
3rd instar ♀	51.2	36.1	34.3	102.0	73.4	189.3	158.9
♂ cocoon	12.7	4.6	4.5	10.1	9.6	27.4	26.8
♀ adult	9.6	5.3	5.0	21.6	18.9	36.5	33.5
ovisacs	3.3	2.0	1.9	7.6	6.9	12.9	12.1
Parasitoids[2]							
immatures[3]	18.2	(9.2)[4]	7.7	(55.6)[4]	27.2	(95.9)[4]	53.1
mummies	3.4	5.0	4.2	45.6	22.3	54.0	29.9

[1] For the 26 August-17 October period, samples were taken of leaves only. However, terminals were rarely infested during this period and thus values are equivalent to whole plant densities as well.

[2] Numbers are for the sum of the all parasitoid species present, nearly all either *Epidinocarsis diversicornis* or *Acerophagus coccois*.

[3] "Immature" stage of parasitoids is the combined egg and larval stages prior to the mummification of the mealybug host.

[4] Numbers of immature parasites (i.e., parasitized live mealybugs) were measured on leaves only; stimates for whole plants are made by extrapolation from data on mummies on leaves only as compared to mummies on whole plants (e.g. for 18 October-2 January, $\frac{4.2}{5.0} = \frac{7.2}{x}$).

example, for the first two seasonal periods are higher for the second instar than the first. We feel this implies that the first instar, being the smallest stage, was detected with lower efficiency. For this reason the stage survival rates of the first instar in these time periods (Table 2) are probably not accurately reflected by the ratios of the Southwood and Jepson estimates of the first and second instars.

The low rate of survival of female mealybugs in the third instar was likely caused, at least in part, by the onset of parasitoid emergence. The third instar is the first stage from which parasitoids are likely to emerge in view of relative mealybug and parasitoid development rates, even if mealybugs were stung as young first instars (Herrera et al. 1989).

The Bellows et al. (1989) estimate of mortality from parasitism and the average percentage parasitism value from pooled samples from the interval were similar in the first seasonal period (26 August-17 October), but the Bellows et al. (1989) estimate was higher for the other two seasonal periods. Sample percent parasitism values have been shown previously to be easily influenced by seasonal patterns of host and parasitoid advancement into and out of the sample stages (Van Driesche 1983). This problem is especially acute in species with distinct generations. For continuously breeding species in areas lacking strong seasonal patterns of breeding, temporal patterns of this nature are likely to be less important. Instead, sample values are more likely to be influenced

TABLE 2. STAGE SURVIVAL OF *PHENACOCCUS HERRENI* AND ITS PARASITOIDS ON WHOLE CASSAVA PLANTS, AT CIAT, CALI, COLOMBIA, 1984-85.

Stage	26 August-17 October	18 October-2 January	3 January-24 April	whole season 26 August-24 April
P. herreni				
First Instar (mixed sexes)	1.00	1.00	0.60	0.84
Second Instar ♀	0.37	0.43	0.52	0.45
Second Instar ♂	0.55	0.48	0.58	0.55
Third Instar ♀	0.19	0.15	0.21	0.19
Adult[1] ♀	0.34	0.38	0.35	0.35
First Instar to Adult[2]	0.11	0.08	0.08	0.09
Parasitoids				
immatures[3]	0.19	0.54	0.82	0.56

[1] Survival from stage entry to first reproduction.

[2] Survival from entry to the first nymphal instar to entry to the adult stage. A 3 ♀:1 ♂ sex ratio of first instar nymphs is assumed based on laboratory values of Varela and Bellotti (1981).

[3] "Immature" stage of parasitoids is the combined egg and larval stages prior to mummification of hosts.

by the relative developmental times of the sampled stages of host and parasitoid. The parasitoids of *P. herreni* complete their development (from oviposition to adult emergence) in approximately 20 days at 25°C (Herrera et al. 1989). *P. herreni*, in contrast, requires about 40 days for females (for first instar through adult death) and about 16 days for males (for first instar through adult emergence; adult males are not subject to parasitism and were not included in sampling). Given a 3:1 female: male sex ratio in the species (Varela & Bellotti 1981), this implies an average lifetime of 34 days for mixed sex groups of mealybugs, 1.7 times greater than the average lifetime of parasitoid stages (egg through adult emergence). This should cause sample percent parasitism to be lower than numbers actually parasitized, as is suggested by estimates obtained from the Bellows et al. (1989) technique.

Population dynamics of *P. herreni* in Colombia differed from those of the closely related *P. manihoti* in Africa in two respects. First, densities of mealybugs per plant in Colombia were dramatically lower (only 3-10%) than those of *P. manihoti* in Africa

TABLE 3. PROPORTION OF TOTAL PARASITISM OF *PHENACOCCUS HERRENI* DUE TO SPECIFIC PARASITOID SPECIES IN EACH SAMPLE MONTH IN A CROPPING CYCLE OF CASSAVA AT CALI, COLOMBIA, 1984-1985.

	Proportion of Total Parasitism Due to Given Species							
Species	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
E. diversicornis	34.8	28.0	18.5	3.8	7.8	8.8	1.9	4.3
A. coccois	0.0	60.0	70.4	84.9	78.9	82.5	79.6	75.4
all others combined	65.2	12.0	11.1	11.3	13.3	8.8	18.5	20.3
sample size	23	25	27	53	90	80	108	69

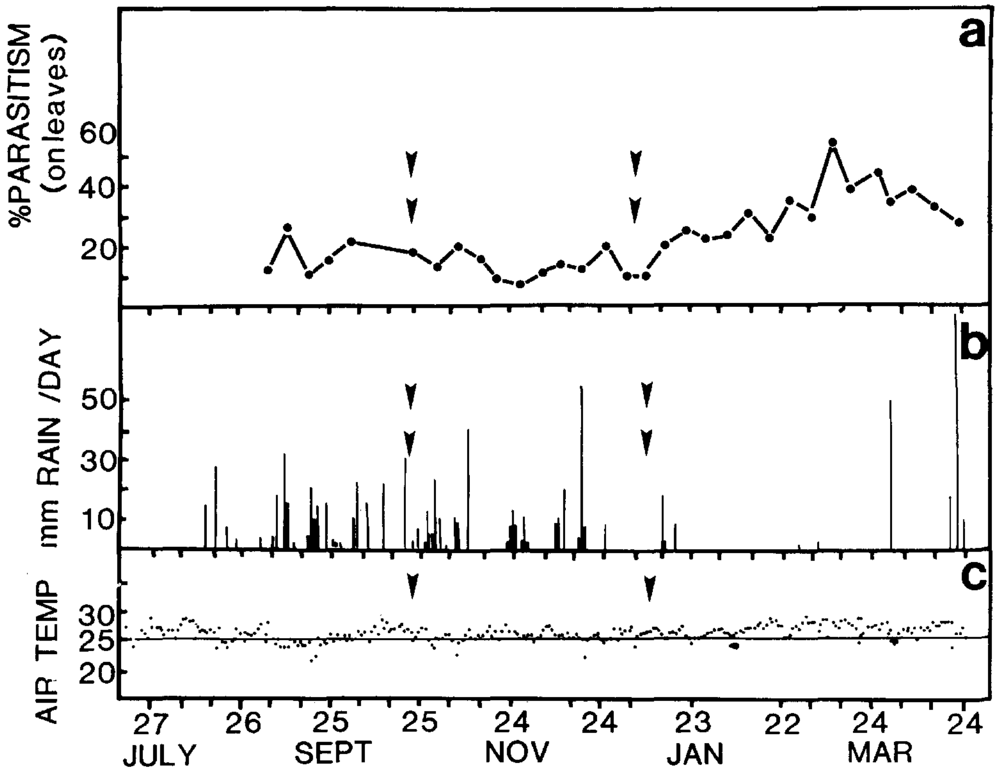

Fig. 3. (a) Percentage of *P. herreni* mealybugs (nymphal stages and female adults combined except for first instars) parasitized by *Acerophacus coccois* or *Epidinocarsis diversicornis*; mummies in samples are included in calculation of percent parasitism; (b) daily rainfall; and (c) daily average temperature (°C) in crop canopy at a cassava field at Cali, Colombia in 1984-85. Arrows denote seasonal divisions used in data analysis, corresponding to a dry, wet, and dry season, respectively.

prior to the introduction of the parasitoid *Epidinocarsis lopezi* (De Santis) (Neuenschwander et al. 1986a) or in study plots where the action of this parasitoid was suppressed by the application of selective insecticides (Neuenschwander et al. 1986b). Second, the population decline observed in this study occurred in late February, well before the onset of the rainy season in late March (Fig. 1, Fig. 3b). In contrast, *P. manihoti* populations, prior to the introduction of *E. lopezi*, in the Popular Republic of the Congo declined after the onset of the rainy season (Fabres 1981). This contrast suggests that where effective natural enemies are lacking (as in Africa prior to the introduction of *E. lopezi*), cassava mealybug populations grow until reduced by unfavorable abiotic factors, but where effective natural enemies are present these can in many cases suppress mealybug populations earlier in the seasonal cycle. In Colombia, the two parasitoids studied, plus a complex of predators (Varela et al. 1979) and other agents, are present and generally maintain *P. herreni* populations at non-pest levels in most regions (Bellotti, personal observation).

ACKNOWLEDGMENT

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TABLE 4. LEVELS OF PARASITOID- CAUSED MORTALITY IN *PHENACOCCUS HERRENI* DUE TO THE ENCYRTID PARASITOIDS *ACEROPHAGUS COCCOIS* AND *EPIDINOCARSIS DIVERSICORNIS* ON CASSAVA IN CALI, COLOMBIA IN 1984-85 AS ESTIMATED BY TWO METHODS, I.E., POOLED SAMPLE PERCENT PARASITISM AND THE METHOD OF BELLOWS ET AL. 1988.

	Estimated Percentage of Hosts Killed by Parasitoids[1]		
	Bellows et al. Method		Pooled Sample Percent Parasitism
	whole plant	leaves only	leaves only
First Dry[2] Season 26 August-17 October	16.5	16.5	18.6
Wet season 18 October-2 January	40.3	37.1	15.3
Second Dry Season 3 January-24 April	70.1	54.1	34.8
Whole Crop Cycle 26 August-24 April	54.9	33.7	25.2

[1] Estimates include parasitism per se and losses due to host feeding and ovipositor piercing.
[2] Actually rather wet although nominally a dry season.

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PREDATION RATE OF LARVAL *CORETHRELLA BRAKELEYI* (DIPTERA: CHAOBORIDAE) ON MOSQUITO LARVAE

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ABSTRACT

Corethrella brakeleyi (Coquillett) larvae were collected from a small roadside pond in Alachua County, Florida, and offered 2nd instar *Anopheles quadrimaculatus* larvae in cups in a laboratory feeding test. The average number of mosquito larvae consumed/day by the 65 predator larvae ranged from 3.00 to 9.32 during the 19 days of the feeding test. The average total number of mosquito larvae consumed/*C. brakeleyi* larva was 76.9. The population of *C. brakeleyi* larvae in the pond, sampled by the standard mosquito larva dipper method between 3 February and 14 November 1989, ranged between 0.62 and 8.3 larvae/dip.

RESUMEN

Se colectaron larvas de *Corethrella brakeleyi* (Coquillet) de una laguna al lado de un camino en el Condado de Alachua en la Florida, y se les ofreció larvas en el segundo estadio de *Anopheles quadrimaculatus* en copas en una prueba de alimentación en el

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Se colectaron larvas de *Corethrella brakeleyi* (Coquillet) de una laguna al lado de un camino en el Condado de Alachua en la Florida, y se les ofreció larvas en el segundo estadio de *Anopheles quadrimaculatus* en copas en una prueba de alimentación en el laboratorio. El promedio del número de larvas de mosquito consumidas por dia por las 65 larvas depredadoras varió de 3.00 a 9.32 durante los 19 dias de la prueba de alimentación. El promedio total del número de larvas de mosquitos consumidas por *C. brakeleyi* fue de 76.9. La población de *C. brakelyi* en la laguna, muestreada por el método patrón de obtener larvas con un jarro, entre el 3 de Febrero y el 14 de Noviembre, varió entre 0.62 y 8.3 larvas por jarra.

Corethrella brakeleyi (Coquillett) is distributed in the North American continent from Texas to Florida and northward into Canada (Stone 1968, Ellis & Wood 1974). The adult females are blood feeders on vertebrates (Williams & Edman 1968) and more specifically on frogs (McKeever 1977). The larvae have been collected in cold springs, bog pools, margins of permanent ponds, swamps and canals (Smith 1902, Williams & Edman 1968), and in a quarry (Chapman et al. 1971). Chapman et al. (1971) also noted that *C. brakeleyi* larvae were voracious predators of 1st instar mosquito larvae. Ellis & Wood (1974) confirmed predation by 4th instar *C. brakeleyi* larvae on small ostracods, 1st instar chironomid larvae, and 1st instar larvae of the mosquito *Culiseta melanura* (Coquillett). I have observed *C. brakeleyi* larvae in rice fields in Louisiana preying upon 1st and 2nd instars of *Anopheles crucians* Wiedemann and *A. quadrimaculatus* Say. Larval densities in nature and predation rates have not been published. This paper presents the first record of rates of predation of mosquito larvae by *C. brakeleyi* from laboratory studies and the persistence of a natural population in a small semipermanent pond in Alachua Co., Florida, during the period 3 February-14 November 1989.

MATERIALS AND METHODS

Laboratory predation rates. Sixty-five late instar *C. brakeleyi* larvae were collected from a semi-permanent pond, (about 100 m at its widest diameter), one edge of which ran alongside a road and bordered on the other sides by a sparse pine thicket, in Alachua Co., Florida, on 20 April 1988. Larvae were placed individually in 400 ml of tap water in white plastic cups (8 cm deep x 10 cm diam). Second instar *A. quadrimaculatus* were placed in each cup each day for the 19 days of the test. The number of mosquito larvae consumed each day was recorded and the remaining prey removed and replaced with new 2nd instars. More mosquito larvae were placed in each cup than had been consumed the previous day to ensure that the predator could feed to repletion. *Corethrella brakeleyi* pupae were held for adult emergence to verify species identification, using the key of Stone (1968).

Usually, the larger the predator the more food it can ingest. Thus, when all the mosquito larvae offered as prey are the same stage, larger predators would be expected to ingest more mosquito larvae. Therefore, calculation of the mean number of prey consumed per calendar day in the test would mask the effects of size (age) of the predator because both 3rd and 4th stage *C. brakeleyi* were collected. The day of pupation for each larva relative to the date the larvae were collected was used as a common reference point. Prey consumption was then related to the number of the day prior to pupation, permitting calculation of the mean number of prey consumed for a group of larvae according to a common age before each of them became a pupa.

Larval sampling in a pond. The *C. brakeleyi* larval population in the small permanent pond was sampled with a standard 400-ml dipper used for collection of mosquito larvae. Five dips were taken from each of 26 sites on 3-II-89, 7-II-89 and 15-III-89, and at 20 sites on 25-VII-89 and 14-XI-89. Samples were taken along the edge of the pond next to the road and were selected by moving several meters further along the edge from the prior sample. The number of each instar of *C. brakeleyi* was recorded for each dip and averaged for the day. *Corethrella brakeleyi* larvae were observed there on 21-VIII-89 but quantitative data were not collected.

RESULTS

Prey consumption. The mean number of prey consumed/predator/day is shown in Table 1, grouped by the day of pupation. Daily consumption of prey for larvae that were youngest when collected and required 19 days of feeding before pupation is listed at the top of the table. Thus, 4 larvae required 19 days of feeding before they pupated, 26 fed for 17 days, and 2 pupated after their 4th day in the test. The average total number of prey consumed/predator was 76.9 (SD = 30.8, range = 13-153). The change from 3rd to 4th stage appears to have occurred at some time centered around the 11th day prior to pupation because this was the day the fewest prey were eaten after a gradual increase from the 19th through the 12th day before pupation. Daily prey consumption then increased from the 11th through the 5th day. The subsequent decrease in prey consumption indicated the pre-pupal period.

Larval occurrence in nature. Table 2 presents the mean number of 2nd, 3rd, and 4th larvae and pupae per dipper sample for the 4 sampling dates. Natural populations of *C. brakeleyi* persisted at least from March through November 1989.

CONCLUSIONS

The predation rates observed in these laboratory tests are estimates of the maximum sustained daily intake of prey by late stage *C. brakeleyi.* There were always living mosquito larvae in the cups at the end of each observation period, indicating that enough

TABLE 1. MEAN NUMBER OF SECOND INSTAR *ANOPHELES QUADRIMACULATUS* EATEN PER DAY PRIOR TO PUPATION BY *CORETHRELLA BRAKELEYI* LARVAE UNDER LABORATORY CONDITIONS.

Days of feeding prior to pupation	Number of *C brakeleyi* larvae feeding	Mean number (± SD) of prey eaten/day
19	4	3.00 (0.00)
18	5	3.00 (0.00)
17	26	3.19 (0.39)
16	27	3.48 (1.50)
15	29	4.21 (1.45)
14	31	4.32 (2.47)
13	39	5.28 (2.83)
12	42	5.64 (3.25)
11	43	3.35 (1.24)
10	58	4.38 (2.41)
9	59	4.58 (2.66)
8	59	5.14 (3.14)
7	60	6.27 (2.14)
6	61	7.77 (3.74)
5	63	9.32 (4.97)
4	65	8.28 (5.80)
3	65	5.75 (2.93)
2	65	6.65 (3.70)
1	65	5.37 (3.48)

TABLE 2. MEAN NUMBER (SD) OF *CORETHRELLA BRAKELEYI* PER DIPPER SAMPLE IN A SEMI-PERMANENT POND IN ALACHUA COUNTY, FLORIDA, 1989.

		LIFE STAGE (instar)				
Date	n	2nd	3rd	4th	Papa	All
3/II-89	130	0.08 (0.52)	0.22 (0.61)	0.56 (1.08)	0.01 (0.09)	0.86 (1.55)
7-II-89	130	0.11 (0.74)	0.09 (0.29)	0.41 (0.89)	0.01 (0.09)	0.62 (1.36)
15-III-89	130	0.05 (0.26)	0.19 (0.50)	0.56 (1.02)	0.02 (0.15)	0.83 (1.34)
25-VII-89	100	0.44 (0.57)	0.53 (0.43)	0.38 (0.38)	0.02 (0.06)	1.37 (1.14)
14-XI-89	100	1.41 (2.66)	0.22 (0.95)	0.0095 (0.0436)	0.0 -	1.65 (2.78)

prey were provided to satiate the predator and also that *C. brakeleyi* does not kill "surplus" larvae in the manner of *Toxorynchites.*

To my knowledge, these data represent the first attempt to quantify *C. brakeleyi* populations in nature. Natural populations of this species have been infrequently reported, and seasonal occurrence and densities of *C. brakeleyi* are unknown. This report documents the persistence of a *C. brakeleyi* population at one habitat from March through November. The importance of this predator as part of the natural mortality of anopheline larvae may therefore be greater than expected based upon the prior reports of its occurrence. The pond studied is similar to those in central Florida in that they are rather small, shallow, have abundant emergent and floating vegetation and are fed mostly by rainstorms. Extensive sampling is needed, however, to determine the distribution and abundance of *C. brakeleyi* in the region.

ACKNOWLEDGMENTS

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NATURAL HISTORY OF THE LEAFHOPPER *CARNEOCEPHALA FLORIDANA* (HOMOPTERA: CICADELLIDAE) IN A NORTH FLORIDA SALT MARSH

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ABSTRACT

Adults of the leafhopper *Carneocephala floridana* Ball are found year round, usually at low to moderate densities, in the salt marshes of north Florida. Although this hopper is oligophagous, the salt-marsh cord grass, *Spartina alterniflora* Loisel, is a primary host plant and serves as the main substrate for both feeding and oviposition for the nymphs and adults. The life history and life cycle of this hopper were investigated in the field and laboratory. In the laboratory, at 21°C and 73% RH, adult females laid an average of 94 eggs over their adult lifetimes, which averaged about 34 days. Egg development of *C. floridana* was completed in 10-12 days. Two undescribed species of egg parasitoids in the genus *Gonatocerus* (Hymenoptera: Mymaridae) were reared from field-collected eggs of *C. floridana.*

RESUMEN

Adultos de saltahojas *Carneocephala floridana* Ball se encuentran todo el año, usualmente en densidadas bajas a moderadas, en los saladares del norte del la Florida. Aunque este saltahojas es oligofogo, la hierba del saladero *Spartina alterniflora* Loise es el principal hospero y sirve como el principal substrato como alimento y el desove de las ninfas y adultos. Se investigó en el campo y en el laboratorio la historia y el ciclo de vida de este saltahojas. En el laboratorio, a 21°C y 73% HR, las hembras adultas pusieron un promedio de 94 huevos durante su vida adulta la cual tuvo un promedio de 34 dias. El desarrollo de los huevos de *C. floridana* se completó de 10-12 dias. Dos especies no descritas del parasitoide de huevos del género *Gonatocerus* (Hymenoptera; Myrmarida) se criaron de huevos de *C. floridana* colectados del campo.

The leafhopper *Carneocephala floridana* Ball is the largest of three species of the genus known to occur in Florida; females are more than 8 mm in length, and males are 6-7 mm in length (Mead 1965). Although Hamilton (1985) replaced *C. floridana* in its original genus, *Draeculacephala*, this work has not been widely accepted by cicadellid taxonomists (F. Mead, personal communication); therefore, this paper will use the commonly accepted name, *Carneocephala floridana*. Like other species of cicadellids, *C. floridana* uses its highly modified mouthparts, the stylets, to pierce the xylem vessels of its host plants (personal observation). Although *C. floridana* is usually not economically important (Mead 1965), it does belong to an economically important subfamily of leafhoppers, the Cicadellinae (Tetigellinae). All of the members of this subfamily studied thus far have proven to be vectors of Pierce's disease (PD) in grapes and of alfalfa dwarf disease (Frazier 1944, Frazier & Freitag 1946, Freitag 1951, Freitag et al. 1952, Stoner 1953). More specifically, several species of *Carneocephala*, including *C. flaviceps* (Riley), *C. fulgida* Nottingham, and *C. triguttata* Nottingham, are all proven vectors of PD (Frazier & Freitag 1946, Stoner 1953) and appear to be some of the most efficient vectors of the disease (Frazier & Freitag 1946). Despite *C. floridana*'s potential importance, its life history has not been detailed. The high probability that it is a vector of PD merits careful description of this leafhopper's natural history.

MATERIALS AND METHODS

Carneocephala floridana is an oligophagous insect found in abundance throughout the salt marshes fringing the mainland of north Florida (personal observation). It is also present on several small islands, including Smith Island, of Oyster Bay in Wakulla County, Florida (Fig. 1).

Laboratory Experiments

Although several species, including *Salicornia virginica* L., *Batis maritima* L., *Distichlis spicata* (L.) Greene, and *Borrichia frutescens* (L.) de Candolle, have occasionally been found to bear eggs of *C. floridana* (personal observation), field and laboratory studies have indicated that *Spartina alterniflora* Loisel is by far its most frequent ovipositional host plant. For this reason, *S. alterniflora* was used exclusively as the host plant for *C. floridana* in all laboratory experiments. All laboratory experiments were performed under a 12:12 (L:D) photoperiod, and the insects were maintained at 23 ± 1°C, RH = 73 ± 2%.

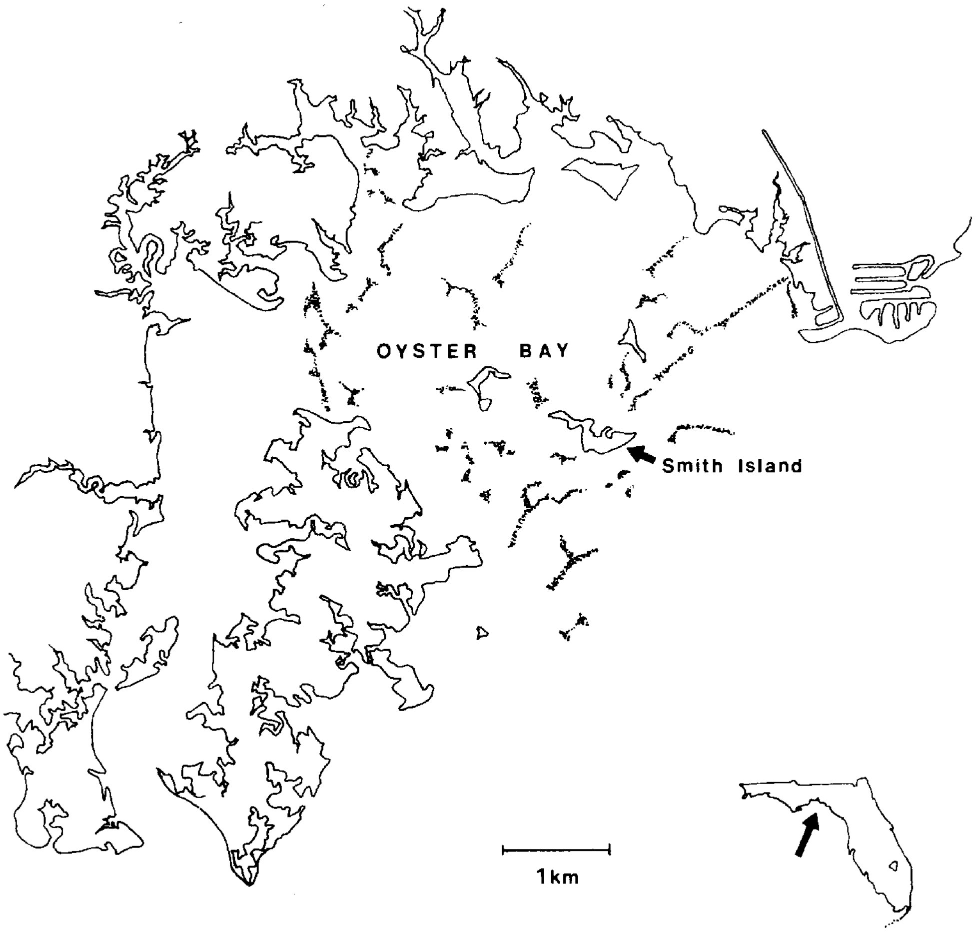


Fig. 1. Map showing the location of the field site, Smith Island, Oyster Bay, Wakulla County, Florida.

