2016

Cockroaches (Blattodea) of Southern Louisiana: Morphology, Diversity, and Life Histories

Forest Brady Huval
Louisiana State University and Agricultural and Mechanical College

COCKROACHES (BLATTODEA) OF SOUTHERN LOUISIANA: MORPHOLOGY, DIVERSITY, AND LIFE HISTORIES

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Masters of Science

in

The Department of Entomology

by
Forest B. Huval
B.S, University of Louisiana at Lafayette, 2012
August 2016

ACKNOWLEDGMENTS

I would like to acknowledge both of my parents Rowdy and Elaine Huval for relentlessly pushing me to archive any and all goals I choose to peruse, regardless of hardship and supposed limitations set by others. Both my mother and father have devoted and an unfathomable amount of time, patience, support, and money to me with no little understanding of how or why I so passionately pursue this career. In addition, to this conditionless love and support they have both allowed me to live at home, allowing me to save money and pursue various other passions within my life, something truly rare among graduate students. Without my parents, there would be significantly less passion and devotion to my current and future studies in entomology. Both are undoubtedly the reason this thesis exists.

I would also like to extend a special appreciation to both of my advisors Dr. Gregg Henderson and Dr. Chris Carlton, Department of Entomology, Louisiana State University, for providing irreplaceable guidance through the attainment of my Masters in Entomology. Neither were experts in the narrow field of Blattodea taxonomy and faunistic, but both continually provided guidance when my direction was waivered. Both strove to enhance what strengths I possessed when entering the program while rigorously coaching me to overcome my weaknesses. Another special thanks is given to Dr. Jim Miller, a dear friend who acted as a mentor, encouraging my pursuit of academic, professional and musical excellence. All of which and more, he has accomplished. His support and guidance is regarded with the utmost respect and appreciation. The last thanks goes to Mitch Andrews and Blake Miller. Two men with busy schedules that through the kindness of their hearts provided a quiet, empty house where the majority of this thesis was written.

I deeply appreciate Dr. Chris Carlton and Dr. Dorothy Prowell for allowing their cabin the West Feliciana Preserve. Keith Blanchard and David Allemon provided transportation to the Atchafalaya Basin Site. Dorothy Prowell and Patty Newell are thanked for the work they did at the Red River WMA, Three River WMA, and Long Leaf Pine Savannah sites, which provided many specimens included in my data. I would like to thank the Entomology Department of Louisiana State University, Louisiana State Arthropod Museum, and LSU Agricultural Center for providing the facilities and financial support necessary to complete this project.

TABLE OF CONTENTS

ACKNOWLEDGMENTS.......... ii

ABSTRACT.......... v

CHAPTER 1: INTRODUCTION.......... 1

CHAPTER 2: LITERATURE REVIEW.......... 4
2.1 Blattodea.......... 4
2.2 Lineages.......... 4
2.3 Taxonomic and Morphological Overview.......... 5
2.4 Morphology.......... 6
2.4.1 Pronotum.......... 7
2.4.2 Leg.......... 7
2.4.3 Abdominal Tergites and Modifications.......... 7
2.4.4 Tegmina and hind wings.......... 8
2.5 Genitalia.......... 9
2.5.1 Spermatophore /Sperm.......... 14
2.5.2 Female genitalia.......... 14
2.6 Reproduction.......... 17
2.6.1 Oviparity.......... 19
2.6.2 Ovoviviparity and Parthenogenesis.......... 19
2.6.3 Ootheca Orientation.......... 20
2.7 Behavior.......... 21
2.7.1 Mating.......... 21
2.7.2 Seduction.......... 23
2.7.3 Seasonal Activity.......... 24
2.8 Habitats.......... 25
2.8.1 Existing structures.......... 26
2.8.2 Insect Nests.......... 26
2.8.3 Desert and Caves.......... 26
2.8.4 Arboreal dwelling species.......... 27
2.8.5 Aquatic Habitats.......... 28
2.9 Ecology.......... 28
2.10 Collection methods.......... 29
2.10.1 Arboreal collection methods.......... 29
2.10.2 Beneath the canopy.......... 30

CHAPTER 3: SURVEY OF COCKROACHES IN SELECTED NON-URBAN HABITATS OF SOUTHERN LOUISIANA.......... 31
3.1 Introduction.......... 31
3.2 Materials and Methods.......... 32
3.2.1 Collections.......... 32
3.2.2 Rearing.......... 32
3.2.3 Data management.......... 33

3.2.4 Data Standardization..33
3.2.5 Study Sites..34
3.2.6 Diversity and Similarity Analysis...35
3.3 Results..35
3.3.1 Species Inventory...42
3.4 Discussion...58

CHAPTER 4: CONCLUSION…..60

LITERATURE CITED..62

APPENDICES
A: EXAMPLE OF DATA SHEET...84
B: ABUNDANCE OF BLATTODEA SPECIES BY SITE AND DATE..........................85
C: SPECIMENS EXAMINED... 86
D: GUIDE TO LOUISIANA (COCKROACHES) BLATTODEA...................................97

VITA..123

ABSTRACT

The state of Louisiana has both temperate and subtropical climates and includes six ecoregions. Two ecoregions in south-central Louisiana were surveyed for members of the order Blattodea to better describe the diversity, life histories, and taxonomy of adult and nymphal cockroaches. Blattodea, excluding the newly included epifamily Termitoidae, is an understudied order of insects in spite of the importance species that are infamous peridomestic pest. The order Blattodea currently contains 9 families comprising of 460 genera. There are approximately 7570 described species 4641 of which are cockroaches and 2929 are termites. Complete information on life histories lacks for the majority of species. Survey methods used included hanging Malaise traps, pitfall traps, mercury vapor light traps, and hand collecting. These methods were utilized monthly, spring through fall, with the first collections being made during summer 2014. To date, 505 field-collected specimens representing 16 species have been identified. These along with specimens examined from the Louisiana State Arthropod Museum have been used to redescribe 17 species based on out of date descriptions and create a key to adult males, adult females, and nymphs of all cockroach species in Louisiana. Significant findings include an expanded parish distribution of *Euthlastoblatta gemma* (Hebard), which had previously been recorded only from Orleans Parish, and detailed documentation of the life cycles of species viewed in the field and reared in the lab. This research on Louisiana cockroaches will contribute to the global knowledge of the diversity and life history of Blattodea that is increasingly utilized as model organisms in biomechanical engineering, insect physiology, and morphology.

CHAPTER 1: INTRODUCTION

Cockroaches are best known globally as pests. The almost universal response to any and all things cockroaches related is the familiar cringed face of disgust that is associated with anything considered disgusting or gross. Besides the unsanitary conditions that coincide with a major infestation of cockroaches, the dislike towards this order is primarily focused on the profoundly unsettling experience of witnessing a hoard of dark, fast moving bugs scurry into the crevices of a room as soon the lights come on. Cockroaches that typically are considered pests in the U.S. include roughly seven species that thrive within and around manmade structures (Brenner and Pierce 1991; Hagenbuch et. al.1988). Infestations that become severe can cause health problems for the residents (Litonjua et al. 2001). The primary goal of all cockroaches seems to be the invasion of any and all manmade structures while perpetually ruining our lives with the spread of allergens and germs. Peridomestic cockroach species make up less than one percent of the order (Nalepa et al. 2001). High densities of cockroaches have been shown to cause asthma as well as other allergic reactions. While pest species may cause allergic reactions it was discovered that different cultures from around the world have used cockroaches for a variety of useful purposes. For example, South American tribes use cockroach legs for medicinal purposes such as a treatment for asthma (Costa-Neto and Oliveira, 2000). The vast majority of the publications and literature that deals with cockroaches typically focus on species such as; *Blattella germanica* or *Periplaneta americana*. The result of which has caused these two species to become the typical representatives of the order (Bell et al. 2007). Pest species of cockroaches are under constant study to understand their life cycle and biological quirks that potentially can be used to more efficiently control and prevent infestations.

During the past decade, numerous studies have shown that cockroaches transcend the stereotypical view of pests or generalist species. Large, easy to maintain roaches like those of the genus *Gromphadorhina* (Madagascar hissing cockroaches) and cockroaches of the genus *Blaberus* are commonly used in morphology studies. Cockroaches display an extraordinary sense of balance, which allows them to traverse rough terrain with ease (Dudek and Full, 2000). When thrown off balance while running, the cockroach regains a balanced stride without re-orientating its center of gravity. This is a product of the cockroach's musculature, exoskeletal morphology. The center of gravity is lies within the support area provided by the legs. Unless completely knocked over the cockroaches examined will naturally fall back into is center of gravity (Jindrich and Full, 2002). By understanding the mechanics of how the members of the genus *Blaberus* move, engineers are currently making strides in developing robots able to traverse a multitude of rough terrains and narrow crevices with a high degree of efficiency (Quin and Ritzmann, 1998; Kingsley et al., 2006; Clark et al., 2001). Even the model of basic insect anatomy is increasingly exemplified by the Madagascar hissing cockroach (Heyborne et al., 2014).

Cockroaches are considered to be among the most ancient terrestrial arthropods. Based on the fossil records they dominated the Carboniferous period (Labandeira, 1994; Vrsanský, 1997; Grimaldi and Engel, 2005). Recent fossil records suggest that an ancient genus of cockroach may have inhabited North America nearly 49 million years earlier than previously hypothesized (Vrsansky et al. 2012, 2014). An extinct cockroach was noted to possess bioluminescence (Zompro and Firtzche, 1999). Advanced fluorescence recording techniques was used to present evidence that *Lucihormetica luckae* seeminly possess bioluminescence. This theory has been disputed due to the lack of an extant bioluminesce relative (Vrsansky and Chordate, 2013; Merrit, 2013).

During the past decade, three species of pollinating cockroaches have been discovered and documented. One of which located in Malasia and the other two in French Guiana (Mackeras, 1970; Grandcolas, 1996; Beccaloni, 2014). This ancient order of insects is now increasingly being used as model organism with an impressive ecological and morphological diversity. This requires a sound taxonomic and life history framework to better understand the diversity of the order. Understanding the ecology of this order can reveal what factors cause different species of roaches to thrive, perish, or never enter particular habitats (Roth and Willis 1960). When compared to other orders such as Coleoptera or Lepidoptera cockroach diversity is typically low. While the number of species in a given area may not be on par with holometabolous orders, the population of a single or group of species is typically high and provides important services such as basal decomposition in ecosystems such as rainforests (Zherikhin, 1993). At first glance pouring time, effort and funding into the study of Blattodea is seemingly not worth the effort. It is important to remember that for any branch of science to develop further, past investigations and new innovative ideas must be explored to understand or even discover how a once considered useless topic of research could further contribute to science.

The major taxonomist of the order Blattodea in the western hemisphere was Dr. Louis M. Roth who was associated with the U.S. Research and Development Laboratories and Harvard University. With his death in 2003 a void in cockroach taxonomy was created. The few Blattodea taxonomists that still exist typically limit their focus to a single taxa within limited geographical areas. These cockroach taxonomists are experts of the families they study within there geographical area of focus. Although various Blattodea taxonomists contributed to the taxonomy and systematics of the order, many phylogenetic discrepancies need to be resolved (Roth, 2003c). One example of an unresolved phylogeny is the family Ectobiidae. The phylogenetic study of Inward et al (2007) showed the paraphyletic nature of the family, but has yet to address it. In addition to the taxonomic problems present many blattoid species, including undescribed species and are threatened by habitat destruction (Tscharntke et al., 2002; Boyer and Rivault, 2003 Grandcolas, 1991, 1994).

The severe lack of Blattodea taxonomists also results in a lack of modern identification guides. Original descriptions potentially solve this problem but the texts are difficult to find and the descriptions are so poor that using them to identify unknown species is futile. Taxonomists who focus on different orders readily produce regional guides or publications that include updated keys to families and localities. Regional identification guides are essential for identifying species occurring in the area for scientific and pest management purposes. Increasing the number of keys and identification guides will increase the ease and accuracy in the identification of cockroaches.

Surveying species in diverse habitats across a region provides a taxonomic inventory of species present and how they are spatially distributed. Samples from five different sites were used in this study. These sites included the Atchafalaya Basin (AB), and West Feliciana Preserve (FP). Specimens from two different studies were sorted to represent a Louisiana longleaf pine savanna (LLP), Red River Wildlife Management area (RRWMA) and Three Rivers Wildlife Management area (TRWMA).

The purpose of this research study was to:

1) Document species of cockroaches that occur in representive habitats in southern Louisiana.

2) Establish cultures of selected cockroach species to document life cycles and identify diagnostic characters that can be used to identify immature Blattodea.

3) Develop an identification guide to the Louisiana cockroach species.

4) Use the biodiversity analysis program EstimateS (Colwell, 2013) to calculate species richness of Blattodea in Louisiana within each site. Compare diversity species richness and shared species among sites.

CHAPTER 2: LITERATURE REVIEW

2.1 Blattodea

Blattodea is currently the order of insects containing cockroaches and termites. The word Blattodea comes from the latinized Greek name for cockroaches, blátta (Capinera, 2008). The accepted name for the order has gone through a few changes over the years. To date all modern cockroaches are reffered to as either Blattodea or Blattaria. The phylogenetic relationship of the once three separate orders Mantodea, Isoptera, and Blattodea, was examined by Henning and was called Blattopteroidea (Hennig, 1969; Deitz, 2003). Kristensen (1991) grouped Mantodea, Isoptera and Blattodea into the single order Dictyoptera. Several phylogenetic studies on the relationships within the order Dictyoptera have revealed conflicting hypotheses on the relatedness between each order (Klass and Meier, 2006). Dictyoptera was separated into the orders Mantodea, Isoptera and Blattodea (Klass and Meier, 2006; Lo et al., 2007; Pellens et al., 2007; Ware et al., 2008; Grandcolas, 1996; Roth et al., 2009;). Molecular studies suggested that termites were a sister clade to the sub-social wood eating *Cryptocercus* genus and have been included in the order Blattodea, leaving only Blattodea and Mantodea (Inward et al., 2007). While few individuals still use Dictyoptera it is now accepted by most as a superorder that includes Mantodea and Blattodea and is regarded as a highly supported monophyletic clade encompassing termites, cockroaches, and mantids (Kristensen, 1991; Klass, 2003; Klass and Eulitz, 2007).

2.2 Lineages

Cockroaches belong to an ancient lineage of insects that comprised 27 families (Wei and Ren, 2013). Fossil records suggest that dictyopteroids were among the first insects to explode in numbers and diversity during the early Carboniferous period. Cockroaches are among only a few organisms with a fossil record complete enough to reveal the changes in morphology during their 320 million year period of existence. The flat body and foldable wings is hypothesized to allow ancient blattoids to better hide from predators. An extinct lineage of blattoid ancestors known as roachoids dominated the Paleozoic era, with over 1,000 species found so far (Greenwalt and Vidlicka, 2015). The earliest fossilized cockroaches were dated late Carboniferous (Wei and Ren, 2013; Brongniart, 1885; Zhang et al., 2012). During the Mesozoic era several lineages of cockroaches arose possessing similar wing veniation. They possessed derived protruding ovipositors that suggested deposition within soil. This is a contrast to modern cockroaches that produce ootheca (Vršanský, 2008).

The families that dominated the Mesozoic era included the ancient family Blattulidae. This family contained small cockroaches with simple wing venation and short external ovipositors. The family Raphidiomimidae was characterized by an elongated pronotum. Based on the morphology of Raphidiomimidae it was hypothesized to have been an active pursuit predator (Vršanský, 2008). The Umenocoleidae contained beetle like representatives (Vršanský, 2008). Fuziidae is a recently discovered family that possessesed earwig-like cerci (Vršanský, 2009). The Liberblattinidae is hypothesized to be the family in which all Dictyoptera stemmed from (Vršanský, 2008). Modern lineages of cockroaches exploded in diversity after the Cretaceous-Permian boundary (Mitchell, 2013; Vršanský et al., 2002, 2011, 2012, 2013).

With an impressively complete fossil record, extinct cockroaches can be used to address several evolutionary questions such as decreased variability throughout time (Vršanský, 2007). Although separate lineages, known extinct roachoids possessed a vast array of morphological adaptations that include cursorial, fossorial, predatory, saltatorial legs, the first evolution of eusociality and a semiaquatic lifstyle. Vršanský (2010) discovered and described an extinct cockroach; *Sociala perlucida*, hailing from the Mesozoic era. Based on morphological similarities to the termite, *Mastotermes darwiniensis*, he hypothesized that although eusociality did occur in cockroaches first it within a different extinct family separate from termites. This conflicts with Inward's (2007) claims that termites are the sister group to the genus *Cryptocercus.*

2.3 Taxonomic and Morphological Overview

Blattodea currently contains approximately 7570 described species 4641 of which are cockroaches and 2929 are termites (Krishna et al., 2013; Beccaloni, 2014). When compared to the diversity of higher orders such as Coleoptera and Lepidoptera, it is a relatively small order. Although low in species diversity, a large array of ecological niches, behavioral responses and evolved traits are represented. Myrmecophilous, eusocial, aquatic, predatory, troglobitic, and pollinating species are represented (Vishniakova, 1973; Zompro and Fritzsche, 1999; Bohn et al., 2010; Vršanský, 2007, 2010; Vršanský and Chorvat, 2013; Greven and Zwanzig, 2013; Mackeras, 1970; Grandcolas, 1996; Beccaloni, 2014; Roth, 1994).

A wide variety of morphological and reproductive characters are used to distinguish Blattodea at all taxonomic levels. Morphological characteristics are commonly used when describing and identifying males. Reproductive strategies are more commonly used when phylogenetically placing, describing and identifying females. Males have the most diagnostically useful characters and new genera or species should be described based on the male representatives (Roth, 2003c). Some species have been described using female or nymphs but are usually proven to be synonyms *(*Roth, 1985b; Roth, 1995a). A common mistake is missidentifying a nymph of one species as a female of a seperate species. Chopard (1929) described a new genus *Parapolyphaga* based on a nymph when in actuality it was an immature of species within the already described genus *Ergaula* (Princis, 1963; Roth, 2003c). The lack of a unifying phylogeny produces many characters that are highly important within a few genera, are absent in related genera, but are present in distantly related genera. Several character types have been used in keys, some requiring dissection such as the key by McKittrick (1964), who used both female and male genitalia to distinguish three subfamilies. Keys by Princis (1960) and Bei-Bienko (1950) rely on external morphological characters. One major problem in cockroach taxonomy is the difficult task of describing or even identifying cockroach juveniles. Unidentified cockroach nymphs can make up a huge bulk of specimens in a collection.

An important external morphological characters used for identifying species of Blattodea is the arrangements of the anteroventral spines on the front ventral surface of the femora. The arrangement of these spines has been classified into four distinct types (Roth, 2003c). Type A is described as a row of stout or "heavy" spines that decrease gradually in size distad, terminating in 2 or 3, rarely 5 large spines members of superfamily Blattoidae typically exhibit this pattern. The arrangement classified as Type B is defined by the presence one or more proximal stout spines succeeded by a row of piliform spinules of uniform length, terminating in 2 or 3 large spines. Common genera exhibiting this arrangement include *Ischnoptera* and *Parcoblatta.* Some

species show intermediates between type A and B possess a few piliform spinules interspersed among the stout spines. The Type C spine arrangement is characterized by a lack of stout proximal spines but possessing a row of piliform spinules only, terminating in 1 or 2 stout spines. The last type of femur spine arrangement is, Type D is defined as lacking stout proximal spines and piliform spinules and possessing, with 1 or 2 stout terminal spines, possibly with a uniform row of slender seta-form setae or "hairs" (Roth, 2003c). The arrangement of femoral spines is useful in genus and species classification in the family Blattellidae. Recent taxonomic papers have broadened the number of spines characters accurate in classifying leg spinal arrangement. In addition to the anteroventral femur spines being listed, the number of spines on the anteroventral and postero-ventral edge of the front middle and hind femur, presence and number of genicular spines on each femur, and number of dorsal, distal and ventral tibia spines is recorded along with the number of tarsi possessing puvilli. The number is entered into a formula and used to precisely characterize leg spine type.

Other leg characters such as presence or absence of puvili on one or multiple tarsi are used to distinguish several genera. The presence, absence or number of tarsi that contain puvilli can be used as defining character in some genera. The genus *Allacta* has puvilli only on the fourth tarsomere of every leg. While useful in some genera they are of minor taxonomic importance in other genera such *Tryonicus,* and *Neostylopyga* (Roth, 1988, 1990a, 1991d, 2003c; Princis, 1974). Tarsal claws are a useful character at multiple levels of taxonomic classification. Tarsal claws are classified as the following types. Simple, symmetrical: with both claws being nearly if not the same size and not serrated. A genus exhibiting this tarsal claw type is *Blattella.* Simple, asymmetrical: one of the tarsal claws is distinctly shorter than the other. Specialized, symmetrical: both claws being the being nearly if not the exact same size with the ventral or internal margin toothed or serrated. The degree and size of the serrations varies and a species may have teeth that are distinct, reduced, sub obsolete, or absent. An even more unique tarsal form is the presence of only one tarsal claw (Shelford, 1911; Chopard, 1929; Bey-Bienko, 1950; Princis, 1962, 1971; Grandcolas, 1994a; Roth, 2003c).

2.4 Morphology

The majority of species of Blattodea are broad flat ovate insects with a large shield-like pronotum that may cover the head. The typical flattened body type is common among cryptic crevice dwelling species, and is variably modified in some taxa and taken to extremes in others. The head is hypognathous with chewing mouthparts. If present and large enough, the wings are folded flat across the abdomen with the forewings (tegmina) slightly overlapping each other. The hindwings are complexly folded radially and transversely with the anal lobe resting under the anterior part of the hindwing. The result is both wings resting flat on abdomen complementing the cockroach's already flat body (Brodsky, 1994).

Cockroaches capable of flight have wings that cover all thoracic and abdominal tergites. The tegmina are slightly sclerotized, with the hindwings being more membranous. Many species of cockroaches show wing reduction or complete loss in one or both sexes. The degree of reduction of the wings varies throughout the order, ranging from fully winged cockroaches capable of flight to species without wings. The sclerotization of the tegmina can be reduced resulting a clear and membranous tegmina, or show heavy sclerotization somewhat resembleing the elytra of Coleoptera. The legs of cockroaches are typically cursorial with the coxa modified to harbor the femur. Leg shape can range from legs modified for maximum speed and agility to

slow moving burrowers that maximize strength and power. The abdomen contains 11 segments. All Blattodea possess two sensory structures called cerci that can vary in size and number of segments. The abdomens of males in the majority of families' posessess modified segment or segments bearing tergal glands that are importatant in the mating process. Tergal glands are rare within the families Polyphagidae and Blaberidae, with only a few genera possessing them (Roth, 1969; Brossut and Roth, 1977). Females typically lack any modified structures on the abdomen but can secrete sex pheromones that attract males (Roth and Willis, 1952a).

2.4.1 Pronotum

The pronotum is the extended dorsal portion of the first thoracic segment. The size of the pronotum can vary, ranging from large enough to entirely cover the head or reduced enough to leave the head exposed. The pronotum can come in a wide variety of shapes that can manifest in startling modifications. Pronota can come in the shovel like shapes or be equipped with horn-like projections that are used in courtship battles (Van Herrewege, 1973; Beccaloni, 1989). Pronotal shapes can vary widely within species and be sexually dimorphic. In addition to being a versatile weapon and tool, the pronotum of certain species can also be used to aid in communication between individuals. See Bell et al., (2007) and Roth, (1960) for more detail.

2.4.2 Leg

Cockroaches are documented to have impressive speed and agility. The insect leg type adapted for running is referred to as cursorial. *Periplaneta americana* is a common household pest, and relative to its mass, one of the fastest invertebrates ever studied, covering 50 body lengths per second (Full and Tu, 1991). The notorious speed and cursorial leg type of cockroaches are so closely associated with cockroaches that they were once placed in a sub-order Cursoria (Blatchley, 1920). Some have taken speed to an extreme, with light, aerodynamic body forms with long legs that maximize speed and agility. Others are specialized for power with modified pro-tibia used for digging (Park, 1990; Tepper, 1894). The muscles in the legs of cockroaches are no different than any running insect but do differ in their orientation. The articulation is notably more ventral. The second and third pair of legs is directed backward in a slanted fashion giving many members of this order a high degree of agility. Many species are able to start and stop running quickly, and change direction almost instantaneously (Hughes, 1952; Full and Tu, 1991).

The tarsi of cockroaches consist of five tarsomeres that may or maynot possess pulvilli and an arolium (Arnold, 1974). Both the arolium and the pulvilli are elastic and can stretch or retract to maximize or minimize contact with the surface. Biological pressures that cause a reduction or loss of adhesive structures are unknown. Reduction or loss of adhesive structures is common in cave dwelling species. See Bell et al., (2007) for more details on cockroach puvilli and arolium.

2.4.3 Abdominal Tergites and Modifications

Abdominal shape, size, along with the presence or absence of glands are important when describing and identifying cockroaches. The abdomen of Blattodea contains 11 segments that end in a supra-anal and sub-anal plate that harbor the genitalia. Two cerci arise from the 11th segment with their bases located under the posterior end of abdominal segment 10 (Klass, 1997).

The number of cercal segments along with shape and length are important characters used at all taxonomic levels. In addition to the eyes and antenna, the cerci serve as sensory structures that detect shifts in the surrounding air. A shift in the surrounding air causes *Periplaneta americana* to move with the direction of the airflow and away from the source of the air disturbance (Camhi et al., 1978).

All families of cockroaches have representatives in which the males' posses modified tergites that are essential in mating. The presence, location, and shape of the tergal glands are valuable characters. Because tergal glands are often different among genera and species, they can be useful in identification (Brossut and Roth, 1977; Bohn, 1993). Tergal glands serve to lure the female into a mating position. The tergites of females are generally unmodified, but are capable of secreting sexual pheromones that attract males in the surrounding area. Tergal glands secrete a mixture of short-range volatiles and non-volatiles comprised of proteins, lipids, and carbohydrates comprised proteins, lipids, and carbohydrates (Brossut et al., 1975; Korchi et al., 1999). Morphologically they can range from highly elaborate structures to sub-cuticular structures that appear absent. Tergal glands can appear as both shallow and deep depressions that possess ridges or projections that can contain setae, hairs, or bristles along with fleshy protuberances. Even tergal glands with no clear structure on the tergite may have sub-cuticular glands that secrete both the volatiles and non-volatiles (Roth, 1969; Brossut and Roth, 1977). Tergal glands are rare in Polyphagidae and Blaberidae. The family Ectobiidae contains the most diverse and complex array of tergal glands, the structure of which can be of taxonomic significance (Brossut and Roth, 1977; Bohn, 1993). Within the family Ectobiidae, the tergal glands typically occur on the first, second, or seventh tergite, but many genera such as *Parcoblatta* have tergal glands on multiple tergites, or can lack visible tergal glands (Hebard, 1917; Roth, 1969; Brossut and Roth, 1977).

Some tergal glands function to keep the female feeding as long as possible. In *B. germanica* adults, the eighth tergite possesses a larger tergal gland that connectes to the primary tergal gland on the seventh tergite. Once feeding on the eighth tergite, a flex of the abdomen puts the seventh tergite into a position to divert the female's attention. The seventh tergite is much smaller and secretes more concentrated attractant than the eighth. Only the female's paraglossa can fit, and this requires more time to feed on the tergal gland. This strategy maximizes the time in which the female is in a pre-mating position while minimizing the amount of attractant the male needs to produce (Nojima et al., 1999). The tergal gland of many species within the genus *Ischnoptera* contains two claws on each side of the tergal gland (Roth, 1969; Brossut and Roth, 1977). Adults of *Cryptocercus punctulatus* have tergal glands located on the eighth tergite and entirely concealed beneath an expanded seventh tergite, a location unsuited to position a female in an effective mating position (Farine et al., 1989).

Abdominal sclerotization can also be a useful character. Hebert (1916) used the degree of sclerotization along with the shape of the male supra-anal plate to determine species relatedness within various genera. The subgenital plate is a useful character within the subfamily Ecobiinae. The size of the apodeme and presence of one or two styli are key characteristics of the taxon (Roth, 1992b; Bohn, 1999).

2.4.4 Tegmina and hind wings

Cockroaches that are capable of flight have two fully developed wings that extend to, or beyond the apex of the abdomen. The forewing when present is usually sclerotized. The hind wing is membranous with less sclerotization. When folded, the anal lobe of the hind wing rests

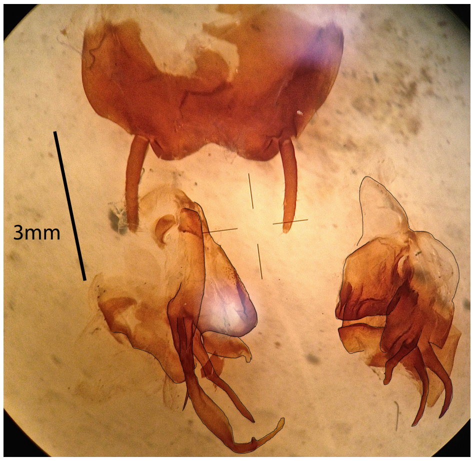
beneath the anterior portion of the hind wing. This is achieved by apical rolling, folding along several apical lines as in a fan, or along eight single fold lines as in the family Corydiidae. In beetle-like cockroaches, the wings can be folded in half before folding along the apical lines, resulting in the protection of a hind wing, which is substantially longer than the tegmina (Fisk and Wolda, 1979; Shelford, 1912a; Roth, 1994). Patterns of wing folding, together with other wing characters, can be useful in cockroach classification (Rehn, 1951; Haas and Wootton, 1996; Haas and Kukalova-Peck, 2001).

The principal form of propulsion for cockroaches capable of flight comes from the hind wings (Brodsky, 1994). The tegmen is an integral component of flight among basal cockroaches while more derived species don't rely on the tegmina as much (Rehn, 1951). During a flight, airflow induces bending of the cerci, which serves as a feedback in regulating wing beat frequency (Lieberstat and Camhi, 1988, as cited in Bell et al., 2007). Flight ability within taxa can vary. There are numerous examples of weak fliers that struggle to maintain flight. Several species are known to be strong fliers. Active flying cockroaches have been documented flying in a strong forward trajectory while increasing altitude, as well as dodging predators mid-flight (Farnsworth, 1972). While many species do retain both wings, many cannot fly. Tegmina and hind wings can also serve as tools in territorial or sexual signaling; males in several species flutter their wings during courtship. They can also serve as physical protection for the abdomen and tergal glands. Tegmina are documented to provide visual defense from enemies via camouflage, mimicry and, in rare cases, as a shelter for early instars (Shelford, 1912a; Reuben, 1988; Roth and Willis, 1954b; Roth, 2003a; Shelford, 1906b; Pruthi, 1933). Factors that cause insects with wings to be strong fliers have been the focus of numerous studies. See Kramer, (1956) and Stokes et al., (1994) for summarazaiton of studies.

2.5 Genitalia

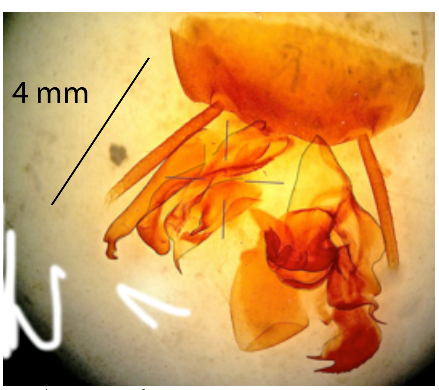
The superorder Dictyoptera contains two orders, Mantodea, and Blattodea. While other morphological differences exist, one significant difference between the two orders is the lack of a genital hook in all species of Mantodea (Klass, 1997). The genitalia and reproductive behaviors of the superorder Dictyoptera are one of the most studied aspects of their biology. The genitalia of Blattodea are used as examples of the complexity of insect genitalia. The genitalia of the superorder Dictyoptera is composed of a complicated asymmetrical mechanism comprised of three primary phallomeres, which can be composed of independently articulating lesser phallomeres (Klass, 1997). These phallomeres sport a vast array of articulating hooks, spikes, pouches, grooves, and tongs that can be distinctly different or nearly identical when comparing closely relates species (Gwynne, 1998). Members of the families Blattidae and Polyphagidae possess more complex phallomere structure than Ectobiidae and Blaberidae (McKittrick, 1964).

The shape and orientation of these phallomeres are important in identifying species, and are used as characters in new species descriptions. Species within the genus *Periplaneta* are readily distinguishable based on phallomeres Plate. 1.1. Species within *Parcoblatta* possess similar phallomeres Plate. 1.1.The orientation of the genital hook is an important taxonomic and phylogenetic character. In posterior view, the genital hook is located on the left side of the genital pouch in the basal superfamilies Corydioidea and Blattoidea Plate. 1.2. Within the superfamily Blaberoidea the genital hook is also located on the left side within the basal subfamilies Blattellinae and Ectobiinae Plate 1.2, Members of the subfamily Pseudophyllodromiinae and the family Blaberidae are unique in having the genital hook located on the right side (McKittrick, 1964) Plate. 1.2. The structure of the phallomere is used to

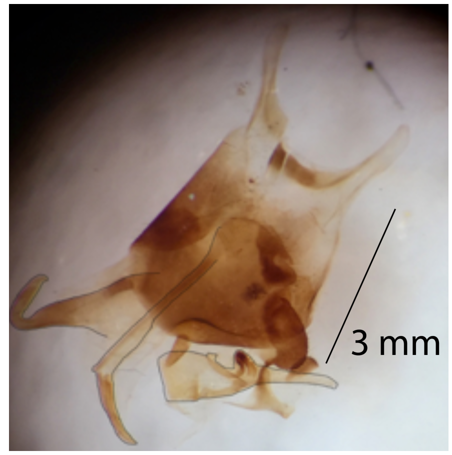


A) *Periplaneta fuliginosa*

B) *Periplaneta brunnea*

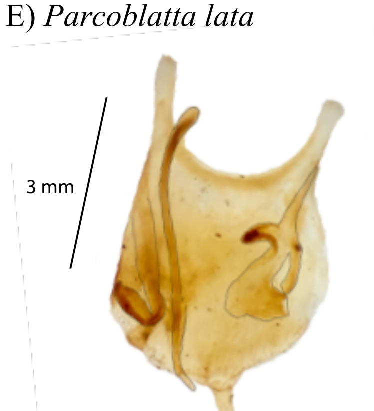


C) *Periplaneta americana*



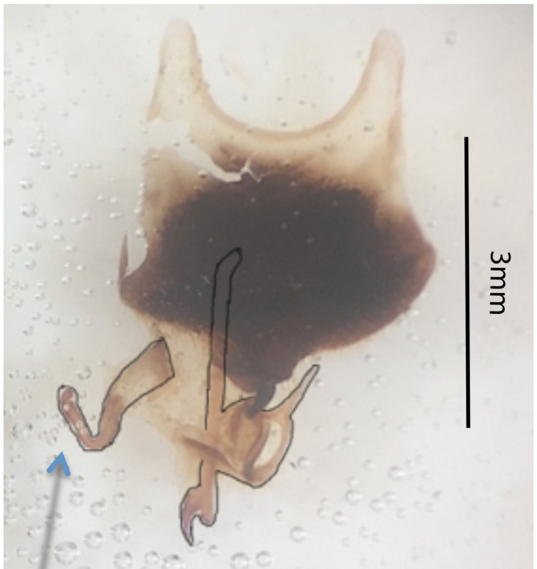
D) *Parcoblatta pennsylvanica*

E) *Parcoblatta lata*



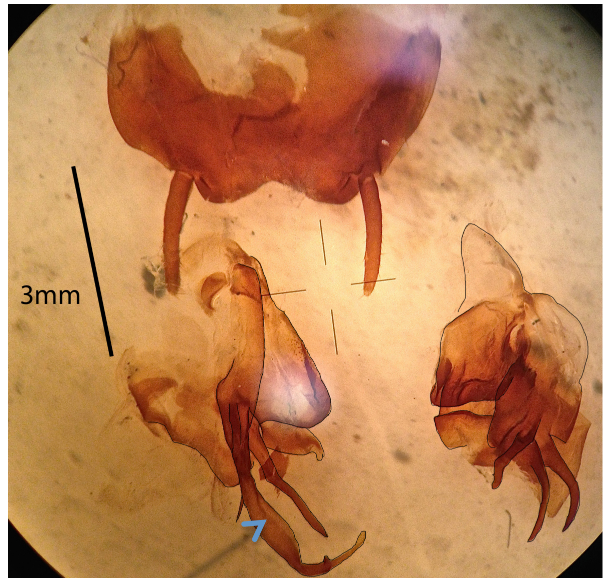
F) *Parcoblatta uhleriana*

Plate. 1.1 Male Phalomeres A) *Periplaneta fuliginosa* genitalia. B) *Periplaneta brunnea* genitalia. C) *Periplaneta americana.* genitalia. D) *Parcoblatta pennsylvanica.* genitalia E) *Parcoblatta lata* genitalia F) *Parcoblatta uhleriana* genitalia. Phallomeres outlined using photoshop.



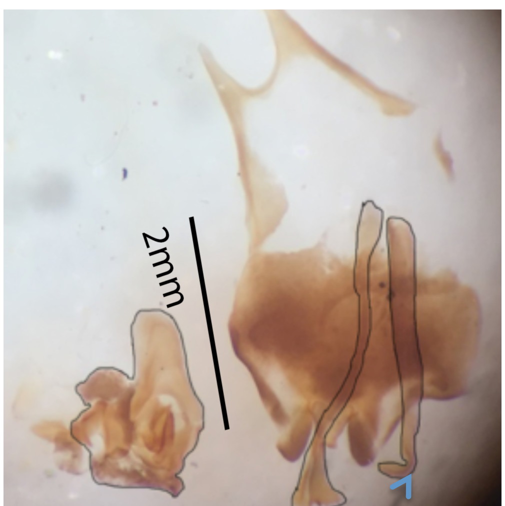
A) *Ischnoptera deropeltiformis*

Genital Hook Sclerite L3 (hla)



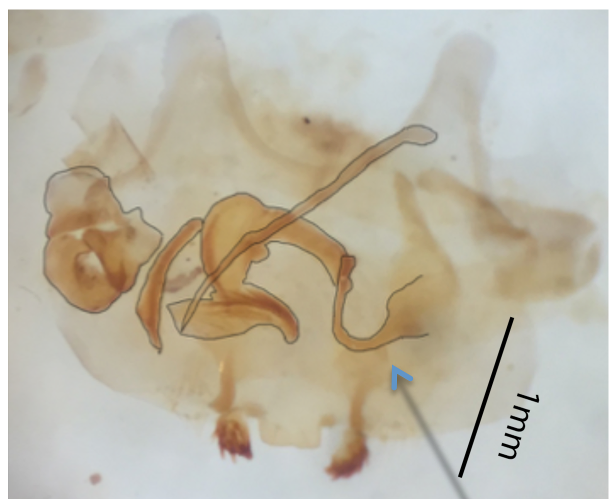
B) *Periplaneta fuliginosa*

Genital Hook Sclerite L3 (hla)



C) *Chorisoneura texensis*

Genital Hook Sclerite L3 (hla)



D) *Cariblatta lutea*

Genital Hook Sclerite L3’ (hla)

Plate 1.2- Male Genital Hooks A) and B) family Blattidae and subfamily Blattellinae (Ectobiidae) with genital hook (hla) on left side C) and D) Subfamily Pseudophyllodromiinae (Ectobiidae) with genital hook (hla) on right side. Phallomeres outlined using photoshop.

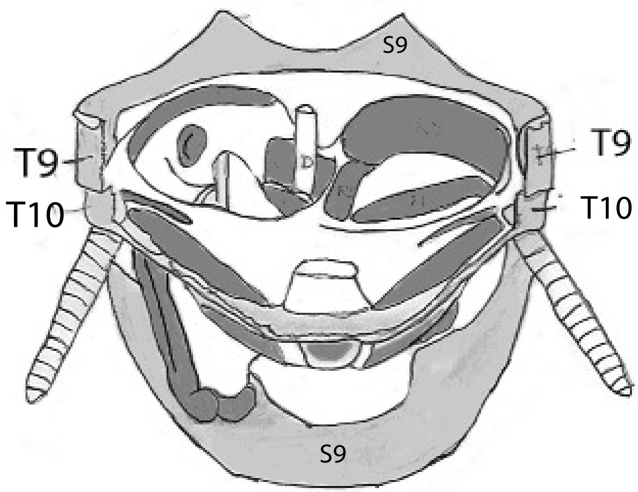
distinguish not only families but species groups within genera (Klass, 1997; Roth, 1970b) One example of genitalia being used to group species within genera is the L2 phallomere within the genus Blaberus. The presence of a curving L2D phallomere and a tumor like growth at the connection of L2vm and L2D is common between *Blaberus gigantus* and *B. cranifer* and are placed in the Gigantus species group. A curving L2D phallomere and the lack of a tumor-like growth is common between *B. colosseus*, *B. brasilianus*, *B. fusiformis*, *B. scutatus*, and *B. minor* are within the Brasilianus species group (Roth, 1970b).

