GENERA OF AMERICAN CICADAS NORTH OF MEXICO

By

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To my family,

Jim,

Cindy, Pam, Jessica

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GENERA OF AMERICAN CICADAS NORTH OF MEXICO

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Cicadas are large, vocal insects, often heard, but seldom seen. Sixteen endemic genera occur in the Nearctic biogeographic region north of Mexico. The genera are *Beameria*, *Cacama*, *Cicadetta*, *Clidophleps*, *Cornuplura*, *Diceroprocta*, *Magiocicada*, *Neocicada*, *Neoplatypedia*, *Okanagana*, *Okanagodes*, *Pacarina*, *Platypedia*, *Quesada*, *Tibicen*, and *Tibicinoides*. Each of these genera is redescribed in a consistent format, thereby facilitating comparisons of common characters. Keys to males and females are included, and diagnostic characters are given for each genus. Radiographs, made with soft x-rays, are used as a taxonomic technique to elucidate internal structures. The following revisions are recognized: *Okanagana rubrocaudata*, a former variety of *O. bella* is raised to species rank; *Okanagana rotundifrons* is transferred to the genus *Clidophleps*; *Tibicinoides hesperia* is moved back to *Okanagana*; *Cicada chisos* is placed in the genus *Neocicada*. A new tribe, Okanaganini, is proposed for six western genera with the possibility of including two palearctic genera. This tribe has two subtribes, Platypedaria and Okanaganaria.

The cicada fauna in North America is old. Earliest fossils date from the Paleocene. Current distribution is dependent on origin,

dispersal patterns, habitat, and past geologic history. Two major radiations of genera have occurred on the North American continent, one allied to *Tibicen*, the other to *Okanagana*. Ancestral and derived characters are proposed and related to the North American genera.

CHAPTER I

INTRODUCTION

Cicadas undoubtedly intrigued the imagination of man before recorded history. A frequently related ancient observation noted how lucky the male cicada is because his mate is mute. The following pages will show that even among cicadas some females have managed to develop a "voice." Myers (1929), in his book Insect Singers, reviewed both the classical and modern literature, summarizing what was known about cicada biology at that time.

The first written references to cicadas, "tettix" in Greek, can be found in those sections of the Iliad attributed to Homer and written around 1,000 B.C. Another poet from the same era, Hesiod, noted that the sound comes from beneath the wings, an observation made and lost many times before sound production organs in cicadas were identified and described. The ancient Greeks apparently found the song of the cicada pleasing and musical. In Greek mythology, cicadas were formerly men who were so enchanted when the Muses brought music to the earth that they became absorbed by the music, neglected to eat and sleep, and eventually wasted away. Their voices may still be heard in the singing of cicadas. In contrast the ancient Romans found the sound of the cicada unpleasant and raucous. Roman mythology tells of the goddess Aurora, who fell in love with a mortal. She asked the gods to grant her lover the gift of immortality, but in her enthusiasm she neglected to ask for eternal youth

for him. As the years passed Tithonus, her lover, became toothless and infirm and prayed for death. However, the gift of the gods could not be returned, so Aurora changed her toothless lover into "the ever complaining cicada." I prefer to think that these differences in the perception of cicada song relate to a taxonomic difference in cicadas rather than a difference in aural perception of ancient Greeks and Romans.

From the fables of Aesop, the stories of ancient India, and the folklore of the Maori tribes of New Zealand come amazingly similar tales contrasting the industrious ant at the foot of a tree with the lazy cicada singing in the sun at the top of its crown. When winter came the ant was well fed and survived, while the cicada begged for food and eventually starved. The Zuni Indians of the American Southwest attribute more cunning to the cicada. They tell the tale of a coyote who wished to learn the song of a cicada singing from the boughs of a pinyon pine. The coyote had difficulty learning the song and twice forgot it on the way home. When he returned for the second time, the cicada, distrustful of the coyote, divested himself of his old skin, filled it with a quartz pebble, sealed the vent with pitch, and flew to the safety of another tree. The coyote became frustrated when this cicada image did not respond, seized it and splintered his teeth on the stone, driving some into his jaw and leaving others protruding as tusks. His descendants inherited these broken teeth. The cicada of the pinyon pine is either *Tibicen duryi* or *Okanagana magnifica*. In the Orient cicada symbolism was developed to its greatest heights by the Taoists. They believe that the soul of the departed escapes the body and is carried aloft by a cicada. Early burials often included a cicada-shaped image, while in later burials a cicada amulet was placed in the mouth of the corpse to facilitate the soul leaving the body.

As the centers of western civilization moved northward to areas where cicadas are less prevalent, literary allusions to cicadas became scarcer. Keats and Browning mentioned them in their poetry, but they had lived in the southern Mediterranean regions of Europe. In the United States nearly all cultural allusions to cicadas center around the genus *Magicalcada*, misnamed "seventeen-year locusts" because their periodical abundance reminded early colonists of the biblical locusts.

The earliest scientific work on cicadas was that of Aristotle. He described the morphology of the cicada mouth, their reproductive behavior, and life history. Taxonomically, he made the distinction between the large ones that sing and the smaller ones that do not sing. This latter observation probably discriminated between our modern family Cicadidae and other auchenorrhynous Homoptera, although we now know many of these produce sounds that are seldom audible to the human ear. Although Aristotle was often quoted, cicada biology remained essentially in suspended animation until Reamur described the sound producing organs and made observations on the nests and eggs in the eighteenth century. Linnaeus established the genus *Cicada* in 1758 in Systemma Naturae. In the nineteenth century Fabre recorded the habits of some Mediterranean Cicadidae. Since that time numerous other writers have described species and various aspects of cicada morphology and biology. These are summarized by Myers (1929). Distant, in a series of papers entitled Rhynochotal Notes appearing in the Annals and Magazine of Natural History (1904-1905), established our current system of cicada taxonomy.

The earliest attempt to treat the classification of North American cicadas comprehensively was Uhler's Preliminary Survey of the Cicadaea of the United States, Antilles, and Mexico, published in two parts in

Entomologica Americana in 1888. Van Duzee published a checklist of genera and species occurring north of Mexico in 1916 and followed this with a catalog of the same genera and species the subsequent year. Davis treated the distribution of the genera and species in 1930. Metcalf's (1963) world catalog is the most recent work to treat North American genera comprehensively. Other papers dealing with several North American genera are Lawson (1920), Beamer (1928), Beamer and Beamer (1930), Froeschner (1952), Simons (1953, 1954), Moore (1966), and Alexander, Pace, and Otte (1972). The writers primarily concerned with each genus are reviewed under the individual genera in the following chapters.

William T. Davis made the most significant contributions to our knowledge of western North American Cicadidae. For Davis the study of cicadas was a second vocation. What began as a hobby during his years as a successful industrialist became, after an early retirement, his primary preoccupation until his death in 1944. Davis described many of our genera and species. He was dependent for most of his specimens on the collections of other people, but in his writings he included whatever biological information was sent to him in letters accompanying the specimens. Since Davis' death most work in North America has centered around the periodical cicadas of the genus *Magicicada*.

Life Cycle

Cicada eggs are laid in nests along the stems and branches of various host plants. The nests may or may not be arranged in a definite order. The female pierces the host with the ovipositor gradually driving into the host tissue with an in-and-out sawing motion of the lateral valves. Some species simply lay the eggs in the dry nest. Other species fill the

ends of the nest or the entire nest with a glue-like secretion, and some, e.g., *Tibicen lyricen*, press the torn tissues of the plant back into place before moving on to the next nest. Beamer (1928) recorded from as few as three to as many as twenty eggs in the nests of Kansas Cicadidae, while Myers (1929) cited estimates of egg production for a single female that range from three hundred to seven hundred. All described eggs resemble each other closely in structure, varying only in size. Some species overwinter as eggs. The eggs of other species hatch the same summer they are deposited.

The hatching embryo ruptures the anterior end of the egg capsule with its egg burster and makes its way to the nest opening, where it sheds the postnatal membrane and falls to the ground. Upon reaching the ground, the young nymph searches for a crevice in the earth to enter. A quick retreat underground is especially important in dry habitats as the newly hatched nymphs appear to be particularly vulnerable to desiccation.

Once in the ground, the nymph continues its downward movement until it locates a suitable spot for a cell. The cell apparently is constructed before food is located (Beamer, 1928). The cell protects the nymphal cicada from both flooding and desiccation and probably provides some protection from predators. The cell consists of walls of hard packed earth. It is cylindrical and large enough to permit the nymph to do a half somersault, his method of turning around. Once the cell is built, the nymph looks for food. If food lies at the edge of the cell, he begins to eat. If there is no food on the periphery of the cell, he searches for food by laboriously moving his cell with him. Digging and packing of the earth is done with special adaptations of the prothoracic

legs. Much of the above was verified by Beamer (1928) from observations made on cicada nymphs in glass-sided cages.

Like most Homoptera, cicadas have five nymphal instars. The shortest life cycle known is four years, a fact established by Beamer (1928) for *Cicadetta calliope*. The longest cycle is the seventeen year cycle of three species of *Magicalicada*.

In the last month before emergence, the fifth nymphal instar extends its cell to within an inch or two of the surface. J.E. Heath (1968) showed that emergence from the ground of seventeen-year cicadas is dependent on soil temperature. Temperature is probably the environmental cue for emergence of other cicadas also. Upon emergence the nymph climbs a nearby stem or trunk before the final molt to an adult.

The primary function of the adult stage is mating and renewal of the life cycle. Adult cicadas live approximately six weeks to two months. In some species, females appear to outlive the males by several days. The two sexes are attracted to each other by a mating call or song usually performed by the male. In *Magicalicada* the song appears to have a congregating function, bringing together both males and females rather than uniting specific pairs. In *Flatypedia* and *Neoplatypedia* both sexes signal in a two-way communication. Several species produce three different sounds: the mating call, a sound used during courtship and mating of specific pairs, and an alarm squawk emitted by males when they are disturbed. Wing fluttering is also used as a signaling device between individual cicadas. After mating, the female lays her eggs and the cycle begins again.

The Problem

In June, 1968, J.E. Heath, P.J. Wilkin, and I began a study of the adaptations to climate of cicadas in Arizona. When we tried to identify our experimental animals, we became frustrated by the lack of taxonomic keys. No key to the genera of North American cicadas existed. Published descriptions of genera were often vague and incomplete. There was usually no way of comparing similar characters in one genus with another. Many of the descriptions were of a comparative nature, but they required identified specimens of the other genus or genera in hand in order to make the comparisons. In some cases a lone female was unidentifiable because only male diagnostic characters had been used.

We were faced with two alternatives. We could compile a list and original descriptions of all species previously reported from the general region and hope that what we had collected was not a range extension or a new species, or we could travel to a large museum collection, and hope that our species were available for comparative identifications. In either case we would be working backward from species to genus or from a larger group to a smaller group. Everyone wishing to identify individual cicada specimens to genus could hardly follow these procedures. Clearly a comprehensive taxonomic study of the genera of American cicadas north of Mexico was needed. This paper presents such a study.

The aims of this dissertation are

1. To provide thorough, consistent descriptions of adults of the genera of cicadas occurring in North America north of Mexico.
2. To provide keys and diagnostic characters for identification of individual specimens to genus.

3. To indicate the general distribution of North American genera north of Mexico.
4. To summarize the known biology of cicada genera found north of Mexico.
5. To indicate evolutionary relationships of the North American genera north of Mexico.

CHAPTER II

MATERIALS AND METHODS

The personal collection of cicadas used in this study dates from 1964. Most of the specimens were collected under the auspices of the University of Illinois and arrangements have been made to deposit these specimens in the Illinois Natural History Survey collection. Several broods of *Magicicada* are included in the collection. Extensive collections of western genera were made in Arizona in June and early July of 1968, 1969, 1970, 1972, and 1973. Additional specimens were collected in Colorado, Illinois, and Florida. Notes were made on location, time of day, and habitat of each collection. Live weights and temperature data were frequently recorded. Specimens were preserved in alcohol and pinned and examined at a later date.

Several museum collections were examined in part or whole. These included the Museum of Zoology, University of Michigan, Ann Arbor; Arizona State University, Tempe; Illinois Natural History Survey, Urbana; the Snow Collection, University of Kansas, Lawrence; the British Museum (Natural History), London; and the Muséum National d'Histoire Naturelle, Paris. Numerous friends and colleagues contributed both specimens and collection data.

Measurements were made using the following tools; a Wild M5 stereoscopic dissecting microscope, calipers, and a plastic rule read easily to the nearest half millimeter. Measurements were made from both

specimens and photographs. The photographic plates found in the collected works of Davis (1921a, 1942) as well as my personal photographs were utilized for proportional measurements. Descriptions were written using the stereoscopic microscope and notes made while using the facilities of the museums visited. Radiographs were made with a Faxitron 804 field emission x-ray unit and Polaroid positive-negative 55 film. Details of exposure are given in the general morphology chapter. Additional prints and enlargements were made by the photographic services of the University of Florida.

Illustrations were drawn with a camera lucida. Original sketches were compared with the descriptions and later reduced on a reducing Xerox prior to the final inking. Three illustrations were made directly from enlarged photographs. Color patterns are indicated, but the decision was made to leave black insects uncolored so that morphological features would not be obscured by the color. Several excellent drawings of male external genitalic segments are found in the literature. Some of these were redrawn from the originals after a comparison was made with specimens in hand.

Unless otherwise indicated in the text, the terminology used in this paper conforms with that found in Torre-Bueno, A Glossary of Entomology, 1962.

CHAPTER III

CLASSIFICATION: HIGHER TAXA

Order

Cicadas are usually placed in the order Homoptera. This order is comprised of hemipteroid insects with a sucking beak arising from the back of the head. The proboscis contains four piercing stylets consisting of two mandibles and two maxillae. In winged members, the forewings are usually of a uniform texture throughout, either membranous or slightly thickened. The hind wings are membranous. Winged forms hold the wings tentlike over the body when at rest. Members of this order are plant feeders.

Suborder

Cicadas belong to the suborder Auchenorrhyncha. Insects in this suborder have three-segmented tarsi and short, bristle-like antennae. The beak arises from the back of the head and not between the fore coxae as in the Sternorrhyncha. Members of the Auchenorrhyncha are described as active insects.

Superfamily

Cicadas are classified in the superfamily Cicadoidea. The designation Cicadoidea, however, means different things to different authors.

Those writers who divide cicadas into two or more families (cf. Kato, Boulard, and Metcalf) define the Cicadoidea as those insects comprising the former family Cicadidae. Authors who still maintain the single family Cicadidae as representing all cicadas use the designation Cicadoidea to separate the families Cicadellidae, Cercopidae, Membracidae, and Cicadidae from the Fulgoroidea. This definition of the Cicadoidea is characterized by antennae which arise on the front of the head between or anterior to the eyes; middle coxae short and contiguous; and no "Y" vein in the anal area of the wing (Borror and DeLong, 1971, and Borror and White, 1970).

Family Cicadidae

History

Lamarck (1801) described the genus *Cicada* and named *Cicada orni* Linn. as the type, thereby establishing the validity of the genus. Essig (1942) gave the following history of the family: "Latrielle grouped these insects as Cicadariae in 1802, and Leach erected the tribe Cicadides and the family Cicadida in 1815. The later was changed to Cicadidae by Samouelle in 1819 and has been generally accepted for this homogeneous group of remarkable insects." Westwood (1840) and Metcalf (1963) attributed the name to Leach, but Leach's description of the tribe Cicadides reads, "Antennae three-jointed. Ocelli two. Tarsi with three joints" (Leach, 1832, First American edition, after Leach, 1815). This description specifically excludes the genus *Cicada* as established by Lamarck. Lamarck's genus falls under Leach's tribe Tettigonides. Leach's family Cicadida also excludes Lamarck's genus *Cicada*. Samouelle's (1819) work follows the classification of Leach. According to Article 10e and

Article 63 of the "International Code of Zoological Nomenclature" (1961), a family name must be based on a valid generic name. Latreille's (1802) "Cicadariae" was roughly equivalent to Linnaeus' genus *Cicada*. It included two subgroups, "Cicadae verae" and "Cicadellae." The genus *Cicada* made up the "Cicadae verae." There were five genera in the "Cicadellae." I believe this example is equivalent to the example given for Tipulidae on page 11 of the 1961 International Code of Zoological Nomenclature and the family Cicadidae, therefore, should be attributed to Latreille. Westwood (1840) was the first author to limit the term "Cicadidae" to this family of homopterous insects as we now recognize it. He equated Cicadidae to "Cicadae maniferae" of Linnaeus, the "Chanteuses" of Latreille, and the "Stridulantia" of Burmeister. Distant (1912), Myers (1929), and Kato (1961) gave credit to Westwood for establishing the family. Metcalf omitted Westwood from his "Bibliography of the Cicadoidea" (1962). Westwood followed his designation by a detailed description of the family. Other descriptions I consulted were Amyot and Serville (1843), Ashmead (1888), Edwards (1896), Distant (1912), Lawson (1920), Metcalf (1951--cohors Cicadida), Kato (1961--superfamily Cicadoidea), and Borrer and DeLong (1971).

Characteristics

The head is short and broad with an enlarged, cross-striated clypeus. Antennae are short and setaceous, arising between the eyes and beneath the supraantennal plates. There are three ocelli arranged triangularly on the epicranium. The head terminates beneath in an elongated, three-jointed rostrum.

The thorax is large and broad. The pronotum is short except in *Tettigarcta* where it covers most of the mesonotum. There are two diagonal grooves on each side of the pronotum. The mesonotum is large and terminates in a raised X or cruciform elevation ("in *Tettigarcta* forming a scutellum," Kato, 1961). The metanotum is short and in some genera only visible laterally. Ventrally the thoracic segments are subequal.

The abdomen consists of eleven segments. The first two are united ventrally and the ninth and tenth segments form the external genitalia. The eleventh segment bears the anal style. The third to seventh spiracles are in the sternites and not the pleura.

The anterior femora are enlarged and spinose in all the genera of North America north of Mexico. Tibiae are slender and subcylindrical. There are no pulvilli or empodia between the tarsal claws. The metathoracic mera are well developed and extend posteriorly. The legs are not adapted for jumping, as in other auchenorrhynchous Homoptera.

Wings may be hyaline, opaque, or both. Venation is distinct. An ambient vein encloses the marginal cells. Forewings contain a basal cell. A nodal line running from the nodus of the costal margin to the anal margin may be indicated by auxiliary bumps and breaks in the venation. Wings are coupled in flight by a recurved flange on the dorsal surface of the costal border of the hind wing which hooks with a similar flange on the ventral surface of the anal border of the forewing.

The ninth segment in both sexes is the pygofer, a more or less cylindrical, strongly chitinized case surrounding the genitalia. The aedeagus is further protected by a projection of the tenth segment known as the uncus. The shape of the uncus has been used as the basis for species determination in many species of North American Cicadidae. The

female external genitalia consist of three pairs of appendages making up the ovipositor and its sheaths. The central pair is fused distally. The apices of the middle pair are highly chitinized and possess cutting teeth or edges. The outer pair forms the sheath.

Because methods of sound production among cicadas vary, the following sound "producing" structures cannot be considered characteristic of the entire family. Sound production has been so closely linked with cicadas, however, that a description of the family would not be complete without some mention of the most common structures associated with sound production and reception. Sounds are most commonly produced by the contraction and expansion of a tymbal organ located lateral to the first abdominal segment of the males. The tymbals may be either partially or totally covered from above by a forward projection of the second abdominal tergite or by a posterior projection of the mesonotum (Boulard, 1976a). Males with functional tymbal organs usually possess posterior metasternal projections called opercula. The hearing or chordotonal organ is located in the second abdominal segment. It may be indicated externally by a lateral bulge on the sternite. Many cicadas have accessory stridulating mechanisms and some produce sound by beating their wings together or against the substrate on which they are sitting.

Current Taxonomic Status of the Family

At least three authors use the superfamilial name Cicadoidea to encompass up to five families of cicadas. All of these divisions are based on sound production mechanisms and/or the coverings associated with them.

Kato (1961) lists four families. The two families Cicadidae and Tettigadidae have tymbal organs. The Tettigadidae have an accessory stridulating organ. The two families Platypediidae and Tettigarctidae lack a functional tymbal organ. Platypediidae produce clicking sounds with the forewings and have a chordotonal mirror. Tettigarctidae lack the usual chordotonal mirror.

Metcalf (1951, 1963) lists two families of cicadas, Cicadidae and Tibicinidae. Cicadidae possess an anterior projection of the second abdominal tergite covering or partially covering the tymbal organ. Tibicinidae lack this projection.

Boulard (1976a) divides cicadas into five families. The Tettigarctidae are separated out by their very long pronotum covering most of the mesonotum. Platypediidae lack a functional tymbal organ. A new family, Plautillidae, is characterized by tymbal coverings emanating from the metanotum and a reduction of the vannal region of the wings. Cicadidae and Tibicinidae include the remaining genera, with Cicadidae possessing an anterior projection of the second abdominal tergite in the males and Tibicinidae lacking such a projection.

A definite difference exists in the philosophy and usefulness of the family taxon between those who place cicadas in a single family, Cicadidae, and the above three authors. If we accept Smith's definition of family as reiterated by Torre-Bueno (1962), we can analyze the above divisions:

Family, a division or classification including a number of genera agreeing in one or a set of characters and so closely related that they are apparently descended from one stem.

Fossil evidence is sparse, but modern characteristics seem to indicate that cicadas evolved from one stem. Almost all authors working

in cicada systematics eventually point out the basic similarity of all cicadas and bemoan the lack of truly separable characters. Most morphological characteristics of cicadas represent a continuum rather than a "have" or "have not" status. Some authors have attempted to explain this basic similarity on the basis of a homogeneous, long, subterranean life shared by the nymphal forms. To me this explanation seems fallacious, as edaphic characteristics of soil and differences in root characteristics of host plants can surely be as varied as the external environment of the imagos. The long life of the nymphs has resulted, however, in fewer generations of cicadas responding to evolutionary pressures than those insects with one or more generation per year. In North America north of Mexico, the shortest confirmed life cycle is the four year cycle of *Cicadetta calliope* (Beamer, 1928). The long life cycle could be a contributing factor to the lack of diversity in cicadan morphology. It seems evident, therefore, that the basic similarity of all cicadas verifies their descent from a single phylogenetic stem.

The family Tettigarctidae used by both Kato and Boulard consists of one genus. Members of this genus are generally considered the most primitive of living cicadas. Although *Tettigarcta* apparently differs considerably from other cicadas, separation of a single genus from its nearest relatives obscures that relationship. A subfamilial ranking seems more logical.

Boulard (1975a, 1976a), himself, recognized that the family Platypediidae is not a natural grouping. The loss of the tymbal organ has occurred at least three times, in North America, in Africa, and in China. In both the African and North American genera, other characteristics relate them more closely to other genera in their respective geographical

areas than to each other. *Platypedia* and *Neoplatypedia* have several characteristics in common with the okanaganoid genera and would be better placed as a subdivision of the same taxa in which these genera are placed. The family as delineated by Kato and Boulard is characterized by a single negative character. If one of the functions of systematics is to clarify phylogenetic relationships rather than obscure them, this is surely not a valid family.

In Kato's family, Tettigadidae, both males and females possess an accessory stridulating surface on the mesonotum. A similar structure is found in four genera of North American cicadas not generally considered to be closely related to the Tettigadidae. In addition Boulard (1976a) has described stridulating files on the posterior margin of the mesonotum in the genus *Moana*. Because of the unavailability of specimens, I have not had an opportunity to examine the stridulating mechanisms of the family Tettigadidae as recognized by Kato. However, the mere presence of accessory stridulating mechanisms now appears to be more widespread among cicadas than previously thought. Therefore, Kato's family, Tettigadidae, as originally circumscribed is no longer valid.

The three remaining families are all diagnosed by the presence or absence and/or derivation of tymbal coverings. Only males have tymbal organs, and hence, only males can be identified by these structures. Even among males, only Boulard's Plautillidae appear definitely to form a phylogenetic group. I think it is safe to assume that the tymbal organ itself developed prior to any accessory protective devices. This structure functions to bring the two sexes into proximity for mating. Because of its importance and relative fragility, the development of strengthening or protective devices seems like the next evolutionary step. If the lack

of a projection of the second abdominal tergite indicates a primitive state, then other characters must be drawn upon to show any special phylogenetic relationship within the Tibicinidae. Myers (1929) was aware of this when he stated, regarding Distant's subfamily Tibicininae from which the family Tibicinidae is drawn, that the "Tibicininae . . . was nothing but a dumping-ground for a miscellany of unrelated forms characterized by a single negative quality." Some cicadas have increased the number of ribs and the degree of rib chitinization within the tymbal itself, and others have lost functional tymbals and replaced them with other sound-producing mechanisms, perhaps as a response to tymbal fragility.

Even among the Cicadidae of Metcalf and Boulard, there is such a variation in second abdominal tergal projections that it is not clear whether this character developed once or many times. In our North American cicadas it ranges from the mere upturned ribbon-like acrotergite of *Quesada gigas* with its small lateral projections to the enormous saddlebags of *Diceroprocta arizona*.

If we consider only males there is at least one other obvious characteristic that may be equally important or more so from an evolutionary standpoint than the presence of tymbal covers. That character is the ability of some males to withdraw some genitalic structures as contrasted with those that do not possess this ability. Thus, even considering only males, it is unclear whether the proposed groupings should rank at the family level. Boulard's Plautillidae may represent a phylogenetic grouping of subfamilial status.

In my opinion, the family taxon in insect systematics serves a utilitarian function. It is the lowest level to which a nonexpert in a group can easily identify a given specimen. While admittedly smaller

groupings may be easier to work with in some cases, I see no justification for the splitting of phylogenetically valid families unless such splitting further elucidates evolutionary and zoogeographic relationships and increases the utilitarian function of the taxon. Any division that obscures the identification of large numbers of a group at the familial level fails to meet these criteria. The proposed family groupings described by Kato, Metcalf, and Boulard are based primarily on male secondary sexual characteristics. At least fifty per cent of the world's cicadas are females. These proposals obscure the identification to family of half of the possible specimens. I, therefore, propose we maintain the family Cicadidae as a single unit until such time as more definitive and useful criteria for familial designations are discovered.

Subfamilies

Several attempts have been made to divide the Cicadidae into subfamilies. Amyot and Serville (1843) erected two subfamilies based on the presence or absence of a reticulate condition of the veins of the forewing. Ashmead (1888) added a third subfamily based on the opaqueness of the wings. Wing characteristics have proven unsuitable at the subfamilial level. The reticulate condition of the veins has apparently arisen at least three times in the family, and several modern genera contain species with both completely membranous, semiopaque, or partially opaque wings (e.g., *Okanagana*). More recent attempts to divide the family(ies) into subfamilies have been based on sound-producing mechanisms and their attendant coverings. Distant (1889) proposed two subfamilies: Cicadinae for those forms with the tymbals completely covered by a forward projection of the second abdominal tergite and Tibicininae for those forms

lacking a projection of the second abdominal segment. Distant's subfamilial divisions proved inadequate. He found many intermediate forms with the tymbals incompletely covered. For these he erected the subfamily Gaeaninae in 1905. Jacobi (1907) erected the Tettigadinae. Handlirsch (1925) attempted to erect a phylogenetic classification and established the subfamily Platypleurinae for those forms with totally covered tymbals. He united forms without tymbal covers or with the tymbals partially covered under the subfamily Cicadinae. Myers (1929) raised *Tettigarcta* to subfamilial level. Kato's family Platypediidae was reduced to subfamilial level by Metcalf (1963). Metcalf (1963) used a combination of tymbal cover characteristics and geographic distribution to delineate subfamilies. His Tibiceninae includes Handlirsch's Platypleurinae and geographically related forms with partially covered tymbals with the exception of the genus *Neocicada* which he placed in the Cicadinae. Boulard (1976a) added Moaninae for those Cicadidae with a stridulatory surface on the posterior border of the mesonotum, Plautillinae to encompass his family Plautillidae, and Ydiellinae as a subfamily of his Platypediidae with a stridulatory surface on the costal margin of the hind wing.