Acceptability of *S. alterniflora* as a host plant for *C. floridana* was assessed on the basis of volume of honeydew produced by field-collected females. For honeydew measurement, these females were placed in clip cages, which consisted of 2-cm (outer diameter) acetate tubing 4 cm long, sealed at both ends with plastic lids. The cages were placed over the leaves gently so as not to damage them, and the hoppers had access to both the upper and lower surfaces of the leaves. A 1.5-ml Eppendorf tube was placed through a hole in the bottom lid to collect the honeydew produced by the hoppers. The honeydew was collected, and the volume produced was determined after 24 h.

The number of instars was determined from the number of exuviae remaining in clip cages that housed nymphs from hatching to adulthood. Nymphs for this experiment were collected as they emerged from eggs laid by females in the laboratory and reared individually in clip cages (the Eppendorf tube was omitted because small nymphs tended to fall in and drown). The clip cages were placed around individual *S. alterniflora* leaves and transferred, with the nymphs, to new leaves at 2- to 3-d intervals.

Average clutch size and stages of egg development were assessed for female leafhoppers collected from the field during July, August, and October of 1988. Females were individually placed on single plants, and the entire plants were enclosed in large (5.5 cm outer diameter) acetate tubes sealed at the top with organdy cloth. The females were transferred to new plants at 2- to 3-d intervals. Plants were examined under a dissecting scope for clutches, and the average number of eggs per clutch was determined. In addition, several clutches from these plants were observed during egg development. The average number of eggs laid per female was determined for females newly eclosed from fifth-instar nymphs, which were collected from the field and reared in the laboratory in clip cages on leaves of *S. alterniflora*. Once the females had molted into adults, they were individually placed on leaves in clip cages. Two adult males were introduced into the cage with each female for 24 h. Next, each female was enclosed, as described above, in an acetate tube on a single plant. Surviving females were transferred to new plants at 2- to 3-d intervals. The plants were carefully dissected, and the numbers of clutches and eggs deposited by each female were recorded.

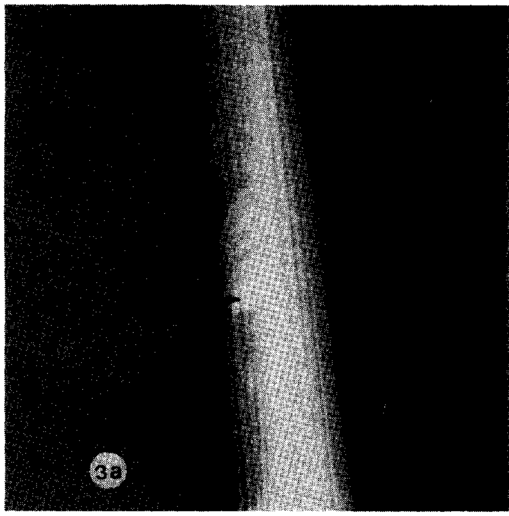
Field Collections

Natural trends in the density of a population of *C. floridana* were assessed by sweep netting from June 1988 through March 1989 at approximately 2-3 week intervals at five sites around the major salt pan at Smith Island. Vegetation at the sites consisted largely of mixed herbaceous plants. A sample consisted of ten individual sweeps at each site, and the number of nymphs and adults were counted in each of the ten sweeps and averaged. In addition, egg clutches were collected from the field at irregular intervals and examined for parasitoids.

RESULTS

Oviposition

In the laboratory, eggs were laid in discrete clutches just beneath the epidermal surface of either the stem or the leaves, although field-collected eggs are almost always found on the stems or at the leaf base of *S. alterniflora.* The clutches are usually located on the abaxial surface beneath the outermost stem sheath. The female cuts through the outer leaf with her ovipositor, and the eggs are generally not obvious unless the plant is dissected.



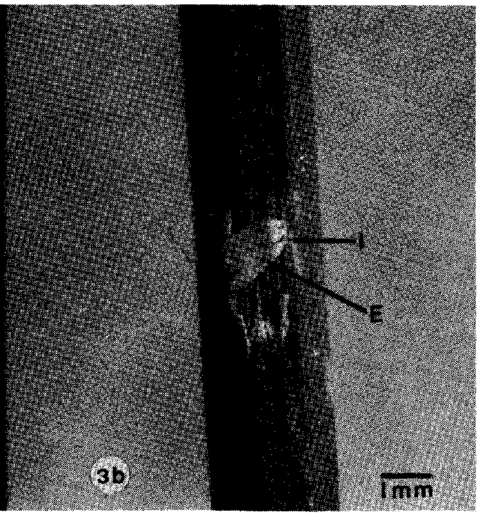


Fig. 2a. Clutch of eggs less than 2 d old as it appears under the stem epidermis of *S. alterniflora*. I = oviposition incision.

Fig. 2b. Clutch of eggs as it appears at 7-8 d. The epidermis has been removed. I = oviposition incision, E = eyespot.

Egg Development

Initially, the egg clutch appears as a blister. The female makes a single oviposition incision and lays the eggs parallel to one another, often in a fan-shaped pattern (Fig. 2a). Individual eggs, which are approximately 1.5 mm in length, are indistinct until 2-3 d after oviposition, when they appear cigar-shaped and dark green. By the third day, the eggs are well-defined and turgid, and the blister appears flaccid. The end of each egg nearest the oviposition incision becomes the nymph's head and takes on an opaque cream color after 5-7 d while the rest of the egg remains clear green. A reddish-brown pigmented spot, which will develop into the compound eye, forms slightly off-center toward the oviposition incision line after 5-7 d. Generally, only a single pigmented spot is visible, because the nymphs develop in profile to the surface of the leaf. By day 7, the eyespot has migrated to its final position, approximately 1/4 of the length from the vertex of the head. Also by day 7, the head takes on its characteristic pointed shape (Fig. 2b). By day 9, the eyespot becomes rounded and dark brown to black. The first-instar nymphs eclose from the eggs on approximately the tenth or twelfth day, making their exit through the leaf epidermis along the original oviposition incision.

Nymph Development

All hoppers reared from egg to adult went through five nymphal instars before eclosion to adult (N = 12). Although we do not have detailed data on nymphal development times, the nymphs took 4-6 weeks to go from first instar to adult.

Reproduction

To determine whether the number of eggs per clutch varied temporally, we performed a one-way ANOVA (Sokal & Rohlf 1969, pp. 181-186) on the data from the three sample dates. The means did not differ significantly (F = 1.58, d.f. = 2,145, p = 0.210;

log-transformed data); therefore, the data for the three months were pooled for calculation of the mean number of eggs per clutch (mean = 3.9 ± 0.2 (SE); range = 2-11; N = 148). Females (N = 19) laid an average of 93.5 ± 8.7 (SE) eggs over their adult lifetimes, which lasted on average 33.7 ± 2.6 (SE) days under laboratory conditions.

Adult Feeding and Sweep Sampling

Complete generations of *C. floridana* were reared on *S. alterniflora*, and the hoppers readily fed upon its xylem fluid. The mean volume of honeydew produced in a 24-h period was calculated to be 0.5 ± 0.1 (SE) ml (N = 33).

The number of nymphs and adults of *C. floridana* at the five sites around the salt pan at Smith Island are given in Figure 3. All five sites showed the same general seasonal trends, so the sweep data from the five sites were pooled. No data were available for the number of nymphs on the three dates indicated by asterisks, two of which occur during the strong spring pulse in population density; therefore, it seems reasonable to assume that this peak is actually much larger than is indicated by the figure. Results of biweekly sweep sampling, along with life-cycle data from the laboratory, suggest that *C. floridana* is at least bivoltine with overlapping generations and that most hoppers overwinter in either the adult or the egg stage.

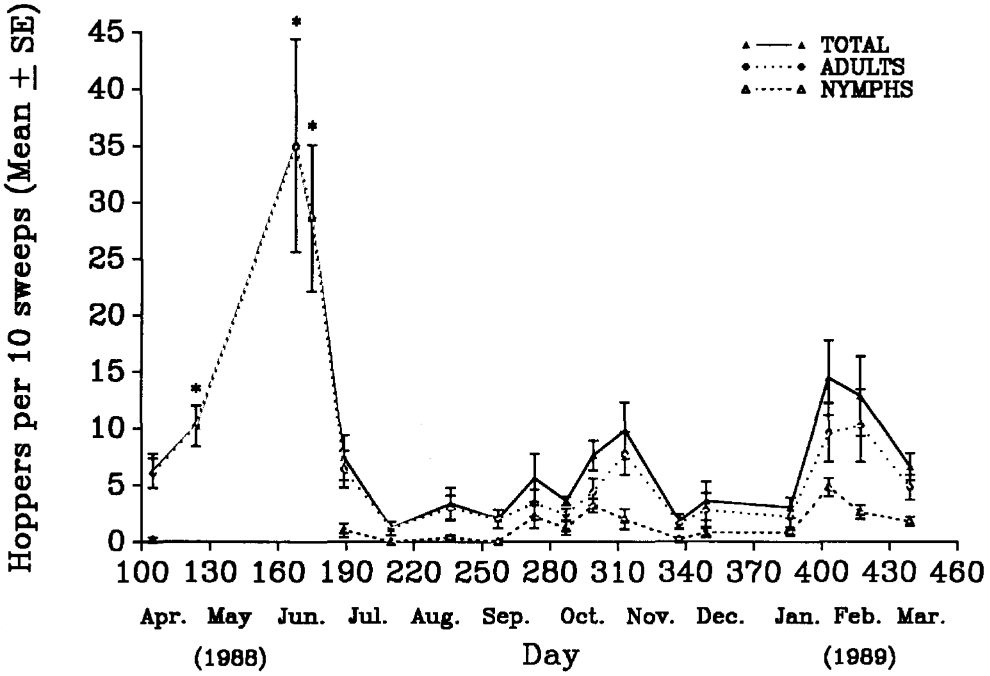


Fig. 3. Mean number of *C. floridana* per ten sweeps at five sites around the major salt pan on Smith Island from April of 1988 through March 1989. Closed triangles and solid line indicate total number of hoppers caught. Closed circles and dotted line indicate adults. Open triangles and dashed line indicate nymphs. Asterisks indicate dates on which no nymph data were available.

Egg Parasitoids

During the course of rearing field-collected *C. floridana* egg clutches, we discovered that approximately 30% of the eggs were parasitized by two species of mymarid wasps. Both wasps are undescribed species belonging to the genus *Gonatocerus* (initial determination by John Huber, Biosystematics Research Centre, K. W. Neatby Building, C.E.F., Ottawa, Ontario, Canada, K1A 0C6).

DISCUSSION

Like both Ball (1927) and Nottingham (1932), we collected *C. floridana* in mixed vegetation, including sea blite (*S. virginica*) and saltwort (*B. maritima*); however, we always found the hopper in close association with the salt-marsh cord grass, *Spartina alterniflora*. Laboratory and field studies clearly indicate that *S. alterniflora* is a primary host plant for *C. floridana*; other feeding and ovipositional hosts include *S. virginica, B. maritima, D. spicata,* and *B. frutescens* (personal observation). The hoppers promptly fed on the cordgrass and produced copious quantities of honeydew. Moreover, females readily laid eggs on the cordgrass, and complete generations of the leafhopper can be reared solely on *S. alterniflora*. Although *S. alterniflora* is certainly not the only host for *C. floridana*, the importance of this grass is consistent with the reports by Mead (1965) and others that members of this genus can become pests of other types of grasses, such as turf and pasture species.

The eggs are laid in a fan-shaped arrangement, sometimes on the abaxial surface of the leaves but more often on the stems, and eclose approximately 12 days after oviposition. This finding is similar to that of Freitag (1951) that another, closely related leafhopper, *Draeculacephala minerva* Ball, lays its eggs parallel in packets of 2 to 18 just below the epidermal surface of the leaves of barley. In addition, we have reared two undescribed species of parasitoids, both of the genus *Gonatocerus* (Hymenoptera: Mymaridae), from field-collected eggs of *C. floridana*. After emergence from the eggs, the hoppers pass through five nymphal instars before maturing into adults.

Adults of *Carneocephala floridana* were collected throughout the year on Smith Island, and the population showed distinct peaks in the spring and fall during 1988. Densities during the spring pulse were an order of magnitude higher than summer densities, whereas those from the fall were twice the summer densities. The population showed another peak in February of the following year. This increase may have been due to the early emergence of overwintering eggs brought about by balmy temperatures during November-January. The seasonal trends in abundance observed in *C. floridana* are similar to those found in another salt marsh homopteran, *Prokelisia marginata* van Duzee (Strong et al., in press; Stiling et al., unpublished).

Frazier (1944) stressed the strong correlation between membership in the subfamily Cicadellinae and the ability of a hopper to transmit Pierce's disease, and any species of the subfamily should be considered a potential vector. Although *C. floridana* is not usually economically important (Mead 1965), it is probably a vector of PD and may become important in spreading of the disease in Florida. The two *Gonatocerus* egg parasitoids discovered in the course of the present study may prove useful as agents for biocontrol of other, more economically important species of *Carneocephala*.

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NEW SPECIES AND FIRST U. S. RECORD OF *AURATONOTA* (LEPIDOPTERA: TORTRICIDAE)

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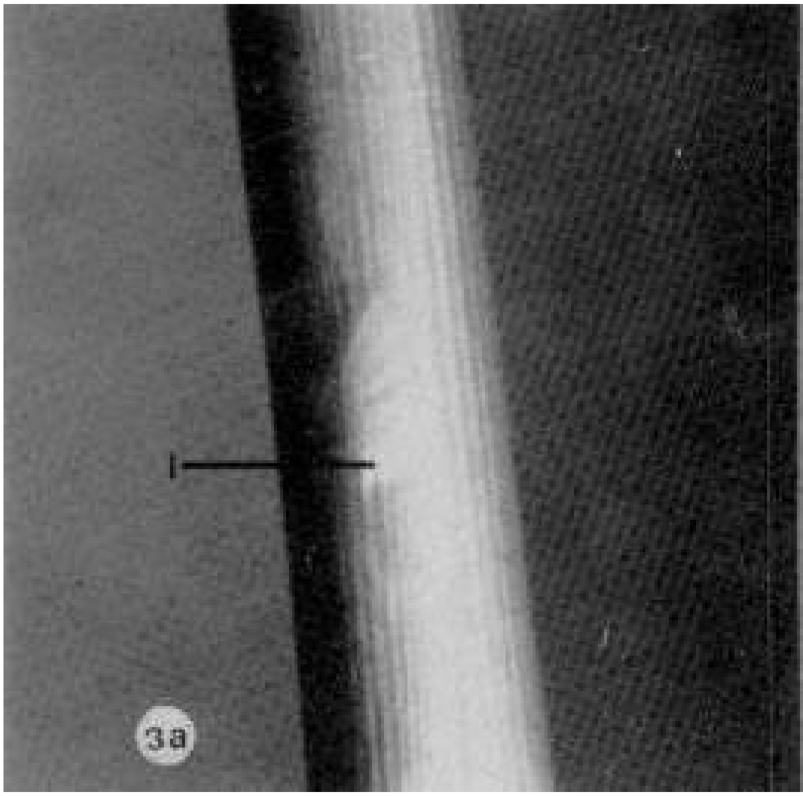
ABSTRACT

Auratonota dispersa n. sp. from Central America is described and figured. It has been collected twice in southern Florida; these captures constitute the first U. S. records of the tortricid tribe Chlidanotini. In addition, *Cnephasia aporema* Dognin is transferred to *Auratonota* Razowski, new combination.

RESUMEN

Se describe e ilustra a *Auratonota dispersa* sp. nov. de Centroamérica. Esta fué collectada dos veces en el sur de la Florida; estas capturas constituyen el primer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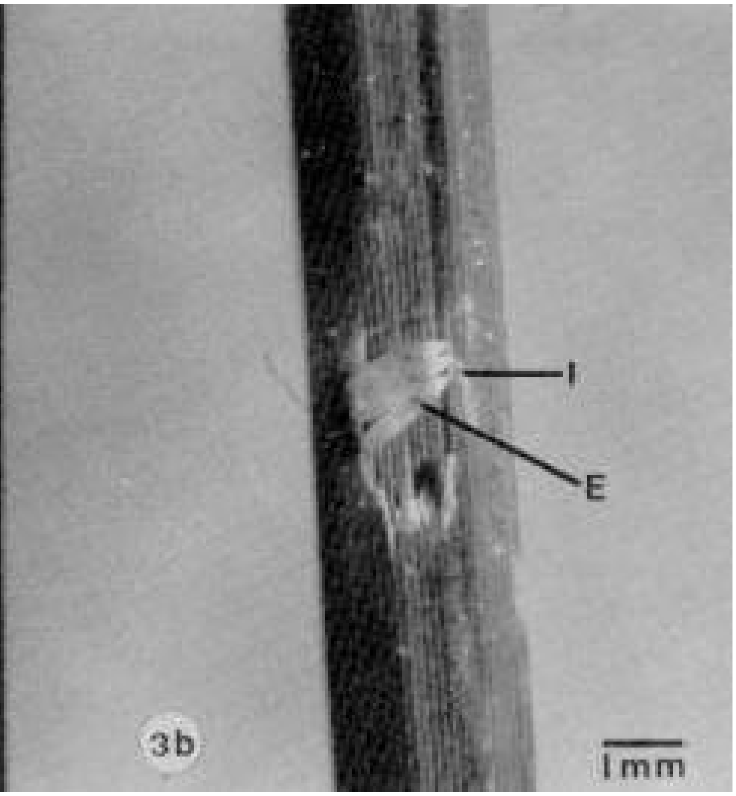
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ABSTRACT

Auratonota dispersa n. sp. from Central America is described and figured. It has been collected twice in southern Florida; these captures constitute the first U. S. records of the tortricid tribe Chlidanotini. In addition, *Cnephasia aporema* Dognin is transferred to *Auratonota* Razowski, new combination.

RESUMEN

Se describe e ilustra a *Auratonota dispersa* sp. nov. de Centroamérica. Esta fué collectada dos veces en el sur de la Florida; estas capturas constituyen el primer registro de tortrícidos de la tribu Chlidanotini para Estados Unidos. Además, se transfiere a *Cnephasia aporema* Dognin a *Auratonota* Razowski, una nueva combinación.

The Chlidanotinae, including the Chlidanotini, Hilarographini, and Polyorthini (Horak & Brown 1990), is the most primitive of three subfamilies that comprise the Tortricidae. The subfamily is primarily pan-tropical in distribution (Diakonoff 1974, Tuck 1981, Heppner 1982). Although three species of Hilarographini are indigenous to the United States, *Thaumatographa youngiella* (Bucsk), *T. regalis* (Waslsingham), and *T. jonesi* (Brower) (Heppner 1982), the remaining two tribes are unrepresented in our fauna (Powell 1983). This paper presents the first U. S. record of the tribe Chlidanotini, and the description of *Auratonota dispersa* n. sp. The species is native to Central America (i.e. from Guatemala to Panama); although it has been found twice in southern Florida, there is no evidence of its establishment. In 1967 a male specimen was intercepted in a shipment of orchids that reportedly originated in Guatemala (label data); in 1970 a single male was collected in a blacklight (UV) trap at an inspection station in Miami (label data).

Dissection methodology follows Powell (1964); nomenclature for genitalia follows Horak (1984); interpretation of forewing maculation follows Nijhout (1978). Depositories are abbreviated as follows: ANSP, Academy of Natural Sciences, Philadelphia; BMNH, British Musuem (Natural History), London, England; UCB, Essig Museum of Entomology, University of California, Berkeley; USNM, United States National Museum of Natural History, Washington, D. C.

Auratonota dispersa n. sp.
(Figs. 1-2)

Male. Forewing length 6.8-8.1 mm ($\bar{x} = 7.4$; $n = 6$). Head: Frons scaling smooth, sparse below mid-eye; suberect above, white with dark brown patches at base of antenna. Labial palpus with second segment moderately upturned, third segment slightly descending, hidden by scaling of second; white mesally, mixed with light brown laterally. Antenna lacking conspicuous cilia, strongly flattened in distal 0.4; scape yellow-ocherous, flagellum light brown. Ocelli present. Chaetosema poorly developed. Thorax: Yellow-gold with dark brown prothoracic collar and posterior lateral band. Legs with alternating bands of yellow and dark brown; scaling on hind femur slightly bushy; no specialized structures on legs. Conspicuous apical setae lacking on all tarsomeres. Forewing: Shiny white with complex pattern of narrow brown and yellow dislocated crossbands; numerous narrow dark brown fasciae extending from costa to hind margin, yellow in mid-wing and dislocated apicad; preapical brown fascia divided by three lateral yellow bands near tornus; median fascia broad at hind margin, bifurcate near lower edge of cell; subbasal fascia ca 0.66 times width of median fascia, broad at hind margin, bifurcate near lower edge of cell; basal facia complete, narrow. Fringe dark brown. Hindwing: White with faint gray-brown marbling. Fringe light gray-brown. Genitalia: As in Fig. 2 (drawn from USNM slide no. 68248; $n = 6$). Uncus moderately long, rod-like, with sparse, fine setae from venter. Socii large, broad basally, attenuate distally, with long, dense, fine setae. Hami narrow, slightly undulate, ca 1.3 x length of uncus; closely associated with, but not fused to, socii. Gnathos weak. Valva moderate in size, rectangular, with rounded apex; costa nearly straight; venter weakly undulate. Aedeagus a simple, narrow, straight tube; vesica with an irregular, weak, distal sclerite.

Female. Unknown.

Fig. 1. Adult male of *Auratonota dispersa.*

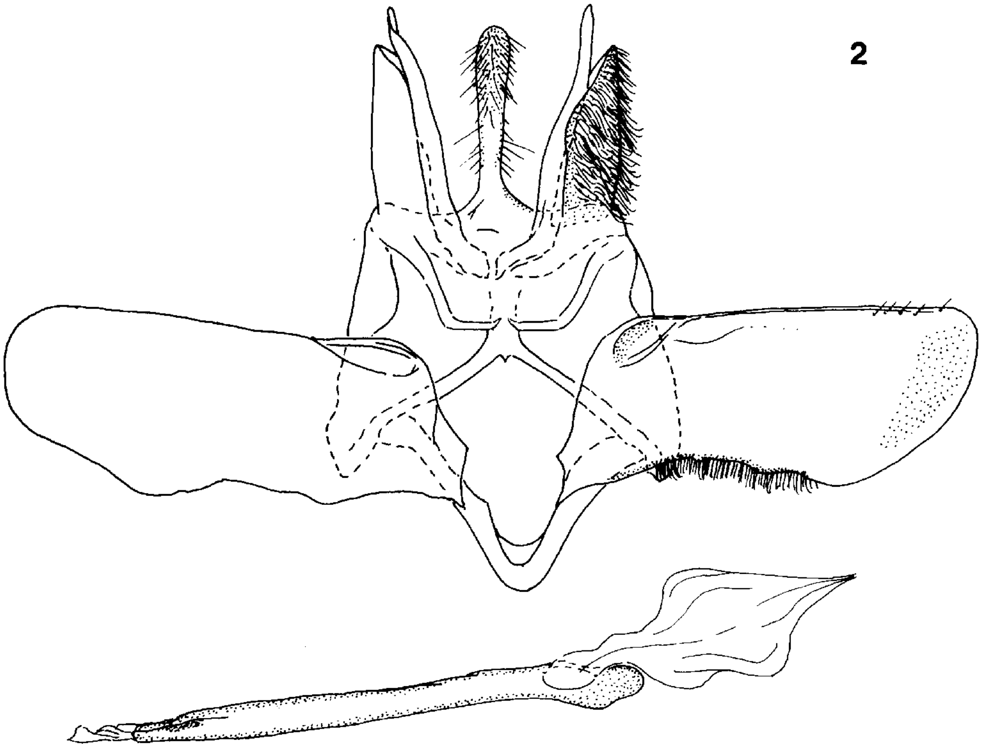

Fig. 2. Male genitalia of *Auratonota dispersa.*

Type material

Holotype male: Panama, Cocle Province, El Valle, 22-IV-65, S. S. & W. S. Duckworth (USNM).

