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The evolutionary biology of Zoraptera (Insecta)

Choe, Jae Chun, Ph.D.

Harvard University, 1990

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Typed name Bruce Waldman

Date 8. May 1990

The Evolutionary Biology of Zoraptera (Insecta)

A thesis presented

by

Jae Chun Choe

to

The Department of Organismic and Evolutionary Biology
in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy
in the subject of
Biology

Harvard University
Cambridge, Massachusetts

May 1990

ABSTRACT

The Zoraptera is among the least explored orders of insects. The order contains a single family, Zorotypidae, a single genus, *Zorotypus*, and less than 30 described species. Here I describe a new species, *Zorotypus gurneyi*, from Panama and redescribe *Z. barberi* Gurney.

Social behavior of this little-known insect order is also described for the first time. Two sympatric species in Panama, *Z. barberi* and *Z. gurneyi*, exhibit marked differences in their behavior and biology. The mating system of *Z. barberi* appears to be promiscuity by both sexes involving an elaborate sequence of courtship, nuptial feeding, and repeated copulations with the same mate. Male *Z. barberi* possess a cephalic gland, from which they secrete liquid substance and use it as a nuptial gift during courtship. Females who have mated three or more times lay considerably more eggs than those who have mated only once or twice, suggesting that the cephalic secretion contains critical resources.

Male *Z. gurneyi* have no such gland and in fact exhibit no apparent courtship. Instead, they establish a highly linear and stable dominance hierarchy in which dominant males obtain the majority of matings. Although body size is clearly the most influential determinant of staged combats among males, the correlation between body size and dominance rank is often weak in field-collected colonies. The effects of age or emergence order override those of size when the information on relative age is available to males. The mating system of *Z. gurneyi* resembles the female defense polygyny which is an extremely rare mating system in insects.

The morphology, systematics, and biology of the entire order is also reviewed. Whether or not the Zoraptera is most closely related to the Isoptera is of particular importance.

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ACKNOWLEDGMENTS

At our first meeting in November 1982 Professor Edward O. Wilson laid out my research strategy, which, I believe, is his own as well. He told me that a good evolutionary biologist must begin with a systematic study of his study organism and related taxa, then conduct a thorough observation on the natural history, and then finally test evolutionary hypotheses. I tried to follow his guideline throughout my dissertation research and will also continue to do so for my future research.

Exploring such an unknown group of insects richly rewarded me, but also made my journey often lonely and frustrating since I had to be an academic jack of all trades. Several people reminded me that I should not be a master of none. Bert Hölldobler has been a willing and patient advisor. He not only helped me set the tone and direction of my research, but also gave me total freedom which enabled me to explore endless possibilities in my research. Edward O. Wilson has been a source of encouragement and comfort. On countless occasions I knocked on his door for help often in the last minute. He was always there for me. Bruce Waldman has been both a tough teacher and good friend. His criticisms and reminders kept me going. My heartfelt thanks go to each one of these three wonderful committee members.

My Smithsonian advisor, William G. Eberhard, and Mary Jane West-Eberhard deserve special thanks for their genuine interests and kindness. Bill has been my mentor and a constant source of inspiration. I will be extremely pleased, if I can become half the man and scholar he is when I grow up. Mary Jane is not only the first member of the National Academy of Sciences who had never held a full-time

academic position but also the most caring member of all. I will never forget when she stayed up till four in the morning to meet a taxi driver so that I could get some sleep before taking one of those red-eye special flights. Numerous evening discussions I had with both of them in their house on a beautiful hill in Costa Rica shaped and clarified my thinking on many issues.

Staff researchers at the Smithsonian Tropical Research Institute in Panama have been so kind and wonderful. Egbert Leigh, Stan Rand, Don Windsor, Joe Wright, Alan Smith, Henk Wolda, Annette Aiello, Ira Rubinoff, I thank you all. Allen Herre, Don Feener, Robert Dudley, Kaoru Kitajima, Betsy Mitchell, Mitch Aide, Jess Zimmermann, Seiji Tanaka, and Andy Green (in no particular order) have taught me how to enjoy field studies and be productive at the same time.

I also thank Peter H. Adler for being a wonderful friend and reading every little thing I have written. David Shetlar first introduced me to the world of Zoraptera. Steven Austad might as well be on my committee, having helped me in many ways. James Carpenter has been a good instructor of systematics and insect taxonomy to me. William Bossert provided his insight in an early phase of my research.

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My parents and parents-in-law have always been cheering and supportive. I owe them a great debt of gratitude. I would also like to send my sincere thanks to my grandparents who still believe that someday I will come back to become a mayor of their little town. I also thank Master Alan Heimert and Mrs. Arline Heimert of Eliot House for providing me and my family with a comfortable nest. Both financially and emotionally they have done much more than they think.

It is not possible to thank my wife enough for all the things she has done for me. Her love and support has been a source of my strength. Suffice it to say that she has supplied my life with purpose and this thesis is really for her. For being a truly wonderful companion and perfect mother for our beautiful son, Ian Matthew, I thank you, H.K.