The phallomere complex is located within a genital pouch beginning at abdominal segment 9, and extending to the apex of the abdomen (Klass, 1997; McKittrik, 1964). The ejaculatory duct opens into the genital pouch with the phallomeres invaginating around the genital opening Plate.1.3. The phallomere complex is always asymmetrical, showing variability within Mantodea, and extreme variability within Blattodea. The genitalia contain many distinct areas of sclerotization, invaginations xthat vary at multiple taxon levels (Klass, 1997; McKittrik, 1964). The genitalia of Matodea differ from Blattodea primarily by the lack of phallomere (L3/hla), which is modified into a genital hook. The genital hook within the Blattodea is hypothesized to be the result of a derived copulation procedure (Snodgrass, 1937; Levereault, 1938; LaGreca& Rainone, 1949; La Greca, 1954; McKittrik, 1964).

The phallomeres of the Blattodea are used to hold and maneuver the female genitalia. McKittrick (1964) described the sclerites of 24 genera of Blattaria and attempted to homologize the genitalia of Blattaria. Due to the lack of detail and musculature in her descriptions, the homology is not well supported (McKittrik, 1964; Klass, 1997; Grandcolas, 1994). McKittrik (1964) terminology is the basis in which Bohn (1987) and Klass (1997) derived their terminology, which differs from McKittrik slightly. Bohn (1987) and Klass (1997) used different nomecladure for side-reversed phallomeres. Both provide detailed explanations in their nomenclatural changes, and all three are accepted as correct nomenclature if stated by the author.

McKittrick's terminology is a derived version of Snodgras's, (1936, 1937) that revolved around three main types of sclerites. Snodgrass, (1936, 1937) classified the phallomere complex into left right and ventral phallomers. Klass (1997) and McKittrik (1964) redefines the phallomere complex into the left (L) and right (R) phallomere complex. The ventral phallomere is closely associated with the ventral lobe (vla) and was redefined as the L2 sclerite (Klass, 1997). McKittrick (1964) used the genitalia of *Cryptocercus punctulatus* as the reference to her terminology due to its relative simplicity and phylogenetic position within the basal superfamily Blattoidea (Klass, 1997). Klass (1997) is the most modern revision of genitalia, and the terminology is as follows: terms used to describe a specific sclerite will have three characters to describe its location.

First the capital letter L or R will be used to dictate whether the sclerite in reference is located on the left or right primary phallomere. A number ranging from 1-5 will follow and be used to distinguish what the main sclerite is being referenced. A capital letter after the number will show what individual sclerite of the main sclerite is being referenced. A small letter following the number is in reference to the position on the main sclerite. The genitalia of *Parcoblatta lata* and *Periplaneta fuliginosa* with examples of terminology can be seen in Plate. 1.4. Members within sub-family Pseudophyllodromiinae and family Blaberidae are examples of taxa within Blattodea that show side reversed phallomeres. The genital hook of this family and subfamily is located on the right side of the genital pouch rather then the left (Bohn, 1987). Terminology for phallomeres that are side-reversed are labeled as mirror images of themselves



A) Genital pouch tergites removed

B) Genital pouch tergites present

Plate. 1.3- Genital Pouch of Blattodea A) Genital pouch shown with tergites removed, sclerotized areas are grey, membranous portions white. B) Genital pouch shown with tergites present, sclerotized areas grey, membranous portions white. Images modified from Klass (1997)

but with the addition of a (‘) either after the letter indicating the side as in Bohn (1987) or after the entire label as in Klass (1997). For example the main sclerite that comprises the genital hook (hla) of a *Parcoblatta lata* is labeled L3. The genital hook of *Blaberus craniifer* is located on the right side but labeled L3’ (Bohn, 1987; Klass, 1997) Plate. 1.4,. The sclerites comprising the surrounding abdominal segments are designate, S: sternite, T: tergite, and E: a sclerotized appendage. Common derivations of internal abdominal segments are abbreviated. One example being the hook like sclerotization on the S10 called the paraprocts (Pp) (Klass, 1997). Membranous structures are designated with the first two letters being arbitrary abbreviations; which are always defined in terminology. The lobe or fold with the orientation of the membrane being designated as a: evaginating, or e: invagination (Klass, 1997).

The genitalia of Blattodea have several main sclerites that make up the main structures of the genitalia. The left phallomere complex contains the primary sclerites L1, L2, L3, and L4. The L1 sclerite can vary in shape or be absent but when present is located as the sclerotized wall of the dorsal pouch (pne) in which the phallomere glands (P) opens. Sclerite L2 is located within the ventral pouch (lve) and is surrounded by the ventral lobe (vla) and in many but not all cases elongate and spear-like Plate. 1.4. Except the families showing side-reversed phallomeres the genital hook is comprised of sclerite L3 and is labeled (hla). The presence of heavily sclerotized genitalia is more prominent within superfamilies' Blattoidea and Corydioidea. The sclerites are typically present with little to no reduction and clearly visible Plate. 1.4. The reduction of sclerites within the superfamily Blaberoidea is common with some groups losing entire sclerites Plate. 1.4.

The right phallomere complex contains sclerites numbering from 1-3. Numbers are assigned based on dorsal-ventral orientation with R1 being the most dorsal and R3 being most ventral (McKittrick, 1964). R3 is a plate-like sclerite that occupies the most anterior right ventral wall of the genital pouch Sclerite R2 in all Blattodea is located left ventrally to a membrane that forms a central buldge **(**cbe**)** and articulates with the left posterior end of the R3 sclerite (Klass, 1997; McKittrick, 1964). R2 and the posterior margin of R1 typical form a toothed ridge of invitations FIG (Klass, 1997). This sclerite shows significant modification and its shape can vary between families. Identification of the sclerite is based primarily on its location in relation to the other two sclerites and the cbe bulge. Sclerite R1 is the most dorsally oriented sclerite that has shifted medially in the Polyphagidae. Nearly all species within Ectobiidae show a reduction or complete loss of R1. All species within Blaberidae show an absence of the R1 sclerite (McKittrick, 1964).

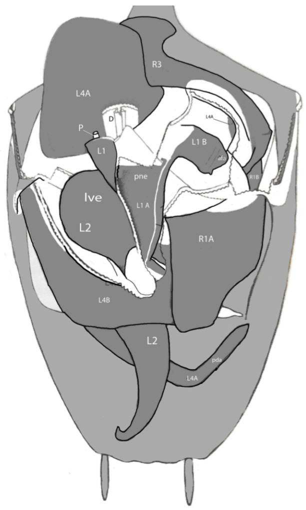
2.5.1 Spermatophore /Sperm

All male cockroaches transfer sperm to the female via spermatophores. The spermatophore is not formed until after the male and female are securely attached in the mating position (Khalifa, 1950; van Wyk, 1952; Roth, 2003a). Once attached the spermatophore descends the ejaculatory duct and is pressed against the female genital sclerites by the male's endophallus. The time it takes to inject the spermatophore varies from species to species with some species taking only 10 minutes and others taking up to an hour (Roth, 1964b; Gupta, 1947). While injecting the spermatophore the male orientates the opening of the sperm sack with the spermathecal pores of the female (Khalifa, 1950; Roth and Willis, 1954b; Gupta and Smith, 1969). According to Gillott (2003), this is not a common phenomenon among insects. The orientation of the spermatophore inside the female differs between taxa. Spermataphore shape size and orientation are summarized in Graves (1969). The orientation of the spermatophore inside the female differs between taxa. Spermataphore shape size and orientation are summarized in Graves (1969).

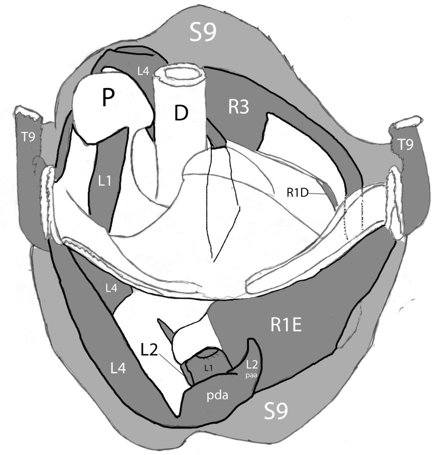
2.5.2 Female genitalia

Female genitalia can be used to differentiate species, but due to lack of study of the female genitalia the taxonomic relevance is limited. Other major taxonomic and phylogenetic characters are the reproductive method and ootheca orientation of females (McKittrick, 1964; Roth, 2003a).

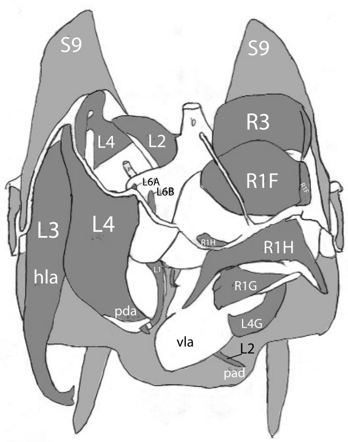
Plate 1.4-A) *Sphodromantis* sp., L1A: Sclerite A of main L1 sclerite, pne: process anterior pouch, L1 B: Sclerite B of main L1 sclerite, afa; apofisia folding anterior process, L2: Main L2 sclerite, lve: lamina ventral pouch, L4 A: Sclerite A of main L4 sclerite, pda; Process dorsal articulation, L4B: Portion B of main L4 Sclerite. R1A: Sclerite A of main R1 sclerite, R1B; Sclerite B of main R1 sclerite, R3: Main R3 sclerite, P; Phallomere gland, D: Ejaculatory duct. B) *Mantoida schraderi*, L1; main L1 sclerite, L2; main L2 sclerite, paa: apical articulating process, L4; Main L4 sclerite, pda; distal articulation process, R1D; Sclerite D of main R1 sclerite. R1E; Sclerite E of main R1 sclerite, R3; Main R3 Sclerite, P; Phallomere gland, D: Ejaculatory duct. Modified from Klass (1997) C) *Eurycotis floridana*, L1; Main L1 sclerite, L2; Main L2 sclerite. paa; apical articulating process, L3: Main L3 sclerite, hla; genital hook left, L4; Main L4 sclerite, pda; distal articulating process. L6A; Sclerite A of main L6 sclerite, L6B; Sclertie B of main L6 sclerite. Modified from Klass (1997) D) *Periplaneta fuliginosa* L1; Main L1 sclertie, L2A; Sclerite A of main L2 sclertie, L2B, Sclerite B of main L2 Sclerite, pda; distal articulating process, L3; Main L3 sclerite, hla; genital hook left, R1A; Sclerite A of main R1 sclerite, R1B; Sclerite B of main R1 sclerite, R2; Main R2 sclerite, R3; Main R3 sclerite. Modified from Takayuki (1987) E) *Parcoblatta lata,* L2: Main L2 sclerite*,* vla; ventral lobe, L3; Main L3 sclerite, hla; genital hook left, L4V; Sclerite V or main L4 sclertie, R1P; Sclerties P of main R1 sclerite, dla; dorsal lobe, fda; dorsal fallomere lobe, R1S; Sclerite 2 of main R1 sclerite, R2; Main R2 sclerite, Sclerites R1S and R2 make up what is referred to as cleft sclerite, pva; Ventrally articulating toothed process, R3; Main R3 sclerite. Modified from Klass (1997) F) *Blaberus craniifer,* L2' Main side reversed L2 sclerite, vla; ventral lobe, lve; ventral pouch, L3'; Main side reversed L3 sclerite, hla; genital hook, L4U'; Sclerite U from main side reversed L4 sclerite, R1S'; Sclerite S from main side reversed R1 sclerite, R2'; Main side reversed R2 sclerite, R3' Main side reversed R3 sclerite, R4'; Main side reversed R4 sclerite. Modified from Klass (1997)



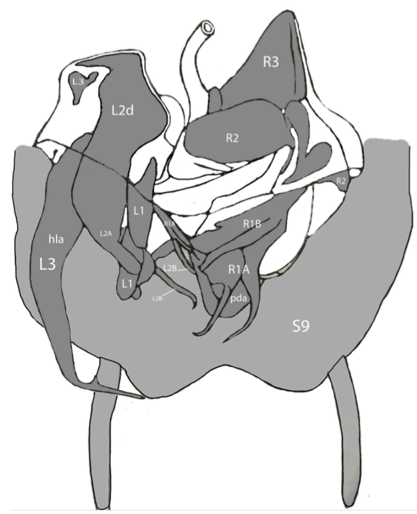
A) *Sphodromantis* sp.



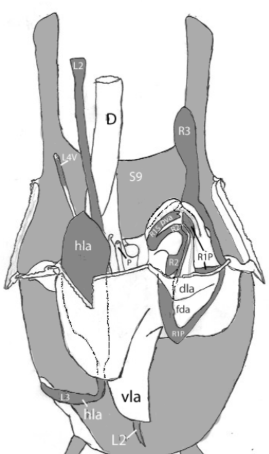
B) *Mantoida schraderi*



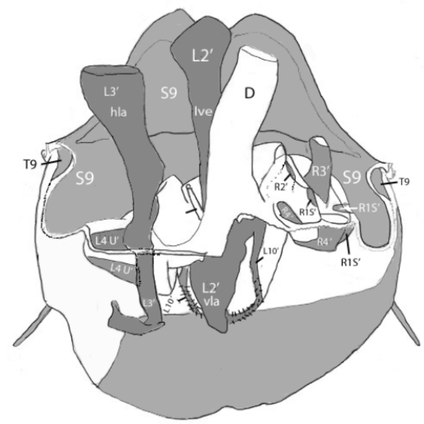
C) *Eurycotis floridana*



D) *Periplaneta fuliginosa*



E) *Parcoblatta lata*



F) *Blaberus craniifer*

For full text on analysis of female genitalia see McKittrick (1964). The genital pouch of female cockroaches is composed of a posteriorly expanded seventh sternite that contains the reproductive tract of the female cockroaches, called the spermatheca (McKittrick, 1964). The pouch is divided into two distinct chambers. The larger posterior chamber is referred to as the vestibulum and produces the ootheca. The roof of this genital pouch is a rigid framework comprised of three genital sclerites of the eighth and ninth tergites. The tergites are joined to the lateralsternal shelf by a band of membranes. These sclerites support the ovipositor valvulae, which are responsible for moving and orientating the eggs and sperm (McKittrick, 1964). A pair of colleterial glands is located within the vestibulum and secretes two separate compounds that harden into the ootheca (Pryor, 1940; McKittrick, 1964). The floor is membranous with the lateral membranes expanded and folded intestinally that expand dorsally embracing the ovipositor valves. The smaller anterior located genital chamber supports the oviduct and contains the spermatheca. The floor of the genital chamber is slightly above the vestibulum roof and is a complex of sclerites that support the slit that is the opening of the oviduct (McKittrick, 1964) Plate. 1.5.

The primary purpose of the spermatheca is to receive and store sperm acquired during mating until fertilization occurs. The size and shape of spermatheca is explained in more detail in McKittrick (1964) and later Bell et al., (2007).

Female cockroahces with multiple spermathecal lobes results in the female possessing multiple storage sites for received sperm. This offers the potential to separate the sperm from different males spatially. Spatial separation of sperm along with the presence of muscular valves and sphincters results in the ability to choose among potential sires and control time of fertilization and oviposition (Eberhard, 1996; Ward, 1993; Hellriegel and Ward, 1998). The form of differentiation and separation of the sperm can come in the form of transport to storage sites, biased sperm survival in different spermathecal lobes, or differential transport from storage to the site of fertilization (Van Wyk, 1952; Marks and Lawson, 1962).

The primary purpose of spermathecal glands is to provide nutrients to the sperm being stored in the spermatheca. The male provides the initial nutrients needed to promote sperm health, while long-term nutrition being supplied by the female (Vijayalekshmi and Adiyodi, 1973). Possessing long-term sperm storage allows females to produce continually ootheca for extended periods of time without the need to re-mate (Griffiths and Tauber, 1942; Cochran, 1986).

2.6 Reproduction

Members of the superfamilies' Blattoidea and Blaberoidea typify the two main reproductive methods in Blattodea (McKittrick, 1964). In Blattoidea, the reproductive method is exemplified by the formation of a hard egg-bearing case called an ootheca. Fertilized eggs are moved down the oviducts and arranged in two rows by the ovipositor valves. The eggs are then covered with a substance that hardens, becoming the ootheca. After complete the ootheca is then dropped. Females within the superfamily Blaberoidea retain the egg case for the entire period of gestation as in the family Ectobiidae, and others that incubate egg cases internally, as in the family Blaberidae (Roth, 2003c Klass, 1997, 2001). The formation of a hard protective egg case is the most obvious method when one thinks of cockroach reproduction. In reality, reproductive strategies of cockroaches can vary and are important diagnostic characters used to separate families. Due to the complexity of reproduction it is assumed that the phylogenetic development of the reproductive process of Blattodea is an irreversible unidirectional trend from oviparity

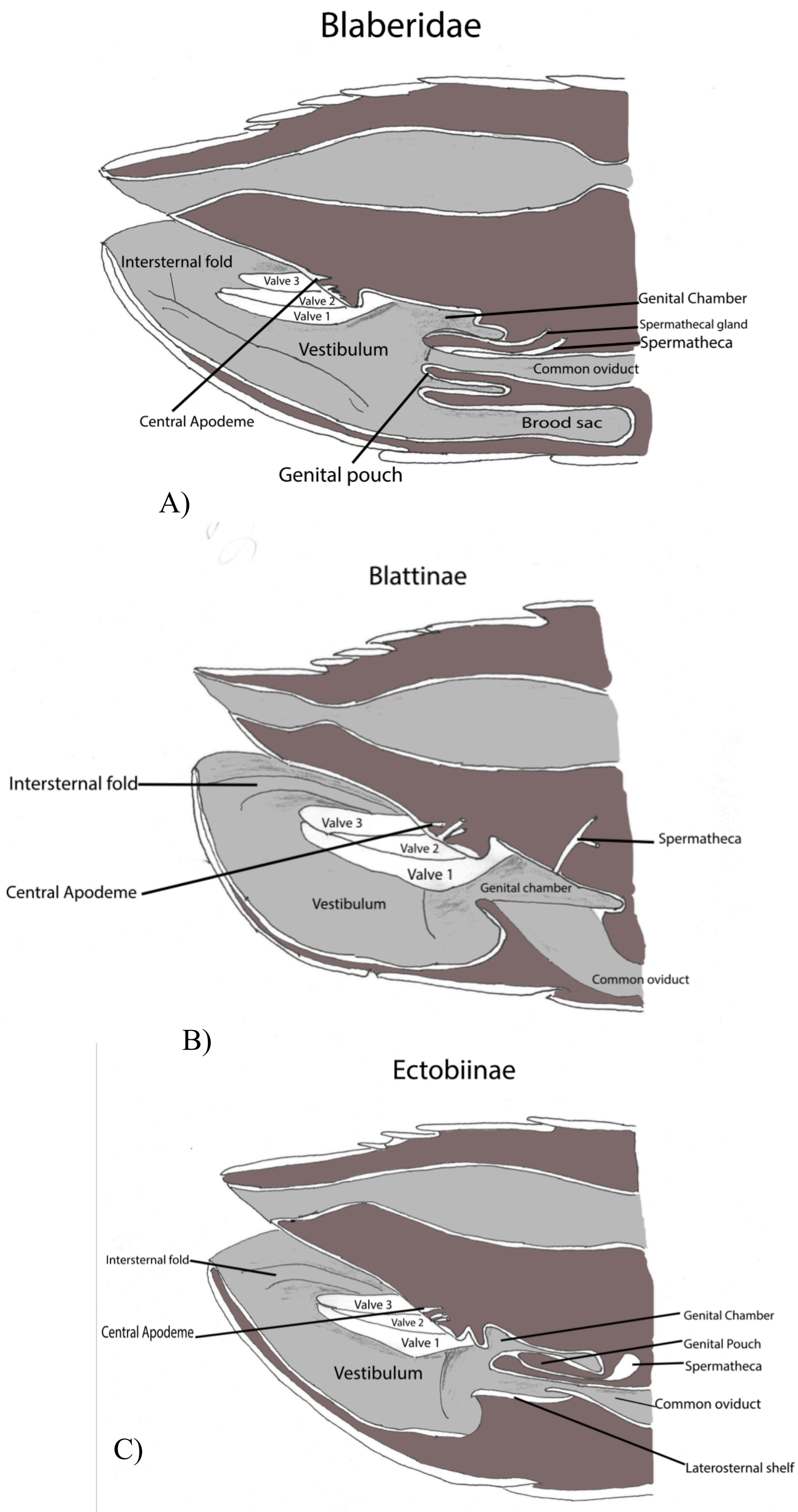


Plate 1.5- A) Blaberidae B) BlattinaeC)-Reproducive chamber of Ectobiidae.

to viviparity (Tinkle and Gibbons, 1977; Crespi and Semeniuk, 2004; as cited in Bell et al., 2007). The initial step from oviparity to viviparity is hypothesized to have initiated when species began waiting to drop their ootheca in a suitable microclimates (Roth, 1989a; Roth and Willis, 1955b). Oothecae are taller than wide, so a rotated ootheca becomes flat like the cockroaches' natural body shape and can fit into a broader variety of places (Roth, 1968a, 1989a). Female *Blatella germanica* carrying a rotated ootheca were found to be capable of traversing smaller crevices than *B. germanica* that had yet to rotated their ootheca (Wille, 1920). The retention of the ootheca eventually led to females providing water and nutrients to the ootheca and halting oogenesis, as seen in *B. germanica*. With the retention and retracting of the ootheca along with the halting of oogenesis, the transition to ovoviviparity would be minor. Ovoviviparity is thought to have evolved in Blaberoidea two or three times, with the most derived outcome being the loss of an ootheca and the further transition to viviparity (Guillette, 1989; Roth, 1970a, 1982, 1989). The two most common types of reproductive strategies seen in Blattodea are oviparity and ovoviviparity.

2.6.1 Oviparity

Oviparity is further classified into two main types. In type A oviparity the female cockroach produces two rows of eggs that are encased in a protective hard shell called an ootheca. The mother provides no further nutrients, and the ootheca is typically dropped after completion. In type B oviparity, the female carries the ootheca externally throughout embryonic development. The proximal end of the ootheca remains within the cockroach and allows for transport of water and nutrients to the eggs through a permeable membrane (Mullins et al., 2002; Roth and Willis, 1955b, 1955c; Willis et al., 1958). Carrying the ootheca throughout the embryos' development allows the cockroach to control how much water and water soluble substances are passed to the developing eggs (Mullins et al., 2002; Ross and Mullins, 1995). The ootheca is typically dropped shortly before it hatches and is seen in the subfamilies Blattellinae and Pseudophyllodromiinae. Both types of oviparity are further described in Bell et al. (2007).

2.6.2 Ovoviviparity and Parthenogenesis

Ovoviviparity is also classified into A and B types. In type A ovoviviparity, the ootheca is developed and extruded as in oviparous taxa but is eventually retracted into the brood sack. The brood sac nymphs rely on the embryonic fluid as nutrition. When nymphs are ready to hatch the ootheca is extruded and the nymphs emerge. In Type B ovoviviparity the eggs are deposited directly in a cluster from the oviducts into the brood sac and no ootheca is produced.

Although no true ootheca is produced, females of the genus *Parapanesthia* were shown to produce an intermediate ootheca that holds the eggs in rows within a thin membrane (Rugg and Rose, 1984a, 1984b). Pregnant females are thought only to provide water to the developing eggs with the primary source of nutrition coming from the yolk (Roth and Willis, 1955b; Roth, 1970a) Plate. 1.6. Both types of ovoviparity are further described in Bell et al., (2007) and Roth and Willis (1955b). Several species of Blattodea have been documented to be capaple of parthenogenesis (Roth and Willis, 1956; Brown, 1973a; Xian, 1998). With the exception of two species, a lack of males causes females to enter a parthenogenic reproductive cycle (Roth and Willis, 1956; Brown, 1973a; Xian, 1998). In this asexual mode, no copulation is needed to reproduce, and all offspring are female. *Pycnoscelus surinamensis* is the best-known species that

is almost exclusively parthenogenetic and does not exhibit decreased fitness levels over successive generations.

2.6.3 Ootheca Orientation

Ootheca orientation in cockroach species is of major taxonomic significance and a crucial aspect in understanding reproductive evolutionary patterns of Blattodea (Roth, 1967a). All members of the superfamily Blattoidea and some of the Blaberoidea (Pseudophyllodromiinae, Anaplectinae) carry their ootheca with the keel oriented dorsally. Within the Blaberoidea, all Blaberidae and most members of the family Ectobiidae (Nyctiborinae, Ectobiinae, Blattellinae) rotate their ootheca 90° with the kneel facing the lateral side of the cockroach at the time of deposition or retraction into the brood sac (McKittrick, 1964) Plate. 1.6. The rotation of the ootheca is a key character used to distinguish subfamilies within Ectobiidae.

Pseudophyllodromiinae and Anaplectinae do not rotate their oothecea and are considered to be more basal taxa. Nyctiborinae, Ectobiinae, and Blattellinae all rotate their ootheca and considered to be closely related to Blaberidae (McKittrick, 1964) Plate. 1.6 ; Plate. 1.7. Oothecal rotation is an important character to distinguish subfamilies. Numerous studies show evidence that ootheca rotation evolved only once. The reproductive method of evolving ootheca rotation is highly complex. The likelihood of species developing rotation then losing it is highly unlikely (McKittrick 1964; Roth, 1967a; Bohn, 1987; Klass, 2001; Klass and Meier, 2006; as cited in Bell et al. 2007). Some members of the family Corydiidae rotate the ootheca and hold it in place by a handle or flange at the apex of the female's abdomen. The ootheca is not connected to the female's vestibular tissues. This is considered "false" ootheca rotation. This is likely a derived character that prevents loss of the oothceae when burrowing through substrates (Roth, 1967a). Plate. 1.7. The ootheca is formed within the large posterior chamber in the female's abdomen and is referred to as the vestibulum. Unfertilized eggs are laid posterior end first from the common oviduct opening (Roth and Willis, 1954c). They are fertilized as the egg passes through the ovipositor valves and are guided to the opening of the vestibulum sac. After fertilization the ovipositor valves arrange the eggs vertically in two rows anterior end up (Snodgrass, 1952). The ootheca takes roughly 24 hrs. to develop depending on the temperature. The ootheca is not made of chitin but contains calcium oxalate crystals that can comprise 8–15% of its dry weight in *Periplaneta americana* (Campbell, 1929; Pryor, 1940; Stay et al., 1960; Rajulu and Renganathan, 1966). The percentage of calcium is less in species that retain their oothecae, and can be completely absent in ovoviviparous species.

Oothecae are produced when the right colleterial gland secretes dihydrophenol onto the eggs. The left colleterial gland secretes a water-soluble proteinase that oxidizes the phenol causing the tanning and hardening of the ootheca (Pryor, 1940; Brunet, 1951,1952,1955; Hagen, 1951; Roth and Willis 1954c). As the ootheca is created the third ovipositor valve creates the kneel that is comprised of two tightly opposing flanges and forms a small air chamber with channels above each egg (Lawson 1951; Brunet, 1951). The ootheca is held by the ovipositor valves with the kneel held between the paraprocts. The hardening of the ootheca begins by a process of quinone tanning arising from the anterior or to posterior end (Mckiddrick, 1964). The degree of hardening can vary among species ranging from heavily tanned dark ootheca, as seen in the family Blattidae, to the complete lack of any tanning seen in members of the family Blaberidae

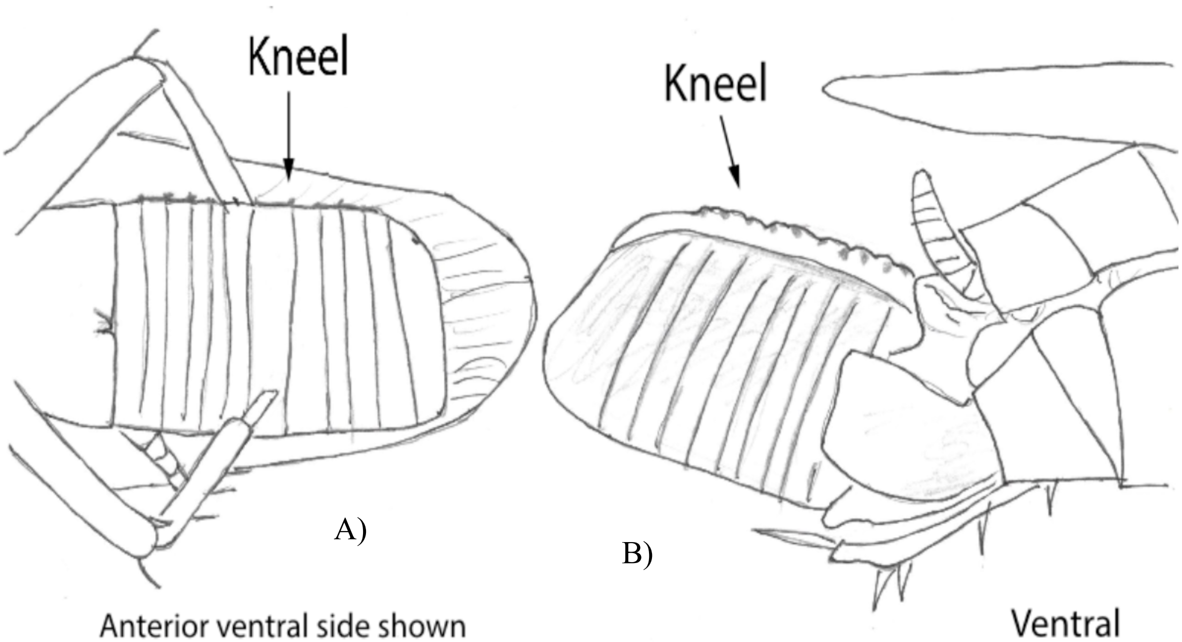


Plate. 1.6- Kneel orientation A) Ventral illustration of rotated ootheca. B) Illustration of non-rotated ootheca with kneel held dorsally.

Retention of the ootheca allows the female to provide protection to the developing nymphs along with water-soluble nutrients as demonstrated by Guillette (1989). The transition from this to the complete retention of the eggs with the loss of the ootheca was short and is thought to have evolved independently two or three times (Roth, 1970a, 1982, 1989). The selective pressures that drive any animal to bearing live young are not well understood. Such pressures may include decreased mobility, increased susceptibility to predators, decreased amount of fertile time, energy requirements for the developing young and the strain of physically carrying young around (Shine, 1989; Goodwin et al., 2002). Parasites and predators are common dangers for oviparous cockroaches (Roth and Willis, 1954a). If one of the developing eggs is parasitized or a predator damages the ootheca, the entire clutch of eggs is unlikely to hatch due to desiccation or the physical incapability to open the kneel (Roth and Willis, 1955b, 1958a; Roth, 1985a). The retraction into the brood sack provides better protection from both cannibalism and parasites (Rau, 1940; Roth and Willis, 1954b). While the transition to internally gestating offspring would come with many physical metabolic and reproductive demands, several studies show that some members of the Blattodea have overcome and even eliminated these drawbacks (Lee, 1994, Meller and Greven, 1996).

2.7 Behavior

2.7.1 Mating

The mating behavior of cockroaches is one of the most well studied aspects of their biology. While the behavior elements are known, the actual processes that are involved

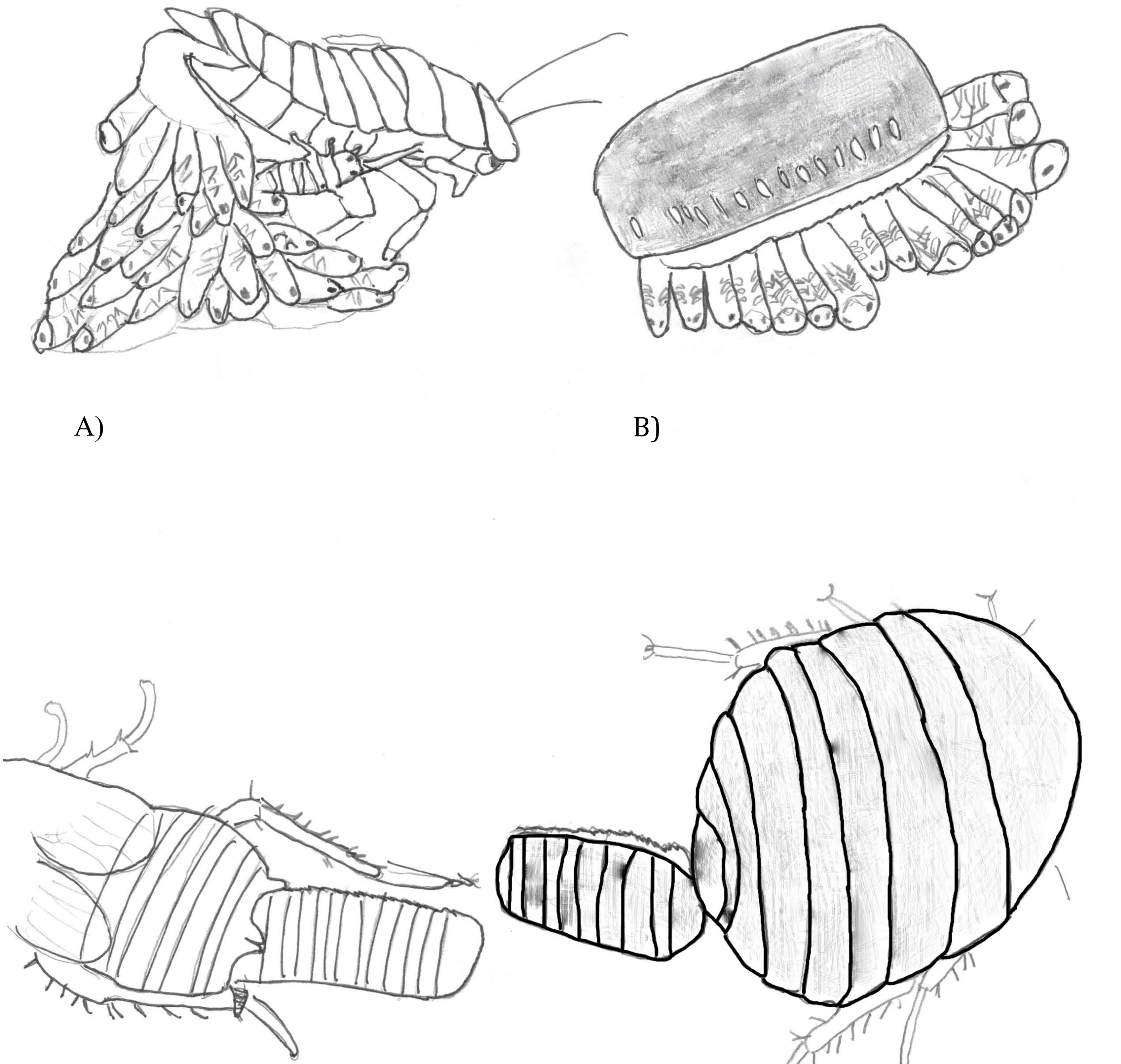


Plate 1.7-Blattodea giving birth A) Illustrations cockroach giving live birth. B) Illustrations dropped ootheca hatching C) True ootheca rotation. D) False ootheca roatation.

are vastly understudied. Behavioral studies primarily focused on the pheromone communication between males and females, reproductive physiology, male competition, and behavioral aspects of courtship in cockroaches (Bell et al., 2007). With the exception of a few species the majority

of male cockroaches will mate with as many females as possible, continuing to do so after they have exhausted all mature, healthy spermatophores (Roth, 1964; Wendelken and Barth, 1987; as cited in Bell et al., 2007). Classifying Blattodea copulation is therefore based on the female's receptiveness and willingness to mate again, rather than the males willingness to mate. The most common form of mating between cockroaches is with one female mating with multiple males whenever she is fertile. Although different mating behaviors have been observed in nature, they are generally considered the exception to the rule. One such exception is the female mating multiple times between each ootheca production. The mating strategy of the genus *Cryptocercus* is one of the few monogamous cockroach genera found thus far excluding termites. Members of this genus pair up during the summer and overwinter together (Nalepa, 1988). A summary of the diffent types of mating frequencies can be found in Bell et al., (2007).

2.7.2 Seduction

Chemical secretions given off by either the male or female are the primary form of attraction among the majority of cockroaches. Among species where at least one sex is capable of flight (usually the male), females tend to secrete the pheromones. The wings if present are held upwards as to allow better dispersion of the pheromones (Hales and Breed, 1983; Gemeno et al., 2004) Plate. 1.8. In addition, to pheromonal secretion, other methods of attraction have been seen among cockroaches. In addition to pheromones, acoustic, visual, and tactile signals have been recorded (Fraser and Nelson, 1982; Roth, 1968c; Hartman and Roth, 1967a, 1967b). Once near each other, both males and females release short-range chemical cues. These chemical cues signal a courtship that is remarkably uniform among the majority of cockroaches (Roth and Willis, 1954b; Roth and Dateo, 1966; Roth and Barth, 1967; Roth, 1969; Simon and Barth, 1977a). These short-range chemical cues are important as they influence mate choice and serve as behavioral releasers. They may even influences physiological processes that can affect the longevity of the female, the rate of nymph development and the sex ratio of the nymphs as in *Nauphoeta cinerea* (Gemeno and Schal 2004; Moore et al., 2001, 2002, 2003).

Once attracted to the general area courtship between two cockroaches begins. When aware of the potential mates presence the male raises his wings, lowers his abdomen and presents the dorsal surface of his abdomen. In many male species, the dorsal abdomen contains one or more tergal glands that secrete a mixture of short-range volatile and non-volatile fractions. The non-volatile fractions are comprised of proteins, lipids, and carbohydrates (Brossut et al., 1975; Korchi et al., 1999). Volatiles are sequestered in the depression that makes up the tergal gland. The female then climbs on the abdomen and proceeds to ingest the sequestered fractions collected within the tergal glands. While the tergal gland occupies the female, the male then extend his abdomen and genital hook, which clasps the female's genitalia. A female that is willing to mate orients her abdomen and spreads her genital atrium to aid in contact with male genitalia (Roth and Willis, 1952a). The male immediately re-orientates his abdomen and genitalia to the normal position. The final position of cockroach coitus is facing away from each other connected posteriorly (Roth and Willis, 1958b; Roth, 1970a; Sreng, 1993) Plate. 1.8.

Two other types of courtships are seen in nature. The first being the male mounting the female. Once mounted the male twists and extends his abdomen clasping the female genitalia, after a good grip is established he dismounts and ultimately ends in the same position as the

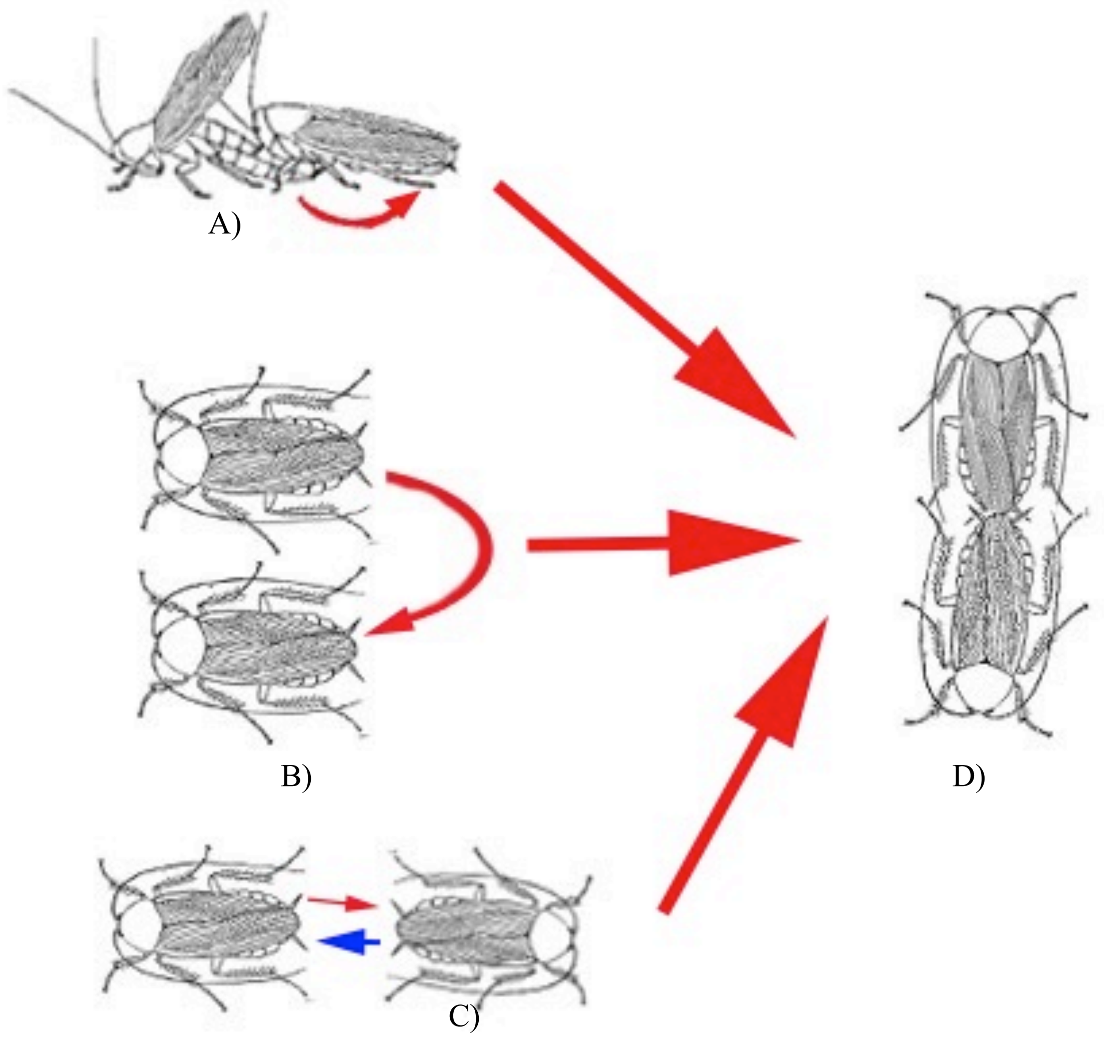


Plate. 1.8- Blattodea mating positions A) Mating position with female mounting male. B) Mating position whith male and female side by side. C) Mating position with male and female facing away from each other. D) Final mating position.

previous form of courtship (Roth and Willis, 1958b; Roth, 1970a; Sreng, 1993). The second type of courtships seen in nature is where neither the male nor the female mounts each other. The male positions himself either on the side of the female (De Fine Licht, 2005; Nutting, 1969). The male then backs up into the female until genital contact is made (Barth, 1968a,1968b; Roth and Willis, 1958b). Several species of Blattodea use other methods such as audible sounds to attract mates. See Bell et al., (2007) for more details on cockorahc mating behavior.