Metcalf (1963) places seven of our North American genera in the Tibiceninae (*Cacama*, *Cornuplura*, *Diceroprocta*, *Tibicen*, *Beameria*, *Pacarina*, and *Quesada*), one in the Cicadinae (*Neocicada*), six in the Tibicininae (*Okanagodes*, *Okanagana*, *Tibicinoides*, *Clidophleps*, *Magiccicada*, and *Cicadetta*), and two in the Platypediinae (*Platypedia* and *Neoplatypedia*). The last eight genera belong to the Tibicinidae of Metcalf, while in Boulard's groupings, the last two are in the family Platypediidae. Their subfamily designations, however, remain the same. The first eight

belong in the family Cicadidae under both arrangements; however, here the resemblance ends. In Boulard's arrangement, by definition, *Tibicen*, *Diceroprocta*, *Cornulplra*, and *Caoama* belong in the Platypleurinae because the tymbals are completely covered, while *Quesada*, *Pacarina*, and *Beameria* would be moved to the Cicadinae because the tymbal coverings are incomplete. The tymbal covers on *Neocicada*, on the other hand, are far more extensive that they are on *Cicada orni*, the type for the genus *Cicada* from which *Neocicada* was removed by Kato in 1932. Individuals following Boulard's key could conceivably place specimens of *Neocicada heiroglyphica* in the Platypleurinae without representative samples of other Platypleurinae genera present for comparison. A comparison of the subfamilial and familial arrangements of Metcalf and Boulard is given in Table 1.

Obviously subfamily designations are dependent on family designations. The problem is that the same terms have now been used with so many variations in meaning that a complete overhauling on a world-wide basis seems desirable. This is, of course, beyond the scope of this paper.

Tribes

Distant was responsible for much of the tribal classification of the Cicadidae in a series of papers in the "Annals and Magazine of Natural History" from 1904 to 1905. These are summarized in his synoptic catalog (Distant, 1906). His work was based on the vast collection of the British Museum. Though his output was tremendous, his techniques have been severely criticized. Myers (1929) sums up the problem thusly:

If any of the [referring to Distant] divisions or tribes prove to be real morphological entities, it will be largely a happy chance, since most of them appear to be cabinet associations of superficially similar genera, for the elucidation of which a study of his collection is the first *desideratum*.

Table 1

A comparison of Metcalf's and Boulard's family and subfamily groupings of the genera of American cicadas north of Mexico.

METCALF	BOULARD
CICADIDAE	
Tibiceninae	Platypleurinae
<i>Cacama</i>	<i>Cacama</i>
<i>Cornuplura</i>	<i>Cornuplura</i>
<i>Diceroprocta</i>	<i>Diceroprocta</i>
<i>Tibicen</i>	<i>Tibicen</i>
<i>Beameria</i>	
<i>Pacarina</i>	
<i>Quesada</i>	
Cicadinae	Cicadinae
<i>Neocicada</i>	<i>Neocicada</i>
	<i>Beameria</i>
	<i>Pacarina</i>
	<i>Quesada</i>
TIBICINIDAE	
Tibicininae	Tibicininae
<i>Cicadetta</i>	<i>Cicadetta</i>
<i>Clidophleps</i>	<i>Clidophleps</i>
<i>Magiccicada</i>	<i>Magiccicada</i>
<i>Okanagana</i>	<i>Okanagana</i>
<i>Okanagodes</i>	<i>Okanagodes</i>
<i>Tibicinoides</i>	<i>Tibicinoides</i>
Platypediinae	
<i>Neoplatypedia</i>	
<i>Platypedia</i>	
PLATYPEDIIDAE	
	Platypediinae
	<i>Neoplatypedia</i>
	<i>Platypedia</i>

Metcalf's "General Catalogue of the Homoptera, Fascicle VII, Cicadoidea" (1963) gives the most recent listing of tribal affiliation.

He placed the North American genera in the following tribes:

Tibicenini

Subtribe Tibicenaria

Cacama

Cornuplura

Tibicen

Diceroprocta

Fidicinini

Beameria

Pacarina

Hyantiini

Quesada

Cicadini

Neocicada

Tibicinini

Okanogodes

Oliadophleps

Okanagana

Tibiccinoides

Magiccicada

Cicadettini

Cicadetta

There are no tribal designations for the two genera *Platypedia* and *Neoplatypedia* which comprise Metcalf's subfamily Platypediinae. Myers (1929)

felt that the tribe Tibicinnini represented a "miscellaneous collection of all those forms which will not go into any of the other gymnotympanate divisions." No improvement seems to have been made since that time.

Tribal classification has not been treated in recent papers on the Cicadidae. Those characteristics which are applicable will be treated in the discussion of individual genera in this paper. The tribal taxon needs to be reworked on a cosmopolitan level.

CHAPTER IV

CLASSIFICATION: GENERA

Linnaeus (1758) separated the genus *Cicada* into five subdivisions. The subdivision Manniferae became the "non saltantes" or true Cicadae. Fabricius (1775) in Systema Entomologiae introduced the genus *Tettigonia* for most of what we now consider cicadas, but the two names were frequently synonymized. The genus *Cicada* remained the only generic designation of the group for a long time. Latrielle founded the genus *Tibicen* in 1825. The name was simply listed without description but with the naming of *C. plebeja* Scop. as type. Some authors tried to use the name with various interpretations, but most ignored it. Several species had been named as types of the genus *Cicada*, among them the species *Cicada tibicen*. In 1914, Van Duzee firmly stated he felt Lamarck (1801) intended to name *Cicada orni* as the type of the genus *Cicada*, thus freeing the name "tibicen" to be used for another genus. He accepted *plebeja* as the type of the genus *Tibicen* following the "International Code" and two years later established many of our North American species as members of this genus in his Check List of the Hemiptera of America, North of Mexico.

Among our American genera north of Mexico, the next genus to be named was *Cicadetta*, Kolenati (1857). *Diceroprocta* appeared in a key in Stal's Hemiptera insularum Philippinarum in 1870 but was not widely used until Davis (1923) moved several North American species from the genus *Tibicen* to *Diceroprocta*. Uhler named *Platypedia* in 1888. *Cacama* was named by Distant in 1904, and the same author named *Pacarina*, *Quesada*,

and *Okanagana* in 1905. Distant added *Tibicinioides* in 1914 and Van Duzee named *Clidophleps* in 1915. All but one of the remaining genera were named by William T. Davis. Those named by Davis include *Okanagodes*, 1919a; *Neoplatypedia*, 1920; *Magicicada*, 1925; *Beameria*, 1934; and *Cornuplura*, 1944. In 1932, Kato transferred our remaining North American representatives of the genus *Cicada* to their own genus, *Neocicada*.

The first attempt to list specifically the genera of America north of Mexico was Van Duzee's checklist of 1916 followed the next year by his catalogue of the same genera and species. Although Van Duzee listed sixteen genera, the same number we have now, only eight of the names remain the same. *Melampsalta* has been synonymized with *Cicadetta*. Our representatives of *Proarna* have become *Beameria*; *Tibicina* have become *Magicicada*; and *Cicada* have become *Neocicada*. *Fidicina*, *Odopoea*, *Tettigades*, and *Herrera* were apparently erroneously attributed to this geographical region by early writers.

The only other paper to deal with the genera as a whole is Davis' 1930 distributional study. He also lists sixteen genera with only twelve that correspond to our current list. Davis omits *Fidicina*, *Odopoea*, and *Herrera* and adds *Neoplatypedia*, *Diceroprocta*, and *Okanagodes*. He replaces *Tibicina* with *Magicicada*. Although Davis retains *Tettigades* as a United States genus, based on Cochise County records, I have never seen specimens of the genus collected north of Mexico. I have collected extensively in Cochise County, Arizona, where Davis reports they occur. I have also consulted with Dr. Thomas Moore of the University of Michigan, who has collected in both the United States and Mexico, and he assures me that the northern distributional limits of *Tettigades* lie far south of the United States border (Moore, 1977, personal communication). *Beameria*,

Neocicada, and *Cornuplura* were not yet named when Davis wrote his 1930 paper, and the synonymy of *Melampsalta* with *Cicadetta* was not widely accepted.

The most recent listing of cicadas is the world wide catalogue of Metcalf (1963). Metcalf occasionally indicates what he thinks is an erroneous location, but he usually reiterates locations given by authors without comment. His generic nomenclature is up to date. Early writers were often obscure in listing their localities, thus one can extract twenty-four possible genera for North American cicadas north of Mexico from Metcalf's list. Errors in Metcalf's catalogue contribute additional genera, for example, *Neocicada chisos* is still listed under the genus *Cicada*.

The current list of American genera from the region north of Mexico is as follows: 1. *Beameria*, 2. *Cacama*, 3. *Cicadetta*, 4. *Clidophleps*, 5. *Cornuplura*, 6. *Diceroprocta*, 7. *Magiciada*, 8. *Neocicada*, 9. *Neoplatypedia*, 10. *Okanagana*, 11. *Okanagodes*, 12. *Pacarina*, 13. *Platypedia*, 14. *Quesada*, 15. *Tibicen*, 16. *Tibicinoides*.

CHAPTER V

GENERAL MORPHOLOGY

The largest Homoptera are found in the family Cicadidae. These insects are generally characterized by a rather short, stout body with moderately long wings. The head is short, but wide, with prominent eyes and three conspicuous ocelli. In the genera north of Mexico, the mesothorax is the largest thoracic segment. Males of most genera contain a sound producing tymbal organ lateral to the first abdominal segment. A chordotonal organ is indicated by a lateral bulge on the second abdominal segment in both sexes.

Although several writers have written on specific aspects of both the internal and external anatomy of cicadas, Myers' study (1928) remains the most comprehensive treatment of cicada morphology. A number of specialized terms have been used in the past to refer to features of cicada anatomy. This paper incorporates several of these terms into the descriptions and keys in order to provide continuity with past work. The following discussion is presented to clarify terms used in the keys and generic descriptions. General characteristics of cicada morphology are illustrated by diagrammatic views of the dorsal and ventral surfaces (Figure 1).

Figure 1. A, dorsal view of a cicada. The following structures are labeled: clypeus (clp), epicranium (ep), pronotum (pr), pronotal collar (pc), prescutum (psc), scutum (sc), scutellum or "cruciform elevation" (scl), metathorax (mt), tymbal cover (tc), pygofer (p). The left tymbal cover is cut away to reveal the tymbal organ (tym). In this example the mesothorax covers most of the metathorax. The arrow points to the location of the lateral carina when viewed laterally. B, ventral view. Legs have been cut away below the coxae (cx). The following structures are labeled: clypeus, operculum (op), propleuron (prp), meron (me), hypandrium (h), epimeron of the metathorax (mep). The right operculum is cut away to reveal the folded membrane (fm) and the mirror or tympanum (m). Roman numerals in both figures indicate abdominal segments.

A

B

General Body Proportions

Two measurements are given for each genus to provide an indication of general range of size of members of the genus. Length of body is measured from the apex of the clypeus to the tip of the abdomen. Expanse of wings is the greatest expanse of the forewings. This measurement is the only wing measurement consistently given in species descriptions. The relationship of abdomen length to overall length of the body is also indicated. This relationship usually is characteristic of a genus. The variability in size range is greater, of course, in specimens of the larger genera. While size ranges overlap considerably, from a practical standpoint, size can often narrow the number of genera under consideration when identifying an individual specimen. Thus, a very large cicada would not fall in the range of *Tibicinoides*, *Beameria*, or *Pacarina*, and a very small cicada is unlikely to be a *Quesada*, *Tibicen*, or *Cornuplura*.

Head

The cicada head contains several characteristic features. Traditional measurements and nomenclature of the head are in some cases obscure and in others a point of controversy in the literature. A characteristic measurement used by Distant and others is a comparison of the width of the head, including the eyes, versus the width of the "base" of the mesonotum. Torre-Bueno (1962) defines the base of a thoracic structure as "that part nearest the abdomen"; however, this is a meaningless measurement in cicadas. Previous writers obviously meant the visible anterior edge of the mesonotum. Since the real anterior edge of the mesonotum is overlapped by the collar of the pronotum, a

sometimes curved structure, this measurement is also awkward. Therefore, the width of the head, including the eyes, in the following descriptions is compared with the width of the mesonotum measured at its broadest point between the forewings, excluding the axillary sclerites.

The eyes in cicadas are prominent and may be narrower, in a line with, or extend laterally beyond the anterior angles of the pronotum. This relationship is usually obvious. However, a straight edge may be lined up with the lateral edge of the eye to determine its relative position with the anterior lateral angles of the pronotum.

The definitions of the head regions are controversial, also. Snodgrass (1935) defined the clypeus as the "region of the cranial wall on which the dorsal dilator muscles of the . . . cibarium take their origin." The frons was interpreted as a triangular region which "bears the median ocellus on its upper part." When a frontoclypeal or epistomal suture is present, it separates these two regions. The anterior tentorial pits are normally associated with the lateral ends of this sulcus and mark the point of articulation with the anterior arms of the tentorium. In some insects the pits have migrated medially on the sulcus. When a frontoclypeal suture is lacking, a line drawn between the anterior tentorial pits is used to delineate the frontal and clypeal regions of the head.

In the cicada the median facial plate is bordered both dorsally and laterally by a continuous suture. The anterior tentorial pits are located in the upper half of the lateral portion of this sulcus. DuPorte (1962) interpreted the transverse portion of the sulcus as a "transfrontal ridge such as found in mantids." The lateral regions between the transverse portion and the anterior tentorial pits, he called "frontogenal

ridges," and those distal to the pits, he interpreted as "clypeogenial ridges." He supported this view by stating that the anterior mandibular articulation would then correspond to that typically found in Hymenoptera. He further stated that the entire head evolved from a hypothetical psocid-like ancestor. In his interpretation, the frons would consist of the region anterior and dorsal to a hypothetical line drawn between the tentorial pits, and the post clypeus would be the region posterior to this line. In reality this interpretation is a return in part to the descriptions of earlier morphologists and taxonomists who called the entire median facial plate the "front" or frons and the remainder of the epicranium the "disk of the vertex." This terminology was used prior to Snodgrass' detailed morphological studies.

DuPorte's interpretation is interesting but requires several assumptions: 1. The frontoclypeal sulcus has disappeared or never existed; 2. the muscles of the cibarium have invaded the frons; 3. The modern cicada head has developed or evolved from both specialized orthopteran and hymenopteran characteristics; 4. The entire head, and by extension, the rest of the organism developed from a psocid-like ancestor. Both Snodgrass and Kramer (1950) cited evidence of a "Y" shaped frontal suture encompassing the median ocellus. They interpreted the arms of this suture as the demarcation of the sides of the modern frons. Kramer further used these ridges as part of his phylogentic evidence that ancestral cicadas branched from a common ancestral stem with cercopids, cicadellids, and membracids much earlier than the separation of the three from each other.

In an attempt to verify DuPorte, I felt that if even part of the lateral edges of the median facial sclerite split during ecdysis, it would

be evidence in favor of his theory. A careful examination of exuviae in my collection indicated that the ecdysial split terminates at the transverse sulcus. This is not, however, inconsistent with other writings of DuPorte (1977).

The dorsum of the cicada head contains three distinct regions, a horizontal vertex, a sloping, sometimes vertical, middle region anterior to the vertex containing the median ocellus, and an anterior horizontal region containing the dorsum of the median facial plate flanked by the supraantennal plates. If we accept DuPorte's ideas, what should we call the central section? If we accept Snodgrass' interpretation, the length of this segment is equivalent to the length of the frons.

There is a much simpler explanation for the dorsal structures of the cicada head than DuPorte's theory. The clypeus has obviously expanded to accomodate the dilator muscles of the cibarium. If it expanded upward as well as outward, the frontoclypeal sulcus would lengthen around the sclerite. Without moving the tentorial pits, the sulcus would attain the current broad "U" shape. The frons would be subsequently shortened as the clypeus expanded. This interpretation does not require the loss of one sulcus and the acquisition of another, the invasion of the frons by the muscles of the cibarium, or other specialized characteristics except those associated with the more efficient acquisition of food.

I have no evidence either in support of or against DuPorte's theory. DuPorte worked with an unidentified *Tibicen*. Until I see additional studies of closely related Homoptera, including *Tettigarcta*, which apparently retains a vestigial subgenal suture (Kramer, 1950), I prefer the simpler explanation. Therefore, in the following descriptions, the length of the frons will refer to the more or less vertical portion of

the head, as distinct from the vertex, and will be compared with the dorsum of the clypeus. The epicranium will be assumed to end with the epistomal or frontoclypeal suture (see Figure 2).

Cicadas have three ocelli. The two lateral ocelli lie on the vertex of the head, the middle ocellus is located on the frons. The relationship of the distance between the two lateral ocelli versus the distance between a lateral ocellus and the corresponding eye usually is characteristic of a genus. Measurements were made from the interior margin of the eye to the exterior edge of the ocellus and between the medial edges of the two lateral ocelli.

The supraantennal plates lie above the insertion of the antennae. The anterior edge of these plates may form a more or less continuous line with the apex of the clypeus or the clypeus may protrude substantially beyond the margins of the supraantennal plates. The dorsal shape of the clypeus and the extent of its protrusion are generically characteristic. The clypeus is flanked laterally on the "face" by the lora (singular, lorum) sometimes referred to as the "cheeks."

The rostrum or proboscis is an extended mouth piece representing the sucking beak in cicadas. The rostrum is comprised of an elongated labium forming the outer sheath and containing the mandibular and maxillary bristles. The maxillary bristles interlock centrally forming two primary ducts, one for the egestion of salivary fluid and one for the ingestion of food. The length of the rostrum may be species specific within a genus; however, a prescribed range of lengths is usually characteristic of a genus. Thus, *Okanagana* have relatively short rostra, extending within the range of the middle coxae; whereas, *Cacama* have long rostra extending to or beyond the hind coxae.

Figure 2. The cicada head. A, face or ventral side showing position of eyes (e), ocelli (oc), frons (fr), supraantennal plates (sap), lora (l), postclypeus (pclp), anteclypeus (aclp), labrum (lm), rostrum (ros). B, dorsum showing the eyes, ocelli, frons, supraantennal plates, the dorsum of the clypeus (clp), and the frontoclypeal or epistomal suture (fcs). The lateral circles just mediad to the eyes mark the location of an unidentified sensory organ. C, cross section of the rostrum showing the relative positions of the mandibular (md) and maxillary (mx) setae. The large central lumen is the food channel. The smaller lumen to the right is the salivary channel. Four smaller lumina, one in each of the setae form passageways for nerves and tracheae. The labium (lab) forms the outer sheath.

A

B

C

Thorax

The pronotum is characterized by two pairs of diagonal grooves. The posterior margin is broad and ends with the dilated lateral posterior angles. The posterior margin is frequently referred to as the pronotal collar. The lateral margins may be amplified or dilated. Laterally the pronotum joins the propleuron. If the pronotum is amplified, when viewed laterally, this juncture forms a continuous keel or carina extending the length of the pronotum. The extent of the lateral amplification determines the extent of the carina. The lateral edges of the pronotum are usually smooth in the genera found north of Mexico. They are irregularly toothed or jagged in *Quesada* and in some species of *Okanagana*. Occasionally the lateral edges will bear one or two spines.

The mesothorax is the largest thoracic segment in the North American genera of cicadas. The anterior part of the notum projects beneath the pronotum forming an anterior phragma. A "U" shaped prescutum is located in the center of the anterior portion of the notum. The scutum occupies the greater part of the notum. The scutellum forms a raised "X" which has been termed the "cruciform elevation" by taxonomists. In some genera the mesonotum is ridged where the forewing sits at rest. A portion of this ridge may project medially on the anterior part of the notum near what is sometimes called the "shoulder." When this occurs, the projection is finely striated and used as an accessory sound producing mechanism with the wing acting as the plectrum. Sometimes the ridged portion bears fine, even striations (see Figure 3).

The metathorax is very short dorsally. In half of the genera found north of Mexico, the scutellum of the mesothorax overlies and conceals

Figure 3. A portion of the thorax of an okanaganoid cicada showing striations on the mesonotum. Large arrow points to the stridulitrum. Small arrow points to the presumed plectrum on the forewing. Terminology follows Ashlock and Lattin (1963). The stridulitrum is frequently located in a pale area on a dark background. This area is indicated on the figure. Drawn from *Clidophleps blaisdelli*.

the central portion of the metathoracic tergum. Ventrally, the epimera in males are usually produced caudally forming the opercula, or lower covers of the tymbal organs.

Legs

The legs of cicadas are normally segmented. They are not modified for jumping as in some of their closest relatives. There are three tarsal segments, but no pulvilli between the tarsal claws. The foreleg of the nymph is fossorial. In the adult the fore femora retain a lessened fossorial expansion and usually bear spines on the ventral margin (Figure 4). The tibia are subcylindrical. The metathoracic mera are elongated and form projecting triangular structures. These projections are the meracanthi of some older works, but more recent publications use mera (singular, meron), e.g., Kramer (1950), Bullough (1950).

Wings

Wing notation is by no means fixed for the family. The most common deviation is the proximal portion of the radius. Some authors combine this portion of the radius with the base of the media where it emerges from the basal cell or the arculus. This of course modifies the notation of the veins at the apex of the wing and also the notation of the intervening cells. The following descriptions follow the modified Comstock-Needham interpretation of venation accepted by Myers (1928, 1929), Cooper (1941), Kramer (1950), and others. This is the interpretation most commonly given in modern general textbooks (e.g., Borrer and DeLong, 1971). In this interpretation the radius is united with the subcosta

Figure 4. Femur of a cicada foreleg showing expanded configuration and spines on the ventral surface. Drawn from *Okanagana fumipennis*.

proximal to the body. This interpretation is used for most original descriptions of North American genera and species. The following remarks, therefore, are consistent with prior descriptions. The modified Comstock-Needham system, which I am following, is shown in Figure 5.

Cell notation in the Comstock-Needham system is complex. The cells or areoles in cicada wings are often referred to by groups, for example, the eight apical areas or marginal cells or the ulnar areas. This is the system of cell notation used and diagrammed by Simons (1954). Simons' notation is simpler and lends itself to use in keys and the more generalized descriptions at a generic level. Simons' system of cell notation is shown in Figure 5 and is utilized in the following text.

A special feature of the forewings is the presence of the nodal line. This line runs from the nodus or node of the costal margin across the width of the wing. Its presence is marked by minute breaks in the sclerotization of some of the principal vein branches. The function of this line became apparent to me during a sequence of a movie showing *Magiccicada septendecim* in the stages of the final molt to an imago (Moore and Kausch, 1975). The wings are apparently folded along this line in the last instar nymph prior to emergence as an adult. The line is well marked in some members of the genus *Tibicinioides* by a rudimentary vein. The line apparently is also present in the Cicadelloid family Hylicidae (Kramer, 1950).

The hindwings of some genera are susceptible to individual variation. Therefore, hindwing characteristics have not been utilized in this dissertation.

Figure 5. Cicada forewing showing two systems of notation in current usage. A, cell notation used by Simons (1954). Abbreviations are as follows: A, anal cell; arc, arcus; Ba, basal cell; C, costa; Cu, cubital cell; M1, M2, etc., marginal cells; Me, medial cell; N, nodus; U1, U2, etc., ulnar cells; 1st and 2nd equal the first and second crossveins. B, Comstock-Needham system used in current textbooks of entomology. Abbreviations used in the notation are longitudinal veins--C, costa; Sc, subcosta; R, radius; M, media; Cu, cubitus; A, anal. Crossveins--m, medial; m-cu, medio-cubital; r-m, radio-medial. Cells are named according to the longitudinal vein on the anterior side of the cell. The general position of the nodal line is indicated by dots in both A and B.

Abdomen

The first two abdominal segments are modified for the production and reception of sound. Pringle (1954, 1957) gives detailed accounts of the morphology of this region. The exterior cuticle is depressed and thickened forming a wide vertical groove. This groove "is divided into dorso-lateral and ventro-lateral portions by a horizontal ridge projecting forwards from the lateral angle of the abdomen" (Pringle, 1957). Ventrally the groove is bounded by two membranes, an anterior "folded membrane" that permits the abdomen to move relative to the thorax and a posterior chordotonal "tympanum" sometimes termed the "mirror." At the base of the groove is a heavily sclerotized skeletal structure that forms the basal attachment of the tymbal muscles and projects dorso-laterally to form the "chitinous V." Dorsally the groove is bounded posteriorly by a strongly sclerotized surface, while the anterior surface is the sound producing "tymbal organ" or simply "tymbal" (Figure 6). The tymbal organ itself is a ribbed membrane whose buckling produces the sound vibrations associated with cicadas. An "auditory capsule" is indicated exteriorly by a lateral bulge on the second segment. Interiorly this capsule contains a number of chordotonal sensilla connected to the thoracic ganglion by an auditory nerve running forward through the base of the chitinous "V" to the thoracic ganglion. In *Neocicada* and *Cicada* this capsule has migrated ventrally. Pringle (1954, 1957) and Vasvary (1966) detail the musculature and nervous connections of this area in *Platyleura capitata* and *Tibicen chloromera*, respectively.

Abdominal segments III through VI are not specialized. The terga form lateral angles and project across the lateral areas of the ventral

Figure 6. Structures associated with the first and second abdominal segments in male cicadas. A, vertical groove, viewed laterally with left opercula and tymbal cover removed. Structures shown are tymbal organ (tym), auditory capsule (a), horizontal ridge (hr), folded membrane (fm), chitinous "V" (V), tympanum or mirror (m), opercula (op), posterior coxae (cx), meron (me). The direction of the thorax (tho) and abdomen (abd) are indicated. B, posterior view of the same area. The tymbal cover (tc) and tymbal organ (tym) are removed on the right to reveal the sclerotized posterior surface. Tymbal muscles (t mus) are shown. Drawn from *Tibicen duryi*.

A

B

side of the abdomen. The terminal segments of the abdomen are discussed under the heading "sexual characteristics."

Sexual Characteristics

One of the primary functions of this study is to enable the reader to identify easily specimens "in hand" to genus. For that reason only external portions of the segments bearing genitalia have been described. These are the parts that are readily seen or easily extracted without complicated dissection. Numerous other genitalic structures are available for use at the specific level. The terminal segments of the abdomen are modified by the genitalic appendages. The ninth and tenth segments form the external genitalia. The eleventh segment is small and bears the anal style. The ninth tergite in both sexes forms the pygofer. The pygofer in cicadas is a simplified structure forming nearly a complete sclerotized ring. Ventrally the ends of the tergite may meet, but they remain unconnected in females to allow for the extrusion of the ovipositor. The posterior portion of the ventral region in males is invaginated into the segment to form the genital chamber that holds the phallus. "Genital plates and genital valve as well as styles and connective are absent" (Tuxen, 1970). The tenth segment in males bears an interesting structure apparently functioning to protect, and in some cases, hold the phallus. This structure may be united or simple as in *Tibicen* and the okanaganoid genera, or it may be bifurcated, consisting of a pair of structures as in *Cicadetta*, *Magicalcada*, and *Diceroprocta*. It has been called by a variety of names, e.g., "copulatory claspers" (Myers, 1928, 1929), "lateral lobes" (Snodgrass, 1935), "anal hooks" (Tuxen, 1970), "ventral processes" (DuPorte, 1977). Taxonomists call it the "uncus," and it

will so be named in this study. The uncus has formed the basis for both generic and specific separation especially in the cicadas found in North America north of Mexico. Six western genera are characterized by an elongated uncus lying dorsally over the phallus. The hypandrium or eighth sternite, a "boat-shaped" sclerite, is correspondingly elongated and protects the phallus from below. The uncus in these genera does not retract into the abdomen. In the remaining genera the pygofer may be substantially withdrawn into the eighth segment. The uncus maintains a ventral position in the noncopulating male. It is hidden ventrally by the correspondingly shorter hypandrium (see Figure 7).

In females the seventh sternite forms the subgenital plate. Its basic shape is frequently characteristic of a genus. The eighth sternite is not visible. It is greatly reduced in size and consists of two lateral sclerites lying under the seventh sternite. In some *Tibicen* and *Cornuplura* the eighth sternite may project into hooks medially. The female possesses three pairs of appendages, or "valves" that make up the ovipositor and its sheaths. The central pair is fused distally. It is united with the middle pair by a series of interlocking grooves that prevent lateral movement but allow the lateral pieces to slide longitudinally relative to the central piece. The middle pair of valves are highly chitinized and possess cutting teeth or edges. The outer pair of valves form the sheath of the ovipositor (Figure 7).