A major portion of my research was supported by the Predoctoral fellowship from the Smithsonian Institution. Additional supports were provided by the Noyes Fellowship from the Organization for Tropical Studies, Theodore Roosevelt Memorial Fund, Grants-in-Aid of Research from Sigma Xi, Graduate Fellowship and Exxon Fellowship from the Smithsonian Institution, Korean Honor Scholarship, and Richmond Fund and deCuevas Fund from Harvard University.

INTRODUCTION

Two of the greatest biological enigmas are the origin of sociality and that of sexuality. Charles Darwin (1859) regarded the evolution of sociality, particularly the phenomenon of sterile castes in social insects, as the greatest challenge to his theory of natural selection. Darwin (1871) also wrote: "We do not even in the least know the final cause of sexuality. The whole subject is hidden in darkness." Why and how have only a handful of animals including humans evolved to be social and dominate the world today? Why does sex exist at all, what allowed it to evolve, and how does it persist? Today both of Darwin's puzzles still remain largely unsolved.

I study a little-known insect order, Zoraptera, not only because it is fascinating in itself but also because it may provide some vital clues to the origin of sociality, particularly that of termite sociality. Zorapterans are minute insects that live colonially under the bark of rotting logs. They belong to the order Zoraptera which contains a single family, Zorotypidae, and only 30 described species of a single genus, *Zorotypus*. Practically nothing was known about zorapteran biology when I began my research six years ago, but I have now gathered a good deal of biological and behavioral information (Choe 1989, 1991). One of the reasons for the lack of information about Zoraptera was that no one could keep them in the laboratory for an extended period. I have developed an excellent culturing method and maintained a number of healthy laboratory colonies.

Ever since Hamilton (1964) proposed a potential evolutionary pathway to true sociality for ants, wasps, and bees, based on their peculiar haplodiploid genetic system, a great deal of both theoretical and empirical research has been conducted.

However, there has been little advance in the study of social evolution in termites, which have a different basis for sociality and exhibit equally as complex social behavior as other social insects. Ironically, studying termites themselves probably will not shed much light on the origin of their sociality, because all living termite species have already evolved to be truly social. I believe that more clues can be found if one looks at evolutionarily less advanced, yet closely related, insects. Zorapterans are an excellent candidate.

Zorapterans have two distinct castes: winged and wingless. Winged zorapterans disperse to new habitats, shed their wings and found new colonies as do winged reproductives of ants and termites. Unlike sterile castes of social insects, however, wingless zorapterans are capable of reproducing themselves to some extent. Although the existence of sterile castes is the most critical feature of true sociality, an 'evolutionary arms race' over reproduction is still going on between reproductive and supposedly sterile castes in many social insects (Choe 1988). The two zorapteran castes may represent an early stage of division of reproductive labor in social insects.

I discovered that zorapterans harbor a variety of protozoans in their guts, as do termites. This is a discovery of particular interest, because symbiotic protozoans are believed to have played a major role in the origin of termite sociality. Whether the protozoans in zorapteran guts are indeed fermentating symbionts and whether they are phylogenetically related to the ones in termite guts are among the critical questions worthy of further research.

Zorapterans are also excellent organisms for studying the dynamics of sexual selection and evolution of sex. Two sympatric species in central Panama, *Zorotypus gurneyi* Choe and *Z. barberi* Gurney, exhibit entirely different sexual behavior (Choe 1991). Male *Z. gurneyi* maintain a well-defined dominance hierarchy and a highly polygynous mating system. In contrast, *Z. barberi* appears to have promiscuous mating system in which males provide cephalic secretion as a nuptial gift and perform an elaborate sequence of courtship behavior. I investigated the ontogeny of dominance hierarchy and its influence on male mating success in *Z. gurneyi*. The dynamics of female choice and male courtship success in *Z. barberi* were also analyzed in detail.

I also found that *Z. gurneyi* females often reproduce asexually, i.e., without fertilization. Asexual females produce only female offspring and appear to do so at a higher rate than sexual females who must also produce male offspring. In spite of this clear disadvantage, sexual colonies are as common as asexual ones in the field.

Topics of my research on Zoraptera range from behavior and ecology to systematics and evolution. The objectives of my dissertation research were: (1) to determine taxonomically important characters in the order Zoraptera and obtain information needed to analyze phylogenetic affinities of Zoraptera to other insect orders, (2) to describe detailed natural histories of *Z. gurnyei* and *Z. barberi*, (3) to observe the dynamics of mate choice and mate competition, and (4) to identify and examine potentially important biological phenomena which may help unveil the evolution of eusociality in insects.

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CHAPTER 1

Zorotypus gurneyi, New Species, from Panama and Redescription of *Z. barberi* Gurney (Zoraptera: Zorotypidae)

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Ann. Entomol. Soc. Am. 82(2): 149–155 (1989)

ABSTRACT A new species of Zoraptera, *Zorotypus gurneyi*, is described from Panama. It is separated from related species by differences in body size, structure of the male genitalia, chaetotaxy on the apical tergites, and the number and arrangement of spines on the posterior margin of the hind femur. *Zorotypus barberi* Gurney is redescribed.