2.7.3 Seasonal Activity

The majority of cockroaches live in relatively stable environments such as caves and tropical rainforests. While theses environment may seem stable when compared to other more

extreme climates they do fluctuate throughout the year. Temperate climates have seasons with distinct temperature, rainfall, and plant growth. Tropical biota goes through seasons of heavy rains and droughts. Other biota such as mountains and desserts can fluctuate wildly within a 24-hour period. By using combinations of movement, habitat choice, life cycle strategies, and physiological mechanisms cockroaches have overcome the strain of a fluctuating climates.

Cockroaches that inhabit climates with distinctly different seasons move from relatively open areas to sheltered areas during the sub-optimal conditions. Others move between areas with available food. This results in different species being active in different parts of the year. Species that are not capable of dealing with drier or colder climates typical change what habitat they inhabit. A common problem with surveying cockroaches is the lack of species during specific parts of the year. Preliminary work shows that surveying cockroaches during certain parts of the year will result in the capture of only nymphs, all adults or no cockroaches at all. Knowing what part of the year yields particular life stages and what habitat they occur in is crucial to collecting the targeted life stages (Daan and Tinbergen, 1997). A complex matrix of interactions that include generation time, size at maturity, age, lifespan, and growing season length interact with development rates. This results in synchronization of lifecycles, diapause, patterns of voltinism and seasonal phenology (Fischer and Fiedler, 2002; Clark, 2003).

Much to the dismay of the typical humanBlattodea have successfully inhabited nearly every type of habitat on this planet. They have been found to inhabit, mines, hollow trees, burrows, sub-bark spaces, dead leaves, rotting logs, streams; within the stream it self and at it's bank, and the water pools in epiphytes. They also invade the homes of other organisms such as the nests of social insects, rodents, reptiles, and birds, and of course man made structures such as dwellings, ships, and aircrafts (Roth and Willis, 1960).

2.8 Habitats

While most cockroaches are capable of living in a huge variety of habitats many show a preference to habitat and microhabitat. Nymphs of many cockroaches species live in the same habitat as the adult but several species exhibit ontogenetic niche shifts. Nymphal instars of *Pseudomops septentrionalis* occur in abundance in the leaf litter. Once adulthood is reach they move up into the brush and canopy and only overlap when adults decent to feed on moss and late instar nymph wander up the bottoms of shrubs or trees (personal observation).

Cockroaches are well known for dwelling in the nooks and crevices that are abundant, both within our homes and nature. These tight compacted spaces are typically dark, humid and may or may not be ventilated. Nearly all cockroach species show high degrees of photonegativity and thigmotaxis, causing them to select tight dark crevices or holes. One cockroach habitat is within the loose substrate of loose soil, leaf litter, dust and even guano. The excavation of long-term or permanent burrows in a fairly solid material such as wood or tightly compact soil is a much more physically demanding task than simply hiding in a crevice. Burrowing in solid substrates usually requires certain degrees of specialization. To dig within compact soil two main methods have been document. The first is digging is common in soil burrowing species. The second method of burrowing is eating through the substrate. The eaten wood is digested with the aid of uricolytic bacteria, cellulolytic bacteria, and methanogens. These gut microbes are also present in lower termites (Breznak et al., 1974; Breznak, 1982; Noirot, 1995). Several examples of habitats are summarized below. For more detailed summary of Blattodea habites see Bell et al., (2007) and Roth and Willis (1960).

2.8.1 Existing structures

Species such as *Blattella germanica* and *Su. longipalpa* are prime examples of cockroaches specializing in using the living quarters, food, supply, and debris of another organism to survive. The method in which these species foster tolerance or elude their hosts is great interest. To date man has yet to succeed in preventing cockroaches from invading their homes, eating their food while creating unsanitary conditions as they do so. Humans are among a very broad group of organisms that cannot prevent cockroaches from invading their homes. This group includes many species of birds, rodents, burrowing mammals, and the nest of other insects such as ants and termites to name a few. The majority of cockroaches that inhabit vertebrate burrows are desert dwellers. Cockroaches take advantage of the cooler temperature, increased moisture and food availability left behind in scraps and fecal residue (Hubbell and Goff, 1939). A North American species *Attaphila fungicola* lives within the fungal gardens of the Texas leafcutter ant *Atta texana* (Wheeler, 1900). Several members within the genus *Nocticola* have been found in the nests of termites and are suspected to be termitophiles**.** Unfortunately, nothing is known about their biology or their relationship with their hosts (Roth and Willis, 1960; Roth, 2003b). The termites that they are associated with include the members within the fungal growing genera *Macrotermes* and *Odontotermes*. Cockroaches have also been found in desert termite mounds (Roth and Willis, 1960). Cockroaches that reside in or scavenge the nests of bees and wasps are much rarer than those found with ants (Bell et al., 2007).

2.8.2 Insect Nests

The life history of cockroaches that reside in the nests of insects are poorly understood. Some cockroach species are exclusively collected in ant and termite colonies and have been determined to be mymercophile and termitophiles, respectively (Roth and Willis, 1960). New world myrmecophiles include the genera *Myrmecoblatta* and *Attaphila. Myrmecoblatta wheeleri* lies within the family Corydiidae and is associated with *Solenopsis geminata* in Guatemala, *Camponotus abdominalis* in Costa Rica and *C. abdominalis floridanus* in Florida (Hebard, 1917). The genus *Attaphila* is located tentatively within the family Ectobiidae. Its exact relation to the other members of the family is poorly understood. The species within the genus *Attaphila* are all associated with leaf-cutting ants of genera *Atta* and *Acromyrmex* (Kistner, 1982). A North American species *Attaphila fungicola* lives within the fungal gardens of the Texas leafcutter ant *Atta texana* (Wheeler, 1900). Several members within the genus *Nocticola* have been found in the nests of termites and are suspected to be termitophiles**.** Unfortunately, nothing is known about their biology or their relationship with their hosts (Roth and Willis, 1960; Roth, 2003b). The termites that they are associated with include the members within the fungal growing genera *Macrotermes* and *Odontotermes*. Cockroaches have also been found in desert termite mounds (Roth and Willis, 1960). Cockroaches that reside in or scavenge the nests of bees and wasps are much rarer than those found with ants (Bell et al., 2007)

2.8.3 Desert and Caves

Cockroaches are well represented in caves throughout the tropics and subtropics, but are uncommon in temperate caves (Izquierdo and Oromi, 1992; Holsinger, 2000). The only US

species found in caves is *Arenivaga grata* (Roth and Willis, 1960; Peck, 1998). Dr. Johanna Darlingon has studied the biology of cave-dwelling cockroaches most extensively in Trinidad and Australia.

The title of “Cave dwelling cockroach” is arbitrary for two main reasons. First, many of the described species are based on few collection records. Second, the term “cave” is typically considered to be an underground space large enough to accommodate a human. In reality caves large enough to accommodate humans are minute. While many cockroaches prefer moist, humid environments, many species inhabit incredibly arid habitats such as grasslands and deserts to name a few. In addition to aridness, the temperature of this kind of habitat can vary depending on the time of year to the time of day. In addition to temperature variability, the low rainfall is a major factor that influences the organisms that reside there. The majority of interest of dessert dwelling cockroaches has been in old world deserts in Egypt and Saudi Arabia (Ghabbour et al., 1977; Ghabbour and Mikhaïl, 1978; Ghabbour and Shakir, 1980) Bei-Bienko, 1950; Grandcolas, 1995a). While one would think scorching heat, and dry barren desserts would be enough to keep any insect population low it would seem that once again cockroaches have found a way to invade. Surveys conducted in Egyptian desserts found cockroaches to be super abundant, comprising nearly a third of the mesofaunal biomass (Ayyad and Ghabbour, 1977). New world species of desert-dwelling cockroaches can be found in Texans, New Mexico Arizona, and Florida (Hopkins and Miller, 2014; Hopkins, 2014).

In order to overcome the harsh climate of the desert, cockroaches that live there must employ behavioral modifications as well as morphological and physiological adaptations. Regulating water balance, finding food and tolerating extreme temperature are crucial to survival. Behavioral tactics for coping with these extreme conditions include diurnal and seasonal shifts in spatial location and prudent choice of microhabitat (Bell et al., 2007). The second form of shift in spatial location is the inhabitation of burrows or other microhabitats. Burrows, caves, rocks can all be suitable microclimates and provide much less extreme microhabitat (Roth and Willis, 1960). Some cockroach species are closely associated with one microhabitat. Others can move freely between them. About half the desert cockroaches whose life histories are understood live in burrows of other organisms (Roth and Willis, 1960). Animal burrows generally offer a more favorable microclimate than surface habitats.

2.8.4 Arboreal dwelling species

When one considers the habitat of cockroaches the idea of them being under foot usually comes to mind. The majority of cockroaches seen are usually running along the ground away from us. Cockroaches however readily inhabit arboreal habitats of both temperate and tropical forest. Canopies are notorious for containing a rich array of biological resources such as sap, bird excrement, plant litter, leaves, flowers, and fruit that are known to make up the typical diet of a cockroach (Novotny et al., 2003). Canopies possess a vast amount of suspended soil that is supported by the compound of leaves and branches. The substantial pool of suspended soil that accumulates in the various nooks and crannies of the canopy may be particularly important in understanding the vertical stratification of cockroach faunas but is typically neglected in studies (Young, 1983; Winchester and Behan-Pelletier, 2003). The soil has a high organic content derived from leaf, fruit and flower litter, epiphyte tissues, decomposing bark, and the feces, food, and faunal remains of canopy-dwelling animals, all of which are food for cockroaches.

In most studies of canopy invertebrates, cockroaches are a consistent a minor component of specimens collected. While considered a minor insect of the canopy. Basset (2001) concluded that while cockroaches represented only 5.3% of the individuals collected, they dominated the amount of invertebrate biomass present. Blattaria were calculated to represent 24.3% of the biomass, with Hymenoptera (primarily ants) coming in second at 19.8%, and Coleoptera ranking third at 18.8%. The revelation that nearly a quarter of the arthropod biomass in tree canopies may consist of cockroaches is particularly significant because the most commonly used canopy techniques almost certainly under sample Blattaria. Both physiological and taxonomically this is important. Studies of arthropods diversity in leaf litter indicate that the soil/litter fauna on the forest floor is in large measure distinct from that of the forest above suggesting a plethora of new unique species that dwell amongst the canopy (Basset et al., 2003b). In-depth surveying of canopies is crucial in gaining a better understanding of just how many species of cockroaches are arboreal and just what morphological and physiological adaptations allow them to survive up there.

2.8.5 Aquatic Habitats

Blattodea have also been documented living within and around aquatic habitats such as bromialiads and streams. Cockroaches who are closely associated with water fall into two basic groups: those that live in phytotelmata (small pools of water within or upon plants) and those associated with rivers, streams, and ponds (Bell et al., 2007). The cockroach lives in close proximity to the surface of the water. When searching for food and escaping predators the cockroaches submerge into their respective water sources. While a plethora of cockroaches that live in and around water has been found, the question if they possess any adaptations to suite an aquatic life style has yet to be definitively answered.

2.9 Ecology

The manner in which Blattodea contribute to the environment is not the major source of public or scientific concern. If unique relationships are seen, they are rarely described with a useful amount of detail. The majorities of cockroaches are detritivores and recycle dead plants, animals, and excrement. These processes are critical in maintaining a balanced environment. Almost all cockroaches are associated with some form of organic matter; dead or otherwise, whether it be decaying logs, stumps, rocks, trees both living and dead, and macro fungi, moss leaves, carcasses or flowers to name a few (Bell et al., 2007). The impact of cockroaches on the environment is important although not as obvious as the primary consumers. The role of cockroaches in the environment lies in their complex and multipart interaction with soil microbes. A major problem faced by the microbes is that they are dormant the majority of the time and are incapable of distributing around the environment. Cockroaches remove this limitation on microbial activity by feeding on decaying leaves and readily moving throughout the area, by fragmenting litter they exposed new substrate to microbial attack.

The role of cockroaches as pollinators is poorly studied. While not common in temperate zones cockroaches do serve as the principal pollinators for a few species of plants. In French Guiana, the species *Epilampra sodalis* and *Amazonina platystylata* were found to frequently visit flowering plants of the genus *Clusia*. *Amazonina platystylata* transferred more pollen that the former and was determined to be its principle pollinator (Vlasakova et al., 2008). Cockroaches

were observed flying during the day to successive inflorescences located 34 m above the ground, ignoring nearby flowers of a different species. The exposed condition of the anthers and stigma of *D. arboreus* and the observed floral fidelity of the cockroach suggest that *Paratropes bilunata* is a likely pollinator (Perry, 1978; Roth, 1979; Bell et. al., 2007). Nagamitsu and Inoue (1997) offer more direct evidence that cockroaches can be the main pollinators of a plant species in the understory of a lowland forest in Borneo. These authors observed Blattellid cockroaches feeding on pollen and stigmatic exudate of *Uvaria elmeri.*

Cockroaches are not limited to the consumption of dead leafs. While the majority feed on dead leaves there are also known species that are herbivores of young plants. The interaction of live plants and cockroaches is rarely studied although the phenomenon is abundant in the literature (Roth and Willis 1960). Most of the evidence comes from commercially grown crops, particularly in the tropics and in greenhouses. One field study found that the frequency of herbivore damage on new leaves in rainforest canopy was significantly correlated with the abundance of Blattaria (Dial and Roughgarden, 1995).

In addition to detritivores, herbivores, and transportation as well as shelter for microbes, cockroaches also serve as food for numerous taxa. The principal food of the Grylloblattid *Galloisiana kurentzovi* in East Asia is juveniles of *Cryptocercus relictus* (Storozhenko, 1979). *Arenivaga investigata* makes up 23% of the prey biomass taken by the scorpion *Paruroctonus mesaensis* (Polis, 1979). *Parcoblatta divisa* along with other members of the genus make up a high proportion of the menu of endangered red-cockaded woodpeckers (*Picoides borealis*) in the Coastal Plain of South Carolina (Horn and Hanula, 2002). Attempts to control urban infestations of *Periplaneta americana* with toxic insecticides may have contributed to the decline of this species on Frégate Island. The birds feed on the dead cockroaches near human structures and ingest lethal doses of insecticides. Cockroaches as prey may be an integral part of the food chain of many insectivores. See Bell et al., (2007) for a detaild summary of Blattodea ecology

2.10 Collection methods

The luxury of studying a non-cryptic insect is never more appreciated than after you attempt to collect cockroaches. These insects spend the majority of their time hiding and when are active are incredibly mobile and difficult to catch even with a net. They also occupy the full vertical spectrum of their habitat with some exclusively arboreal and other burrowers. Many species have wingless sexes that are completely missed in flight traps. While the diversity of cockroaches is assumed to be low the general methods used in surveying for a diverse array of cockroaches may not be ideal. With an order that possesses representatives that show amazing behavioral, morphological, physiological adaptations, collecting the full spectrum of cockroaches could reveal missing links or new adaptations that could shake the foundations of what we consider a cockroach. There are many published surveys of cockroaches in a given area (Peck, 1989; Prat, 1988; Evangelista et al., 2015). A major problem is that few list collection methods or even descriptions of the species. It is almost certain that cockroaches are under-surveyed in nearly every part of the world.

2.10.1 Arboreal collection methods

One example of under-surveyed cockroaches would be canopy dwelling cockroaches. Collection methods for a survey of a canopy or arboreal habit typically include fogging with

pyrethrum and if the surveyors choose, light traps, suspended soil cores, beating foliage, bromeliad bagging, and branch bagging. While effective on other insects, it was recently found that this is not the case with cockroaches. A recent review of canopy arthropods of the world reveled that although cockroaches represented only 5.3% of the individuals collected, they dominated in the amount of invertebrate biomass present. Blattaria represented 24.3% of the biomass, with Hymenoptera coming in second at 19.8%, and Coleoptera ranking third at 18.8% (Basset, 2001). The revelation that nearly a quarter of the arthropod biomass in tree canopies may consist of cockroaches is particularly significant because the most commonly used canopy techniques almost certainly under sample Blattaria. Each method of collection is biased and can miss many species. While fogging's is the most effective at surveying canopies, it is usually done during the time of day when the air is still. Few fogging's are done and night and night which is typically the active period of cockroaches. Cockroaches are known to hide in very secure places that hide them from potential predators. Even if fogging kills them, they are still within their shelter and are likely not to drop down to the sheet below. Many cockroaches are negatively phototaxic and will not go to light traps (Basset et al., 2003). Any person that has tried to squash much less hand catch cockroaches becomes well aware that they can be highly athletic and move amazingly quick to and successfully hide almost as quick. Branch bagging is flawed in losing many of these highly mobile species (Schowalter and Ganio, 2003). Collecting in the canopy is by far the most difficult although similar problems occur when collecting in other areas.

2.10.2 Beneath the canopy

Many cockroaches traverse up and down trees foraging on moss and other sources of food. Collecting species that roam the area between the canopies and ground is far less difficult than canopy collecting but collection methods are still biased. Hanging santé malaise and flight intercept traps are useful in collecting flying insects but miss any sex or species that show reduction in wings. Tree trunk traps are useful and collect both sexes as they climb up and down the tree. Hand collecting is by far the most effective way to collect cockroaches at this altitude. Hand collecting allows the capture of both sexes. Collecing live specimins provides a better understanding of their behavior. Hand collecting, however, is extremely difficult, and many specimens can be lost and is open to the human error. When collecting insect that are known to scurry around the ground the pitfall traps are usually used. While effective in arid areas with litter precipitation areas that recieve heavy rain fall on short notice is not an ideal habitat to put a pitfall as they are subject to flooding on a regular basis. Hand collecting is still one of the most effective methods in collecting cockroaches on the ground. Combining multiple collection methods is one way of increasing the effectiveness of a survey (Basset et al., 1997). A difficulty in documenting cockroach diversity is that in collections nymphs are common. It is rarely possible to identify cockroach nymphs, and these can make up the bulk of Blattaria collected; 90% of the cockroaches collected by Fisk (1983) in Central American canopies were nymphs.

CHAPTER 3: SURVEY OF COCKROACHES IN SELECTED NON-URBAN HABITATS OF SOUTHERN LOUISIANA

3.1 Introduction

The diversity of insects has been the source of numerous studies ever since the vast number of insect species became apparent. Synoptic surveys of Blattodea provide a list of cockroach species recorded within the studied areas. While useful, many provide little or no information that can aid in identification or provide data that can be helpful in later studies. Recording dates, collection methods and coordinates are standard protocol when collecting. The exclusion of this valuable data creates a gap of information within orders that lack regular revisions. Only listing species recorded in the area with references to original descriptions and re-description provides no help in identification. The original descriptions of Blattodea are typically vague and difficult to find. Surveys with information useful in identifying the species listed along with the standard information recorded while collecting will provide an easier source of identification information while making more data available for future studies.

A total of 3 inventories were included in this study. Two were conducted from May 2014 to August 2015 within the Atchafalaya Basin and West Feliciana Preserve. The Atchafalaya basin is predominantly forested wetland consisting of bald cypress (*Taxodium distichum*) and multiple species of oak (*Quercus* spp.*)*. The Feliciana Preserve is a mixture of disturbed and relatively mature upland deciduous forest containing a large concentration of the Loblolly Pine (*Pinus taeda*). Surveys from two other similar studies were sorted and included. Areas surveyed include a longleaf pine savannah, which consists of scattered longleaf pine trees (*Pinus palustris*) and a rich grass and shrub ground flora (Colby and Prowell, 2006). The other study surveyed the Red River and Three Rivers Wildlife Management Areas consisting of overcup oak-bitter pecan (*Quercus lyrata*/*Carya aquatica*) bottom lands (Newell, 2008).

No previous studies have documented cockroach diversity in Louisiana. Our current knowledge is based on specimens collected as a byproduct of various past studies. Collecting from areas in which the habitats differ has provided a better understanding of biodiversity and habitat preferences of Blattodea that inhabit Louisiana. Cockroaches are best known as generalists. They also possess the capability to survive on minimal food and water (Durbin and Cochran, 1985; Willis and Lewis, 1957). Factors such as temperature changes, amount of food available, moisture gradients, and other aspects can restrict certain species of cockroaches to one habitat at one or all stages of its life (Hubbell and Goff, 1939; Corbet, 1961; Grandcolas, 1997). Live specimens were kept and reared to document life cycles and maturation times. Adults were preserved and used for taxonomic evaluations in order to prepare a key to southern Louisiana Blattodea.

The goal of this study was to build a data matrix for diversity studies of the Blattodea of Louisiana, gain a better understanding the biogeographic relationships of the cockroaches between each biota, and build a modern list of the cockroaches that inhabit Louisiana. Species collected were listed along with useful identification characters. Range expansions and new species were recorded. This study contributes new information about the ecology and distribution of the cockroaches within southern Louisiana.

3.2 Materials and Methods

3.2.1 Collections

Two sites were surveyed for cockroaches by the author. These were located in the Atchafalaya Basin (AB) (30 17' 2" N 91 44' 1"), and at a private nature reserve, Feliciana Preserve (FP) (30.797471, -91.253081). Three other areas were included in the survey using specimens collected from studies done by Landau and Prowell (1999), Colby and Prowell (2006), and Newell (2008). Cockroaches were sorted and identified to species or morphospecies. These studies were conducted in the Red River Wildlife Management area (RRWMA)(31.247596, -91.695556), the Three Rivers wildlife management area (TRWMA)(31.076615, -91.649551) Bayou Cocodrie WMA (31.547452, -91.612469), Big Lake WMA (32.200070, -91.472636), and a long leaf pine savannah located at Abita Creek Flatwoods Preserve Louisiana (LLP)(30.5236, -89.9686).

A 1.8288 by 1.8288 m Santé malaise trap was used in all locations surveyed Plate. 3.1. Pit fall traps were used during the first summer of the study but due to constant flooding they were deemed ineffective and not used after the first summer. The tree trunk traps were modeled after Hanula and Kirsten's (1996) design and used during the second summer. This trap uses a modified funnel to steer insects into a chamber where they fall into a collection jar containing 1:3 ratio of propylene glycol and soapy water. Active methods of collecting were done at AB and FP, which included light trapping, beat sheeting and hand collecting. Hand collecting consisted of physically removing cockroaches from tree trunks, shrubs and leaf litter.

Because the active time for adults and nymphs can vary depending on species, collecting was done throughout the spring, summer, and into fall in order to adequately sample during all seasons (Brown, 1983). Traps were serviced when the average temperature at night 15 ºC and continue during the spring and summer months until the temperature is below 15 ºC. The Santé malaise traps were serviced during the afternoon. Hand collecting began during the daylight and continued eleven o'clock at night. Hand collections and other active collecting were done once a month when the Santé malaise traps and tree trunk traps were serviced. The individuals were documented and identified to species. A brief description was provided for each species caught along with any unique behavioral patterns observed. Roth (1968, 1971) was referenced for terminology and McKittrick (1964) and Roth (2003) for higher taxonomic categories. Original descriptions and synonyms for each taxon are referenced using the Blattodea species file (Beccaloni, 2014).

3.2.2 Rearing

100% of live nymphs and 50% of live adult specimens were placed in ventilated petri dishes Plate. 3.2. Petri dishes were modified by cutting a square hole in the lid. Using hot glue, a screen was attached to allow ventilation. Cockroaches from each sample were sorted and morphologically similar specimens were kept together. Cockroaches were fed Fluker's Orange cubes Louisiana **®,** apple slices and watered as needed (typically twice weekly). Rearing chambers were kept in a room within the Louisiana State Arthropod Museum with an average temperature of 30.2° C. Light was present during weekdays between the hours of 8:30 and 5. Once adulthood was reached all members of the same species were documented in the data sheet

and then either killed, or put into the same container in order to establish a colony. Morphological characters for each nymph was documented, described, and illustrated.

Plate 3.1-Santé Malaise trap hung in tree at height of 8ft. (Photo, Forest Huval).

3.2.3 Data management

A standard data sheet used for each collection included the date, temperature and humidity. All samples were recorded separately; methods of capture, and number of species collected were recorded on an Excel sheet as shown in Appendix A.

3.2.4 Data Standardization

For each site the primary collection method for each site was the Santé malaise trap. Collecting specimens using the same method is required for diversity and shared species analysis. Only specimens that were caught in Santé malaise traps were included when comparing species diversity and site similarity. All specimens were included in species documentation regardless of collection method.

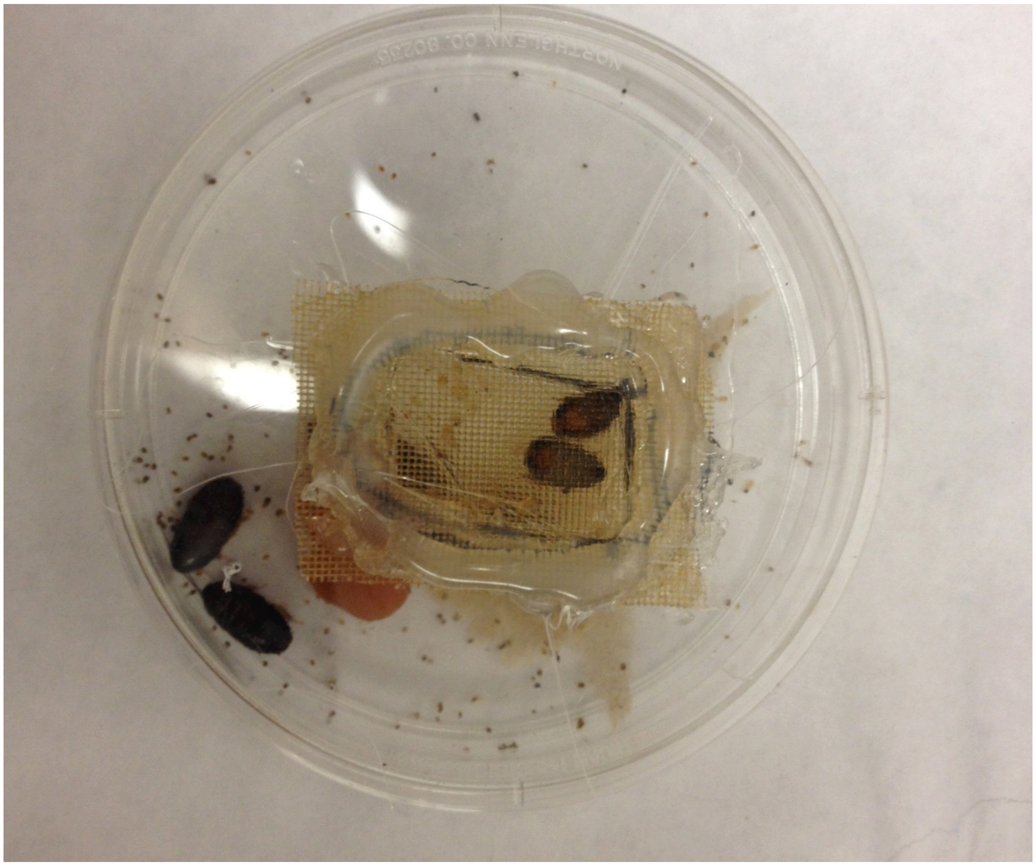


Plate 3.2- Cockroach rearing petri dish with *Pseudomops septentrionalis* nymphs (Photo, Forest Huval).

Specimens from Bayou Cocodrie and Big Lake Wildlife Management Area were included in the survey but not the diversity analysis due to different collecting methods.

3.2.5 Study Sites

The AB is the largest forested wetland in the U.S. consisting of 1,400,000 ac. The AB spans across multiple parishes but the site studied is located within St Martin Parish Louisiana. The site studied consists bald cypress (*Taxodium distichum*) and live oak (*Quercus* spp.*).* The AB was heavily deforested but after perseveration efforts stable cypress forests and swamps have returned. The land within the basin is prone to periods of heavy flooding depending on the river levels and manmade spillways. The FP is a privately owned preserve located within West Feliciana Parish, Louisiana. The private reserve contains 150 ac and consists of mature upland deciduous forest containing the Loblolly Pine (*Pinus taeda*). The LLP surveyed is located in Abita Creek Flatwoods Preserve in St Tammy Parish, Louisiana; containing 835ac. Long leaf pine savannahs are floristically rich, herb-dominated wetlands containing a sparse longleaf pine (*Pinus palustris*). The LLP once dominated the gulf coast but now are one of the most threatened biota in North America. The remnants of this biota are small when compared to the vast savannahs that once existed. The LLP contains rich diversity of both plants and insects.

Frequent fires are critical for flora to perpetuate. Due to the need of frequent fires to clear out invasive fire intolerant plants scheduled burnings are controlled within the area. The TRWMA is considered a bottomland hardwood and is owned by the Louisiana Department of Wildlife and Fisheries. This site is located within Concordia Parish, Louisiana and consists of 26,295 ac. The majority of the site is flat and at the site studied consists primarily of overcup-oak (*Quercus lyrata)*. Springtime flooding is common and heavily influences the understory fauna. The RRWMA is located within Concordia Parish, Louisiana and contains 1,377 ac of bottomland hardwoods and cypress swamps. The site studied within RRWMA consists primarily of overcup-oak *(Quercus lyrata*) and pecan *(Carya aquatic)*.

3.2.6 Diversity and Similarity Analysis

To assess differences in diversity and species similarity between different sites, the abundance, diversity and species similarity for each site was quantified. All specimens were deposited at the Louisiana State Arthropod Museum (LSAM). Date collected and method of capture were recorded for each specimen. Original descriptions were referenced when identifying the species (Beccaloni, 2014). Species diversity curves were calculated for each site using Estimate S (Colwell, 2013). ACE, ICE, Jack2 and Chao 2 diversity estimators were also calculated. Jaccard's coefficient is a measure of similarity between finite sample sets. Each site was compared using Jaccard's classic Similarity analysis, which compares similarity based on the presence or absence of a species within the site surveyed Plate 3.3. The Chao-Jaccard-Raw Abundance-based analysis incorporates species abundances when determining similarity and was also run between each site. Jaccard's coefficient analyses determined the percent of species shared between the sampled populations (Real and Vargas, 1996). Chao et. al (2005) proposed a new approach to the classic Jaccard coefficient that incorporated species abundance. This new approach was also used to measure the similarity between sites. Estimate S software was used to predict the number of species that may be at each site based on the number of species observed in aggregate samples using multiple diversity algorithms.

3.3 Results

A total of 1386 cockroaches were collected. *Euthlastoblatta gemma* was documented for the first time in central Louisiana with six specimens found in the AB and one specimen collected at the LLP. *Pseudomops* sp. is yet to be identified or described. *Pseudomops septentrionalis* was the most abundant species collected (934), followed by *Parcoblatta divisa* (78*), Ischnoptera deropeltiformis* (74), and *Parcoblatta bolliana* (67). *Plectoptera picta* was the least abundant (2) followed by *Parcoblatta fulvescens* (3), and *Periplaneta fuliginosa* (4).

Several species were only collected in certain sites. *Plectoptera picta* was only found in AB. *Parcoblatta uhleriana* was only found in LLP. *Euthlastoblatta gemma* was only found in AB and LLP. Several species were abundant in all areas but one. *Pseudomops septentrionalis*, *Parcoblatta lata*, and *Parcoblatta divisa* were all collected in every site except the LLP site. Abundance for each species at all sites surveyed are documented in appendix B.

All sites were shown to be adequately surveyed with all sites predicted to possess a number of species that does not differ from the observed species. The Long Leaf Pine Savannah was shown to be the most diverse area surveyed and is predicted to contain between 12 and 16 species. The second most diverse area was the Atchafalaya Basin. The species richness curve

indicates additional species and predicts between 13 and 15 species in the area. TRWMA was predicted to possess between 10 and 14 species, followed by West Feliciana Preserve (10), and RRWMA (8) Plate. 3.3.The similarity between sites was shown to be much less once species abundance was included Plate. 3.4. The areas showing the greatest species overlap are the RRWMA/TRWMA areas and the AB/WF areas. Both areas show over 95% species similarity. The areas showing the least species similarity were the LLP and RRWMA showing only a 0.9% similarity.

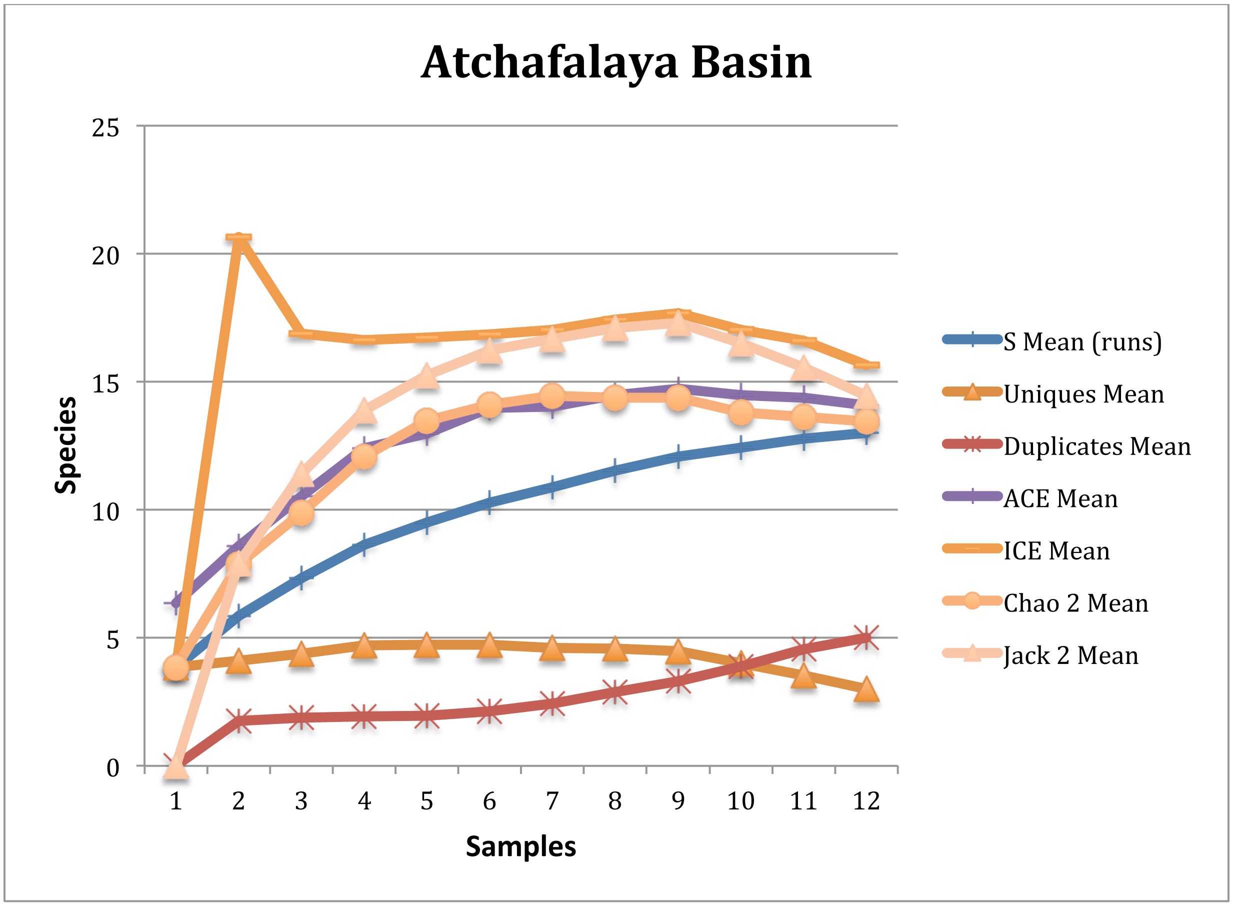


Plate 3.3-Projected total cockroach diversity at Atchafalaya Basin site generated using Estimate S software. Sample based mean (S Mean); Number of species in *t* pooled samples, given the reference sample (mean among runs). Unique Mean; Number of uniques (species that occur in a only one sample) in *t* pooled samples (mean among runs) (Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). Duplicates Mean; Number of duplicates (species that occur in a only two samples) in *t* pooled samples (mean among runs)(Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). ACE Mean; Abundance Coverage-based Estimator of species richness (mean among runs) (Chao et al. 2000; Chazdon et al. 1998). ICE Mean; Incidence Coverage-based Estimator of species richness (mean among runs) Chao et al. 2000; Chazdon et al.1998). Chao2 Mean; Chao 2 richness estimator (mean among runs) (Chao 1984, 1987). Jack 2 Mean; Second-order Jackknife richness estimator (mean among runs)(Burnham & Overton1978, 1979; Smith & van Belle1984; Palmer 1991).

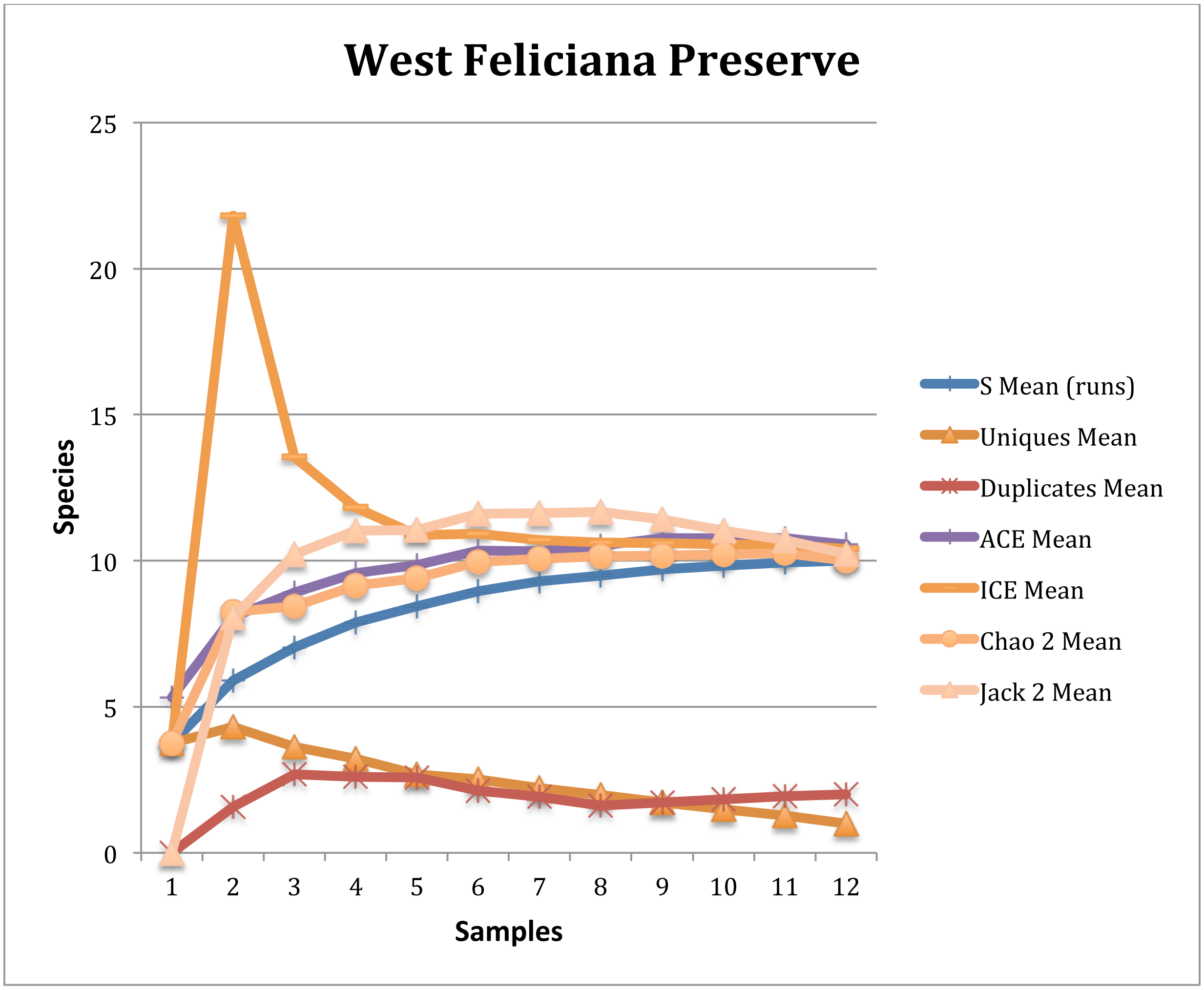


Plate 3.4- Projected total cockroach diversity at West Feliciana Preserve site generated using Estimate S software. Sample based mean (S Mean); Number of species in *t* pooled samples, given the reference sample (mean among runs). Unique Mean; Number of uniques (species that occur in a only one sample) in *t* pooled samples (mean among runs) (Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). Duplicates Mean; Number of duplicates (species that occur in a only two samples) in *t* pooled samples (mean among runs)(Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). ACE Mean; Abundance Coverage-based Estimator of species richness (mean among runs) (Chao et al. 2000; Chazdon et al. 1998). ICE Mean; Incidence Coverage-based Estimator of species richness (mean among runs) Chao et al. 2000; Chazdon et al.1998). Chao2 Mean; Chao 2 richness estimator (mean among runs) (Chao 1984, 1987). Jack 2 Mean; Second-order Jackknife richness estimator (mean among runs)(Burnham & Overton1978, 1979; Smith & van Belle1984; Palmer 1991).