Internal Structure Revealed by Radiographs

Systematists have recognized for a long time that characteristics other than external anatomical features could be useful in identification and in correlating relationships of various taxonomic units. Numerous

Figure 7. External genital bearing segments of cicadas. A through E are males. A, lateral view of retractable form with the pygofer (p) and uncus (u) pulled out; B, same as above in a normal resting position; C, caudal view. D, lateral view of nonretractable form with the uncus raised; E, same in a normal resting position with the uncus lying in the trough of the hypandrium (h). F through H show female characters. F, caudal view showing hooks of sternite VIII lying under the subgenital plate (sp). This character occurs in *Cornuplura* and some *Tibicen*. G, ventral view showing the pygofer (p) surrounding the ovipositor. H, female ovipositor showing saw valves (v1), middle piece (v2), sheaths (v3). Terminology after Myers (1929).

A

B

C

D

E

F

G

H

approaches have been taken ranging from simple internal dissections to complicated chemical extractions. While most of these techniques yield valuable information, they may be impractical for the average entomologist to use. They frequently require fresh specimens or at least freshly preserved specimens for best results. Many techniques are extremely expensive. They all require destruction of part or all of the specimen, and, therefore, cannot be used on museum types. Professor H.L. Cromroy of the University of Florida suggested I explore the use of low energy x-rays (soft x-rays) to elucidate internal characteristics. The results are only preliminary, but a few remarks can be made regarding the technique. The model [Faxitron 804] used is small and fits on a table-top. It is a relatively inexpensive piece of scientific equipment and is as easy to operate as a kitchen oven. It in no way alters or damages the appearance of the specimen and, therefore, should be safe to use even on type specimens. Two series of radiographs were taken. Dorsal views were made at 50 KVP (kilovolt potential) with exposures ranging from 45 to 60 seconds, and ventral views at 25 KVP with an exposure time of 60 seconds. Polaroid P/N 55 film was used, and the resulting radiographs were enlarged for analysis. At these exposures and times, elements of dried internal musculature are the most obvious features revealed. The median dorsal indirect flight muscles show clearly in both sexes. The other thoracic musculature is less distinct. Elements of the reproductive musculature are also seen in some of the pictures. The most significant muscular feature of taxonomic value revealed is the generalized shape of the male tymbal muscles.

Pringle (1954) defines the tymbal muscles as, "The main muscles of the sound-producing apparatus, attached basally to the base of the

chitinous V and distally to a thin approximately circular disk from the centre of which a flat apodeme runs to the tymbal." While the muscle runs dorso-ventrally through the insect, a characteristic pattern is shown by x-rays made of a dorsal or ventral view. Thus the four North American genera having complete tymbal covers and belonging to the tribe Tibicenini have a characteristic deep V shape to the x-rayed tymbal muscle. The V is united posteriorly forming a Y in both *Tibicen* and *Cornuplura*. This pattern holds for both the parallel sided and gently tapering forms of *Tibicen* discussed later in the text. Kato (1961) has also taken radiographs of cicadas. He pictures two genera of Tibicenini found in Japan (Kato, 1961, Plate XIX). The x-rayed tymbal muscle in *Tibicen bihamatus* (Motschulsky) illustrated by Kato agrees perfectly with the pattern seen in North American *Tibicen*, while *Cryptotympana japonensis* Kato lacks the united posterior extension of the V. *Cacama* also lacks the posterior extension, its V shape being broader and shallower than *Tibicen*. The pattern in *Diceroprocta* shows the greatest deviation from the other Tibicenini. Although the central posterior V is present, the lateral connections are broader. Additional partial anterior muscles extend upward, almost forming a hexagonal pattern. The pattern in *Diceroprocta* is very similar to that found in *Magicicada* which lacks tymbal covers completely. *Pacarina* has a similar pattern, but the arms do not meet posteriorly. In *Neocicada* the distal connections are narrow. The four okanagancoid genera, *Okanagana*, *Tibicinoides*, *Okanagodes*, and *Clidophleps* exhibit a rather flat latitudinal pattern indicating a more vertical structure within the insects. This pattern appears broadest in *Okanagana*. *Quesada* shows a broad latitudinal pattern and *Beameria* falls between *Okanagana* and *Quesada*. *Cicadetta* has a narrow pattern projecting

slightly anteriorly. X-rays of *Platypedia* and *Neoplatypedia* reveal no sign of tymbal muscles. While all the patterns of tymbal muscles generated by North American genera occurring north of Mexico appear to be deviations of two basic patterns, they do not group the genera completely around traditional lines. The most notable exception is the pattern exhibited by *Magiccicada*, resembling more closely the muscular pattern in the group containing tymbal covers rather than the group lacking tymbal covers. The tymbal covers in *Beameria* and *Quesada* are minimal. Handlirsh (1925) felt that cicadas with partial tymbal covers should be considered more closely related evolutionarily to those lacking covers than to those with complete covers. The two genera with extensive, but not complete covers, *Pacarina* and *Neocicada*, are more similar to those genera with tymbal covers than they are to those without. Although variation in the tymbal musculature patterns found in the North American genera are not as striking as one might hope for, quite different patterns are illustrated by Kato for the genera *Tanna* and *Graptopsaltria* from Japan, indicating that both this character and the technique that reveals it are worth pursuing further. Figure 8 shows examples of the radiographs.

Other morphological features exhibited by all or several of the x-ray radiographs are the shape and position of the frontoclypeal suture, the insertion of the forelegs, and the extent of ovarian development.

All the specimens x-rayed were dry, pinned specimens. Therefore, care must be used in interpretation of the radiographs. Comparative studies need to be made between fresh specimens and dry ones to see the extent and variation of change with time. Various exposures and times may reveal different structures. For these reasons, the above analysis

Figure 8. Radiographs of cicadas. A through H are males. Arrows point to the location of the tymbal muscles. A, *Tibicen*, and B, *Cornuplura*, show a Y configuration. C, *Cacama*, shows a broad V. D, *Diceroprocta*, and E, *Magicicada*, are almost hexagonal. F, *Quesada*, and G, *Tibicinoides*, are transverse. H, *Platypedia*, lacks a tymbal muscle. I through L are females. Large arrows point to the ovaries. Small arrows on I, *Quesada*, point to the frontoclypeal sulcus and the insertion of the foreleg. The small arrow on J, *Tibicen*, points to the muscles surrounding the ovipositor. K and L are *Magicicada* and *Cacama*, respectively. E, G, and H are enlarged. The remainder approximate the actual size.

A

B

C

D

E

F

G

H

I

J

K

L

is regarded as both speculative and preliminary. The technique does show promise, however, not only in taxonomy but in ecology as well. Structure and utilization of nests, nymphal development, analysis of parasitism, and infestations within plants are but a few of the possibilities. The greatest advantage of low energy x-ray radiography in taxonomy is that it reveals additional information without damaging the source.

CHAPTER VI

KEYS TO THE GENERA

Males

- 1 Posterior margin of metanotum partially covered by mesonotum; lateral anterior projections of 2nd abdominal tergite covering or partially covering the tymbal organ (Fig. 1) 2
- 1' Posterior margin of metanotum completely visible behind mesonotum; lateral anterior projections of 2nd abdominal tergite absent (Fig. 12) 10
- 2 (1) Tymbal covers complete dorsally; opercula meeting or nearly meeting (Fig. 2) 6
- 2' Tymbal covers incomplete dorsally; opercula may meet (Fig. 20) . . . 3
- 3 (2') Tymbal covers triangular and concave medially; opercula meeting or nearly meeting (Fig. 20) *Pacarina*
- 3' Tymbal covers not triangular or concave medially; opercula separated (Fig. 9) 4
- 4 (3') 1st and 2nd crossveins of forewings parallel (Fig. 5) 5
- 4' 1st and 2nd crossveins of forewings not parallel (Fig. 9) . . . *Beameria*
- 5 (4) Lateral edges of pronotum smooth (Fig. 16) *Neocicada*
- 5' Lateral edges of pronotum jagged or irregularly toothed (Fig. 22) *Quesada*
- 6 (2) Ninth abdominal tergite produced posteriorly to a central spine or point (Fig. 6) 7
- 6' Ninth abdominal tergite without a central spine (Fig. 14) 9
Diceroprocta and *Tibicen* in part
- 7 (6) Width of head including eyes much narrower than the width of the mesonotum; length of body less than 2 1/2 times the width of the mesonotum; abdomen broadly rounded caudally (Fig. 10) . . . *Cacama*

- 7' Width of head including eyes about as wide or wider than mesonotum;
length of body at least 2 1/2 times the width of the mesonotum;
abdomen tapering caudally (Fig. 1) 8
- 8 (7') Ninth abdominal tergite with a pair of spines protruding backward
from the ventral edge (Fig. 13). *Cornuplura*
- 8' Ninth abdominal tergite lacking ventral spines (Fig. 23 and
Fig. 7). *Tibicen*
- 9 (6') Length of body greater than 35 mm; uncus simple
(Fig. 23). *Tibicen*
- 9' Length of body less than 35 mm; uncus bifurcated (Fig. 14) *Diceroprocta*
- 10 (1') Uncus retractable (Fig. 7). 11
- 10' Uncus exposed; hypandrium elongated (Fig. 7). 12
- 11 (10') Medial and cubital veins joined when emerging from basal cell
of forewing (Fig. 11) *Cicadetta*
- 11' Medial and cubital veins emerging separately from basal cell of
forewing (Fig. 15). *Magisicada*
- 12 (10') Tymbal organs present (Fig. 1) 14
- 12' Tymbal organs absent (Fig. 21). 13
- 13 (12') Eight marginal cells in forewing (Fig. 21) *Platypedia*
- 13' Seven marginal cells in forewing (Fig. 17). *Neoplatypedia*
- 14 (12) Pronotum flared laterally forming longitudinal ridge or carina
when viewed from the side; ocelli variously colored 15
- 14' Pronotum constricted, rounding laterally; ocelli ruby red
(Fig. 19) *Okanagodes*
- 15 (14) Marginal cells of forewing about 1/2 the length of ulnar cells
U1 and U2 (Fig. 24) *Tibicenoides*
- 15' Marginal cells of forewing at least 2/3 the length of ulnar cells
U1 and U2 (Fig. 5). 16
- 16 (15') Costal margin of radial cell at least 2 1/2 times longer than
the medial vein anterior to the first branch
(Fig. 18). *Okanagana*
- 16' Costal margin of radial cell less than 2 1/2 times longer than the
unbranched segment of the medial vein (Fig. 12) *Clidophraps*

Females

- 1 Posterior margin of metanotum partially covered by mesonotum
(Fig. 1). 2
- 1' Posterior margin of metanotum completely visible behind mesonotum
(Fig. 12) 11
- 2 (1) Width of head including eyes about as wide or wider than width
of mesonotum (Fig. 1) 3
- 2' Width of head including eyes much narrower than the width of the
mesonotum (Fig. 10). *Cacama*
- 3 (2') First and second crossveins of forewing parallel or nearly
parallel (Fig. 5). 4
- 3' First and second crossveins of forewing not parallel (Fig. 9). . . . 9
- 4 (3) Longitudinal veins with infuscated dots near the ambient vein
(Fig. 16). *Neocicada*
- 4' Longitudinal veins without infuscated dots near the ambient vein
(Fig. 5) 5
- 5 (4') Lateral edges of pronotum jagged or irregularly toothed
(Fig. 22) *Quesada*
- 5' Lateral edges of pronotum smooth (Fig. 1). 6
- 6 (5') Subgenital plate sinuous and/or length of R_{4+5} between the first
and 2nd crossveins equal to or greater than length of R_{4+5}
from first crossvein to the ambient vein in the forewing
(Fig. 14). *Diceroprocta*
- 6' Subgenital plate produced into two symmetrical, smooth lobes; length
of R_{4+5} between the first and second crossveins less than the
length of R_{4+5} from the first crossvein to the ambient vein in
the forewing (Fig. 23) 7
- 7 (6') Eighth abdominal sternite visible as 2 hook-like projections
beneath the subgenital plate when viewed caudally (Fig. 7) . . 8
Cornuplura and *Tibicen* in part
- 7' Eighth abdominal sternite not visible beneath subgenital plate or
or lacking hook-like projections (Fig. 23) *Tibicen*
- 8 (7) Basal cell of forewing green or brown (Fig. 23) *Tibicen*
- 8' Basal cell of forewing predominantly black (Fig. 13) *Cornuplura*
- 9 (3') Length of 7th marginal areole more than 2 times the width
(Fig. 14). *Diceroprocta*

- 9' Length of 7th marginal areole not greater than 2 times the width
(Fig. 9). 10
- 10 (9') Eyes extending laterally away from pronotum; abrupt color change
on face (Fig. 20). *Pacarina*
- 10' Eyes not extending laterally away from anterior edge of pronotum;
no abrupt color change on face (Fig. 9). *Beameria*
- 11 (1') Medial and cubital veins joined when emerging from basal cell
of forewing (Fig. 11). *Cicadetta*
- 11' Medial and cubital veins emerging separately from basal cell of
forewing (Fig. 5). 12
- 12 (11') Nodus of forewing located centrally on the costal margin
(Fig. 5). 14
- 12' Nodus of forewing located on the distal third of the costal margin
(Fig. 21). 13
- 13 (12') Eight marginal cells in forewing (Fig. 21). *Platypedia*
- 13' Seven marginal cells in forewing (Fig. 17) *Neoplatypedia*
- 14 (12') Pronotum expanded laterally forming a longitudinal carina for
its entire length 15
- 14' Pronotum rounded laterally, lacking a complete longitudinal
carina 17
- 15 (14) Marginal cells of forewing about 1/2 the length of ulnar cells
U1 and U2 (Fig. 24). *Tibicenoides*
- 15' Marginal cells of forewing at least 2/3 the length of ulnar cells
U1 and U2 (Fig. 5) 16
- 16 (15') Costal margin of radial cell at least 2 1/2 times longer than
the medial vein anterior to the first branch
(Fig. 18) *Okanagana*
- 16' Costal margin of radial cell less than 2 1/2 times longer than the
unbranched segment of the medial vein (Fig. 12). . . . *Clidophleps*
- 17 (14') First crossvein of forewing oblique (Fig. 15) . . . *Magicticada*
- 17 First crossvein of forewing perpendicular (Fig. 19) . . . *Okanagodes*

CHAPTER VII

Beameria

Taxonomy

Beameria Davis (1934, p. 47)

Type Species

Beameria venosa (Uhler) (Davis, 1934)

= *Pruanasis venosa* Uhler

= *Proarna venosa* (Uhler)

Species

There are two species in this genus, *Beameria venosa* (Uhler) and *B. wheeleri* Davis. Both occur in North America north of Mexico.

Descriptive History

Davis' remarks are less a description than a comparison of the new genus with the two genera in which *Beameria venosa* was previously placed. Neither *Pruanasis* nor *Proarna* occur in North America north of Mexico so these comparisons are of little value in distinguishing this genus from other American genera north of Mexico.

Description

General Body Proportions

Length of body 11.0 to 17.0 mm

Expanse of forewings 31.0 to 40.0 mm

The abdomen represents approximately one-half the body length.

Head

Width of head including eyes about the same as the width of the mesonotum; eyes not prominently projecting laterally; epicranium in a continuous gentle slope with dorsum of clypeus; width between ocelli about the same as width between lateral ocelli and eyes; clypeus rounded and prominently produced beyond the supraantennal plates; dorsum of clypeus longer than frons; rostrum reaching posterior coxae. Dorsum and venter of head similarly colored.

Thorax

Pronotum adpressed laterally except at posterior angles, lacking a continuous lateral carina. Length of pronotum shorter than length of mesonotum; mesonotum obscuring central portion of metanotum. Opercula in males large, broadly rounded, separated medially by a third, centrally projecting schlerite.

Legs

Anterior femora with two prominent spines beneath, sometimes with a minute third spine distally. Posterior femora triangular, frequently curved.

Wings

Forewing venation is illustrated in Figure 9. Both wings hyaline. First crossvein in forewing perpendicular, second crossvein slightly oblique, first and second crossveins not parallel; medial and cubital veins arising separately from the arculus; basal cell clear; nodus central; costal margin of forewings minutely spinose.

Abdomen

First abdominal segment in males containing tymbal organs; central dorsal sclerite modified to resemble a "bow tie." Second abdominal segment produced anteriorly on each side into a small tymbal covering that leaves approximately two-thirds to three-fourths of the tymbal organ exposed; sternal sclerite produced into lateral bulges.

Sexual Characteristics

Ninth dorsal segment in males not prominently produced centrally, lateral margins produced into two upturned points; uncus withdrawable, notched both caudally and laterally (see Figure 9). Subgenital plate of female shallowly notched (Figure 9).

Diagnostic Characters

The adpressed pronotal margins and non parallel first and second crossveins in the forewings are primary diagnostic characters. Secondly, small size, basically light coloration, and the relatively small eyes are helpful. Males are easily identified by the shape and extent of the tymbal covers and the central sclerite separating the opercula (Figure 9).

Figure 9. *Beameria*. A, dorsal view of male; B, ventral view of male abdomen; C, ventral view of terminal segments of female abdomen; D, caudal view of male abdomen showing uncus (after Davis, 1934); E, map showing distribution of the genus by state. Arrows point to diagnostic characters of the genus. Species illustrated is *Beameria venosa*.

E

Distribution

Beameria is apparently confined to America north of Mexico. It has been recorded in the literature from Texas, New Mexico, Arizona, Oklahoma, Kansas, Colorado, and Nebraska.

Discussion

Changes in morphology of the nymphs of four of the five nymphal instars of *B. venosa* are described in Beamer (1928). *Beameria venosa* adults frequently inhabit high, dry, rocky hillsides or hilltops where sparse grass and occasional yucca make up the only vegetation (Beamer, 1928). Davis (1921b) also reports *B. venosa* as a grassland species living in desert grass. It has been reported singing from thistle (Davis, 1921b). I have personally captured only one specimen of this genus, a *B. venosa* singing in *Juniperus* sp. just south of Sedona, Arizona. There was sparse grass in the area. It is not unusual for grass or weed inhabiting cicadas to utilize a higher perch for singing if one is available. Altitudes recorded for specimens taken in Arizona fall in the range of 1,500 to 2,500 meters. The song of *B. venosa* is shrill but difficult to hear beyond a few meters. The light coloration of *B. venosa* makes it inconspicuous among the dry grass it inhabits.

Beamer (1928) records *B. venosa* as sluggish and not easily frightened into flight. He describes the nests as arranged serially in a single row along a stem. Each nest contains three to four white eggs and there may be a dozen or more nests in a series.

Very little is known about *Beameria wheeleri*. It is also presumed to be a grassland species. Dates of capture on specimens of this genus I have examined range from June 9 to July 14.

CHAPTER VIII

Cacama

Taxonomy

Cacama Distant (1904b, p. 429)

Type Species

Cacama maura (Distant) (Distant, 1904b)

= *Proarna maura* Distant

Species

The five species of *Cacama* reported from North America north of Mexico are

C. californica Davis

C. crepitans (Van Duzee)

C. dissimilis (Distant)

C. valvata (Uhler)

C. variegata Davis

Discriptive History

The genus *Cacama* was described more completely than most North American genera. I have added additional features in the following description, and Distant's remarks are referred to in the appropriate

sections. In 1919, Davis considered the genus as a whole, adding four species to the list of *Cacama* and providing a key to *Cacama* identification. No new species have been described since that time.

Description

General Body Proportions

Length of body 21.0 to 30.0 mm

Expanse of forewings 64.0 to 83.0 mm

Cacama are robust insects with the abdomen representing approximately one-half the body length. The length of the abdomen is less than two and one-half times the width of the mesonotum.

Head

Width of head, including eyes, much narrower than the width of the mesonotum; eyes in a line with or extending slightly beyond the anterior edge of the pronotum; vertex of epicranium horizontal, frons sloping or vertical, forming an obtuse to right angle with the dorsum of the clypeus; distance between lateral ocelli about the same to slightly less than distance between lateral ocelli and eyes; clypeus moderately truncate, extending only slightly beyond the supraantennal plates and giving the head a blocky appearance; dorsum of clypeus shorter than frons; "rostrum reaching or passing the posterior coxae" (Distant, 1904b).

Thorax

Pronotum amplified posteriorly, strongly arched anteriorly, lateral carinae complete but minimal on the anterior half, lateral edges

smooth; length of pronotum shorter than mesonotum; "Mesonotum somewhat convexly gibbous" (Distant, 1904b); mesonotum obscuring central portion of metanotum; opercula in males large, "about half the length of abdomen above, broad, their apical margins convexly rounded, their lateral margins almost straight" (Distant, 1904b), overlapping medially.

Legs

Anterior femora with two prominent spines beneath; posterior tibiae short, sometimes blunt, usually equilateral.

Wings

Forewing venation is illustrated in Figure 10. Both "wings (excepting base) hyaline . . . apical areas [of forewings] eight in number, the two lowermost small, subquadrangular" (Distant, 1904b); first and second crossveins may or may not be parallel; medial and cubital veins arising separately from the arculus; nodus central; costal margin of forewings not noticeably spinose, may have a few tiny spines proximal to body.

Abdomen

"Abdomen short, broad, convex above" (Distant, 1904b); first abdominal segment in males containing tymbal organs, central dorsal sclerite with two rounded lateral lobes (Figure 10); second dorsal segment in males produced anteriorly on each side into a complete tymbal cover; "lateral margins of the tympanal coverings subparallel to the abdominal margins" (Distant, 1904b); lateral bulge inconspicuous.

Figure 10. *Cacama*. A, dorsal view of male; B, ventral view of male abdomen; C, ventral view of terminal segments of female abdomen; D, caudal view of male abdomen showing uncus (after Davis, 1919b); E, map showing distribution of genus by state. Arrows point to diagnostic characters of the genus. Species illustrated is *Cacama valvata*.

1cm

A

D

C

B

E

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, produced into a central spine dorsally; uncus withdrawable, simple (Figure 10). Subgenital plate of female shallowly notched centrally, smooth, not sinuous (Figure 10).

Diagnostic Characters

Cacama is easily recognized by its stout gestalt. The combination of the mesonotum overlapping the metanotum and the narrow, blocky head will identify both males and females. In addition the abdomen is broadly rounded caudally.

Distribution

Cacama extends from Yucatan, Mexico, northward to the southwestern United States. Within the United States it has been captured in Texas, Oklahoma, New Mexico, Colorado, Arizona, Utah, Nevada, and Southern California.

Discussion

Cacama is the only cicada genus found north of Mexico that might be considered a mimic. Their black or nearly black, robust bodies superficially resemble bumble bees. They initiate flight by hovering away from a perch rather than jumping into flight. The behavior of *Cacama* when captured in a net also is reminiscent of a bumble bee. Live *Cacama* are marked with a light colored pruinosity usually not seen in museum specimens. Heath, Wilkin, and Heath (1972) showed that *C. valvata* from

Arizona extended activity in the sun by orienting the reflective surface of the white, pruinose venter toward the sun's rays thereby diminishing the rate of heat gain. I have consistently found peak activity in *C. valvata* and *C. dissimilis* to range between 8:00 AM and 1:00 PM mountain standard time. Beamer and Beamer (1930) reported a similar activity period for *C. crepitans*. No data are available on the other two American species found north of Mexico. In Arizona I have captured *Cacama* from the desert plant formations to the pinyon-juniper plant formation. Although Beamer and Beamer (1930) reported capturing *C. valvata* from a yucca, sagebrush, and cedar habitat, and again, from a "habitat of small cedars" and *C. dissimilis* from palo verde, I have found the same two species almost always associated with some species of *Opuntia*. All other reports in the literature are from *Opuntia*. *Cacama* will sing from higher perches when these are available. I have observed them on barbed-wire fences and telephone poles. I cannot help but wonder if some *Opuntia* was not present in the habitats reported by Beamer and Beamer. *Cacama valvata* was observed to spend the night feeding near the base of clusters of the flat pads of prickley pear by Heath, Wilkin, and Heath (1972). Beamer and Beamer (1930) found that wetting nests of *C. valvata* laid in cane cactus or exposing the nests to a cold morning rain approximately three months after egg laying precipitated the emergence of the nymphs. They concluded that moisture, and consequently reduced soil temperatures, would increase the survival of nymphs from arid, hot habitats. *Cacama* has been given the popular name "cactus dodger." The song of *Cacama* resembles the sound of a chain saw cutting logs.

Cacama dissimilis was described by Distant (1881) from Mexico. I have seen the type specimen in the British Museum and believe it to be a

different species from that commonly identified as *C. dissimilis* in the southwestern United States. Dr. Thomas Moore of the University of Michigan has a manuscript in preparation naming the U.S. species. Remarks on *C. dissimilis* given above will be pertinent to this new species when Dr. Moore's description appears.

CHAPTER IX

Cicadetta

Taxonomy

Cicadetta Kolenati (1857, p. 417)

Type Species

Cicadetta montana (Scopoli) (Kolenati, 1857)

- = *Cicada montana* Scopoli
- = *Cicada orni* (nec Linné)
- = *Tettigonia montana* (Scopoli)
- = *Cicada pygmea* Olivier
- = *Cicada tibialis* Latreille (nec Panzer)
- = *Cicada anglica* Samouelle
- = *Cicada haematodes* Linné (nec Scopoli)
- = *Cicadetta* Amyot (nonbinomial)
- = *Tettigonia haematodes* (Linné) (nec Scopoli)
- = *Tettigonia dimidiata* Fabricius
- = *Cicada schaefferi* Gmelin
- = *Cicada parvula* Walker
- = *MeLampsalta montana* (Scopoli)
- = *Cicada saxonica* Hartwig
- = *Tettigia montana* (Scopoli)

Species

Four species and one named variety occur in North America north of Mexico. The species are

C. calliope (Walker)

C. cameroni (Davis)

C. kansa (Davis)

C. texana (Davis)

Alexander (unpublished) considers the geographical variety *Cicadetta calliope floridensis* (Davis) a distinct species. *Cicadetta calliope floridensis* is distinguishable by color and patterning.

Descriptive History

At least six generic names have been used for all or part of the genus *Cicadetta*. Metcalf (1963) catalogs the names and synonymies while Chen (1943) gives a brief history of the status of the names. They each come to different conclusions regarding the proper name. References to North American species prior to Metcalf (1963) use the generic name *Melampsalta*. In 1847, Amyot published descriptions of *Melampsalta*, *Cicadetta*, and *Tettigetta* in that order. Although he included the range of body lengths, the major part of the descriptions deals with color patterning and not anatomical features. In this sense each description resembles a species description and not a generic description. Amyot apparently intended these names as part of a monomial system of nomenclature and meant to refer only to what we now consider single species. Kolenati (1857) picked up Amyot's names and gave them subgeneric status using the species described by Amyot as the types and attributing the names to Amyot. In Kolenati's work the names appear in the following

order: *Cicadetta*, *Tettigetia*, *Melampsalta*. Kolenati's descriptions are morphological. According to Metcalf (1963) Stål was the first to synonymize the three in 1861. He, however, recognized Amyot as the author and used the name *Melampsalta*. Since that time various authors have recognized the same synonymy. The favored name depends on whether Amyot or Kolenati is recognized as author. Other authors have attempted to separate portions of the genus into new genera, but most of these names have not been generally accepted. The current status rests on the argument that Amyot did not intend to describe part of a binomial name. The species described by Amyot already had valid specific names. According to article 11c of the International Code of Zoological Nomenclature, a name does not become available unless the author consistently applied the principles of binomial nomenclature in the work in which the name is published. Since Amyot was proposing monomial names, the names cannot be attributed to him. Kolenati, therefore, becomes the author. The subgenera described by him constitute the establishment of the genus and *Cicadetta* becomes the valid name. This is apparently the view taken by Metcalf and now accepted on a world-wide basis. I have consulted the descriptions of Amyot (1847), Kolenati (1857), Ortega (1957), and Kato (1961). The following description is intended to encompass only those species found in North America north of Mexico.

Description

General Body Proportions

Length of body 12.0 to 20.0 mm

Expanse of forewings 25.5 to 40.0 mm

The abdomen represents more than one-half the body length.