KEY WORDS Insecta, *Zorotypus*, Zoraptera, zorapteran phylogeny

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THE ZORAPTERA is among the smallest and least known orders of insects. Since the order was established by Silvestri (1913), only 28 species have been described (Choe in press). The order contains a single family, Zorotypidae, and a single genus, *Zorotypus*.

Zorapterans are basically pantropical, occurring on all continents except Australia. Although 14 species have been recorded from various localities in the Neotropical Region (Fig. 1), no zorapterans have been reported previously from Panama. In the following account, I describe a new species, *Zorotypus gurneyi*, and I redescribe *Z. barberi* Gurney, which was described originally from a single apterous male from Cocos Island, Costa Rica (Gurney 1938). *Z. barberi* is redescribed to provide more detail, because some important characters were omitted in the original description.

All measurements were made on live or freshly killed specimens. For the study of fine structure, specimens were cleared in potassium hydroxide or disarticulated and then mounted on slides. I follow the scheme for wing venation given by Weidner (1970). All measurements are in millimeters.

Zorotypus gurneyi Choe, n. sp.
(Fig. 1–5, 10–13, and 19)

Apterous Male. Brown to brownish black; body length without antennae 2.4–2.6. Antennae 9-segmented, 1.40–1.65 long; segments long, slender; segment II or pedicel shortest, curved; segments VIII, IX, apex of segment VII usually pale. Pronotum 0.40–0.50 long, 0.48–0.58 wide. Hind femur (Fig. 2) 0.75–0.85 long, 0.25–0.33 wide, with posterior row of 9–11 (usually 11) spines; central spines (usually the 3rd to 6th spines from proximal end) thicker, longer. Abdomen 11-segmented; tergum IX (Fig. 3) expanded anteromedially, with group of 7–10 thick setae, 2 thin setae along posterior margin, and 1 very thin short seta on each side posterior to transverse membranous tissue; tergum X (Fig. 3) with 2 pairs of weakly sclerotized plates and 1 hookshaped projection fused by membranous tissue; tergum XI with a pair of unsegmented cerci. Basal plate (Fig. 4) wider medially, with spiral-shaped duct tightly packed between bifurcated posterior arms. Sternite VIII (Fig. 4) small, slightly emarginate, with a pair of depressed regions anterior to rugose surface.

Apterous Female. Color, general shape similar to those of apterous male; body length without antennae 2.2–2.4. Antennae 1.35–1.65 long; pronotum 0.35–0.45 long, 0.45–0.53 wide. Hind femur 0.60–0.75 long, 0.20–0.25 wide, with spines less pronounced than those of apterous male; number and arrangement of spines similar to those of apterous male. Abdominal tergite IX expanded anteromedially as in males. Sternite VIII (Fig. 5) round, broad, emarginate medially; sternite IX (Fig. 5) shallow, with a pair of small projections on anterior margin. One spermatheca, connected by long slender duct (Fig. 5).

Alate Female. Darker than apterous individuals. With compound eyes, 3 ocelli, each ocellus half dark, half pale. Two pairs of wings (Fig. 10–13); forewing 2.6–2.8 long, hindwing 2.1–2.3 long; forewing venation variable where Rs meets M (Fig. 12 showing most common venation); Cu_1 of hindwing absent; Cu_2 of hindwing present or absent (Fig. 13).

Nymph. Pale, but similar in general structure to adults. Antennae of later instars 9-segmented; those of earlier ones 8-segmented.

Egg. Oblong, cream-colored; 0.60–0.63 long, 0.40–0.43 wide; surface with hexagonal or sometimes pentagonal patterns with 2 micropyles; operculum absent (Fig. 19).

Type Material. HOLOTYPE, apterous ♂, Pipeline Road, Gamboa, Panama, 7-III-87, J. C. Choe. PARATYPES: Panama: 3 apterous ♂♂, same data

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This paper is dedicated to the late Dr. Ashley Buell Gurney.