12M Paratypes as follows: COSTA RICA: Alajuela Province: 8 km N Vera Blanca, Volcan Poas, 1500 m, 1M, 11-V-85, bl. (J. Chemsak, P. Opler & J. Powell, UCB), 1M, 26-V-85, bl. (J. Powell, UCB); N slope Volcan de Rincon, 2 km W Dos Rios, 550 m, 22-V-85, bl. (J. Powell & P. Opler, UCB); Estacion Pitilla, 9 km S Santa Cecilia, 700 m, 1M, VI-88, bl. (D. Janzen & W. Hallwachs, ANSP). Puntarenas Province: 2 km E Monteverde, 1M, 19-V-85, bl. (J. Powell, P. Opler, UCB), 1M, 13-VI-88, bl. (J. Brown & J. Powell, UCB). San Jose Province: La Montura, Braulio Carillo Nat. Park, 1100 m, lM, 17-XII-81 (D. Janzen & W. Hallwachs, ANSP). U.S.A.: Florida: Dade Co: Miami, black light trap, inspection station, 1M, 17-II-70 (USNM); Miami, "from Guatemala", with orchid plants, 26-V-67 (J. C. Buff, USNM).

Diagnosis

Auratonota dispersa appears most closely related to *A. aenigmatica* (Meyrick) from Colombia (holotype BMNH), to which it is superficially and morphologically similar. *A. dispersa* can be distinguished from *A. aenigmatica* (figured in Clarke 1958:117) by the absence of white dots in the dark brown transverse fasciae of the forewing and by the presence of long, fine setae from the venter of the uncus. *A. aenigmatica* and *A. dispersa* are not similar in forewing size or pattern to other species of *Auratonota.*

Heppner (1982) assigned *aenigmatica* to *Hilarographa* Meyrick (Hilarographini); Razowski (1987) included the species in *Auratonota* (Chlidanotini). Although Razowski's generic assignment may be provisional since *aenigmatica* is fairly distinct from its congeners, his tribal assignment is almost certainly correct. Neotropical Hilarographini have smooth-scaled, strongly upturned labial palpi, huge ocelli, and typical ciliate antennae. In contrast, Neotropical Chlidanotini have bushy-scaled, porrect palpi, small ocelli, and inconspicuous antennal cilia. These character states support Razowski's tribal assignment of the species.

DISCUSSION

Prior to Razowski (1987), the dozen or so described species of Neotropical Chlidanotini were without meaningful generic assignment. Razowski (1987) described *Auratonota* to accommodate *hydrogramma* (Meyrick, 1912), *petalocrossa* (Meyrick, 1926), *aurantica* (Busck, 1920), and *aenigmatica* (Meyrick, 1912). In addition, *Cnephasia aporema* Dognin, 1912, is congeneric with the above species, and herewith is transferred to *Auratonota* (new combination). Species of *Auratonota* are characterized by the following symplesiomorphies: 1) socii and hami not fused; 2) uncus lacking spine-like setae ventrally; and 3) valva simple, nearly rectangular, with rounded outer margin. Although fairly homogenous in overall appearance, with the exception of *aenigmatica* and *dispersa,* no convincing synapomorphies have been identified to support the monophyly of the genus.

ACKNOWLEDGMENTS

I thank J. F. G. Clarke (USNM), K. R. Tuck (BMNH), D. H. Janzen, University of Pennsylvania, whose material is deposited in the ANSP, and J. A. Powell (UCB) for allowing me to examine specimens in their care. I thank J. B. Heppner and J. A. Powell for comments and suggestions on the manuscript. This study was completed under the support of a Smithsonian Postdoctoral Fellowship.

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NEW NEOTROPICAL SPECIES OF "STICK-TICK" (DIPTERA: CERATOPOGONIDAE) FROM KATYDIDS

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ABSTRACT

Forcipomyia (Microhelea) tettigonaris Wirth and Castner new species is described from two females captured while attached tick-like to the scutellum of the katydid *Roxelana crassicornis* (Stal)(Orthoptera: Tettigoniidae) near Iquitos, Peru, on the Amazon River. Hosts of the four previously described species of this group of tick-like biting midges have been confined to stick insects (Orthoptera: Phasmatidae). A third female of this species is reported from a katydid in Costa Rica.

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RESUMEN

Se describe la nueva especie *Forcipomyia (Microhelea) tettigoniaris* Wirth y Castner, de dos hembras capturadas cuando estaban pegadas al estilo-garrapata, al escutelo del cigarrón *Toxelana crassicornis* (Stal) (Ortóptera: Tetigonida), cerca de Iquitos, Perú, en el rio Amazona. Hospederos de las cuatro especies previamente descritas de este grupo de mosquitas que pican parecido a las garrapatas, han sido confinados a los insectos de palo (Ortóptera: Fasmítida). Se reporta una tercera hembra de esta especie de un cigarrón de Costa Rica.

Female midges of the dipterous family Ceratopogonidae have evolved an amazing variety of feeding habits dependent on the basic nematocerous piercing-sucking arrangement of their mouthparts (Downes 1955, 1958, 1978). Distinct patterns of feeding have generally evolved in parallel with structural features which form the basis of subfamily and tribal classification, even as far as genera. For example, most Leptoconopinae as well as the genus *Culicoides* Latreille in the tribe Culicoidini are blood-feeders on vertebrates. All members of the subfamily Ceratopogoninae, except those in the tribe Culicoidini, are predaceous. They capture and suck haemolymph from insects smaller or not much larger than themselves, causing death of the prey. All members of the subfamily Dasyheleinae are autogenous and subsist on nectar and sugar-rich plant products. It is in the subfamily Forcipomyiinae that the most amazing variety of feeding habits has evolved, ranging from carrion and pollen-feeding, to feeding on haemolymph of meloid beetles (Wirth 1956b, 1980). In the genus *Forcipomyia* Meigen, various subgenera have evolved a variety of parasitic feeding patterns, none of which seriously harms the host (Wirth 1956a). Midges of the subgenus *Lasiohelea* Kieffer have retained what is thought to be the primitive habit of sucking vertebrate blood; species of *Trichohelea* Goetghebuer and *Pterobosca* Macfie are ectoparasitic on the wings of dragonflies or on the bodies or appendages of a wide variety of insects and other arthropods larger than themselves. In the subgenus *Microhelea* Kieffer one group of species sucks haemolymph from a variety of smooth-bodied caterpillars and sawfly larvae (Wirth 1972), while another group feeds on phasmid stick-insects. The abdomens of the latter swell with developing eggs to grotesque tick-like proportions, for which the common name "stick-ticks" was coined (Wirth 1971).

The junior author has recently collected a new species of this group of "stick-ticks" on the River Amazon near Iquitos (Department of Loreto), Peru. It was observed feeding on the katydid *Roxelana crassicornis* (Stal) (Orthoptera: Tettigoniidae), a habit previously unrecorded in the New World. Wirth (1971) summarized our knowledge of the "stick-ticks," pointing out the difference in structure and habits separating this group of species from the caterpillar parasites in the subgenus *Microhelea*; giving host records for the two common and widespread species, *F. ixodoides* (Fiebrig-Gertz) and *F. obesa* Costa Lima, known to feed on stick insects; and describing two new species, *F. amazonica* Wirth from Manaus, Brazil, and *F. willistoni* Wirth from Brazil, Jamaica and Puerto Rico. The present new species from Peru also feeds on an orthopteran, but is the first American species known to feed on a host other than a phasmid.

Debenham (1987) recorded two females of *Forcipomyia (Microhelea) willisi* Debenham feeding on the abdomen of a katydid (*Polichne* sp.: Tettigoniidae, Phaneropterinae) in Queensland, Australia, the first record of a *Microhelea* species from this host family. *Forcipomyia willisi* is closely related to *F. fuliginosa* (Meigen) and the group of caterpillar parasites, and does not have the morphological modifications of the Neotropical "stick-ticks." An unidentified species of *Microhelea* which Wirth (1971) placed close to but not identical with *F. fuliginosa* was reported by Edwards (1926) from a large phasmid on Buru Island, Indonesia, as *F. hirtipes* (de Meijere).

The terminology used in this paper is the same as that used in previous papers by Wirth (1971, 1972) on Neotropical species of the *Forcipomyia* subgenus *Microhelea.*

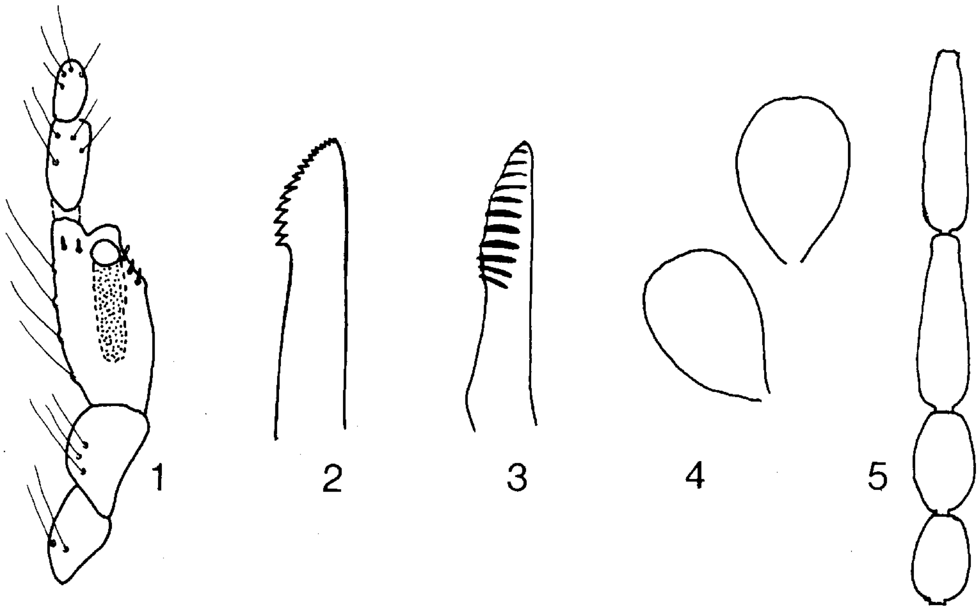
Forcipomyia (Microhelea) tettigonaris Wirth and Castner, new species
(Figs. 1-5)

Holotype Female.—Wing length 1.25 mm; breadth 0.51 mm.

Head: Dark brown, antennal segments 3-10 yellowish. Antenna with lengths of flagellar segments in proportion of 12-11-11-11-11-11-12-15-26-28-x-x-x (segments 13-15 missing); segment 11 2.0 times as long as 10 (Fig. 5). Palpus (Fig. 1) with lengths of segments in proportion of 12-15-31-15-8; third segment swollen on one side from base nearly to tip, swollen portion obliquely truncated distally, sensory pit extending from pore near tip of swollen portion of segment nearly to base of segment; several tear-shaped hyaline sensilla scattered on surface near pore opening; palpal ratio 2.2. Mandible (Fig. 2) with 15 dark brown teeth in a curving row, gradually increasing in size from minute teeth at apex to large, somewhat proximally curved teeth at base of row, proximal teeth forming a distinct lateral expansion of mandible. Maxilla (Fig. 3) well sclerotized and gradually tapering distally, with 11 well-sclerotized, dark-pigmented, transverse corrugations.

Thorax: Dark brown; mesonotum with moderately long yellowish setae. Legs yellowish including coxae and trochanters, with long yellow setae; tarsal ratios (T1/T2) of fore, mid and hind legs 0.68, 0.43, and 0.54 respectively. Wings damaged, much abraded; membrane infuscated; costal ratio of paratype 0.54. Halter color not observed.

Abdomen: Both specimens gravid witih abdomen much distended tick-like, with numerous fully-developed, spindle-shaped, yellowish eggs. Terga and sterna reduced to small, quadrate, transverse, brownish sclerites with long yellowish setae on lateral ends. Pleural membrane much distended, with sparse vestiture of short, pale brown setae arising from brownish-pigmented punctures. Spermathecae (Fig. 4) two, ovoid, without necks, slightly unequal, measuring 0.091 by 0.070 mm and 0.082 by 0.065 mm.



Figs. 1-5. *Forcipomyia tettigonaris*, female: 1, palpus; 2, mandible; 3, maxilla; 4, spermathecae; 5, antennal segments 9-12.

Male.—Unknown.

Distribution.—Peru, Costa Rica.

Types.—Holotype female, 1 female paratype, both taken from scutellum of the katydid *Roxelana crassicornis* (Stal), Iquitos, Loreto Department, Peru, 30.vii.1987, J. L. Castner (Holotype deposited in National Museum of Natural History, Smithsonian Institution, Washington, D.C.; paratype in Florida State Collection of Arthropods, Gainesville, Florida).

Etymolgy.—The species takes its name from the family name of the host insect, a katydid in the subfamily Pseudophyllinae and tribe Pterachrozini.

Discussion.—When he reviewed this paper, Art Borkent of Agriculture Canada recalled a female specimen in the Canadian National Collection which he kindly loaned us. The female, collected from a katydid thorax, La Selva, Costa Rica, 18.ii.1980, D. M. Wood, is conspecific with the types from Peru. This extension of the range of the species indicates to us that perhaps these midges are not rare in nature, and that special efforts should be made to look for them when observing katydids.

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HYMENOPTERA OF BERMUDA

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ABSTRACT

A recent survey of Bermuda's Hymenoptera resulted in 88 new records. This brings the number of known species to 199, representing 28 families. Approximately 25% of the species are cosmopolitan or tropicopolitan. A further 37% are common to Bermuda and eastern North America, and 24% originate from the Caribbean region. Two species are known to be endemic; at least six species remain undescribed.

RESUMEN

Una reciente encuesta de Himenópteros de las Bermudas resultó en 88 registros nuevos. Esto trae el número de especies conocidas a 199, representando a 28 familias. Aproximadamente el 25% de las especies son cosmopolitas o tropiolitas. El 37% son comunes de las Bermudas y del este de Norteamérica, y el 24% originan de la región del Caribe. Se sabe que dos especies son endémicas, y por lo menos seis especies se mantienen sin describir.

Bermuda is a small archipelago in the North Atlantic centered at 32°18′ N, 64°46′ W. Total land area of the seven main islands is only 54km^2. The climate is subtropical and frost-free, however, due to its small size, isolation, and geologically young age, Bermuda's native terrestrial fauna is depauperate. A survey of Bermuda's insects was inititated in 1987. For a review of entomology in Bermuda and an introduction to this project see Hilburn & Gordon (1989).

This report on the Hymenoptera (bees, wasps, and ants) includes all the species in the collection of the Bermuda Department of Agriculture and Fisheries (BDAF). It is now housed at the Bermuda Natural History Museum (BNHM) in Flatts, except for a small reference collection retained at BDAF"s laboratory in Paget. Sweepnet and Malaise trap collecting by the authors in 1987 and 1988 added a large amount of new material to this collection. In addition, all records listed in Wheeler (1906), Ogilvie (1928), Bequaert (1929), Banks (1938), Waterston (1940), Crowell (1968), Haskins & Haskins (1965) and Gould (1988) are repeated here, though as noted in the text some were apparently misidentified or are no longer established on Bermuda. In many cases the original specimens could not be found.

Several dozen species of parasitic Hymenoptera have been intentionally released in Bermuda as biological control agents; only the ones which are thought to be established are reported here. For a complete list of introduced species see Bennett et al. (1985), Bennett & Hughes (1959), and Simmonds (1957).

One hundred ninety-nine species in 28 families are listed along with information on biology and world distribution. Included are 88 new Bermuda records. Approximately 25% of the species are cosmopolitan or tropicopolitan. A further 37% are common to Bermuda and eastern North America, and 24% originate from the Caribbean region.

Two species are known to be endemic. At least six species are underscribed, some of these may be endemic. In many cases only generic names are given, either because the species were not identifiable as a named Nearctic, Neotropical or Holarctic species, or because the genus (or family in some cases) needs study before the species can be named. Because a large number of the species are apparently adventive from North America, we hope this list encourages taxonomists to include Bermuda in future studies of Nearctic or Western Hemisphere species.

This list is arranged by superfamily, and then alphabetically by families within superfamilies and genera and species within families. Voucher specimens of most species are housed at the BNHM and/or the U.S. National Museum of Natural History (USNM), Washington, DC.

ICHNEUMONOIDEA

BRACONIDAE

Agathis gibbosa (Say)
(Bennett et al. 1985). "Native" parasite of potato tuber moth, *Phthorimaea operculella* (Zell.). Occurs throughout North America; probably adventive in Bermuda.

Apanteles carpatus (Say) New Record
One specimen in BDAF collection; Paget, 1966. Cosmopolitan; probably adventive in Bermuda.

Apanteles sp. near *feltiae* Viereck New Record
Numerous specimens collected Paget, 1987; probably an undescribed species.

Apanteles sp. near *laevicoxis* Musesebeck New Record
Seven specimens collected St. George's, Paget and Sandy's Parishes, 1966 and 1987. Close to North American *laevicoxis*, also similar to *insularis* Muesebeck from Grenada and St. Vincent; appears to be undescribed.

Apanteles sp. near *paranthrenidis* Musesebeck New Record
Ten specimens collected in St. George's, Smith's, and Sandy's Parishes, 1987. *A. paranthrenidis* occurs in eastern USA; also similar to several Caribbean species but appears distinct; probably undescribed.

Aphaereta pallipes (Say) New Record
Occurs throughout North America; probably adventive to Bermuda. One specimen collected Smith's Parish, 1987.

Aphidius matricariae Haliday New Record
Holarctic and Neotropical in distribution; attacks a wide variety of aphids. A specimen in USNM labeled "With lilies from Bermuda at Chicago 1961"; apparently caught in quarantine in Chicago. Probably adventive in Bermuda, although no other specimens seen.

Chelonus (Microchelonus) phthorimaeae Gahan
(Bennett et al. 198t). Introduced to Bermuda from California in 1945 for control of potato tuber moth. Specimens in U.S. National Museum from Bermuda collected 1948 indicate recovery after the initial release. Lack of recent specimens suggests no longer established.

Cotesia marginiventris (Cresson) New Record
Placed in *Apanteles* prior to 1981, occurs throughout Western Hemisphere. Of 14 specimens in BDAF collection, earliest date of collection is 1966. However, one specimen of *marginiventris* in BDAF collection incorrectly identified as *Apanteles solitarius* collected in 1923; probably the specimen mentioned by Ogilvie (1928). Apparently adventive in Bermuda.

Desmiostoma parvulum (Wesmael) New Record

Six specimens collected St. George's and Smith's Parishes, 1967 and 1987. Holarctic; probably adventive in Bermuda from eastern USA.

Diaeretiella rapae (M'Intosh)

(=*Diaeretus rapae* Curtis; Ogilvie 1928). Reported by Ogilvie (1928) to be parasitic on *Aphis pseudobrasicae*. No specimens found in BDAF collection; cosmopolitan.

Eubazus sp.

(=*Calyptus* sp.; Ogilvie 1928). No specimens in BDAF collection, however, one *Eubazus* collected Smith's Parish, 1988, may be species identified by Ogilvie.

Habrobracon gelechiae (Ashmead)

(=*Bracon gelechiae*; Bennett et al. 1985). Occurs throughout North America, Caribbean, and India; introduced and established in Bermuda 1945 and 1948 for control of potato tuber moth.

Habrobracon hebetor (Say) New Record

One specimen in BDAF collection reared from peanut shell, 1967. Cosmopolitan; adventive in Bermuda.

Heterospilus sp. near *chittendenii* Ashmead New Record

Genus presently being revised; several hundred species primarily from Western Hemisphere; species probably undescribed.

Lysiphlebus testaceipes (Cresson)

(=*Aphidius testaceipes*; Ogilvie 1928). Occurs throughout Western Hemisphere; probably adventive in Bermuda.

Meteorus autographae Muesebeck New Record

Occurs throughout eastern USA, adventive to Bermuda. Of six specimens in BDAF collection, two labelled as associated with potatoes infested with tuber moth. Known hosts of *autographae* mostly noctuid moths, one of these pests probably actual host.

Opius concolor Szepligeti

(Bennett et al. 1985, =*Opius humilis* Silv.; Ogilvie 1928). Parasite of Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), imported from Hawaii, 1926-27. Recovered in 1936, but not observed during 1950s and not collected since. Mediterranean fruit fly eradicated from Bermuda 1962.

Opius confundens Fischer New Record

One specimen collected Smith's Parish, 1987; occurs in South Carolina, Florida, Louisiana and Texas.

Phanerotoma sp.

(Ogilvie 1928). BDAF collection contains 17 specimens, some reared from lepidoptera larvae in oleander and cedar berries. Genus in need of study for the Western Hemisphere; species probably undescribed.

Pholetesor bedelliae (Viereck) New Record

Placed in *Apanteles* prior to 1981; occurs throughout eastern half of USA and parts of western states. Apparently adventive in Bermuda.

Pseudapanteles dignus (Muesebeck)

(=*Apanteles dignus* (Mues.); Bennett et al. 1985). "Native" parasite of potato tuber moth; occurs in Florida, California, Mexico, and Caribbean; probably adventive in Bermuda.

ICHNEUMONIDAE

Campoletis sonorensis (Cameron)

Two specimens in BDAF collection: 'Camden', Paget Parish, Nov. 1966; Devonshire Bay, Devonshire Parish, June 1987 with sweepnet. Widespread in North, Central, and South America.

Daidegma compressa (Cresson)
(=*Angitia blackburni* Cam.; Waterston 1940, Bennett and Hughes 1959, =*Diadegma blackburni* (Cram.); Bennett et al. 1985). Parasite of potato tuber moth when it attacks potato foliage or tomato fruit. First collected in 1932, now common; also occurs in eastern USA, California, and northern Mexico.

Enicospilus flavus (F.)
(Bequaert 1929; =*Henicospilus concolor* Cress; Ogilvie 1928). Collections throughout the year at lights; not common. West Indies, Central and South America.

Enicospilus doylei Gould
(Gould 1988). Also known from Florida, Louisiana, Bahamas, and Nicaragua.

Enicospilus purgatus (Say)
(Gould 1988). Parasite of various noctuid larvae. Widespread in New World.

Enicospilus trilineatus (Brulle)
(Gould 1988). Southeast USA, West Indies, Central and South America.

Itoplectis conquisitor (Say)
(=*Ephialtes* (*Itoplectis*) *conquisitor* (Say); Cushman 1920). No specimens in BDAF collection. North America; many hosts.

Labena nigra Rohwer
(Rohwer 1920). Described from five Bermuda specimens collected 1909. No recent collections; no specimens in BDAF collection.

Netelia sp.
(?=*Paniscus rufus* Brulle; Ogilvie 1928). Apparently an undescribed species; three specimens in BDAF collection: April and May 1967, Mount Hill, Pembroke Parish, at lights; Feb. 1967, Wreck Rd., Sandy's Parish, at light.

Ophion bermudensis Cushman
(Cushman 1940). Described from five Bermuda specimens. No recent collections; no specimens in BDAF collection.

Ophion sp.
(Ogilvie 1928). No specimens in BDAF collection; possibly *O. bermudensis*.

Rubicundella perturbatrix Heinrich
Collected from Devonshire Marsh, Devonshire Parish, 1955, and BDAF laboratory, Feb. 1964. Widespread in eastern USA, also occurs in California and Hawaii.

CHALCIDOIDEA

AGAONIDAE

Odontofroggatia galili Wiebes New Record
Lives within syconia of *Ficus microcarpa*; does not pollinate florets. Native to eastern Asia; established in Israel and Florida.

Parapristina verticillata (Waterston) New Record
Pollinator of *Ficus microcarpa*; accidentally introduced early 1980's; epiphytic seedlings have become serious weeds in stone walls, roadcuts, palm tree crowns, and similar habitats. Native to Old World tropics and subtropics, now widespread in North, Central, and South America wherever *F. microcarpa* introduced.

Walkerella yoshiroi (Ishii) New Record
Like, *O. galili*, lives within syconia of *F. microcarpa*, but does not pollinate florets. probably native to Asia; now also occurs in Florida and Brazil.

APHELINIDAE

Aphelinus sp. New Record
Specimens collected with sweepnet; Spittal Pond, Smith's Parish; Nonsuch Island, St. George's Parish; and Gibbon's Nature Reserve, Devonshire Parish, June 1988.

Aphytis diaspidis (Howard)
(Simmonds 1957, Bennett & Hughes 1959, Bennett et al. 1985, =*Aphytis fuscipennis* Howard; Waterston 1940, Simmonds 1957, Bennett & Hughes 1959, =*Aphelinus diaspidis* Howard; Ogilvie 1928). Introduced from Italy 1923 for control of *Pseudaulacaspis pentagona* (Targ.); also parasitizes *Acutaspis agavis* (Tns. & Ckll.), *Selenaspidus articulatus* (Morg.), and *Comstockiella sabalis* Comst. Simmonds (1957) reports identity somewhat in doubt; *Aphytis* collected in Bermuda not typical *diaspidis*. *A. diaspidis* occurs eastern USA and California.

Aphytis mytilaspidis (LeBaron)
(Waterston 1940, Simmonds 1957, Bennett & Hughes 1959, Bennett et al. 1985). Cosmopolitan; attacks palmetto scale, *C. sabalis*, in Bermuda.

Aphytis sp.
(Bennett & Hughes 1959). Parasite of cedar scale, *Carulaspis minima* (Targ).