Head

Width of head, including eyes, subequal with the width of the mesonotum; eyes prominent, may or may not project laterally beyond the anterior angles of the pronotum; vertex of epicranium horizontal; frons sloping, forming a broad obtuse angle with the dorsum of the clypeus; vertex and clypeus centrally sulcate; dorsum of clypeus somewhat centrally depressed; distance between lateral ocelli about the same or narrower than distance between lateral ocelli and eyes; clypeus and supraantennal plates forming the more or less continuous sides of a broad triangle with the sides notched where the clypeus and supraantennal plates meet; dorsum of clypeus shorter than frons; rostrum reaching to or barely beyond the intermediate coxae.

Thorax

Pronotum strongly arched laterally, not strongly amplified, but usually having continuous carinae where the notal and pleural regions meet, lateral margins smooth, posterior angles lobately dilated; length of pronotum shorter than mesonotum; posterior margins of metanotum completely visible behind mesonotum; opercula in males well developed, separated, rounded.

Legs

Anterior femora with at least three distinct spines; a fourth, less developed, distal spine is usually present. Posterior femora narrowly drawn out at the tip.

Wings

Forewing venation is illustrated in Figure 11. Wings hyaline. First and second crossveins in the forewings perpendicular and usually parallel; medial and cubital veins coalescent where they arise from the arculus; nodus more or less central, may be slightly further from the base of the wing than from the apex; costal margin of forewing may have several very fine spines.

Abdomen

First abdominal segment in males containing tymbal organs, posterior margin of central dorsal sclerite concave centrally; anterior margin of second dorsal sclerite curved smoothly ventrad laterally behind the tymbal organs; lateral bulge on sternite well developed in both sexes; tymbal organs exposed.

Sexual Characteristics

The ninth dorsal segment of the males may or may not project into an acute point dorsally, posterior margin with a caudally projecting, ventral lobe, a third lobe may be present along the ventral margin; uncus retractable, short, bifurcated with the two parts diverging outward from a caudal view and the apices subacute, curved inwardly from a lateral view (Figure 11). Subgenital plate of female with a large simple, triangular notch extending nearly to the base of the sternite (Figure 11).

Figure 11. *Cicadetta*. A, dorsal view of male; B, ventral view of male abdomen; C, ventral view of terminal segments of female abdomen; D, lateral view of extended male pygofer, caudal view of uncus (after Davis, 1920); E, map showing distribution of the genus by state. Open circle is a questionable report. Arrow points to the coalesced media and cubitus emerging together from the arculus. Species illustrated is *C. kansa*.

Diagnostic Characters

The coalesced medial and cubital veins in the forewings emerging together from the apex of the basal cell will separate *Cicadetta* from all other genera found in North America north of Mexico. In the other genera in this region the medius and cubitus leave the arculus separately.

Distribution

Cicadetta is widely distributed throughout all the world's biogeographic regions except the Neotropical. Within the Nearctic region it is found throughout the southeastern United States, as far west as eastern Colorado, and north to Nebraska, Iowa, Illinois, Ohio, and Virginia. *Cicadetta cameroni* and *C. texana* have thus far been reported only from Texas. *Cicadetta calliope floridensis* is found in Florida and Georgia. Davis (1930) records *C. kansa* from Kansas, Colorado, Oklahoma, and Texas. *Cicadetta calliope calliope* is the most widely distributed species. It is found in all of the above states except Oklahoma. Additional state records are from Missouri, Arkansas, Louisiana, Mississippi, Alabama, Tennessee, and North Carolina. There is a doubtful report from New Jersey. There are no records from Indiana, Kentucky, South Carolina, or West Virginia, but part or all of these states fall within a more generalized distributional pattern, particularly if the Ohio designation is accurate. These four states represent likely extensions of the reported distribution.

Discussion

Cicadetta is the most widespread genus in the family Cicadidae. Several factors may influence the widespread dispersal of *Cicadetta*, among which are the age of the genus, size of the insects, and the period of development. There are, at present, no known fossil *Cicadetta* to give us a clue to the age of the genus. If, however, *Cicadetta* does represent a single phylogenetic line, the wide distribution would seem to infer that it is a very old genus. The majority of *Cicadetta* species are small. Beamer (1928) remarks on the effects of wind in lengthening the flight of *C. calliope* in Kansas. Because of the small size of the adults, wind may well be a factor in *Cicadetta* dispersal. Myers (1929) suggests that the entire New Zealand cicada fauna derives from a single immigrant species of *Cicadetta*. Whether this invasion resulted from rafting, wind, or a combination is difficult to say. Most cicadas spend a lengthy immature period underground. Although some cicadas have received popular names such as "annual cicada" and a two year life cycle has been proposed frequently, the shortest documented life cycle of a cicada is the four year cycle of *Cicadetta calliope* (Beamer, 1928). If a relatively short life cycle is characteristic of the genus, more generations of *Cicadetta* have been available for dispersal than have been available among those cicada genera of equal age with a longer subterranean existence.

The probable habitat of the species of *Cicadetta* in North America is perennial grasses and weeds. Like other cicadas, they will utilize the higher perches of shrubs or trees when singing. Beamer (1928) studied *C. calliope calliope* in detail in Kansas. This species is abundant frequently in meadowlands as long as fires or serious flooding do not prevail. Females oviposit in live material and the eggs wither if the

branch dies. Nests are placed in a single row on pithy stems. Maturation of the eggs takes about two months. The song of the males is audible for only a distance of a few meters. Adults are preyed upon extensively by both robber flies (Asilidae) and spiders. Eggs are parasitized by chalcids of the genus *Syntomaspis*. *Cicadetta* in North America are active as adults from late April to August. Beamer (1928) also observed the behavior of the nymphs in glass sided cages. Cells are generally about one inch long. If the host plant dies the cell may be extended for several inches as the nymph searches for a new host. Loose dirt is dug from the front of the cell with the forelegs. It is then packed into a ball between the forelegs and the postclypeus and subsequently carried to the rear of the cell. Beamer found nymphs in the field usually six to ten inches beneath the surface. A disturbed nymph will rear and prepare to fight the offender with its fore femora. Beamer described the morphology of the five nymphal instars of *C. calliope* in detail.

CHAPTER X

Clidophleps

Taxonomy

Clidophleps Van Duzee (1915, p. 31)

Type Species

Clidophleps distanti (Van Duzee) (Van Duzee, 1915)

= *Okanagana distanti* Van Duzee

= *Okanagana pallida* Van Duzee

= *Okanagana pallidus* Van Duzee

= *Clidophleps pallida* (Van Duzee)

Species

Seven species and one named variety of *Clidophleps* occur in North America north of Mexico. The species are

C. beameri Davis

C. blaisdelli (Uhler)

C. distanti (Van Duzee)

C. rotundifrons (Davis)

C. tenuis Davis

C. vagans Davis

C. wrighti Davis

There is one named variety of *Clidophleps distanti*.

Descriptive History

The original description of Van Duzee (1915) compares features of *Clidophleps* with similar features in *Okanagana* and *Platypedia*. A few diagnostic features are given. Simons (1954) keys and illustrates a generalized wing and the terminal abdominal segments of the males of the California species. No other general work on the genus has appeared, and no complete description has been written.

Description

General Body Proportions

Length of body	19.0 to 26.5 mm
Expanse of forewings	44.0 to 71.0 mm

The abdomen represents approximately one-half the body length. In addition the long, slender body has a "bullet or torpedo-shaped" appearance.

Head

Width of head, including eyes, narrower than the mesonotum; eyes in a line with or slightly wider than the anterior angles of the pronotum; vertex of epicranium horizontal, centrally sulcate; frons steeply slanted to vertical, forming an obtuse to right angle with the dorsum of the clypeus; distance between lateral ocelli greater than distance between lateral ocelli and eyes; clypeus broadly rounded, extending beyond the supraantennal plates, centrally sulcate apically and ventrally; dorsum of clypeus about the same to slightly longer than frons; rostrum reaching intermediate coxae.

Thorax

Pronotum steeply arched laterally; lateral carinae continuous but varying between minimal and amplified on a species specific basis; lateral edges usually smooth, posterior angles dilated; length of pronotum shorter than mesonotum; mesonotum with a raised striated surface located next to the base of the forewing when folded against the body; posterior margin of metanotum completely visible behind mesonotum; opercula in both sexes small, transverse, rounded, widely separated, not extending beyond the base of the abdomen.

Legs

Anterior femora with two prominent spines; posterior femora broadly triangular.

Wings

Forewing venation is illustrated in Figure 12. Wings hyaline, basal cell clear; first and second crossveins in forewings usually oblique and parallel; third marginal cell at least two-thirds the length of second ulnar cell; costal margin of the radial cell less than two and one-half times longer than the medial vein anterior to the first branch; radial cell of forewing frequently expanded; the transverse crossvein between M_8 and Cu usually thickened; medial and cubital veins arising separately from the arculus; the cubital vein with at least a slight arch; nodus central; costal margin of forewing with a few very minute spines.

Figure 12. *Clidophleps*. A, dorsal view of male; B, ventral view of terminal segments of male abdomen; C, ventral view of terminal segments of female abdomen; D, lateral view of terminal male abdominal segments showing uncus in profile, dorsal view of uncus (after Simons, 1954); E, map showing distribution of the genus by state. Arrows point to diagnostic characters. Species illustrated is *C. vagans*.

Abdomen

First abdominal segment in males containing tymbal organs, central dorsal sclerite visible as a thin band centrally, turned outward laterally proximal to the tymbal organs (Figure 12); anterior margin of second dorsal sclerite turned outward forming a ribbon-like structure posterior to the tymbals; lateral bulge obvious; tymbal organs exposed.

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, caudal margin concave dorsally; uncus stationary, not retractable, simple (Figure 12); hypandrium elongated. Subgenital plate of female broadly and doubly notched (Figure 12).

Diagnostic Characters

Males can be identified by the exposed tymbals flanked posteriorly by the ridged anterior edge of the second abdominal tergite and the long unbranched portion of the medial vein in the forewing. Females can be identified by the combination of a visible metanotum, broadly rounded clypeus, complete carina formed by the lateral edge of the pronotum, and forewing characteristics.

Distribution

In North America north of Mexico, *Clidophleps* occurs in California and Arizona. Five species appear to be restricted to California. *Clidophleps rotundifrons* is found in Arizona. *Clidophleps tenuis* extends

into Lower California and *C. astigma* is known only from the Mexican side of the border in Baja or Lower California.

Discussion

An accessory stridulatory surface on the anterior, lateral portions of the mesonotum reaches its greatest development north of Mexico in the genus *Clidophleps*. Boulard (1976a) illustrates this structure in *C. blaisdelli* and *C. vagans*. The verification of two songs from the same individual was reported by Davis (1943) for *Clidophleps beameri* from observations made by J. Beamer. The sound was characterized as starting "with a clicking, and then run into a rattle or whir, which is made by the drumming of the wings." The Beamers at first felt there were two species present until they identified both songs in a single individual. I have had a similar experience with *Okanagana synodica* (Say) and was further confused by two color forms which subsequently turned out to be a sexual dimorphism. A mesonotal stridulatory surface is present in four genera found in America north of Mexico. This feature further confirms the close phylogenetic relationship between *Clidophleps*, *Okanagana*, *Okanagodes*, and *Tibicinoides*.

Little is known about the ecology of *Clidophleps*. They are active as adults from late May to early August. Most species seem to prefer a scrub or chaparral type habitat. They have been captured from the seashore to the mountains in California and from desert to mountain forest conditions. *Clidophleps rotundifrons* from Arizona has been taken at 1,100 meters from scrub oak and red mahonia by M. Kolner (1976--personal communication). Several species have been described as singing in a unified chorus normally initiated by the singing of a single individual. The

song can be stimulated artificially by the sound of an automobile engine (Beamer and Beamer, 1930). The song is usually of short duration making individuals difficult to locate. Beamer and Beamer (1930) reported *C. distanti* ovipositing in the twigs of a young orchard containing peach, plum, and citrus trees. They also found the same species associated with a vineyard.

CHAPTER XI

Cornuplura

Taxonomy

Cornuplura Davis (1944, p. 217)

Type Species

Cornuplura curvispinosa (Davis) (Davis, 1944)

= *Tibicen curvispinosa* Davis

Species

One species of *Cornuplura*, *C. nigroalbata* (Davis), occurs in North America north of Mexico. *Cornuplura rudis* (Walker) was reported from Arizona by Uhler (1892) from a single fragmentary specimen, but that report now appears to be erroneous.

Descriptive History

Davis' (1944) description is in the nature of a comparison between *Tibicen*, *Diceroprocta*, and *Cornuplura*. No complete description of the genus has been written.

Description

General Body Proportions

Length of body 34.0 to 38.0 mm

Expanse of forewings 95.0 to 102.0 mm

The abdomen represents about one-half the body length. It may be slightly longer in males with the genitalia extended.

Head

Width of head, including eyes, broader than the mesonotum; eyes extending slightly beyond the anterior margin of the pronotum; vertex of epicranium horizontal, frons nearly vertical; distance between ocelli less than distance between lateral ocelli and eyes; clypeus moderately tumid, projecting beyond the supraantennal plates; dorsum of clypeus as long as frons; rostrum reaching just short of posterior coxae (in *C. rudis* it reaches the anterior portion of the coxae).

Thorax

Pronotum amplified laterally forming definite lateral carinae, lateral edges smooth, not toothed; length of pronotum shorter than mesonotum; mesonotum obscuring central portion of metanotum; opercula in males large, longitudinal, overlapping medially.

Legs

Anterior femora with two prominent spines beneath and the remnant of a third distal spine; posterior femora elongated, acute, with a slight inward curvature.

Wings

Forewing venation is illustrated in Figure 13. Both wings hyaline; first and second crossveins in forewings oblique, parallel, may be very slightly infuscated; length of R_{4+5} between the first and second crossveins less than R_{4+5} between the first crossvein and the ambient vein, medial and cubital veins arising separately from the arculus; nodus central, costal margin of the forewing may have a few very minute spines.

Abdomen

First abdominal segment in males containing tymbal organs, central dorsal sclerite with basically the same curvature as succeeding tergites; second dorsal segment in males produced anteriorly on each side into a complete tymbal cover, lateral bulge lacking.

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, produced into a central spine dorsally and two spines extending from the ventral margin; uncus withdrawable, deeply cleft or bifurcated (Figure 13). Subgenital plate of female smoothly bilobed, eighth sternite visible beneath subgenital plate, produced into two medial hooks (Figure 13).

Diagnostic Characters

Males can be distinguished by the two spines extending from the ventral margin of the pygofer. Females can be distinguished by hooks on the eighth sternite combined with a black basal cell in the forewings.

Figure 13. *Cornuplura*. A, dorsal view of male; B, ventral view of male abdomen; C, ventral and caudal views of terminal segments of female abdomen. Caudal view shows hooks on eighth sternite lying under the subgenital plate. D, lateral and caudal views of terminal male abdominal segments (after Smith and Grossbeck, 1907). Lateral view shows ventral spines on extruded pygofer. E, map showing distribution of the genus north of Mexico. Arrows point to diagnostic characters. Species illustrated is *C. nigroalbata*.

Distribution

Cornuplura has been reported in central Mexico from Jalisco, Colima, Vera Cruz, Moreles, and the Distrito Federal. North of Mexico it has been recorded only from Santa Cruz County, Arizona.

Discussion

The above description was written to include the male *Cornuplura rudis* in my possession. In *C. rudis* the ventral spine on the ninth dorsal segment of the males is much shorter and stouter than in *C. nigroalbata*. In general appearance *Cornuplura* resembles the parallel sided *Tibicen* found in the southwestern United States. It is, however, larger than species that make up this group of *Tibicen*. Species of *Cornuplura* have also been compared favorably with *Tibicen plebeja*, the type of the genus *Tibicen*. Davis (1944) places the genus *Cornuplura* between *Tibicen* and *Diceroprocta*. In almost all characteristics except male genitalia it agrees with *Tibicen*. The deeply cleft uncus is somewhat similar to *Diceroprocta* but is fused at the base. In *C. rudis* the uncus is simple for part of its length and then divides. In females the hooked eighth sternite is shared with some members of the genus *Tibicen*. This character should be viewed caudally.

Little is known of the biology of *C. nigroalbata*. The type is a female captured from an oak on August 15, 1935. Four males and a female were captured near the type locality on July 12 and 13, 1940. On June 21, 1972, J.E. Heath captured a male on the mountainside overlooking Lago Pena Blanca, a few miles east of the type locale. Although this individual was captured singing on mountain mahogany, others were singing from black

oak in the general vicinity. The 1935 and 1940 specimens were also captured from "oaks." As far as I know, these are the only specimens taken. The animals were actively singing in mid afternoon (2:30-4:30 PM mountain standard time) from perches near the periphery of the host plant. They were widely scattered, solitary animals. The song was the loudest I have heard, although this may have been amplified by the nature of the small valley. The song also had a strong metallic quality. Experiments to determine thermal parameters of this species showed it required a mean body temperature of 18.1°C to fly. It stopped basking and moved into shade at a mean body temperature of 37.8°C and reached heat torpor at 44°C. Temperature measurements were made with a thermistor probe described by Heath and Adams (1969). I returned to the same locality exactly one year later but did not hear this species. Analysis of the years of capture indicates there is probably more than one brood of *C. nigroalbata* in Santa Cruz County, Arizona.

CHAPTER XII

Diceroprocta

Taxonomy

Diceroprocta Stål (1870, p. 714)

Type Species

Diceroprocta alacris (Stål) (Stål, 1870)

= *Cicada transversa* Walker

= *Cicada alacris* Stål

Species

There are nineteen species and five named varieties of *Diceroprocta* in America north of Mexico. A twentieth species *D. bicosta* has been reported from Florida, but the identification is in doubt (Davis, 1938; Mead, 1978--personal communication). The species are

<i>D. apache</i> (Davis)	<i>D. cinetifera</i> (Uhler)
<i>D. arizona</i> (Davis)	<i>D. delicata</i> (Osborn)
<i>D. averyi</i> Davis	<i>D. eugraphica</i> (Davis)
<i>D. azteca</i> (Kirkaldy)	<i>D. knighti</i> (Davis)
<i>D. bequaerti</i> (Davis)	<i>D. marevagans</i> Davis
<i>D. bibbyi</i> Davis	<i>D. olympusa</i> (Walker)
<i>D. biconica</i> (Walker)	<i>D. semicincta</i> (Davis)
<i>D. canescens</i> Davis	<i>D. swalei</i> (Distant)

D. texana (Davis)

D. viridifascia (Walker)

D. vitripennis (Say)

In addition there are two named varieties of *D. cinatifer*a and one each of *D. delicata*, *D. semicincta*, and *D. swalei*.

Descriptive History

The generic name *Diceroprocta* appears in a key in Stål's Hemiptera Insularum Philippinarum. Two characters are given, one for males, one for females; however, neither will separate the genus as currently recognized. *Diceroprocta* was essentially ignored until Davis, in 1928, moved the United States species and three others into this genus. He added two more characters, but neither of these stand alone as diagnostic of the genus. A complete description of *Diceroprocta* has never been written.

Description

General Body Proportions

If *Diceroprocta bicosta* is subsequently shown to occur in North America north of Mexico, it will be the largest *Diceroprocta* in the region with a body length circa 34 mm and a forewing expanse circa 102 mm. *Diceroprocta biconica* from the Florida Keys approaches this size range. With the exception of the two species, *D. bicosta* and *D. biconica*, body dimensions range as follows:

Length of body	17.0 to 30.0 mm
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Expanse of forewings	52.0 to 85.0 mm
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The abdomen represents approximately one-half the body length.

Head

Width of head including eyes about as broad or broader than mesonotum; eyes projecting slightly beyond the anterior margin of the pronotum; vertex of epicranium horizontal, frons sloping vertically, sometimes continuous with dorsum of clypeus, sometimes forming an obtuse angle with the dorsum of the clypeus; distance between ocelli less than distance between lateral ocelli and eyes; clypeus in a more or less continuous line with supraantennal plates, not projecting prominently, dorsum as long or longer than frons; rostrum reaching posterior coxae or beyond.

Thorax

Pronotum amplified laterally forming definite lateral carinae, lateral edges smooth; length of pronotum shorter than mesonotum; mesonotum obscuring most of metanotum; opercula in males large, either rounded or triangular, meeting or nearly meeting centrally.

Legs

Anterior femora with two prominent spines beneath; posterior tibiae narrow and angulate.

Wings

Forewing venation is illustrated in Figure 14. Both wings hyaline, infuscated markings various. Davis (1928) gives the following forewing characteristic for *Diceroprocta*, ". . . the first cross vein of the fore wing does not, as a rule, start as far back or near to the base of the wing from radius 3 as it does in *Tibicen*." Length of R_{4+5} between the

first and second crossveins usually equal to or greater than R_{4+5} between the first crossvein and the ambient vein; first and second crossveins usually parallel; medial and cubital veins arising separately from the arculus; nodus central; costal margin of forewings minutely spinose. (See discussion section for further elaboration of the above characters.)

Abdomen

First abdominal segment in males containing tymbal organs, central dorsal sclerite variable in shape and visibility; second dorsal segment in males produced anteriorly on each side into a complete tymbal cover; lateral bulge inconspicuous.

Sexual Characteristics

Ninth dorsal segment of males not produced into a central spine, lateral margins usually produced into two upturned points, uncus withdrawable, bifurcated with a dorsal projection (Figure 14). Subgenital plate of female usually "sinangulate at middle of apex and on each side very obtusely rounded sinuate" (Davis, 1928 translation of Stål, 1870) (Figure 14).

Diagnostic Characters

No single diagnostic character is consistent throughout the genus except the bifurcated, "wishbone shaped" uncus of the males. In most cases deviations from the general description are on an individual basis and not characteristic of a species as a whole. Both males and females can be identified by a combination of characters. The position of the

Figure 14. *Diceroprocta*. A, dorsal view of male; B, ventral view of male abdomen; C, terminal segments of female venter; D, lateral view of terminal male segments, caudal view of uncus; E, map showing the distribution of the genus by state. The report from New Jersey is questionable and is indicated by an open circle. Wisconsin records are unverified. Arrows indicate diagnostic characters. Species illustrated is *D. apache*.

first crossvein in the forewings and its relationship to the longitudinal veins and/or the sinuate subgenital plate will identify females. The position of the first crossvein of the forewings and/or the shape of the ninth dorsal segment will identify males without dissecting out the uncus. The ninth dorsal segment in males has two diagnostic characters, the lack of a central spine and the acute lateral lobes. Males have a complete tymbal cover. In size, *Diceroprocta* is larger than *Pacarina*, and United States species, with a few exceptions, are smaller than United States species of *Tibicen*.

Distribution

Diceroprocta extends from northern South America, where it has been recorded from Brazil, Guyana, and Venezuela, north throughout Central America, Mexico, the islands of the Caribbean and into the United States. Within the United States, the genus extends along the Atlantic coast from New Jersey to the Florida Keys. *Diceroprocta* is found in all states comprising the southern boundary of this country, from southern California to Florida. The range of *Diceroprocta apache* extends into southern Nevada, Utah, and Colorado, while *D. eugraphica* is found from Texas north to southern Kansas. One species, *Diceroprocta vitripennis*, inhabits many of the midwestern states. It is recorded from Nebraska, Kansas, Oklahoma, Missouri, Arkansas, Illinois, Indiana, and the southern tip of Michigan in addition to more southerly states. Dr. Moore tells me it may also reach into southern Wisconsin (Moore, 1977, personal communication).

Discussion

The variation in generic characters may be individual, confined to a single deme, or specific in nature. I have observed the following exceptions to the five morphological characters used to diagnose the genus. All specimens of *Diceroprocta azteca* I have seen lack the acutely pointed lateral lobes on the last dorsal segment of the males. This character is the source of the generic name. The lack of these acute lobes appears to be a species characteristic in *D. azteca*. Specimens of *Diceroprocta arizona* from the Chiracahua mountains, Arizona, have a central spine on the ninth dorsal segment of the males, whereas, paratypes from the Santa Rita mountains, also in Arizona, lack this spine. I interpret the presence of the spine in the Chiracahua population as a local phenomenon. The sinuous posterior margin of the female subgenital plate is one of the original characteristics cited by Stål (1870). The sinuations are present to some extent in almost all specimens of the genus I have seen; however, they occasionally may be reduced in an individual specimen so that the plate appears smoothly bilobed. I have observed specimens of *D. olympusa* like this, and Lawson (1920) pictures the subgenital plate of a female *D. eugraphica* from Kansas as smoothly bilobed. The last of the five diagnostic characters is the position of the first crossvein in the forewings. The position and cant of this vein is highly variable within the genus. It may be perpendicular to strongly oblique. Usually the first and second crossveins are parallel, but in an occasional individual, the first crossvein will be less oblique than the second. For this reason *Diceroprocta* occurs twice in the key to the females. Wherever Davis mentions this character, it is always compared with the genus *Tibicen*. In an attempt to quantify the character so that

a comparison specimen of *Tibicen* is not required, I measured the distance between the first and second crossveins versus the distance between the first crossvein and the ambient vein along R_{4+5} . The result in ninety per cent of the measurements was an equal or greater length between the crossveins than between the first crossvein and the ambient vein. In similar measurements on *Tibicen* the distance between the crossveins was always shorter than the distance between the ambient vein and the first crossvein.

From 1916 when Van Duzee published his Check List of the Hemiptera of North America North of Mexico to 1928 when Davis separated out the *Diceroprocta*, this genus was considered part of the genus *Tibicen*. The two genera appear to be closely related, and except for a general size differential north of Mexico and the five diagnostic characters mentioned above, they are difficult to separate. Exceptions to diagnostic characters in *Diceroprocta* overlap the corresponding characters in *Tibicen*. Internal structures revealed by X-rays confirm this basic similarity. *Tibicen* is the dominant genus in the Eastern United States while *Diceroprocta* reaches its greatest diversity in the southern states west of the Mississippi river. Only five species of *Diceroprocta* occur in the southeast with fourteen additional species in the southwest from Texas to California. *Diceroprocta* continues to flourish farther south in what Metcalf (1946) calls the Caribbean region while the number of *Tibicen* species drops to a handful.

Ecologically it is difficult to characterize a genus this large and diverse. Different members of the genus have adapted to most plant types from grass to trees. Some, such as *Diceroprocta knighti*, seem restricted to one host plant while others, such as *D. vitripennis* and *D. apache*, in

addition to their endemic hosts, have adapted to various cultivated plants on which they occasionally have been considered pests. Davis (1928) cited *D. vitripennis* as a destructive pest of cotton and Brown and Eads (1967) cited *D. apache* as a pest of ornamental elms in southern California. The distribution of several members of the genus has been expanded by following stream or river courses. *Diceroprocta cinetifera* is found along such courses and *D. apache*, which is prevalent in the desert around Phoenix but absent at altitudes above the Pinyon-Juniper plant formation, follows the Colorado river through the Grand Canyon and thus occurs in extreme northern Arizona and southern Utah. Adult *Diceroprocta* tend to be sedentary in their habits, singing from a continuous perch rather than singing then flying like *Magicicada*. *Diceroprocta* are preyed upon by birds, other insects, and small mammals. Davis (1924) records *Erax interruptus*, an asilid fly, attacking *Diceroprocta olympusa*. Desert species of *Diceroprocta* avoid severe predation by being active during midday periods when ambient temperatures are beyond the thermal tolerances of their predators. Heath and Wilkin (1970) documented this behavior for *D. apache*. Additional data indicate a similar activity pattern for *D. semicincta*. *Diceroprocta apache* is preyed upon in the Phoenix desert by a cicada killer wasp. Cranford (1978, personal communication) found heteromyid rodents feeding extensively on *D. apache* adults in northern Arizona and southern Utah. An analysis of fecal pellets showed cicada parts comprised up to sixty-five per cent of the fecal mass of *Dipodomys spectabilis* and *D. ordii*.

CHAPTER XIII

Magicalcada

Taxonomy

Magicalcada Davis (1925), p. 43)

Type Species

Magicalcada septendecim (Linné) (Davis, 1925)

= *Cicada septendecim* Linné

= *Tettigonia septendecim* (Linné)

= *Tettigenia costalis* Fabricius

= *Tibicen septendecim* (Linné)

= *Tibicina septendecim* (Linné)

Species

There are six species of *Magicalcada* in America north of Mexico.