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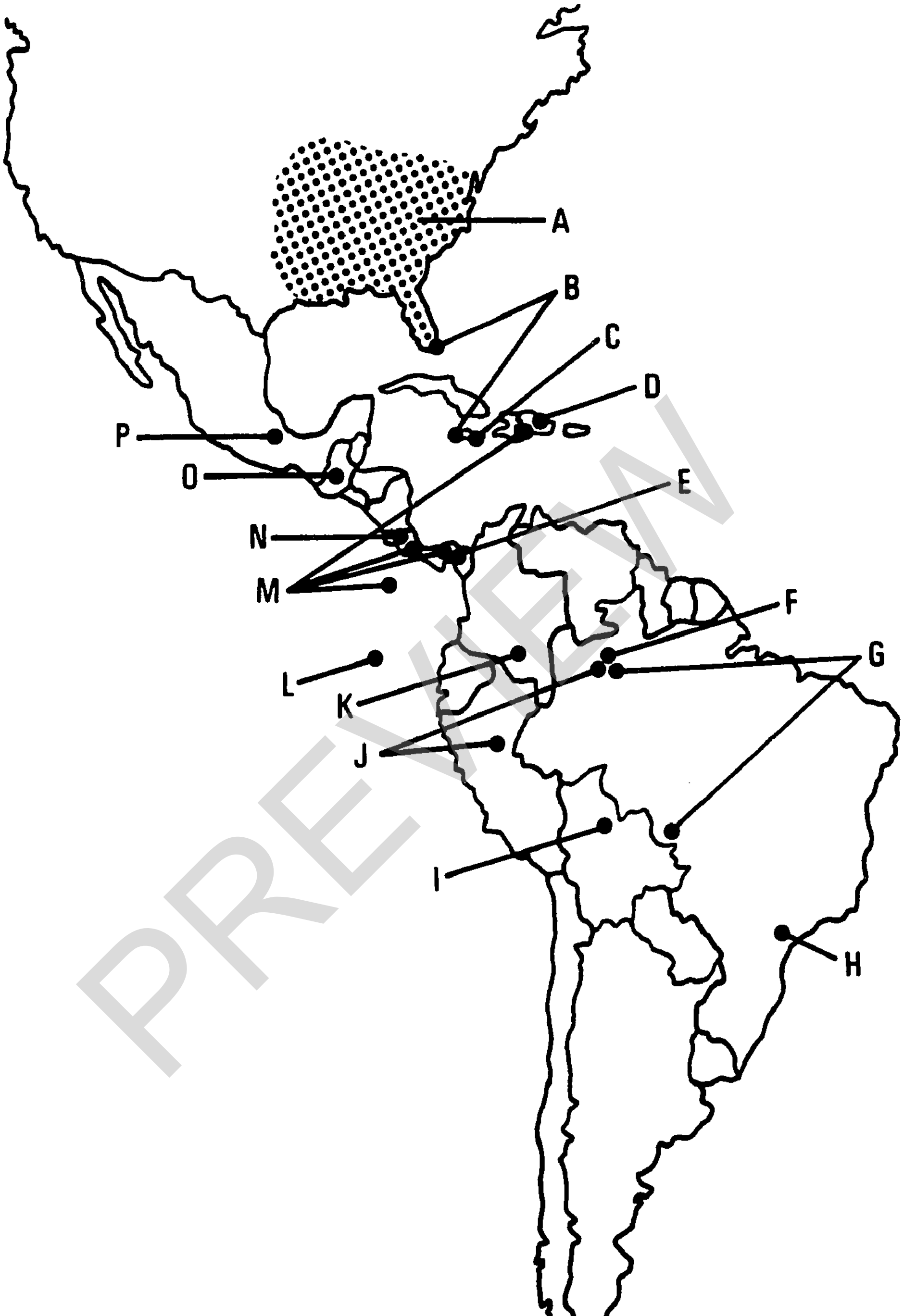

Fig. 1. Distribution of neotropical Zoraptera: A, *Zorotypus hubbardi* Caudell; B, Z. *snyderi* Caudell; C, Z. *longicercatus* Caudell; D, Z. *palaeus* Poinar (fossil); E, Z. *gurneyi* Choe; F, Z. *weidneri* New; G, Z. *shannoni* Gurney; H, Z. *brasiliensis*, Silvestri; I, Z. *manni* Caudell; J, Z. *huxleyi* Bolivar y Pieltain & Coronado; K, Z. *hamiltoni* New; L, Z. *leleupi* Weidner; M, Z. *barberi* Gurney; N, Z. *neotropicus* Silvestri; O, Z. *cramptoni* Gurney; P, Z. *mexicanus* Bolivar y Pieltain.