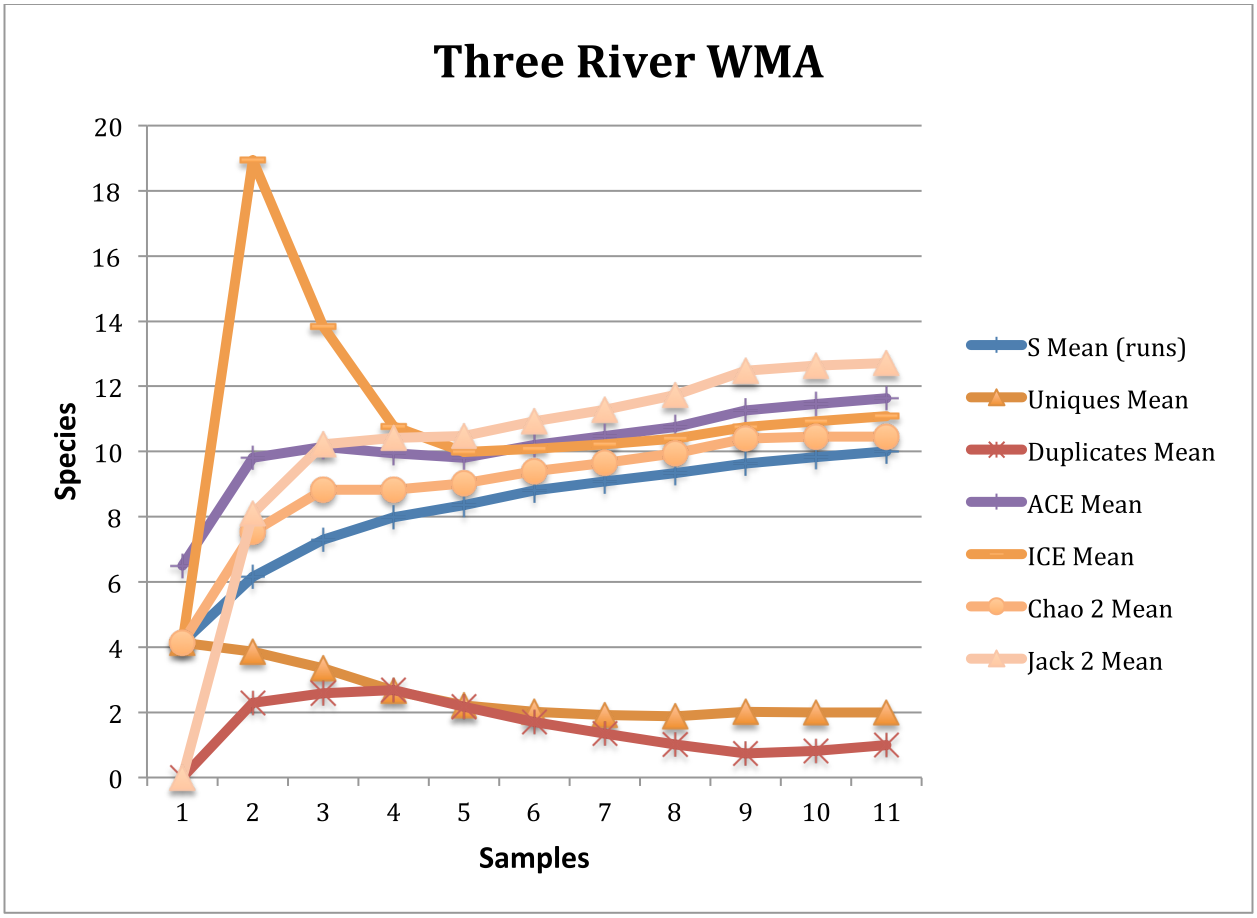


Plate 3.5- Projected total cockroach diversity at Three River site generated using Estimate S software. Sample based mean (S Mean); Number of species in *t* pooled samples, given the reference sample (mean among runs). Unique Mean; Number of uniques (species that occur in a only one sample) in *t* pooled samples (mean among runs) (Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). Duplicates Mean; Number of duplicates (species that occur in a only two samples) in *t* pooled samples (mean among runs)(Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). ACE Mean; Abundance Coverage-based Estimator of species richness (mean among runs) (Chao et al. 2000; Chazdon et al. 1998). ICE Mean; Incidence Coverage-based Estimator of species richness (mean among runs) Chao et al. 2000; Chazdon et al.1998). Chao2 Mean; Chao 2 richness estimator (mean among runs) (Chao 1984, 1987). Jack 2 Mean; Second-order Jackknife richness estimator (mean among runs)(Burnham & Overton1978, 1979; Smith & van Belle1984; Palmer 1991).

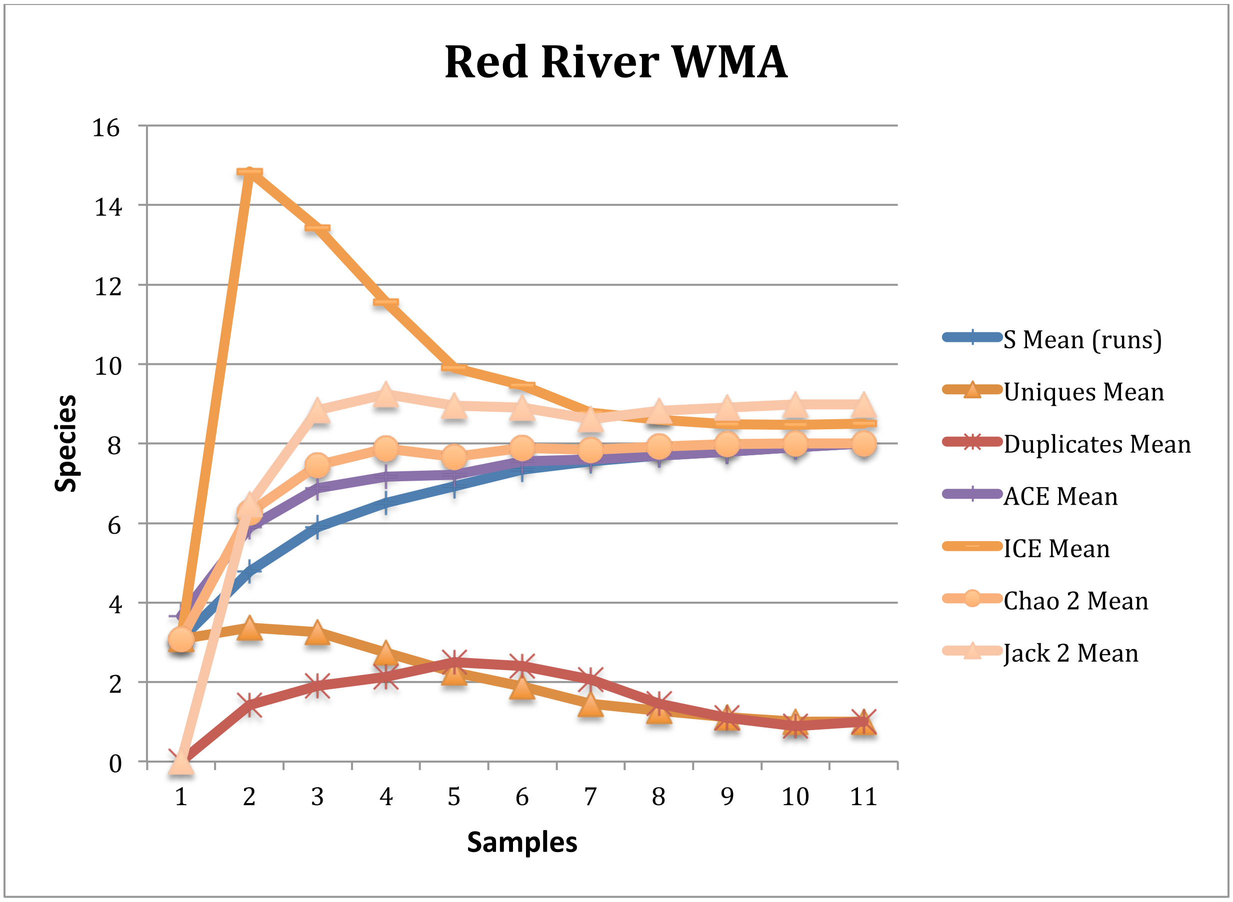


Plate 3.6- Species richness curve Red River A) Projected total cockroach diversity at Red River site generated using Estimate S software. Sample based mean (S Mean); Number of species in *t* pooled samples, given the reference sample (mean among runs). Unique Mean; Number of uniques (species that occur in a only one sample) in *t* pooled samples (mean among runs) (Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). Duplicates Mean; Number of duplicates (species that occur in a only two samples) in *t* pooled samples (mean among runs)(Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). ACE Mean; Abundance Coverage-based Estimator of species richness (mean among runs) (Chao et al. 2000; Chazdon et al. 1998). ICE Mean; Incidence Coverage-based Estimator of species richness (mean among runs) Chao et al. 2000; Chazdon et al.1998). Chao2 Mean; Chao 2 richness estimator (mean among runs) (Chao 1984, 1987). Jack 2 Mean; Second-order Jackknife richness estimator (mean among runs)(Burnham & Overton1978, 1979; Smith & van Belle1984; Palmer 1991).

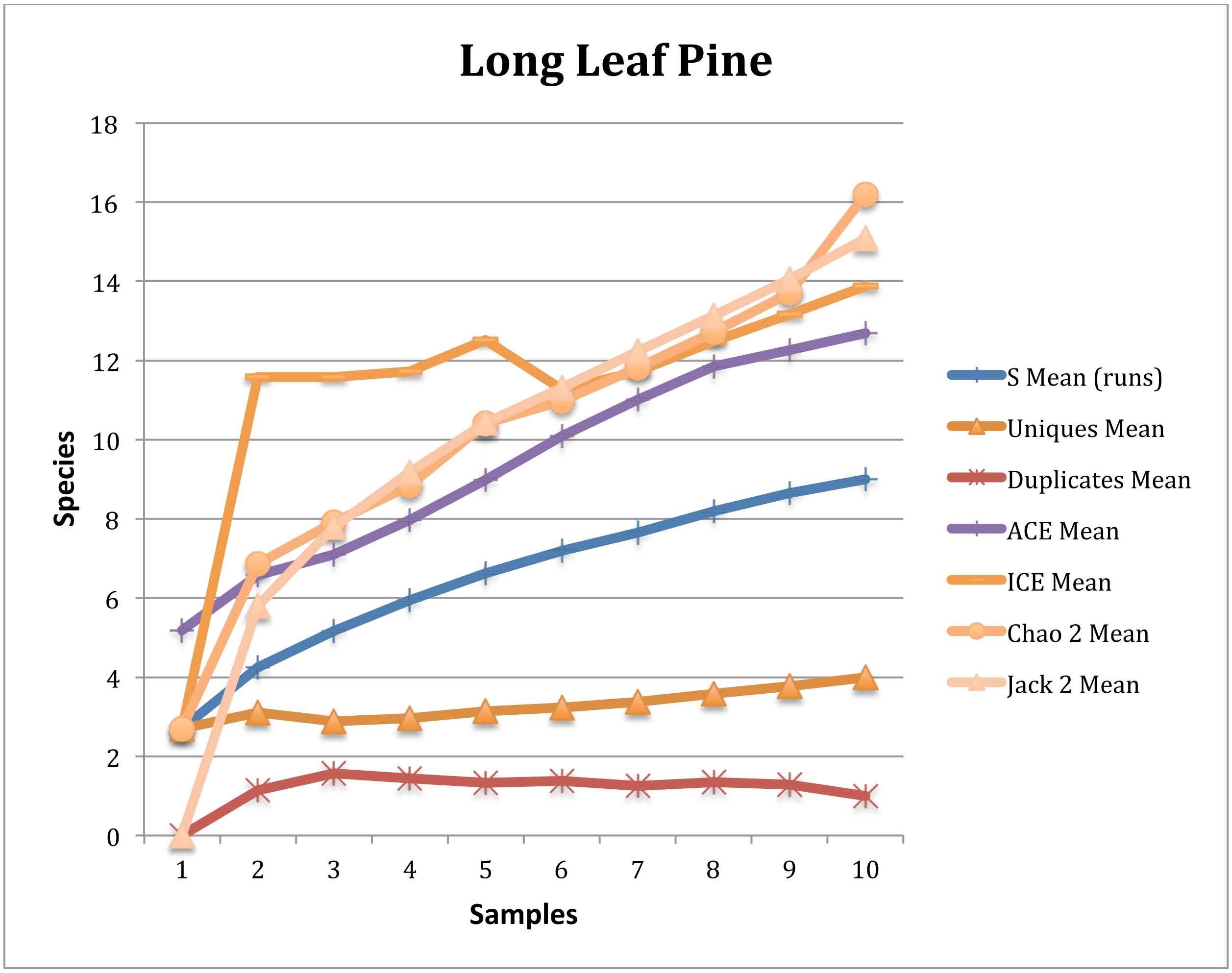


Plate 3.7- Species richness curve Long leaf Pine A) Projected total cockroach diversity at Long Leaf Pine site generated using Estimate S software. Sample based mean (S Mean); Number of species in *t* pooled samples, given the reference sample (mean among runs). Unique Mean; Number of uniques (species that occur in a only one sample) in *t* pooled samples (mean among runs) (Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). Duplicates Mean; Number of duplicates (species that occur in a only two samples) in *t* pooled samples (mean among runs)(Colwell & Coddington, 1994; Chazdon et al. 1998; Colwell et al. 2012). ACE Mean; Abundance Coverage-based Estimator of species richness (mean among runs) (Chao et al. 2000; Chazdon et al. 1998). ICE Mean; Incidence Coverage-based Estimator of species richness (mean among runs) Chao et al. 2000; Chazdon et al.1998). Chao2 Mean; Chao 2 richness estimator (mean among runs) (Chao 1984, 1987). Jack 2 Mean; Second-order Jackknife richness estimator (mean among runs)(Burnham & Overton1978, 1979; Smith & van Belle1984; Palmer 1991).

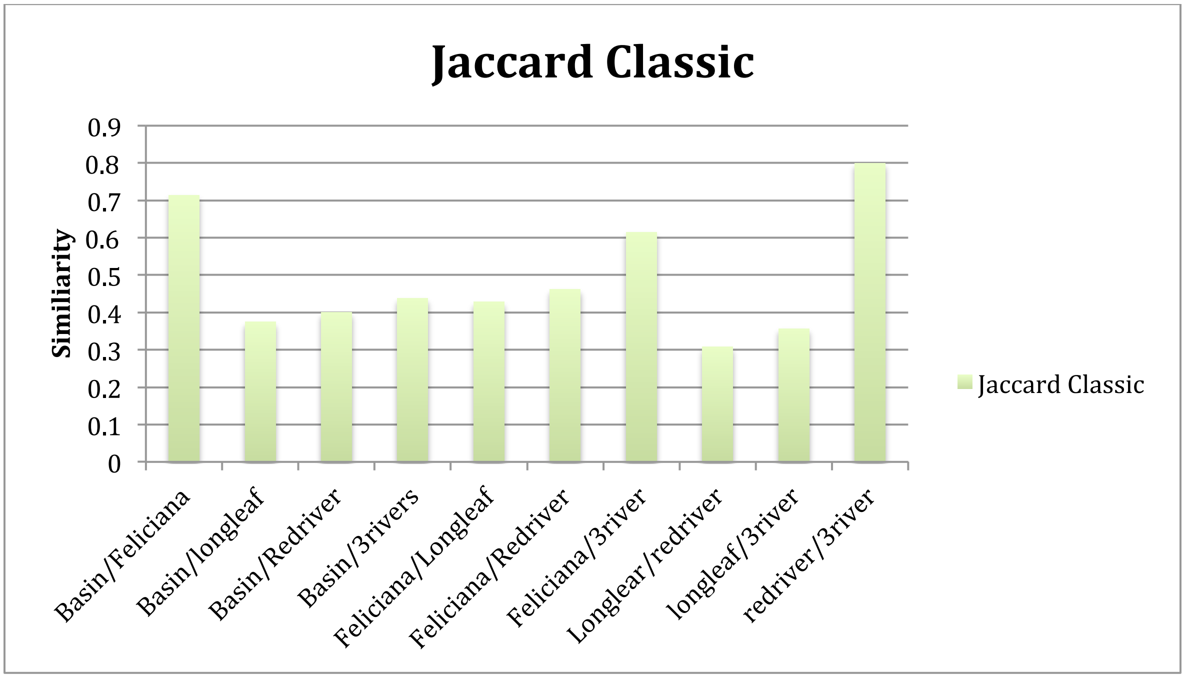


Plate 3.8-Jaccard's Classic based similarity between each site surveyed.

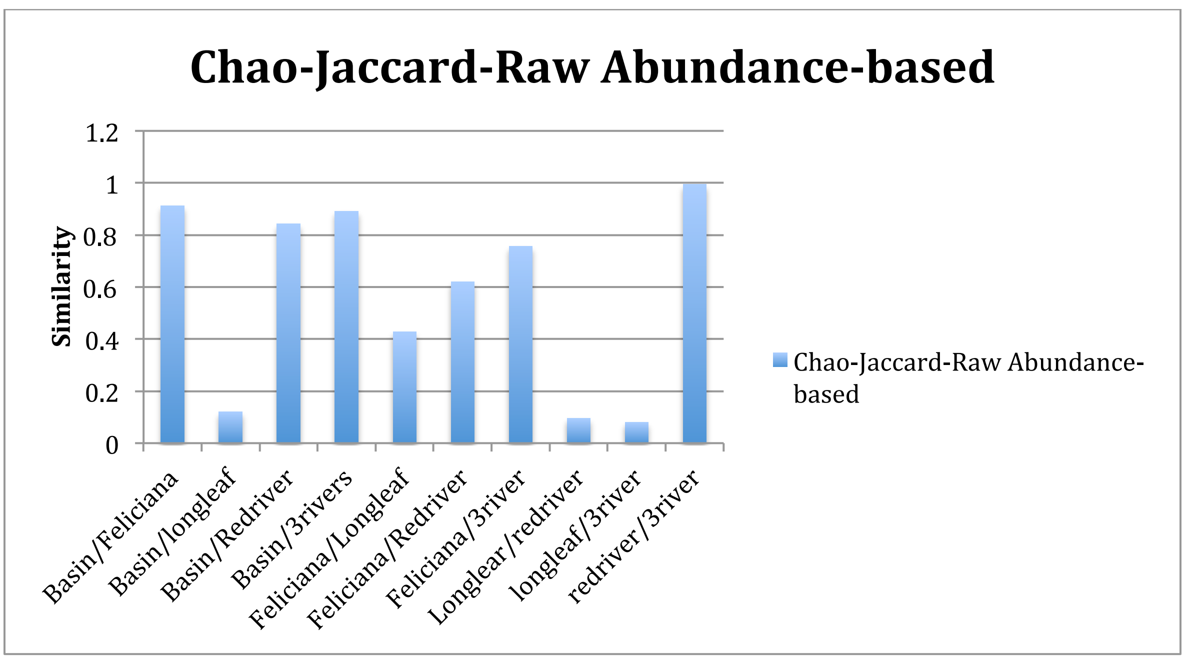


Plate 3.9-Chao-Jaccard- Raw Abundance based similarity between each site surveyed.

3.3.1 Species Inventory

Plate 3.10-*Panchlora nivea* (Linnaeus)
Linnaeus. 1758. Systema naturae 1, ed. 10, Holmiae 424 >> *Blatta nivea.*
Kirby, W. F. 1904. A synonymic Catalogue of Orthoptera. Orthoptera, Euplexoptera, Cursoria, et Gressoria. 1:153 >> *Panchlora.*
Panchlora nivea. (Photo, Forest Huval).

Diagnosis: Males and females with fully developed tegmina. Coloration green with yellow margins on pronotum. Front femora posses small or lacking uniform spines with no distal or genicular spines. Second femora posses no spines except for one genicular spine. Size ranges from 25-27 mm.

Comments: One out of 49 species of *Panchlora* is documented in the US. The majority of species are found in Central and South America. Two species are documented in Africa and three in the West Indies (Beccaloni, 2007). Adults readily came to lights. Nymphs were found in leaf litter, burrowing within and under decaying logs. Adults were caught year round but at much lower amounts. This species was absent from LLP and RRWMA. N=37

Plate 3.11-*Parcoblatta bolliana* (Saussure & Zehntner)
Saussure & Zehntner. 1893. Biol. Centr. Amer., Zool., Orthopt. 1(12):40 >> *Ischnoptera bolliana* .
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):715 >>*Parcoblatta bolliana.* (Photo, Forest Huval).

Diagnosis: Males with fully developed tegmina and females with reduced wings. Males not possessing modified abdominal tergites. Coloration consists of pale tan tegmina with dark brown pronotum possessing pale spot in the center. Females possess tegmina in the form of small slightly veinated wing-pads that never overlap. Front femora possessing four large spines followed by a row of minute pilliform spines ending with three large distal spines. Interocular space not wider that interoceli space. Body size between 12-13mm.

Comments: Males found perched on ferns and bushes after sunset. Few females found in leaf litter with no nymphs collected. The 88% adults were caught between the months of May and July with post July capture records declining until winter. Lawson (1967) documented *P. bolliana* as a strict grassland species but specimens were readily collected in forested areas. Adults were present in all sites surveyed. N=67.

Plate 3.12-*Parcoblatta caudelli* Hebard
Hebard. 1917. Mem. Amer. Ent. Soc. 2:122 >> *Parcoblatta caudelli.*
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):722 >> *Parcoblatta caudelli.* (Photo, Forest Huval).

Diagnosis: Males and females with fully developed tegmina and are capable of flight. Coloration uniformly pale in both sexes. Males possess modified median and first abdominal segment in the form of a pair of slightly elevated cetaceous clumps those segments. Front femora armed with more than 3 heavy spines followed by a row of smaller pilliform spines ending in three large distal spines. Size between 15.7 -15.9 mm.

Comments: Unique within the genus as both sexes are capable of flight. Adults were seen perching on trees logs and low hanging tree branches after sunset. This species was not collected from RRWMA and AB. 100% of Adult specimens were caught between months of June and July. N=20.

Plate 3.13-*Parcoblatta divisa* (Saussure & Zehntner)
Saussure & Zehntner. 1893. Biol. Centr. Amer., Zool., Orthopt. 1(12):40 >> *Ischnoptera divisa.*
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):723 >> *Parcoblatta divisa.* (Photo, Forest Huval).

Diagnosis: Males with fully developed tegmina and are capable of flight. Female tegmina reduced covering only 2/3 the length of the abdomen. Males possess modified median tergite in the form of mesal ridges overhanging a concave segment with ventral faces overhanging and bearing two extremities supplied with short hairs. Sizes range between 18- 21mm.

Comments: Males and females found in late evening into the night perched on trees and low hanging tree branches. Species found in all sites except LLP. Adults were caught between the months of May and August with the 76% of adults collected between June and July. N=78.

Plate 3.14-*Parcoblatta fulvescens* (Saussure & Zehntner)
Saussure & Zehntner. 1893. Biol. Centr. Amer., Zool., Orthopt. 1(12):36 >> *Ischnoptera uhleriana* variety *fulvescens*
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):721 >> *Parcoblatta fulvescens.* (Photo, Forest Huval).

Diagnosis: Males with fully developed tegmina and capable of flight. Females with reduced tegmina overlap and cover only 1/3 the length of the abdomen. Males possess modified median tergite represented by weakly raised mesal ridges supplied with two heavy tufts of hairs. Male coloration uniformly pale. Females possess reddish tan pronotum with uniformly dark abdomen. Size ranges from 14.6-16mm.

Comments: No specimens captured in the TRWMA or RRWMA. N=3.

Plate 3.15-*Parcoblatta lata* (Brunner von Wattenwyl)
Brunner von Wattenwyl. 1865. Nouveau Système des Blattaires. 135 >> *Ischnoptera lata*.
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):722 >> *Parcoblatta lata.* (Photo, Forest Huval).

Diagnosis: Males with fully developed tegmina and capable of flight. Female tegmina overlapping and reduced covering only 1/3 the length of the abdomen. Males possess modified median and first abdominal tergites represented by weakly elevated cephalic faces supplied with two heavy tufts of hair. Coloration uniformly tan in males and females. Last abdominal segments and cerci in both males and females black. Size ranges from 18-21mm.

Comments: Males and females usually found in bushes and low hanging tree branches. Specimens collected in all sites except for the Long Leaf Pine Savannah. N=15.

Plate 3.15-*Parcoblatta uhleriana* (Saussure)
Saussure. 1862. Rev. Mag. Zool. 2(14):169 >> *Ischnoptera uhleriana*.
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):719 >> *Parcoblatta uhleriana.* (Photo, Forest Huval).

Diagnosis: Males with fully developed tegmina and are capable of flight. Female tegmina not overlapping and reduced to small wing pads. Males possess modified median tergite represented by weakly raised mesal ridges supplied with two heavy tufts of hairs. Coloration in males uniformly pale with last four inner joints of cerci acutely produced and pointed. Female uniformly dark brown/black with last four inner cerci joints acutely pointed. Size ranges from 15-16.8 mm.

Comments: Only collected in LLP between the months of May and July. N=6.

Plate 3.16-*Parcoblatta virginica* (Brunner von Wattenwyl)
Brunner von Wattenwyl. 1865. Nouveau Système des Blattaires. 86 >> *Temnopteryx virginica*.
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae.
Orthopterorum Catalogus(13):718 >> *Parcoblatta virginica.* (Photo, Forest Huval).

Diagnosis: Males with fully developed tegmina and are capable of flight. Female tegmina overlapping and reduced, covering only 1/3 the length of the abdomen. Males possess modified median tergite represented by large mesal portion supplied with scattered minute hairs. Coloration in males uniformly pale. Female coloration similar to *P. fulvescens* but coloration of tegmina and pronotum less reddish tan and more hazel. Female abdomen may possess hazel spots or be completely dark. Size ranges from 14.5-15.2mm.

Comments: Collected at all sites. N=34.

Plate 3.17- *Parcoblatta zebra* (Brunner von Wattenwyl)
Hebard. 1917. Mem. Amer. Ent. Soc. 2:89 >> *Parcoblatta zebra.*
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):717 >> *Parcoblatta zebra.* (Photo, Forest Huval).

Diagnosis: Males with fully developed tegmina and capable of flight. Female tegmina overlapping and reduced, covering only 1/3 the length of the abdomen. Males possess modified median tergite represented by large tuft of agglutinated hairs. Tegmina in both sexes uniformly pale with two bands of brown in anterior portion of pronototum. Male abdomen possesses two ventral bands that continue the length of the abdomen. Female abdomen colored with brown band on the posterior of tergite and white band on the anterior portion of the tergite.

Comments: Absent from Atchafalaya Basin and West Feliciana preserve. N=25.

Plate 3.18-*Ischnoptera deropeltiformis* (Brunner von Wattenwyl)
Brunner von Wattenwyl. 1865. Nouveau Système des Blattaires. 87 >> *Temnopteryx deropeltiformis.*
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):747 >>*Ischnoptera deropeltiformis.* (Photo, Forest Huval).

Diagnosis: Males with fully developed tegmina capable of flight. Female tegmina overlapping and reduced, covering only 1/3 the length of the abdomen. Males possess modified sixth and seventh abdominal tergite represented by raised portion between two chitinous projections armed with teeth. Coloration for both sexes uniformly dark with bright red legs. Size ranges from 16-17mm.

Comments: Present in all areas surveyed. Males, female and nymphs were found in leaf litter after dark. Only males were seen perched on trees and low hanging branches. Males were only sex caught in santé malaise traps. N=72.

Plate 3.19-*Pseudomops septentrionalis* Hebard
Hebard. 1917. Mem. Amer. Ent. Soc. 2:156 >> *Pseudomops septentrionalis.*
Princis. 1969. In Beier [Ed.]. Blattariae: Subordo Epilamproidea. Fam.: Blattellidae. Orthopterorum Catalogus(13):945 >> *Pseudomops septentrionalis.* (Photo, Forest Huval).

Diagnosis: Males and females with fully developed tegmina and are capable of flight. Males possess modified second, third, sixth and seventh abdominal tergites. Both sexes possess red pronotum and black tegmina outlined in cream-colored margins. Females are notable more contrast than males with the dark tegmina being darker and the red pronotum being a slightly deeper red. Size ranges from 11.8-12 mm.

Comments: Most common and abundant species captured. Captured in all sites except for LLP. Nymphs were readily found in leaf litter. Adults were found perched on tree trunks bushed and low hanging tree branches. Adults were captured both at night and during the day. Both sexes were caught in santé malaise traps. N=934.

Plate 3.20-*Pseudomops* sp.
Pseudomops sp. (unidentified) (Photo, Forest Huval).

Diagnosis: Males and females with fully developed tegmina and are capable of flight. Males possess modified second, third, sixth and seventh abdominal tergites. Both sexes possess dark pronotum with red spot and band extending posteriorly with cream-colored margins. Tegmina black outlined in cream colored margins. Size ranges from 11.8-12 mm.

Comments: This species is yet to be identified and represents a new record for Louisiana. Only caught at RRWMA and TRWMA. N=18.

Plate 3.21- *Chorisoneura texensis* Saussure & Zehntner
Brunner von Wattenwyl. 1865. Nouveau Système des Blattaires. 255 >> *Chorisoneura*. (Photo, Forest Huval).

Diagnosis: Males and females with fully developed tegmina and are capable of flight. Hind wing possessing large appendicular field. Front femora possessing very small to no pilliform spines ending with only one large distal spine. Coloration uniformly tan. Size ranging from 9.5-10mm.

Comments: Only captured in Atchafalaya Basin and west Feliciana preserve. Adults collected perching on tree trunks in bushes and low-lying vegetation. Nymphs found in leaf litter and during colder times hidden under tree bark. N= 24.

Plate 3.22-*Cariblatta lutea* (Saussure & Zehntner)
Hebard. 1916. 147(Tabelle) >> *Cariblatta*. (Photo, Forest Huval).

Diagnosis: Males and females with fully developed tegmina. Male possessing modified sixth abdominal tergite. Male tegmina extending to apex of abdomen while females are slightly reduced. Tegmina uniformly pale tan with pronotum bearing distinct pattern. Size ranges from 6-6.5mm.

Comments: Species found in all sites except for RRWMA. Adults and nymphs found in leaf litter and perch in low-lying vegetation. N= 43.

Plate 3.23-*Plectoptera picta* Saussure & Zehntner
Saussure & Zehntner. 1893. Biol. Centr. Amer., Zool., Orthopt. 1(12):85 >> *Plectoptera picta.*
(Photo, Forest Huval).

Diagnosis: Males and females with fully developed tegmina capable of flight. Beetle like in appearance. Coloration consists of white with specks of maroon pattern on tegmina and large maroon spot on prontotum outlined in white. Front femora possessing only single distal spine. Size ranges from 2.5-3mm.

Comments: Only captured in Atchafalaya basin. Several other members of this geneus are known to be arboreal dwelling species. Likely that this species is arboreal and rarely descends pass the treetops. N=2.

Plate 3.24-*Euthlastoblatta gemma* Hebard (new record)
Hebard. 1917. Mem. Amer. Ent. Soc. 2:32 >> *Aglaopteryx gemma.*
(Photo, Forest Huval).

Diagnosis: Wings reduce to slightly overlapping wing pads in both sexes. Coloration yellow with pronotum bearing distinct pattern. Size ranges 8-9mm.

Comments: First record of *E. gemma* being found past the Mississippi Louisiana border. Collected at the Atchafalaya basin and Long leaf Pine Savannah sites. Viewed descending from tops of trees to feed on moss after sunset. Failed to capture in tree trunk traps and occurred once in santé malaise trap. Several members of this genus are known to be arboreal dwelling flightless species. N=7.

Plate 3.25- *Periplaneta fuliginosa* Serville
Serville. 1838[1839]. Librairie Encyclopédique de Roret [Collection des Suites à Buffon] 70 >> *Periplaneta fuliginosa.* (Photo, Forest Huval).

Diagnosis: Males and females with fully developed tegmina and are capable of flight. Front femor contains uniform row of heavy spines. Coloration mahogany.

Comments: Only species caught that is regarded as a pest or peridomestic. All other species documented, as pests were not collected in this survey. *P. fuliginosa* is the only peridomestic species to be native to North America. N= 4.

3.4 Discussion

This study was the first to survey the cockroach fauna of Louisiana. Louisiana is shown to have an impressive diversity of Blattodea. A total of 17 species were document in this survey. When other documented species are included the total number of species comes to 27 species. Eight out of the eleven species of *Parcoblatta* were collected. Lawson (1967) documented *Parcoblatta bolliana* as a strict grassland species but was readily collected in all biomes surveyed, none of which were grasslands. Two species collected acquired their first documentation in the area. These species include *Euthlastoblatta gemma* and *Pseudomops* inde. *Plectoptera picta* and *Euthlastoblatta gemma* were both rare species that are likely arboreal and likely won't occur often in any non-arboreal survey. Recorded species that were absent from the survey include *Blattella germanica, B. asahinai, B. vaga; Supella longipalpa; Parcoblatta pennsylvanica; P. americana, P. australasiae, P. brunnea; Blatta orientali; Supella longipalpa, Attaphila fungicola, Ischnoptera bilunata,* and *Pycnoscelus surinamensis*. Half of the species that were not collected were all cosmopolitan species that are pests. *Attaphila fungicola* is documented to be a myrmecophile of the Texas leaf cutter ant *Atta texana*. Traps weren't set in

cosmopolitan areas and within nests of *A. texana* the failure to collect specimens does not indicate a poor surveying method.

It was evident that the bulk of adult activity occurred between the months of May and August with nymphs either developing thought the winter months or going into diapause. The species diversity curves suggest that all areas in the study were adequately surveyed of species. When looking at Jaccards classic species similarity indices each site is shown to have large species overlap. The Chao-Jaccard-Raw Abundance-based similarity indices showed that when incorporating abundance each sites becomes much less similar. The LLP area showed a greater degree of differences between biota. LLP dropped from 37% to 12% when compared to the AB, 30% to 9% when compared to RRWMA and 35% to 8% when compared to TRWMA. Several species including *Pseudomops* inde, *Parcoblatta zebra* and *Euthlastoblatta gemma* were found within a limited range of areas while other common species such as *Pseudomops septentrionalis* and *Parcoblatta divisa* are absent from a single biota This is also seen by the lack of peridomestic species collected. With the exception of *Periplaneta fuliginosa,* no peridomestic species were collected in rural areas. This suggests that rural species of Blattodea show some degree of habitat preference, which is paralleled by the peridomestic species' preference of manmade structures.

CHAPTER 4: CONCLUSION

This study was the first to survey and document Blattodea species found within five different sites in Louisiana. One minor range extension and a possible new species of *Pseudomops* were documented. This study encompasses all three uses of faunistic surveys. The first documents the majority of species that occupy the areas surveyed, including range extensions and new species. The second provides information on how to more efficiently collect the species within the surveyed areas. The third provides general descriptions of each species collected using appropriate taxonomic characters. This will aid researchers and conservation biologists by providing a list species within the sites. This study also allows for accurate identification regardless of their level of expertise of the Blattodea within the study area.

Another objective of this study was a comparison of diversity of Blattodea and compare the similarity between each site. Sites showing the highest richness were the LLP and AB. *Euthlastoblatta gemma* and *Parcoblatta zebra* were only found in specific sites. *Pseudomops septentrionalis* was the most abundant species, but no specimens were collected at LLP. Only one state in the U.S. has published a checklist of Blattodea. When compared to the species checklist of Florida the species diversity of Louisiana was shown to be lower. The Florida checklist documented 38 species of Blattodea while Louisiana is only know to have 28 (Atkinson et al., 1990). Excluding pest species only 15 species are found in both Florida and Louisiana. A checklist from Puerto Rico documented a total of 58 species with only one found in Louisiana (Gutiérrez and Fisk, 1998). Both checklists were created using literature reviews and past documentations of species. While Louisiana showed low diversity when compared to Florida only a portion of the state was properly surveyed. A complete survey of the state and inclusion of all species documented would likely increase the species count of Louisiana.

The most recent key that focused on all species of cockroaches within North America was Hebard (1917). This current study provided the first key in almost a century that does not focus primarily on pest species. It also provides the first key to immature cockroaches. This key will aid future scientist and pest control agents in identifying cockroaches regardless of life stage or gender. These identification tools expand the knowledge of species in the study area, allowing rapid awareness of new and introduced species.

Lastly, an extensive literature review was compiled. This consolidation of information touches on morphological, taxonomical, behavioral, evolutionary and ecological aspects of this order. The majority of this information is spread out amongst literature both old and relatively new. This literature review also reveals that many taxonomic and systemic problems are still left unresolved. Many unique morphological traits along with previously unknown ecological relationships require further study. The consolidation of this information allows future researchers to gain a strong fundamental knowledge of this order, in addition to gaining knowledge of areas that require further study.

All three aspects of this thesis were designed to further the understanding of Blattodea as a whole. This thesis included behavioral, ecological and taxonomic realms of study. The most comprehensive portion was the literature review largely drway from Bell (2007) with updates. The literature review encompassed many facets of Blattodea literature touching on both intensively studied and weakly studied aspects of Blattodea. The survey reveals that while possessing a relatively low species number, several species can go undocumented and undescribed due to the absence of surveys. A larger survey encompassing the eastern half of the US may reveal previously unknown species and knowledge of habitat associations amongst

Blattodea species. An expansion of this key to the entirety of North America would provide the first all-encompassing Blattodea guide since Hebard (1917).

LITERATURE CITED

Arnold, J. W. (1974). Adaptive features on the tarsi of cockroaches. *International Journal of Insect Morphology and Embryology.* 3:317–334.

Atkinson, T. H., Koehler, P. G., & Patterson, R. S. (1990). Annotated checklist of the cockroaches of Florida (Dictyoptera: Blattaria: Blattidae, Polyphagidae, Blattellidae, Blaberidae). *Florida Entomologist*, 303-327.

Ayyad, M. A., Ghabbour, S. I., & Goodall, D. W. (1986). Hot deserts of Egypt and the Sudan. *Ecosystems of the World*, *12*, 149-20.

Barth, R. H. (1968a). The comparative physiology of reproductive processes in cockroaches. Part I. Mating behaviour and its endocrine control. *Advances in Reproductive Physiology.* 3:167–207.

Barth, R. H. (1968b). The mating behavior of *Gromphadorhina portentosa* (Schaum) (Blattaria, Blaberoidea, Blaberidae, Oxyhaloinae): an anomolous pattern for a cockroach. *Psyche.* 75:124–131.

Bartholomew, C. S., & Prowell, D. (2005). Pan compared to malaise trapping for bees (Hymenoptera: Apoidea) in a longleaf pine savanna. *Journal of the Kansas Entomological Society*, *78*(4), 390-392.

Bartholomew, C. S., & Prowell, D. (2006). Comparison of bee diversity in Upland and Wet flatwood longleaf Pine Savannas in Louisiana (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society*, *79*(2), 199-206.

Basset, Y. (2001). Invertebrates in the canopy of tropical rain forests. How much do we really know? *Plant Ecology.* 153:87–107.

Beccaloni, G. (1989). Why not study cockroaches? *Amateur Entomologists' Society Bulletin.* 48:176–178.

Beccaloni, G. W. (2014). Cockroach Species File Online. Version 5.0/5.0. World Wide Web electronic publication. <http://Cockroach.SpeciesFile.org> [accessed 1 December 2015*]

Bei-Bienko, G. Y. (1950). Blattodea. *In* Faune de l'URSS New Series 40. Akademiya Nauk SSSR, St. Petersburg. 332–336.