The species are

M. cassini (Fisher)

M. septendecim (Linné)

M. septendecula Alexander and Moore

M. tredecassini Alexander and Moore

M. tredecim (Walsh and Riley)

M. tredecula Alexander and Moore

Descriptive History

Davis' (1925) description is in the nature of a comparison of features primarily between *Magiacada septendecim* and *Tibicina haematodes* (Scopoli), the type species of the genus *Tibicina* in which *M. septendecim* was at that time placed. *Tibicina* does not occur in North America. Alexander and Moore (1962) give diagnostic characters to separate *Magiacada* from other eastern North American cicadas.

Description

General Body Proportions

Length of body 19.0 to 33.0 mm

Expanse of forewings 55.0 to 83.0 mm

The abdomen is greater than one-half the body length in both sexes.

Head

Width of head, including eyes, subequal with the width of the mesonotum; "head including eyes is distinctly wider than the front edge of the pronotum and distinctly narrower than the rear edge of the pronotum" (Alexander and Moore, 1962). Epicranium broadly rounded from a horizontal position at the base of the vertex to a nearly vertical position where the frons joins the clypeus; frons forming a slightly obtuse angle emarginate with the dorsum of the clypeus; distance between lateral ocelli less than distance between lateral ocelli and eyes; clypeus triangular, extending well beyond the supraantennal plates; length of dorsum of clypeus about the same as length of frons; rostrum reaching posterior coxae.

Thorax

Pronotum adpressed laterally except at posterior angles, lacking continuous lateral carinae. Length of pronotum shorter than mesonotum; posterior margin of metanotum completely visible behind mesonotum; opercula in males broadly rounded, not extending beyond the second abdominal sternite.

Legs

Anterior femora with two or three prominent spines; posterior tibiae sharply elongate.

Wings

Forewing venation is illustrated in Figure 15. Both wings hyaline; first and second crossveins in the forewings oblique, nearly parallel, and frequently infuscated; medial and cubital veins arising separately from the arculus; basal cell infuscated; nodus central; costal margin of forewing minutely spinose.

Abdomen

First abdominal segment in males containing tymbal organs; central dorsal sclerite rounded laterally, somewhat sinuous along posterior margin (Figure 15); anterior margin of second dorsal sclerite turned smoothly inward posterior to tymbals; lateral bulge present; tymbal organs exposed.

Figure 15. *Magiccicada*. A, dorsum of male; B, venter of male; C, terminal segments of the female venter; D, caudal view of male abdomen showing uncus; E, distribution map of the genus by state and province. Small dots are used for the small northeastern states and the panhandle of Florida. Arrows point to the location of diagnostic characters. Species illustrated is *M. septendecula*.

B

C

D

E

Sexual Characteristics

Ninth dorsal segment in males prominently produced into an acuminate central spine; 9th segment bears small mediad projections caudally; uncus withdrawable, bifurcated, "viewed caudally it has the form of two sclerites extending downward from the anal tube, encircling the penis, and widening below it into two triangular processes which taper to acute apices. The penis is usually strongly protruded from between the two parts of the uncus and possesses terminally two very characteristic little sclerites . . . whose rounded margins are strongly serrate" (Lawson, 1920) (Figure 15). Subgenital plate of female with a single, large broad "incision posteriorly which reaches over one-half the distance to the base" (Lawson, 1920) (Figure 15).

Diagnostic Characters

Males can be distinguished by a combination of the lack of tymbal covers, retractable uncus, and medial and cubital veins arising separately from the arculus. Females can be distinguished by a combination of the visible metanotum, adpressed pronotum lacking complete lateral carinae, and the triangular clypeus. The dorsal thorax in both sexes is black without patterning.

Distribution

Magisicada is distributed throughout the eastern United States with one record from Quebec, Canada, reported by Alexander and Moore (1962). Within the United States they have been found in all the states east of the Mississippi River except New Hampshire and Maine. Their southern

limit in the east is the panhandle of Florida. West of the Mississippi River the range of *Magicicada* extends to eastern Texas, Oklahoma, Kansas, and Nebraska; the range is bounded by Iowa on the north and Louisiana on the south.

Discussion

Because of their long life cycle, periodicity, and enormous synchronous emergences, *Magicicada* have attracted as much attention as all the other genera found north of Mexico combined. *Magicicada* consists of three sets of sibling species. Each set contains a thirteen year species and an, as yet, inseparable seventeen year species. The three seventeen year species have the longest known insect life cycle. Early settlers recorded the large emergences of these cicadas and *Magicicada septendecim* is an original Linnaean species. A smaller "dwarf" variety was recognized in the 1830's, but it was so difficult for early naturalists to accept the concept of two long-lived synchronized species that the second species, *M. cassini*, was not named until 1851. The thirteen and seventeen year "decim" siblings were separated in the 1860's. Almost one hundred years passed before Alexander and Moore (1962) described the third set of siblings and also separated *M. tredecassini* as a separate thirteen year species.

Magicicada inhabits the eastern deciduous forest. Although specimens have been recorded each year, there are apparently eighteen successful broods, thirteen with seventeen year life cycles and five with thirteen year life cycles (Alexander and Moore, 1962). Three species occur in at least thirteen of the eighteen broods. Although the distribution of the

thirteen and seventeen year broods overlaps, the thirteen year broods represent the more southerly parts of the distribution of the genus, and the seventeen year broods comprise the most northerly portions of the distribution except for a southwestern extension of *M. cassini* (Brood IV) into eastern Texas. The presence of only *M. cassini* in the southwestern extremes of the range and only *M. septendecim* in the northern extremes of the range combined with the upland, xeric, habitat preferences of the "*decula*" siblings led Alexander and Moore (1962) to propose a southwestern origin for the "*cassini*" siblings, a south-central origin for the "*decim*" ancestor, and a southeastern origin for "*decula*." They also feel that the present distribution is the result of at least two periods of brood formation with Pleistocene glaciation involved in the most recent period. Individual broods of cicadas may also overlap, but the overlapping broods do not occur as adults in consecutive years. Consecutive broods are frequently contiguous in distribution, and a small amount of gene flow from one brood to the next may occur through stragglers emerging out of synchrony and joining an active emergence of another brood.

When two or three species emerge together, they tend to divide the available habitat both behaviorally and ecologically. Alexander and Moore (1962) recorded maximal chorusing of *M. tredecim* in midmorning, *M. tredecula* in midday, and *M. tredecassini* in midafternoon. Dybas and Davis (1962) found a definite preponderance of *M. septendecim* in upland areas of oak-hickory and *M. cassini* in an adjacent floodplain area in a study of Brood XIII in northern Illinois. Dybas and Lloyd (1962), in the same study area, reported overlapping of the species on the intermediate slope and also on a grove of young, previously uninhabited, ash growing in a recently cleared area nearby. *Magicicada septendecula* was

not present. While "*cassini*" and "*decim*" appear somewhat catholic in their host plants "*decula*" is apparently restricted to hickory, *Carya* spp. (J.E. Heath, 1978, personal communication).

The most potent isolating mechanism is the song. *Magicicada cassini* and *M. tredecassini* have evolved a highly elaborate synchronous chorus in which all male members sing in unison followed by a short burst of flight. J.E. Heath (1967) found the synchronous chorus occurred when males reached a body temperature of 30°C or more. The "*decula*" chorus appears less synchronous and the "*decim*" species do not sing in synchrony, but males of all six species follow the song with flight. The auditory stimulus of the song combined with the visual stimulus of flight tend to aggregate both males and females of the same species in the same location. In more solitary cicadas, it is the song of the individual male that attracts a mate. These males tend to be more sedentary in behavior. In *Magicicada* it is the chorus that attracts both sexes to a common location. J.E. Heath (1978, personal communication) has observed an isolated *M. septendecim* calling without the accompanying flight.

The attraction of a *Magicicada* chorus is not limited to cicadas. Both the movement of the flight and the sound of the song are powerful attractants for predators, especially birds. There are numerous reports of the annihilation of small emergences prior to reproduction. Most cicadas are wary. Many are protectively patterned or colored. *Magicicada* are both conspicuous and docile. Lloyd and Dybas (1966b) have labeled them "predator-foolhardy." This suggests that the group behavior of the congregational chorus has been selected over the incompatible secretive behavior of predator avoidance (Lloyd and Dybas, 1966b). In order for this to occur, large populations of the cicadas must emerge synchronously.

No one knows how *Magicicada* "count" the thirteen or seventeen years between emergences, but J.E. Heath (1968) showed that emergence is thermally synchronized. Emergence occurs when soil temperatures 20 cm below the surface reach 18°C. The other essential parameter is population density. The synchronous emergence of more than one species decreases the predator pressure on each individual species. Although density varies from place to place and generation to generation, millions of *Magicicada* can emerge within the space of a few miles. Dybas and Davis (1962) found a density of 1,500,000 cicadas per acre in a floodplain habitat in northern Illinois. They calculated the biomass of this same population at 1,913 to 3,685 kg/ha (1,707 to 3,288 lbs/acre), the highest mean biomass per unit of habitat recorded for a terrestrial animal under natural conditions. Their net average annual productivity of cicada protoplasm, 112 to 216 kg/ha (100-193 lbs/acre), is comparable to controlled beef production.

With such high population densities verified, are there any controls on *Magicicada* populations? Predator satiation apparently occurs quickly in a large *Magicicada* emergence, but the long term effects of an increase in predator populations have disappeared before the next generation of cicadas appears. Predator pressure probably eliminates the possibility of consecutive broods developing in the same locality. Lloyd and Dybas (1966a) suggested that moles are important predators of late instar nymphs. They also cited evidence that larvae of the predacious burrowing fly, *Coenomyia pallida* Say, will attack nymphal cicadas. Green muscardine disease will infect mature nymphs. The fungus *Massospora cicadina* Peck attacks the adults and is apparently the only specific organism that remains viable during the seventeen years between emergences. Lloyd and

Dybas (1966a) conclude that "food and space" (i.e., the scarcity of feeding sites) may be important in limiting *Magicicada* populations.

Magicicada have been implicated as severe pests in orchards, particularly on apples. The pruning caused by oviposition usually encourages new growth in the natural forest habitat. In a cultivated orchard, however, young trees can be killed by a large emergence. There is also some evidence that large nymphal populations underground may reduce production of fruit.

CHAPTER XIV

Neocicada

Taxonomy

Neocicada Kato (1932, p. 168)

Type Species

Neocicada hieroglyphica (Say) (Kato, 1932)

= *Cicada hieroglyphica* Say

= *Cicada caracterea* Germar

= *Cicada sexguttata* Walker

= *Tettigia hieroglyphica* (Say)

= *Tettigia caracterea* (Germar)

= *Tettigia sexguttata* (Walker)

= *Tibicen hieroglyphica* (Say)

Species

There are two species and one named variety of *Neocicada* in America north of Mexico. The species are

N. hieroglyphica (Say)

N. chisos (Davis)

Neocicada hieroglyphica johannis is found principally in peninsular Florida. Alexander (unpublished) does not consider *johannis* a good subspecies.

Descriptive History

Kato's (1932) description is short and incomplete. Although Kato's monograph is in Japanese, the description is given in English, a language that appears somewhat unfamiliar to the author. Kato was unaware of *N. chisos* and its relationship to *N. hieroglyphica*. He stated that the species (*N. hieroglyphica*) previously belonged to the genus *Cicada*, but that the characters differ from *Cicada orni*, the genotype of *Cicada*. He did not say how they differ, however. Davis (1925) stated *N. hieroglyphica* is allied closely to *Cicada orni*. The two genera are zoogeographically separated. External morphological differences are compared in the following discussion.

Description

General Body Proportions

Length of body	22.0 to 27.0 mm
Expanse of forewings	54.0 to 68.0 mm

In male specimens the abdomen is elongated and greater than one-half the body length. In females, the abdomen represents approximately one-half the body length.

Head

Width of head, including eyes subequal with the width of the mesonotum; eyes projecting laterally beyond the anterior angles of the pronotum; "Head with the front deflected before the eyes" (Kato, 1932), making the profile slightly emarginate at the juncture of the clypeus and the epicranium; width between ocelli less than width between lateral

ocelli and eyes; clypeus and supraantennal plates in a more or less broadly rounded, continuous curve; clypeus not prominently produced anteriorly; dorsum of clypeus subequal in length to frons; rostrum reaching at least the posterior margins of the metathoracic coxae.

Thorax

Pronotum amplified laterally forming definite lateral carinae, lateral edges smooth, not toothed; length of pronotum shorter than mesonotum; "lateral margins obliquely narrowed anteriorly . . . posterior lateral lobe somewhat developed" (Kato, 1932); mesonotum obscuring central portion of metanotum; opercula in males small, rounded, widely separated, and not extending beyond the base of the abdomen; opercula in females similar to those of males.

Legs

Anterior femora usually with three distinct spines, distal spine occasionally lacking, rarely armed with four spines; posterior femora slender, elongated.

Wings

Forewing venation is illustrated in Figure 16. Both wings hyaline; first, second, third, and fourth crossveins infuscated; infuscated dots on longitudinal veins near the ambient vein; first and second cross veins oblique, virtually parallel; medial and cubital veins arising separately from the arculus; basal cell clear; nodus central; costal margin of forewings with a few very minute spines.

Abdomen

First abdominal segment in males containing tymbal organs, central dorsal sclerite with basically the same curvature as succeeding tergites; second dorsal sclerite in males produced anteriorly on each side into an incomplete, rounded tymbal cover (Figure 16) that leaves the tymbal organ partially exposed laterally; bulges marking the lateral ends of the second sternite are located ventrally on the insect. Abdominal cuticle thin, may be translucent, particularly in males.

Sexual Characteristics

Ninth dorsal segment of males slightly produced centrally, rounded laterally; uncus withdrawable, simple, shallowly notched caudally (Figure 16), not notched laterally. Subgenital plate of female projecting slightly centrally, projecting region notched medially* (Figure 16).

Diagnostic Characters

Males can be easily identified by the rounded partial tymbal covers. Both males and females can be identified by the combination of the mesonotum partially covering the metanotum, first and second cross veins parallel, and infuscated markings on the longitudinal veins near the ambient vein. The usual diagnostic character used to identify *Neocicada* is the translucent abdomen. While this is very evident in male specimens, it is not very apparent in dried females. *Quesada* also has a somewhat translucent abdomen. Therefore, I prefer the above characters to identify members of this genus.

*I have not been able to verify this character in a female *N. chisos*.

Figure 16. *Neocicada*. A, dorsal view of male; B, ventral view of male abdomen; C, terminal segments of female venter; D, caudal view of male abdomen showing uncus; E, map showing the distribution of the genus by state. Small dots indicate smaller eastern states. Arrows point to diagnostic characters. Species illustrated is *N. hieroglyphica*.

A

D

C

B

E

Distribution

Neocicada occurs from Long Island, New York, southward along the east coast of the United States to Florida. It inhabits all of the gulf coast states and extends up the Mississippi valley to Missouri and Illinois. Its western range extends from Tamaulipas, Mexico, to southeastern Kansas.

Discussion

Through the courtesy of Dr. Michel Boulard of the Muséum National d'Histoire Naturelle, Paris, I have in my possession two male specimens of *Cicada orni*, the type species of the genus *Cicada*. I do not know the full range of characters in *Cicada*, but from a comparison of these specimens with our North American species, it appears that *Neocicada* has a relationship to *Cicada* similar to that of *Diceroprocta* to *Tibicen*. It does not appear closely related to any of the other genera found in North America north of Mexico. I have not explored a relationship with more tropical American genera. There are also no closely related fossils in North America. Outside of the obvious size, color, and pattern differences which usually distinguish species, there are morphological differences in both forewing venation and the structure of the male uncus between *Cicada* and *Neocicada*. In the forewing, R_3 is proportionately longer in *Neocicada* and is subsequently bisected more evenly by the first crossvein than in *Cicada orni*. In *C. orni* the section of R_3 anterior to the first crossvein is short as in *Tibicen*. In *Neocicada* the medial and cubital veins are very close together where they arise from the arculus (Figure 16). In *Cicada* the degree of separation is again similar to *Tibicen* (Figure 23). The male uncus in *Neocicada* is simple, but shallowly

notched. In *Cicada* it is deeply cleft into two distinct forks or prongs. These morphological differences appear to justify Kato's separation of our North American species into their own genus on a morphological as well as zoogeographical basis.

In north central Florida, *Neocicada hieroglyphica* is the first cicada to emerge each year, appearing around mid April (T.J. Walker, 1976, personal communication). The songs of scattered individuals may be heard into early October. In the more northerly parts of its range, the appearance of adults is much more restricted. Beamer (1928) recorded imagos in Kansas from June 7 to August 7. Dates reported for *N. chisos* are in June and July. *Neocicada hieroglyphica* are most active at dawn and dusk, but on warm summer days, individuals may be heard singing throughout the day and early evening. I have even heard them in the middle of the night in mid-summer when they were perched near a street lamp. The preferred host plants for *Neocicada* appear to be oaks. Davis (1916) reported them from the "Pine Barrens" of New Jersey. In the mixed pine/oak forests of the south, they sing from both types of trees. Beamer (1928) noted that they are only found in Kansas in regions with sandy soil. The relationship between soil characteristics and cicadas has not been explored but may be very important in determining the distribution of genera and species. Beamer (1928) observed the eggs are laid in dead twigs with three eggs per nest. He also described the five nymphal instars. *Neocicada* are cryptically colored. Beamer (1928) stated these basically straw and green insects with disruptive black markings "blend almost perfectly with the lichen-covered trunks of the oak trees on which they are found making individuals very difficult to find." I have had similar experiences in Florida. Both species are wary and

difficult to capture and observe (Beamer, 1928; Davis, 1932). The cant of the wings on resting *Neocicada* is flatter and less tent-like than the other genera found north of Mexico. The thin cuticle and largely vacuous abdomen of males makes *Neocicada* light in weight for its size. Weights of live male *N. hieroglyphica* range from 215 mg to 240 mg.

CHAPTER XV

Neoplatypedia

Taxonomy

Neoplatypedia Davis (1920, p. 121)

Type Species

Neoplatypedia ampliata (Van Duzee) (Davis, 1920)

= *Platypedia ampliata* Van Duzee

Species

Both species of *Neoplatypedia* occur in North America north of Mexico.

They are

N. ampliata (Van Duzee)

N. constricta Davis

Descriptive History

Davis' (1920) description compares features of *Neoplatypedia* that differ from corresponding characters in *Platypedia*. No complete description has been written. Davis included a key to both species in his 1920 paper. Since both species occur in California, a complete key to the genus is found in Simons (1954).

Description

General Body Proportions

Length of body 15.0 to 19.0 mm

Expanse of forewings 38.0 to 44.0 mm

The abdomen is greater than one-half the body length. The following general characters cited by Uhler (1888a) in his description of *Platypedia* also apply to *Neoplatypedia*, "Elongate, acutely tapering posteriorly, with a sub-carinate ridge on the tergum, extending from near the base to beyond the middle." Davis (1920) remarks, "When the insect is turned over, the wings, if closed, are seen to cover about the apical third of the abdomen." *Neoplatypedia* are black, with the exception of the following body regions which are normally pale: part of the supraantennal plates, a median line and the posterior edge of the pronotum, the propleura, the posterior edge of the mesonotum including the posterior half of the cruciform elevation, the posterior edge of the metanotum.

Head

Width of head, including eyes, slightly narrower than the width of the mesonotum; eyes may or may not project beyond the anterior angles of the pronotum; vertex of epicranium horizontal; frons gently sloping forming a broad obtuse angle with the dorsum of the clypeus; vertex and clypeus centrally sulcate; distance between lateral ocelli narrower than distance between lateral ocelli and eyes; clypeus strongly convex, narrowing anteriorly, prominently protruding beyond the supraantennal plates, longer than frons; rostrum reaching beyond the intermediate coxae.

Thorax

Pronotum strongly arched laterally, not amplified, but having continuous carinae where the notal and pleural regions meet, lateral margins smooth, sides parallel except at dilated posterior angles; length of pronotum shorter than mesonotum; posterior margin of metanotum completely visible behind mesonotum; opercula not developed.

Legs

Anterior femora armed with two prominent spines, sometimes showing the rudiments of a third distal spine; posterior femora long, triangular.

Wings

Forewing venation is illustrated in Figure 17. Wings hyaline; first and second crossveins in the forewing parallel; "costal vein is strongly expanded and bent beyond the middle of the radial cell" (Davis, 1920), expansion extending both anteriorly and ventrally; radial cell long, extending more than one-half the length of the forewing; U_2 nearly triangular; medial and cubital veins arising separately from the arculus; cubital vein arched; nodus of forewing about two-thirds out on the costal margin; costal margin of forewing may have a few minute spines; marginal cells seven in number.

Abdomen

Tymbal organs of males rudimentary; first abdominal tergite in both sexes with the anterior margin somewhat indented dorso-laterally forming a small gap between the abdomen and the metathorax, reduced to a narrow

band centrally, frequently covered by the metanotum; laterally a colored membrane is visible between the thorax and abdomen when the wings are spread. Second dorsal sclerite resembles succeeding tergites, not specialized; lateral bulge on sternite may be inconspicuous.

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, caudal margin slightly concave dorsally; uncus stationary, not retractable, simple, "remarkably long and upturned at the extremity" (Davis, 1920) (Figure 17); hypandrium extremely elongate; subgenital plate of female with a simple deep notch nearly reaching the base of the segment (Figure 17). The terminal segments in both sexes are narrow and acutely tapering.

Diagnostic Characters

Neoplatypedia is the only genus found in North America north of Mexico with seven marginal cells in the forewings. The other genera have eight. The position of the nodus about two-thirds out on the costal margin of the forewing separates *Neoplatypedia* from all other genera found north of Mexico except *Platypedia*.

Distribution

Neoplatypedia is known only from North America north of Mexico. Both species occur in California. *Neoplatypedia ampliata* is reported from Oregon, and *N. constricta* is recorded from Arizona, Colorado, Idaho, and Utah.

Figure 17. *Neoplatypedia*. A, dorsal view of male; B, venter of male; C, terminal segments of female venter; D, lateral view of terminal male segments and dorsal view of uncus (after Davis, 1920); E, map showing distribution of the genus by state. Arrows indicate diagnostic characters. Species illustrated is *N. constricta*.

Discussion

Neoplatypedia is most closely related to the genus *Platypedia* from which it can be distinguished by having forewings with seven marginal cells instead of eight and a greater expansion and bend in the costal margin. In *Platypedia* the venter is completely visible when the wings are closed, but in *Neoplatypedia*, the closed wings meet and obscure the apical third. The distal tip of the uncus is turned upward in *Neoplatypedia* and not in *Platypedia*.

As in *Platypedia*, the male tymbal organ is no longer functional in *Neoplatypedia*. Sounds are made by clicking or rubbing the costal margins of the forewing together beneath the body or by "banging" these margins against the substrate on which the insect sits. The costal margin is expanded ventrally at the point at which it bends, bringing the two forewings into close proximity. Since the sound is made by both sexes, it may function as a congregating device rather than a specific mating call or, as suggested by Dugdale and Fleming (1969) for *Amphipsalta*, the two-way communication may "speed the coming together of the sexes." The reasons for considering the lack of a functional tymbal organ a secondary loss rather than a primitive characteristic are discussed under the genus *Platypedia*.

Neoplatypedia appears to be derived from *Platypedia*. Like *Platypedia* it shares a number of characteristics with the okanaganoid genera, *Okanagana*, *Okanagodes*, *Tibicinoides*, and *Clidophleps*. Among these are the visible metanotum and the nonretractable uncus. Wing expansion can be traced from the narrow wings of *Okanagana*, through *Clidophleps* and *Platypedia*, to *Neoplatypedia* which exhibits the greatest modifications of the forewings.

Very little is known of the ecology of *Neoplatypedia*. Adults are active from April through midsummer. *Neoplatypedia constricta* is recorded from sagebrush (*Artemesia sp.*) (Davis, 1927; Fautin, 1946). It is an important midsummer invertebrate component of the northern desert shrub biome in Western Utah, providing a primary source of food for lizards (Fautin, 1946). Fautin further stated that they "tend to remain close to the main branches of the sagebrush." Similar shaded, somewhat cooler, microhabitats are inhabited by *Diceroprocta* during midday on mesquite (Heath and Wilkin, 1970). In Colorado, *N. constricta* was collected at about 1,850 meters (Davis, 1921b). The same article describes the song as a "zip, zip, zip, zip continued for a long time."

CHAPTER XVI

Okanagana

Taxonomy

Okanagana Distant (1905c, p. 23)

Type Species

Okanagana rimosa (Say) (Distant, 1905e)

= *Cicada rimosa* Say

= *Tibicen rimosa* (Say)

Species

There are fifty-two named species and four named varieties of *Okanagana* in America north of Mexico. A fifty-third species *O. rotundifrons* belongs in the genus *Clidophleps* (M.S. Heath, 1976). The species are

<i>O. albibasalis</i> Wymere	<i>O. cruentifera</i> (Uhler)
<i>O. annulata</i> Davis	<i>O. davisii</i> Simons
<i>O. arboraria</i> Wymere	<i>O. ferrugomaculata</i> Davis
<i>O. arctostaphylae</i> Van Duzee	<i>O. formosa</i> Davis
<i>O. aurora</i> Davis	<i>O. fratercula</i> Davis
<i>O. balli</i> Davis	<i>O. fumipennis</i> Davis
<i>O. bella</i> Davis	<i>O. gibbera</i> Davis
<i>O. canadensis</i> (Provancher)	<i>O. hesperia</i> (Uhler)
<i>O. canescens</i> Van Duzee	<i>O. hirsuta</i> Davis

<i>O. lurida</i> Davis	<i>O. simulata</i> Davis
<i>O. luteobasalis</i> Davis	<i>O. sperata</i> Van Duzee
<i>O. magnifica</i> Davis	<i>O. striatipes</i> (Haldeman)
<i>O. mariposa</i> Davis	<i>O. sugdeni</i> Davis
<i>O. napa</i> Davis	<i>O. synodica</i> (Say)
<i>O. nigriviridis</i> Davis	<i>O. tanneri</i> Davis
<i>O. nigrodorsata</i> Davis	<i>O. triangulata</i> Davis
<i>O. noveboracensis</i> (Emmons)	<i>O. tristis</i> Van Duzee
<i>O. occidentalis</i> (Walker)	<i>O. uncinata</i> Van Duzee
<i>O. opacipennis</i> Davis	<i>O. utahensis</i> Davis
<i>O. oregona</i> Davis	<i>O. vanduzeei</i> Distant
<i>O. ornata</i> Van Duzee	<i>O. vandykei</i> Van Duzee
<i>O. pallidula</i> Davis	<i>O. venusta</i> Davis
<i>O. rimosa</i> (Say)	<i>O. villosa</i> Davis
<i>O. rubrocaudata</i> Davis	<i>O. viridis</i> Davis
<i>O. rubrovenosa</i> Davis	<i>O. wymerei</i> Davis
<i>O. schaefferi</i> Davis	<i>O. yakimaensis</i> Davis

In addition there is one named variety each of *O. tristis*, *O. synodica*, *O. rimosa*, and *O. mariposa*. *Okanagana striatipes* variety *beameri* equals *O. hesperia* (M.S. Heath, 1976). An additional species, *O. georgi*, described by Heath (M.S. 1976) is unpublished.

Descriptive History

Distant's (1905a) description of *Okanagana* covers a number of important features that will be referred to in the appropriate places in the following description. However, because of the limited number of species available to Distant, several of his features are now not consistent

throughout the genus as it is currently recognized. Van Duzee in A Preliminary Review of the West Coast Cicadidae (1915) wrote a key to twenty species of *Okanagana*. Davis (1919a) treated the genus in depth. He added the nonretractable status of the male uncus as a generic feature. Davis covered thirty-five species in his remarks. Two of the species covered by Van Duzee and Davis have subsequently been moved to the genus *Tibicinioides*, and one covered by Davis belongs in the genus *Clidophleps*. Simons covered thirty-five species of *Okanagana* in The Cicadas of California (1954), and M.S. Heath (1976) treated thirteen species from Arizona. Specimens of a fourteenth species from Arizona, *O. schaefferi*, have subsequently been discovered.

Description

General Body Proportions

Length of body 15.0 to 35.0 mm

Expanse of forewings 37.0 to 90.0 mm

The length of the abdomen is equal to or greater than one-half the body length.