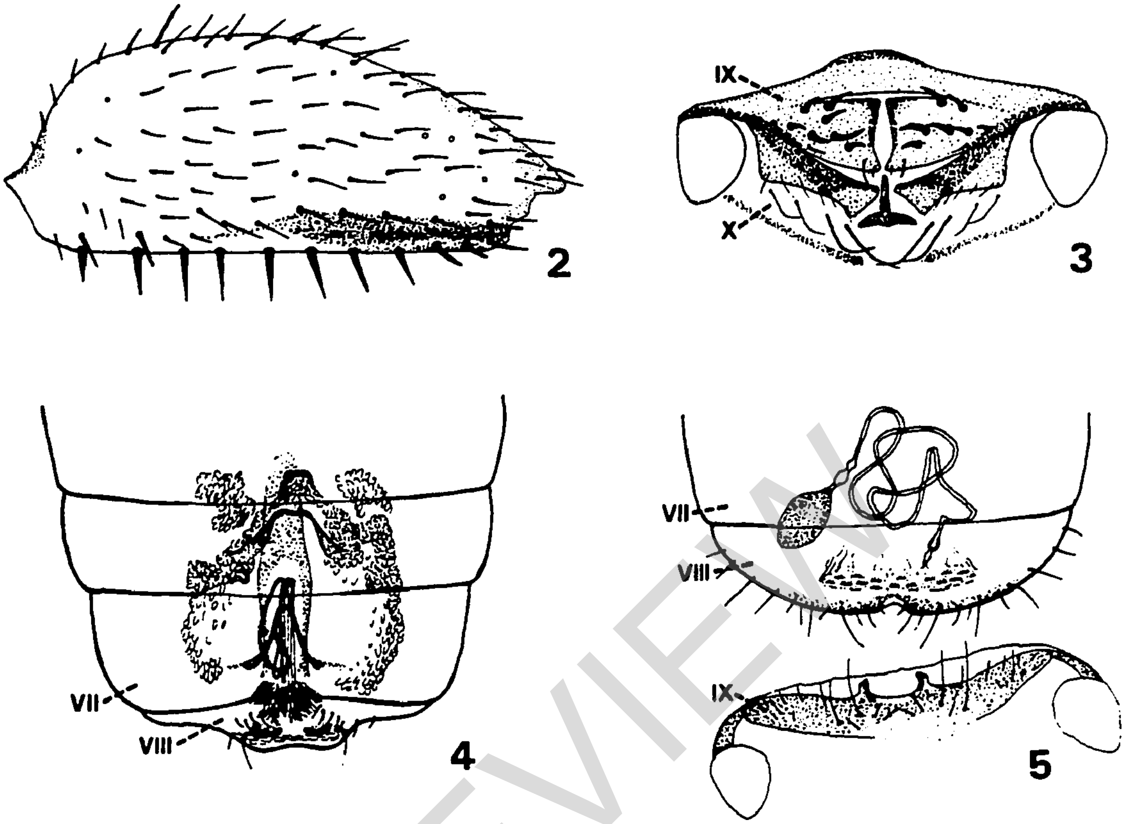

Fig. 2–5. *Zorotypus gurneyi*. (2) Male hind femur. (3) Male apical terga. (4) Male genitalia. (5) Female apical sterna and reproductive system.

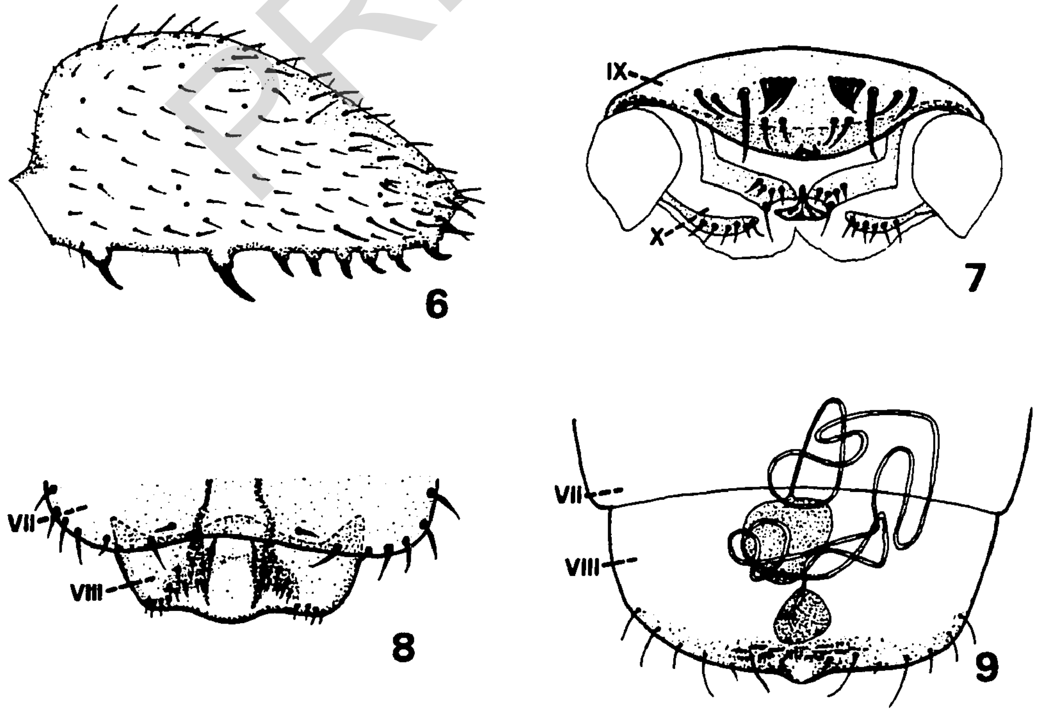

Fig. 6–9. *Zorotypus barberi*. (6) Male hind femur. (7) Male apical terga. (8) Male apical sterna. (9) Female apical sterna and reproductive system.