Bell, W. J., Roth, L. M., & Nalepa, C. A. (2007). *Cockroaches: ecology, behavior, and natural history*. JHU Press. Pp. 273

Bey-Bienko, G. Ya., (1950). Fauna of the U.S.S.R. Insects. Blattodea. Zoo!. Inst. Akad. Nauk, S.S.S.R., Moskva, n.s. 40, 342 pp. (Russian).

Blatchley, W. S. (1920). Orthoptera of Northeastern America, with Special Reference to the Faunas of Indiana and Florida. The Nature Publishing Company, Indianapolis. 784 pp.

Bohn, H. (1987). Reversal of the right-left asymmetry in male genitalia of some Ectobiinae (Blattaria: Blattellidae) and its implications on sclerite homologization and classification. *Insect Systematics & Evolution*, *18*(3), 293-303.

Bohn, H. (1993). Revision of the *panteli* group of *Phyllodromica* in Spain and Morocco (Blattaria: Blattellidae: Ectobiinae). *Entomologica Scandinavica.* 24:49–72.

Bohn, H., Picker, M., Klass, K.-D., and Colville, J. (2010). A Jumping Cockroach from South Africa, Saltoblattella montistabularis, gen. nov., spec. nov. (Blattodea: Blattellidae). *Arthropod Systematics and Phylogeny*, 68:53-69.

Boyer, S., and Rivault C.. (2003). La Réunion and Mayotte cockroaches: impact of altitude and human activity. *Comptes Rendus Biologies.* 326:S210–S216.

Braack, L.E.O. (1989). Arthropod inhabitants of a tropical cave "island" environment populated by bats. *Biological Conservation.* 48:77–84.

Breed, M. D., Hinkle, C. M. and Bell. W. J. (1975). Agonistic behavior in the German cockroach, *Blattella germanica. Zeitschrift für Tierpsychologie.* 39:24 – 32.

Brenner, R. J., & Pierce, R. R. (1991). Seasonality of peridomestic cockroaches (Blattoidea: Blattidae): mobility, winter reduction, and effect of traps and baits. *Journal of economic entomology*, *84*(6), 1735-1745.

Breznak, J. A. (1982). Biochemical aspects of symbiosis between termites and their intestinal microbiota. *In* Invertebrate- Microbial Interactions. J.M. Anderson, A.D.M. Rayner, and D.W.H. Walton, editors. Cambridge University Press, Cambridge. 173–203.

Breznak, J. A., Mertins, J. W. and Coppel. H.C. (1974). Nitrogen fixation and methane production in a wood eating cockroach *Cryptocercus punctulatus* Scudder (Orthoptera: Blattidae). *University of Wisconsin Forestry Notes.* 184:1–2.

Brodsky, A. K. (1994). The Evolution of Insect Flight. Oxford University Press, Oxford. 229 pp.

Brongniart, C. (1885). Les insectes fossiles des terrains primaires. Coup d'oeil rapide sur la faune entomologique des terrains paléozoïques. Bull. Soc. Amis Sci. Nat. Rouen 1885, 50—68.

Brossut, R., Dubois, P., Rigaud, J., & Sreng, L. (1975). Etude biochimique de la sécrétion des glandes tergales des Blattaria. *Insect Biochemistry*, *5*(6), 719-732.

Brossut, R., and Roth. L. M. (1977). Tergal modifications associated with abdominal glandular cells in the Blattaria. *Journal of Morphology.* 151:259–298.

Brousse-Gaury, P. (1977). Starvation and reproduction in *Periplaneta americana* L.: Control of mating behaviour in the female. *In* Advances in Invertebrate Reproduction. Vol. 1. K.G. Adiyodi and R.G. Adiyodi, editors. Peralam-Kenoth, Kerala,India.328–343.

Brown, V. K. (1973a). Aspects of the reproductive biology of three species of *Ectobius* (Dictyoptera: Blattidae). *Entomologia Experimentalis et Applicata.* 16:213–222.

Brown, V. K. (1983). Developmental strategies in British Dictyoptera: seasonal variation. *In* Diapause and Life Cycle Strategies. V.K. Brown and I. Hodel, editors. Dr W. Junk Publishers, The Hague. 111–125.

Brunet, P. C. J. (1951). The Formation of the Ootheca by *Periplaneta americana* I. The Microanatomy and Histology of the posterior part of the Abdomen. *Quarterly Journal of Microscopical Science*, *3*(18), 113-127.

Brunet, P. C. J. (1952). The formation of the ootheca by *Periplaneta americana* II. The structure and function of the left colleterial gland. *Quarterly Journal of Microscopical Science*, *3*(21), 47-69.

Brunet, P. C. J., & Kent, P. W. (1955). Observations on the mechanism of a tanning reaction in Periplaneta and Blatta. *Proceedings of the Royal Society of London B: Biological Sciences*, *144*(915), 259-274.

Burnham, K. P. & Overton. W.S. (1978). Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65, 623-633.

Burnham, K. P. & Overton. W.S. (1979). Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60, 927-936.

Camhi, J. M., Tom, W., & Volman, S. (1978). The escape behavior of the cockroach Periplaneta americana. *Journal of comparative physiology*, *128*(3), 203-212.

Campbell, F. L. (1929). The detection and estimation of insect chitin; and the irrelation of "chitinization" to hardness and pigmentation of the cuticula of the American cockroach, Periplaneta americana L. *Annals of the Entomological Society of America*, *22*(3), 401-426.

Capinera, J. L. (2008). Cockroaches (Blattodea). In *Encyclopedia of Entomology* (pp. 937-948). Springer Netherlands.

Chao, A. (1984). Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11, 265-270.

Chao, A., W.-H. Hwang, Chen Y.-C., and Kuo. C.-Y. (2000). Estimating the number of shared species in two communities. *Statistica Sinica* 10:227-246.

Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43, 783-791.

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, *8*(2), 148-159.

Chazdon, R. L., R. K. Colwell, Denslow, J. S. & Guariguata. M. R. (1998). Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. Pp. 285-309 in F. Dallmeier and J. A. Comiskey, eds. *Forest biodiversity research, monitoring and modeling: Conceptual background and Old World case studies.* Parthenon Publishing, Paris.

Chopard, L., (1929). Orthoptera palaearctica critica. Les Polyphagiens de la faune palearctique (Orth., Blatt.). Eos, 5: 215-358.

Clark, A. (2003). Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology & Evolution.* 18:573 – 581.

Clark, J. E., Cham, J. G., Bailey, S., Froehlich, E. M., Nahata, P. K., Full, R. J., & Cutkosky, M. R. (2001). Biomimetic design and fabrication of a hexapedal running robot. In *Robotics and Automation, 2001. Proceedings 2001 ICRA. IEEE International Conference on* (Vol. 4, pp. 3643-3649). IEEE.

Cochran, D. G. (1986). Biological parameters of reproduction in *Parcoblatta* cockroaches (Dictyoptera: Blattellidae). *Annals of the Entomological Society of America.* 79:861–864.

Cohen, A. C., and Cohen. J.L. (1976). Nest structure and microclimate of the desert cockroach *Arenivaga apacha* (Polyphagidae, Dictyoptera). *Bulletin of the Southern California Academy of Sciences.* 75:273–277.

Colby, D., & Prowell, D. (2006). Ants (Hymenoptera: Formicidae) in wet longleaf pine savannas in Louisiana. *Florida Entomologist*, *89*(2), 266-269.

Colwell, R. K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. 2006. *Consultado en: http://viceroy. eeb. uconn. edu/estimates*.

Colwell, R. K., & Coddington. J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society* (Series B) 345, 101-118.

Colwell, R. K., Chao A., GotellN. J. i, Lin S.-Y., Mao C. X., Chazdon R. L., and Longino. J. T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. *Journal of Plant Ecolog*y 5:3-21.

Corbet, P. S. (1961). Entomological studies from a high tower in Mpanga forest, Uganda. XII. Observations on Ephemeroptera, Odonata, and some other orders. *Transactions of the Royal Entomological Society of London.* 113:356–368.

Costa-Neto, E. M., & Oliveira, M. V. M. (2000). Cockroach is good for asthma: zootherapeutic practices in Northeastern Brazil. *Human Ecology Review*, *7*(2), 41-51.

Crespi, B. J., and Semeniuk. C. (2004). Parent-offspring conflict in the evolution of vertebrate reproductive mode. *The American Naturalist.* 163:635–653.

Daan, S., and Tinbergen. J. M. (1997). Adaptation of life histories. *In* Behavioural Ecology, an Evolutionary Approach. J.R. Krebs and N.B. Davies, editors. Blackwell Science, Ox- ford. 311–333.

de Carvalho Moretti, T., Quirán, E. M., Solis, D. R., Rossi, M. L., & Thyssen, P. J. (2011). Pycnoscelus surinamensis (Linnaeus, 1758)(Blaberoidea: Blaberidae), a cockroach with a possible association with the ant Brachymyrmex cordemoyi Forel, 1895 (Hymenoptera: Formicidae) and which may be exhibiting a domiciliation trend. *Symbiosis*, *53*(1), 37-39.

De Fine Licht, H. H., Andersen, A., & Aanen, D. K. (2005). Termitomyces sp. associated with the termite Macrotermes natalensis has a heterothallic mating system and multinucleate cells. *Mycological research*, *109*(03), 314-318.

Deitz, L. L., Nalepa, C., & Klass, K. D. (2003). Phylogeny of the Dictyoptera re-examined (Insecta). *Entomologische Abhandlungen*, *61*(1), 69-91.Ewing, L.S. 1967. Fighting and death from stress in a cockroach. *Science.* 155:1035–1036.

Dial, R., and Roughgarden. J. (1995). Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology.* 76:1821–1834.

Dudek, D. M., and Full. R. J. (2000). Spring-like behavior of the legs of running insects. *American Zoologist.* 40:1002–1003.

Durbin, E. J., & Cochran, D. G. (1985). Food and water deprivation effects on reproduction in female Blattella germanica. *Entomologia experimentalis et applicata*, *37*(1), 77-82.

Eberhard, W. G. (1996). Female Control: Sexual Selection by Crypic Female Choice. Princeton University Press, Prince- ton. 501 pp.

Edmunds, L. R. (1957). Observations on the biology and life history of the brown cockroach *Periplaneta brunnea* Burmeister. *Proceedings of the Entomological Society of Washington.* 59:283–286.

Evangelista, D. A., Chan, K., Kaplan, K. L., Wilson, M. M., & Ware, J. L. (2015). The Blattodea ss (Insecta, Dictyoptera) of the Guiana Shield. *ZooKeys*, (475), 37.

Farine, J.-P., R. Brossut, and Nalepa. C. A. (1989). Morphology of the male and female tergal glands of the woodroach *Cryptocercus punctulatus* (Insecta, Dictyoptera). *Zoomorphology.* 109:153–164.

Farnsworth, E. G. (1972). Effects of ambient temperature, humidity, and age on wingbeat frequency of *Periplaneta* species. *Journal of Insect Physiology.* 18:827–839.

Fischer, K., and Fiedler. K. (2002). Reaction norms for age and size at maturity in response to temperature: a test of the compound interest hypothesis. *Evolutionary Ecology.* 16:333 – 349.

Fisk, F. W., and Wolda. H. (1979). Key to the cockroaches of Central Panama. Part I. Flying species. *Studies on Neotropical Fauna and Environment.* 14:177–201.

Fraser, J., and Nelson. M. C. (1982). Frequency modulated courtship song in a cockroach. *Animal Behaviour.* 30:627– 628.

Full, R.J., and Tu. M. S. (1991). Mechanics of a rapid running insect: two, four, and six-legged locomotion. *Journal of Experimental Biology.* 156:215–231.

Gemeno, C., K. Snook, N. Benda, and Schal. C. (2003). Behavioral and electrophysiological evidence for volatile sex pheromones in *Parcoblatta* wood cockroaches. *Journal of Chemical Ecology.* 29:37–54.

Ghabbour, S. I., and Shakir. S. H. (1980). Ecology of soil fauna of Mediterranean desert ecosystems in Egypt. III. Analysis of *Thymelaea* mesofauna populations at the Mariut frontal plain. *Revue d' Écologie et de Biologie du Sol.* 17:327–352.

Ghabbour, S. I., and Mikhaïl. W. Z. A. (1978). Ecology of soil fauna of Mediterranean desert ecosystems in Egypt. II. Soil mesofauna associated with *Thymelaea hirsuta. Revue d' Écologie et de Biologie du Sol.* 15:333 – 339.

Ghabbour, S. I., Mikhaïl, W. and Rizk. M. A. (1977). Ecology of soil fauna of Mediterranean desert ecosystems in Egypt. I. Summer populations of soil mesofauna associated with major shrubs in the littoral sand dunes. *Revue d' Écologie et de Biologie du Sol.* 14:429 – 459.

Gillott, C. (2003). Male accessory gland secretions: modulators of female reproductive physiology and behavior. *Annual Review of Entomology.* 48:163–184.

Goodwin, N. B., N. K. Dulvey, and Reynolds. J.D. (2002). Lifehistory correlates of the evolution of live bearing in fishes. *Philosophical Transactions of the Royal Society of London B.* 357:259–267.

Gorb, S., & Beutel, R. (2001). Evolution of locomotory attachment pads of hexapods. *Naturwissenschaften*, *88*(12), 530-534.

Gorton, R. E. J. (1979). Agonism as a function of relationship in a cockroach *Shawella couloniana* (Dictyoptera: Blattellidae). *Journal of the Kansas Entomological Society.* 52:438 – 442.

Grandcolas, P. (1993). The origin of biological diversity in a tropical cockroach lineage: a phylogenetic analysis of habitat choice and biome occupancy. *Acta oecologica*, *14*(2), 259-270.

Grandcolas, P., (1994). Phylogenetic systematics of the subfamily Polyphaginae, with the assignment of *Cryptocercus* Scudder, 1862 to this taxon (Blattaria, Blaberoidea, Polyphagidae). Sys. Ent. 1994: 145-158.

Grandcolas, P. (1995a). Bionomics of a desert cockroach, *Heterogamisca chopardi* Uvarov, 1936 after the spring rainfalls in Saudi Arabia (Insecta, Blattaria, Polyphaginae). *Journal of Arid Environments.* 31:325–334.

Grandcolas, P. (1996) The phylogeny of cockroach families: a cladistic appraisal of morphoanatomical data. *Canadian Journal of Zoology*, 74, 508–527.

Grandcolas, P. (1997). *Gyna gloriosa,* a scavenger cockroach dependent on driver ants in Gabon. *African Journal of Ecology.* 35:168–171.

Greenwalt, D. E., & Vidlička, Ľ. (2015). Latiblattella avita sp. nov.(Blattaria: Ectobiidae) from the Eocene Kishenehn Formation, Montana, USA. *Palaeontologia Electronica*, *18*(1), 1-9.

Greven, H. and Zwanzig, N. (2013). Courtship, Mating, and Organisation of the Pronotum in the Glowspot Cockroach *Lucihormetica verrucosa* (Brunner von Wattenwyl, 1865) (Blattodea: Blaberidae). *Entomologie heute*, 25:77-97.

Grillou, H. (1973). A study of sexual receptivity in *Blabera craniifer* Burm. (Blattaria). *Journal of Insect Physiology.* 19:173–193.

Grimaldi, D., & Engel, M. S. (2005). *Evolution of the Insects*. Cambridge University Press.

Guillette, L. J., Jr. (1989). The evolution of vertebrate viviparity: morphological modifications and endocrine control. *In* Complex Organismal Functions: Integration and Evolution in Vertebrates. D.B. Wake and G. Roth, editors. John Wiley & Sons, Chichester, England. 219–233.

Gupta, A. P. (1947). On copulation and insemination in the cockroach *Periplaneta americana* (Linn.). *Proceedings of the National Institute of Sciences, India.* 13:65–71.

Gupta, B. L., and Smith. D.S. (1969). Fine structural organization of the spermatheca in the cockroach *Periplaneta americana. Tissue & Cell.* 1:295 – 324.

Gurney, A. B., & Roth, L. M. (1966). Two new genera of South American cockroaches superficially resembling Loboptera, with notes on bionomics (Dictyoptera, Blattaria, Blattellidae). *Psyche*, *73*(3), 196-207.

Gutiérrez, E., & Fisk, F. W. (1998). Annotated checklist of Puerto Rican cockroaches. *Transactions of the American Entomological Society*, 333-354.

Gwynne, D. T. (1998). Genitally does it. *Nature.* 393:734–735.

Haber, V. R. (1920). Oviposition by a cockroach, *Periplaneta americana* Linn. (Orth.). *Entomological News.* 31:190–193.

Hagan, H. R. (1951). Embryology of the viviparous insects.

Hagenbuch, B. E., Koehler, P. G., Patterson, R. S., & Brenner, R. J. (1988). Peridomestic cockroaches (Orthoptera: Blattidae) of Florida: their species composition and suppression. *Journal of medical entomology*, *25*(5), 377-380.

Hanula, J. L., & New, K. C. (1996). A trap for capturing arthropods crawling up tree boles.

Hawke, S. D., and Farley. R. D. (1973). Ecology and behavior of the desert burrowing cockroach, *Arenivaga* sp. (Dictyoptera, Polyphagidae). *Oecologia.* 11:262–279.

Hebard, M. (1916). Studies in the group Ischnopterites (Orthoptera, Blattidae, Pseudomopinae). *Transactions of the American Entomological Society*, 337-383.

Hebard, M. (1917). The Blattidae of North America north of the Mexican boundary. *Memoirs of the American Entomological Society.* 2:255–258.

Hellriegel, B., and Ward. P. I. (1998). Complex female reproductive tract morphology: its possible use in postcopulatory female choice. *Journal of Theoretical Biology.* 190:179 – 186.

Hennig, W. (1969). Die Stammesgeschichte der Insekten. Senckenbergbuch (Frankfurt a. M.) 49: 1–436.

Heyborne, W. H., Fast, M., & Goodding, D. D. (2012). The Madagascar Hissing Cockroach: A New Model for Learning Insect Anatomy. *The American Biology Teacher*, *74*(3), 185-189.

Holsinger, J. R. (2000). Ecological derivation, colonization, and speciation. *In* Ecosystems of the World. Vol. 30: Subterranean Ecosystems. H. Wilkens, D.C. Culver, and W.F. Humphreys, editors. Elsevier, Amsterdam. 399 – 415.

Hopkins, H. (2014). Phylogenetic revision of the genus Arenivaga (Rehn)(Blattodea: Corydiidae), with descriptions of new species, a key to the males, and an investigation of its ecological niche (Doctoral dissertation, The University of New Mexico).

Hopkins, H., & Miller, K. B. (2014). A first total evidence phylogeny of the genus Arenivaga (Rehn)(Blattodea, Corydiidae). Phylogenetic Revision of the Genus Arenivaga (Rehn)(Blattodea: Corydiidae), with Descriptions of New Species, a Key to the Males, and an Investivation of its Ecological Niche, 388.

Hubbell, T. H., and Goff. C.C. (1939). Florida pocket-gopher burrows and their arthropod inhabitants. *Proceedings of the Florida Academy of Sciences.* 4:127–166.

Inward, D., Beccaloni, G.,& Eggleton, P. (2007). Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biology Letters*, *3*(3), 331-335.

Izquierdo, I., and Oromi. P. (1992). Dictyoptera—Blattaria. *In* Encyclopaedia Biospeologica. Vol. 1. C. Juberthie and V. Decu, editors. Academie Roumaine, Bucharest. 295 – 300.

Johns, P. M. (1966). The cockroaches of New Zealand. *Records of the Canterbury Museum*, *8*(2), 93-136.

Juberthie, C. (2000a). Conservation of subterranean habitats and species. *In* Ecosystems of the World. Vol. 30: Subterranean Ecosystems. H. Wilkens, D.C. Culver, and W.F. Humphreys, editors. Elsevier, Amsterdam. 691–700.

Khalifa, A. (1950). Spermatophore formation in *Blattella germanica. Proceedings of the Royal Society of London A.* 25:53 – 61.

Kingsley, D., Quinn, R. D., & Ritzmann, R. E. (2006). A cockroach inspired robot with artificial muscles. In *Intelligent Robots and Systems, 2006 IEEE/RSJ International Conference on* (pp. 1837-1842). IEEE.

Kistner, D. (1982). The Social Insects' Bestiary. *In* Social Insects. Vol. III. H.R. Hermann, editor. Academic Press, New York.1–244.

Klass, K. D. (1997). *External male genitalia and phylogeny of Blattaria and Mantodea*. Zoologisches Forschungsinstitut; Museum Alexander Koenig.

Klass, K. D. (2003). Relationships among the principal lineages of Dictyoptera inferred from morphological data. *Entomologische Abhandlungen*, 61, 134–137.

Klass, K. D. & Eulitz, U. (2007). The tentorium and anterior head sulci in Dictyoptera and Mantophasmatodea (Insecta). *Zoologischer Anzeiger*, 246, 205–234.

Klass, K. D. & Meier, R. (2006). A phylogenetic analysis of Dictyoptera based on morphological characters. *Entomologische Abhandlungen*, 63, 3–50.

Klass, K.-D. (2001). Morphological evidence on blattarian phylogeny: "phylogenetic histories and stories" (Insecta, Dictyoptera). *Mitteilungen aus dem Museum für Naturkunde in Berlin, Deutsche Entomologische Zeitschrift.* 48:223–265.

Korchi, A., Brossut R., Bouhin H., and Delachambre. J. (1999). cDNA cloning of an adult male putative lipocalin specific to tergal gland aphrodisiac secretion in an insect (*Leucophaea maderae*). *FEBS Letters.* 449:125–128.

Kramer, S. (1956). Pigmentation in the thoracic musculature of cockroaches and related Orthoptera and the analysis of flight and stridulation. *Proceedings of the 10th International Congress of Entomology.* 1:569–579.

Krishna, K., Grimaldi, D. A., Krishna, V. & Engel, M. S. (2013). Treatise on the Isoptera of the world. Bulletin of the American Museum of Natural History, 377(Volumes 1–7), 1-2704. http://www.bioone.org/doi/abs/10.1206/377.1

Kristensen, N. P. (1991). Phylogeny of extant hexapods. *The insects of Australia*, *1*, 125-140.

Kugimiya, S., Nishida R., Sakuma M., and Kuwahara Y. (2003). Nutritional phagostimulants function as male courtship pheromone in the German cockroach *Blattella germanica. Chemoecology.* 13:169–175.

La Greca, M. (1954). Sulla struttura morfologica dell'apparato copulatore dei Mantoidei. *Annali dell'Istituto Superiore di Scienze e Lettere "S. Chiara" di Napoli*, *4*, 1-28.

Labandeira, C. C. (1994). *A compendium of fossil insect families*. Department of Paleobiology, National Museum of Natural History.

Landau, D., & Prowell, D. (1999). A partial checklist of moths from longleaf pine savannas in Louisiana (Insecta: Lepidoptera). *Transactions of the American Entomological Society*, 127-138.

Lawson, F. A. (1967). Ecological and collecting notes on eight species of *Parcoblatta* (Orthoptera: Blattidae) and certain other cockroaches. *Journal of the Kansas Entomological Society.* 40:267–269.

Lee, H.-J. (1994). Are pregnant females of the German cockroach too heavy to run? *Zoological Studies.* 33:200–204.

Levereault P. (1938).The morphology of the Carolina mantis. *University of Kansas* Science Bulletin 25: 577-633

Liang, J, Vrsansky, P. Ren, D. (2012). Variability and symmetry of a Jurassic nocturnal predatory cockroach (Blattida: Raphidiomimidae) *Revista Mexicana de Ciencias Gelogicas, 29 (2):411-421.*

Libersat, F., & Camhi, J. M. (1988). Control of sensory feedback by movement during flight in the cockroach. *Journal of Experimental Biology*, *136*, 483-488.

Litonjua, A. A., Carey, V. J., Burge, H. A., Weiss, S. T., & Gold, D. R. (2001). Exposure to cockroach allergen in the home is associated with incident doctor-diagnosed asthma and recurrent wheezing. *Journal of Allergy and Clinical Immunology*, *107*(1), 41-47.

Livingstone, D., and R. Ramani. (1978). Studies on the reproductive biology. *Proceedings of the Indian Academy of Sciences B.* 87:229–247.

Lo, N., Beninati, T., Stone, F., Walker, J. & Sacchi, L. (2007). Cockroaches that lack *Blattabacterium* endosymbionts: the phylogenetically divergent genus *Nocticola*. *Biology Letters*, 3, 327–330.

Lu, W., Valentine, B. D., Perez-Gelabert, D. E., & Gutiérrez, E. (2014). 0349. Ecology and Diversity of Cockroaches (Dictyoptera: Blattaria) from the Virgin Islands. *Insecta Mundi*, *2014*(0345-0355).

Mackerras, M. J. (1967). A blind cockroach from caves in the Nullarbor Plain (Blattodea: Blattellidae). *Journal of the Australian Entomological Society.* 6:39–44.

Mackerras, M. J. (1970). Blattodea (cockroaches). *Insects of Australia*.

Marks, E. P., and Lawson. F. A. (1962). A comparative study of the Dictyopteran ovipositor. *Journal of Morphology.* 111:139–172.

Mckittrick, E. A.,(1964). Evolutionary studies of cockroaches. Cornell Univ. Agric. Exp. Sta., N.Y. State ColI. of Agric. Mem. 389, 197 pp., PIs. 1-64.

Meller, P., and Greven. H. (1996b). Locomotor activity patterns of the viviparous cockroach *Nauphoeta cinerea* and their relation to the reproductive cycle. *Zoologische Beitraege.* 37:217–245.

Merritt, D. J. (2013). Standards of evidence for bioluminescence in cockroaches. *Naturwissenschaften*, *100*(7), 697-698.

Mizukubo, T., Hirashima, Y., & 平嶋義宏. (1987). Homology of Male Genital Sclerites in Cockroaches (Blattaria) by Means of Analysis of Their Association Patterns'. *九州大学農学部紀要*, *31*(3), 247-277.

Moore, A. J., Haynes K. F., Preziosi. R. F., and Moore. P. J. (2002). The evolution of interacting phenotypes: genetics and evolution of social dominance. *The American Naturalist.* 160:S143–S159.

Moore, A. J., Gowaty P. A., and Moore. P. J. (2003). Females avoid manipulative males and live longer. *Journal of Evolutionary Biology.* 16:523–530.

Moore, A. J., Gowaty P. A., W. Wallin, and Moore P. J.. (2001). Fitness costs of sexual conflict and the evolution of female mate choice and male dominance. *Proceedings of the Royal Society of London B.* 268:517–523.

Mullins, D. E., K. J. Mullins, and K. R. Tignor. (2002). The structural basis for water exchange between the female cockroach (*Blattella germanica*) and her ootheca. *Journal of Experimental Biology.* 205:2987–2996.

Nagamitsu, T., and Inoue. T. (1997). Cockroach pollination and breeding system of *Uvaria elmeri* (Annonaceae) in a lowland mixed dipterocarp forest in Sarawak. *American Journal of Botany.* 84:208–213.

Nalepa, C. A. (1988). Reproduction in the woodroach *Cryptocercus punctulatus* Scudder (Dictyoptera: Cryptocercidae): mating, oviposition and hatch. *Annals of the Entomological Society of America.* 81:637–641.

Newell, P. J. (2008). Pileated woodpeckers (Dryocopus pileatus) and saproxylic beetles in partial cut and uncut bottomland hardwood forests (Doctoral dissertation, University of New Brunswick).

Noirot, C. (1995). The gut of termites (Isoptera). Comparative anatomy, sytematics, phylogeny. I. Lower termites. *Annales de la Societe Entomologique de France, nouvelle série.* 31:197–226.

Nojima, S., M. Sakuma, Nishida. R, and Kuwahara. Y. (1999). A glandular gift in the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): the courtship feeding of a female on secretions from male tergal glands. *Journal of Insect Behavior.* 12:627–640.

Novotny, V., Basset, Y. and Kitching. R. L. (2003). Herbivore assemblages and their food resources. *In* Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy. Y. Basset, V. Novotny, S.E. Miller, and R.L. Kitching, editors. Cambridge University Press, Cambridge. 40 – 53.

Nutting, W. L. (1969). Flight and colony foundation. *In* Biology of Termites. Vol. 1. K. Krishna and F.M. Weesner, editors. Academic Press, New York. 233–282.

Palmer, M. W. (1991). Estimating species richness: The second-order jackknife reconsidered. *Ecology* 72, 1512-1513.

Parker, E. D. J. (2002). Geographic parthenogenesis in terrestrial invertebrates: generalist or specialist clones? *In* Reproductive Biology of Invertebrates. Vol. XI. R.N. Hughes, editor. John Wiley & Sons, Chichester. 93–114.

Parker, E. D. J., Selander R. K., Hudson R. O, and Lester. L. J. (1977). Genetic diversity in colonizing parthenogenetic cockroaches. *Evolution.* 31:836 – 842.

Peck, S. B., & Beninger, C. (1989). A survey of insects of the Florida Keys: cockroaches (Blattodea), mantids (Mantodea), and walkingsticks (Phasmatodea). *Florida Entomologist*, 612-617.

Pellens, R., D'Haese, C. A., Belle´s, X., Piulachs, M.-D., Legendre, F., Wheeler, W. C. & Grandcolas, P. (2007). The evolutionary transition from subsocial to eusocial behaviour in Dictyoptera: phylogenetic evidence for modification of the "shift-in-dependent-care" hypothesis with a new subsocial cockroach. *Molecular Phylogenetics and Evolution*, 43, 616–626.

Perry, D. R. (1978). *Paratropes bilunata* (Orthoptera: Blattidae): an outcrossing pollinator in a Neotropical wet forest canopy. *Proceedings of the Entomological Society of Washington.* 80:656–657.

Perry, D. R. (1986). Life Above the Jungle Floor. Simon and Schuster, New York. 170 pp.

Pitnick, S., T. Markow, and Spicer. G. S. (1999). Evolution of multiple kinds of female sperm-storage organs in *Drosophila. Evolution.* 53:1804–1822.

Polis, G. (1979). Prey and feeding phenology of the desert sand scorpion *Paruroctonus mesaensis* (Scorpionidae: Vaejovidae). *Journal of Zoology, London.* 188:333 – 346.

Pratt, H. D. (1988). Annotated checklist of the cockroaches (Dictyoptera) of North America. *Annals of the Entomological Society of America*, *81*(6), 882-885.

Princis, K., (1960). Zu Systematik der Blattarien, Eos 36: 427-449.

Princis, K., (1962). Blattariae: Subordo Polyphagoidea; Fam. Polyphagidae. In Beier, M. (ed.), Orthopterorum Catalogus, pars 3, pp. 1-74 (W Junk; s'Gravenhage).

Princis, K., (1963). Blattariae: Subordo Polyphagoidea; Fam. Homoeogamiidae, Euthyrrhaphidae, Latindiidae, Anacompsidae, Atticolidae, Attaphilidae. Subordo Blaberoidea; Fam. Blaberidae. In Beier, M. (ed.), Orthopterorum Catalogus, pars 4, pp. 75-172 (W Junk; s'Gravenhage).

Princis, K., (1974). Ergebnisse der Osterreichischen Neukaledonien Expedition 1965. Blattariae - Schaben. Ann. Naturhist. Mus. Wien 78: 513-521.

Pruthi, H. S. (1933). An interesting case of maternal care in an aquatic cockroach, *Phlebobotus pallens* Serv. (Epilamprinae). *Current Science (Bangalore).* 1:273.

Pryor, M. G. M. (1940). On the hardening of the ootheca of Blatta orientalis. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, *128*(852), 378-393.

Quinn, R. D., & Ritzmann, R. E. (1998). Construction of a hexapod robot with cockroach kinematics benefits both robotics and biology. *Connection Science*, *10*(3-4), 239-254.

Ragge, D. R. (1965). Grasshoppers, crickets and cockroaches of the British Isles.

Rajulu, J. S., and Renganathan. K. (1966). On the stabilization of the ootheca of the cockroach *Periplaneta americana. Naturwissenschaften.* 53:136.

Rau, P. (1940). The life history of the American cockroach, *Periplaneta americana* Linn. (Orthop.: Blattidae). *Entomological News.* 51:121–124, 151–155,186–189, 223–227, 273–278.

Real, R., & Vargas, J. M. (1996). The probabilistic basis of Jaccard's index of similarity. *Systematic biology*, 380-385.

Real, R. (1999). Tables of significant values of Jaccard's index of similarity. *Miscellània Zoològica*, *22*(1), 29-40.

Rehn, J. W. H. (1951). *Classification of the Blattaria as indicated by their wings (Orthoptera)* (No. 14). American Entomological Society.

Reuben, L. V. (1988). Some aspects of the bionomics of *Trichoblatta sericea* (Saussure) and *Thorax porcellana* (Saravas Saussure) (Blattaria). Ph.D. thesis, Department of Zoology. Loyola College, Madras, India. 211 pp.

Rocha e Silva Albuquerque, I., R. Tibana, J. Jurberg, and Rebordões. A. M. P. (1976). Contribuição para o conheci- mento ecológico de *Poeciloderrhis cribosa* (Burmeister) e *Poeciloderrhis verticalis* (Burmeister) comum estudo sobre a genitália externa (Dictyoptera: Blattariae). *Revue Su- isse de Zoologie.* 36:239–250.

Ross, M. H., and Mullins. D. E. (1995). Biology. *In* Understanding and Controlling the German Cockroach. M.K. Rust, J.M. Owens, and D.A. Rierson, editors. Oxford University Press, New York. 21–47.

Roth, L. M. (1962). Hypersexual activity induced in females of the cockroach *Nauphoeta cinerea. Science.* 138:1267–1269.

Roth, L. M. (1964). Control of reproduction in female cockroaches with special reference to *Nauphoeta cinerea.* I. First oviposition period. *Journal of Insect Physiology.* 10:915 – 945.

Roth, L. M. (1968). Oviposition behavior and water changes in the oöthecae of *Lophoblatta brevis* (Blattaria: Blattellidae: Plectopterinae). Psyche 75: 99–106.

Roth, L. M. (1967a). The evolutionary significance of rotation of the oötheca in the Blattaria. *Psyche.* 74:85–103.

Roth, L. M. (1968a). Oothecae of Blattaria. *Annals of the Entomological Society of America.* 61:83–111.

Roth, L. M. (1968b). Oviposition behavior and water changes in the oothecae of *Lophoblatta brevis* Blatteria: Blattellidae: Plectopterinae. *Psyche.* 75:99–106.

Roth, L. M. (1968c). Reproduction in some poorly known species of Blattaria. *Annals of the Entomological Society of America.* 61:571–579.

Roth, L. M. (1969). The evolution of male tergal glands in the Blattaria. *Annals of the Entomological Society of America.* 62:176–208.

Roth, L. M. (1970a). Evolution and taxonomic significance of reproduction in the Blattaria. *Annual Review of Entomology.* 15:75–96.

Roth, L. M. (1970b). The Male Genitalia of Blattaria. IV. Blaberidae Blaberinae. *Psyche: A Journal of Entomology*, *77*(3), 308-342.

Roth, L. M. (1971). Additions to the oöthecae, uricose glands, ovarioles, and tergal glands of Blattaria. Annals of the Entomological Society of America 64(1): 127–141.

Roth, L.M. (1973). Brazilian cockroaches found in birds nests, with descriptions of new genera and species. *Proceedings of the Entomological Society of Washington.* 75:1–27.

Roth, L. M. (1979). Cockroaches and plants. *Horticulture.* August:12–13.

Roth, L. M., (1988). Some cavernicolous and epigean cockroaches with six new species, and a discussion of the Nocticolidae (Dictyoptera: Blattaria). Rev. Suisse Zoo!. 95: 297-321.

Roth, L. M. (1982). Ovoviviparity in the blattellid cockroach, *Symploce bimaculata* (Gerstaecker) (Dictyoptera: Blattaria: Blattellidae). *Proceedings of the Entomological Society of Washington.* 84:277–280.

Roth, L. M. (1985a). A taxonomic revision of the genus *Blattella* Caudell (Dictyoptera, Blattaria: Blattellidae). *Entomologica Scandinavica Supplement.* 22:1–221.

Roth, L. M., (1985b). A revision of the cockroach genus *Parasymploce* (Dictyoptera: Blattaria: Blattellidae). J. Nat. Hist. 19: 431-532.

Roth, L. M. (1990a). A revision of the Australian Parcoblattini (Blattaria: Blattellidae: Blattellinae). *Memoirs of the Queens- land Museum.* 28:531–596.

Roth, L. M., (1990b). Cockroaches from the Krakatau Islands (Dictyoptera: Blattaria). Mem, Mus. Viet, 50: 357-378.

Roth, L. M. (1994). The beetle-mimicking cockroach genera Prosoplecta and Areolaria, with a description of Tomeisneria furthi gen. n., sp. n. (Blattellidae: Pseudophyllodromiinae) Insect Systematics & Evolution, 25(4): 419 – 426.

Roth, L. M., (1995a). The cockroach genera *Hemithyrsocera* Saussure, and *Symplocodes* Hebard (Dictyoptera: Blattellidae: Blattellinae). Invert. Tax. 9: 959-1003.

Roth, L. M. (2002). The cockroach genus Ischnoptera Burmeister. Part II. Species from the United States (Blattellidae: Blattellinae). *Transactions of the American Entomological Society*, 345-360.

Roth, L. M. (2003a). Blattodea (Cockroaches). *In* Grzimek's Animal Life Encyclopedia. Vol. 3. M. Hutchins, D.A. Thoney, and M.C. McDade, editors. Gale, Detroit. 147– 159.

Roth, L. M. (2003b). Some cockroaches from Africa and islands of the Indian Ocean, with descriptions of three new species (Blattaria). *Transactions of the American Entomological Society.* 129:163–182.

Roth, L. M. (2003c). Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). *Oriental Insects*, *37*(1), 1-186.

Roth, L. M., & Dateo, G. P. (1966). A sex pheromone produced by males of the cockroach Nauphoeta cinerea. *Journal of Insect Physiology*, *12*(2), 255-265.

Roth, L. M., and Willis. E. R. (1952a). A study of cockroach behavior. *American Midland Naturalist.* 47:66–129.

Roth, L. M., and Willis. E. R. (1952b). Tarsal structure and climbing ability in cockroaches. *Journal of Experimental Zoology.* 119:483–518.

Roth, L. M., and Willis. E. R. (1954a). *Anastus floridanus* (Hymenoptera: Eupelmidae) a new parasite on the eggs of the cockroach *Eurycotis floridana. Transactions of the American Entomological Society.* 80:29–41.

Roth, L. M., and Willis. E. R. (1954b). The reproduction of cockroaches. *Smithsonian Miscellaneous Collections.* 122:1–49.

Roth, L. M., & Willis. E. R. (1954c). Anastatus floridanus (Hymenoptera: Eupelmidae) a new parasite on the eggs of the cockroach Eurycotis floridana. *Transactions of the American Entomological Society*, 29-41.

Roth, L. M., and Willis. E. R. (1955a). Relation of water loss to the hatching of eggs from detached oothecae of *Blattella germanica* L. *Journal of Economic Entomology.* 48:57–60.

Roth, L. M., and Willis. E. R. (1955b). Water content of cockroach eggs during embryogenesis in relation to oviposition behavior. *Journal of Experimental Zoology.* 128:489– 509.

Roth, L. M., and Willis. E. R. (1956). Parthenogenesis in cockroaches. *Annals of the Entomological Society of America.* 49:31–37.

Roth, L. M., and Willis. E. R. (1957). The medical and veterinary importance of cockroaches. *Smithsonian Miscellaneous Collections.* 134:147.

Roth, L. M., and Willis. E. R. (1958a). An analysis of oviparity and viviparity in the Blattaria. *Transactions of the American Entomological Society.* 83:221–238.

Roth, L. M., and Willis. E. R. (1958b). The Biology of *Panchlora nivea* with observations on the eggs of other Blattaria. *Transactions of the American Entomological Society.* 83:195–207.

Roth, L. M., and Willis. E. R. (1960). The biotic associations of cockroaches. *Smithsonian Miscellaneous Collections.* 141:1–470.

Roth, L. M., and Willis. E. R. (1961). A study of bisexual and parthenogenetic strains of *Pycnoscelus surinamensis* (Blattaria, Epilamprinae). *Annals of the Entomological Society of America.* 54:12–25.

Roth, L. M., and Dateo. G. P. (1964). Uric acid in the reproductive system of males of the cockroach *Blattella germanica. Science.* 146:782–784.

Roth, L. M., and Naskrecki. P. (2003). A new genus and species of cave cockroach (Blaberidae: Oxyhaloinae) from Guinea, West Africa. *Journal of Orthoptera Research.* 12:57–61.

Roth, L. M., and Barth. R. H. (1967). The sense organs employed by cockroaches in mating behavior. *Behaviour.* 28:58 – 94.

Roth, L. M., and Cohen. S. H. (1968). Chromosomes of the *Pycnoscelus indicus* and *P. surinamensis* complex (Blattaria: Blaberidae: Pycnoscelinae). *Psyche.* 75:53–76.