Head

Width of head, including eyes, narrower than the mesonotum; eyes in a line with or slightly narrower than the anterior angles of the pronotum; vertex of epicranium horizontal, frons steeply slanted to vertical, forming an obtuse to right angle with the dorsum of the clypeus; "vertex centrally sulcate" (Distant, 1905c); distance between lateral ocelli about the same to slightly greater than distance between lateral ocelli

and eyes; clypeus triangular, extending well beyond the supraantennal plates; "face more or less centrally sulcate" (Distant, 1905c); dorsum of clypeus usually longer than frons, but this ratio is species specific; "rostrum reaching the intermediate coxae" (Distant, 1905c).

Thorax

Pronotum amplified laterally forming definite lateral carinae, lateral edges smooth or jagged (irregularly toothed), "anterior angles in a line with eyes . . . posterior angles dilated" (Distant, 1905c); length of pronotum shorter than mesonotum; mesonotum frequently striated where the base of the forewing folds against the body; posterior margin of metanotum completely visible behind mesonotum; opercula in both sexes small, transverse, rounded, widely separated, not extending beyond the base of the abdomen.

Legs

Anterior femora with two prominent spines; posterior tibiae broadly triangular (Figure 18).

Wings

Forewing venation is illustrated in Figure 18. Wings hyaline, frosty, opaque, or partially opaque, rarely more than slightly infuscated except within the basal cell; first and second crossveins in forewing usually oblique and parallel; marginal cells of forewing at least two-thirds the length of the corresponding ulnar cells; costal margin of radial cell at least two and one-half times longer than the medial vein

anterior to the first branch; "basal cell [of forewing] about or almost twice as long as broad" (Distant, 1905c); medial and cubital veins arising separately from the arculus; nodus central; costal margin of forewing usually with a few very minute spines, occasionally spinose proximal to the body.

Abdomen

First abdominal segment in males containing tymbal organs, central dorsal sclerite, when visible, somewhat sinuous posteriorly, central portion frequently obscured by posterior margin of metanotum; anterior margin of second dorsal sclerite turned outward forming a ribbon-like structure posterior to the tymbals; lateral bulge obvious; tymbal organs exposed.

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, posterior margin concave dorsally; uncus stationary, not retractable, simple (Figure 18); hypandrium elongated. Subgenital plate of female either singly or doubly notched (Figure 18).

Diagnostic Characters

A combination of characters is necessary to distinguish *Okanagana*. The amplified pronotum, exposed tymbals, nonretractable uncus, and forewing venation will identify males. The visible metanotum, forewing characteristics, and amplified pronotum will distinguish females. The distinctly triangular rather than broadly rounded clypeus is a secondary diagnostic feature for both sexes.

Figure 18. *Okanagana*. A, dorsal view of male; B, venter of male; C, terminal segments of female venter; D, lateral view of terminal male segments and dorsal view of uncus (after Davis, 1919a); E, map showing the distribution of the genus by state and province. Small dots are used for the smaller New England states. The open circles in New Jersey and Virginia are doubtful reports. Although no *Okanagana* have been reported from Saskatchewan, the species found in Alberta and Manitoba is presumed to be there and is indicated by an open triangle. Arrows indicate the location of diagnostic characters. Species illustrated is *O. bella*.

Distribution

Although several species of *Okanagana* have been described since Davis wrote his paper on cicada distribution in 1930, his delineation of the range of *Okanagana* north of Mexico remains accurate. One species, *O. aurantiaca*, is known only from Baja, California. The currently recorded distribution of the remaining species is confined to North America, north of Mexico. *Okanagana* extends across southern Canada and the northern half of the United States from coast to coast. In the northeastern United States its range extends southward to Pennsylvania, Ohio, Indiana, and Illinois with one possible location reported from Virginia. *Okanagana* has been recorded in every state west of the Mississippi River except Oklahoma and Louisiana. One species, *O. viridis*, has been reported from Mississippi, Tennessee, Arkansas, and eastern Texas. *Okanagana* is apparently absent from the remaining southeastern states.

Discussion

Okanagana is the western counterpart of *Tibicen*. While species of *Tibicen* have proliferated in the eastern United States with relatively few species invading the southwestern states, *Okanagana* reaches its greatest diversity west of the Rocky Mountains with relatively few species present in the northeastern regions of the North American continental range of the Cicadidae. Simons (1954) records the greatest diversity in a single state with thirty-five species of *Okanagana* in California. *Okanagana* does not occur in tropical or low desert habitats. In Arizona, I have found *Okanagana* from the lower altitudinal limits of the Pinyon to the Hudsonian life zones of Merriam (1890) at altitudes of 915 to

3,200 meters. The latter, a female *O. rubrocaudata* captured on a small aspen on Mount Humphries, is the highest reported altitudinal record for a cicada. The species of *Okanagana* apparently extend their range southward in the western United States by following the mountain ranges.

It is difficult to characterize the habitat of a genus as large as *Okanagana*. *Okanagana* adults are found in grass, shrub, and arboreal habitats. Each species is associated with one or more distinct vegetation types which in turn are dependent on climate, altitude, and edaphic features for their distribution. M.S. Heath (1976) proposes that *O. bella*, *O. synodica*, and *O. magnifica* are key faunal indicator species of pine, steppe, and Pinyon-Juniper plant formations, respectively, in Arizona. Many species of *Okanagana* appear restricted to a single host plant. *Okanagana rubrovenosa*, *O. arctostaphylae*, and *O. opacipennis* all inhabit only manzanita, and each exhibits a protective coloration that blends with the dull red color of the host plant stems. Some species appear more catholic in their taste. Simons (1954) reports *O. vanduzeei* ovipositing "in a variety of plants including goldenrod, sage, *Baccharis*, and *Pinus* spp."

The behavior and activity of *Okanagana* appear to be more influenced by thermal parameters of their environment than by size or morphological features. Thus, those species living in environments where the body heat generated by long flights would thermally stress the insects tend to be congregating species, inhabiting a restricted portion of their potential habitat. Those species living in environments where they are unlikely to encounter thermal stress tend to disperse throughout the available habitat and become solitary species. *Okanagana utahensis*, *O. magnifica*, *O. synodica*, probably *O. fumipennis*, *O. rubrovenosa*, *O. mariposa*, and

O. georgi (*nomen nudum*) are all congregating species, while *O. bella*, *O. rubrocaudata*, and *O. hesperia* are solitary. The body temperature for heat torpor circa 43.5°C, appears remarkably consistent throughout the genus, but other thermal parameters appear linear with altitude. J.E. Heath et al. (1971) and M.S. Heath (1972) record minimum temperatures for flight and the temperatures at which basking ceases and individual cicadas seek the shelter of shaded locations for four species. Shade seeking temperatures range between 31.8°C and 37.6°C for *Okanagana*. Adult *Okanagana* live between one and two months, with females apparently outliving males. A major cause of death is predation by birds. Myers (1929) lists several bird predators of *Okanagana*. Soper, Shewell, and Tyrrell (1976) report on a sarcophagid parasite of *O. rimosa* apparently attracted by the song of the male cicada. Soper (1963) records a fungus, *Massospora levispora* Soper, attacking the same species.

The genus *Okanagana* appears closely related to *Clidophleps*, *Tibicinoides*, and *Okanagodes*. *Okanagana* share a number of characteristics with *Platypedia* and *Neoplatypedia*, implying a more distant relationship with these two genera.

CHAPTER XVII

Okanagodes

Taxonomy

Okanagodes Davis (1919a, p. 221)

Type Species

Okanagodes gracilis Davis (1919a)

Species

Both species in this genus occur in America north of Mexico. The species are

O. gracilis Davis

O. terlingua Davis

There is one named variety or subspecies of *O. gracilis*.

Descriptive History

Davis' (1919a) description is brief and concerned basically with the general habitus of the genus. Features are compared with *Okanagana*. No complete description has been written and no comparisons are made with the other two closely allied genera.

Description

General Body Proportions

Length of body 16.5 to 23.0 mm

Expanse of forewings 42.0 to 58.0 mm

The abdomen represents one-half the body length. *Okanagodes* are slim, parallel sided cicadas. Known species range in color from green to brownish, with some demes a light beige or straw color.

Head

Width of head, including eyes, narrower than the mesonotum; eyes prominent and may extend slightly beyond the anterior angles of the pronotum; vertex of epicranium horizontal, centrally sulcate; frons slanted, forming an obtuse angle with the dorsum of the clypeus; distance between lateral ocelli about the same or greater than distance between lateral ocelli and eyes; ocelli large, ruby red; clypeus steeply rounded, swollen, protruding prominently beyond the supraantennal plates, length about one and one-half times the length of the frons; rostrum reaching intermediate coxae.

Thorax

Pronotum constricted, adpressed laterally except at posterior angles, sides more or less parallel, lacking distinct lateral carinae; length of pronotum shorter than mesonotum; mesonotum striated where base of forewing folds against the body; posterior margin of metanotum completely visible behind metanotum; opercula small, rounded, widely separated, not extending beyond the base of the abdomen.

Legs

Anterior femora usually armed with two spines, although poor development of one or both spines seems to be a common anomaly in this genus. Posterior femora broad, somewhat rounded triangles.

Wings

Forewing venation is illustrated in Figure 19. Wings hyaline. First crossvein in forewing nearly perpendicular; second crossvein slightly oblique; first and second crossveins not parallel; ratio of costal margin of radial cell to the unbranched portion of the medial vein 2:1; marginal cells of forewing at least two-thirds the length of the corresponding ulnar cells, e.g., M_3 to U_2 ; medial and cubital veins arising separately from the arculus; nodus central; costal margin of forewing with a few very minute spines.

Abdomen

First abdominal segment in males containing tymbal organs, posterior margin of central dorsal sclerite sinuous; anterior margin of second dorsal sclerite curved smoothly ventrad laterally behind the tymbal organs; lateral bulge well developed; tymbal organs exposed.

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, posterior margin may or may not be concave dorsally; uncus stationary, not retractable,

Figure 19. *Okanagodes*. A, dorsal view of male; B, ventral view of male abdomen; C, terminal segments of female venter; D, lateral view of terminal male segments and dorsal view of uncus (after Simons, 1954); E, map showing the distribution of the genus by state. Arrows indicate the location of diagnostic characters. Species illustrated is *O. gracilis*.

simple (Figure 19); hypandrium elongated. Subgenital plate of female broadly and doubly notched (Figure 19).

Diagnostic Characters

The extremely produced, steeply rounded clypeus and relatively shallow frons will identify *Okanagodes*. Secondarily, the large ruby red ocelli and forewing are helpful characteristics.

Distribution

Okanagodes gracilis extends into Lower California; otherwise, *Okanagodes* is known only from North America north of Mexico. *Okanagodes gracilis* is reported from Utah, Arizona, California, and Nevada. *Okanagodes terlingua* is known only from Texas.

Discussion

Davis (1919a) gives the following characteristics to distinguish *Okanagodes* from *Okanagana*, ". . . the pronotum is much narrower behind the eyes. . . . The body is slim with the sides more parallel than in any known species of *Okanagana*." *Tibicinoides* and *Clidophleps* are also closely related to *Okanagodes*. *Tibicinoides* most closely approaches *Okanagodes* in the prominence and shape of the clypeus, but the short marginal cells in the forewings and the short unbranched section of the medial vein will in *Tibicinoides* clearly distinguish these two genera. The wing venation of *Okanagodes* lies intermediate between *Okanagana* and *Clidophleps*. The unbranched portion of the medial vein in the forewing is longer proportionally than in most *Okanagana* but shorter than most

Clidophleps. In *Okanagana* Cu is relatively straight as it is in *Okanagodes terlingus*. In *Clidophleps* Cu is arched. It is also arched in *Okanagodes gracilis*.

Okanagodes have an accessory stridulatory surface on the anterior, lateral portions of the mesonotum similar to that found in the three related genera above. Beamer and Beamer (1930) reported that, when approached, *Okanagodes* will cease the normal intermittant "Z'---Z'---Z' --- . . . song or change to a more broken one." It is possible the more broken sound may be made by stridulation rather than the tymbal organs.

The species of *Okanagodes* occur primarily on low-lying desert vegetation. They are adaptively colored, with the green forms preferring green stems, and the pale tan or straw forms occurring "in a habitat which looks to be almost entirely dry and dead" (Beamer and Beamer, 1930). Sage is apparently a common host, but singing males have been captured from many kinds of desert vegetation, grass, weeds, and even bare rock. They seldom fly when approached, probably because of the excessive ambient temperatures of their environment. The body heat generated by flight would quickly raise the internal body temperature to the point of heat torpor. A torporous animal would fall to the unprotected, hot, desert floor and experience thermal death. Like *Diceroprocta apache*, *Okanagodes gracilis* are active when ambient temperatures are between 40° and 50°C. They are able to avoid severe predation by being active when predators are not. The only predator reported for *Okanagodes gracilis* is a bird, *Geococcyx californianus* (Less.) (Myers, 1929).

CHAPTER XVIII

Pacarina

Taxonomy

Pacarina Distant (1905a, p. 314)

Type Species

Pacarina puella (Distant, 1905a)

= *Pacarina signifera* (Walker)

= *Cicada signifera* Walker

Species

The type species *Pacarina puella* is the only described species that occurs in North America north of Mexico.

Descriptive History

Distant (1905a) bases his description on general body proportions, head characteristics, pronotal characters, tympanal coverings, opercula, anterior femora, and forewing characters. His remarks will be referred to in the appropriate sections.

Description

General Body Proportions

Length of body	13.0 to 14.0 mm
Expanse of forewings	34.5 to 41.5 mm

In addition, Distant (1905a) gives the length of the abdomen as "about as long as the space between the apex of head and base of cruciform elevation," i.e., the abdomen represents approximately one-half the body length.

Head

Width of head, including eyes, broader than the mesonotum; eyes projecting laterally beyond the anterior angles of pronotum, appearing somewhat stalked; epicranium in a continuous gentle slope with the dorsum of the clypeus; width between ocelli less than width between lateral ocelli and eyes; clypeus and supra antennal plates rounded; dorsum of clypeus shorter than frons; rostrum reaching posterior coxae. United States specimens exhibit a sharp color demarcation between a dark dorsum and light venter. This line occurs just posterior to the anterior edge of the venter on the "face."

Thorax

Pronotum strongly arched laterally; lateral carinae continuous but minimal; lateral edges smooth, "slightly sinuous," with "posterior angles moderately lobately produced." Length of pronotum shorter than length of mesonotum; mesonotum obscuring most of metanotum; opercula in males large, broadly rounded, meeting or nearly meeting centrally.

Legs

Distant (1905a) states the "anterior femora armed with two strong spines beneath." United States specimens frequently have a third smaller

spine posterior to the larger distal spine. The posterior mera are narrow and angulate.

Wings

Forewing venation is illustrated in Figure 20. Both wings hyaline; infuscated markings various; first crossvein perpendicular, second crossvein slightly oblique, first and second crossveins not parallel; medial and cubital veins arising separately from the arcus; basal cell clear; nodus central; costal margin of forewings spinose.

Abdomen

First abdominal segment in males containing tymbal organs, central dorsal sclerite modified to resemble a "bow tie." Second abdominal segment produced anteriorly on each side into a triangular tymbal cover; covers concave medially exposing tympanal cavities; sternal sclerite produced into lateral bulges.

Sexual Characteristics

Ninth dorsal segment in males slightly produced centrally, produced region setaceous, lateral margins produced into two upturned points; uncus withdrawable, bifurcated, notched laterally (Figure 20). Seventh sternite of female shallowly notched, Figure 20.

Diagnostic Characters

The prominent eyes projecting laterally beyond the anterior edges of the pronotum combined with the small size and abrupt facial color

Figure 20. *Pacarina*. A, dorsal view of male; B, ventral view of male abdomen; C, terminal segments of female venter; D, lateral view of terminal male segments and caudal view of male abdomen showing uncus; E, face showing color pattern; F, map showing the distribution of the genus by state. Arrows indicate diagnostic characters. Species illustrated is *P. puella*.

change will distinguish this genus from all other American genera north of Mexico. This is the only genus in this region with triangular tymbal covers in the males. The nonparallel status of the first and second crossveins in the forewings is a secondary diagnostic character.

Distribution

The range of the genus *Pacarina* extends from Central America northward into the United States. Within the United States it has been recorded in the literature from Louisiana, Texas, Oklahoma, and Arizona. I have also seen specimens from New Mexico.

Discussion

Very little is known about the biology of *Pacarina*. Davis (1917) mentioned that it was captured on *Prosopis glandulosa*, mesquite, at Gillette, Texas. Beamer and Beamer (1930) recorded a capture from "cedar" near Ashfork, Arizona. Cedar is frequently used as a common name for the plant genus *Juniperus*. Collection dates on specimens I have seen range from May through mid August.

Wing markings of *Pacarina* collected within the United States vary from immaculate to highly infuscated markings on all the crossveins at the bases of the marginal cells and on portions of the longitudinal veins surrounding the marginal cells. Thoracic notal markings also vary widely.

Both the ecological notes and the diverse wing and notal markings make me suspect that the current species *Pacarina puella* is in reality a complex of two or more species.

CHAPTER IXX

Platypedia

Taxonomy

Platypedia Uhler (1888a, p. 23)

Type Species

Platypedia areolata (Uhler) (Distant, 1905d)

= *Cicada areolata* Uhler

Species

There are twenty-three described species of *Platypedia*, twenty-two of which have been reported from North America north of Mexico. They are

<i>P. affinis</i> Davis	<i>P. middlekauffi</i> Simons
<i>P. aperta</i> Van Duzee	<i>P. minor</i> Uhler
<i>P. areolata</i> (Uhler)	<i>P. mohavensis</i> Davis
<i>P. balli</i> Davis	<i>P. putnami</i> (Uhler)
<i>P. barbata</i> Davis	<i>P. rufipes</i> Davis
<i>P. bernardinoensis</i> Davis	<i>P. scotti</i> Davis
<i>P. falcata</i> Davis	<i>P. similis</i> Davis
<i>P. gressitti</i> Kato	<i>P. sylvesteri</i> Simons
<i>P. laticapitata</i> Davis	<i>P. tomentosa</i> Davis
<i>P. latipennis</i> Davis	<i>P. usingeri</i> Simons
<i>P. mariposa</i> Davis	<i>P. vanduzeei</i> Davis

There are four subspecies of *P. putnami* and one of *P. mohavensis*.

Descriptive History

Uhler's (1888a) description is the most complete original description of any of our American genera north of Mexico. Only two species were known to Uhler when he described the genus. He subsequently added a third the same year (Uhler, 1888b). Van Duzee (1915) added three more species and wrote a key to the genus as then known. He also added a generalized statement about the color patterning found in the genus. Davis (1920) added four more species and three varieties to the list of *Platypedia* in an in-depth treatment of the genus. He synonymized two of the known species. Davis added three additional generic morphological features. Simons (1953) named three species and rearranged the status of several others. In 1954, he keyed eighteen species known from California and listed their locations. Simons omitted one species described from California specimens. He may not have been aware of Kato's 1932 Monograph of Cicadidae written in Japanese in which *P. gressitti* is described. It is possible that *P. gressitti* may be synonymous with a species covered by Simons.

Description

General Body Proportions

Length of body	13.5 to 23.0 mm
Expanse of forewings	34.0 to 59.0 mm

The abdomen is greater than one-half the body length. Uhler (1888a) adds the following about the general appearance, "Elongate, acutely tapering posteriorly, with a sub-carinate ridge on the tergum, extending from near the base to beyond the middle; wing covers when at rest almost

vertical." *Platypedia* are black insects with normally the following pale markings: "sides of the face, supra-antennal plates in part, median line and hind edge of the pronotum, hind margin of the metanotum including the posterior one-half of the elevated X [of the mesonotum], the costal nervure as far as the node and the propleura superiorly" (Van Duzee, 1915).

Head

Width of head, including eyes, subequal with width of the mesonotum; eyes may project laterally slightly beyond the anterior angles of the pronotum; vertex of epicranium horizontal; frons gently sloping forming a broad obtuse angle with the dorsum of the clypeus; vertex centrally sulcate; "the anterior ocellus placed in a longitudinal groove, which later is continued upon the tumid front [i.e., clypeus]" (Uhler, 1888a); distance between lateral ocelli slightly narrower than distance between lateral ocelli and eyes; clypeus "quite prominent, strongly convex; exterior cheeks long and narrow; supra-antennal plates narrow, thick, bounded on each side with a notch" (Uhler, 1888a); clypeus longer than frons; rostrum reaching the posterior margin of the intermediate coxae or beyond. Uhler (1888a) adds, "Head bluntly triangular, hirsute."

Thorax

"Pronotum short . . . with the dorsal surface feebly convex . . . , the lateral margins almost straight, with the anterior angles feebly reflexed, and the posterior angles narrowly, but abruptly turned up" (Uhler, 1888a). Pronotum strongly arched laterally, not amplified, but

having small, continuous carinae where the notal and pleural regions join; lateral edges smooth; length of pronotum shorter than length of mesonotum; posterior margin of metanotum completely visible behind mesonotum; opercula not developed.

Legs

"Anterior femora short and stout, swollen in the middle" (Uhler, 1888a), armed with two prominent spines, sometimes showing the rudiments of a third distal spine; posterior tibiae broadly triangular.

Wings

Forewing venation is illustrated in Figure 21. Wings hyaline. First and second crossveins may or may not be parallel. "Wing covers [i.e., forewings] wide, strongly bowed on the costal margin, the areoles large and mostly wide, basal areole oblong, the radial areole occupying more than one-half the length of the wing-cover, the second ulnar areole short, wide, almost triangular; the apical areoles narrow, and the third, fourth, and sixth of equal length, with their inner tip triangular, while the inner end of the second, fifth, and seventh is truncated; wings [i.e., hind wings] narrow, not reaching as far as the tip of the discoidal areole of the hemelytra, with the anal-flaps broadly rounded, and separated by a deep emargination from the other member of the wing" (Uhler, 1888a). Medial and cubital veins arising separately from the arculus; cubital vein arched; nodus of forewing about two-thirds out on the costal margin; costal margin of forewings with at least a few minute spines; eight marginal cells.

Abdomen

"Sonorus valves [i.e., tymbal organs] of the males rudimentary, inconspicuous" (Uhler, 1888a). First abdominal tergite in both sexes with the anterior margin indented dorso-laterally forming a gap between the abdomen and the metathorax, reduced to a narrow band centrally, frequently covered in part by the metanotum; laterally a colored membrane is visible between the thorax and abdomen when the wings are spread. Second dorsal sclerite resembles succeeding tergites, not specialized; united first and second sternite may or may not be well developed (lateral bulge).

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, caudal margin slightly concave dorsally; uncus stationary, not retractable, simple (Figure 21); hypandrium extremely elongate; subgenital plate of female with a simple deep notch (Figure 21). The terminal segments in both sexes are "narrow and compressed, acutely tapering" (Uhler, 1888a).

Diagnostic Characters

Both male and female *Platypedia* can be distinguished by a combination of the position of the nodus and eight marginal cells in the forewing. The nodus is not located centrally, but lies about two-thirds out on the costal margin.

Figure 21. *Platypedia*. A, dorsal view of male; B, ventral view of male abdomen; C, terminal segments of female venter; D, lateral view of terminal male segments and dorsal view of uncus (after Davis, 1920); E, map showing the distribution of the genus by state and province. Arrows indicate diagnostic characters. Species illustrated is *P. putnami lutea*.

Distribution

One species of *Platypedia*, *P. australis* Davis, is known only from Nuevo Leon, Mexico. The remaining species are restricted to the western United States and Canada. Davis (1930) records *P. areolata* from British Columbia. Within the United States, *Platypedia* are recorded from Washington, Oregon, Idaho, Montana, Wyoming, South Dakota, Nebraska, Colorado, New Mexico, Arizona, Utah, Nevada, California, and western Texas. A fossil *Platypedia*, *P. primigenia* Cockerell, is recorded from Miocene deposits at Florissant, Colorado.

Discussion

Members of the genus *Platypedia* lack a functional tymbal organ and, therefore, do not produce sound in the manner normally associated with cicadas. They do, however, possess the auditory "mirrors" found in cicadas. Both sexes of *Platypedia* produce a clicking sound with the forewings. Simons (1954) feels this sound is made by rubbing the forewings together. Dr. Thomas Moore (1975, personal communication), of the University of Michigan, calls *Platypedia* and *Neoplatypedia* "wing bangers." He apparently feels that some species may produce sound by beating the wings against the substrate on which they are perched. The specialized costal margin of the forewings seems to indicate that the sound is produced with that margin rather than clicking the hind margin over the ridge formed where the resting wing sits against the mesonotum. The mesonotum lacks the even striations found in *Clidophleps*, *Okanagodes*, *Tibicinioides*, and some *Okanagana*. The upper surface of the ridge, however, is irregular in many species. A slow motion photographic analysis

of *Platypedia* in the act of sound production is needed to determine exactly how the sounds are made.

Several writers have in the past considered *Platypedia* and the related genus *Neoplatypedia* primitive because of the rudimentary nature of the tymbal organs. I am inclined to agree with Simons (1954) when he says, "In the genus *Platypedia* the tympana are so reduced they *no longer function* as sounding organs" (italics mine). Two lines of evidence support this conclusion. Other Auchenorrhyncha have fully developed tymbal organs and tymbal muscles for the production of sound (Ossiannilsson, 1949; Pringle, 1954). The lack of a functional tymbal organ has also been discovered in African cicadas of the genus *Ydiella* (Boulard, 1973a) and *Lamotialna* (Boulard, 1975a). *Ydiella gilloni* Boulard bears a stridulatory surface on the anal margin of the forewing and the costal margin of the hind wing (Boulard, 1973b). The African genera and the two North American genera, *Platypedia* and *Neoplatypedia*, have other morphological characters that relate them to genera within their own geographical regions. If a rudimentary tymbal organ is an indication of a primitive state, it would be difficult to explain present zoogeographical distribution without invoking the parallel evolution of nearly identical sound producing tymbal organs, an unlikely hypothesis at best. I, therefore, feel that the rudimentary tymbal organ in *Platypedia* and *Neoplatypedia* represents a distant departure from an ancestral North American cicada rather than a close relationship with a primitive ancestor.

Van Duzee (1915) remarked, "approaching *Platypedia* in its expanded elytra" in his original description of the genus *Clidophleps*. While the nodus remains central in *Clidophleps*, the radial cell in the forewing is

expanded and the costal margin in some species is strongly arched resembling the shape in some of the lesser arched species of *Platypedia*. In both *Clidophleps* and *Platypedia*, the cubital vein in the forewing is arched. The length of the medial vein prior to the first branch also resembles that character in *Clidophleps*. Davis (1920) remarked, "In *Platypedia*, as in *Clidophleps*, *Okanagana*, *Okanagodes*, and *Tibicinoides* the metanotum is conspicuous behind the mesonotum, and the uncus cannot be withdrawn into the abdomen." *Platypedia* is obviously most closely related to *Neoplatypedia*, from which it can be distinguished by having eight marginal cells in the forewings, whereas *Neoplatypedia* has only seven marginal cells. The above remarks, however, indicate a secondary relationship of these two genera with the okanaganoid group.

Like the okanaganoid genera, *Platypedia* reaches its greatest diversity in California with at least eighteen species occurring in that state. *Platypedia* is one of the larger genera of cicadas found in America north of Mexico. As such, different species have invaded a variety of habitats. They are reported from the California seacoast to elevations as high as 2,750 meters, and from desert shrubs to stream-side trees. *Platypedia* adults are active from March to late July. Several species are very setose. It would be interesting to know if this "hair" has any insulating value to the individual. *Platypedia* do not fly readily. *Platypedia putnami lutea* drops to the ground when approached (Davis, 1943), a reaction similar to the death feint of *Tibicinoides mercedita*. The only known predators of *Platypedia* are birds (Myers, 1929). Simons (1954) states that *P. minor* and *P. areolata* have been implicated in oviposition damage to economic plants in Northern California.

Platypedia is one of two modern North American genera documented in the fossil record. A nearly complete specimen of *Platypedia primigenia* was found in the Miocene deposits at Florissant, Colorado. Cooper (1941) stated this fossil "is in striking agreement" proportionally with *P. putnami*. It varies in details of venation. Another fossil, *Lithocicada perita* Cockerell, from the same deposits exhibits a forewing radial cell extending beyond the middle of the wing and may be related to the modern genus *Platypedia*.