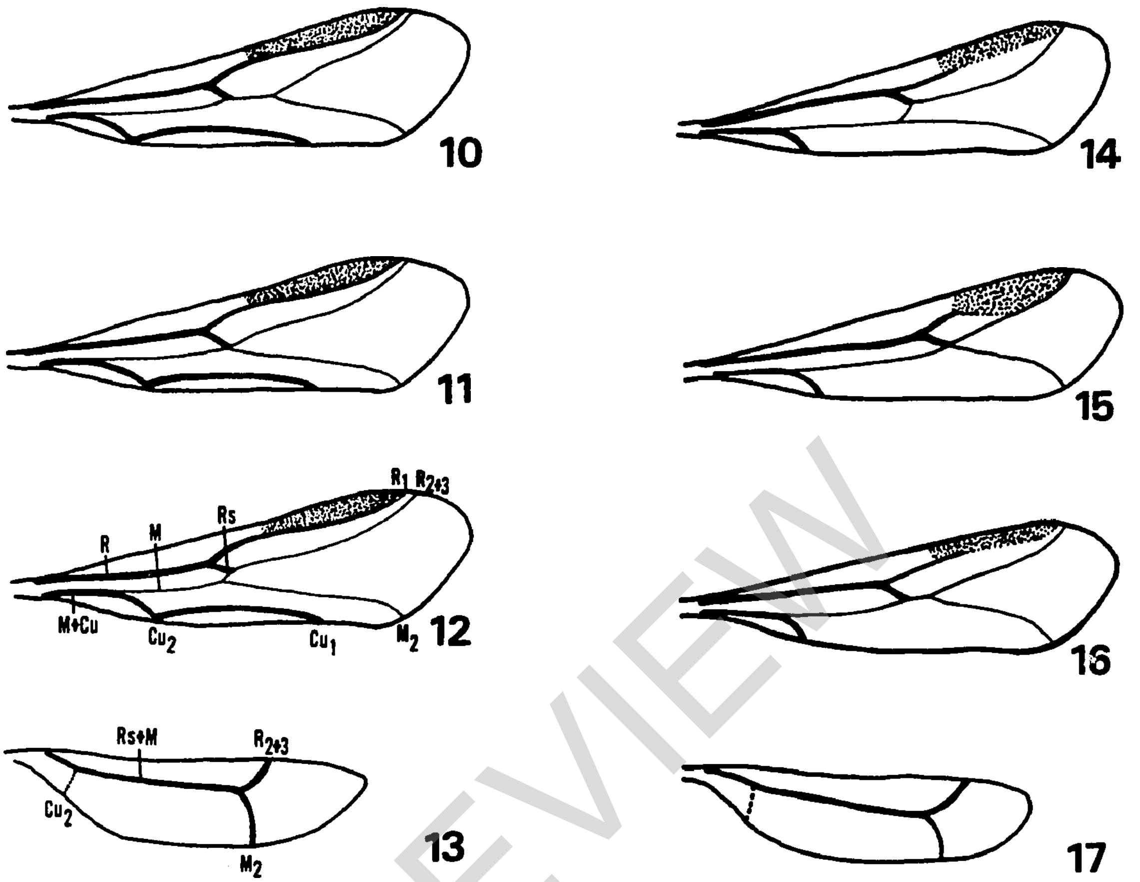

Fig. 10–17. Variations in wing venation of *Zorotypus*. (10–12) Forewings of *Z. gurneyi*. (13) Hindwing of *Z. gurneyi*. (14–16) Forewings of *Z. barberi*. (17) Hindwing of *Z. barberi*.

as holotype; 1 dealate and 5 apterous ♀♀, 6 nymphs, Barro Colorado Island, 9-X-86, J. C. Choe. Holotype and 6 paratypes (1 apterous ♂, 1 dealate and 2 apterous ♀♀, 3 nymphs) are in the Museum of Comparative Zoology, Harvard University, and 8 paratypes (2 apterous ♂♂, 3 apterous ♀♀, 3 nymphs) in the U.S. National Museum of Natural History.

Etymology. I name this species for the late Dr. Ashley Buell Gurney, who has worked extensively on Zoraptera.

Habitat. *Zorotypus gurneyi* live under the bark of decaying logs. Whether they live in only certain species of trees is not known, but they seem to prefer trees with relatively thick bark.

Remarks. This species is most similar to *Z. neotropicus* Silvestri from Costa Rica (Silvestri 1946) and *Z. hamiltoni* New from Colombia (New 1978). According to the descriptions of these species, *Z. gurneyi* is considerably smaller and differs in the chaetotaxy of the hind femur and the ninth abdominal tergum. The bifurcated arms of the basal plate in *Z. hamiltoni* expand posteriorly (New 1978), whereas those in *Z. gurneyi* are narrower than the midregion (Fig. 4). A comparison with *Z. neotropicus* is not possible because *Z. neotropicus* was described only from females (Silvestri 1946).