Roth, S., Fromm, B., Ga¨de, G. & Predel, R. (2009). A proteomic approach for studying insect phylogeny: CAPA peptides of ancient insect taxa (Dictyoptera, Blattoptera) as a test case. *BioMed Central Evolutionary Biology*, 9, 12 pp.

Rugg, D., and Rose. H. A. (1984c). Reproductive biology of some Australian cockroaches (Blattodea: Blaberidae). *Journal of the Australian Entomological Society.* 23:113 – 117.

Rugg, D., and Rose. H. A. (1984b). The taxonomic significance of reproductive behavior in some Australian cockroaches. *Journal of the Australian Entomological Society.* 23:118.

Rugg, D., and Rose. H. A. (1990). Nymphal development and adult longevity of the Australian wood-feeding cockroach *Panesthia cribrata* (Dictyoptera: Blaberidae). *Annals of the Entomological Society of America.* 83:766–775.

Rugg, D., and Rose. H. A. (1991). Biology of *Macropanesthia rhinoceros* (Dictyoptera: Blaberidae). *Annals of the Entomological Society of America.* 84:575–582.

Schal, C. (1982). Intraspecific vertical stratification as a mate finding strategy in cockroaches. *Science.* 215:1405–1407.

Schowalter, T. D., & Ganio, L. M. (2003). Diel, seasonal and disturbance-induced variation in invertebrate assemblages. *Arthropods of tropical forests. Cambridge University Press, Cambridge*, 315-328.

Shelford, R. (1906). Studies of the Blattidae. VII. A new genus of symbiotic Blattidae. *Transactions of the Entomological Society of London.* 1906:515–519.

Shelford, R. (1907). Aquatic cockroaches). *Zoologist,* Ser. 4. 11:221–226.

Shelford, R. (1911). Descriptions of some new species of Blattidae. Ann. Mag. Nat. Hist. Ser. 8, vol.8: 1-13.

Shelford, R. (1912a). Mimicry amongst the Blattidae; with a revision of the genus *Prosoplecta* Sauss., and the description of a new genus. *Proceedings of the Zoological Society of London.* 82:358–376.

Shelford, R. (1916). A Naturalist in Borneo. T.F. Unwin, London. 331 pp.

Shine, R. (1989). Ecological influences on the evolution of vertebrate viviparity. *In* Complex Organismal Functions: Integration and Evolution in Vertebrates. D.B. Wake and G. Roth, editors. John Wiley & Sons, New York. 263–278.

Simon, D., and Barth. R. H. (1977a). Sexual behavior in the cockroach genera *Periplaneta* and *Blatta.* I. Descriptive aspects. *Zeitschrift für Tierpsychologie.* 44:80–107.

Simon, D., and Barth. R. H. (1977b). Sexual behavior in the cockroach genera *Periplaneta* and *Blatta.* III. Aggression and sexual behavior. *Zeitschrift für Tierpsychologie.* 44:306 – 322.

Smith, E. P. & van Belle, G. (1984). Nonparametric estimation of species richness. *Biometrics* 40, 119-129.

Smithsonian Institution, & Snodgrass, R. E. (1936). *Morphology of the Insect Abdomen-Part 3-the Male Genitalia*.

Snodgrass, R. E. (1937). The male genitalia of orthopteroid insects. *Smithsonian Miscellaneous Collections.* 96:1–107.

Snodgrass, R. E. (1952). Textbook of arthropod anatomy.

Snodgrass, R. E. (1957). *A revised interpretation of the external reproductive organs of male insects*. Smithsonian Institution 96 (5):1-107

Sreng, L. (1993). Cockroach mating behaviors, sex pheromones, and abdominal glands (Dictyoptera: Blaberidae). *Journal of Insect Behavior.* 6:715–735.

Stay, B., King A., and Roth. L. M. (1960). Calcium oxalate in the oothecae of cockroaches. *Annals of the Entomological Society of America.* 53:79–86.

Stehr, F. W. (1987). *Immature insects [Vol. 1]*. Kendall/Hunt Publishing Co..

Stokes, D. R., J. Malamud. G., and Schreihofer. D. A. (1994). Gender specific developmental transformation of a cockroach bifunctional muscle. *Journal of Experimental Zoology.* 268:364 – 376.

Storozhenko, S. Y. (1979). Behavioral and habitation conditions of the grylloblattid *Galloisiana kurentzovi* in the southern primorski krai—SFSR USSR (in Russian; English abstract). *Biologicheskie Nauki Moscow.* 2:18–21.

Tepper, J. G. O. (1894). The Blattariae of Australia and Polynesia: supplementary and additional descriptions and notes. *Transactions of the Royal Society of South Australia.* 18:165–189.

Tinkle, D. W., and Gibbons. J. W. (1977). The distribution and evolution of viviparity in reptiles. *Miscellaneous Publications of the University of Michigan.* 154:1–55.

Tscharntke, T., Steffan-Dewenter. I, Kruess, A. and Thies. C. (2002). Characteristics of insect populations on habitat fragments: a mini-review. *Ecological Research.* 17:229–239.

Van Herrewege, C. (1973). Contribution a l'étude des Blattaria de la faune Malgache. II. Description de huit espèces nouvelles appartenant aux genres *Gromphadorhina* Brunner v.W. et *Elliptorhina* gen. nov. *Bulletin de la Société Linnéenne de Lyon, 42 année, spécial du 150 anniversaire:*75 – 10.

Van Wyk, L. E. (1952). The morphology and histology of the genital organs of *Leucophaea maderae* (Fab.) (Blattidae, Orthoptera). *Journal of the Entomological Society of South Africa.* 15:3 – 62.

Vannier, G., and Ghabbour. S. I. (1983). Effect of rising ambient temperature on transpiration in the cockroach *Het- erogamia syriaca* Sauss. from the Mediterranean coastal desert of Egypt. *In* New Trends in Soil Biology. P. Lebrun, H.M. André, A. De Medts, C. Grégoire-Wibo, and G. Wauthy, editors. Dieu-Brichart, Louvain la Neuve. 441–453.

Vijayalekshmi, V. R., and Adiyodi. K. G. (1973). Accessory sex glands of male *Periplaneta americana* (L.). Part I. Quantitative analysis of some non-enzymatic components. *Indian Journal of Experimental Biology.* 11:512–514.

Vishniakova, V. N. (1973). New cockroaches (Insecta: Blattodea) from the Upper Jurassic sediments of Karatau ridge, p. 64-77. In Narchuk, E.P. (ed.), *Problems of the Insect Palaeontology*. *Lectures on the XXIV Annual Readings in Memory of N.A. Kholodkovsky (1-2 April, 1971*). Nauka, Leningrad.

Vlasáková, B., Kalinová, B., Gustafsson, M. H., & Teichert, H. (2008). Cockroaches as pollinators of Clusia aff. sellowiana (Clusiaceae) on inselbergs in French Guiana. *Annals of botany*, *102*(3), 295-304.

Vršanský, P. (2004). Cretaceous Gondwanian Cockroaches (Insecta, Blattaria). *Entomol Probl*, *34*, 49-54.

Vršanský, P. (2007). Jumping cockroaches (Blattaria, Skokidae fam. n.) from the Late Jurassic of Karatau in Kazakhstan. *Biologia, Bratislava*, 62:588-592.

Vršanský, P. (2008). New blattarians and a review of dictyopteran assemblages from the Lower Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, *53*(1), 129-136.

Vršanský, P. (2010). Cockroach as the earliest eusocial animal. *Acta Geologica Sinica (English Edition)*, *84*(4), 793-808.

Vršanský, P. and Chorvát, D. (2013). Luminescent system of *Lucihormetica luckae* supported by fluorescence lifetime imaging. *Naturwissenschaften*, 100(11):1099-1101.

Vršanský, P., Cifuentes-Ruiz, P., Vidlička, L., Čiampor, F. Jr., and Vega, F.J. (2011). Afro-Asian cockroach from Chiapas amber and the lost Tertiary American entomofauna. *Geologica Carpathica*, 62:463-475.

Vršanský, P., Oružinský, R., Barna, P., & Labandeira, C. C. (2014). Native Ectobius (Blattaria: Ectobiidae) From the Early Eocene Green River Formation of Colorado and Its Reintroduction to North America 49 Million Years Later. *Annals of the Entomological Society of America*, *107*(1), 28-36.

Vršanský, P., Vidlička, L., Barna, P., Bugdaeva, E., and Markevich, V. (2013). Paleocene origin of the cockroach families Blaberidae and Corydiidae: Evidence from Amur River region of Russia. *Zootaxa,* 3635:117-126.

Vršanský, P., Vidlička, L., Čiampor, F. Jr., and Marsh, F. (2012). Derived, still living cockroach genus *Cariblattoides* (Blattida: Blattellidae) from the Eocene sediments of Green River in Colorado, USA. *Insect Science*, 19:143-152.

Vršanský, P., Vishniakova, V. N., and Rasnitsyn, A. P. (2002). Order Blattida Latreille, 1810, p. 263-270. In Rasnitsyn, A.P. and Quicke, D.L.J. (eds). *History of Insects.* Kluwer Academic Publishers.

Ward, P. I. (1993). Females influence sperm storage and use in the yellow dung fly *Scatophaga stercoraria* (L.). *Behavioral Ecology and Sociobiology.* 32:313–319.

Ware, J. L., Litman, J., Klass, K.-D. & Spearman, L. A. (2008). Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. *Systematic Entomology*, 33, 429–450.

Wei D. and Ren D. (2013). Completely preserved cockroaches of the family Mesoblattinidae from the Upper Jurassic-Lower Cretaceous Yixian Formation (Liaoning Province, NE China) *Geologiva Carpathica*, 64, 4, 291—304.

Wendelken, P. W., and Barth. R. H. (1987). The evolution of courtship phenomena in Neotropical cockroaches of the genus *Blaberus* and related genera. *Advances in Ethology.* 27:1–98.

Wheeler, W. M. (1900). A new myrmecophile from the mushroom gardens of the Texan leaf-cutting ant. *The American Naturalist.* 34:851–862.

Wheeler, W. M. (1910). Ants: Their Structure, Development and Behavior. Columbia University Press, New York. 663 pp.

Wille, J. (1920). Biologie und Bekämpfung der deutschen Schabe (*Phyllodromia germanica* L.). *Monographien zur angewandten Entomologie.* 5:1–140.

Willis, E. R., & Lewis, N. (1957). The longevity of starved cockroaches. *J. Econ. Entomol*, *50*, 438-440.

Willis, E. R.,Riser G. R., and Roth. L. M. (1958). Observations on reproduction and development in cockroaches. *Annals of the Entomological Society of America.* 51:53–69.

Wolda, H., and Fisk. F.W. (1981). Seasonality of tropical insects. II. Blattaria in Panama. *Journal of Animal Ecology.* 50:827–838.

Wolda, H., and Wright. S. J. (1992). Artificial dry season rain and its effects on tropical insect abundance and seasonality. *Proceedings of the Koninklijke Nederlandse Akademie vanWetenschappen.*95:535–548.

Xian, X. (1998). Effects of mating on oviposition, and possibility of parthogenesis of three domestic cockroach species, the American cockroach, *Periplaneta americana;* the Smoky brown cockroach, *Periplaneta fuliginosa;* and the German cockroach, *Blattella germanica. Medical Entomology and Zoology.* 49:27–32.

Zhang Z. J., Schneider J.W. & Hong Y.Q. (2012). The most ancient roach (Blattida): A new genus and species from the earliest Late Car- boniferous (Namurian) of China, with discussion on the phylomorphogeny of early blattids. J. Systematic Palaeont. 11, 27—40.

Zherikhin, V. V. (1993) "HISTORY OF TROPICAL RAIN-FOREST BIOME." *Zhurnal Obshchei Biologii* 54.6: 659-666.

Zompro, O. and Fritzsche, I. (1999). *Lucihormetica fenestrata* n.gen., n.sp., the first record of luminescence in an orthopteroid insect (Dictyoptera: Blaberidae: Blaberinae: Brachycolini). *Amazoniana*, 15:211-21

APPENDIX A: EXAMPLE OF DATA SHEET

	Date:May 6 2014	
Colectors:l	Forest Huval, Zoe Huval	
temp		85
humidity		60%
Dayes since last precipitation:	7 days	
Location: lat long: 30 17' 2'' N 91 44' 1'' (Basin)		
Moon Phase:	First Quarter	
Dayes since last precipitation:	7 days	
Malaise 1 top:		0
malais 1 bottom		
Malaise 2 top:		0
Malais 2 bottom		
Malaise 3 top :	1 Pseudomops septentrionalis (top)	
Malaise 3 bottom:		
Pitfall Trap 1:		0
Pitfall Trap 2:	1 Nymph	
pitfall trap 3:		0
pitfall trap 4 :		0
pitfall trap 5 :		0
pitfall trap 6 :		0
pitfall trap 7 :		0
pitfall trap 8:		0
pitfall trap 9 :		0
pitfall trap 10:		0
Pit fall trap11:		0
pitfall trap12:		0
Hand collect day		0
hand collect night:	13 nymphs	
Light trap:		0
Beat Sheet:		0
nymph maturation	2- Psudomops septentrionalis may 16 2014 ,1- psudomops septentrionalis may 21 2014	
Locations: Atchalafay basin : 30 17' 2'' N 91 44' 1''		
Cabin:30.797471, -91.253081		
Bluebonnet swamp 30.368849,-91.107377		
Total (subject to change)	4- Psudomops septentrionalis 14- nymphs	
Comments		
	Hand colllecting yeilded most roaches but all were nymphs, nymphs appear to be late instar and majority were kept alive to reer and ID uppon maturation. Light trap beat sheet malais trap yeilde few to no blattodea.	

APPENDIX B: ABUNDANCE OF BLATTODEA SPECIES BY SITE AND DATE

Species are listed phylogenetically. (AP=Atchafalaya Basin 2014-2015; FP=Feliciana Preserve 2014-2015; LLP= Long Leaf Pine Savannah 1999-2001;RRWMA=Red River Wildlife Management Area 2006-2007; TRWMA=Three Rivers Wildlife Management area 2006-2007)

Species	AB	FP	LLP	RRWMA	TRWMA	Total
Blattidae						
Periplaneta fuliginosa	4	0	0	0	0	4
Ectobiidae						
Pseudomops septentrionalis	258	65	0	187	424	934
Pse. ind	0	0	0	8	10	18
Ischnoptera deropeltiformis	6	42	21	2	1	72
Cariblatta lutea	6	21	16	0	0	43
Parcoblatta bolliana	25	16	1	7	18	67
P. divisa	33	6	0	7	32	78
P. lata	2	2	0	5	6	15
P. fulvescens	1	1	1	0	0	3
P. caudelli	0	12	6	0	2	20
P. uhleriana	0	0	6	0	0	6
P. virginica	1	4	14	9	6	34
P. zebra	0	0	2	6	17	25
Euthlastoblatta gemma	6	0	1	0	0	7
Chorisoneura texensis	2	22	0	0	0	24
Plectoptera picta	2	0	0	0	0	2
Blaberidae						
Panchlora nivea	18	18	0	0	1	37
Total capture	364	209	68	231	517	1389

APPENDIX C SPECIES EXAMINED

USA Louisiana

St Martin Par. Atchafalaya Basin 30.282528, -91.728755 Col. Forest Huval

6 May 2014 20 May 2014
Malaise 1 top: 2- *Pseudomops septentrionalis*, 1-*Parcoblatta bolliana.*
Malaise 2 top: 3- *Pseudomops septentrionalis*, 2-*Parcoblatta divisa.*
Malaise 3 top: 1- *Pseudomops septentrionalis*, 1-*Parcoblatta divisa.*
Pitfall trap 4: 1-*Cariblatta lutea.*
Pit fall trap11: 1- *Pseudomops septentrionalis*, 1-*Cariblatta lutea*, 1-nymph.
Hand Collect Night: 5 nymphs (2-*Panchlora nivea*, 3-*Pseudomops septentrionalis)*, 6-*Pseudomops septentrionalis*, 1-*Plectoptera picta,* 2-*Cariblatta lutea*.

5 June 2014
Malaise 1 top: 10- *Pseudomops septentrionalis*, 1-*Parcoblatta divisa.*
Malaise 1 bottom1-*Parcoblatta bolliana.*
Malaise 2 top: 4- *Pseudomops septentrionalis* (2 destroyed).
Malaise 2 bottom2- *Pseudomops septentrionalis*
Malaise 3 top: 12- *Pseudomops septentrionalis*, 1-*Parcoblatta bolliana*.
Pitfall Trap 1: 1- *Pseudomops septentrionalis.*
Pitfall Trap 2: 1- *Pseudomops septentrionalis*.
Pitfall trap 9: 1- *Pseudomops septentrionalis*, 1-*Parcoblatta bolliana.*
Hand collect: 1-*Periplaneta fuliginosa*, 1- *Pseudomops septentrionalis*, 2-*Parcoblatta divisa*,
1-*Panchlora nivea*, 7-Nymph.
Beat Sheet: 1- *Pseudomops septentrionalis.*

28 July 201418 August 2014
Malaise 1 top: 4- *Pseudomops septentrionalis*
Malaise 3 top: 1- *Pseudomops septentrionalis*
Hand collect: 4-*Euthlastoblatta gemma*, 1-*Periplaneta fuliginosa* 3-nymphs (*Pseudomops septentrionalis*)

11 September 2014
Hand collect: 19nymphs(6 *Pseudomops septentrionalis*, 5-*Ischnoptera deropeltiformis*, 8-*Panchlora nivea*), 1-*Euthlastoblatta gemma*

4 November 2014
Hand collect: 28 nymphs (25-*Pseudomops septentrionalis*, 2-*Cariblatta lutea*, 1-*Parcoblatta divisa)*5-*Parcoblatta bolliana.*

Continued.

22 March 2015
Hand collect: 9- Parcoblatta nymph 2-*Panchlora nivea,* 2-*Chorisoneura texensis* 2 late instars roach (*Periplaneta fuliginosa*).

20 April 2015
Hand collect: 2-*Pseudomops septentrionalis*. 2- *Parcoblatta divisa*. 11- nymphs, (3-*Panchlora nivea*, 8-*Pseudomops septentrionalis*)

21 May 2015
Malaise 1 top: 3-*Parcoblatta bolliana*, 2-*Parcoblatta divisa*, 15-*Pseudomops septentrionalis*
Malaise 3 top: 1-*Parcoblatta bolliana*, 6-*Pseudomops septentrionalis*
Tree trunk trap 1: 5-*Pseudomops septentrionalis* 1-*Parcoblatta divisa*
Tree trunk trap 2:1-*Pseudomops septentrionalis*, 5-*Parcoblatta divisa*
Hanging Blacklight trap: 1-*Pseudomops septentrionalis*
Hand collect: 8-*Parcoblatta divisa* (females and nymphs), 13-*Pseudomops septentrionalis* (3nymphs), 7-*Parcoblatta bolliana*, 1-*Parcoblatta virginica*,1-*Parcoblatta fulvescens,* 1-*Parcoblatta lata*.

23 June 2015
Malaise 1 Top: 34-*Pseudomops septentrionali,s* 3-*Parcoblatta divisa*, 7-*Parcoblatta bolliana*
Malaise 2 Top: 10-*Pseudomops septentrionalis*, 2-*Parcoblatta divisa*, 2-*Parcoblatta bolliana*
Malaise 2 Bottom: 2-*Pseudomops septentrionalis.*
Malaise 3 Top: 3-*Pseudomops septentrionalis.*1-*Periplaneta fuliginosa*
Malaise 3 Bottom: 1-*Pseudomops septentrionalis.*
Tree trunk trap 1: 2-*Parcoblatta divisa.*
Tree trunk trap 2: 4- *Pseudomops septentrionalis.*
Hand collect night: 1-*Parcoblatta bolliana*, 1-*Pseudomops septentrionalis*, 1-*Parcoblatta divisa*, 2-*Periplaneta fuliginosa*

29 July 2015
Malaise 1 bottom: 1-*Parcoblatta divisa*, 1-*Pseudomops septentrionalis.*
Malaise 2 top: 3-*Parcoblatta zebra*, 1-*Pseudomops septentrionalis,*1-*Plectoptera picta.*
Tree trunk trap 1: 2-*Parcoblatta zebra*.
Hand collect: 1-*Panchlora nivea*, 3-*Parcoblatta bolliana*, 6-*Pseudomops septentrionalis*, 2-*Parcoblatta divisa*.

Continued.

West Feliciana Par. West Feliciana Preserve 30.765987, -91.271229 Col. Forest Huval

13 May 2014
Hand collect: 1- *Ischnoptera deropeltiformis.*

27 May 2014
Pitfall trap 5: 2- *Ischnoptera deropeltiformis*, 4- roach nymph (3-*Ischnoptera deropeltiformis,* 1- *Parcoblatta bolliana*)
Pitfall trap 6: 2- roach nymph (*Ischnoptera deropeltiformis*) 1-Parcoblatta
Pit fall trap11: 1-roach nymph
1-*Ischnoptera deropeltiformis*, 1- roach nymph
Hand collect day: 5-*Parcoblatta bolliana.*

14 June 2014
Malaise 1 Top: 1-*Parcoblatta divisa,* 1-*Parcoblatta virginica*, 2-*Parcoblatta caudelli*
Malaise 2 Top: 2-*Pseudomops septentrionalis.*
Hand collect night: 6-*Ischnoptera deropeltiformis*, 4-*Parcoblatta bolliana*, 1-*Chorisoneura texensis.*
Light trap: 1-*Panchlora nivea.*

30 July 2014
Malaise 1 Top: 1-*Ischnoptera deropeltiformis*, 1-*Panchlora nivea*, 2-*Pseudomops septentrionalis*,
2-*Parcoblatta caudelli*.
Malaise 1 bottom: 1-*Pseudomops septentrionalis.*
Malaise 2 Top: 10-*Pseudomops septentrionalis*, 2-*Ischnoptera deropeltiformis*,
1-panchlora niva, 1-*Parcoblatta bolliana*, 2-*Parcoblatta caudelli*.
Malaise 3 top: 1-*Parcoblatta caudelli*, 1-*Parcoblatta divisa,* 2-*Pseudomops septentrionalis.*

1 September 2014
Hand collect: 21 nymphs;(10-*Panchlora nivea*, 5-*Pseudomops septentrionalis*, 5-*Ischnoptera deropeltiformis*, 1-*Parcoblatta divisa*), 1-*Panchlora nivea*, 2-*Parcoblatta caudelli*.

2 October 2014
Hand collect: 22 nymphs:(19-*Pseudomops septentrionalis*, 1- *Parcoblatta bolliana*, 2-*Parcoblatta divisa*).

Continued.

24 November 2014
Hand collect: 9-nymphs (1-*Cariblatta lutea*, 8-*Chorisoneura texensis*)

17 March 2015
Hand collect: 9-nymphs (5- *Chorisoneura texensis*, 1-*Cariblatta lutea*).

29 April 2015
Malaise 3 Top: 1-*Parcoblatta bolliana.*
Hand collect: 4-*Chorisoneura texensis*, 9-*Cariblatta lutea.* 1-*Parcoblatta lata*, 5-*Ischnoptera deropeltiformis*, 1-*Parcoblatta bolliana*,

22 May 2015
Malaise 1 Top: 1-*Parcoblatta virginica,* 1-*Parcoblatta divisa*, 1-*Pseudomops septentrionalis*
Malaise 2 Top: 5-*Pseudomops septentrionalis*, 1-*Parcoblatta lata.*
Malaise 3 Top: 2-*Ischnoptera deropeltiformis*, 3-*Pseudomops septentrionalis*
Hand collect: 1-*Ischnoptera deropeltiformis*, 1-*Panchlora nivea*, 5-*Cariblatta lutea*, 1-*Chorisoneura texensis*, 1-*Pseudomops septentrionalis*, 1-*Parcoblatta divisa.*

25 June 2015
Malaise 1 Top: 4-*Pseudomops septentrionalis.*
Malaise 2 Top: 3-*Pseudomops septentrionalis*, 1-*Ischnoptera deropeltiformis*, 1-*Parcoblatta caudelli.*
Hand collect night: 3-*Cariblatta lutea*, 3-*Chorisoneura texensis*, 7-*Ischnoptera deropeltiformis*,
3-*Parcoblatta caudelli.*

30 July 2015
Malaise 1 Top: 3-*Pseudomops septentrionalis* 1-*Parcoblatta fulvescens*, 1-*Parcoblatta virginica.*
Malaise 2 Top: 1-*Cariblatta lutea*, 1-*Pseudomops septentrionalis*, 1-*Parcoblatta virginica.*
Malaise 3 top: 1-*Parcoblatta divisa*. 1-*Parcoblatta virginica.*
Hand collect night: 1-*Panchlora nivea*, 1-*Cariblatta lutea*, 2-*Chorisoneura texensis*, 1-*Parcoblatta caudelli.*
Total: 2-*Cariblatta lutea*, 4-*Pseudomops septentrionalis*, 3-*Parcoblatta virginica*, 1-*Parcoblatta divisa*, 3-*Pseudomops septentrionalis*, 1-*Parcoblatta fulvescens*

Continued.

Tensas. Tensas Par. 32.327334, -91.379875 Collectors C. Carlton

June-10-2006- June-24-2006
M35 B: 1-*Parcoblatta zebra.*
M36 T: 3-*Parcoblatta divisa*, 6-*Pseudomops septentrionalis*, 3-*Parcoblatta caudelli.*
M33T: 6-*Parcoblatta zebra.*
M34T: 1- *Parcoblatta fulvescens.*
M35 T: 5-*Parcoblatta zebra*, 1-*Parcoblatta divisa*, 3-*Pseudomops septentrionalis*
M36 B: 1-*Pseudomops septentrionalis*

Long Leaf Pine Savannah 30.476726, -90.046908 Collector D. Prowell

19 May 1999
MalaisC1: 6-*Ischnoptera deropeltiformis.*
Malaise C2: 1-*Parcoblatta zebra*, 1-*Parcoblatta virginica*, 1-*Cariblatta lutea*, 1-*Parcoblatta uhleriana*, 1-*Periplaneta fuliginosa.*
Malaise C3: *Ischnoptera deropeltiformis.*

16 June 1999
Malaise C1: 1-*Cariblatta lutea*, 1-*Parcoblatta caudelli*, 1- *Parcoblatta zebra.*
Malaise C2: 1-*Cariblatta lutea*, 1-*Ischnoptera deropeltiformis* 5- *Parcoblatta virginica*, 1-*Parcoblatta bolliana.*
Malaise C3: 1- *Cariblatta lutea.*

14 July 1999
Malaise C1: 2-*Ischnoptera deropeltiformis.*
Malaise C2: 2- *Parcoblatta virginica*, 3-*Cariblatta lutea.* 3-*Ischnoptera deropeltiformis.*

11 August 1999
Malaise C2: 2-*Parcoblatta virginica*, 1-*Ischnoptera deropeltiformis.*

18 April 2000
Malaise C1: 1-*Ischnoptera deropeltiformis.*
Malaise C2: 1-*Ischnoptera deropeltiformis*
Malaise C3: 2-*Ischnoptera deropeltiformis*

6 June 2000
Malaise C1: 1-*Ischnoptera deropeltiformis*
Malaise C2: 1-*Parcoblatta bolliana*

Malaise C3: 2-*Parcoblatta virginica*, 1-*Parcoblatta caudelli.*

6 July 2000
Malaise C3: 3-*Parcoblatta caudelli*, 2-*Parcoblatta virginica.*

1 August 2000
Malaise C1: 9-*Cariblatta lutea.*
Malaise C2: 1-*Ischnoptera deropeltiformis.*
Malaise C3: 1-*Euthlastoblatta gemma.*

1 May 2001
Malaise C1: *Ischnoptera deropeltiformis.*

1 June 2001
Malaise C1: 6-*Parcoblatta uhleriana*, 1-*Parcoblatta fulvescens*, 1- *Parcoblatta zebra.*

Concordia Par. Bayou Cocodrie 31.552973, -91.606610 Collector Patty Newell

May-6-May20-2006
M30T: 1-*Parcoblatta virginica.*

May-3-may-17-2007
M25 T: 1-*Parcoblatta divisa.*

June-2-june16-2007
M25 T-1: 1-*Pseudomops septentrionalis*
M25 B-1: 1-*Pseudomops septentrionalis*, 1-*Parcoblatta zebra*.
M26 T: 3-*Pseudomops septentrionalis*
M27 T: 1-*Parcoblatta zebra*, 2-*Pseudomops septentrionalis.*

July-2-July-16-2007
M25 T: 7- *Pseudomops septentrionalis*, 1-*Parcoblatta lata.*
M25 B: 1-*Parcoblatta zebra.*
M26 T: 3-*Pseudomops septentrionalis.*
M27 T: 3-*Pseudomops septentrionalis.*
M28 T: 8-*Pseudomops septentrionalis.*
M 30 T: 1-*Parcoblatta virginica.*
M29 T: 1-*Parcoblatta divisa.*

Tensas Par. Big Lake Wildlife Management Area 32.208662, -91.464083 Col. Patty Newell

May-6-2006-May-20-2006

Continued.

M31T: 1- *Ischnoptera deropeltiformis*
M35 B: 1-*Parcoblatta virginica.*
M36 T: 1-*Parcoblatta divisa.*
M36 B: 1-*Parcoblatta virginica.*

June-11-2006-June-24-2006
M31T: 3-*Parcoblatta divisa.*
M32 T: 1-*Parcoblatta divisa.*
M36 T: 1-*Parcoblatta caudelli*, 1-*Parcoblatta zebra*
M27 T: 2-*Pseudomops septentrionalis*, 1-*Ischnoptera deropeltiformis*, 1-*Parcoblatta zebra*
M29 T: 1-*Parcoblatta divisa.*
M30 T: 1-*Parcoblatta divisa*, 1-*Parcoblatta caudelli*, 1-*Parcoblatta zebra*
M31 B: 1-*Parcoblatta divisa.*

May-3-2007-May-17-2007
M31T: 1-*Parcoblatta divisa.*
M29 T: 1-*Parcoblatta divisa.*
M30 T: 2-*Parcoblatta divisa.*

June-2-2007-June-16-2007
M31T: 1-*Parcoblatta lata.*
M32 T: 1-*Parcoblatta zebra.*
M35 T: 1-*Parcoblatta zebra.*
M35 B: 1-*Parcoblatta lata.*
M36 T: 1-*Pseudomops septentrionalis*, 1-*Parcoblatta divisa.*
M36 B: 1-*Parcoblatta divisa*, 1-*Parcoblatta caudelli*, 1-*Parcoblatta zebra*
M34 T: 1-*Parcoblatta divisa.*

Franklin Par. Red River Wildlife Management Area 31.247596, -91.695556 Collector Patty Newell

May-5-2006-May-16-2006
M19 T: 1-*Pseudomops septentrionalis*.

May-24-2006-June-7-2006
M13 T: 4-*Pseudomops septentrionalis*.
M14 T: 27- *Pseudomops septentrionalis* 1-*Parcoblatta divisa*, 1-*Parcoblatta virginica*.
M 15T: 5-*Pseudomops septentrionalis*, 1-*Parcoblatta bolliana*
M16 T: 6-*Pseudomops septentrionalis* 1-*Parcoblatta zebra*, 1-*Parcoblatta divisa.*
M16B: 1-*Parcoblatta divisa.*
M17 T: 3-*Pseudomops septentrionalis.*

Continued.

M17 B: 1- *Parcoblatta zebra.*
M18 B: 1-*Parcoblatta bolliana.*

May-25-2006-June-8-2006
M10 T: 9-*Pseudomops septentrionalis.*
M11 T: 3-*Pseudomops septentrionalis,* 1-*Parcoblatta bolliana.*
M12 T: 2-*Pseudomops septentrionalis* 1-*Parcoblatta bolliana*, 1-*Parcoblatta divisa.*

June-6-2006-July-11-2006
M13 T: 8- *Pseudomops septentrionalis.*

June-27-2006-July-11-2006
M14 T: 7- *Pseudomops septentrionalis* 1- *Parcoblatta zebra.*
M14 B: 1- *Pseudomops septentrionalis* 1-*Parcoblatta zebra*, 1-*Parcoblatta virginica.*
M 15: T4- *Pseudomops septentrionalis* 1-*Parcoblatta virginica*
M16 T: 2- *Pseudomops septentrionalis.*
M17 T: 4- *Pseudomops septentrionalis*.
M17 B: 2- *Pseudomops septentrionalis*
M18T: 8- *Pseudomops septentrionalis*.

July-13-2006-July-24-2006
M20 T: 1- *Pseudomops septentrionalis.*

July-11-2006-July-24-2006
M19 T: 5- *Pseudomops septentrionalis*, 1-*Parcoblatta zebra.*
M19 B: 1- *Pseudomops septentrionalis.*
M21 T: 1- *Pseudomops septentrionalis.*

Mar-16-2007-Mar-30-2007
M06 T: 1-*Parcoblatta divisa.*

May-18-2007-June-6-2007
M01T: 1-*Pseudomops septentrionalis*
M01B: 1-*Parcoblatta bolliana.*
M03 T: 2-*Parcoblatta lata*, 1-*Parcoblatta virginica.*
M03 B: 1-*Pseudomops septentrionalis*
M04 T: 1-*Pseudomops septentrionalis*
M04 B: 1-*Parcoblatta divisa.*
M05 T: 1-*Pseudomops septentrionalis* 1-*Parcoblatta lata.*
M06 T: 1-*Pseudomops septentrionalis* 1-*Parcoblatta virginica.*

Continued.

M06 B: 1-*Parcoblatta virginica*, 1-*Parcoblatta bolliana.*

June-17-2007-July-1-2007
M01T: 2- *Parcoblatta lata*, 2-*Pseudomops septentrionalis.*
M02 T: 11-*Pseudomops septentrionalis.*
M03 T: 6-*Pseudomops septentrionalis* 1-*Parcoblatta zebra*, 1-*Parcoblatta virginica*
M04T: 7-*Pseudomops* indet 1-*Parcoblatta divisa.*
M04 B: 1-*Pseudomops septentrionalis.*
M05 T: 6-*Pseudomops septentrionalis* 1-*Parcoblatta divisa.*
M06 T: 12-*Pseudomops septentrionalis*
M06 B: 1 *Pseudomops septentrionalis* 1-*Parcoblatta virginica.*

June-10-2007-June-24-2007
M19 T: 1-*Parcoblatta virginica*, 4-*Pseudomops septentrionalis*
M20 T: 5-*Pseudomops septentrionalis* 1-*Ischnoptera deropeltiformis,* 1-*Parcoblatta bolliana.*
M20 B: 1-*Parcoblatta zebra.*
M21 T: 3-*Pseudomops septentrionalis*
M22 T: 14-*Pseudomops septentrionalis* 1-*Parcoblatta zebra.*
M23 T: 2-*Pseudomops septentrionalis*
M24 T: 5-*Pseudomops septentrionalis,* 1-*Ischnoptera deropeltiformis*.
M24 B: 1-*Parcoblatta zebra*

Franklin Par. Three Rivers Wildlife Management Area 31.076615, -91.649551 Collector Patty Newell

April-19-2006-May-19-2006

M06 T: 1-*Pseudomops septentrionalis*
M07B: 1-*Parcoblatta zebra.*
M14B: 1-*Parcoblatta zebra.*

May-5-2006-May-19-2006
M24 T 1-*Pseudomops septentrionalis,* 1-*Parcoblatta divisa.*

May-25-2006-June-8-2006
M01T: 9-*Pseudomops septentrionalis*
M02 T: 19-*Pseudomops septentrionalis*, 2- *Parcoblatta virginica*, 1-*Parcoblatta bolliana* 1- *Pseudomops* indet
M03T: 18- *Pseudomops septentrionalis,* 1-*Parcoblatta divisa*, 2-*Parcoblatta zebra*, *Parcoblatta virginica*, 1-*Parcoblatta bolliana*
M03 B: 2- *Pseudomops septentrionalis*
M04T: 18- *Pseudomops septentrionalis*.1-*Pseudomops* Indet, 3-*Parcoblatta zebra.*

Continued.

M04B: 1-*Pseudomops septentrionalis* 1-*Parcoblatta bolliana*, 1-*Parcoblatta zebra*
M05 T: 18-*Pseudomops septentrionalis*, 2-*Parcoblatta zebra*, 1-*Parcoblatta bolliana*,

1-*Cariblatta lutea.*
M06 T: 15-*Pseudomops septentrionalis* 2-*Parcoblatta divisa*, 1-*Parcoblatta caudelli.*
M07T: 5-*Pseudomops septentrionalis*, 2-*Parcoblatta divisa.*
M08 T: 5-*Pseudomops septentrionalis,* 1-*Parcoblatta zebra*
M09 T: 8-*Pseudomops septentrionalis,* 1-*Parcoblatta virginica.*

June-26/27-2006-July-10-2006
M01T: 11-*Pseudomops septentrionalis*
M02 T: 7-*Pseudomops septentrionalis*, 1-*Parcoblatta lata*, 1- *Parcoblatta virginica*
M03T: 1-*Pseudomops septentrionalis.*
M07T: 6-*Pseudomops septentrionalis,* 1-*Parcoblatta divisa*.
M08 T: 7-*Pseudomops septentrionalis.*
M09 T: 6-*Pseudomops septentrionalis*.
M10 T: 8-*Pseudomops septentrionalis*, 1-*Ischnoptera deropeltiformis*
M10B: 1- *Parcoblatta virginica.*
M11 T: 5- *Pseudomops septentrionalis*, 1-*Pseudomop* Indet, 1-*Parcoblatta zebra.*
M11B: 2-*Pseudomops septentrionalis.*

July-11-July-24- 2006
M22 T: 5-*Pseudomops septentrionalis.*
M23 T: 2-*Pseudomops septentrionalis.*
M24 T: 1-*Pseudomops septentrionalis,* 1-*Parcoblatta virginica.*

2-May-2007-16-May-2007
M19 T: 1-*Parcoblatta bolliana*, 1-*Parcoblatta divisa.*
M20 T: 4-*Parcoblatta bolliana.*
M 21 T: 1-*Parcoblatta divisa.*
M23 T: 1- *Parcoblatta virginica.*

May-16/18-2007-June-1-2007
M08 T: 3-*Pseudomops septentrionalis,* 2-*Parcoblatta divisa*
M09 T: 5-*Pseudomops septentrionalis.*
M10 T: 2-*Pseudomops septentrionalis.*
M11 T: 4-*Pseudomops septentrionalis*, 3- *Parcoblatta divisa*, 1-*Parcoblatta lata*, 1-*Parcoblatta bolliana.*
M13 T: 6-*Pseudomops septentrionalis.*
M 13 B: 1-*Pseudomops septentrionalis.*
M14 T: 2-*Pseudomops septentrionalis,* 1-*Parcoblatta caudelli*, 2-*Parcoblatta lata.*
M15 T: 5-*Pseudomops septentrionalis.*

Continued.

M16 T: 5-*Pseudomops septentrionalis,* 2-*Parcoblatta bolliana*, 1-*Parcoblatta caudelli.*
M17 T: 6-*Pseudomops septentrionalis*, 1-*Parcoblatta bolliana.*
M18 T: 3-*Pseudomops septentrionalis,* 2-*Parcoblatta divisa.*

June-2-2007-June-16-2007

M20 T: 4-*Pseudomops septentrionalis,* 2-*Parcoblatta bolliana.*
M 20 B: 1-*Parcoblatta zebra.*
M 21 T: 6-*Pseudomops septentrionalis.*
M23 T: 1- *Parcoblatta divisa.*
M24 T: 9- *Pseudomops septentrionalis,* 1- *Parcoblatta divisa*.

June-6-2007-July-1-2007
M10 T: 3-*Pseudomops septentrionalis*.
M11 T: 5-*Pseudomops septentrionalis*.
M07T: 13-*Pseudomops septentrionalis*.
M08 T: 21-*Pseudomops septentrionalis,* 1-*Parcoblatta divisa*, 1-*Parcoblatta zebra.*
M09 T: 12-*Pseudomops septentrionalis,* 1-*Parcoblatta divisa*, 2-*Parcoblatta lata.*
M12 T: 2-*Pseudomops septentrionalis.*
M13 T: 3-*Pseudomops septentrionalis*, 1-*Parcoblatta divisa.*
M14 T: 6-*Pseudomops septentrionalis,* 1-Panchlora nivea, 1-*Parcoblatta divisa*, 1-*Parcoblatta caudelli.*
M15 T: 3-*Pseudomops septentrionalis.*
M16 T: 11-*Pseudomops septentrionalis* 1-*Parcoblatta zebra*, 1-*Parcoblatta divisa.*
M16B: 2-*Pseudomops septentrionalis.*
M17 T: 17- *Pseudomops septentrionalis*, 1-*Parcoblatta divisa.*
M18 T: 1- *Parcoblatta zebra*, 6-*Parcoblatta divisa*.