CHAPTER XX

Quesada

Taxonomy

Quesada Distant (1905b, p. 478)

Type Species

Quesada gigas (Olivier) (Distant, 1905b)

- = *Cicada gigas* Olivier
- = *Cicada triupsilon* Walker
- = *Cicada senans* Walker
- = *Cicada consonans* Walker
- = *Cicada vibrans* Walker
- = *Tympanoterpes sibilatrix* Berg
- = *Tympanoterpes gigas* (Olivier)

Species

The type species *Quesada gigas* is the only representative of this genus that occurs in North America north of Mexico.

Descriptive History

Distant's (1905b) description covers the major body regions; however, several additional features may be added to the characterization of *Quesada* in North America north of Mexico.

Description

General Body Proportions

The following ranges are based on specimens in my possession and photographs in Davis (1944).

Length of body 29.0 to 45.0 mm

Expanse of wings 95.0 to 120.0 mm

In addition, Distant (1905b) indicates that the body is broad and robust and that the abdomen represents about one-half the body length.

Head

Width of head, including eyes, about as wide as the mesonotum. Distant (1905b) gives the following length comparison--length of head "about as long as pronotum without its posterior margin." Eyes conspicuous, projecting laterally beyond the anterior edge of the pronotum; slope of epicranium emarginate where it joins the clypeus; width between ocelli less than width between lateral ocelli and eyes; supraantennal plates triangular; clypeus rounded; dorsum of clypeus longer than frons; "rostrum reaching base of posterior coxae."

Thorax

Pronotum strongly arched laterally; lateral carina present; anterior half of lateral edges jagged or irregularly toothed; "posterior angles moderately dilated." Length of pronotum shorter than length of mesonotum; mesonotum obscuring most of metanotum. "Metasternum centrally elevated, the process posteriorly triangularly produced between the posterior coxae" (Distant, 1905b). Opercula in males small, widely separated, and

not extended beyond the base of the abdomen; opercula in females similar to those of males.

Legs

Anterior femora with two prominent spines beneath, sometimes a minute third spine posterior to the larger distal spine. Posterior tibiae elongated triangles.

Wings

Forewing venation is illustrated in Figure 22. Both wings hyaline, first and second crossveins of forewings slightly infuscated. The forewing is "long, somewhat narrow, greatest breadth not quite one-third of length" (Distant, 1905b). First and second crossveins oblique, virtually parallel; medial and cubital veins arising separately from the arculus; basal cell half opaque, half clear, "almost as broad as long"; nodus central; costal margin of forewings minutely spinose.

Abdomen

First abdominal segment in males containing tymbal organ; central dorsal sclerite reduced to a thin band medially. Anterior margin of second dorsal sclerite turned outward forming a ribbon-like structure posterior to the tymbals with a small lateral triangular projection; tymbal organ exposed; sternal sclerite not prominently bulged.

Sexual Characteristics

Ninth dorsal segment of males produced centrally, rounded laterally; uncus withdrawable, bifurcated with a central dorsal projection (see

Figure 22. *Quesada*. A, dorsal view of male; B, ventral view of male abdomen; C, terminal segments of female venter; D, caudal view of male abdomen showing uncus; E, map showing the distribution of the genus north of Mexico. Arrows indicate diagnostic characters. Species illustrated is *Q. gigas*.

E

Figure 22), not notched laterally. Subgenital plate of female with a small central notch, not bilobed (Figure 22).

Diagnostic Characters

The short, definitely triangular head with its prominent, laterally projecting eyes and the strongly arched pronotum with the irregularly serrated lateral margins will identify this genus. The "ribbon-like" projection of the second abdominal tergite in the males and the shape of the subgenital plate in the females are also characteristic.

Distribution

The genus *Quesada* extends from southern Texas to Argentina north of a line drawn between Buenos Aires and Mendoza. In Texas, it has been recorded from Starr, Hildalgo, Cameron, Bexar, Nueces, and Bee counties.

Discussion

Myers (1929) and Davis (1944) summarize most of the literature on *Quesada gigas*. Davis points out that owing to its remarkable north-south distribution of some 6,500 kilometers, *Quesada gigas* is the only cicada found north of Mexico that is active in the adult form somewhere in its range every month of the year. In southern Texas, adults have been recorded from May to October.

Quesada is arboreal and apparently eclectic in its choice of trees. In Texas, it has been taken from live oaks and mesquite. It sings chiefly at dawn and dusk but may also be active on warm, moonlit nights. It frequently occurs in broods and sings in chorus. An individual starts

singing with one or two tentative croaks. These are repeated by its neighbors. After this brief "warm-up" the entire area will resound with a loud, shrill, unison cry that has been likened to the whistle of a "first-rate locomotive."

Because of its size, sound, and habits, *Quesada gigas* has acquired a number of colorful common names. Among these are "Locomotive cicada," "Popcorn-Whistler," and "Soupbug" in the United States and "Chichara grande" and "Coyoyo" in Argentina. The "Soupbug" appellation comes from its occasional attraction to lights during its evening flights and its consequent appearance on the dinner table.

Quesada is subject to a fungus disease which attacks the terminal portions of the abdomen. It is also attacked by a "Cicada killer," a sphecid wasp.

CHAPTER XXI

Tibicen

Taxonomy

Tibicen Latreille (1825, p. 426)

Type Species

Tibicen plebeja (Scopoli) (Latreille, 1825)

= *Cicada plebeja* Scopoli

= *Tettigonia orni* Fabricius (nec Linné)

= *Tettigonia fraxini* Fabricius

= *Tettigonia obscura* Fabricius

= *Cicada obscura* (Fabricius)

= *Lyristes plebeja* (Scopoli)

= *Cicada fraxini* (Fabricius)

Species

There are thirty species of *Tibicen* in North America north of Mexico and eight additional named varieties. The species are

T. auletes (Germar)

T. chisosensis Davis

T. aurifera (Say)

T. chloromera (Walker)

T. bifida (Davis)

T. cultriformis (Davis)

T. canicularis (Harris)

T. davis (Smith and Grossbeck)

T. chiricahua Davis

T. dealbata (Davis)

<i>T. dorsata</i> (Say)	<i>T. latifasciata</i> (Davis)
<i>T. duryi</i> Davis	<i>T. winnemanna</i> (Davis)
<i>T. figurata</i> (Walker)	<i>T. resh</i> (Haldeman)
<i>T. inauditus</i> Davis	<i>T. resonans</i> (Walker)
<i>T. linnei</i> (Smith and Grossbeck)	<i>T. robinsoniana</i> Davis
<i>T. longiopercula</i> Davis	<i>T. similaris</i> (Smith and Grossbeck)
<i>T. lyricen</i> (De Geer)	<i>T. superba</i> (Fitch)
<i>T. montezuma</i> (Distant)	<i>T. texanus</i> Metcalf
<i>T. parallela</i> Davis	<i>T. townsendii</i> (Uhler)
<i>T. pruinosa</i> (Say)	<i>T. walkeri</i> Metcalf

Metcalf (1963) lists two additional species of *Tibicen* with ranges north of Mexico, *T. variegata* (Fabricius) and *T. ocreoptera* (Townsend). Davis (1918) tried to identify Fabricius' *T. variegata* but concluded "owing to a faulty description" it might "be one of several of our well-known species." He apparently could not locate an identified specimen, and the species still remains unidentifiable. The name has not been used for sixty years except in Metcalf's catalogue. Myers (1929) cites *T. ocreoptera* as a *nomen nudum*. No subsequent description or types have established this species, and it has not been referred to since Myer's work except in Metcalf's catalogue. I have, therefore, dropped these two names from the list. Both Metcalf (1963) and Alexander (unpublished) consider *T. latifasciata* and *T. winnemanna* as varieties or subspecies of *T. pruinosa*; however, both Davis and Van Duzee treated them as separate species in their writings so I have listed them as such. There are three recognized varieties of *T. lyricen* and one each of *T. pruinosa*, *T. walkeri*, *T. bifida*, *T. chloromera*, and *T. davisi*.

Descriptive History

Confusion as to what actually constituted the genus *Tibicen* was intimately entangled for almost a hundred years with a similar confusion over what was intended by the original Linnean genus *Cicada*. In 1825, Latreille named *Tibicen* for *plebeja* Scopoli without description. Had he left well enough alone, the confusion might not have arisen, but in 1829 he named "one distinguishing character (of no value) . . . and four species (belonging to three genera)" (Van Duzee, 1914). Since *plebeja* was frequently used as the type for *Cicada*, subsequent authors felt free to use the other species named in 1829 as types for *Tibicen*. Some authors, notably Distant, ignored the genus altogether. Distant, in Genera Insectorum (1912), used *plebeja* as his type for the genus *Cicada*. Van Duzee (1912) quickly pointed out that *Cicada* as characterized by Distant no longer included any of the original Linnean species. In 1914, Van Duzee declared *C. orni* the type for *Cicada* based on Lamarck's naming of *orni* in 1801 and other evidence indicating Linnaeus intended *orni* as the type for his section "Manniferae." He returned to the original naming of *Tibicen* in 1825 and reiterated *plebeja* as the type for the genus. He further established the genus by placing our American species in *Tibicen* in his Check List of Hemiptera (Excepting the Aphididae, Aleurodidae and Coccidae) of America North of Mexico (1916) and his subsequent catalog of the same species (1917). *Tibicen*, as recognized by Van Duzee, included the then described species of our presently recognized genera *Tibicen*, *Diceroprocta*, and *Cornuplura*. Van Duzee did not describe *Tibicen*. Various short descriptions, usually relating to diagnostic characters of local species, have appeared, but I have been unable to locate a fuller treatment of the genus.

Description

General Body Proportions

Length of body 22.0 to 41.0 mm

Expanse of forewings 60.0 to 125.0 mm

The above size range applies only to *Tibicen* from North America north of Mexico. Both larger and smaller species have been described from other areas. The abdomen represents about one-half the body length in females but is generally slightly longer in males because of the extended male genitalia. The length of the body is at least two and one-half times the width of the mesonotum.

Head

Width of head, including eyes, about as broad or broader than mesonotum; eyes may extend slightly beyond the anterior margin of the pronotum; vertex of epicranium horizontal, frons nearly vertical, forming a right or sharply obtuse angle with the dorsum of the clypeus; distance between ocelli less than distance between lateral ocelli and eyes; clypeus ranges from more or less truncate, in a continuous line with the supraantennal plates, to moderately tumid; dorsum of clypeus about as long or longer than frons; length of rostrum species specific, ranging from middle coxae to beyond posterior coxae.

Thorax

Pronotum amplified laterally forming definite lateral carinae, lateral edges smooth, not toothed, occasionally spinose; length of pronotum shorter than mesonotum; mesonotum obscuring central portion of

metanotum; opercula in males large, longitudinal, meeting or overlapping medially.

Legs

Anterior femora with two prominent spines beneath, sometimes with a third smaller spine distally; posterior tibiae triangular.

Wings

Forewing venation is illustrated in Figure 23. Both wings hyaline; first and second crossveins in forewings oblique, virtually parallel, and frequently infuscated; length of R_{4+5} between the first and second crossveins less than R_{4+5} between the first crossvein and the ambient vein; medial and cubital veins arising separately from the arculus; nodus central; costal margin of the forewings with at least a few minute spines.

Abdomen

First abdominal segment in males containing tymbal organs, central dorsal sclerite with basically the same curvature as succeeding tergites; second dorsal segment in males produced anteriorly on each side into a complete tymbal cover; lateral bulge inconspicuous.

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, usually produced into a central spine dorsally; uncus withdrawable, simple (Figure 23). Subgenital plate of female smoothly bilobed (Figure 23).

Figure 23. *Tibicen*. A, dorsal view of male; B, ventral view of male abdomen; C, terminal segments of female venter; D, caudal view of male abdomen showing uncus; E, map showing the distribution of the genus by state and province. Small dots are used for the smaller eastern states and provinces. Although *Tibicen* has not been reported from Wyoming, this state falls within the north-south range of *T. dealbata*, which is presumed to be there. This presumed distribution is marked by an open triangle. Arrows indicate diagnostic characters. Species illustrated is *T. duryi*.

E

Diagnostic Characters

Tibicen is most notable for its lack of diagnostic characters. Therefore, combinations of characters must be used to identify the genus. Males can be distinguished by the complete tymbal cover, broad head, opaque abdomen, simple uncus, and smooth ventral edge of the pygofer. Female identification requires the following combination of features: a) mesonotum covering central portion of metanotum, b) first and second crossveins of wings parallel, c) no infuscated markings on longitudinal veins of forewings, d) head about as broad or broader than mesonotum, e) lateral edges of pronotum smooth, not jagged or toothed, f) subgenital plate smoothly bilobed, not sinuous, g) distance between the crossveins along R_{4+5} less than distance between the first crossvein and the ambient vein. To distinguish female *Tibicen* from female *Cornuplura*, it is necessary to look under the subgenital plate for the eighth abdominal sternite. If the subgenital plate lies flush against the body and the eighth sternite can, therefore, not be seen from a caudal view, the above characters will identify *Tibicen*. If two "hook-like" projections emanating from the eighth sternite are visible, the specimen is either *Cornuplura*, *Tibicen townsendii*, or *T. cultriformis*. The basal cell of the forewing in both species of *Cornuplura* north of Mexico is predominantly black. In *T. cultriformis* it is green and in *T. townsendii* it is a light brown.

Distribution

The genus *Tibicen* is widely dispersed throughout the north temperate areas of the world in both the Palearctic and Nearctic biogeographic regions. There are also several species in the Neotropical region.

There are scattered reports of *Tibicen* from all the commonly recognized biogeographic regions except the Australian. *Tibicen* reaches its greatest known diversity in the Nearctic. The number and diversity of *Tibicen* seems, however, to be a part a consequence of the location and conceptual outlook of the taxonomists who have worked since Van Duzee firmly established the genus in 1916. Thus, Van Duzee and Davis clarified the status of *Tibicen* in North America. Kato has thoroughly studied the cicada fauna of Japan during the past half century and records seven species and several named varieites in Fauna Japonica, Cicadidae (1961).

I am hesitant to accept reports from the Ethiopian, Oriental, and Oceanic regions without further verification. For example, the lone *Tibicen* from the Ethiopian region comes from Madagascar. While this distribution is improbable, it is no less improbable than the distribution of iguanid lizards which are restricted to the Americas, Madagascar, and Fiji (Darlington, 1957). *Tibicen*, which also is recorded from Fiji, is at least present currently on some Old World continental land masses. Further exploration and reworking of museum specimens may indeed reveal a truly cosmopolitan distribution for *Tibicen*, or they may prove earlier records spurious. Boulard is currently working extensively on the African cicada fauna. In several recent papers on African cicadas, he has yet to record the presence of *Tibicen* in the Ethiopian region of the African continental land mass (Boulard, 1972a, 1972b, 1974a, 1974b, 1975b, 1975c, 1976b).

In North America north of Mexico, *Tibicen* is distributed from Manitoba to Nova Scotia in the north and from Florida to Arizona in the south. *Tibicen* is found from the east coast to Manitoba, Montana, Utah, and Arizona. Although I have seen neither specimens nor reports from

Wyoming, I assume *Tibicen* is found in at least the eastern portion of that state since Davis (1930) records *T. dealbata* as extending from "Montana and North Dakota southward to New Mexico and Texas."

Discussion

If I were asked to select a generalized cicada from among the North American genera, it would have to be the genus *Tibicen*. From the broad head to the simple uncus, there is not a single feature, I have observed, that *Tibicen* fails to share with at least one other genus. *Diceroprocta* and *Cornuplura* appear obviously closely related to *Tibicen* and the three genera form a natural grouping. Nevertheless, the more distant genera that do not retract the male genitalia, have a simple uncus. This occurrence of common features is not only found in living forms but also among fossil Cicadidae. Cooper (1941) states the oldest known fossil cicada, *Davispia bearcreekensis* Cooper from the Paleocene, resembles *Tibicen* more closely than it resembles any other modern genus. He also finds no reason why the fossil *Cicada grandiosa* Scudder from the Miocene should not be considered *Tibicen*. Both of these fossil species are from North American deposits. The fossil record seems to indicate that *Tibicen* and its immediate antecedents have been in North America north of Mexico for several million years.

Among living *Tibicen*, Davis (1930) recognizes three distinct groups in America north of Mexico. The first group he characterizes as large, usually black and green cicadas. These cicadas inhabit the eastern half of the United States and Canada. The second group averages somewhat larger than the first group and is characterized by two "pipe-shaped" marks on the mesonotum resembling the inverted Hebrew letter resh. These

cicadas also frequently have a row of dorsal spots on the abdomen. This group inhabits the central portion of the United States with one, *Tibicen cultriformis*, occurring in Arizona. Both of these groups have gently tapering abdomens. The third group contains the smallest species of American *Tibicen* north of Mexico. They inhabit the southwestern United States and are characterized by having the sides of the abdomen conspicuously parallel to each other. While the first two groups may be distinct in color and patterning, I see no basic morphological differences between them. The difference in shape between the third group and the other two is quite obvious. Davis states the third group most closely resembles the type species, *Tibicen plebeja*. The first two groups seem to resemble more closely the species of *Tibicen* illustrated by Kato (1961) in Fauna Japonica.

The majority of *Tibicen* species are arboreal, but, as might be expected in a genus this large, different species have adapted to a wide variety of plant types. Beamer (1928) records panic grass, *Panicum virgatum*, as the favored host of *T. aurifera*, and dead yucca fruiting stalks as the predominant oviposition site of *T. bifida*. *Tibicen* also vary in the temperature and moisture requirements of their habitat, ranging from the "swampy woods" dwelling *T. chloromera* in Michigan (Moore, 1966) to the xerophilous *T. chiricahua* and *T. duryi* of Arizona. *Tibicen* are frequently solitary species, and males, at least, appear to be somewhat sedentary. I have observed a male *T. pruniosa* singing from the same hackberry tree throughout his adult life of several weeks in central Illinois. *Tibicen* occasionally occur in large broods, and several individuals may be heard singing from the same tree or clump of trees. This clumping appears to be the result of an accident of

birth rather than the congregating behavior seen in *Magicalicada*. The song of one individual frequently evokes singing by nearby males, but the songs are not necessarily synchronous. In *T. figurata* from Florida, one male will sing, then another, and when the second individual stops, the first male and sometimes a third will take up the song. Moore and Kausch (1975) record the mating clicks in *Magicalicada septendecim* in the film, Seventeen-Year Cicadas (*Magicalicada septendecim*). I have observed similar mating sounds in *T. duryi*. Birds are probably the most common predators of *Tibicen*. Attacks recorded by other insects include the asilid fly *Dasyllis grossa* (Fabr.) on *Tibicen chloromera*, the sarcophagid *Sarcophaga helioides* (Town.) on *Tibicen linnei*, and a braconid egg parasite of *Tibicen walkeri* (Myers, 1929). Davis (1924, 1925) records *Vespa crabro* (Linn.) eating *T. lyricea* and *T. chloromera*, while the cicada killer wasp, *Sphecius speciosus* Dru. collects several species of *Tibicen* as food for its young. In addition, I have observed several large dipteran puparia associated with a dead *T. figurata* male in Florida. Members of the genus *Tibicen* are known throughout the eastern United States and into Canada as the "dog-day cicadas" because of their presence during the hot days of mid and late summer. *Tibicen auletes* is the largest cicada in North America north of Mexico.

CHAPTER XXII

Tibicinoides

Taxonomy

Tibicinoides Distant (1914, p. 166)

Type Species

Tibicinoides cupreosparsa (Uhler) (Distant, 1914)

= *Tibicen cupreosparsa* Uhler

= *Tibicina cupreosparsa* (Uhler)

Species

There are two species of *Tibicinoides* in North America north of Mexico. The species are

T. cupreosparsa (Uhler)

T. mercedita (Davis)

A third species *T. minuta* (Davis) is considered synonymous with *T. mercedita* by Simons (1954). *Tibicinoides hesperia* belongs in the genus *Okanagana* (Davis, 1919a; M.S. Heath, 1976).

Descriptive History

All of Distant's (1914) characters are well illustrated by the type species; however, not all occur in *T. mercedita*. The following description

is inclusive of the genus as currently recognized. Both Davis (1919a) and Van Duzee (1915) include the species of *Tibicainoides* in their keys.

Description

General Body Proportions

Length of body 16.0 to 20.5 mm

Expanse of forewings 33.0 to 44.5 mm

The abdomen longer than space between apex of head and base of cruciform elevation (Distant, 1914).

Head

Width of head, including eyes, narrower than the mesonotum; eyes in a line with the anterior angles of the pronotum; vertex of epicranium centrally sulcate and horizontal; frons steeply slanted, forming an obtuse angle with the dorsum of the clypeus; distance between lateral ocelli slightly greater than distance between lateral ocelli and eyes; clypeus steeply rounded, extending well beyond the supraantennal plates; dorsum of clypeus longer than frons; "rostrum reaching the intermediate coxae" (Distant, 1914).

Thorax

Pronotum amplified laterally forming definite lateral carinae, lateral edges smooth, sinuate, posterior angles dilated; pronotum gradually narrowing anteriorly; length of pronotum shorter than mesonotum; mesonotum striated where base of forewing folds against the body; posterior margin of metanotum completely visible behind mesonotum;

opercula small, transverse, rounded, widely separated, not extending beyond the base of the abdomen.

Legs

Anterior femora armed with two prominent spines; posterior tibiae broadly triangular.

Wings

Forewing venation is illustrated in Figure 24. Wings hyaline to semiopaque, the basal half of the forewings sometimes heavily infuscated especially behind a rudimentary crossvein marking the transverse fold of the forewing, that may be well developed in some specimens of this genus. First and second crossveins in forewing slightly oblique and usually parallel; marginal cells of forewings short, about one-half the length of the ulnar row, especially the ratio of M_3 to U_2 ; "basal cell about twice as long as broad" (Distant, 1914); medial and cubital veins arising separately from the arculus; nodus central; costal margin not notably spinose; wings may be setose, especially in opaque areas and around veins.

Abdomen

First abdominal segment in males containing tymbal organs, posterior margin of central dorsal sclerite broadly curved anteriorly, margin occasionally sinuous (Figure 24); anterior margin of second dorsal sclerite ending abruptly, may or may not turn outward to form a ribbon-like structure posterior to the tymbals; lateral bulge well developed; tymbal organs exposed.

Figure 24. *Tibicinoides*. A, dorsal view of male; B, ventral view of male abdomen; C, lateral view of terminal segments of the male and dorsal view of the uncus (after Simons, 1954); D, map showing the distribution of the genus by state. Arrows indicate diagnostic characters. Species illustrated is *T. cupreosparsa*.

A

C

B

D

Sexual Characteristics

Ninth dorsal segment of males rounded laterally, caudal margin with an anterior curve dorsally; uncus stationary, not retractable, simple (Figure 24); hypandrium elongated. Subgenital plate of female with a deep, single U or V shaped notch (Davis, 1915).

Diagnostic Characters

The short marginal cells on the forewing will identify *Tibicinoides* from other cicada genera found in North America north of Mexico.

Distribution

North of Mexico, the genus *Tibicinoides* is reported only from California. Simons (1954) states, "The genus *Tibicinoides* is found primarily in the western part of the state (California), extending as far north as Lake County and reaching southward into Lower California."

Discussion

Tibicinoides, as currently recognized, consists of two, small okanaganoid species. The genus appears to be the nucleus of a group in transition with the type species, *Tibicinoides cupreosparsa*, the most divergent from *Okanagana*. The semiopaque (or heavily infuscated) wings sometimes accompanied by a well developed rudimentary vein running from the base of the first ulnar area to the base of the "lower apical area," and included by Distant (1914) in his original description of *Tibicinoides*, appears to be a polymorphism found in both *Tibicinoides* and some species of *Okanagana*. *Okanagana hesperia* exhibits distinct,

independent polymorphism in body and wing coloration with intermediate forms occurring in both. A transverse fold, or rudimentary vein, crossing the forewings at the node may or may not be developed. The dark winged forms have been frequently placed in the genus *Tibicinoides*, whereas the clear winged form was described originally as a variety of *Okanagana striatipes*. The species conforms in all other features with *Okanagana* and has been placed there by Davis (1919a) and M.S. Heath (1976). Since wing patterning can no longer be considered diagnostic of the genus, we must look for structural features. The clypeus is much more rounded in *Tibicinoides* than it is in *Okanagana*. In that feature it more closely resembles the other two okanaganoid genera, *Okanagodes* and *Clidophleps*. The anterior margin of the second abdominal tergite in *T. mercedita* resembles the same structure in *Okanagana* and *Clidophleps*, while the tergite in *T. cupreosparsa* resembles that of *Okanagodes*. The only unique feature of the genus is the short marginal cells in the wing. *Tibicinoides* is thus closely related to *Okanagana*, *Clidophleps*, and *Okanagodes*.

Tibicinoides are active as adults from late April to late June. Both species are found in grass (Van Duzee, 1914; Simons, 1954). Davis (1936) records an interesting behavioral note on *T. mercedita*. This species feigns death when disturbed. Both males and females fold their legs and drop to the ground. They remain comatose even when handled and will wait several minutes before resuming activity.

Tibicinoides possess a striated surface where the forewing folds against the mesonotum. A similar structure is found in *Clidophleps*, *Okanagodes*, and some species of *Okanagana*. This is apparently the stridulitrum (Ashlock and Lattin, 1963) of a secondary sound producing mechanism used for communication by both males and females.

CHAPTER XXIII

DISCUSSION AND CONCLUSIONS

Origins and Dispersal

The entire cicada fauna of North America north of Mexico is endemic. At least two genera appear to have their origins in the Neotropical biogeographic region. *Quesada* barely slips over the southern border of the United States into southern Texas, yet its range extends southward into Argentina. *Pacarina* presently is represented by one species in the American southwest, and diversification occurs only in the Neotropical region. A third genus, *Beameria*, may have its closest relatives in the neotropics. The type species *B. venosa* was originally classified as a member of a neotropical genus. Although *Beameria* is known to occur only north of Mexico, Metcalf (1963), who relies heavily on geographical centers of origin for all taxonomic levels, places *Beameria* in the same tribe with *Pacarina*.

Neocicada has its closest morphological affinity with the genus *Cicada*, a widely distributed Palearctic genus. A *Cicada*-like ancestor probably crossed the Bering land bridge at some point in the geologic past. The most widely distributed of all cicada genera, *Cicadetta*, is represented in the Nearctic region by only four species. It is not found in the Neotropical region. *Cicadetta*'s invasion of North America must have occurred in a manner similar to that of *Neocicada*.

Magiccicada is a North American phenomenon. There is nothing else quite like it. Several anatomical features suggest, that despite its remarkable synchronous periodicity, *Magiccicada* is a somewhat primitive cicada. It may well be that remnant of an ancient cicada fauna once inhabiting the North American continent. There seems to be no justification for the traditional lumping of *Magiccicada* in the same tribe, Tibicinini, with *Okanagana* and its derivatives. Myers (1929) considers Tibicinini a catchall of unrelated genera, and I agree that a thorough reworking of the material within this tribe is called for.

The above six genera, with the possible exception of a loose relationship between *Beameria* and *Pacarina*, stand as solitary generic representatives in the region of North America north of Mexico. The current distribution of both *Neocicada* and *Cicadetta* suggest that, like the other North American cicadas, the presence of both antidesates Pleistocene glaciation in North America. Several writers have noted the effects of glaciation on the distribution of broods of *Magiccicada*.

The remaining ten genera can be divided into two primary groups, those derived from the genus *Tibicen* or its immediate predecessor and those derived from *Okanagana* and/or its predecessor. This latter group is comprised of two subgroups, one containing *Platypedia* and *Neoplatypedia* and the other comprised of the four okanaganoid genera.

There are two basic shapes found in the genus *Tibicen*. One is the parallel sided habitus characteristic of the type species *Tibicen plebeja* from Europe. The other is a gradually tapering form characteristic of the Japanese *Tibicen* as illustrated by Kato (1961). Both forms are found in North America north of Mexico. Parallel sided species are found predominantly in the southwestern United States and on the eastern

slopes of the Rocky Mountains. Their eastern border appears to be the Great Plains. The tapering species are found predominantly in the eastern United States and Canada. Although some species appear to have followed river courses into the eastern fringe of the parallel sided group, and one species, *Tibicen cultriformis*, is found in Arizona, their western dispersal also seems limited by the Great Plains. I believe that there were two invasions of *Tibicen* or *Tibicen*-like ancestors into North America, one representing each of the two basic forms.