Aspidiotiphagus citrinus (Craw)
(Waterston 1940, Simmonds 1957, Bennett & Hughes 1959, =*Encarsia citrina* (Craw); Bennett et al. 1985). Accidentally introduced around 1940; further shipments imported from California 1955-56; parasitizes the following scale insects: *C. sabalis*, *P. pentagona*, *C. minima*, and *A. agavis*; cosmopolitan.

Aspidiotiphagus lounsburyi (Berlese & Paoli)
(Simmonds 1957, Bennett & Hughes 1959). Accidentally introduced around 1940; parasite of *C. minima*, *Diaspis boisduvalii* Sign., *Lepidosaphes beckii* (Newm.), *Pinnaspis aspidistrae* (Sign.), and *Pinnaspis strachani* (Cooley); also occurs in Florida.

Azotus sp. New Record
Collected with sweepnet Gilbert Nature Reserve, Sandy's Parish, June 1988.

Coccophagoides sp. New Record
Collected Berry Hill Rd., Paget Parish, June 1988.

Coccophagus flavoscutellum Ashmead
(Ogilvie 1928). Reportedly reared from *P. pentagona*; not found by later collectors; probably a misidentification.

Coccophagus ochraceus Howard
(Simmonds 1957). Parasite of *Pulvinaria psidii* Mask. and *Saissetia coffeae* Walk; occurs in Louisiana and California.

Coccophagus scutellaris (Dalman)
(Simmonds 1957). Parasite of *Coccus hesperidum* L., *Coccus viridis* (Green), *P. psidii*, *S. coffeae*, *Parasaissetia nigra* (Nietn.), and *Saissetia oleae* (Bern); known from Florida, and west coast USA.

Coccophagus sp. *lycimnia* group
(Simmonds 1957). Parasitizes *C. hesperidum*, and *S. coffeae*.

Coccophagus sp.
Collected in Malaise trap Berry Hill Rd., Paged Parish, June 1988.

Encarsia fasciata (Malenotti)
(=*Prospaltella fasciata* Malenotti; Simmonds 1957). Parasite of *C. minima*.

Encarsia formosa Gahan
(Bennett et al. 1985). Parasitizes *Metaleurodicus cardini* (Back) which attacks fiddlewood, *Citharexylum spinosum* L.; cosmopolitan.

Encarsia portoricensis Howard
(Waterston 1940, Simmonds 1957, Bennett & Hughes 1959, Bennett et al. 1985). Introduced from USA 1926 and 1928; parasitizes palmetto scale, *C. sabalis.*

Encarsia sp.
(= *Prospaltella* sp.; Bennett & Hughes 1959). Parasite of *C. minima*; collected Spittal Pond, Smith's Parish, June 1988.

Eretmocerus sp. New Record
Collected in Malaise trap Berry Hill Rd., Paget Parish, and with sweepnet Gilbert Nature Reserve, Sandy's Parish, June 1988.

Marietta sp.
(Simmonds 1957). Hyperparasite associated with *S. nigra.* Collected in Malaise trap Paget Parish Sept. 1987.

Physcus sp. near *testaceus* Masi
(Simmonds 1957). Parasite of *C. sabalis.*

CHALCIDIDAE

Spilochalcis sp. New Record
First collected 1955; a large chalcid now fairly common in sweepnet samples.

ENCYRTIDAE

Acerophagus pallidus Timberlake
(Simmonds 1957, Bennett et al. 1985). Introduced successfully from California, 1951 for control of *Phenacoccus madeirensis* Green (= *P. gossypii*). Hyperparasitized by *Chartocerus niger* (Ashm.).

Anagyrus fusciventris (Girault)
(Simmonds 1957, Bennett & Hughes 1959, Bennett et al. 1985). Imported from Australia 1951-53 and 1955 as a biological control agent for *Pseudococcus adonidum* L. Established successfully in Bermuda; also introduced to California.

Anagyrus sp New Record
Collected in Malaise trap Berry Hill Rd., Paget Parish, and with sweepnet Gilbert Nature Reserve, Sandy's Parish June 1988.

Anicetus annulatus Timberlake
(Simmonds 1957). Parasite of *C. hesperidum*; also occurs Texas and California.

Arrhenophagus chionaspidis Aurivillius
(Simmonds 1957). Attacks both *D. boisduvalii*, and *P. strachani*; southeastern USA.

Carabunia waterstoni Subba Rao
(Bennett et al. 1985, = *Carabunia myersi* Waterston; Bennett et al. 1985). Imported from Jamaica 1959-61; parasitizes casuarina spittlebug, *Clastoptera undulata* Uhl. Recovered 1960, 1961, and 1965; not in recent collections (Bennett et al. 1985).

Cheilonerus pulvinariae Dozier
(Simmonds 1957, Bennett & Hughes 1959). Hyperparasite of *Microterys kotinsky* (Fullaway); southeastern USA.

Cheiloneurus sp.
(Simmonds 1957). Hyperparasite associated with *P. nigra*; in Malaise trap Spittal Pond, Smith's Parish. August 1987.

Coccidencyrtus ochraceipes Gahan
(Simmonds 1957). Attacks *D. boisduvalii*; known from eastern USA.

Coccidoxenoides peregrinus (Timberlake)
(= *Pauridia peregrina* Timberlake; Simmonds 1957, Bennett & Hughes 1959, Bennett et al. 1985). Imported from south China 1951-53 as a biological control agent for *Planococcus citri* (Risso); established successfully in Bermuda and California.

Copidosoma floridanum (Ashmead) New Record

Reared from unidentified caterpillars feeding on potato leaves November 1966; eastern USA.

Copidosoma sp. New Record

Collected with sweepnet various locations 1988.

Encyrtus barbatus Timberlake

(Simmonds 1957). Attacks *C. hesperidum*; also found California.

Encyrtus infelix (Embleton)

(Simmonds 1957). Parasitizes *S. coffeae*; eastern USA.

Encyrtus lecaniorum (Mayr)

(Simmonds 1957). Attacks *P. nigra*; known from Europe and North America.

Epidinocarsis sp.

(=*Apoanogyrus* sp.; Simmonds 1957). Parasite of *P. madeirensis*; collected with sweepnet Nonsuch Island, St. George's Parish, June 1988.

Epitetracnemus sp.

(=*Anabrolepis* sp.; Simmonds 1957). Parasitizes *P. adonidum*; collected in Malaise trap Berry Hill Rd., Paget Parish, June 1988.

Gahaniella sp. (not *tertia* Kerr)

(Simmonds 1957). Hyperparasite associated with *P. nigra*.

Leptomastidea abnormis (Girault)

(Simmonds 1957). Introduced from Sicily 1953 as a biological control agent; attacks *P. citri*; widespread in North America.

Leptomastidea dactylopii (Howard)

(=*Leptomastix dactylopii* Howard; Simmonds 1957, Bennett and Hughes 1959, Bennett et al. 1985). Introduced from Brazil 1952; mealybug parasite; apparently already present (Bennett et al. 1985). Widespread and common in sweepnet samples; also widespread in North America.

Litomastix sp. New Record

Collected in sweepnets and Malaise traps at several locations June 1988.

Metaphycus flavus (Howard)

(Simmonds 1957, Bennett et al. 1985, =*Aphycus flavus* How.; Bennett & Hughes 1959). Imported from Morocco and Spain 1953-54; apparently already present. Parasitizes *P. psidii*, and *S. coffeae* in Bermuda; widespread in eastern and southern North America.

Metaphycus stanleyi Compere

(Simmonds 1957, Bennett et al. 1985, =*Aphycus stanleyi* (Comp.); Bennett & Hughes 1959). Parasite of: *P. psidii*, *C. hesperidum*, *S. oleae*, and *P. nigra*; also occurs in California.

Metaphycus sp.

(Simmonds 1957). Reared from *Pulvinaria floccifera* (Westwood); additonal *Metaphycus* collected with sweepnet several locations June 1988.

Microterys kotinskyi (Fullaway)

(Simmonds 1957, Bennett & Hughes 1957, Bennett et al. 1985). Introduced from Hawaii and California 1953-55 for control of *P. psidii*; well established and occurs throughout the islands.

Neodusmetia sangwani (Subba Rao)

(Bennett et al. 1985). Introduced from Texas 1968 as a biological control agent for Rhodes grass scale, *Antonia graminis* (Mask.); occurs in southern USA. *Neodusmetia* sp. possibly *sangwani* collected with sweepnet Paget, Smith's, and Sandy's Parishes 1987.

Plagiomerus sp.

(Simmonds 1957). Parasitizes *Howardia biclavis* (Comst.).

Procheiloneurus sp.
(Simmonds 1957, Bennett & Hughes 1959). Members of genus are hyperparasites; collected 1987 and 1988 in sweepnets and Malaise traps.

Pseudectroma europaeus (Mercet)
(=*Timberlakia europaea* (Merc.); Bennett et al. 1985). Attacks Rhodes grass scale, *A. graminis*. *Pseudectroma* sp. collected with sweepnet Spittal Pond, Smith's Parish, June 1988, possibly this species.

Psyllaephagus sp. New Record
Collected with sweepnet Botanical Gardens, Paget Parish, June 1988.

Tetracnemoidea peregrinus (Compere)
(=*Arhopoideus peregrinus* (Comp.); Bennett et al. 1985, =*Tetracnemus peregrinus* Comp.; Simmonds 1957, Bennett and Hughes 1959). Imported from Argentina 1951 as a biological control agent for longtailed mealybug, *P. adonidum* L.; established successfully; also introduced to California. *Tetracnemoidea* sp. collected Berry Hill Rd., Paget Parish, June 1988, with Malaise trap possibly this species.

Trichomasthus portoricensis (Crawford)
(=*Coccidoxenus portoricensis* Crawf.; Simmonds 1957). Hyperparasite associated with *P. nigra*.

EULOPHIDAE

Aprostocetus spp. New Record
At least five species in genus collected various locations 1987 and 1988.

Ceranisus sp. New Record
A single specimen collected with sweepnet Gilbert Nature Reserve, Sandy's Parish, June 1988.

Chrysocharis sp. New Record
Fairly common in sweepnet and Malaise trap samples June 1988.

Chrysonotomyia sp. New Record
Collections made Sept. 1973 from eggs of *Calpodes* and June 1988 various locations with sweepnet.

Cirrospiloideus sp. New Record
Collected Gilbert Nature Reserve, Sandy's Parish, and Ferry Reach, St. George's Parish August 1987.

Closterocerus sp. New Record
Common in sweepnet samples many locations June 1988.

Diaulinopsis callichroma Crawford New Record
Widespread and common in sweepnet samples June 1988; occurs in New World tropics and subtropics.

Diglyphus spp. New Record
At least three species in genus collected June 1988; group needs revision.

Elachertus cidariae Ashmead New Record
Collected with Malaise trap Berry Hill Rd., Paget Parish, June 1988.

Elachertus sp. New Record
Collected with sweepnet Spittal Pond, Smith's Parish, June 1988.

Euderus sp. New Record
Collected Spittal Pond, Smith's Parish, and Admiralty House Park, Pembroke Parish, 1987 and 1988.

Euplectrus comstockii Howard New Record
Very common and widespread June 1988; known from USA, Central and South America.

Euplectrus sp. New Record
Very common August 1987 several locations.

Horismenus sardus (Walker) New Record
Collections made Spittal Pond, Smith's Parish and Gilbert Nature Reserve, Sandy's Parish, June 1988; known from Florida.

Horismenus texanus (Girault) New Record
Widespread and very common 1987 and 1988; known from eastern and southern USA.

Neotrichoporoides viridimaculatus (Fullaway) New Record
Collected several locations 1988; known from North and South America.

Pediobius williamsoni (Girault) New Record
Collected Spittal Pond, Smith's Parish, June 1988; eastern USA.

Pnigalio sp. New Record
Collected with sweepnet Spittal Pond, Smith's Parish, June 1988. Previously, one specimen collected Nonsuch Island, St. George's Parish, February 1967.

Sympiesis sp. New Record
Collected Spittal Pond, Smith's Parish, June 1988.

Tetrastichus spp. New Record
At least three species collected 1987 and 1988; group needs revision.

Zagrammosoma multilineatum (Ashmead) New Record
Collected Spittal Pond, Smith's Parish, June 1988 with sweepnet; known from USA, Puerto Rico, and South America.

EUPELMIDAE

Anastatus sp. New Record
Collected Berry Hill Rd., Paget Parish, June 1988 in Malaise trap.

Brasema sp. New Record
Collected Spittal Pond, Smith's Parish, June 1988 with sweepnet.

Eupelmus sp. New Record
Collected Spittal Pond, Smith's Parish, June 1988 with sweepnet; group needs revision.

Lecaniobius cockerelli Ashmead
(Ogilvie 1928, Simmonds 1957). Parasite of *P. nigra*; occurs in Florida, the West Indies, and Central and South America.

EURYTOMIDAE

Eurytoma spp. New Record
At least two species collected 1987 and 1988 several different locations.

MYMARIDAE

Alaptus sp.
(Simmonds 1957). Reared from *C. minima*; also collected Gilbert Nature Reserve, Sandy's Parish, June 1988 with sweepnet; genus nearly cosmopolitan.

Anagrus sp. New Record
Collected several locations June 1988; genus nearly cosmopolitan.

Anaphes sp. New Record
Collected Spittal Pond, Smith's Parish, June 1988 with sweepnet; genus nearly cosmopolitan.

Gonatocerus spp. New Record
In June 1988, at least three species collected various locations; genus nearly cosmopolitan.

Mymar sp. New Record
Collected Gilbert Nature Reserve, Sandy's Parish, June 1988; genus nearly cosmopolitan.

Polynema sp. New Record
Common many locations 1987 and 1988; genus nearly cosmopolitan.

PTEROMALIDAE

Anisopteromalus calandrae (Howard) New Record
Two specimens collected Southampton Parish Dec. 1982.

Asaphes sp. New Record
One specimen reared from aphid collected Paget Parish 1982.

Bubekia fallax Gahan New Record
One specimen collected in Malaise trap Paget Parish Oct. 1987.

Halticoptera sp. New Record
Very common many locations 1987 and 1988.

Heteroschema sp. New Record
Collected Horseshoe Bay, Southampton Parish June 1988.

Pachyneuron sp. New Record
Common many locations June 1988.

Pteromalus puparum (L.) New Record
Introduced 1988 from Virgina; gregarious pupal parasite of imported cabbageworm, *Pieris rapae* (L.). Recoveries made May 1988, one month after release; cosmopolitan.

Pteromalus sp. New Record
Collected several locations June 1988.

Spalangia sp. New Record
One specimen collected August 1987, Penhurst Park, Smith's Parish; a second in Malaise trap Paget Parish October 1987.

Thinodytes sp. New Record
Collected Penhurst Park, Smith's Parish, August 1987.

Zatropis sp. New Record
Collected Penhurst Park, Smith's Parish and Nonsuch Island, St. George's Parish, 1987 and 1988.

SIGNIPHORIDAE

Chartocerus niger (Ashmead)
(Bennett et al. 1985, =*Thysanus niger* Ashm.; Waterston 1940, Simmonds 1957). Hyperparasite of *A. pallidus*; occurs in eastern USA and California.

Signiphora louisianae (Dozier)
(=*Thysanus louisianae* Dozier; Simmonds 1957). Hyperparasite associated with *C. minima*; occurs in extreme southeastern USA.

Signiphora sp. New Record
Collected Gilbert Nature Reserve, Sandy's Parish, June 1988 with sweepnet.

TRICHOGRAMMATIDAE

Trichogramma exiguum Pinto & Planter
(prob. =*Trichogramma* sp.; Bennett & Hughes 1959, and Bennett et al. 1985). Speciments in BDAF collection reared from eggs of *Calpodes ethlius* August 1983; no locality given.

Trichogramma sp. New Record
Collected in Malaise trap Berry Hill Rd., Paget Parish, June 1988.

CYNIPOIDEA

EUCOILIDAE

Didyctium sp. New Record
Two females collected in BDAF laboratory June 1966. Known hosts Phoridae (humpbacked flies).

Hexacola sp. New Record
A single specimen collected Hog Bay Level, Sandy's Parish, Aug. 1987 with sweepnet.

Kleidotoma sp. New Record
One specimen collected Admiralty House Park, Pembroke Parish, Aug. 1987 with sweepnet.

Leptopilina boulardi (Barbotin et al.) New Record
Collected from rotting pawpaws, 'Camden', Paget Parish, May 1966; parasite of *Drosophila melanogaster* Meigen; widely distributed in warmer parts of North and South America, Europe, and Africa.

EVANIOIDEA

EVANIIDAE

Evania appendigaster (L.)
(Ogilvie 1928). Common indoors during summer; parasitic on cockroach egg cases; nearly cosmopolitan, especially in warmer climates.

PROCTOTRUPOIDEA

DIAPRIIDAE

Trichopria spp. New Record
At least three species collected 1987 and 1988; genus badly in need of revision for Western Hemisphere.

PLATYGASTRIDAE

Platygaster sp. New Record
One specimen caught in Malaise trap Paget Parish, Sept. 1987; a second collected Horseshoe Bay, Southamptom Parish, June 1988 with sweepnet; genus in need of study for Western Hemisphere.

Synopeas sp. New Record
Three specimens collected Smith's and Paget Parishes 1987 and 1988; genus in need of revision for Western Hemisphere.

SCELIONIDAE

Idris binotatus (Ashmead) New Record
Collected Paget Parish 1987; occurs in northeastern North America and probably adventive in Bermuda. Species in genus parasitic on spider eggs.

Telenomus spp. New Record
Several species collected 1986 and 1987. One series reared from Lepidoptera egg mass on *Mangifera indica*. Genus presently being studied; species not yet identifiable.

CERAPHRONOIDEA

CERAPHRONIDAE

Ceraphron sp. New Record

Three specimens collected Paget Parish 1987. Some species in genus develop as primary parasites, others as secondary parasites; hosts Diptera, Hymenoptera and Homoptera; entire family in need of study.

CHRYDIDOIDEA

BETHYLIDAE

Sclerodermus sp. New Record

Two specimens found in house Paget Parish May 1987; not an American species; may be adventive from Europe or Africa; probably not established.

Unidentified sp. New Record

A single specimen collected on flowers Spittal Pond, Smith's Parish, January 1988.

DRYINIDAE

Anteon funestus Perkins New Record

Known from Arizona; first collected in Bermuda Admiralty House Park, Pembroke Parish, and Hog Bay Level, Sandy's Parish, August 1987.

Unidentified sp. of Gonatopodinae

First collected 1966; recent collections from Spittal Pond and Penhurst Park, Smith's Parish, and Paget Parish. Genital armature of males different from known USA species; possibly new species or USA species with unknown males.

FORMICOIDEA

FORMICIDAE

Brachymyrmex heeri Forel

(Wheeler 1906, Ogilvie 1928). Probably introduced with plants from West Indies; found on citrus leaves and amongst grass, sometimes attending *Pseudococcus* spp. (Ogilvie 1928). Collected from *Cassia* tree Warwick Parish, July 1987; widespread in neotropics and West Indies.

Brachymyrmex sp.

Numerous males collected at Trott's Pond, Hamilton Parish, July 1966 in grass and in McPhail trap baited with torula yeast Warwick Parish; may be *B. heeri.*

Camponotus novaeboracensis (Fitch) New Record

Intercepted in imported Christmas trees Dec. 1983 and Dec. 1986; a northern North American species; not established in Bermuda.

Cardiocondyla emeryi Forel

(Wheeler 1906, Ogilvie 1928). Not common, but widespread in Bermuda; most abundant Aug. and Sept.; a tramp specie distributed by commerce throughout tropics.

Crematogaster sp. New Record

Intercepted in coconuts from West Indies, July 1967.

Hypoponera opaciceps (Mayr)

(=*Ponera opaciceps* Mayr; Wheeler 1906, Ogilvie 1928). No specimens in BDAF collection; probably misidentified or no longer established. Spread by commerce; found in both New and Old World tropics and subtropics.

Iridomyrmex humilus (Mayr)

Argentine Ant. (Haskins & Haskins 1965, Crowell 1968). First detected 1948 (Bennett & Hughes 1959); presumably arrived in imported nursery stock. Now common islandwide; distribution patchy. Native to South America; distributed by commerce, now tropicopolitan.

Lasius niger L.

(Wheeler 1906, Ogilvie 1928). Wheeler (1906) felt probably introduced; holarctic. May no longer be established in Bermuda; no specimens in BDAF collection, and no sightings in recent years.

Monomorium pharaonis (L.)

Pharaoh Ant. (Wheeler 1906, Ogilvie 1928). According to Ogilvie (1928), a common house species; listed by earlier collectors as *M. minutum.* Cosmopolitan; not an important household pest in Bermuda in recent years.

Monomorium sp.

(Crowell 1968). First reported by Crowell (1968); one specimen in BDAF collection Spittal Pond, Smith's Parish, Sept. 1987, with sweepnet.

Ochetomyrmex auropunctatus (Roger)

Little Fire Ant. (=*Wasmannia auropunctata* Roger; Crowell 1968). First reported St. Geroge's Parish by Crowell (1968); now fairly common. Often nests in trees; capable of stinging; occurs in Florida, California, West Indies, and Central and South America.

Odontomachus brunneus (Patton)

(=*Odontomachus haematodes insularis* Guerin; Wheeler 1906, Ogilvie 1928, Haskins & Haskins 1965, Crowell 1968). Common in 1927; rare by 1968 Crowell (1968). No specimens in BDAF collection; may no longer be established. Occurs in southern USA, West Indies, and Central and South America. *O. insularis* known only from Cuba, Bahamas, and ?Hispaniola.

Paratrechina longicornis (Latreille) New Record

Crazy Ant. Intercepted on plants from Holland July 1971 and *Dahlia* bulbs from Holland Jan. 1987; not established; transported by commerce; pantropical.

Paratrechina vividula (Nylander)

(=*Prenolepis kincaidi* Wheeler; Wheeler 1906, Ogilvie 1928). Wheeler (1906) found amongst grass and attending *Pseudococcus* on sugarcane; known from Mexico and southern USA; no specimens in BDAF collection.

Paratrechina spp.

(Crowell 1968). First reported Crowell (1968) Ferry Point, St. George's Parish; now common and widespread.

Pheidole megacephala (F.)

Bigheaded Ant. (Wheeler 1906, Ogilvie 1928). Ubiquitous in Bermuda; frequently found attending aphids and scale insects and sometimes invades houses (Ogilvie 1928). Still Bermuda's most common ant though displaced in some areas by *I. humilus* (Haskins & Haskins 1965, Crowell 1968). Tropicopolitan species able to propagate rapidly and exterminate indigenous ant fauna (Wheeler 1906).

Tetramorium caespitum L.

(Wheeler 1906, Ogilvie 1928). More likely *T. bicarninatum* (Nylander) (=*T. guineense*) according to Wheeler (1906). No specimens in BDAF collection; misidentified or no longer be established. *T. bicarinatum* is pantropical.

VESPOIDEA

EUMENIDAE

Euodynerus hidalgo hidalgo (Saussure) New Record

Rare in Bermuda. Collections on Nonsuch Is., St. George's parish, July 1963; Cobb's Hill, Warwick Parish, 1955; and Elbow Beach Area, Paget Parish, 1955. Common throughout eastern USA.

Stenodynerus bermudensis (Bequaert)

(Bequaert 1929). Rare endemic species. Collections Nonsuch Is., St. Geroge's Parish, Aug. 1967, and Serpentine Rd., Pembroke Parish, June 1970.

VESPIDAE

Polistes carolina (L.)

(=*P. carolinus*, Richards 1978). Intercepted at airport 1972; eastern USA.

Polistes fuscatus fuscatus (F.)

(Richards 1978; =*P. fuscatus* (F.), Bequaert 1929; =*P. bellicosus* Cress., *P. pallipes* Lep., *P. perplexus* Cress.; Ogilvie 1928). Known locally as "red bee"; common during summer and fall. Nests usually fastened to branches of wild sage (Lantana spp.); common North American species.

Vespa arenaria F.

(Bequaert 1929). One specimen collected by J. M. Jones in Bermuda late 1800's; not established; common throughout northern North America.

POMPILOIDEA

POMPILIDAE

Anoplius bermudensis (Banks)

(Banks 1938, =*Psammochares funereus* Lep., *P. philadelphicus* Lep., and *P. scelestus* Cress; Ogilvie 1928). Once common on sandy banks (Ogilvie 1928). Endemic; recent collections Spittal Pond, Smith's Parish and Warwick Pond, Warwick Parish in grasses near ponds using sweepnet.

SPHECOIDEA

SPHECIDAE

Chalybion cyaneum (Klug)

(Bequaert 1929). No specimens in BDAF collection; common mud-dauber in eastern USA. Originally misidentified or no longer established.

Liris sp. New Record

Three specimens in BDAF collection: Flatts, Hamilton Parish, Oct. 1968; two intercepted in soil from West Indies Oct. 1948.

Mimesa sp.

(Ogilvie 1928, Bequaert 1929). Reproted by early collectors but not after 1921; probably no longer established.

Sceliphron caementarium (Drury)

(Ogilvie 1928, Bequaert 1929, =*S. fasciatum* St. Farg.; Ogilvie 1928). Reported to be most common mud-dauber wasp in Bermuda (Ogilvie 1928). No longer common, but still widespread; common in eastern USA.