Zorotypus barberi Gurney
(Fig. 1, 6–9, 14–17, 18, and 20)

Apterous Male. Light amber to brown; body length without antennae 1.9–2.2. Antennae 1.0–1.1, with short, almost round segments; segment II shortest; segment III only slightly longer than segment II; segments IV, V much darker than others; segments VII, VIII, IX pale. Distinct fontanelle or cephalic gland (Fig. 18) present in center of head. Vestigial eyespots often visible. Pronotum 0.33–0.38 long, 0.40–0.43 wide. Hind femur (Fig. 6) 0.60–0.65 long, 0.28–0.33 wide, with posterior row of 8 or 9 unusually thick curved spines; from proximal end, first spine medium-sized, second largest, rest relatively small (Fig. 6). Abdomen 11-segmented; tergum IX (Fig. 7) with 4 or 5 (usually 5) light-colored setae tightly arranged in vertical row and 5 dark-colored setae on each side, and small rectangular process near posterior margin; tergum X (Fig. 7) with 2 pairs of weakly sclerotized plates, 1 hookshaped projection fused by membranous tissue; tergum XI with a pair of unsegmented cerci. Sternite VIII (Fig. 8) much narrower than sternite VII, expanded anteriorly in middle and at corners. Genitalia (Gurney 1938, Fig. 37–39) composed of

1 weakly sclerotized ventral plate, moderately sclerotized paired dorsal lobes, and 1 long needle-like aedeagus surrounded by paired mesal lobes and membranous flaps.

Apterous Female. Color, general shape similar to those of apterous male; body length without antennae 1.8–2.3. Antennae 1.0–1.1 long. Pronotum 0.30–0.33 long, 0.38–0.40 wide. Hind femur 0.50–0.55 long, 0.20–0.28 wide, with spines less pronounced than those of apterous male; number and arrangement of spines similar to those of apterous male. Head often with vestigial eyespots but without fontanelle gland. Abdominal sternite VIII (Fig. 9) much longer and darker than sternite VII, elevated posteromedially. Reproductive system (Fig. 9) composed of spermatheca connected by long duct.

Alates. Darker than apterous individuals. With compound eyes, 3 ocelli. Two pairs of wings (Fig. 14–17); forewing 2.2–2.4 long, hindwing 1.9–2.0 long; forewing venation variable where Rs meets M (the pattern in Fig. 16 most common); extent of pterostigma also variable in forewing; Cu_1 absent in both forewing and hindwing; Cu_2 of hindwing present or absent.

Nymph. Pale, but general structure similar to that of adults. Antennae of later instars 9-segmented; those of earlier instars 8-segmented.

Egg. Oblong, but somewhat flat on top, cream-colored; 0.58–0.60 long, 0.30–0.35 wide; surface sculpture similar to that of *Z. gurneyi* (Fig. 20).

Material Examined. HOLOTYPE, apterous ♂, Costa Rica: Cocos Island, 1-III-33, W. Schmidt (USNM). PANAMA: 6 apterous and 1 dealate ♂♂, 6 apterous and 2 dealate ♀♀, 6 nymphs, Barro Colorado Island, 11-VI-85, J. C. Choe (J. C. Choe [JCC], personal collection); 4 apterous ♂♂, 4 apterous ♀♀, 4 nymphs, Gigante Peninsula, Barro Colorado Nature Monument, 23-XI-86, J. C. Choe (JCC); 1 apterous ♂, 2 apterous ♀♀, Nusagandi, 13-III-87, J. C. Choe (JCC); 2 apterous ♀♀, La Fortuna (elevation 1.100 m), 19-IX-85, S. Tanaka (JCC); 2 apterous ♂♂, 3 apterous ♀♀, Bocas del Toro, 15 km north of La Fortuna, 27-I-87, E. S. Ross (California Academy of Sciences). COSTA RICA: 6 apterous ♂♂, 6 apterous ♀♀, 6 nymphs, La Selva, 5-VII-84, J. C. Choe (JCC). DOMINICAN REPUBLIC: 1 apterous ♂, 1 apterous ♀, 5 km north of Polo, Barahoga, 23-VII-87, E. S. Ross (California Academy of Sciences).

Habitat. *Zorotypus barberi* live under the bark of decaying logs. They sometimes occur together with *Z. gurneyi* in Panama and *Z. neotropicus* in Costa Rica.

Remarks. Although this species was previously known only from a single specimen collected from Cocos Island (Gurney 1938), it appears to be common. It has now been recorded from Panama, Costa Rica, and the Dominican Republic (Fig. 1).