July-1-2007-July-15-2007
M19 T: 6-*Pseudomops septentrionalis,* 1- *Pseudomops* Indet.
M20 T: 15-*Pseudomops septentrionalis*, 1-*Parcoblatta zebra*, 1-*Parcoblatta divisa.*
M 21 T: 3-*Pseudomops septentrionalis,* 1-*Parcoblatta divisa*.
M22 T: 1-*Pseudomops septentrionalis.*
M23 T: 2-*Pseudomops septentrionalis*, 1-*Parcoblatta lata*.
M24 T: 4- *Pseudomops septentrionalis.*

APPENDIX D: GUIDE TO LOUISIANA (COCKROACHES) BLATTODEA

Over the past decade, the majority of Cockroach taxonomists have passed away leaving a huge gap in the scientific community. The majority of studies done by these elite few were predominantly genus revisions, descriptions of new species and systemic groupings of closely related taxa. Comprehensive keys to taxa in a particular area are essential to allow non-specialist to identify unknown species and to help foster future generations' interest in studying specific taxa. The last comprehensive key to North American Blattodea was published in 1917 by Morgan Hebard and failed to provide even a basic key to Blattodea nymphs. Since this publication numerous genus revisions, species descriptions and introduced species have arisen in North America. This publication will provide the most modern key to the Blattodea of Southern Louisiana, offering keys to males, females and nymphs. This publication will be the first to provide a comprehensive key to the nymphal stages of the Blattodea life cycle while submitting a new format of species level plates that provide a broad representation of all relevant morphological characters used in family, genus and species level identification. Multiple keys and plates were modified and merged in addition to adding several new characters. Keys modified include Roth (2003), Heberd (1917) and Ster (1987). The keys were formatted to provide basic novel characters in addition to systemic and taxonomically relevant morphological characters when describing given species. This bridges the gap between novel diagnoses and taxonomically accurate diagnoses of species allowing novices to identify a species and a seasoned entomologist to recognize the important morphological characters common amongst taxa.

Key to Families (Males)

1) Genitalia complex; structure heavily sclerotized; femoral spines of legs typically heavy and uniform (Plate. 4.5, D); oviparous…….Blattidae …….Key 1
-- Genitalia not as complex; structure less heavily sclerotized; with spines on femora not present, consisting of a row of heavy spines followed by a row of shorter spines, or spines gradually reducing in size (Plate. 4.8, E),…….2

2) Cerci relatively long, extending much further than sub-genital plate and obviously segmented; genitalia less complex, typically with three principle sclerites,, one of which comprises a hook-shaped phallomere …….Ectobiidae
…….Key 2.
-- Cerci generally short, not extending past, or just barely extending past, sub-genital plate, may or may not be segmented, with similarly shaped styles present; hook like sclerotized phallomere always on right side, may be reduced…….Blaberidae
Key 3

Key 1
Blattidae

1) Structure heavily sclerotized; femoral spines heavy and typically uniform in size…….2

2) Arolia present; reduction of tegmina to pads…….3
-- Arolia absent (Plate. 4.1, B); size medium (< 30 mm); tegmina only covering roughly "two-thirds" of abdomen…….*Blatta orientalis* Linnaeus

3) Tegmina reduced to pads…….4
-- Tegmina and wings developed either extending beyond apex of abdomen or covering roughly two thirds of abdomen…….5

4) Tegmina represented by sub-quadrate pads that may touch or weakly overlap with each other and second thoracic segment; abdominal tergites acute at the posterior lateral margins (Plate. 4.2,A); color dark brown (Plate. 4.2, A) …….*Eurycotis floridana* Stål
-- Tegmina represented by sub-ovate lateral pads that extend somewhat over second thoracic segment but never touching opposing wing-pad; tergites with black and yellow pattern coloration (Plate. 4.3, A)…….*Neostylopyga rhombifolia* Stoll

5) Dorsal segments specialized; coloration reddish brown; pronotum pattern ill defined yellow ring that form point on anterior with two yellow areas on posterior (Plate. 4.4, A)…….*Periplaneta americana* Linnaeus
-- Dorsal segments of abdomen with median segment un-modified,; color ranging from reddish brown to dark blackish brown…….6

6) Ventral surface of sub-genital plate simple; pronotum bearing yellow outlining on lateral margins ..…….7
-- Ventral surface of sub-genital plate modified (Plate. 4.5, B) ; coloration dark blackish brown(Plate. 4.5, A)…. *Periplaneta fuliginosa* Serville

7) Tegmina reddish brown; pronotum bearing ill defined yellow ring fig (Plate. 4.6, A)…….*Periplaneta brunnea* Burmeister
-- Tegmina dark brown; two yellow spots on the marginal field with pronotal pattern having clearly defined yellow ring (Plate. 4.7, A) …….*Periplaneta australasiae* Fabricius

Key 2
Ectobiidae

1) Distal end of front femora armed with at least three heavy spines (Plate. 4.8, E); genital hook located on left side(Plate. 4.8, C)….. (Ectobiinae,) (Blattellinae), (Attaphilinae) (Nyctiborinae) …….2

-- Distal end of front femora armed with less than three heavy spines (Plate. 4.25 , E); genital hook located on right side (Plate. 4.25, C)…….(Psudophyllodromiinae)…….18

2) Ventral margin of front femora with 3 heavy spines followed by row of smaller spines;
-- Ventral margin of front femora with row of 4 heavy spines followed by row of smaller spines (Plate. 4.10, E), coloration ranging from light tan to dark brown never showing bright colors…….4

3) Pronotum distinctly colored red with a creamy margin; tegmina colored black with creamy margin and fully developed, extending past the apex of abdomen; second, third sixth and seventh abdominal segment specialized (Plate. 4.8, A)…….*Pseudomops septentrionalis* Hebard
-- Pronotum black with creamy margin, red spot in the center of the pronotum with red band extending to posterior of the pronotum (Plate. 4.9, A)……..*Pseudomops indet*

4) Pronotum distinctly marked with two longitudinal bands that extend along the body; abdomen with sixth, seventh and supra anal plate modified …….Blattella…….5
-- Pronotum typically not bearing obvious longitudinal bands, if bands are present they do not extend along body.......7

5) Face bearing dark vertical band starting from between eyes extending down to more than two thirds of face (Plate. 4.10, B)…… *Blattela vaga* Hebard
-- Face not bearing dark vertical band…….6

6) Tegmina significantly longer that abdomen, capable of flight; typically found outdoors (Plate. 4.11, B)…….*Blatta asahinai* Mizukubo
-- Tegmina exceeding to or slightly past apex of abdomen, not capable of flight; typically found indoors…….*Blatta germanica* Linnaeus

7) Only sixth and seventh dorsal abdominal segment bearing mesad modification; coloration either dark black with bright red legs or dark brown with pronotum bearing longitudinal stripes that do not continue along the body……. *Ischnoptera* …….8
-- Median and/or abdominal segment modified, or not; with sixth and seventh abdominal segment never specialized; color ranging from dark brown to light tan, never brightly colored……. *Parcoblatta*…….9

8) Coloration black with bright red orange legs (Plate. 4.13, A)……. *Ischnoptera deropeltiformis* Brunner von Wattenwyl
-- Coloration dark brown; two lateral stripes on pronotum that do not extend along the body (Plate. 14.4, A)……. *Ischnoptera bilunata* Saussure

9) Dorsal surface un-modified, showing no setae or ridges on any tergites; interocular space no wider than space between ocelli (Plate. 4.15, B); pronotum dark with lighter markings in center (Plate. 4.15, A)…….*Parcoblatta bolliana* Saussure & Zehntner, 1893
-- Dorsal surface modified bearing setae and either weak or strong ridges ……..10

10) Only median segment specialized…….11
--Median and first abdominal segment modified…….15

11) Median segment has a single modification in middle of tergite(Plate. 4.16, B; 4.17, B) …….12
-- Median tergites showing twin modifications (Plate. 4.18, B; 4.19, B) …….13

12) Modified area represent by a large mesal portion with scattered minute setae fig (Plate. 4.16, B) ……. *Parcoblatta virginica* Brunner von Wattenwyl
--Modified area represented by large tuft of setae (Plate. 17 ,B); pronotum and abdomen banded fig (Plate. 4.17, A)…….*Parcoblatta zebra* Hebard

13) Modified segment with weak or no ridges bearing heavy tuffs of hairs (Plate. 4.19,B; 4.20, B)…….14
-- Pronotum pattern as in (Plate. 4.18, A); modified segment with distinct mesal ridges with over hanging parts bearing heavy tufts of hairs (Plate. 4.18, B)…….*Parcoblatta divisa* Saussure & Zehntner

14) Cerci with inner apical points acutely protruding (Plate. 14.9, D)…….*Parcoblatta uhleriana* Saussure
-- Cerci with inner apical points simple and not protruding (Plate. 4.20, D)…….*Parcoblatta fulescens* Saussure & Zehntner

15) Tegmina and pronotum colored tan; modified segments with weak to no ridges which bear two sets of heavy tufts of hair on each segment (Plate. 4.22, B; 4.23, B)…….16
-- Tegmina dark brown; pronotum maroon distinctly lined with white on margins (Pl. 4.21, B); modified segments with distinct measal and first abdominal segment ridges with overhanging areas bearing tufts of hair(Plate. 4.21, B)…….*Parcoblatta pennsylvanica* De Geer

16) Size less than 15mm ; abdomen uniformly colored…….*Parcoblatta caudelli,* Hebard
-- Size larger than 15 mm; last 4 abdominal segments including cerci darker than first abdominal segments…….*Parcoblatta lata,* Brunner von Wattenwyl

17) Ventral margin of front femora with numerous spines, row of heavy spines followed by row of smaller spines (Plate. 4.24, E)…….18
--Ventral margin of front femora unarmed or with few spines…….21

18) Tegmina not reduced, just reaching to or exceeding apex of abdomen…….19
-- Tegmina reduced to wing pads ,…….20

19) Tegmina pale yellow with two bands of brown stretching horizontally (Plate. 4.24, A); with strong oblique discoid sectors; sixth abdominal segment specialized *Supella longipalpa* Fabricius

-- Tegmina just reaching apex of abdomen; dorsal surface not specialized; pronotum with pale but distinct pattern (Plate. 4.25, A); sub-genital plate symmetrical with two small pubescent styles with produced portion in between them broad leaving no empty space (Plate. 4.25, B)…….*Cariblatta lutea lutea* Saussure & Zehntner

20) Only fourth tarsal joint bearing a pulvillus; dorsal surface not specialized and tegmina reduced; pronotum with distinct pattern (Plate. 4.26, D)……. *Euthlastoblatta gemma* Princis
-- Tegmina reduced, only covering roughly two thirds of abdomen; sub-genital plate with two small pubescent styles, with produced portion between them not broader than long, leaving empty space between them (Plate 4.25, H); only found in Florida…….*Cariblatta lutea minima* Hebard

21) Tarsal claw simple not possessing teeth; wing contains appendicular field that is slightly wider than long (Plate. 4.27, B); not beetle like…….*Chorisoneura texensis* Saussure & Zehntner
-- Tarsal claws specialized with microscopic teeth in internal margin; appendicular field of hind-wing large; beetle like…….*Plectoptera*…….22

22) Beetle like; tan coloration; thin dark band stretching horizontally between eyes …….*Plectoptera poeyi* Saussure
-- Beetle like; creamy white coloration with small spots of dark maroon on tegmina; large dark maroon spot on pronotum (Plate. 4.26, A); cream colored band stretching horizontally between eyes…….*Plectoptera picta* Saussure & Zehntne.

Key 3
Blaberidae

1) Ventral margin of front femora with no or few spines (Plate. 4.28, B); tegmina present; size coloration lime green(Plate. 4.28, A)…….*Panchlora nivea* Linnaeus

Key to Families (Females)

1) Front femora equipped with stout spines either uniform in size or large spines followed by row of smaller spines (Plate. 4.5, D) (Plate. 4.8, E); Female produces hard ootheca that is carried and eventually dropped; cerci obviously segmented, relatively long usually extending past sub genital plate…….2
-- Ventral margin of front femora with no or weak spines (Plate. 4.28, B); cerci generally short rarely extending further than sub-genital plate; female has brood sack in which eggs are incubated internally, typically ovoviviparous, rare viviparous…….Blaberidae…….Key 4

2) Heavily sclerotized insect; femoral spines all heavy and of relative equal size(Plate. 4.5, D); sub-genital plate divided into a pair of valves by a longitudinal groove

(bivalvulat); when female carries ootheca it is kept vertically and not rotated or retracted oviparous…….Blattidae…….Key 5
--Sub-gential plate not valvular; when female is carrying ootheca it is rotated retracted into abdomen…….Ectobiidae…….Key 6

Key 4
Blaberidae

1) Small size coloration lime green (Plate. 4.28, A)……. *Panchlora nivea*
-- Small size tegmina brown; pronotum black with anterior portion of pronotum brown (Plate. 4.29, A)…….*Pycnoselus surinamensis*

Key 5
Blattidea

1) Arolia present large in size…….2
-- Arolia absent (Plate. 4.1, B); size ranging 20–27 mm tegimina represented by small rounded wing pads; coloration blackish brown (Plate. 4.1, A)…….*Blatta orientalis*

2) Tegmina severely reduced…….3
-- Tegmina showing little or no reduction, still reaching or extending past apex of abdomen……4

3) Tegmina represented by sub quadrate pads that may touch or weakly overlap with each other at second thoracic segment if at all; abdominal tergites acute at the posterior lateral margins; color dark brown (Plate. 4.2, A)…….*Eurycotis floridana*
-- Tegmina represented by sub-ovate lateral pads that extend somewhat over second thoracic segment but never touching opposing wing-pad; coloration black with unique yellow coloration pattern (Plate. 4.3, A)…….*Neostylopyga rhombifolia*

4) Coloration solid, shining blackish brown(Plate. 4.5, A)…….*Periplaneta fuliginosa*
-- Coloration not solid; pronotoum colored brownish red and yellow…….5

5) Pronotum patterned with brownish red with ill defined yellow ring that form point on anterior with two yellow areas on posterior end; tegmina unicolorous…….6
-- Tegmina dark brown with two yellow spots on the marginal field with pronotal pattern having clear defined yellow ring (Plate. 4.7, A)…….*Periplaneta australasiae*

6) Supra-anal plate with a deep acute angulate median emargination, cerci elongate and slender (Plate. 4.4, C); pronotal pattern more defined.…….*Periplaneta Americana*
-- Supra-anal plate with a much less deep median emargination; cerci less elongate not as slender (Plate. 4.6, B); pronotal pattern much less defined…….*Periplaneta brunnea*

Key 6
Ecotbiidae

1) Distal end of front femora armed with at least three heavy distal spines (Plate. 4.8, E)…….2
--Distal end of front femora armed with less that three heavy distal spines (Plate.24.7, D)…….18

2) Tegmina not reduced; pronotum red with creamy outline; tegimina black with creamy outline; ventral margin of front femora armed with row of 3 heavy spines followed by row of smaller spines (Plate. 4.8, E)…….3 *Psudomops septentrionalis*
-- Tegmina severely or somewhat reduced; pronotal coloration ranging from black to dark brown to light tan; ventral margin of front femora with row of 4 heavy spines followed by row of smaller spines…….4

3) Pronotum red with creamy outline……. *Psudomops septentrionalis*
-- Pronotum black with creamy margin, red spot in the center of the pronotum with red band extending to posterior of the pronotum (Plate. 4.9, A)……..*Pseudomops indet*

4) General coloration solid shining black with limbs bright red; tegmina reduced to weakly overlapping sub-quadrate pads (Plate. 4.13, A)…….*Ishnoptera deropeltiformis*
-- General coloration ranging from light tan to dark brownish black; limbs never bright red …….5
5) Coloration light tan with two distinct longitudinal bands on pronotum that extend along body…….17
-- Coloration ranging from dark brown to pale tan but never showing the two longitudinal bands that extend along body……. *Parcoblatta* …….6

6) Wings severely reduced, represented by small lobiform pads (Plate. 4.15, A); compact form; interocular space less than space between antennal socket (Plate. 4.15, B); tegmina show little venation …….*Parcoblatta bolliana*
-- Reduced wings present…….7

7) Tegmina decidedly to greatly reduced…….8
-- Tegmina moderately reduced neither lateral nor truncate distad …….11

8) Tegmina roundly sub-triangular lateral pad; general color dark; supra-anal plate with lateral margin convergent and weakly concave…….*Parcoblatta ulheriana*
-- Tegmina represented by sub-quadrat slightly overlapping pads…….9

9) Tegmina truncate extending to apex of anal field…….10
-- Tegmina truncate extending beyond apex of anal field; size large; coloration tannish brown hays russet blackish brown, sixth abdominal segment as in fulvescens (Plate 4.23, A)…….*Parcoblatta lata*

10) Size small; with slender form; hazel coloration; margin of sixth dorsal abdominal segment weakly convex mesad; supra-anal plate with lateral margin normally straight and converging to sharply round apex (Plate. 4.16, A)…….*Parcoblatta virginica*
-- Size medium; form broad; color blackish brown sixth dorsal abdominal segment weakly convex mesad supra-anal plate with lateral margins normally straight and convergent to sharply rounded apex (Plate. 4.20, A)…….*Parcoblatta fulvescens*

11) Apex of tegmina not reaching beyond apex of supra-anal plate; sustained flight impossible; general color dark brown with various paler markings …….12
-- Tegmina with apices reaching beyond apex of supra-anal plate; capable of flight; color ochraeous tawny (Plate. 4.22, A)…….*Parcoblatta caudelli*

12) Distinct pronotal pattern; pale bands on abdominal segments as in (Plate 4.17, A)…….*Parcoblatta* zebra
--Dorsal surface of abdomen not banded…….13

13) Size medium to large; coloration less solid; with lateral margin of pronotum paler in center and contrast of white medial margins less defined (Plate. 4.18, A)…….*Parcoblatta divisa*
-- Large size; coloration solid brown with well defined strikingly pale lateral margins (Plate. 4.21, A)…….*Parcoblatta pensylvanica*

14) Face bearing dark vertical band starting from between eyes extending town to more than two thirds of face (Plate. 4.10, B)…….*Blattela vaga*
-- Face not bearing dark vertical band…….15

15) Tegmina significantly longer that abdomen; capable of flight typically found outdoors (Plate. 4.11, B)…….*Blatta asahinai*
-- Tegmina exceeding to or slightly past apex of abdomen; not capable of flight; found indoors considered pest…….*Blatta germanica*

16) Distal end of front femora armed with only one heavy spine (Plate. 4.27, D)…..17
-- Distal end of front femora armed with two heavy spines (Plate. 4.24, E)…….19

17) Tarsal claw simple; wing contains appendicular field (Plate. 4.27, B)…….*Chorisoneura texensis* Saussure & Zehntner
-- Tarsal claws specialized with microscopic teeth; internal margin appendicular field large; beetle like…….*Plectoptera*…….18

18) Beetle like; tan coloration with thin dark band stretching horizontally between eyes (Plate. 4.26, E)…….*Plectoptera poeyi* Saussure
-- Beetle like; creamy white coloration with small spots of dark maroon on tegmina; large dark maroon spot on pronotoum; creamy band stretching horizontally between eyes (Plate. 4.26, A)…….*Plectoptera picta*

19) Tegmina reduce to two small wing pads; distinct pronotal and body pattern as in (Plate. 4.26, D)....... *Euthlastoblatta gemma*
-- Tegmina present with little to no reduction…….20

20) Color of tegmina pale yellow with two bands of brown stretching horizontally as in (Plate. 4.24, A)…….*Supella longipalpa*
-- Tegmina just reaching apex of abdomen dorsal; surface not specialized; pronotum with distinct markings as in (Plate. 4. 25, A)…….*Cariblatta lutea lutea*

Key to Blattodea Nymphs of Southern Louisiana

1) Mid and hind femur with numerous strong spines along ventral margin (Plate. 4.4, E)…….4
--Mid and hind femora without strong spines except at distal end (Plate. 4.27, D)…….2

2) Color dark brown blackish showing no lateral stripes or markings…….3
-- Lateral margins of prontoum and thoracic segments bearing two stripes that extend to a dark colored abdomen, later instars will show reduction in lateral stripes (Plate. 4.27, G,H) …….*Chorisoneura texensis*

3) First and second leg armed with distal spine (Plate. 4.29, B); Dorsal surface of abdomen roughened; posterior to third segment abdominal tergites come to points at the posterior end of each side (Plate. 4.29, C) …….*Pycnoscelus surinamensis*
-- First and second led not armed with distal spine (Plate. 4.28, B); Entire abdomen and thorax smooth; posterior with abdominal tergites do not come to points at the posterior end of each side of tergite (Plate. 4.28 , C)…….*Panchlora niva*

4) Ventro-anterior margin of front femora with continuous row of stout spines of roughly equal length (Plate. 4.4, E)…….5
-- Ventro-anterior margin of front femora that contain a row of large spines followed by row of smaller spines (Plate. 4.8, E)…….14

5) Dorsal surface uniformly black or dark mahogany colored…….6
--Dorsal surface not uniformly dark; predominate color reddish brown often with pal transverse marking laterally…….8

6) Tarsi with arolia absent; cerci stout…….*Baltta orientalis*
Tarsi with arolia present…….7

7) Bbdominal tergites acute at the posterior lateral margins (Plate. 4.2, D)…….*Eurycotis floridana*
-- Abdominal tergite not acute at posterior end of each side; cerci slender; color reddish brown to mahogany (Plate. 4.5, F)…….*Periplaneta fuliginosa*

8) Early instar larva (<8mm) …….9

--Late instar larva (>8mm) …….11

9) Antenna un-banded; body palely colored at lateral margins…….10
--- Antenna banded with white near base; pale band on mesonotum and second abdominal tergite…….*Periplaneta australiasiae, Periplaneta brunnea or Periplaneta fuliginosa* (early instar)

10) Arolia large; pale lateral margins on thoracic terga…….*Neostylopyga rhombifolia* (early instar)
--Arolia absent; abdominal terga uniformly colored…….*Periplaneta americana* (early instar)

11) Pronotum bearing light yellowish tan markings near posterior (Plate. 4.4, G); arolia barley visible; cerci slender (Plate. 4.4, C)…….*Periplaneta americana*
-- Tarsi with obvious arolia; pronotum may or may not be colored…….12

12) Obvious lateral pale spots on sixth abdominal tergite (Plate. 4.6, E); cerci stout (Plate. 4.6, B); pronotum not showing lighter spots; pronotum pale not showing any spots…….*Periplaneta brunnea*
-- Pronotum showing obvious marks …….13

13) Pronotom with ring of tan yellowish markings; spots of yellow on lateral margins of thoracic and abdominal segments (Plate. 4.7, E) …….*Periplaneta australasiae*
-- Pronotum with striking yellow markings; yellow patterns continues on both abdominal and thoracic segments (Plate. 4.3, E)…….*Neostylopyga rhombifolia*

14) Ventro-anterior margin of front femora containing only 3 large spines before the row of smaller spines (Plate. 4.8, E); color light tan (early instars); or dark brown (late instars); pronotum uniformly colored with pale lateral margins extending to both thoracic segments (Plate. 4.8, F,G)…….*Pseudomops septentrionalis*
-- Ventro-anterior margin of front femora containing more than 3 large spines before the row of smaller spines (Plate. 4.10, E); coloration ranges…….15

15) Pronotal pattern consisting of two longitudinal dark stripes that extend along the body…….22
-- Pronotal pattern not consisting of two longitudinal stripes that extend along the body …….16

16) Color uniformly dark with bright orange red legs (Plate. 4.13, G)…….*Ischnoptera deropeltiformis*
-- Color not as above…….17

17) Tan coloration with distinctive black pattern on pronotum; body as in (Plate. 4.25, F,G)…….*Cariblatta lutea*
-- Coloration ranging from tan, to brown to dark reddish brown; pronotum may or may not show pattern…….18

18) Abdomen uniformly black with reddish tan pronotum and thoracic segments…….19
--Abdomen not uniformly colored…….24

19) Entire body uniformly colored dark redish brown(Plate. 4.16, F)……. *Parcoblatta virginica*
-- Entire body not uniformly colored possessing dark abdomen with either lighter reddish tan pronotum or a pale oval marking in center of pronotum…….20

20) Thoracic and pronotum color reddish brown…….21
-- Thoracic and pronotum colored dark brown with pronotum possessing a pale spot in center…….*Parcoblatta bolliana*

21) Pronotum and thoracic segments posteriorly lined with dark coloration; (Plate. 4.23, F,G) increasing with later instars…….*Parcoblatta lata*
-- Pronotum and thoracic segment uniformly colored reddish tan as in (Plate. 4.20, F,G)……. *Parcoblatta fulvescens*

22) Dark longitudinal stripes widely separated (Plate. 4.10, F); later instars will have colored portion of face as a wide median stripe (Plate. 14.0, B…….*Blattella vaga*
-- Dark longitudinal stripes not widely separated; later instars will have colored faces that is not confined to median stripe and less confined…….23

23) Color pale with abdomen contains pale bands between two longitudinal bands in the entirety of the abdomen (Plate. 4.11, E,D); typically found outdoors or in greenhouses……. *Blattella asahinai*
-- Color dirty tan with abdomen almost uniformly dark, pale spots on abdomen rarely occure and never extend to apex of abdomen (Plate. 4.12, F); commonly found indoors and is considered a pest species…….*Blattella germanica*

24) Abdomen possessing pale bands on anterior ends of abdominal tergites (Plate. 4.17, F; 4.18, E,F; 4.21, E,F) …….25
--Abdomen nearly uniform in color except for reddish tan band at the anterior of the abdomen (Plate. 4.19, F)…….*Parcoblatta uhleriana*

25) Pronotum outlined in white with distinct paler portion in the middle of the pronotum(Plate. 4.18, F; 4.17, F)…….26
--Pronotoum outlined in white and uniformly colored bearing no pale band in the center (Plate. 4.21, E,F)……. *Parcoblatta pensylvanica*

26) Abdominal bands not extending the entirety of the abdominal tergites; color brown (Plate. 14.8, F)…….*Parcoblatta divisa*
Abdominal band extending the entirety of the abdominal tergites showing clear complete pale bands on each abdominal segment; color pale tan (Plate. 4.17, F)……. *Parcoblatta zebra*

Plate. 4.1
Blatta orientalis

Plate .4.2
Eurycotis floridana

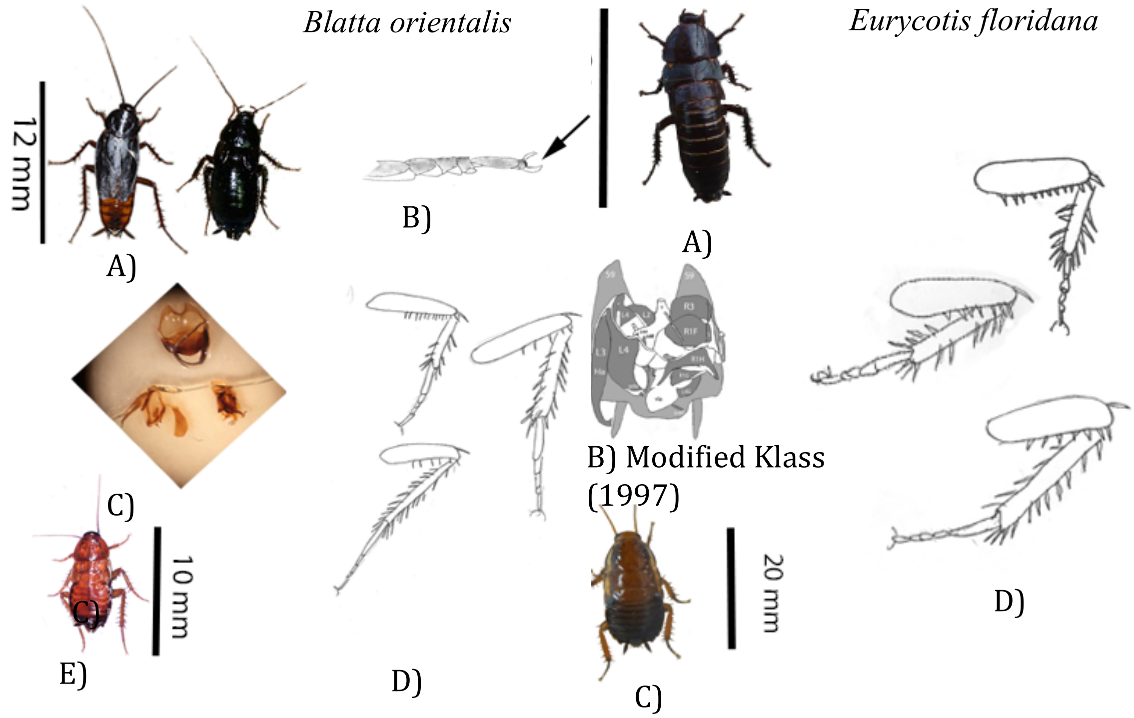


Plate. 4.3
Neostylopyga rhombifolia

Plate. 4.4
Periplaneta americana

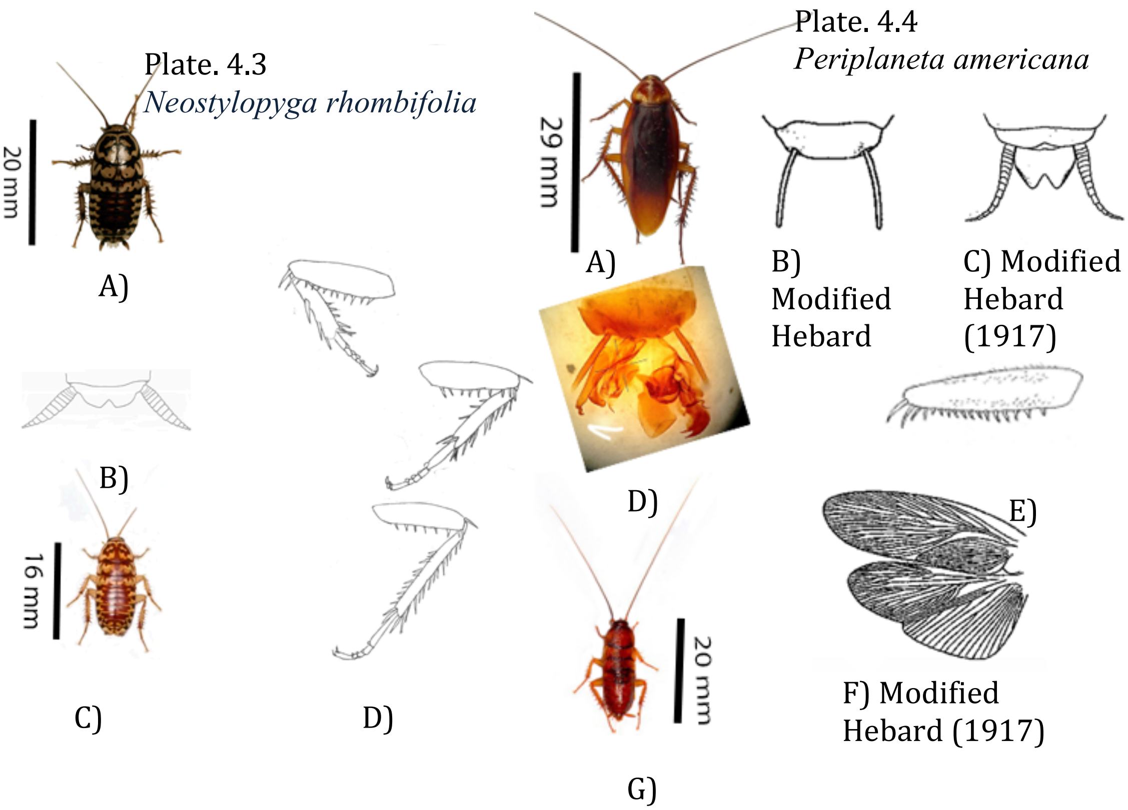


Plate 4.1

A)-*Blatta orientalis*. Image of adult male (right) and female (left); dorsal view.
B)-*Blatta orientalis*. Tarsi lacking arolia.
C)-*Blatta orientalis*. Male genitalia; dorsal view.
D)-*Blatta orientalis*. Image of mid instar nymph; dorsal view.
E)-*Blatta orientalis*. Legs with uniform femoral spine arrangement and distal spines.

Plate 4.2

A)- *Eurycotis floridana*. Image of adult; dorsal view.
B)- *Eurycotis floridana*. Male Genitalia; dorsal view.
C)- *Eurycotis floridana*. Legs with uniform femoral spine arrangement and distal spines.
D)- *Eurycotis floridana*. Image of mid instar nymph; dorsal view

Plate 4.3

A)- *Neostylopyga rhombifolia*. Image of adult; dorsal view.
B)- *Neostylopyga rhombifolia*. Male supra-anal plate and cerci; ventral view
C)- *Neostylopyga rhombifolia*. Image of mid instar; dorsal view
D)-*Neostylopyga rhombifolia*. Legs with uniform femoral spine arrangement and distal spines.

Plate 4.4

A)- *Periplaneta americana*. Image of adult; dorsal view.
B)- *Periplaneta americana*. Male supra-anal plate and cerci; ventral view Modified (Hebard,1917).
C)- *Periplaneta americana*. Male distal portion of abdomen with cerci; dorsal view Modified (Hebard, 1917).
D)- *Periplaneta americana*. Male genital; dorsal view
E)- *Periplaneta americana*. Front femora with uniform spine arrangement.
F)- *Periplaneta americana*. Outline of left tegmen and wing Modified (Hebard, 1917).
G)- *Periplaneta americana*. Image of mid instar nymph; dorsal view.

Plate. 4.5
Periplaneta fuliginosa

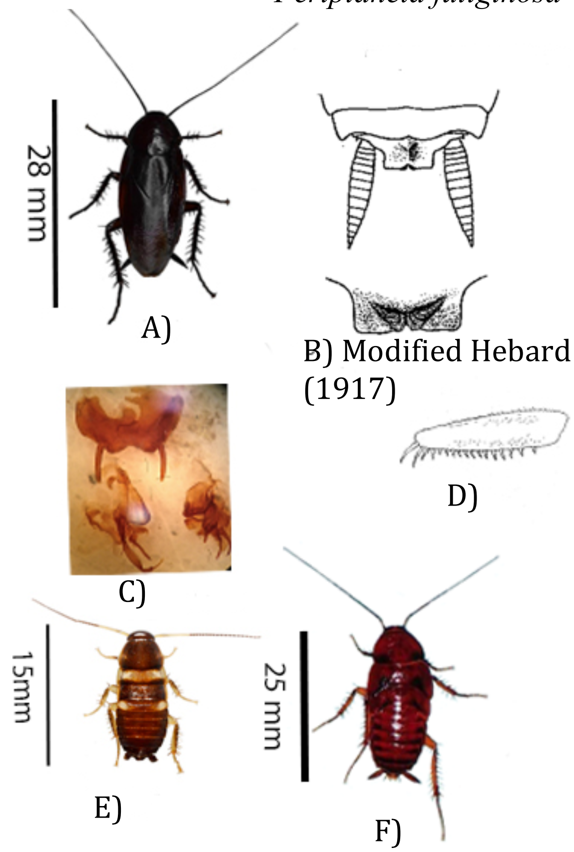


Plate. 4.6
Periplaneta brunnea

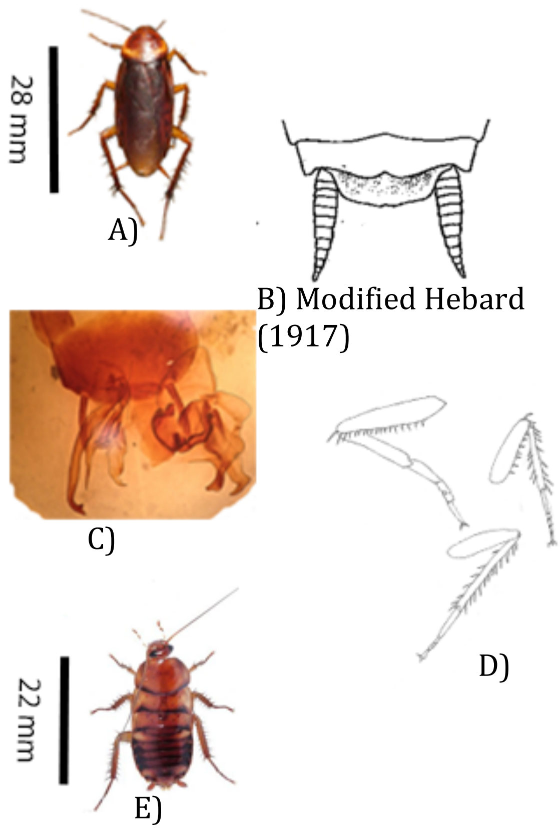


Plate. 4.7
Periplaneta australasiae

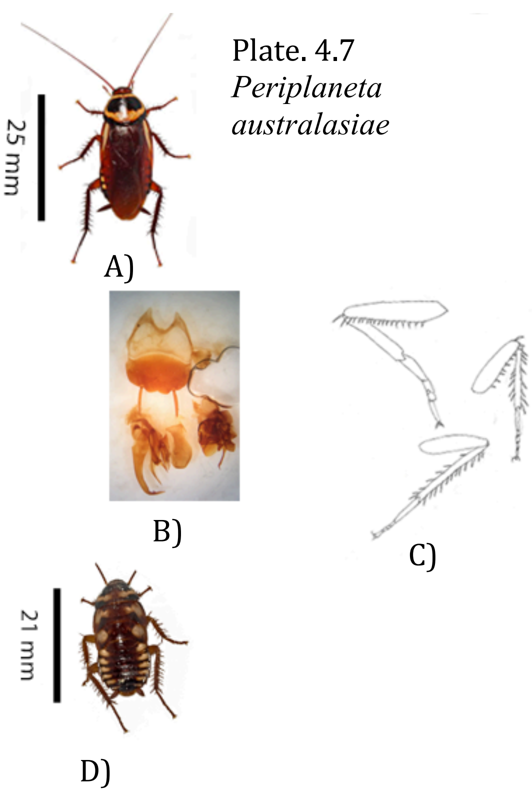


Plate. 4.8
Pseudomops septentrionalis

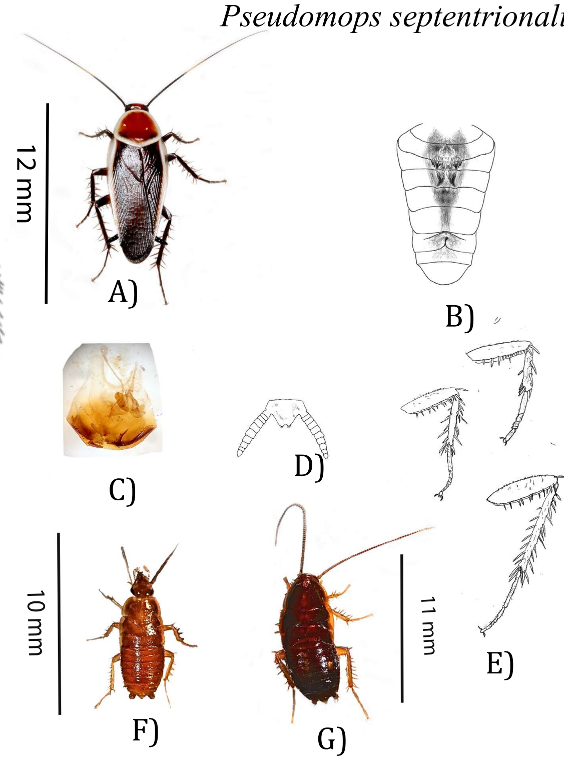


Plate 4.5

A)- *Periplaneta fuliginosa*. Image of adult; dorsal view.
B)- *Periplaneta fuliginosa*. Male distal portion of abdomen with cerci with tergal modification shown under; dorsal view Modified (Hebard,1917).
C)- *Periplaneta fuliginosa*. Image of male genitalia; dorsal view.
D)- *Periplaneta fuliginosa*. Front femora with uniform spine arrangement.
E)- *Periplaneta fuliginosa*. Image of early instar; dorsal view.
F)- *Periplaneta fuliginosa*. Image of late instar; dorsal view.

Plate 4.6

A)- *Periplaneta brunnea*. Image of adult; dorsal view
B)- *Periplaneta brunnea*. Male distal portion of abdomen with cerci with tergal modification shown under; dorsal view. Modified (Hebard,1917).
C)- *Periplaneta brunnea*. Image of male genitalia; dorsal view.
D)- *Periplaneta brunnea*. Front femora with uniform spine arrangement.
E)- *Periplaneta brunnea*. Image of late instar; dorsal view.

Plate 4.7

A)- *Periplaneta australasiae*. Image of adult; dorsal view.
B)- *Periplaneta australasiae*. Image of male genitalia; dorsal view.
C)- *Periplaneta australasiae* . Legs with uniform femoral spine arrangement and distal spines.
D)- *Periplaneta australasiae*. Image of late instar; dorsal view.

Plate 4.8

A)- *Pseudomops septentrionali*. Image of adult; dorsal view.
B)- *Pseudomops septentrionalis*. Adult male abdomen with modified tergites; dorsal view.
C)- *Pseudomops septentrionalis*. Image of male genitalia; dorsal view.
D)- *Pseudomops septentrionalis*. Super anal plate with cerci; dorsal view.
E)- *Pseudomops septentrionalis* . Legs with three spines followed by a row of smaller spines and distal spine.
F)- *Pseudomops septentrionalis*. Image of early instar; dorsal view.
G)- *Pseudomops septentrionalis*. Image of late instar; dorsal view.