Sceliphron caeruleum L.
(Ogilvie 1928). Clay nests once found on old walls; provisioned with spiders (Ogilvie 1928). Two specimens in BDAF collection: June 1925, Smith's Parish, and April 1963, no locality given; may no longer be established.

Tachysphex sp. near *ruficaudis* New Record
Two males collected Aug. 1968 Nonsuch Is., St. George's Parish; probably underscribed. *T. ruficaudis* ranges from Argentina to Jamaica, Arizona, and southern California.

APOIDEA

APIDAE

Apis mellifera L.
Honey bee. (Ogilvie 1928). Introduced from England about 1616 (Kevan 1981). In 1988 thirty part-time beekeepers managed 400 hives. Well managed hives yield approximately 55 kg of honey per year. Native to Europe, Asia, and Africa; introduced to all parts of the world.

HALICTIDAE

Halictus semiviridis Friese
(Bequaert 1929, =*Augochlora* sp. and *Halictus* sp.; Ogilvie 1928). Once very common, especially among fennel flowers; not collected or seen this century.

MEGACHILIDAE

Megachile pruina pruina Smith
(=*Megachile* sp.; Ogilvie 1928, =*M. p. bermudensis* Mitchell; Bequaert 1929, Mitchell 1929). Made circular incisions in rose leaves and nested in walls (Ogilvie 1928). No longer present on main islands; survives on Nonsuch, Is., St. George's Parish; utilizes Jamaica dogwood, *Dodonaea viscosa*; also occurs in North Carolina, Georgia, and Florida.

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TWO NEW SPECIES AND A KEY TO THE ADULTS OF *ALEOCHARA* OF FLORIDA (COLEOPTERA: STAPHYLINIDAE)

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ABSTRACT

Two new species, *Aleochara* (*Aleochara*) *pseudolustrica* Klimaszewski, and *Aleochara* (*Calochara*) *beckeri* Klimaszewski, from Florida, are described on the basis of structures of adults. A key is given to adults of the eleven species of *Aleochara* now known to occur in Florida. Additional distributional data are given for *Aleochara* (*Coprochara*) *notula* Erichson and *A.* (*A.*) *lustrica* Say.

RESUMEN

Dos nuevas especies, *Aleochara (Aleochara) pseudolustrica* Klimaszewski y *Aleochara (Calochara) beckeri* Klimaszewski, de Florida, son descritas en base a estructuras de los adultos. Una clave para adultos de 11 especies de *Aleochara* conocidas de Florida es proveida. Datos adicionales de distribución son reportados para *Aleochara (Calochara) notula* Erichson y para *A. (A.) lustrica* Say.

Larvae of all *Aleochara* species are internal parasitoids of dipterous pupae, as far as is known. Dipterous eggs and larvae are major dietary items of adult *Aleochara.* Interest has accordingly been shown in *Aleochara* as natural regulatory agents and as biological control agents of pest fly populations. Although some *Aleochara* species have been introduced into North America as biological control agents of pest flies, knowledge of classification and natural history of native North American species remained very poor until Klimaszewski's (1984) revision began to provide a sound basis for identification. This paper provides a basis for ecological studies of the *Aleochara* species occurring in Florida. Most of the material comes from an extensive sampling program by S. B. Peck in natural habitats in extreme south Florida (Peck 1989).

MATERIALS AND METHODS

Most specimens were collected in flight-intercept traps in hardwood hammocks, or in carrion-baited pitfall traps, or by Tullgren funnel extraction of sifted organic materials. Flight-intercept traps were large-area intercept traps combined with Townes-style Maise trap heads [Malaise-FIT traps]. Materials sifted included dog- and horse-dung, hammock leaf litter, and sea beach litter. Most specimens were collected by S.

& J. Peck, and some by S. Peck & J. Klimaszewski. Some specimens were collected by E. C. Becker in the Gainesville area using malt-baited pitfall traps in pine-oak forest.

Many specimens were dissected. Genitalic structures were dehydrated in alcohol, transferred to xylene, mounted in Canada balsam on plastic slides, and pinned with the specimens from which they came. Holotypes and allotypes from this study are deposited in the Canadian National Collection [CNC], Ottawa. Paratypes are deposited in the collections of the authors [JKC, JHFC, SPC] and in the Florida State Collection of Arthropods [FSCA] as indicated in the text. Authorship of the new species names is attributed to the senior author alone, as recommended by Blackwelder (1967) in the case of multi-authored taxonomic works.

KEY TO ADULTS OF *ALEOCHARA* SPECIES OCCURRING IN FLORIDA

1\. Pronotum with 2, longitudinal, subparallel rows of setigerous punctures near the middle line of the disc; elytra brown to black, each elytron with paler apico-medial spot colored yellowish-brown to bright yellow 2

1′. Pronotum evenly pubescent, without 2 longitudinal rows of setigerous punctures near the middle line of the disc; elytra not colored as above (except in *A. lacertina*) 4

2\. Pronotum and head highly glossy with sparse punctation and fine pubescence; median line of pronotum outlined on each side with a broken row of about 12 punctures; each elytron with a bright-yellow apico-medial spot .... *A.* (*C.*) *notula* Erichson

2′. Pronotum and head glossy with moderately dense punctation and coarse pubescence; median line of pronotum outlined on each side with an unbroken row of >20 punctures; each elytron with a dull yellowish-brown apico-medial spot 3

3\. Setigerous punctures of head and pronotum deeply impressed; smaller (2.0-4.0 mm long) .... *A.* (*C.*) *verna* Say

3′. Setigerous punctures of head and pronotum shallowly impressed; larger (4.0-8.0 mm long) .... *A.* (*C.*) *bimaculata* Gravenhorst

4\. Basal terga of abdomen with prominent, scale-shaped microsculpture; elytra black; most specimens with a pale, yellowish-brown spot in apico-medial part of each elytron .... *A.* (*X.*) *lacertina* (Mäklin)

4′. Basal terga of abdomen without scale-shaped microsculpture; elytra not colored as above 5

5\. Body slender; head, pronotum, elytra and abdominal terga with distinct hexagonal microsculpture; pro- and mesotibiae each with double row of prominent spines; occurring on seashores .... *A.* (*E.*) *litoralis* (Mäklin)

5′. Body robust; head, pronotum, elytra and abdominal terga with surface smooth between punctures; pro- and mesotibiae with moderate spines, inconspicuous because interspersed among finer setae; generally in habitats other than seashores 6

6\. Elytra with pubescence directed approximately straight posteriorly; last maxillary palpomere as long as penultimate; antennomeres V-X strongly transverse, each at least twice as wide as long; some specimens large (3.0-9.0 mm long) 7

6′. Elytra with pubescence directed obliquely posteriorly toward postero-lateral angles, in some specimens forming slightly sinuate lines near the angles; last maxillary palpomere slightly or distinctly shorter than penultimate; antennomeres V-X at most slightly transverse 10

7\. Elytra uniformly black; some specimens large (4.0-9.0 mm long) .... *A.* (*A.*) *lata* Gravenhorst

7′. Elytra yellowish to rust-brown or bicolored; smaller (3.0-7.0 mm long) 8

8\. Elytra yellowish-brown to rust-brown; antennomere IV longer than wide, V-X quadrate or longer than wide; tergite VIII of male without apical serration .... *A.* (*A.*) *gracilicornis* Bernhauer

8′. Elytra dark brown to black with paler brownish to rust-brown oblique belt on each elytron, extending from basal outer angle to apico-medial angle; antennomeres IV-X transverse; tergite VIII of male with distinct apical serration 9

9\. Head and pronotum moderately densely pubescent and moderately glossy, punctation fine; abdominal apex of most specimens dark; tergite VIII of male unicolorous; apex of median lobe of aedeagus produced into a small hook laterally; spermatheca connected to membranous, inconspicuous vagina with one inconspicuous, U-shaped sclerite; widely distributed except on Florida Keys .... *A.* (*A.*) *lustrica* Say

9′. Head and pronotum sparsely pubescent and highly glossy, punctation deeply impressed; abdominal apex paler, rust-brown; tergite VIII of male bicolored; apex of median lobe of aedeagus acute, pointed slightly ventrally, and with small subapical projection; spermatheca connected to well-sclerotized vagina with 2 distinct sclerites near its opening; known only from lower Florida Keys .... *A.* (*A.*) *pseudolustrica* Klimaszewski

10\. Body evenly, narrowly elongate; pronotum sparsely pubescent with deeply impressed coarse punctation and with narrow, transverse basal impression; elytra unicolorous, black; last maxillary palpomere spindle-shaped, only 0.25X length of penultimate .... *A.* (*C.*) *beckeri* Klimaszewski

10′. Body robust with sides arcuate; pronotum densely pubescent with slightly impressed fine punctation and with basal impression absent; elytra black with paler, rufous or yellowish-brown belt on each side, ranging from basal outer angle to apico-medial one; last maxillary palpomere as long as penultimate or almost so .... *A.* (*X.*) *puberula* Klug

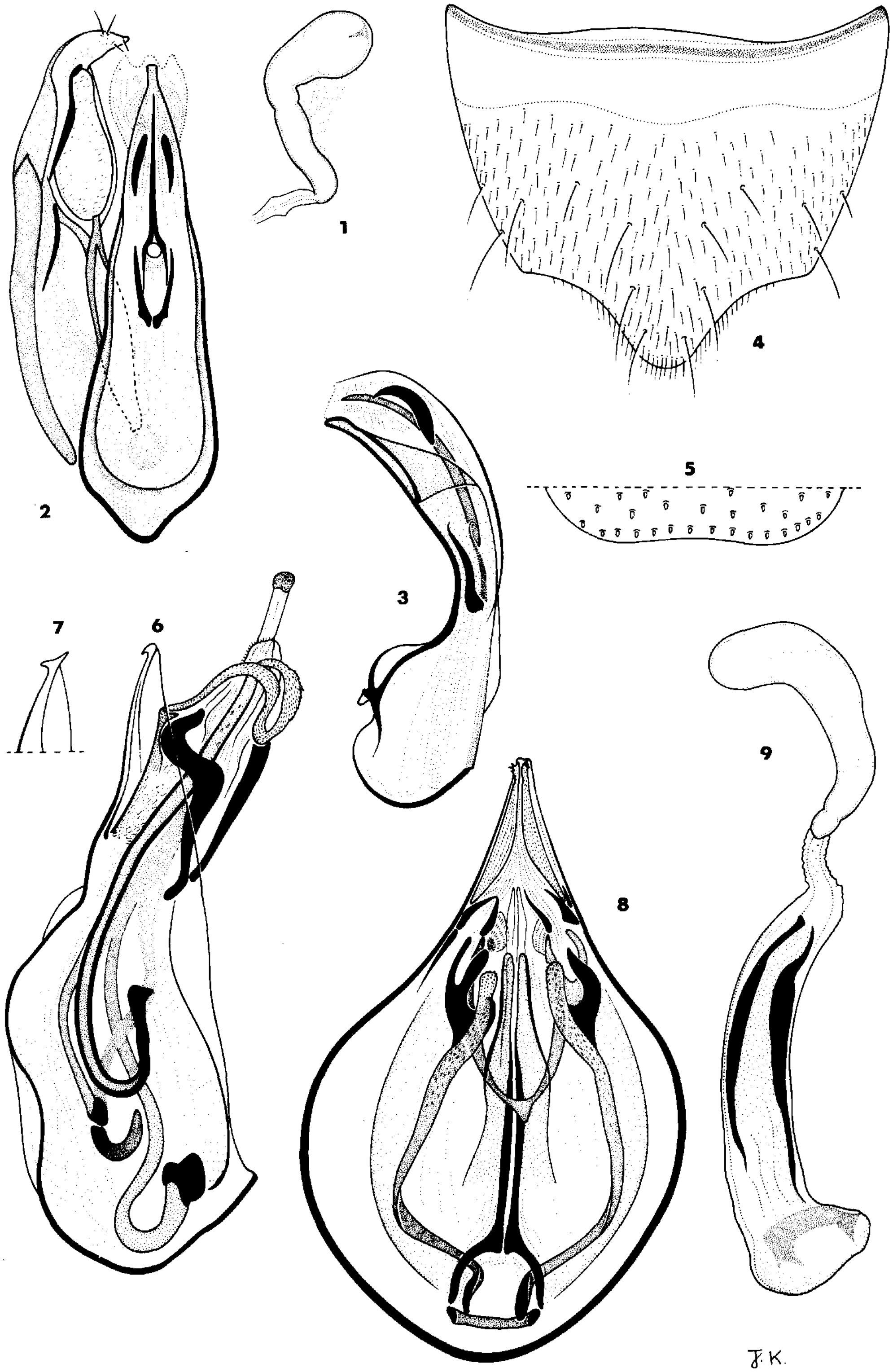
SUBGENUS *ALEOCHARA* MULSANT & REY

For definition of the subgenus see Klimaszewski (1984).

Aleochara pseudolustrica Klimaszewski, new species
(Fig 7-12)

ETYMOLOGY. The name adds the prefix *pseudo-* (false) to the epithet *lustrica* (as in *Aleochara lustrica* Say).

DIAGNOSIS. Adults of this species are distinguished by the following combination of characters: body robust, of medium size (average 4.5 mm long), glossy (slightly less so on elytra), dark brown to black with oblique, paler, rust-brown belt on each elytron, abdomen with apical part also paler, usually rust-brown; punctation deep, especially on head and pronotum; male tergum VIII serrated apically and bicolored (Fig. 12); median lobe of aedeagus with a complex arrangement of sclerites (Fig. 8), and with apex acute, slightly pointed ventrally and with a subapical small projection (Fig. 7); spermatheca L-shaped with a short duct and seminal canal connected to a broad, long, and usually well-sclerotized or pigmented vagina whose opening has a semicircular sclerite bearing a small tooth on side (Fig. 9); in vicinity of vaginal opening there is an additional



Figs. 1-9. *Aleochara* spp.: 1-5 *A. beckeri* sp. n.: 1, spermatheca; 2, aedeagus in ventral view (one paramere removed); 3, median lobe of aedeagus in lateral view; 4, sternite VIII of male; 5, apex of tergite VIII of male with peg-shaped setae; 6: *A.*

U-shaped sclerite (Fig. 10, 11). Specimens resemble those of *A.* (*A.*) *lustrica* Say, but differ in coarser punctation and in genitalic structures described above. *Aleochara pseudolustrica* is known only from the lower Florida Keys (Cudjoe Key, Sugarloaf Key), where *A. lustrica* has not been found. Adults also are similar to those of two Neotropical species (*A. chrysorrhoa* Erichson and *A. lateralis* Erichson), but differ in the same ways as they do from *A. lustrica* (see also description of *A. lustrica* by Klimaszewski 1984 and of *A. chrysorrhoa* and *A. lateralis* by Klimaszewski et al. 1987).

DESCRIPTION. Dark brown to black, with tarsi and in some specimens tibiae, maxillary and labial palpi, antennomeres I-II, and apical part of abdomen paler, usually rust-brown. Each elytron with a more-or-less well-defined rust-brown belt extending from basal outer angle to apico-medial angle. Pubescence brownish, paler on elytral belts, and denser on elytra than elsewhere. Punctation moderately deep. Length 2.5-6.0 mm.

Head capsule slightly transverse, sparsely pubescent, and with punctures deeply impressed, surface between punctures without microsculpture and glossy, pubescence directed anteriorly and inward; antennomeres I-III elongate and glossy, IV transverse and glossy, IV-X transverse and matt, each at least twice wider than long; last maxillary palpomere as long as penultimate or almost so. Pronotum slightly transverse, broadly rounded basally and insignificantly sinuate basally near the sides, sparsely pubescent with punctures deeply impressed and surface between them without microsculpture and glossy, pubescence directed posteriorly along midline of the disc and postero-laterally elsewhere. Elytra transverse, densely pubescent, with pubescence directed more-or-less straight posteriorly, punctures less pronounced than those on head and pronotum, and surface less glossy than the latter. Abdomen robust, broadly arcuate laterally and gradually narrowed posteriorly, glossy and sparsely pubescent, punctures deeply impressed and slightly, longitudinally elongate; first five abdominal tergites narrowly, transversely impressed at base.

MALE. Tergite VIII bicolored, brown with paler, usually yellowish, apical third; sparsely pubescent and with a few prominent setae in apical third; apex serrate (Fig. 12). Sternite VIII of most specimens bicolored, with apex truncate, pubescence sparse, slightly elongate toward apex. Apex of median lobe of aedeagus acute and slightly dorsally oriented and with small subapical projection in lateral view (Fig. 7); internal sac with complex sclerites (Fig. 8) similar to those of *A. lustrica* and *A. lateralis*.

FEMALE. Tergite and sternite VIII similar to those of male, but tergite lacking serrate apex. Spermatheca L-shaped with short duct and seminal canal connected to broad, long and in most specimens well-sclerotized vagina which bears near the opening a semicircular sclerite (Fig. 9). In vicinity of the vaginal opening there is an additional U-shaped sclerite (Fig. 11).

HABITAT. All specimens examined were collected in hardwood hammocks.

GEOGRAPHIC DISTRIBUTION. The species is known only from Cudjoe and Sugarloaf Keys, in the lower Florida Keys, USA, though it may occur also in the West Indies. Although identical traps were operated on the southern mainland of Florida, in the upper Keys and lower Keys, specimens were collected only in the lower Keys.

MATERIAL EXAMINED. In total, 219 specimens, including 37 males, 39 females, and 143 specimens of undetermined sex. Specimens are deposited in CNC, JKC, JHFC, and SPC.

←

lustrica Say: median lobe of aedeagus with everted internal sac; 7-9 *A. pseudolustrica* sp. n.: 7, apical portion of median lobe of aedeagus in lateral view; 8, median lobe of aedeagus in ventral view; 9, spermatheca with seminal canal and vagina. [Note: the dorsal side of the aedeagus is considered to be the side with the vas deferens].

HOLOTYPE. The holotype is a female and is deposited in the Canadian National Collection, and labelled: Florida, Monroe Co., Sugarloaf Key, Kitchings Hammock, Section 25, 29.viii-14.xii.86, S. & J. Peck (86-80), hammock forest Malaise-FIT.

ALLOTYPE. The allotype is a male, bears the same collection labels, and is deposited in CNC.

PARATYPES. Florida, Monroe Co., Cudjoe Key, SE 1/4, Section 20, 21.xi.1985-26.ii.1986, S. & J. Peck (86-28), hammock, Malaise-FIT, (JKC, SPC) 3 males, 4 females, 5 sex undetermined; same data but 5.vi.-28.viii.1986 (JKC) 2 males; same data but 29.viii.-14.xii.1986 (86-79), (JKC) 8 males, 5 females, (FSCA) 1 male, 1 female; Sugarloaf Key, SE 1/4, Section 25, 4.viii.-19.xi.1985, S. & J. Peck, hammock, Malaise-FIT, (JKC) 35 sex undetermined; same data but 5.viii-19.xi.1985, (JKC) 2 males, 2 females; Kitchings, 9.xi.1985-26.ii.1986, (JKC) 4 females, 8 sex undetermined; 19.xi.1985-26.ii.1986, (JKC) 5 males, 6 females, 33 sex undetermined; 6.vi.-29.viii.1986, S. & J. Peck (86-30), hammock forest, Malaise-FIT, (JKC) 1 male, 1 female, 61 sex undetermined, (JHFC) 1 female, 6 sex undetermined; SE 1/4, Section 25, 26.ii.-6.vi.1986, (86-29) remaining data as above, (JKC) 2 males, 1 female, (JHFC) 1 male; same data as above but 6.vi.-29.viii.1986, (JKC) 2 males, 5 females.

Aleochara (Aleochara) lustrica Say
(Fig. 6)

This species is widely distributed in the eastern USA, from New York, Michigan and Illinois in the north to Florida and Texas in the south, with a few records from Arizona and southern Mexico (Klimaszewski 1984). NEW FLORIDA RECORDS are: Florida, Dade Co., Everglades National Park, Palma Vista Hammock, 15 km NW of Royal Palm, 15.xi.1985 24.ii.1986, hardwood hammock, Malaise-FIT, S. & J. Peck, (JKC) 3 females; Long Pine Key, 8.vi.-26.viii.1986, pinelands, Malaise-FIT, S. & J. Peck, (JKC) 1 female; Royal Palm Hammock, 28.vii.-15.xi.1985, hardwood hammock, Malaise-FIT, S. & J. Peck, (JKC) 4 males, 4 females; South Miami, Old Cutler Hammock, 21.ii.-1.vi.1986, hardwood hammock, Malaise-FIT, S. & J. Peck, (JKC) 6 males; South Miami, Deering Estate Park, 21.ii.-1.vi.1986, old hammock, Malaise-FIT, S. & J. Peck, (JKC) 1 male, 1 female; 50 km SW of Miami, Chekika State Recreation Area, 15.xi.1985-24.ii.1986, Malaise-FIT, S. & J. Peck, (JKC) 2 males.

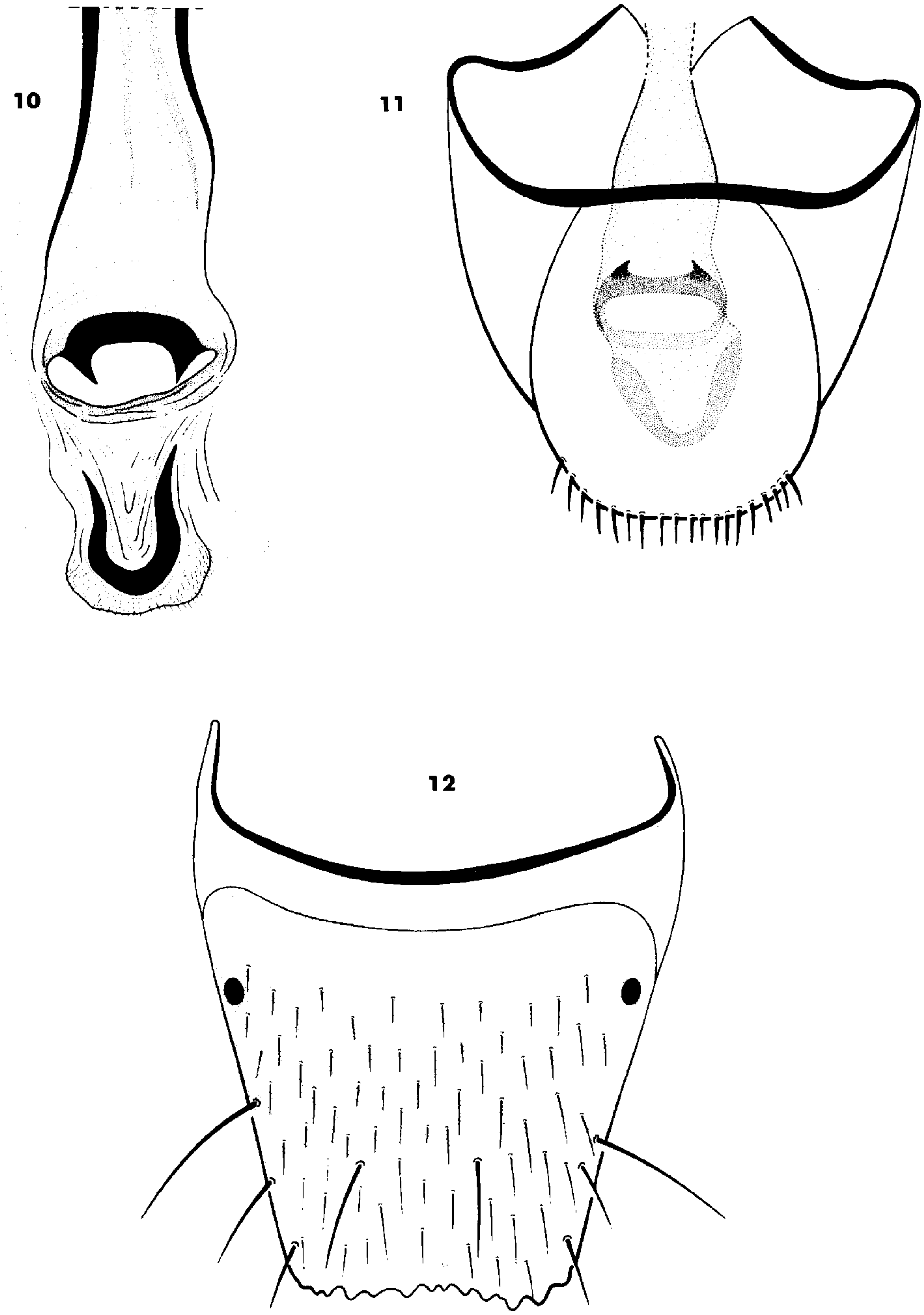
SUBGENUS *CALOCHARA* CASEY

For definition of the subgenus see Klimaszewski (1984).

Aleochara beckeri Klimaszewski, new species
(Fig. 1-5)

ETYMOLOGY. The species is named for our colleague E.C. Becker, Ottawa, Canada, collector of the type series.