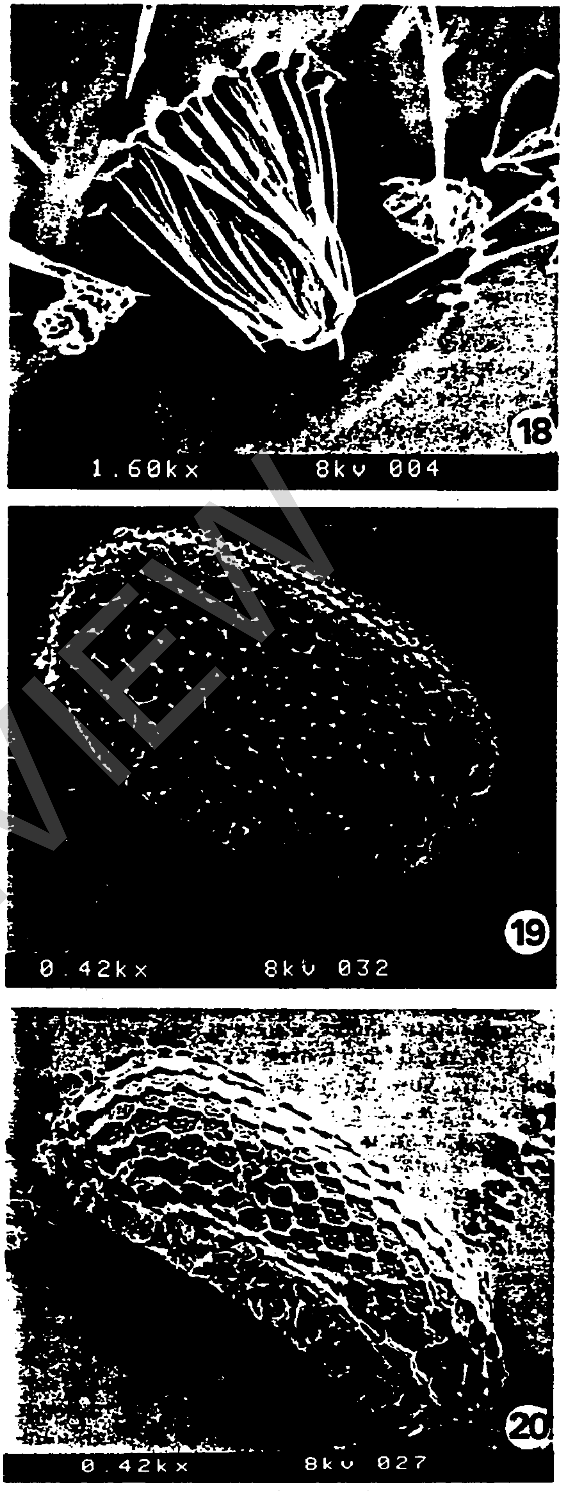

Fig. 18–20. Scanning electron photomicrographs of *Zorotypus*. (18) Fontanelle gland on the head of a *Z. barberi* male. (19) *Z. gurneyi* egg. (20) *Z. barberi* egg.

The fontanelle gland was not mentioned in the original description (Gurney 1938). Both apterous and alate males possess the gland in this species. Similar glands have been observed in *Z. congensis* Van Ryn-Tournel from Zaire (Van Ryn-Tournel 1971), *Z. delamarei* Paulian from Madagascar (Paulian 1949), and *Z. hubbardi* Caudell from the United States (Riegel 1987).

Several apterous individuals have pigments corresponding to the position of the compound eyes, but whether such individuals can detect light is not known. Some other individuals have caudolaterally extended meso- and metathoracic nota. Such intermorphs between apterous and alate morphs also were found in Z. *delamarei* (Delamare-Deboutteville 1951) and Z. *hubbardi* (Riegel 1963, Shetlar 1978).

Discussion

A fossil species, Z. *palaeus* Poinar, was described recently from Dominican amber of the lower Miocene–upper Eocene (Poinar 1988). The affinities of the Zoraptera are perhaps the most difficult puzzle in constructing the phylogeny of insects. Hennig (1969) suggested that the Zoraptera are the most primitive Paraneoptera, whereas Delamare-Deboutteville (1952) and Weidner (1969) argued that they are highly autapomorphic descendents of a predictyopteran stock. Kristensen (1975) successfully ruled out most claims of close relationship between the Zoraptera and Isoptera. It is also unlikely that the zorapteran fontanelle gland is homologous to the isopteran frontal gland, because the former is used in courtship (unpublished data), whereas the latter is used in defense (Prestwich 1984). Recently, however, Boudreaux (1979) revived the possibility of the Zoraptera–Isoptera affinity based on similarities in wing muscles and associated structures. In short, the phylogenetic affinities of the Zoraptera remain unsolved, and more rigorous collecting and systematic revision are needed.

Male genitalia form the most important characters for species identification. Species determination is often difficult because at least eight species were described from females or nymphs only (Caudell 1927, New 1978). Female genitalia are generally simple and not very species-specific.

Zorotypus gurneyi has the same general type of male genitalia as an array of species that range from Jamaica and Mexico to northern South America (Fig. 1), including Z. *snyderi* Caudell, Z. *mexicanus* Bolivar y Pieltain, Z. *cramptoni* Gurney, Z. *neotropicus*, and Z. *hamiltoni*. Their genitalia consist of an intromittent organ coiled between the bifurcated arms of the basal plate. These characters seem to define these zorapterans as a clear species group within the genus. These species also are similar in general body shape and color but differ in chaetotaxy on the ninth abdominal tergum, number and arrangement of spines on the hind femur, and some of the finer structures of the male genitalia.

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