Plate. 4.9
Pseudomops sp.

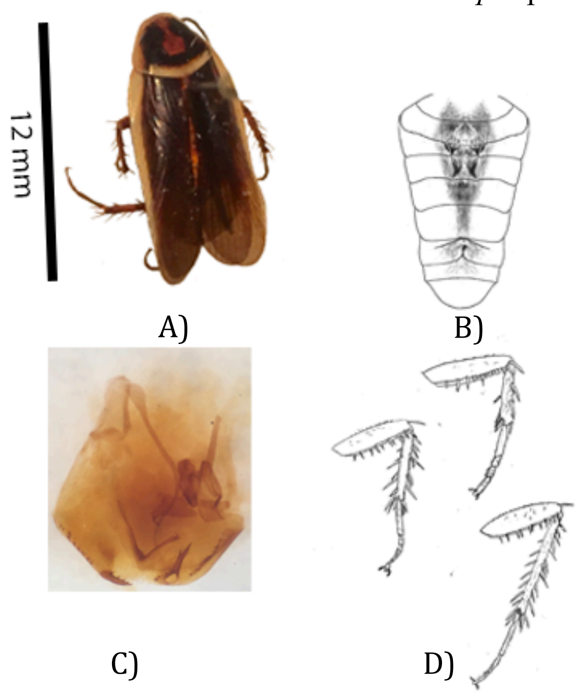


Plate. 4.10
Blattella vaga

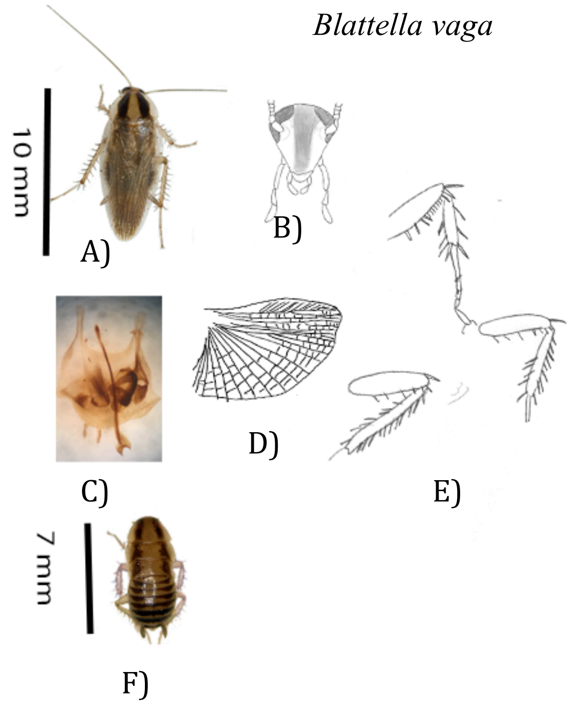


Plate. 4.11
Blattella asahinai

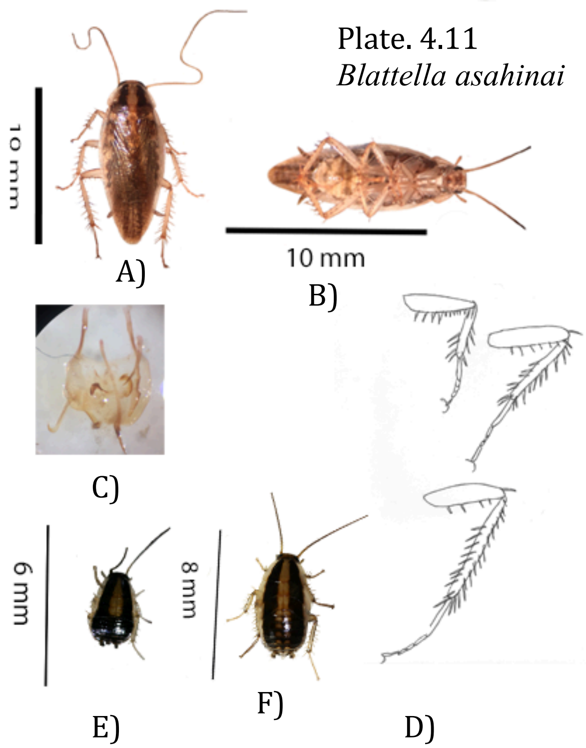


Plate. 4.12
Blattella germanica

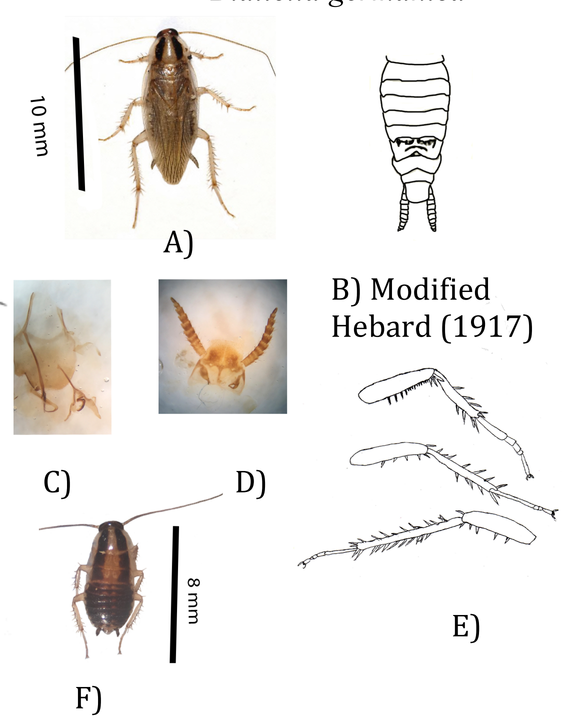


Plate 4.9

A)- *Pseudomops* sp. Image of adult; dorsal view.
B)- *Pseudomops* sp. Adult male abdomen with modified tergites; dorsal view.
C)- *Pseudomops* sp. Image of male genitalia; dorsal view.
D)- *Pseudomops* sp. Legs with three spines followed by a row of smaller spines and distal spine.

Plate 4.10

A)- *Blattella vaga*. Image of adult; dorsal view.
B)- *Blattella vaga*. Face with lateral band.
C)- *Blattella vaga*. Image of male genitalia; dorsal view.
D)- *Blattella vaga*. Outline of right wing.
E)- *Blattella vaga*. Legs with four spines followed by a row of smaller spines and distal spines.
F)- *Blattella vaga*. Image of late instar; dorsal view.

Plate 4.11

A)- *Blattella asahinai*. Image of adult; dorsal view.
B)- *Blattella asahinai*. Image of adult with tegmina extending past abdomen; ventral view.
C)- *Blattella asahinai*. Image of male genitalia; dorsal view.
D)- *Blattella asahinai*. Legs with four spines followed by a row of smaller spines and distal spines.
E)- *Blattella asahinai*. Image of early instar; dorsal view.
F)- *Blattella asahinai*. Image of late instar; dorsal view.

Plate 4.12

A)- *Blattella germanica*. Image of adult; dorsal view.
B)- *Blattella germanica*. Male abdomen with modified tergites. Modified (Hebard,1917).
C)- *Blattella germanica*. Image of male genitalia; dorsal view.
D)- *Blattella germanica*. Image of male super-anal plate; dorsal view.
E)- *Blattella germanica*. Legs with four spines followed by a row of smaller spines and distal spines.
F)- *Blattella germanica*. Image of late instar; dorsal view

Plate. 4.13
Ischnoptera deropeltiformis

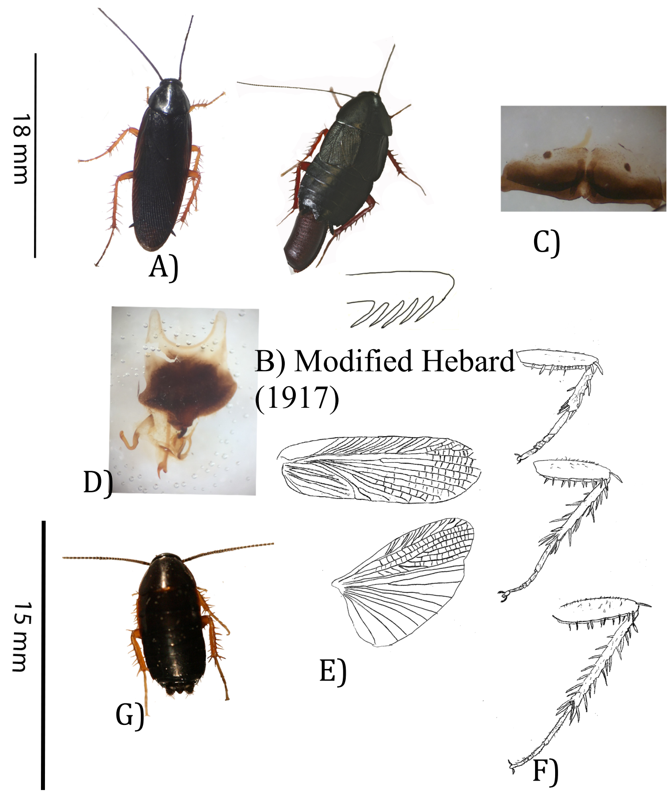


Plate. 4.14
Ischnoptera bilunata

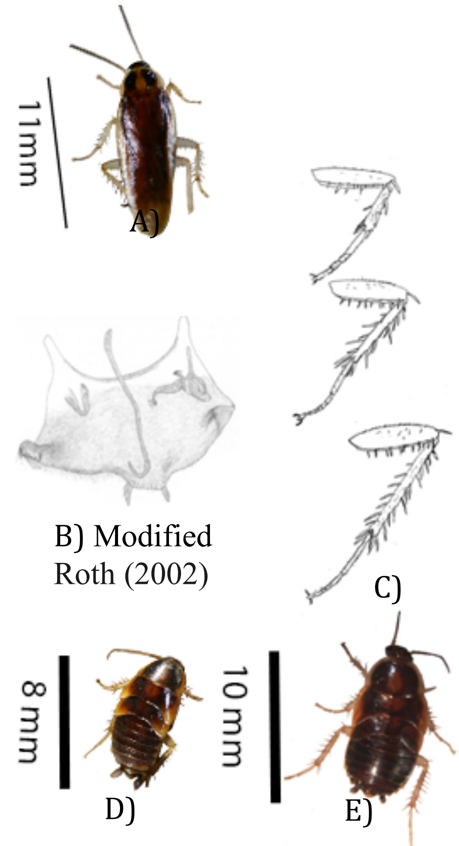


Plate. 4. 15
Parcoblatta bolliana

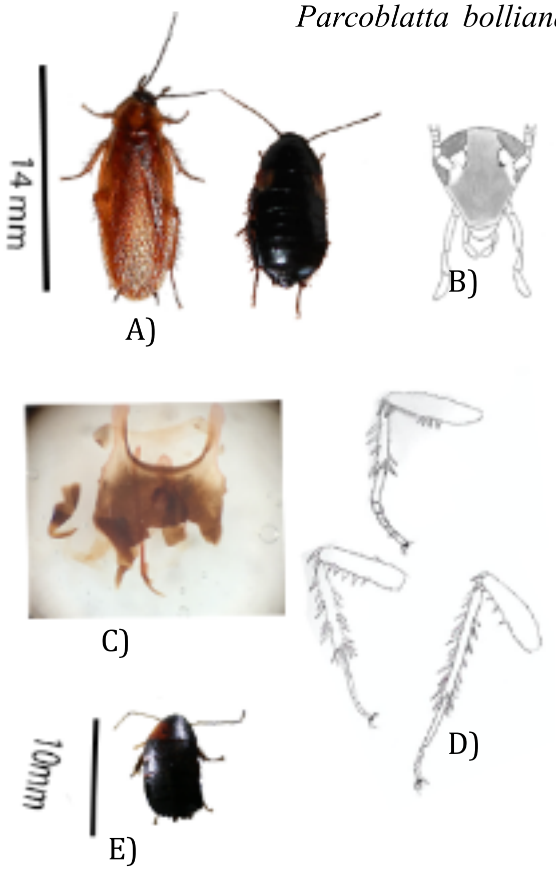


Plate. 4.16
Parcoblatta virginica

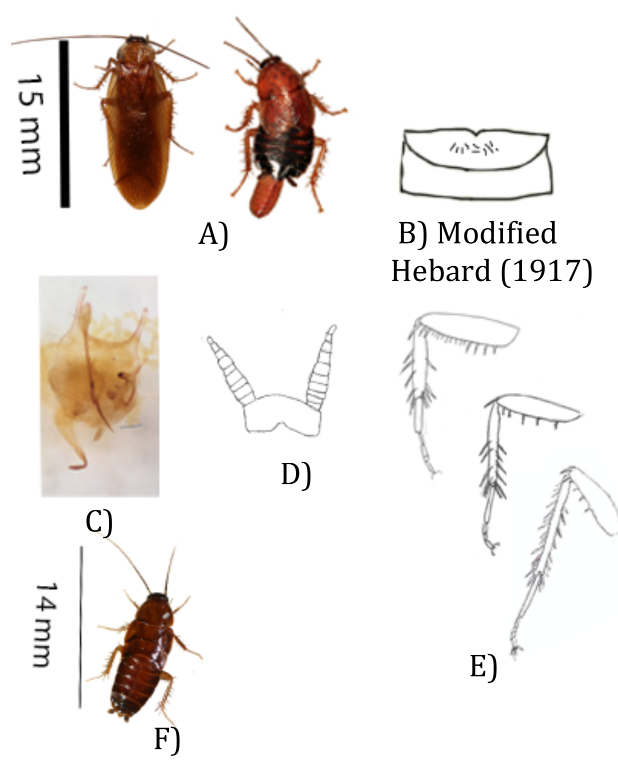


Plate 4.13

A)- *Ischnoptera deropeltiformis*. Image of adult male (right) and female (left); dorsal view.
B)- *Ischnoptera deropeltiformis*. Image of modified tergite; dorsal view.
C)- *Ischnoptera deropeltiformis*. Claw like appendage within the tergite modification Modified (Hebard,1917).
D)- *Ischnoptera deropeltiformis*. Image of male genitalia; dorsal view.
E)- *Ischnoptera deropeltiformis*. Outline of right tegmen and wing.
F)- *Ischnoptera deropeltiformis*. Legs with four spines followed by a row of smaller spines and distal spines.
G)- *Ischnoptera deropeltiformis* Brunner von Wattenyl. Image of late instar; dorsal view.

Plate 4.14

A)- *Ischnoptera bilunata*. Image of adult dorsal view.
B)- *Ischnoptera bilunata*. Male genitalia dorsal view Modified (Roth, 2002).
C)- *Ischnoptera bilunata*. Legs with four spines followed by a row of smaller spines and distal spines.
D)- *Ischnoptera bilunata*. Image of early instar nymph; dorsal view.
E)- *Ischnoptera bilunata*. Image of late instar nymph; dorsal view.

Plate 4.15

A)- *Parcoblatta bolliana*. Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta bolliana*. Face with inter-ocular space not exceeding with of oceli.
C)- *Parcoblatta bolliana*. Image of male genitalia; dorsal view.
D)- *Parcoblatta bolliana*. Legs with four spines followed by a row of smaller spines and distal spines.
E)- *Parcoblatta bolliana*. Image of early instar nymph; dorsal view.
F)- *Parcoblatta bolliana*. Image of late instar nymph; dorsal view.

Plate 4.16

A)- *Parcoblatta virginica*. Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta virginica*. Modified median tergite; dorsal view Modified (Hebard,1917).
C)- *Parcoblatta virginica*. Image of male genitalia; dorsal view.
D)- *Parcoblatta virginica*. Male super-anal plate and cerci; dorsal view.
E)- *Parcoblatta virginica*. Legs with four spines followed by a row of smaller spines and distal spines.
F)- *Parcoblatta virginica* . Image of late instar nymph; dorsal view.

Plate 4.17
Parcoblatta zebra

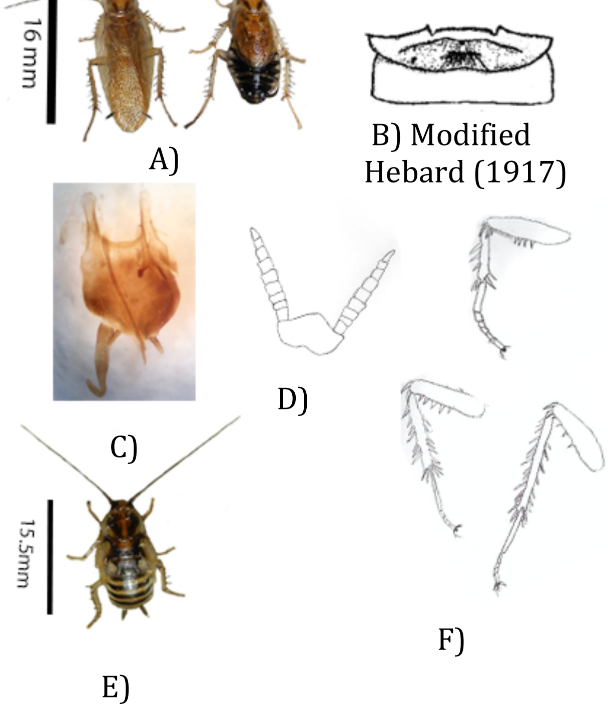


Plate 4.18
Parcoblatta divisa

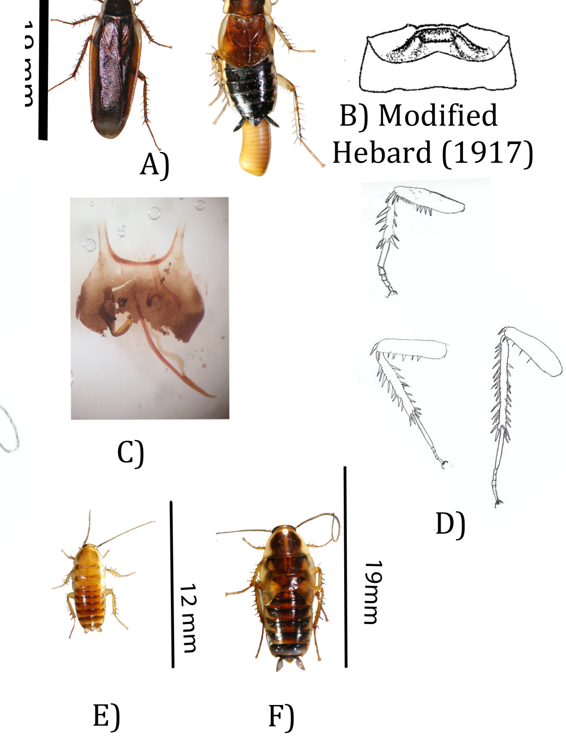


Plate. 4.19
Parcoblatta uhleriana

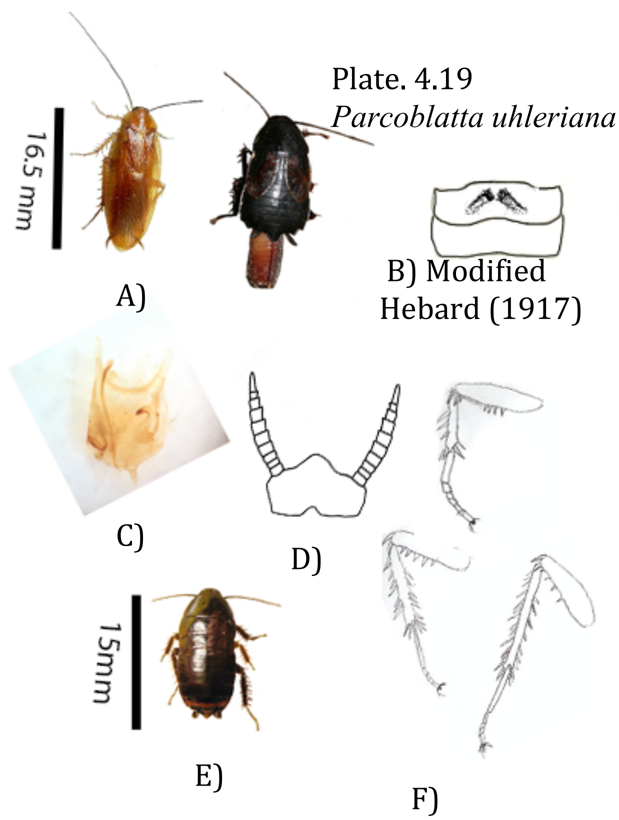


Plate. 4.20
Parcoblatta fulvescens

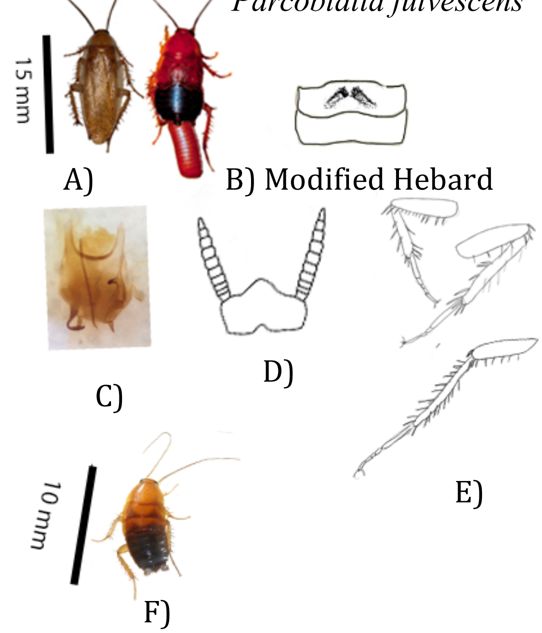


Plate 4.17

A)- *Parcoblatta zebra*. Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta zebra*. Modified median tergite; dorsal view Modified (Hebard,1917).
C)- *Parcoblatta zebra*. Image of male genitalia; dorsal view.
D)- *Parcoblatta zebra*. Male super-anal plate and cerci; dorsal view.
E)- *Parcoblatta zebra*. Image of late instar nymph; dorsal view.
F)- *Parcoblatta zebra*. Legs with four spines followed by a row of smaller spines and distal spines.

Plate 4.18

A)- *Parcoblatta divisa* . Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta divisa*. Modified median tergite; dorsal view Modified (Hebard, 1917).
C)- *Parcoblatta divisa*. Image of male genitalia; dorsal view.
D)- *Parcoblatta divisa*. Legs with four spines followed by a row of smaller spines and distal spines.
E)- *Parcoblatta divisa*. Image of early instar nymph; dorsal view
F)- *Parcoblatta divisa*. Image of late instar nymph; dorsal view

Plate 4.19

A)- *Parcoblatta uhleriana*. Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta uhleriana*. Modified median tergite; dorsal view Modified (Hebard,1917).
C)- *Parcoblatta uhleriana*. Image of male genitalia; dorsal view.
D)- *Parcoblatta uhleriana*. Male super-anal plate and cerci; dorsal view.
E)- *Parcoblatta uhleriana*. Legs with four spines followed by a row of smaller spines and distal spines.
F)- *Parcoblatta uhleriana*. Image of late instar nymph; dorsal view.

Plate 4.20

A)- *Parcoblatta fulvescens*. Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta fulvescens*. Modified median tergite; dorsal view Modified (Hebard,1917).
C)- *Parcoblatta fulvescens* . Image of male genitalia; dorsal view.
D)- *Parcoblatta fulvescens*. Male super-anal plate and cerci; dorsal view.
E)- *Parcoblatta fulvescens*. Legs with four spines followed by a row of smaller spines and distal spines.
F)- *Parcoblatta fulvescens*. Image of early instar nymph; dorsal view.
G)- *Parcoblatta fulvescens*. Image of late instar nymph; dorsal view.

Plate. 4.21
Parcoblatta pennsylvanica

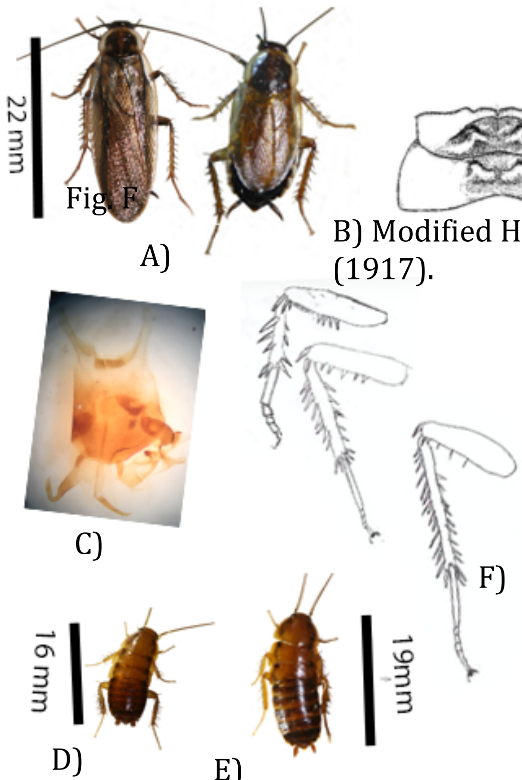


Plate. 4.22
Parcoblatta caudelli

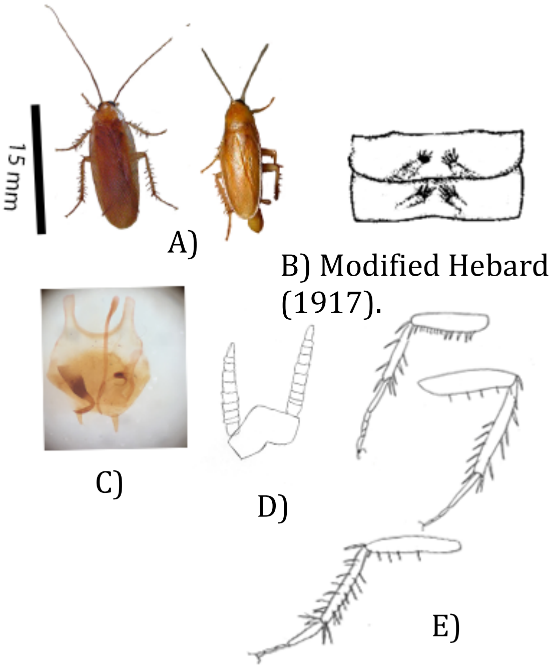


Plate. 4.23
Parcoblatta lata

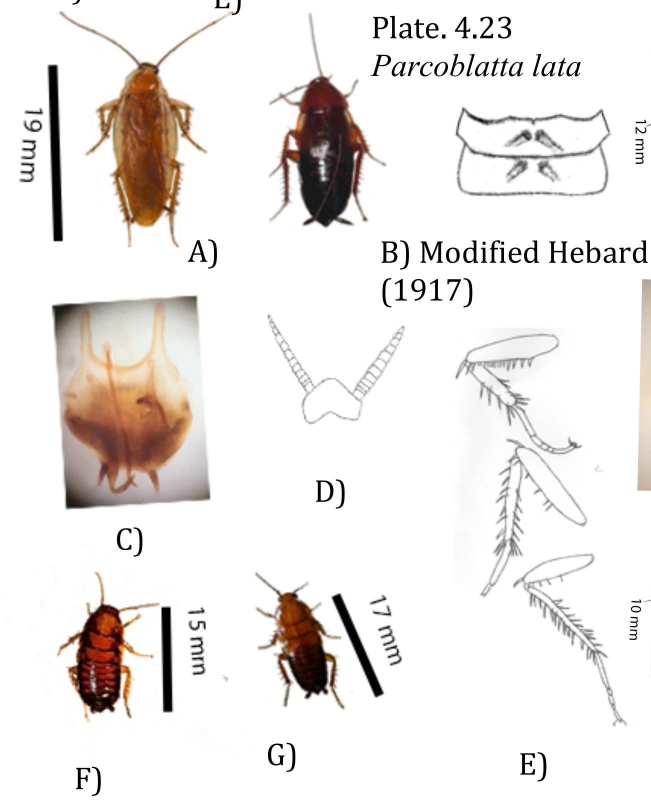


Plate. 4.24
Supella longipalpa

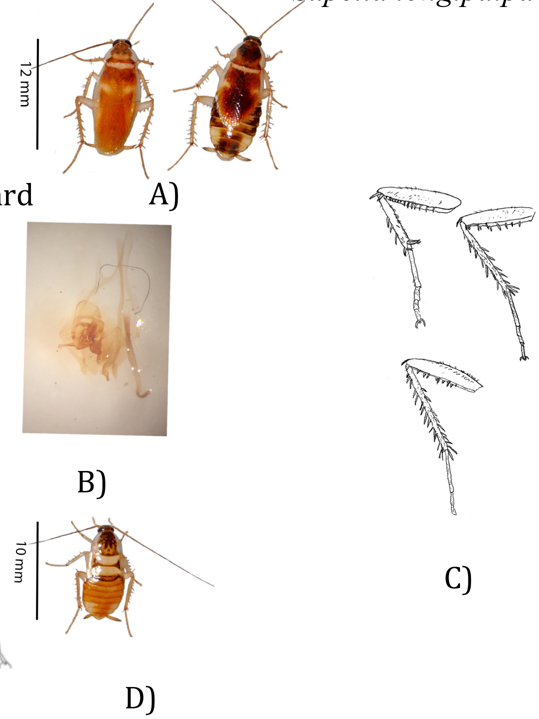


Plate 4.21

A)- *Parcoblatta pensylvanica*. Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta pensylvanica*. Modified median and first tergite; dorsal view Modified (Hebard,1917).
C)- *Parcoblatta pensylvanica*. Image of male genitalia; dorsal view.
D)- *Parcoblatta pensylvanica*. Male super-anal plate and cerci; dorsal view.
E)- *Parcoblatta pensylvanica*. Image of early instar nymph; dorsal view.
F)- *Parcoblatta pensylvanica*. Image of late instar nymph; dorsal view.
G)- *Parcoblatta pensylvanica*. Legs with four spines followed by a row of smaller spines and distal spines.

Plate 4.22

A)- *Parcoblatta caudelli*. Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta caudelli*. Modified median and first tergite; dorsal view Modified (Hebard,1917).
C)- *Parcoblatta caudelli*. Image of male genitalia; dorsal view.
D)- *Parcoblatta caudelli*. Male super-anal plate and cerci; dorsal view.
E)- *Parcoblatta caudelli*. Legs with four spines followed by a row of smaller spines and distal spines.

Plate 4.23

A)- *Parcoblatta lata*. Image of adult male (left) and female (right); dorsal view.
B)- *Parcoblatta lata*. Modified median and first tergite; dorsal view Modified (Hebard,1917).
C)- *Parcoblatta lata*. Image of male genitalia; dorsal view.
D)- *Parcoblatta lata*. Male super-anal plate and cerci; dorsal view.
E)- *Parcoblatta lata*. Legs with four spines followed by a row of smaller spines and distal spines.
F)- *Parcoblatta lata*. Image of early instar nymph; dorsal view.
G)- *Parcoblatta lata*. Image of late instar nymph; dorsal view.

Plate 4.24

A)- *Supella longipalpa*. Image of adult male (left) and female (right); dorsal view.
B)- *Supella longipalpa*. Image of male genitalia; dorsal view.
C)- *Supella longipalpa*. Male super-anal plate and cerci; dorsal view.
D)- *Supella longipalpa*. Image of late instar nymph; dorsal view.
E)- *Supella longipalpa*. Legs with femoral spines and distal spines.

Plate. 4.25
Cariblatta lutea

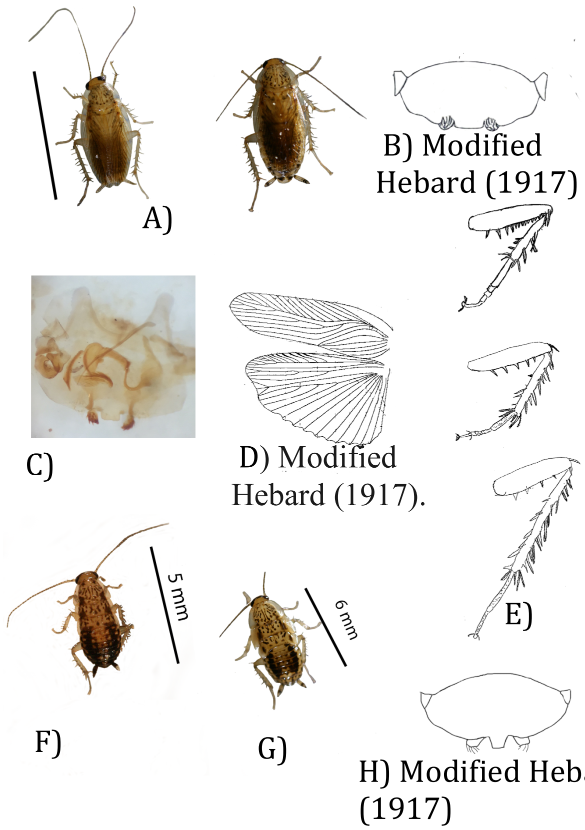


Plate. 4.26
Plectoptera picta/Euthlastoblatta gemma

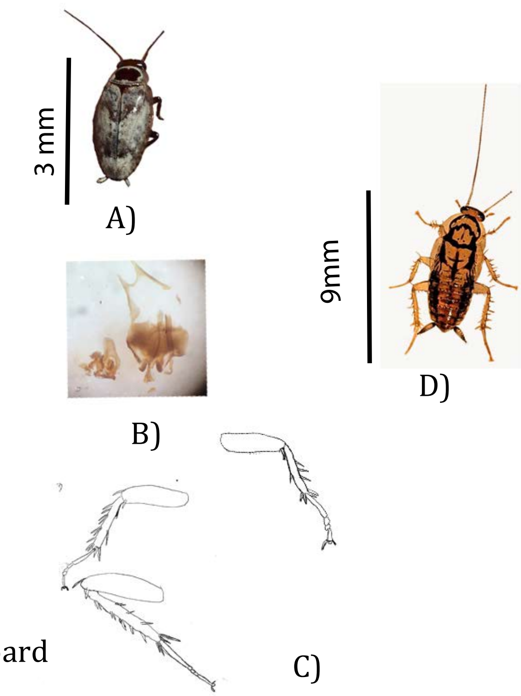


Plate. 4.27
Chorisoneura texensis

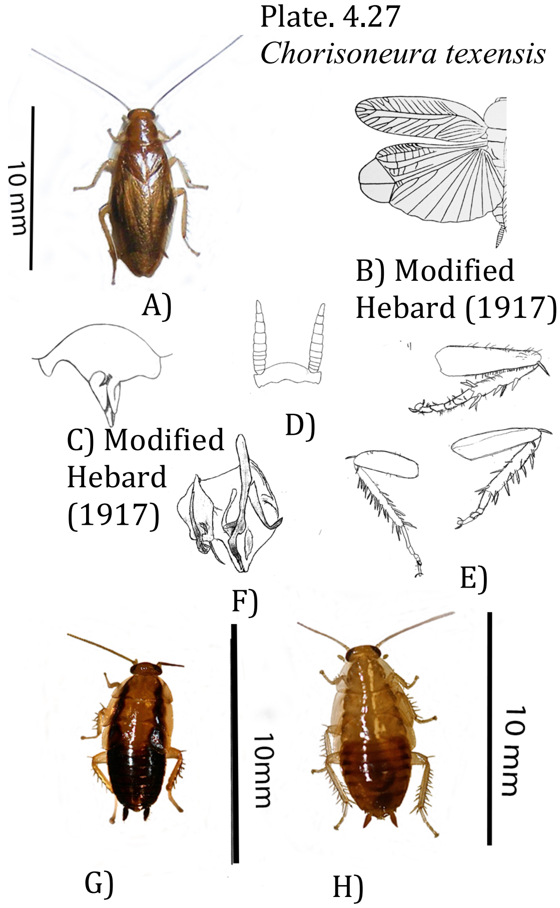


Plate. 4.28
Panchlora nivea

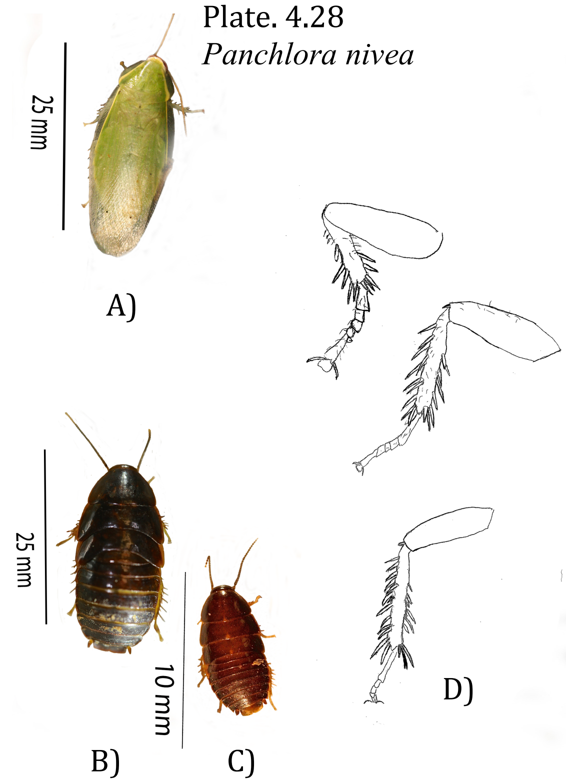


Plate 4.25

A)- *Cariblatta lutea lutea*. Image of adult male (left) and female (right); dorsal view.
B)- *Cariblatta lutea lutea* Sub-genital plate Modified (Hebard,1917).
C)- *Cariblatta lutea lutea*. Image of male genitalia; dorsal view.
D)- *Cariblatta lutea lutea*. Outline of left tegmen and wing. Cite
E)- *Cariblatta lutea lutea*. Legs with femoral spines and distal spines.
F)- *Cariblatta lutea lutea*. Image of early instar nymph; dorsal view.
G)- *Cariblatta lutea lutea*. Image of late instar nymph; dorsal view.
H)- *Cariblatta lutea minima*. Sub-genital plate Modified (Hebard,1917).

Plate 4.26

A)- *Plectoptera picta*. Image of adult; dorsal view.
B)- *Plectoptera picta*. Image of male genitalia; dorsal view.
C)- *Plectoptera picta*. Legs with femoral spines and distal spines.
D)- *Euthlastoblatta gemma*. Image of adult; dorsal view.
E)- *Plectoptera poeyi* Saussure.

Plate 4.27

A)- *Chorisoneura texensis*. Image of adult; dorsal view.
B)- *Chorisoneura texensis*. Body illustrated with tegmen and wing outlined Modified (Hebard, 1917).
C)- *Chorisoneura texensis*. Sub genital plate.
D)- *Chorisoneura texensis*. Legs with femoral spines and distal spines.
E)- *Chorisoneura texensis*. Male super-anal plate and cerci; dorsal view.
F)- *Chorisoneura texensis*. Image of male genitalia; dorsal view.
G)- *Chorisoneura texensis*. Image of early instar nymph; dorsal view.
H)- *Chorisoneura texensis*. Image of late instar nymph; dorsal view.

Plate 4.28

A)- *Panchlora nivea*. Image of adult; dorsal view.
B)- *Panchlora nivea*. Legs with femoral spines and distal spines.
C)- *Panchlora nivea*. Image of late instar nymph; dorsal view.
D)- *Panchlora nivea*. Image of early instar nymph; dorsal view.

Plate. 4.29
Pycnoscelus surinamensis

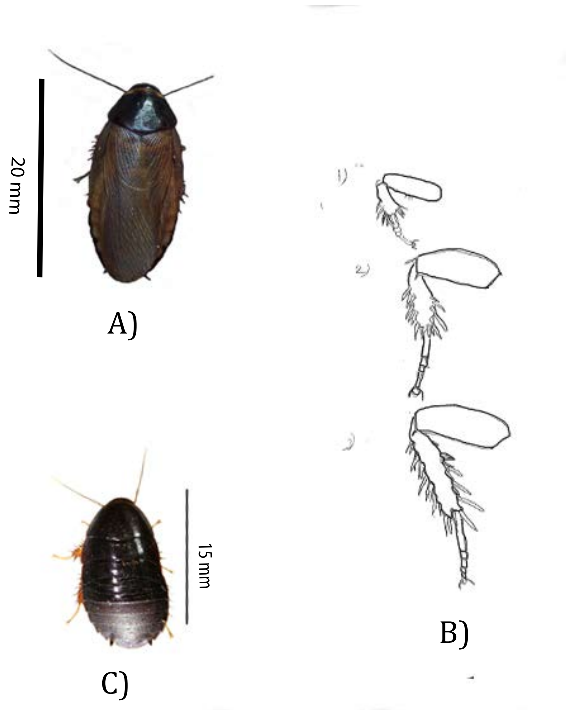


Plate 4.29

A)- Pycnoselus surinamensis. Image of adult; dorsal view.
B)- Pycnoselus surinamensis. Legs with femoral spines and distal spines.
C)- Pycnoselus surinamensis. Image of late instar nymph; dorsal view.

VITA

Forest Brady Huval is a native of Cecilia, Louisiana received his bachelors degree in resource biology and biodiversity at the University of Louisiana at Lafayette in 2012. Thereafter he applied to Louisiana State University graduate program within the entomology department to pursue a master's degree in entomology. He plans to receive his master's degree in August of 2016 and continue towards a doctorate upon graduation.