DIAGNOSIS. Adults of this species are distinguished by the following combination of characters: body dark brown to black; evenly, narrowly elongate; of medium size (3.0-5.0 mm long); punctures on head, pronotum and elytra coarse; pubescence sparse and yellowish; median lobe of aedeagus slender in ventral view (Fig. 2), its apex in lateral view projecting dorsally and pointed (Fig. 3), the internal sac with two pairs of sclerites (Fig. 2, 3), the flagellum about 0.3X length of median lobe (Fig. 2); sternite VIII of male with triangular, median, apical projection (Fig. 4), tergite VIII of both sexes with peg-shaped apical setae (Fig. 5); spermatheca with spherical capsule and slightly sinuate and narrowly elongate chamber (Fig. 1). Known only from Florida.



Figs. 10-12. *A. pseudolustrica* sp. n.: 10, posterior portion of vagina with sclerites; 11, apical abdominal segments of female with internal sclerites; 12, tergite VIII of male (shaded area indicates colors brown to dark brown, and unshaded area indicates colors yellowish brown to yellow).

DESCRIPTION. Dark brown to black, with tarsi (or entire legs, maxillary and labial palpi, antennae, labrum, apex of abdomen, and posterior portion of elytra) brown with rusty tinge. Pubescence sparse, uniformly yellowish; punctures on head, pronotum and elytra coarse. Length 3.0-5.0 mm.

Head capsule approximately as wide as long, sparsely pubescent, with pubescence directed toward vertex, punctures round and deeply impressed, surface between punctures without evident microsculpture and glossy; antennomeres I-III elongate and glossy, IV as wide as long and glossy basally, V-X each slightly transverse and matt; last maxillary palpomere spindle-shaped and 0.25X length of penultimate. Pronotum slightly elongate, broadest in apical third, emarginate and with narrow basal impression, base broadly rounded, anterior and posterior angles acute, lateral margins broadly curved; pubescence moderately dense, directed obliquely outward from the midline of the disc; punctures deeply impressed, and either rounded or somewhat irregular in shape, surface between punctures glossy and without evident microsculpture. Elytra approximately as long as wide, as densely pubescent as pronotum pubescence directed obliquely or in slightly sinuate pattern outward from the suture and toward posterior angles; punctures deep, rounded or slightly irregular in shape, surface between them glossy. Abdomen evenly, narrowly elongate, sparsely pubescent and glossy; punctures not as coarse as on forebody; first four abdominal terga broadly and deeply impressed at base.

MALE. Tergite VIII unicolorous, with sparse pubescence and with peg-shaped apical setae (Fig. 5), apex truncate or with insignificant, shallow, median emargination. Sternite VIII unicolorous, sparsely pubescent with a few prominent setae in apical third and with triangularly shaped apical projection (Fig. 4). Median lobe of aedeagus slender in ventral view (Fig. 2), in lateral view with apex acute and projecting ventrally (Fig. 3); internal sac with two pairs of sclerites and flagellum about 0.3X length of median lobe (Fig. 2).

FEMALE. Tergite VIII similar to that of male, with shallow apical emargination. Sternite VIII as pubescent as that of male, but with shorter apical, median projection. Spermatheca as in Fig. 1.

HABITAT. Specimens were collected in January in pine/oak forest, using malt-baited pitfall traps. Species of this subgenus are associated with animal burrows (Klimaszewski 1984).

GEOGRAPHIC DISTRIBUTION. Known only from Gainesville, Florida.

MATERIAL EXAMINED. Two males, 5 females, 1 sex undetermined.

TYPES. HOLOTYPE. Florida, Gainesville, 1-5.ii.1979, E. C. Becker, malt traps, pine/oak forest, (CNC) 1 male. ALLOTYPE: labelled as holotype, (CNC) 1 female. PARATYPES: with same label data, (CNC) 4 females, (FSCA) 1 sex undetermined, (JKC) 1 male, 1 female.

REMARKS. Distinct from the other 9 Nearctic species of the subgenus (Klimaszewski 1984, Klimaszewski & Genier 1987) in the following combination of characters: coarse (and on pronotum irregularly shaped) punctures of forebody, lack of microsculpture, uniformly yellowish pubescence, deep basal pronotal impression, mesosternum with carina slightly shorter than half length of mesosternum and with deep and narrow basal impression, peg-shaped setae on apical part of tergite VIII, and distinctively shaped spermatheca and median lobe of aedeagus. The number of these differentiating characters places the species at some phylogenetic distance from the other species of the subgenus. The only other species of this subgenus occurring in the eastern Nearctic is *A.* (*C.*) *rubripennis* (Casey), whose range includes the western Nearctic, and whose aedeagal and spermathecal structures are similar (for illustrations see Klimaszewski 1984).

SUBGENUS *COPROCHARA* MULSANT & REY

For definition of the subgenus see Klimaszewski (1984).

Aleochara notula Erichson

This is a widely distributed species known from the southern USA, with several records from the West Indies, Venezuela, and Chile (Klimaszewski 1984). It is widely distributed in Florida, but in the Keys it was known only from a single record from Key West. We provide here the first records from Big Pine Key and Sugarloaf Key. They were collected from dog dung, and from horse dung in association with *Leptagria perexilis* Casey and *Tinotus* sp.

NEW RECORDS: Florida, Monroe Co., Big Pine Key, 15.xii.1986, J. Klimaszewski & S. B. Peck, by sifting horse dung, (JKC) male, 5 sex undetermined; same locality data and collectors, 18.xii.1986, sifting dog dung, (JKC) 4 males, 1 female, 23 sex undetermined; Sugarloaf Key, Pirates Cove, 15.xii.1986, J. Klimaszewski & S. B. Peck, (JKC) 1 male, 3 females, 5 sex undetermined.

ACKNOWLEDGMENTS

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SCIENTIFIC NOTES

NEW RECORDS OF NEUROPTERA, MALLOPHAGA, AND STREPSIPTERA FROM BERMUDA

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A new survey of Bermuda's insects was initiated in 1987. Hilburn & Gordon (1989) provides an introduction to this project and a review of entomology in Bermuda.

In his survey of Bermuda's insects, Ogilvie (1928) lists three Neuroptera: *Myrmeleon* sp., *Chrysopa rufilabris* Burmeister, and *Chrysopa* sp. *C. rufilabris*. *C. rufilabris* is a common species in eastern U.S. which is also common in Bermuda and present year round. *Chrysopa* sp. is listed without comment. The *Myrmeleon* sp. was collected by J. M. Jones in the middle of the last century, but not by later collectors, including Ogilvie. This is probably the same species listed below, although Jones's specimens could not be located for comparison. Three additional species were brought in as biological control agents (Bennett et al. 1985). The hemerobiid *Sympherobius barberi* (Banks), a mealybug predator, was imported from California in 1955. *Semidalis aleyrodiformis* (Stephens) and *Heteroconis picticornis* (Banks), two coniopterygid scale predators, were imported from England in 1950 and Hong Kong in 1955 respectively. None of these intentionally introduced species became established.

Ogilvie also lists three Mallophaga collected by A. E. Verrill: *Trinoton querquedulae* L., from tropic bird; *Docophorus subflavescens* Geoff., from redbird; and *D. incisus* Kell., from bluebird.

Eight new Bermuda records are listed below, including five new species of Neuroptera, two new species of Mallophaga, and the first Strepsiptera ever reported. Determinations were provided by O. S. Flint (Neuroptera), R. Palma (Mallophaga), and J. Kathirithamby (Strepsiptera).

NEUROPTERA

CHRYSOPIDAE

Chrysopa externa Hagen

A common neotropical species collected twice in November 1987 with a sweepnet: Shelly Bay, Hamilton Parish, and Admiralty House Park, Pembroke Parish.

Chrysopa sp. near *harrisii* Fitch

C. harisii is found in eastern U.S. Two specimens were collected at Fort Scaur, Sandy's Parish, in January 1988.

HEMEROBIIDAE

Hemerobius stigma Stephens

A species common in eastern U.S. and Europe. One specimen was collected at Spittal Pond, Smith's Parish, in February 1988.

Micromus posticus (Walker)

A species common in eastern U.S. Widespread in Bermuda and not uncommonly collected while beating trees and shrubs.

MYRMELEONTIDAE

Myrmeleon sp. prob. *crudelis* Walker
Three adults collected on Nonsuch Island, St. George's Parish, July 1969. Larval pits seen July 1987 at the same location, but not subsequently and never on the main islands.

MALLOPHAGA

PHILOPTERIDAE

Halipeurus sp.
An undescribed species which is apparently shared by Bermuda's endemic cahow, *Pterodroma cahow,* and *Pterodroma madeira* of Madeira.

Trabeculus sp. poss. *schillingi*
A second species collected from *P. cahow.*

STREPSIPTERA

ELENCHIDAE

Elenchus spangleri Fox
Males were collected in a Malaise trap on Berry Hill Rd., Paget Parish, in March and September 1987. Females identifiable only as *Elenchus* sp. are not uncommon in delphacids.

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OVICIDAL EFFECTS OF FENOXYCARB ON EGGS OF FULLER ROSE BEETLE, *PANTOMORUS CERVINUS* (COLEOPTERA: CURCULIONIDAE)

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The need for a quarantine treatment affecting 100% mortality of Fuller rose beetle, *Pantomorus cervinus* (Boheman), eggs on export citrus by 1990 (Anonymous 1988)

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The need for a quarantine treatment affecting 100% mortality of Fuller rose beetle, *Pantomorus cervinus* (Boheman), eggs on export citrus by 1990 (Anonymous 1988) requires that novel control measures be examined. Promising chemicals for effective and selective insect control are the insect growth regulators (IGRs). One class of these compounds is known as the phenyl carbamates.

One of these phenyl carbamates, fenoxycarb (ethyl [2-(4-phenoxyphenoxy) ethyl] carbamate, RO 13-5223, Maag Agrochemicals, Vero Beach, Florida), was granted registration by the U. S. Environmental Protection Agency in 1985. It has been shown to be very effective in controlling a number of insects (Dorn et al. 1980, Masner et al. 1981) and is marketed under the names of Logic^R, Torus^R, and Insegar^R for control of fire ants, fleas and roaches, and orchard pests, respectively.

The effects of fenoxycarb as an ovicide has been reported in the literature for *Heliothis virescens* (Masner et al. 1987). As one probable mode of action of the phenyl carbamates relates to their ability to interfere with the polymerizing enzyme in the chitin synthetase system (Cohen & Casida 1980), fenoxycarb also has good potential as an ovicide against coleoptera. This study investigated the effectiveness of fenoxycarb as an ovicidal dip for control of Fuller rose beetle eggs.

Fuller rose beetle adults were collected from field-emergence cages per Coats and McCoy (1989) and maintained in 4 liter glass jars with screened lids placed in an environmental growth chamber at 28°C and 60% RH. The adults fed on fresh citrus flush supplied twice weekly and deposited their eggs between folded wax paper strips taped to the inside walls of the jars. Eggs were collected from 1-2 month-old adults. Individual egg masses were cut from the strips, by cutting around each egg mass, leaving the egg mass attached to the wax paper piece on one side. Each egg mass was then dipped into fenoxycarb solutions. Eggs were allowed to air dry before being placed into presterilized 3 dram plastic cups. A few drops of distilled water were placed on the underside of the lid of each cup before sealing to approximate 100% RH. To retain the RH near 100%, trays of cups were placed in plastic boxes (22 x 30 cm) with lids with a 2 cm layer of deionized water maintained in the bottom of these containers. All eggs were left to hatch in the growth chamber at 28°C, and checked twice weekly for viability for at least 30 days until no more hatching occurred.

TABLE 1. OVICIDAL EFFECTS OF FENOXYCARB ON FULLER ROSE BEETLE EGGS.

Treatment date	Dose (ppm)	Age of egg (days)	No. egg masses	Total No. eggs	Total No. hatch	Total Mortality (%)
Trial 1						
11/23/88	0	1-6	20	381	307	19.4
11/23/88	1,000[1]	1-6	20	397	0	100.0
11/23/88	2,000[1]	1-6	20	419	0	100.0
Trial 2						
06/15/89	0	1-6	20	442	368	16.7
06/15/89	100[2]	1-6	30	476	27	94.4
06/15/89	1,000[2]	1-6	30	431	0	100.0
06/27/89	0	7-12	20	505	415	17.8
06/27/89	100[2]	7-12	30	490	0	100.0
06/27/89	1,000[2]	7-12	30	606	0	100.0
06/27/89	10,000[2]	7-12	30	514	0	100.0

[1] Formulation used was 99% pure technical grade fenoxycarb resuspended in acetone (w/v) on 11/23/88.

[2] Formulated as a 25% wettable powder, concentrations (w/v) prepared 06/15/89 as suspensions in double distilled H_2O and well mixed just before eggs were dipped. All chemicals were supplied by Maag Agrochemicals, Inc.

Two trials were performed using 1-6 day-old eggs in trial 1, and 1-6 and 7-12 day-old eggs in trial 2. In trial 1, doses of 1,000 and 2,000 parts per million (ppm) were made by diluting a 99% pure technical grade of fenoxycarb (w/v) with reagent grade acetone. In trial 2, 100, 1,000, and 10,000 ppm suspensions were made by dilution of a 25% wettable powder formulation with distilled water. Controls were dipped in the solvent used to make the dilutions.

Individual replications consisted of one egg mass with a mean of 20 eggs/mass. Each dose, including controls, was replicated a minimum of 20 times/trial.

Except at 100 ppm on 06/15/89 in Trial 2, all of the fenoxycarb-treated eggs failed to hatch (Table 1). Excellent viability, in excess of 80% hatch, was observed for all control eggs.

Use of the IGR, fenoxycarb, as a dip for citrus fruit appears to be a viable method for affecting complete mortality of Fuller rose beetle eggs laid on the fruit surface. This compound is extremely safe to mammals (LD_{50} rat, acute oral = > 10,000 mg/kg; LD_{50} rat, dermal = > 2,000 mg/kg) and birds (LD_{50} = 3,000 and 7,000 mg/kg for Mallard duck and quail, respectively). It is also non-mutagenic, has a low environmental mobility with no bioaccumulation tendency in fish, and a low potential for environmental persistence (Maag Agrochemicals, Inc. 1985). All of these factors make fenoxycarb a prime candidate for consideration as a safe and effective quarantine treatment for control of Fuller rose beetle eggs on citrus fruit exported to Japan.

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STEINERNEMATID NEMATODE DRENCHES FOR CONTROL OF FIRE ANTS, *SOLENOPSIS INVICTA*, IN FLORIDA

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Recent developments in low-cost, large-scale production of entomogenous nematodes of the genera *Steinernema* and *Heterorhabditis* (Bedding 1984) have facilitated large-scale field testing against various soil-infesting insect pests (Kaya 1985, Poinar 1986), with good potential for commercial control in some applications. Early research by Poole (1976) and Quattlebaum (1980) showed promise that entomogenous nematodes have potential for controlling fire ants, *Solenopsis* spp. Furthemore, these nematodes have the ability to invade adult insects, and thus potential to kill fire ant queens. Agents which only kill worker ants do not effectively eliminate colonies, although they may temporarily reduce their size.

A variety of entomopathogens, including viruses, bacteria, fungi, protozoa, and other species of nematodes have been evaluated for fire ant control. These organisms, with the possible exception of a fungus (*Beauveria* sp.) isolated from fire ants in Brazil (Stimac et al. 1987), produced little or no mortality in laboratory and/or field tests. Jouvenaz (in press) recently reviewed these evaluations and discussed the special problems attending the development of biological formicides.

We selected a strain of *Steinernema feltiae* produced by Biosys Inc. (Palo Alto, CA) for field evaluation after screening several strains of *Steinernema* and *Heterorhabditis* spp. in the laboratory. In the laboratory tests, groups of ants composed of queens (from a polygynous colony), about 25-30 workers, and a small quantity of brood were placed in 16 x 125 mm glass culture tubes containing 25 mm of slightly moistened sandy soil. The tubes were capped with plastic tops which allowed gas exchange and were maintained at 29° C. After two or three days of acclimation, one ml of deionized water without nematodes or containing 5,000 or 50,000 nematodes was added to each tube, and survival of queens was scored daily for four days. Ten replicates (a total of 50 queens) were used for each nematode concentration and for the control. After 96 h, the strain we selected had produced queen mortalities of 40% and 58% in 5,000 and 50,000 nematode dosaged, respectively. Mortality of workers and brood, although not quantitatively determined, was estimated to be at least 80%. Mortality of queens, workers or brood was not observed in the control group. In separate tests we observed that colonies of ants vacated soil treated with high concentrations of nematodes.

The first of the two field evaluations reported here was conducted in October and November, 1987, at Site No. 1 in southeast Gainesville, Alachua Co., Florida. This site was a utiities right-of-way measuring about 365 x 23-30 m, with sandy soil and surrounded by trees. The site had been mowed regularly prior to the test, but was not mowed during the test period. The second test was conducted during June and July, 1988, at Site No. 2, 4 mi north of LaCrosse, Alachua Co., Florida. This site was an approximately rectangular plot 1.4 ha in size on a sod farm and was also bordered by trees. On both plots, the grass varied from 10-30 cm high, and was not mowed during the test period.

Site no. 1 was divided crosswise into four areas of approximately equal size (about 90 x 23-30 m); mounds on the site (including abandoned mounds) were marked with wooden stakes and color-coded according to treatment with flagging ribbon. The active mounds were rated by the population index method of Williams & Lofgren (1983) before treatment and at intervals of 7, 14, 28, and 45 days after treatment. Abandoned mounds were also checked to determine whether treated colonies had moved into them. Four treatments (one treatment per plot) were used in which all mounds in the plot were either: 1) drenched with one gallon of water; 2) drenched with one gallon of water containing 5 x 10^6 infective juvenile nematodes (the viability of the nematodes was verified microscopically within 1 h before they were transported to the field in styrofoam chests containing ice); 3) treated with 5 tablespoons of Amdro fire ant bait according to the label recommendations, or 4) received no treatment. The mounds were examined with minimal disturbance several times weekly to monitor colony movement. No rainfall occurred during the first 28 days of the test. The results of this test are presented in Table 1.

Site no. 2 was divided into 12 plots which were randomly assigned one of three treatments: 1) 2 x 10^6 infective juvenile nematodes (dessicated product) in one gallon of water; 2) Amdro fire ant bait; or 3) no treament. All mounds were marked with wire survey flags, color coded for treatment, and rated as at Site No. 1 prior to treatment and 40 days after treatment. During the interim, each mound was checked 48 hours after treatment and at approximately weekly intervals thereafter by stamping the ground nearby to disturb the ants and thereby verify that the mound was still active. If ants did not appear from this disturbance, a search for new, unmarked mounds in the vicinity (up to 10 m) was made to determine whether the colony had moved. The results of this test are presented in Table 2.

Although the strain of *S. feltiae* used in these tests killed up to 58% of queens exposed in the laboratory and also produced very high mortality in adult and immature workers, it was not effective against colonies in either field test. In the first test (Site No. 1), we suspected that very dry soil affected the nematodes adversely. The increase in population index of the non-treated colonies 45 days after treatment (Table 1) followed a rain which occurred 30 days after treatment. The Amdro treatment was significantly different (Waller-Duncan K-Ratio t-Test; PC-SAS 6.03, SAS Institute Inc., Cary, NC) from all other treatments, whereas there was no significant difference ($p = 0.05$) between the water and nematode treatments, or between the untreated and nematode treated. At least one inch of rain fell during each week of the second test; however, there was no difference in population index reduction between the nematode treated

TABLE 1. REDUCTION IN POPULATION INDICES (P.I.) OF IMPORTED FIRE ANT MOUNDS AT SITE #1.

Treatment	No. Active Mounds	Initial P.I.	P.I. Reduction (%) Days after treatment			
			7	14	28	45
Amdro[1] A[2]	25	367	25.1	46.6	60.5	65.1
Water[3] B	21	339	10.0	18.0	20.9	23.6
Nematode[4] BC	19	292	10.6	25.7	31.5	7.9
Untreated C	18	353	10.5	17.3	15.0	–15.1

[1] 5 Tablespoons per mound.

[2] Treatments followed by the same letter are not significantly different. Regardless of treatment, there are no significant differences over time (Waller-Duncan K-Rtio t-Test).

[3] 1 gallon of water.

[4] 5x10^6 *S. feltiae* per mound in 1 gallon of water.

TABLE 2. REDUCTION OF POPULATION INDICES (P.I.) AND ACTIVE MOUNDS OF IMPORTED FIRE ANTS AT SITE NO. 2, 40 DAYS AFTER TREATMENT. DATA ARE SUMS OF FOUR PLOTS FOR EACH TREATMENT.

	Before Treatment		After Treatment	
Treatment	# Active Mounds	Initial P.I.	# P.I. Reduction After Treatment	% Reduction Active Mounds
Amdro[1]	52	624	96.5%	92.3
Nematode[2]	44	588	15.0%	27.3
Untreated	49	743	6.1%	12.2

[1] 5 Tablespoons per mound.

[2] 5 x 10^6 *S. feltiae* per mound in 1 gallon of water.

and untreated plots (the population index increased on one of the untreated plots, but the reduction in the remaining three plots averaged 10.9% vs. 15.0% for the nematode plots).

Quattlebaum (1980) reported mound mortalities of 88.2 to 96.8% using 2 x 10^6 *Neoaplectana carpocapsae* ("DD-136") per mound, and 75 to 86.3% using *Heterorhabditis heliothidis* ("NC-19") in South Carolina. Poole (1976) reported mound mortalities of 35% (fall treatment) and 45% (spring treatment) using 10^6 *Neoaplectana dutkyi* per mound in Mississippi. Their criteria for evaluating treatments differed from ours, however, and they apparently did not consider mound movement. Poole (1976) reports spading up mounds and spraying the workers with paint to identify them and of destroying "new migratory colonies". If mound movement is ignored (all treated and control mounds uninhabited after treatment are scored as dead), control by *S. feltiae* appears to be ca. 78% in our second test. These investigators also applied treatments under more favorable conditions such as during early morning or late evening precipitation.

Colony movement was stimulated by the presence of nematodes. After 72 h, 10 (52.6%) of the 19 colonies treated with nematodes in the first test had moved, whereas only four (16.7%) of the 24 colonies treated with Amdro, five (23.8%) of the 21 colonies treated with water, and none of the untreated colonies moved. In the second test, stimulation of colony movement by nematodes was even more pronounced. After 48 h, 27 (61.3%) of the 44 colonies treated with nematodes had moved, whereas only four (7.6%) of the 52 colonies treated with Amdro, and five of the 49 colonies (10.2%) of the control colonies had moved.

S. feltiae applied to dry sandy soil may lose activity before infecting insect hosts (Molyneux & Bedding 1984). Even with adequate soil moisture, the pathogenic lifespan of entomogenous nematode is limited by the ambient microfauna present in field soils (Ishibashi & Kondo 1986, 1987). Thus, any attempt to control fire ants with entomogenous nematodes will need to overcome these disadvantages either through selection of a superior strain or through improved formulation of existing strains. Efficacy of drench treatments of fire ants may always be limited by the tendency of colonies to relocate some distance from the antagonistic agent. Thus, alternative application strategies such as uniform application (through a sprinkler or irrigation system, for example) to create areas void of fire ants, bait traps containing nematodes, or slow release formulations in hygroscopic polymers (Schroeder, in press) may offer improvements in efficacy.

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AGE OF FIRST MATING IN FIELD CRICKETS, *GRYLLUS INTEGER* (ORTHOPTERA: GRYLLIDAE)

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This experiment was performed to determine the age at which female field crickets, *Gryllus integer* Scudder, first mate when exposed to conspecific males daily following the adult molt. Such information adds to an understanding of the ontogeny of behavior, and was also needed to plan additional observations on *G. integer* mating behavior.

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This experiment was performed to determine the age at which female field crickets, *Gryllus integer* Scudder, first mate when exposed to conspecific males daily following the adult molt. Such information adds to an understanding of the ontogeny of behavior, and was also needed to plan additional observations on *G. integer* mating behavior.

Adult male and female *G. integer* were collected in and near Austin Texas, and used to establish laboratory cultures. This species is routinely referred to as *G. integer*, but this designation may be incorrect (Smith & Cade 1987, Weissman *et al.* 1980). Cultures were maintained in plastic garbage cans (45 l) with a 100 W light at the top. Cultures were on a light/dark cycle of 12:12 h at a temperature of approximatly 25 C°. Newly molted male and female *G. integer* were removed daily from the containers. Male *G. integer* first produce spermatophores and thus are capable of mating at 4.4 days on average (range = 3-7, SD = 1.2, N = 51) after the adult molt (Cade & Wyatt 1984). Newly molted adult *G. integer* were therefore virgins when removed from the laboratory culture. To determine cricket adult age, the day a new adult was removed was designated day 0 since these individuals were less than 24 h of adult age.

Females were marked individually on the pronotum with typewriter correction fluid and introduced into a plastic observation chamber (36 x 30 x 17 cm). A maximum of 4 female *G. integer* were placed in the chamber at a time ($\bar{X} = 3.1$). The same numbers of adult male *G. integer* were placed in the chamber. Males were at least 7 days of adult age, thus ensuring they were sexually mature and also capable of producing the female-attracting calling songs (Cade & Wyatt 1984). Food (Purina Cat Chow©) and water (cotton-plugged test tubes) were present.

Females were observed for 5 h each day until they mated. Once mated an individual was no longer observed. When observations were not being conducted, females were placed in individual plastic containers (500 ml) with food and water. The individual containers and the mating chambers were on a light/dark cycle of 12:12 h. Observations were conducted approximately 1 h into the light portion of the cycle since field observations on *G. integer* show a high frequency of matings at about dawn (French & Cade 1987).

The distribution of the age at which female *G. integer* first mated is presented in Figure 1. Females mated at an average age of 3.6 days since the adult molt (SD = 2.3,

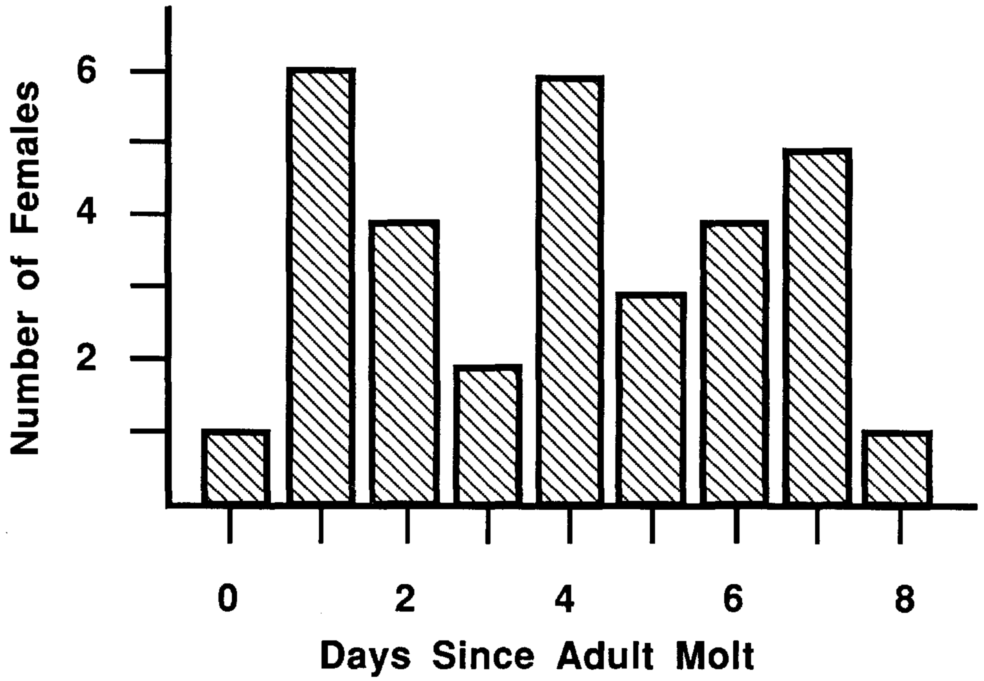

Fig. 1. The adult age at which female *G. integer* first mate.

N = 32). One female mated the day she molted and was placed in the observation chambers. All females had mated by 8 days after the final molt.

The data presented here are similar to data presented from a single observation on 3 female *G. integer* where females also mated soon after the adult molt (Sakaluk & Cade 1980). Female *Teleogryllus commodus* (Walker) mate within hrs of the adult molt (Loher & Edson 1973), and female house crickets, *Acheta domesticus* (L.) become sexually receptive approximately 2 days after the adult molt (Sakaluk 1982).

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COMPARATIVE TOXICITY OF FIVE *BACILLUS THURINGIENSIS* STRAINS AND FORMULATIONS AGAINST *SPODOPTERA EXIGUA* (LEPIDOPTERA: NOCTUIDAE)

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The beet armyworm, *Spodoptera exigua* (Hübner), is a polyphagous noctuid that is a primary pest on agricultural crops in the United States and Mexico (Metcalf et al. 1962, Alvarado-Rodriguez 1987). Low economic thresholds, and apparent resistance to pesticides (Poe et al. 1973, Meinke & Ware 1978) have increased chemical use, leading to higher control costs and harmful effects on beneficial insects suppressing other pest species such as the *Liriomyza* spp. leafminers (Trumble 1985).

Insecticides containing *Bacillus thuringiensis* subsp. *kurstaki* (Berliner) have been registered since 1961, but recommended field rates in many vegetable crops result in unsatisfactory *S. exigua* control (Wyman & Oatman 1977). *B. thuringiensis* subsp. *kurstaki* has proven to be virtually non-toxic to key parasite species of *Liriomyza* leafminers (Carson et al. 1987), and therefore would be a good insecticide to use in an integrated pest management system.

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An approach to resolving this problem of *B. thuringiensis* field efficacy has been the recent commercial release of the NRD-12 isolate of *B. thuringiensis* subsp. *kurstaki*, marketed as Javelin, which has improved activity against *Spodoptera* species. Moar et al. (1986) also demonstrated that the commercial wettable powder formulation of Javelin was 3-4 times more toxic to *S. exigua* in diet incorporation studies than Dipel 2X. Since various *Spodoptera* spp. cause economic damage on numerous crops, there is increasing interest in developing more efficacious *B. thuringiensis* products. Therefore, the purpose of this study was to determine the toxicity of new commercial formulations of *B. thuringiensis* to *S. exigua*.

Wettable powder/granule test materials included Dipel 2X containing the HD-1 isolate of *B. thuringiensis* subsp. *kurstaki* with 32,000 international units (IU)/mg, ABG-6218 (Abbott Laboratories), and SAN 415 WG 354 (Sandoz Corp.). Flowable liquid test materials included SAN 415 SC 353 (commercially available as Javelin), and SAN 415 SC 363 (Sandoz Corp.).

Bioassays with *B. thuringiensis* were conducted with seven-eight concentrations plus a control for individual treatments. Concentration ranges for wettable powder/granule compounds (μg/ml diet) tested were as follows: Dipel 2X; 25-800; ABG-6218; 20-320; SAN 415 WG 354; 5-80. Suspensions were made by adding materials to 50 ml 0.1% Tween 80 solution. Suspensions were chilled to 10°C and suspended for 30 seconds with a sonic dismembrator. Concentration ranges for flowable liquid compounds (μl/ml diet) tested were as follows: SAN 415 SC 353; 0.05-0.70; SAN 415 SC 363; 0.02-0.12. Suspensions were made by adding materials to an aqueous 0.1% Tween 80 solution to produce 50 ml. Suspensions were chilled to 10°C and vortexed for one min. Controls consisted of 50 ml of an aqueous 0.1% Tween 80 solution.

Each concentration was added to artificial diet (Patana 1969), mixed, poured into 30 ml plastic cups, and a single neonate *S. exigua* (0-4 h old) placed in each cup as described by Moar et al. (1986). The neonate *S. exigua* larvae used in all tests were taken from a stock culture which was maintained on the same artificial diet as described previously at 27 ± 1°C, and a photoperiod of 16:8 (L:D). This temperature and photoperiod also were used in the bioassays. At least 30 insects were tested with each concentration; tests with each concentration were replicated five-six times. Larval mortality was assessed at 7 days in all treatments.

Data were analyzed using the Proc Probit procedure (SAS Institute 1985) after correction for control mortality with Abbott's (1925) formula, and then judged for suitability as described by Vandekar & Dulmage (1982). Remaining values were pooled. Control mortality was $\leq$ 10%.

The LC_{50}'s for SAN 415 WG 354 (26.4 μg/ml diet) and ABG-6218 (55.1 μg/ml diet) were 7.0 and 3.35 times lower than the LC_{50} for Dipel 2X (184 μg/ml diet) (Table 1). The LC_{50} value for Dipel 2X is consistent with a previous report indicating 50% mortality at 196 μ/ml diet (Moar & Trumble 1987). Comparisons of the toxicities of the liquid formulations determined that the LC_{50} value for SAN 415 SC 363 (0.05 μ/ml diet) was ca. 3.0 times lower than for SAN 415 SC 353 (0.15 μ/ml diet) (Table 1). Thus, these new *B. thuringiensis* products are more efficacious in the laboratory against *S. exigua* than the commercially available Dipel 2X and Javelin. However, outdoor testing of these products must be conducted to determine if similar results will occur under the relatively more adverse environmental conditions associated with production agriculture in the field.

We thank K. Kamrath for her assistance in bioassays. This research was supported in part by the California Celery Research Advisory Board, the Western Regional pesticide Impact Assessment Program, the California Department of Food and Agriculture, Abbott Laboratories, and Sandoz Corporation.

TABLE 1. Lethal concentrations of various wettable powder (μg/ml diet) and flowable liquid (μl/ml diet) formulations of *Bacillus thuringiensis* against neonate *S. exigua*.

Treatment	n[a]	Slope ± SEM	LC_{50} (95% FL)	LC_{90} (95% Fl)
	Solid formulations (granule and wettable powders)			
Dipel 2X	1200	1.82 ± 0.13	184 (154-220)	950 (719-1381)
ABG-6218	1440	2.06 ± 0.14	55.1 (48.9-61.2)	231 (198-280)
SAN 415 WG 354	1220	2.60 ± 0.14	26.4 (24.4-28.4)	82.1 (73.1-94.2)
	Liquid formulations (soluble concentrates)			
SAN 415 SC 353	1220	2.63 ± 0.13	0.15 (0.13-0.16)	0.45 (0.40-0.51)
SAN 415 SC 363	1050	3.90 ± 0.40	0.05 (0.048-0.062)	0.12 (0.097-0.152)

[a] Number of total insects assayed from 7-8 concentrations and 5-6 replicates.

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DAMAGE TO NORTH CAROLINA AND FLORIDA HIGHWAYS BY RED IMPORTED FIRE ANTS (HYMENOPTERA: FORMICIDAE)

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The increasing importance of the red and black imported fire ants, *Solenopsis invicta* Buren and *S. richteri* Forel as economic pests is documented in reviews (Lofgren 1986, Adams 1986) and bibliographic lists (Banks et al. 1978, Wojcik & Lofgren 1982, and Wojcik 1986). This report of damage by red imported fire ants (RIFA) to highways in North Carolina and Florida further emphasizes their pestiferous nature.

Depressions or potholes (2.5-15 cm deep and up to 1.4 m long and 45 cm wide), adjacent to RIFA mounds, were observed in three highways in Onslow Co., NC (CDR. Roger Grothaus, U. S. Naval Medical Field Laboratory, Camp Lejeune, NC—personal communication). Investigation by one of the authors (CTA) revealed that removal of soil from beneath the roadway by RIFA caused the road to collapse under vehicular traffic. The larger depressions were hazardous to vehicles and all caused sufficient breakup of the asphalt surface to require repairs.

The North Carolina Department of Transportation (NCDOT) indicated that proper repair of the damage required removal of the asphalt over the area excavated by the ants, replacement and repacking of the roadbed, and repaving. Repair costs averaged $200 per depression.

Forty km along the three roads averaged four depressions or potholes per km. Although no other roads were damaged, the presence of numerous fire ant mounds indicated the potential for additional depressions unless the ants were controlled.

NCDOT reported that ant excavation appeared more frequent during the colder months. We suspect that this behavior resulted from the ants seeking the warmth absorbed by the highway from the sun's rays.

In Florida, damage by RIFA to the expansion joint sealant (Dow Corning® 888 silicone highway joint sealant—Dow Corning Corporation, Midland, MI. 48640) between newly-completed concrete sections of Interstate Highway 75 near Tampa was detected by Florida Department of Transportation (FLDOT) personnel. Open tunnels (approximately 1.25 X 7.5 cm) underneath the sealant, extending laterally across the highway from shoulder to shoulder and longitudinally along the traffic lanes, were invaded by RIFA from nests on either shoulder. Damage occurred as the ants chewed away a styrofoam backer rod and made exit holes through the silicone to the surface. Backer rod and cured silicone exposed to ants in laboratory colonies was chewed, but neither material was particularly attractive to the ants.

Damage by the ants is important because expansion joints in concrete highway must be tightly sealed, with material pliable enough to withstand concrete contraction and expansion, against rainwater entry. The silicone provides a better and much longer lasting seal than the tar that is usually used.

Although ant penetration of the sealant appeared to be random, about twice as many holes were found in sealant in lateral joints as in longitudinal joints. We found 226 holes, ranging in size from about 1.0 to 50 mm, in a total of 2820 m of sealant at 12 randomly selected sites near the junction of I-75 and FL-574. Penetration of all the sealant by RIFA at this observed frequency would give a total of about 555 penetrations in the 6930 m of sealant in each km of highway.

Repair or replacement of the RIFA-damaged sealant was required for release of Federal highway funds to FLDOT. Replacement costs were approximately $45,100 per km, thus, FLDOT chose to repair the damage with a patch of silicone over each ant penetration. Repairs cost an estimated $82 to $187 per km.

Continuing damage to the sealant was prevented by application of Amdro® Fire Ant Bait (1.12 kg/ha) to the highway median and shoulders. Initial control costs were ca $28 per km for material and labor. RIFA reinfestation of the highway right-of-way has required twice yearly retreatment with Amdro at an increased annual highway maintenance cost of approximately $56 per km.

Damage to highways in the United States by other ant species has not been reported, however, no other ant species are as wide-spread and abundant as RIFA. We have observed only one other instance of damage by RIFA to highways; potholes like those observed in NC were found adjacent to RIFA mounds along asphalt roads at the Martin Co., Florida electric power plant. Nevertheless, highway engineers and maintenance personnel need to be aware that RIFA can cause serious damage and should take steps to prevent damage and associated repair costs.

Mention of a proprietary product does not constitute an endorsement or a recommendation by the USDA for its use.

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BOOK REVIEWS

LEWIS BERNER AND MANUEL L. PESCADOR, 1988: The Mayflies of Florida. Revised Edition. University Presses of Florida. Florida A&M University Press/Tallahassee and University of Florida Press/Gainesville. xvi + 416 pp. ISBN 0-8130-0845-X. Clothbound. Price: $35.00.

The Mayflies of Florida by Prof. Berner, an eminent specialist in water insects, appeared almost four decades ago. It was truly pioneer work, unprecedented by any monograph that would treat mayflies of a territory of comparable size in such detail. The book has become a classic, which is evident among other things from hundreds of citations in entomological literature.

Naturally, the book has been published again. We see the co-authorship of Dr. Berner and Dr. Pescador, professor at the A&M University, as a happy combination. Prof. Berner's contribution—his long experience and thousands of field data gathered during his studies of Florida water biotopes—is complemented by Prof. Pescador's valuable data resulting from his detailed study of some regions (e.g., Ochlockonee River Basin and others). The taxonomical part of the new edition has been substantially revised, many species have been reclassified, and newly described taxa have been included. Although we are no experts in Nearctic fauna we consider the taxonomic part excellent. Even a non-specialist or beginner using this publication can get a very clear picture of the mayfly fauna of Florida. Keys are concise and lucid, with geographic distribution, ecology, seasonal occurrence and life history given for most species. Most of the illustrations have been taken over from the first edition, some—especially those of morphological structures of some species—are new. There is a noticeable difference between the drawing techniques. However, none of the figures is redundant and no illustration of an important structure is lacking. The extended general part, based on the latest published data on this order of aquatic insects, is a particular improvement on the first edition. The authors accept modern phylogenetic hypotheses, their characterization of the whole group is brief and precise, primitive and derivative characters are pointed out, and Florida mayflies are compared with the rest of Nearctic ephemeropteran fauna. Chapters on the abundance, life cycles, dispersal of mayflies and habitats of Florida mayflies are especially stimulative. These chapters, exceeding the framework of mayfly research, are useful for limnological studies in general.

The book is technically perfect, with a well-constructed index facilitating orientation by species, subject entries and literary sources. The selection of references is very good, complementing the bibliography of the first edition. The authors did an excellent piece of work. Their book is very useful not only to ephemeropterists but also to limnologists, ecologists and hydrobiologists.

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Coreidae of Florida (Hemiptera: Heteroptera). R. M. BARANOWSKI AND J. A. SLATER. Arthropods of Florida and Neighboring Land Areas. Vol. 12. 82 pp. Gainesville, FL, 1986. Paper-bound. Price $12.00.

The large family Coreidae (about 1,800 species worldwide) is mainly a tropical group. Even though most species are larger than those in many other heteropteran families, the Coreidae generally have not received the biological or taxonomic attention given to terrestrial families such as the Lygaeidae, Miridae, Pentatomidae, or Tingidae. World catalogs are available for lygaeids, mirids, and tingids, and the coreoid family Rhopalidae also has been catalogued recently. But the most recent world catalog of coreids is that of Lethierry & Severin (1894), with a supplement by Bergroth (1913).

Drs. Baranowski and Slater are to be commended for synthesizing information on the coreid fauna of Florida. They treat the Coreidae in a restricted sense, that is, excluding the coreoid families Alydidae and Rhopalidae, which at one time were considered coreid subfamilies. The authors emphasize that Florida's diverse habitats, complex geological history, and wide climatic differences between north and south provide for a large and diverse fauna. For a knowledge of its fauna to attain the maturity of that of many other states requires more comprehensive collecting and greater familiarity with extralimital species. As they admit, knowledge of Florida Coreidae remains incomplete, but because of their research it is considerably more mature.

Introductory material includes a summary of previous work in Florida: early collecting by E. P. Van Duzee, Annie T. Slosson, and W. S. Blatchley; studies by R. F. Hussey in the 1940s and 1950s; and extensive field work by the first author in recent years. The number of coreids known from the state has increased from 29 in Barber's (1914) list, 33 recorded by Blatchley (1926), to the 41 given in the present work. Four of these species were not seen by the authors, who feel that at least two species do not actually occur there. I note that the number of coreid species they say is found in the United States and Canada, 120, contrasts with the 87 recorded from America north of Mexico by Froeschner (1988).

Among other preliminary sections, I found the discussion of faunal composition particularly useful. They categorized coreids as endemic (or indigenous) to Florida (5% of the fauna); widespread in North America (21%); found in the Southeast or Gulf Coast region (13%); occurring in the southern United States, including the Southwest (13%); representing a disjunct Florida-southwestern U.S. element (10%); members of a Neotropical component (Florida, West Indies, Central America) (21%); and belonging to a West Indian-Floridian element (16%).

Most of the volume consists of a taxonomic account of the fauna. There is a key to coreid subfamilies occurring in Florida and, for subfamilies having more than one tribe represented in the state, a tribal key. Generic keys and diagnoses are provided, and for each species there is reference to the original description, a listing of synonymy and the different combinations used, diagnosis, distribution, and Florida distribution. The last-named category includes data for all collections and a map. There also are 26 excellent illustrations of adult habitus.

The authors intend for the keys to allow field identification of most species and positive laboratory determination of all species. In this aim they have succeeded. The keys seem workable and the diagnoses accurate. Nonspecialists, however, will be unfamiliar with some of the terminology used. A glossary, perhaps in combination with a labeled illustration showing key characters, would have been helpful.

In two cases the authors propose new synonymy. *Leptoglossus australis* (F.) is considered a junior synonym of the Old World *L. gonagra* (F.); the reasons for this taxonomic decision are clearly stated. *Sephina grayi* Van Duzee is proposed as a junior synonym of *S. gundlachi* (Guérin-Méneville).

Valuable biological information, including host plants and references, is included in the species accounts; a complete list of associated plants is given as an appendix. A comprehensive treatment of biological literature would have been inappropriate, and most relevant papers are cited. Nearly all biological papers that might have been mentioned are readily available in Schaefer and Mitchell's (1983) list of coreoid host plants. An additional Florida host of *Chariesterus antennator* is *Euphorbia blodgettii* Engelm. ex Hitchc. (Wheeler 1981). Baranowski and Slater, in discussing *Merocoris typhaeus*, add that the similar and extralimital *M. distinctus* is known to have been collected on carrion. I note that three coreids known from Florida—*Acanthocephala terminalis*, *Ceraleptus americanus*, and *Euthochtha galeator*—have been similarly recorded from bird droppings or carrion (Adler & Wheeler 1984).

I found several, mostly minor, problems in the taxonomic section. In the key to *Leptoglossus* spp. (p. 17), *L. fulvicornis* is said to have a reddish-brown head, whereas later (p. 20) the head is described as nearly uniformly brown. The relative size given for certain species could be confusing. For example, small is said to be 8-9 or 10-13 mm (pp. 69-70); rather small, 11-13 mm (p. 46); moderate or moderate-sized, 10-12 and 15-17 mm (pp. 32, 59); medium-sized, 12 and 13-18 mm (pp. 57, 61); and moderately large, 13-15 and 15-20 mm (pp. 63, 65).

In addition, typographical and other errors were found. "Blatchely" was noted on p. 31, "fuscus" on p. 38, and orange "medium" (for median) stripe on p. 49; the Yonke and Medler paper listed as 1969d on p. 13 should read 1969c. There also were inconsistencies, such as nondeclivent and non-declivent (p. 14), *Amphiachyris dracunculoides* (p.24) and *A. draconculoides* (p. 72), Ebling (pp. 24, 34) and Ebeling (p. 77), *Cestrum pargui* (p. 29) and *C. pargui* (p. 72), *Solanum sisymbrifolium* (p. 29) and *S. sisymbriofolium* (p. 76), *Amphicarpaea* (p. 34) and *Amphicarpa* (p. 72), Nematopini (p. 36) and Nematopodini (p. 82), McCullough (p. 36) and McCollough (p. 79), Kurczewski (p. 47) and Kurzewski (p. 78), *Ooencyrtus* (p. 56) and *Oencyrtus* (p. 82), and *Coccoloba* (p. 57) and *Cocoloba* (p. 73).

Occasional lack of attention to detail is illustrated by citation of the authors of the plant name *Citrullus lanatus* as Matsumara (p. 21) or Matsomara (p. 73) & Naki; it should be Matsumura & Nakai. In some cases there is failure to distinguish in the text two papers by Mayr in 1866, Van Duzee in 1909, and Barber in 1914, as well as redundancies such as "ellipsoidal in shape" (p. 44) and "orange in color" (p. 49). *Chariesterus antennator* (F.) is listed in the table of contents as *C. alternatus* (F.), the date of a paper by Gmelin is cited as 1778 in the text (p. 55) but 1789 in the literature cited, the 1913 paper by Bergroth (p. 31) and Basso et al. in 1974 (p. 43) are omitted from Literature Cited, Palisot de Beauvois is cited once (p. 54) as Palisot Beauvois, and the original description of the type species of *Ceraleptus* is undated (p. 69). In addition, *however* and *thus* are used several times as coordinating conjunctions, and in one sentence (p. 1) the subject and verb do not agree: "Ecological, behavioral, and seasonal information usually is lacking or are of a very preliminary nature."

Baranowski and Slater recognize *Piezogaster alternatus* (Say) and *P. calcarator* (F.). They apparently overlooked O'Shea (1980b), who followed Lethierry and Severin (1894) in synonymizing *alternatus* under *calcarator.*

Baranowski and Slater's treatment of the genus *Corecoris* appears to be based on that of Van Duzee, who considered *Spartocera* Laporte 1833 a *nomen nudum.* Recent authors, however, recognize *Spartocera* and treat *Corecoris* Hahn 1833 as a junior synonym. The species they record from Florida as *C. diffusus* (Say) is *S. diffusa* (tribe Spartocerini). Their *C. fusca* (Thunberg) is (at least in part) *Sagotylus confluens* (Say) (Acanthocerini). For a partial explanation of a complex nomenclatural problem, the reader is referred to O'Shea (1980a) and Froeschner (1988).

But enough said about trivial errors and some taxonomic problems. This is a significant work for pulling together scattered data on a rather neglected group and contributing new information on distribution and ecology. The *Coreidae of Florida* not only permits specimens to be determined with accuracy, but it provides a point of departure for additional biological and systematic work. This well-illustrated, attractive publication is essential for anyone interested in Florida Coreidae. It should prove useful to a diverse audience—from general entomologists to ecologists and biogeographers.

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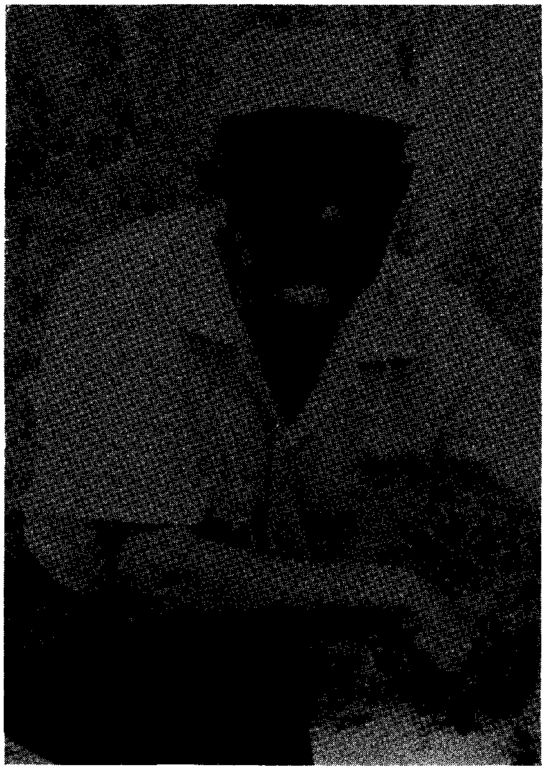

IN MEMORIAM

MARTIN HAMMOND MUMA
1916-1989

Martin Hammond Muma, Department of Entomology and Nematology, University of Florida, Emeritus Professor, was born in Topeka, Kansas, 24 July 1916. He died 1 December 1989 in Portal, Arizona after a short illness.

His professional training was obtained at Western Maryland College Extension Night School in 1933-34, Frosburg State Teachers College in 1935-36, and the University of Maryland in 1936-43. He received his B.S. degree in 1939, his M.S. in 1940, and his Ph.D. in 1943. From 1940-45, he served as Instructor in Entomology and Assistant Entomologist at the University of Maryland; from 1945-51, he was Extension Entomologist, Associate Entomologist, Associate Professor, and Associate Curator of the Museum at the University of Nebraska; 1951-71 he was Associate Entomologist, Associate Professor, and Entomologist and Professor at the University of Florida where he was involved in research on the taxonomy, biology, ecology, and nonchemical control of injurious citrus insects and mites. Since 1971 Dr. Muma had continued his association with the University of Florida as an Emeritus Professor of Entomology. Since 1963 he had been a Research Associate of the Florida Collection of Arthropods.

Although Dr. Muma's formal education and much of his official professional experience had been in the field of economic entomology, his favorite avocational fields were arachnology and speleology. In entomology he had investigated and contributed to the taxonomy, biology, ecology, and control of deciduous fruit insects and mites. In arachnology he had studied and contributed to the taxonomy, biology, and ecology of mites, spiders, tarantulas, scorpions, whip-scorpions, and solpugids. In speleology he had studied and contributed to cave biology, cave ecology, and cave terminology. He is author of a book, *Common Spiders of Maryland*, and author or coauthor of 195 articles, research articles, bulletins, and papers.

Dr. Muma was a member of Alpha Zeta, Gamma Sigma Delta, Phi Kappa Phi, and Sigma Xi honor societies and was a member of several professional organizations:

Florida Entomological Society, Ecological Society of America, Society of Systematic Zoology, and Society of Animal Behavior. Dr. Muma received the Entomologist of the Year Award from the Florida Entomological Society in 1970. He received the Outstanding Research Faculty Membership SHARE Award for $1,000 in 1971.

On 14 September 1940, Martin married Katherine Elizabeth Short. He is survived by his wife and their 6 children: Bonnie, Leslie, Merrie, Sallie, Cherie, Elsie; and 9 grandchildren. Martin was a Presbyterian. In addition to arachnids and caves, Martin enjoyed poetry writing, fishing, and his large family.

H. A. Denmark
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EDITED MINUTES OF THE 72ND ANNUAL MEETING FLORIDA ENTOMOLOGICAL SOCIETY

A meeting of the Executive Committee was held the evening preceding the Society's 72nd annual meeting. The meeting was called to order by President Richard Patterson at 5:10 p.m., August 7, 1989, in the Executive Conference Room of the Daytona Beach Hilton, Daytona Beach Florida. Minutes of the May 5, 1989 Executive Committee meeting at Lake Alfred were distributed and accepted. The Business Manager then distributed reports on the Society's finances. Following a discussion of the financial status of the Society, the reports were accepted. The Business Manager also reported that she had received requests from 2 retired entomologists requesting emeritus status; following a brief discussion, the Committee unanimously elected A. K. Burditt, Jr. and D. W. Anthony to Emeritus status. President Patterson proposed that the Society recognize the accomplishments and contributions of C. S. Lofgren and W. H. Whitcomb by offering their names in nomination to be considered by the entire membership for Honorary Membership; following a brief discussion, the Secretary was instructed by contact S. Whitney to include a ballot in this regard in the next Newsletter. J. Knapp discussed the status of plans for the annual meeting to be held in Cancun, Mexico in 1990. President Patterson encouraged members of the various committees to participate in the recruitment of new members. Preliminary reports were also heard from the Program Committee, Local Arrangements Committee, Publications Committee, Public Relations Committee, Resolutions Committee, and the Newsletter Committee.

The final business meeting was called to order by President Patterson at 5:05 p.m., Tuesday, August 8, 1989. The minutes of the 1988 meeting at Clearwater Beach, Florida, were accepted as published in the Florida Entomologist 72(1):230-239. Reports of the various standing and ad hoc committees of the Society are presented herein. President Patterson passed the gavel to the new President J. S. Eger who called for additional business from the floor. No further business was forthcoming, and the meeting adjourned at 5:45 p.m.

REPORT OF THE BUSINESS MANAGER
July 1, 1988 to June 30, 1989

RECEIPTS:		
Membership		$14,082.80
Subscriptions		6,500.00
Annual Meeting		6,930.00
Interest Earned		3,935.34
Back Issues		376.25
Contributions		70.00
Entomology Directories		37.00
Refunds		(85.00)
TOTAL		$31,846.39
EXPENSES:		
Telephone		$ 33.45
Postage		355.32
Contract Labor:		
J. M.	$1525.00	
A. C.	4700.00	6,225.00
Travel Expenses		16.29

Grants & Scholarships	1,950.00
Editing Expenses	145.62
Dues & Subscriptions	100.00
Bank Charges	125.00
Annual Meeting	7,926.21
Miscellaneous	143.47
Newsletter	1,322.94
TOTAL EXPENSES	$18,343.30
NET GAIN	$13,503.09

ASSETS:		MEMBERSHIPS:
Petty Cash	$ 100.00	Full 440
Cash in Bank	55,578.57	Student 88
		Sustaining 34

A. C. KNAPP, BUSINESS MANAGER

REPORT OF THE FISCAL COMMITTEE

Status of Society Financial Books

An examination of the FES books was performed by the Fiscal Committee on August 8, 1989. The committee found no inadequacies in the financial records.

W. T. MINTER, CHAIRMAN; J. HOGSETTE; R. JANSSON

REPORT OF THE PROGRAM COMMITTEE

The Program Committee developed the 1989 program to consist of approximately 100 papers. Papers are scheduled among one Keynote Address by Dr. Dorothy Pashley, three symposia, a student paper contest with 4 participants, a student poster paper contest with five entrants, ten regular poster papers, and various other submitted papers. The deadline for paper submission was scheduled originally one month earlier (1 May) than in the recent past. The Program Committee suggests that the May deadline should be used in the future for early August meetings.

A booklet of submitted abstracts was prepared and printed by IFAS Editorial. Printing costs to the Society were restricted to the costs of paper. The booklet contributes significantly to the effectiveness of the program and should be produced in future years.

The printed program of the Annual Meeting was distributed to members one month prior to the meeting. This early distribution was possible only through the earlier paper submission deadline and the excellent cooperation of Dick Johnston of E. O. Painter Printing Co. Tony Aquilino of the Program Committee secured sales of six advertisements at $100 each to the Society. His efforts offset most of the cost of printing the program.

J. F. PRICE, CHAIRMAN; D. J. SCHUSTER; J. E. EGER; T. AQUILINO; R. K. JANSSON; J. H. FRANK; H. L. CROMROY

REPORT OF THE LONG-RANGE PLANNING COMMITTEE

The Committee offers the following items for consideration by the Executive Committee and general membership:)

(1) The Executive Committee should develop a formal mechanism by which the recommendations from this Committee are routinely considered and acted upon by adopting, rejecting, tabling, otherwise disposing of such proposals.

(2) A position of Official Historian for the Society should be created in order to keep all of the historical information, photographs, news clippings, and other items of interest to the members for future generations of Florida entomologists.

(3) The Society should publish a brochure listing the addresses, phone numbers, staffs, and type of research conducted by all experiment stations in the state of Florida dealing with entomology. University, State, Federal and Industry locations should be included in the publication.

(4) Society membership levels should be a concern of all members, and the Society should address this issue. Members who have suggestions regarding increasing memberships levels should be encouraged to bring these to the attention of the Membership and Executive Committees.

D. F. WILLIAMS, CHAIRMAN; W. T. MINTER; F. W. MEAD; N. Y. SU; R. F. MIZELL

REPORT OF THE HONORS AND AWARDS COMMITTEE

The objective of this Committee is to recognize and in some way reward those entomologists who have made significant contributions to their profession and society. This year, the Honors and Awards Committee has selected 18 individuals for recognition of their worthy contributions.

Entomologist of The Year: James B. Kring

Dr. Kring had a distinguished career as an Assistant, Associate, and Professor of Entomology at the Connecticut Agricultural Experiment Station and as Head, Department of Entomology and Acting Dean, College of Agriculture at the University of Massachusetts. Dr. Kring retired to the Gulf Coast Research and Education Center, Bradenton, Florida. There, his vast knowledge of entomology made him a valued and respected member of the staff. Through the years, Dr. Kring has authored or coauthored more than 100 publications. In addition, Dr. Kring has served the profession of entomology in many capacities, including President of the Entomological Society of America. In addition to many committee assignments, Dr. Kring has served as Editor and Co-Editor of the FES Newsletter.

Achievement Award For Research: David J. Schuster

Dr. Schuster has provided IPM research to support tomato, melon, cole crop and other vegetable industries in Florida. He also provides basic biological, behavioral, and ecological research to address fundamental questions in entomology. He has given the scientific support to alleviate formidable losses from leafminer, tomato pinworm, beet armyworm, melonworm, pepper weevil, and sweetpotato whitefly. He is currently working on the uneven ripening effects of the sweetpotato whitefly in tomatoes. Dr. Schuster has been recognized both nationally and internationally for his research on the biology and control of vegetable insects. Dr. Schuster has recently completed a 9-month sabbatical, working on tomato pinworm in California. Dr. Schuster has been author and coauthor on many publications.

Achievement Award For Teaching: Frank Slansky Jr.

Dr. Slansky has made a significant impact on the graduate student program at the Department of Entomolohy and Nematolohy, University of Florida. His obvious grasp and knowledge of the interactions between insects and their host plants coupled with his relaxed, friendly interaction with students contribute to the popularity of his course in nutritional ecology. He unceasingly updates his course with modern theory and current literature. He has served on over 26 graduate supervisory committees, as chairman or committee member. He has served as outside examiner on many doctoral qualifying examinations where his participation in the oral examinations makes the students think and synthesize the information they have accumulated.

Achievement Award For Extension: Philip G. Koehler

Dr. Koehler has been a leader in the transfer of new scientific technology to the private citizens and the pest control industry of Florida. Through his research efforts, he has devised innovative control strategies for the suppression of such important urban pests as cockroaches and fleas, resulting in the savings of millions of dollars in control costs to the taxpayers of the state. His humorous and informative talks at extension meetings are famous not only in Florida where they draw large numbers of people, but throughout the nation. He is unceasing in his efforts to aid the Florida pest control industry by assisting in seminars, monthly and annual meetings, and training sessions. He has produced, singly and in cooperation with others, numerous training aids, extension publications, and research publications.

Certificate of Merit: May Buckingham

Museum collections are chronically undercurated and the Florida State Collection of Arthropods is no exception. Over the past 3 years, May Buckingham has volunteered more than 2,000 hours of labor to the state's reference insect collection, labelling specimens and incorporating accessions. Many thousands of specimens have thus been made available to specialists for study. The Honors and Awards committee would like to recognize May Buckingham for her unselfish contribution of time and talent which have immeasurably increased the value of the FSCA as a tool for the protection and improvement of Florida agriculture.

Certificate of Appreciation: Susan P. Whitney

One of the thankless, time-consuming jobs which has to get done is the publication of the society's newsletter. Dr. Whitney has given unstintingly of her time to co-edit and produce our newsletter, under difficult circumstances and changing formats. The Honors and Awards Committee would like to recognize Dr. Susan P. Whitney for her co-editorship of the Newsletter of the Florida Entomological Society.

Certificate of Appreciation: Fred D. Bennett

Many people work tirelessly to make our Annual Meeting a success, but none any more than the Chairman of the Local Arrangements Committee. The Honors and Awards Committee would like to recognize Dr. Fred. D. Bennett for his efforts in making the 1989 Annual Meeting a success.

Certificates of Appreciation: Associate Editors

Publication of the *Florida Entomologist* is one of the society's main functions, and the one which probably brings the Society the most acclaim. The success of *Florida Entomologist* is due in large part to the unselfish efforts of the Associate Editors. The

Honors and Awards Committee would like to recognize the following individuals for their years of unselfish devotion to editing the Society's journal: Dr. Arshad Ali, 6 years; Dr. Carl S. Barfield, 4 years; Dr. Ronald H. Cherry, 3 years; Dr. John B. Heppner, 6 years; Dr. Michael D. Hubbard, 7 years; Dr. Lance S. Osborne, 3 years; Dr. John Sivinski, 2 years; Dr. Omelio Sosa, Jr., 6 years; Dr. Howard V. Weems Jr., 17 years; and Dr. Willis W. Wirth, 6 years.

Certificate of Appreciation: Margaret R. Martin

Behind every successful President, there is one unsung hero who never gets the credit. That person's job is to not be noticed but to get her boss's work out on time. The Honors and Awards Committee would like to recognize our President's secretary, Ms. Margaret R. Martin, for her unselfish herculean efforts, often under adverse conditions, in doing her job, making our President's term a successful one.

Presidential Recognition Award: Lewis Wright, Jr.

President Patterson presented a special award to Mr. Lewis Wright, Jr., for his dedication and timeless effort to the Florida Entomological Society.

Recognition of the President: Richard S. Patterson

The Honors and Awards Committee would like to recognize the outstanding job done by our outgoing President, Dr. Richard S. Patterson. Being elected president of the Florida Entomological Society demands a tremendous commitment for a year's service but also demonstrates many previous years of such service to the Society. This award is presented as an appreciation of this year's untiring efforts this office represents and hopes for many more years to come.
D. P. WOJCIK, CHAIRMAN; R. F. MIZELL; L. S. WOOD

REPORT OF THE STUDENT ACTIVITIES COMMITTEE

Mini-grant funding was increased from $50 to $100 this year and funding for scholarships remained at $500 each. Grant/scholarship applications were widely solicited, with applications received from several universities (University of Florida, Florida State University, Florida A & M, and University of Miami). Funding was provided for 8 (66% of applicants) mini-grants as follows: V. Banschbach (Miami), J. Capogreco (FSU), C. LeDuc (Florida A & M), D. McInnes (FSU), M. Minno (UF), D. Riley, (UF), T. Rossi (FSU), and G. Storey (UF).

Three scholarships were awarded (50% of applicants) as follows: M. Camara (FSU), R. Coler (UF), and G. Storey (UF).

Fourteen papers and five posters were submitted for entry in the student competitions at the Annual meeting. Winners in the oral paper contest were : 1st Place- D. Riley (UF), 2nd Place- D. Ritland (UF), and tied for 3rd Place were N. Epsky (UF) and N. Hinkle (UF). Winners in the Poster contest were: 1st Place- B. Lenczewski (UF), 2nd Place- A. Rueda (UF), 3rd Place- S. Yocum (UF).
J. CAPINERA, CHAIRMAN; P. LAWRENCE; J. SIVINSKI

REPORT OF THE RESOLUTIONS COMMITTEE

Resolution No. 1:

WHEREAS, the 72nd Annual meeting of the Florida Entomological Society at the Daytona Beach Hilton, Daytona Beach, Florida, has enjoyed outstanding facilities and hospitality which immensely contributed to the success of the meeting, AND WHEREAS, The representative from the City of Daytona Beach generously give his time and efforts to welcome the Society for the City of Daytona Beach, which effectively opened the 72nd Annual Meeting of the Society.

THEREFORE, BE IT RESOLVED that the Secretary of the Society be instructed to forward a copy of this resolution to the hotel and to the City of Daytona Beach.

Resolution No. 2:

WHEREAS, The Local Arrangements Committee has provided excellent organization and facilities for the 72nd Annual meeting of the Society,

AND WHEREAS J. F. Price and the Program Committee have prepared a high quality and well-balanced program for the Society's meeting,

AND WHEREAS the speakers who presented papers, both invited and submitted, shared their outstanding work and ideas with our Society,

AND WHEREAS excellent and timely symposia were organized by J. H. Frank, E. D. McCoy, B. R. Wiseman, D. J. Schuster, D. H. Habeck and J. E. Eger,

AND WHEREAS The Committee on Student Activities encouraged excellent student participation in and contribution to our Annual Society Meeting,

THEREFORE BE IT RESOLVED that the Society expresses its deepest appreciation to these individuals who helped make the meeting a success.

Resolution No. 3:

WHEREAS President Richard S. Patterson, and the other members of the Executive Committee have provided our Society with dedicated leadership and invaluable service,

AND WHEREAS J. R. McLaughlin and the Associate Editors of the *Florida Entomologist* have done a magnificent job in maintaining the highest standards for the Society's journal,

AND WHEREAS J. B. Kring and S. Whitney and H. G. Hall have excelled in the production of an informative and timely newsletter for the Society,

AND WHEREAS members of other committees have generously contributed their time and efforts to the Society this past year,

THEREFORE BE IT RESOLVED that the Society commends these individuals and expresses its appreciation for their services to the Society and to the Science of Entomology.

Resolution No. 4:

WHEREAS members of industry continue to provide much needed financial support to the Society by way of Sustaining Memberships, advertising in the program, support for the journal and numerous other Society functions,

THEREFORE BE IT RESOLVED that the Society hereby expresses its appreciation to these groups.

L. BLOOMCAMP, CHAIRMAN; D. HARRIS; F. HASSUT; S. NARANG

REPORT OF THE NEWSLETTER COMMITTEE

Three issues of the Newsletter were published with the November 1988 and March, 1989 issues of 4-6 pages costing the Society $410.49 and $710.73, respectively. A new format began with the June 1989 issue with an 8 page format at a cost to the Society of $55.09. The new format and procedures represent a large savings to the Society, and provide more space than was previously available.

SUSAN WHITNEY AND GLENN HALL, Co-editors

REPORT OF THE MEMBERSHIP COMMITTEE

Committee members wrote to approximately 75 individuals who had not renewed their membership in the Society for this year. Committee members promoted membership among various groups, including students at UF. FSU and FAMU, science fair participants, co-workers, and others with identified interests in insects or entomology. A target for next year could be to identify one person at every university/college/community college in Florida and to provide that person with Society and membership information, and request active recruitment for the FES.
J. L. NATION, CHAIRMAN; A. D. GETTMAN; L. S. OSBORNE; M. L. PESCADOR; R. H. SCHEFFRAHN; D. F. WILLIAMS

REPORT OF THE PUBLIC RELATIONS COMMITTEE

The committee sent special announcements of the 72nd FES meeting to a number of universities and other organizations in the state with entomological affiliations. Letters of invitation were also sent to Dr. Dorothy Feir, President of the Entomological Society of America; Mosquito Control Association, and the Florida Pest Control Association.
J. E. PEÑA, CHAIRMAN; J. R. CASSANI; F. PETIT

REPORT OF THE PUBLICATIONS COMMITTEE

The Publications Committee thoroughly reviewed the fiscal aspects of journal publication and has proposed the following items for consideration at the October, 1989 Executive Committee meeting: (1) Continue base page charges of $45. (2) Beginning with Volume 73(1), add a $10 surcharge for tables and figures (additional charge for any page containing a figure or table). (3) Beginning January 1990, the finances of the journal will be separated from the general Society budget with a fiscal year beginning January and ending December 31.
J. R. MCLAUGHLIN, EDITOR

REPORT ON THE 1990 MEETING SITE

J. Knapp provided those present at the Annual meeting with detailed information regarding the 73rd Annual Meeting of the Society to be held in Cancun, Mexico 9-12 August, 1990. The hotel has been selected and price information has been sent to all members. President Eger encouraged all members to plan to attend the meeting, and to make their plans as early as possible.

REPORT OF THE NOMINATING COMMITTEE

The Nominating Committee submitted the following slate of nominees for FES offices:

President	Joe Eger
President-Elect	James Price
Vice-President	Joe Knapp
Secretary	Jim Coffelt
Executive Committee Member-at-Large	Jorge Peña

This slate of nominees subsequently was elected to office by the FES for 1989-1990.
JAMES L. TAYLOR, CHAIRMAN; J. H. FRANK; D. H. HABECK

JAMES A. COFFELT
Secretary

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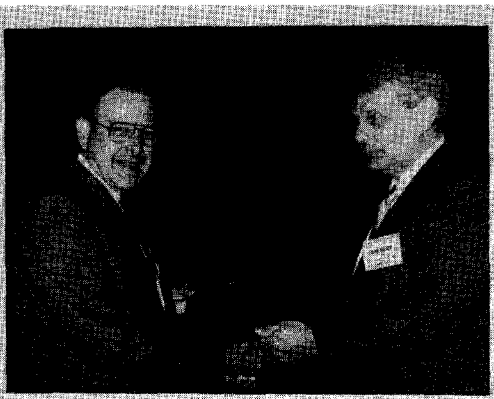

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Fig. 1. Outgoing President Richard S. Patterson is presented a plaque as a token of appreciation for his dedication and service to the Society from Dan Wojcik, Chairman, Honors and Awards Committee. (All photos courtesy of Frank W. Mead). Fig. 2. James B. Kring receives the Entomologist of the Year Award. Fig. 3. David J. Schuster accepts the Annual Achievement Award for Research. Fig. 4. Frank Slansky. Jr. receives the Annual Achievement Award for Teaching. Fig 5. Philip G. Koehler accepts the Annual Achievement Award for Extension. Fig. 6. May Buckingham is awarded a Certificate of Merit for her contributions to the Florida State Collection of Arthropods.

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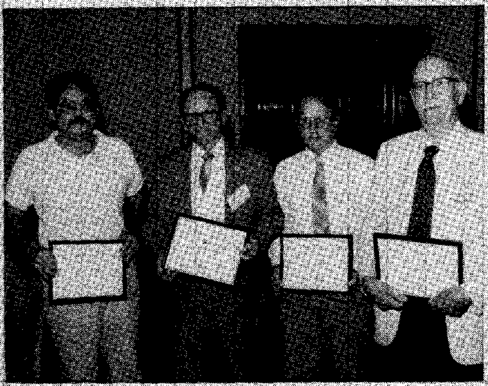

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Fig. 7. Susan F. Whitney receives a Certificate of Appreciation for her many contributions as Editor of the Society's Newsletter. Fig. 8. Margaret R. Martin receives a Certificate of Appreciation for her contributions to the Society as Secretary to President Patterson. Fig. 9. The Associate Editors of *Florida Entomologist* received Certificates of Apprecation for their contributions to the success of the Society's major publication. (Left to Right: M. Hubbard, H. Weems. Jr., L. Osborne, ard W. Wirth; not pictured: A. Ali, C. Barfield, R. Cherry, J. Heppner, J. Sivinski, and O. Sosa). Fig. 10. Participants in Insect Behavior and Ecology Symposium. (Left to Right: J. Lloyd D. Pearson, B. Witz, H. Frank, E. McCoy, J. Allen, and J. Linley. Fig. 11. D. Riley accepts his award from John Capinera, Chairman, Student Affairs Committee, for placing First in the Student Paper Contest. Fig. 12. D. Ritland receives his award for placing Second in the Student Paper Contest.

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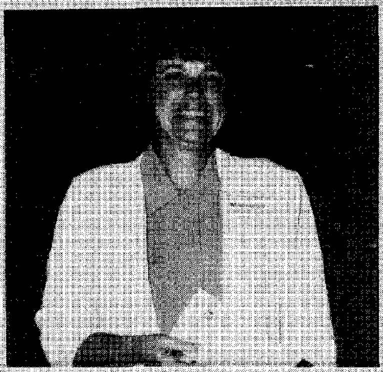

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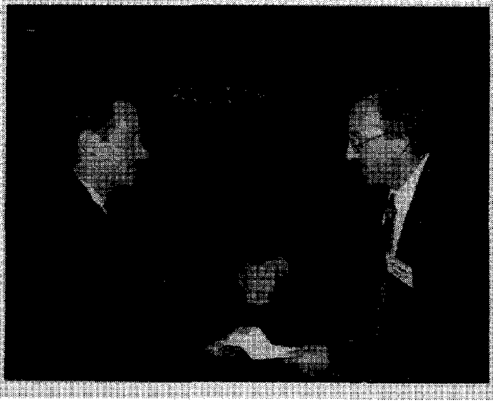

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Fig. 13. N. Epsky displays her award for placing Third (tie) in the Student Paper Contest. Fig. 14. N. Hinkle receives her award for placing Third (tie) in the Student Paper Contest. Fig. 15. B .Lenczewski accepts her award for First Place in the Student Poster Contest. Fig 16. A. Rueda is awarded Second Place in the Student Poster Contest. Fig. 17. S. Yocum receives the award for Third Place in the Student Poster Contest. Fig. 18. R. Coler receives one of 3 scholarships awarded by the Society.

Fig. 19. A. Rossii Receives his mini-grant award. Fig. 20. C. LeDuc receives her mini-grant award. Fig. 21. J. Capogreco receives his mini-grant award. Fig. 22. Linda Tindale receives the Society's award from incoming President J. Eger for her prize winning exhibit in the Florida State Science Fair.

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SUSTAINING MEMBERS, JANUARY, 1990

Abbott Labs—Chem & Ag. Products Div.
Att: R. Cibulsky, Dept. 986
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North Chicago, IL 60064

All American Termite & Pest Control, Inc.
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Orlando, FL 32854

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Att: Emil A. Moherek
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Att: John B. O'Neil
2997 Gant Place
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ASGROW Florida Company
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ICI Americas, Inc.
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P.O. Drawer "A"
South Bay, FL 33493

Sun Refining & Marketing Co.
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Marcus Hook, PA 19061-0835

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