The parallel sided group appears to be the earlier invader because Neotropical *Tibicen* have the parallel sided appearance, and this group has diversified into three additional genera. The tapering habitus is more limited in distribution and has not diversified into additional genera. Parallel sided *Tibicen* apparently spread southward along the eastern slopes of the Rockies into Mexico and eventually into South America. Somewhere in central Mexico this group radiated into *Diceroprocta*, *Cornuplura*, and *Cacama*. These three genera then spread back northward. *Diceroprocta* spread across the southern United States from the Colorado River valley to the eastern seaboard and is now found as far north as Michigan, Wisconsin, and Virginia. *Cornuplura* has reached southern Arizona, and *Cacama* inhabits the southwestern United States including southern California. *Tibicen* and its three related genera are still found in Mexico.

The gently tapering *Tibicen* form entered North America later. It did not disperse southward along the eastern slopes of the rockies probably because the *Tibicen* niches already were occupied. Instead, it dispersed eastward along a northerly route until it reached territory unoccupied by other *Tibicen* east of the Great Plains. There ensued a

radiation of species southward throughout the eastern United States. This group has not spawned any new genera.

The second major group of genera in North America north of Mexico is that derived from or sharing a common ancestor with *Okanagana*. This group apparently has a loose relationship with the Palearctic genera *Tibicina* and *Subsaltria* and the Neotropical genera making up the subfamily Tettigadinae with which they share an accessory stridulatory surface near the "shoulder" of the mesonotum. *Tibicina* and *Okanagana* have other characters in common. I propose that a common ancestor of these two genera entered North America across the Bering land bridge, and that this ancestor developed into an *Okanagana* somewhere in northwestern Canada. From there it spread eastward to the Atlantic. There is a small radiation of species of *Okanagana* in the eastern United States and Canada. This radiation was probably restricted by the presence of other cicada genera already occupying the cicada niche in eastern North America. *Okanagana* also spread southward west of the Rocky Mountains. Here it found a territory unclaimed by other cicadas. It radiated into a variety of species and genera particularly in the diversified habitats afforded in California. It is probably fortuitous that the distribution of the type species of *Okanagana*, *O. rimosa*, follows both the eastward and southward distribution today.

All six of the genera in this group, *Okanagana*, *Clidophleps*, *Tibicinoides*, *Okanagodes*, *Platypedia*, and *Neoplatypedia*, reach their greatest diversity of species in California. Four species comprise one subgroup. *Okanagana* has remained boreal in the western United States extending its range southward along the mountain ranges. *Tibicinoides* is restricted to western California and Baja California. *Clidophleps* and

Okanagodes have adapted to more arid habitats. *Okanagodes* has spread across the southwestern deserts to Texas, while *Clidophleps* has remained in southern California and Baja California with the exception of one species found in Arizona.

The other subgroup consists of *Platypedia* and *Neoplatypedia*. It is probably an earlier diversification than that of the above genera. Although these two genera have deviated strikingly from other North American cicadas, the deviations are all related directly to the loss of the traditional sound producing tymbal organ and the development of a different method of sound communication. The nonretractable, simple uncus definitely relates them to the okanaganoid group. *Platypedia* probably had its origins in an okanaganoid-like ancestor that lacked a mesonotal stridulatory surface. *Neoplatypedia* derived from *Platypedia*. Both have a basin and range distribution, with *Platypedia* reaching the northern plains.

It appears to me that the above six genera, and possibly *Tibicina*, and *Subpsaltria*, should form the basis of a new tribe. The new tribe would consist of at least two subtribes. Traditionally *Tibicina* and the four okanaganoid genera have been placed in the Tibicinini with *Platypedia* and *Neoplatypedia* placed in their own subfamily or family because of the lack of a functional tymbal organ. I believe evolutionary relationships would be more clearly shown by a new tribal designation. I propose the name Okanaganini for the tribe with Platypedaria for one subtribe containing *Platypedia* and *Neoplatypedia* and Okanaganaria as the other subtribe encompassing the other genera.

It is difficult to establish a time line for these various invasions and dispersals. Cicadas disperse slowly. Although cicadas are capable

of strong flight, females usually oviposit in the general region where they mate. They do not fly away in search of a new, suitable location. Dybas and Lloyd (1962) did observe *M. cassini* and *M. septendecim* colonizing a grove of young ash across a clearing from a more mature habitat where the nymphs emerged. The fossil record is not particularly helpful either. The oldest fossil, *Davispsia bearcreekensis* from Montana, is a wing that dates from the Paleocene (Cooper, 1941). This wing resembles the wing of *Tibicen*. Cooper also considers *Cicada grandiosa* from Miocene beds in Colorado a *Tibicen*. *Lithocicada perita* and *Platypedia primigenia* are from the same Miocene beds. Cooper feels *Lithocicada perita* has an expanded radial cell approaching *Platypedia*. It is probably reasonable to assume that the current genera were present somewhere in North America before the Pleistocene.

Ecology and Distribution

Very little is known of the ecology of North American cicadas other than the genus *Magicicada*, and man has altered their natural habitat considerably. Nevertheless, a few generalizations can be proposed regarding the division of the habitat on an ecological basis. Six genera inhabit the eastern United States and Canada. *Magicicada* is associated with the eastern deciduous forest. It thrives in areas with deep, fertile forest soils. *Neocicada*, on the other hand, is associated with oaks growing in sandy soil. Both are arboreal. *Cicadetta*, with much the same state by state distribution as *Neocicada*, inhabits grasses and weeds. The boreal origins of *Okanagana* have already been mentioned. In the eastern United States with the exception of one species, *Okanagana* is restricted to more northerly states. Ambient temperature and/or temperature fluctuations may

have an effect on the distribution of *Okanagana*. *Tibicen* overlaps the distribution of the other genera and is found throughout the eastern United States and southeastern Canada. Most *Tibicen* are arboreal. The large number of species suggests that each species is associated with a particular habitat or more narrowly defined niche. *Tibicen* are more wary of predators than *Cicadetta* or *Magicalicada*. They are frequently solitary. Some species may escape predator pressure by being distributed sparsely among large numbers of other cicadas. I would not expect to find a large population of *Tibicen* in the same location the year following an emergence of *Magicalicada*. The final eastern genus, *Diceroprocta*, spreads across the southern United States from the Colorado River basin to the Atlantic coast. It is found in the arid southwest and along the Gulf and eastern coastlines. The "salt-marsh" cicada, *Diceroprocta veridifascia*, belongs to this genus. It is not clear what limits the distribution of *Diceroprocta*; however, many species, even in the southwest, have obviously expanded their ranges by following stream or river courses. Food tolerances may be important in their distribution.

Tibicen, *Diceroprocta*, and *Okanagana* are also found in the West, although *Tibicen* does not reach the far western states. *Okanagana* have expanded their western distribution by following mountain chains. Isolated populations of *Okanagana* found on the disjunct mountains of the Southwest attest to their geologic history. *Cornuplura* is associated with oaks in southern Arizona while the distribution of *Cacama* is closely tied to the distribution of *Opuntia*. *Quesada* is an arboreal genus throughout its range. Our knowledge of *Pacarina* is scant, but Juniper may be a factor in its distribution. *Beameria* inhabits dry, rocky grasslands. *Yucca* may also influence *Beameria*'s distribution. Another

grass dwelling genus is *Tibicainoides*, which inhabits the grassy slopes found in western California. *Okanagodes* live in true desert conditions, while *Clidophleps* prefers chaparral. The ecology of *Platypedia* and *Neoplatypedia* is not well known. Some species definitely have adapted to the high northern deserts where they inhabit sagebrush, but others live in streamside vegetation, and still others may inhabit the scrubby elements of a forest understory.

Three major geographic features appear to be major deterrents to cicada dispersal in North America north of Mexico. These are the Rocky Mountains, the Great Plains, and the southwestern deserts.

Another element of cicada ecology is the relationship of cicadas to other organisms in their environment. During large emergences, cicadas may be a primary food source of birds and rodents. They are attacked by predaceous insects and spiders. Some of the insects known to feed on cicadas are mantids, dragonflies, and robberflies. Cicada killer wasps use them to stock their nests as food for developing larvae. Chalcids have been reported as egg parasites, and some Diptera, apparently summoned by the song of the males, parasitize adults. At least three genera are subject to fungus diseases, *Magiccicada*, *Okanagana*, and *Quesada*. In the past man has utilized cicadas as a source of food. I am told the flavor resembles a nut.

Evolution of Higher Taxa

Schaefer (1976) points out that higher taxa, including genera, are the result of real biological phenomena, exemplified by the occupation of a new niche, such as a new behavior, a new locality, or a new food resource. Three examples stand out among the cicadas found north of

Mexico. One is the invasion of the western United States, particularly California, by an *Okanagana* prototype. The release from competition in a favorable climatic habitat with a wide variety of suitable cicada niches resulted in a burst of species and genera which should be regarded as a supergeneric or tribal taxon. In this case the new niche was an unoccupied locale. Undoubtedly the early radiation was specific. As the favorable niches became filled with species of *Okanagana*, those on the fringes adapted to utilize the other unoccupied habitats, such as desert and grass, and new genera were formed.

Somewhere in the radiation of the *Okanagana* ancestor, a new means of communication developed. This resulted eventually in a second supergeneric group represented by *Platypedia* and *Neoplatypedia*. This was the occupation of a new behavioral niche.

Cacama is an example of a group that has arisen because of its ability to utilize a new food resource. The bumble-bee mimicry of body shape and color along with a hovering takeoff and landing pattern may have developed first as examples of protective coloration and behavior. These changes enabled *Cacama* to exploit *Opuntia* as a food resource with the subsequent radiation of species. This is an example of both a new behavioral and a new food niche providing the impetus for the evolution of a new genus.

Evolution and Morphology

It is not possible on the basis of the sixteen North American genera found north of Mexico to construct a complete phylogeny since many of these genera have their "roots" in other geographical regions. It is possible, however, to indicate some characteristics which appear to be

ancestral and some that appear to be derived on the basis of this limited sample.

Structures Associated with the Tymbal Organs

Since the discovery of tymbals and tymbal muscles in other auchenor-
rynchous Homoptera by Ossiannilsson (1949), it has become clear that this
character, long associated only with cicadas, is ancestral. In the
Cicadelloidea and Fulgoroidea, this structure may be associated with
both sexes, or it may be better developed in one or the other sex.
Pringle (1954) attributes the loud call of the male cicada to the develop-
ment of a resonating chamber in the form of a largely hollow, air-filled
abdomen. The origins of this chamber and associated modifications of
internal abdominal structure in nymphal cicadas is not completely re-
solved. Pringle feels it is part of the tracheal system. Female cicadas
were unable to develop a resonating chamber of similar magnitude because
the abdomen is largely occupied by the developing ovaries. Therefore,
the loss of the tymbal organ and associated muscles in female cicadas
is a derived state. The loss of a functional tymbal and associated
muscles in males of two North American genera, *Platypedia* and
Neoplatypedia, is derived. A similar loss has been noted by Boulard
(1973a, 1975a) for the African genera *Ydiella* and *Lamotialna*, and by
Chen (1943) for the Chinese genus *Sinosensa*.

The "chitinous V" is an infolding of the exoskeleton forming the
basal attachment of the tymbal muscles. The tymbal muscles fold around
the arms of the "V." A second strut arises on each side near the base
of the chitinous V. In the genus *Platypleura* these struts or ridges fuse
medially providing a strong additional surface for the attachment of the

muscles (Pringle, 1957). In *Tibicen* these ridges almost meet (Myers, 1928). However, in *Magiicada* the chitinous V is merely "buckled inward" (Pringle, 1957). Pringle considers the condition as found in *Magiicada* primitive, the condition in *Platypleura* the most advanced status, and the structure of *Tibicen* somewhere in between. If the shape of the chitinous V affects the shape of the tymbal muscles as seen in the radiographs (Figure 8), then the modified hexagon seen in *Magiicada* can be considered ancestral or primitive for this character.

Externally the tymbal organ is protected on the dorsal side by a protrusion of the second abdominal tergite in some genera. Other genera completely lack a dorsal tymbal cover, while in some the tymbal organ is only partially protected. These tymbal covers vary in shape and size. They apparently have arisen several times. One group of cicadas has tymbal covers emanating from the metanotum (Boulard, 1976a). It appears, therefore, that a lack of tymbal covers is the ancestral state and the presence of tymbal covers is derived. Similarly shaped covers probably indicate a phylogenetic relationship, as in the case of *Cacama*, *Diceroprocta*, *Tibicen*, and *Cornuplura*, or *Neocicada* and *Cicada*.

The opercula protect the tymbal organs ventrally. While it is not possible to ascertain a primitive or derived state for the opercula from the limited sample represented by the North American genera, two characteristics appear to be important. The opercula may be widely separated or they may meet centrally. They may be short, curving inward, or they may extend longitudinally over the abdomen. Similar opercular development may indicate an evolutionary relationship. Thus, the four okanaganoid genera have short, transverse, rounded, widely separated opercula. *Tibicen* and its derived genera have longitudinal, overlapping

opercula. *Diceroprocta* exhibit both rounded and triangular opercula. The triangular shape may be considered derived. Opercular development does not correspond necessarily with tympanal covering development. *Magiccicada* has well developed opercula but no tymbal covers. A large medial extension of the metathorax is found in *Beameria* between the two opercula. This projection is assumed to be a derived character.

Distant, Metcalf, and others have used tymbal covers, or the lack of them, for major divisions of cicadas. Cicadas can indeed be divided into the two major groups suggested by Metcalf (1963) but not on the basis of tymbal covers. The line between partial tymbal covers and no tymbal covers becomes ambiguous in genera such as *Quesada* and *Beameria*. A more reliable character is the visibility of the metanotum behind the mesonotum, or whether it is obscured centrally by an overlapping mesonotum. This character is more valuable because it can be seen in both male and female specimens. All the genera considered here with tymbal covers have the metanotum obscured centrally. This is, therefore, considered the derived state, and the exposed metanotum is considered the ancestral state.

Male Sexual Characteristics

The male uncus has been used extensively as a taxonomic character in North American Cicadidae. There are two primary characteristics. One is the retraction of the uncus with the pygofer so that in a non-copulatory male the uncus lies in a ventral, unexposed position. This is the general cicada condition and, therefore, is considered ancestral. In the other character state the uncus is elongated, remains exposed, and forms a dorsal shield for the phallus. This condition or structural

arrangement is found in six North American genera, *Okanagana*, *Okanagodes*, *Clidophleps*, *Tibicinoides*, *Platypedia*, and *Neoplatypedia* and is considered derived. The second taxonomic characteristic of the uncus is its shape. The shape is species specific, but a generalized pattern is characteristic of a genus. The generalized shape of the male unci in the genera north of Mexico form a "phenocline" (as defined by Ross, 1974) with *Magicicada* at one end and *Cornuplura* at the other. In *Magicicada* the uncus forms two distinct lateral lobes. These lobes are close together but remain distinct in *Pacarina* and *Cicadetta*. In *Diceroprocta*, *Beameria*, and *Quesada* the two sclerites meet at the base. In the remaining genera they are fused into a single piece. This piece may be notched posteriorly. In *Cornuplura* the notch has expanded to form two separate prongs, but the uncus remains fused at the base. Although the majority of North American genera north of Mexico have a simple, fused uncus, because six of these genera derived from a common ancestor, this is not considered the primitive condition. The ancestral state is more likely closer to *Magicicada* or *Pacarina* with the other states being derived. The simple, exposed uncus was likely derived from a simple retractable uncus.

Accessory Sound Producing Mechanisms

An accessory stridulatory surface on the anterior, lateral portions of the mesonotum is found in four genera of cicadas occurring in North America north of Mexico. Within this region the mechanism reaches its greatest development in the genus *Clidophleps*. This feature was initially described by Jacobi (1907) in the Tettigadinae and has subsequently been used by taxonomists as a key feature at all taxonomic levels from

species to family. It is the only key feature used by Kato (1961) to identify the family Tettigadidae. Boulard (1976a) has subsequently discovered the presence of a "tettigadien" type stridulitrum (Ashlock and Lattin, 1963) in a variety of genera from very diverse geographical areas. He specifically identifies *Tettigades*, *Calliopsida*, *Babras*, and *Chonosia*. Presumably other genera making up the Neotropical subfamily Tettigadinae also exhibit this character. *Zammara* is another Neotropical genus exhibiting mesonotal striations. Among the Palearctic and Nearctic genera mentioned by Boulard (1976a) are *Tibicina*, *Subpsaltria*, and *Clidophleps*. Chen (1943) used these mesonotal striations as the principal distinctive feature of the genus *Subpsaltria* from northwest China. I have verified the presence of this striated surface in *Tibicina haematodes*, the type species of the genus *Tibicina*. It resembles the degree of development in several species of *Okanagana*. *Okanagana*, *Okanagodes*, and *Tibicinoides* may now be added to the list of Nearctic genera possessing a mesonotal stridulatory surface. These three genera obviously are related closely to *Clidophleps*. The discovery of several genera containing mesonotal striations should help elucidate evolutionary relationships. The discovery, however, reduces the value of the present usage of mesonotal striations as a discriminating taxonomic character for some current groups.

Wing fluttering when two cicadas approach each other has been observed for a long time. This was thought to be a purely visual cue, but the rustling also produces a sound. This sound is distinctly audible at night in a forest filled with *Magicicada* (J.E. Heath, 1978, personal communication) or in a darkened room with caged cicadas. In many cicadas a ridge is formed where the forewing rests against the mesonotum. The

sclerotized anal margin of the forewing passing over this ridge could produce a sound. It is easy to see how striations could amplify and specialize this signal. The ridge, itself, is often rough and irregular. The advantage of an accessory sound mechanism is the two way communication between males and females. It is unlikely that such a mechanism would develop independently again and again. It is assumed, therefore, that those genera with similarly positioned striations are somehow loosely related. The accessory stridulatory mechanism is considered a derived character.

The wing tapping of *Platypedia* and *Neoplatypedia* probably also developed as an accessory sound producing mechanism. In this case it was such a successful communication device that the tymbal organ was lost. A similar accessory wing tapping is performed by New Zealand cicadas of the genus *Amphipsalta* (Dugdale and Fleming, 1969). There appears to be no relation between this genus and the two wing tapping genera in North America. Wing tapping is also a derived character.

Boulard (1973b, 1976a) has found other stridulatory surfaces on cicadas. I predict additional methods of sound communication in cicadas will be discovered as investigators become more aware of this phenomenon.

Wings

An analysis of wing venation and structure on a world-wide basis is needed to ascertain ancestral and derived characters. The movement of the nodus from a more or less central position to the edge of the distal third of the wing in *Platypedia* and *Neoplatypedia* is definitely derived as is the expanded radial cell in these two genera and in some *Clidophleps*.

Eight marginal cells in the forewings is an ancestral trait; the seven in *Neoplatypedia* are a derived character.

Summary

Sixteen endemic genera of cicadas are found in North America north of Mexico. Each of these genera is redescribed in a consistent format, thereby facilitating comparisons of common characters. Keys to both males and females are presented, and the known biology of each genus is summarized. The use of soft x-rays to reveal internal characters is a new technique in insect taxonomy. Reasons for maintaining the family Cicadidae as a single taxonomic unit encompassing all cicadas are given.

Five of the genera, *Quesada*, *Pacarina*, *Cacama*, *Diceroprocta*, and *Cornuplura* have entered the geographical area north of Mexico from the south. Two genera, *Tibicen* and *Cicadetta*, are cosmopolitan in distribution, apparently entering North America across a Bering land bridge. The remaining genera have evolved in place. Six of these, *Okanagana*, *Okanagodes*, *Clidophleps*, *Tibicinoides*, *Platypedia*, and *Neoplatypedia*, appear to have shared a common ancestor. A new tribe, Okanaganini, is proposed for these genera. This tribe has two subtribes Okanaganaria and Platypedaria.

The following revisions are recognized: *Okanagana rubrocaudata*, a former variety of *O. bella* is raised to species rank; *Okanagana rotundifrons* is transferred to the genus *Clidophleps*; *Tibicinoides hesperia* is moved back to *Okanagana*; *Cicada chisos* is placed in the genus *Neocicada*. Two species of *Tibicen*, *T. variegata* and *T. ocreoptera*, are removed from the list of North American cicadas.

Current distributions are related in this paper to origins, dispersal patterns, habitat, and past geologic history. Two major radiations of genera, one allied to *Tibicen* and the other to *Okanagana*, have occurred on the North American continent.

The evolution of new genera can result from the exploitation of new niches. Three examples are given for North American genera. The evolutionary position of each of several primary characters is discussed.

Cicadas are large, loud, obvious insects found in practically all habitats in North America. It is surprising that only the genus *Magicicada* has been well studied. Very little is known about the other genera found in the Nearctic region north of Mexico. It is hoped that this taxonomic work will lay the foundation for further studies on the biology of North American Cicadidae.

LITERATURE CITED

- Alexander, Richard D.
unpublished. Key to species of cicadas occurring in the United States
east of the Mississippi River, 3rd revision. 6 pp.
- Alexander, Richard D. and Thomas E. Moore
1962. The evolutionary relationships of 17-year and 13-year cicadas,
and three new species (Homoptera, Cicadidae, *Magistercicada*).
Misc. Publ. Mus. Zool., Univ. Michigan, 121:1-59.
- Alexander, Richard D., Ann E. Pace, and Daniel Otte
1972. The singing insects of Michigan. Great Lakes Ent. 5(2):33-69.
- Amyot, Charles Jean Baptiste
1847. Rhynchotes. Ordre deuxième. Homoptères. Homoptera. Latr.
Entomologie Française. Rhynchotes. Méthode Mononymique.
Soc. Ent. de France, Ann. (2)5:143-238.
- Amyot, C.J.B. and J.G.S. Serville
1843. Histoire Naturelle des Insectes. Hemiptères 1843:i-lxxvi;
1-676.
- Aristoteles
1908. The works of Aristotle translated into English by D'Arcy
Wentworth Thompson. Oxford, Clarendon Press, 1908, 7 vol.
- Ashlock, Peter D. and John D. Lattin
1963. Stridulatory mechanisms in the Lygaeidae, with a new American
genus of Orsillinae (Hemiptera:Heteroptera). Ann. Ent. Soc.
Amer. 56:693-703.
- Ashmead, William H.
1888. A generic synopsis of the Cicadidae. Ent. Amer. 4:140-141.
- Beamer, L.D. and R.H. Beamer
1930. Biological notes on some Western Cicadas. N.Y. Ent. Soc.
Jour. 38:291-305.
- Beamer, Raymond Hill
1928. Studies on the biology of Kansas Cicadidae. Kans. Univ.
Sci. Bul. 18:155-263.
- Borror, Donald Joyce and D.M. DeLong
1971. An introduction to the study of insects, 3rd ed. 1971:1-812.

Borror, Donald Joyce and Richard E. White

1970. A field guide to the insects of America north of Mexico.
1970:v-xi, 1-404.

Boulard, Michel

- 1972a. Les Cigales de la République Centrafricaine; I. les espèces forestières. Cahiers de La Maboke, 1971, IX(2):133-161.

Boulard, Michel

- 1972b. Contribution à l'étude de la faune Cicadéenne de l'Angola (Insecta-Auchenorrhyncha). Publçoes Cult. Co. Diam. Ang., Lisboa 84:151-178.

Boulard, Michel

- 1973a. Les Ydiellinae, sous-famille nouvelle de Cigales Platypediidae. Ann. Soc. Ent. France (N.S.) 9(4):841-852.

Boulard, Michel

- 1973b. Un type nouveau d'appareil stridulant chez les Cigales. C.R. Acad. Sci. Paris, 877 ser. D:1487-1489.

Boulard, Michel

- 1974a. Sur une Cigale africaine nouvelle présentant une adaptation melanique très probablement liée aux feux de brousse. Ann. Soc. Ent. France 10(2):381-393.

Boulard, Michel

- 1974b. *Spoerryana llewelyni*, n.g., n. sp., une remarquable cigale d'Afrique orientale [Hom. Cicadoidea]. Ann. Soc. Ent. France 10(3):729-744.

Boulard, Michel

- 1975a. Sur une deuxième Cigale africaine dépourvue d'appareil sonore [Homoptera]. Bull. IFAN 37, A(3):629-636.

Boulard, Michel

- 1975b. *Iruana rougeoti* n. sp. interessante Cigale éthiopienne. Bull. Soc. Ent. France 80:176-179.

Boulard, Michel

- 1975c. Les Cigales des Savanes centrafricaines. Systématique, notes biologiques et biogéographiques. Bull. Mus. Natn. Hist. Nat. Paris, 3^e Ser. 315, Zool. 222:869-928.

Boulard, Michel

- 1976a. Un type nouveau d'appareil stridulant accessoire pour les Cicadoidea; Révision de la classification supérieure de la superfamille [Hom.]. Jour. Nat. Hist. 10(4):399-407.

Boulard, Michel

- 1976b. Cigalles nouvelles de Côte d'Ivoire et de Guinée. Bull. IFAN 38, A(1):112-123.

- Brown, Leland R. and Clark O. Eads
1967. Insects affecting the elm tree in Southern California. Pest Control Operators News 27(2):20-21.
- Bullough, W.S.
1950. Practical invertebrate anatomy 1950:v-xi, 1-463.
- Chen, Kia-ziang
1943. New genera and species of Chinese Cicadas with synonymical and nomenclatorial notes. N.Y. Ent. Soc. Jour. 51:19-52.
- Cooper, Kenneth W.
1941. *Davisia bearcreekensis* Cooper, a new cicada from the Paleocene, with a brief review of the fossil Cicadidae. Amer. Jour. Sic. 239:286-304.
- Cranford, Jack A.
1978. Personal communication.
- Darlington, Philip J.
1957. Zoogeography: The geographical distribution of animals 1957: vii-xi, 1-675.
- Davis, William Thompson
1915. New species of cicadas from California and Utah. N.Y. Ent. Soc. Jour. 23:11-27.
- Davis, William Thompson
1916. Notes on cicadas from the United States with descriptions of several new species. N.Y. Ent. Soc. Jour. 24:42-64.
- Davis, William Thompson
1917. Sonoran cicadas collected by Harry H. Knight, Dr. Joseph Bequaert and others, with descriptions of new species. N.Y. Ent. Soc. Jour. 25:203-215.
- Davis, William Thompson
1918. Mississippi cicadas, with a key to the species of the South-eastern United States. N.Y. Ent. Soc. Jour. 26:141-155.
- Davis, William Thompson
1919a. Cicadas of the genera *Okanagana*, *Tibicainoides* and *Okanagodes*, with descriptions of several new species. N.Y. Ent. Soc. Jour. 27:179-223.
- Davis, William Thompson
1919b. Cicadas of the genus *Cacama*, with descriptions of several new species. N.Y. Ent. Soc. Jour. 27:68-79.
- Davis, William Thompson
1920. North American cicadas belonging to the genera *Platypedia* and *Melampsalta*. N.Y. Ent. Soc. Jour. 28:95-145.

Davis, William Thompson

- 1921a. North American Cicadas. A collection of papers published in the Journal of the New York Entomological Society from 1915 to 1921. Staten Island, N.Y., 1921. Vol. 1 (each article paged separately).

Davis, William Thompson

- 1921b. An annotated list of the cicadas of Colorado with description of a new species. N.Y. Ent. Soc. Jour. 29:43-57.

Davis, William Thompson

1924. Cicada-killing wasps and flies. N.Y. Ent. Soc. Jour. 32:113.

Davis, William Thompson

1925. *Cicada tibicen*, a South American species, with records and descriptions of North American Cicadas. N.Y. Ent. Soc. Jour. 33:35-51.

Davis, William Thompson

1927. New cicadas from the Western United States with notes on several other species. N.Y. Ent. Soc. Jour. 35:373-389.

Davis, William Thompson

1928. Cicadas belonging to the genus *Diceroprocta* with descriptions of new species. N.Y. Ent. Soc. Jour. 36:439-459.

Davis, William Thompson

1930. The distribution of cicadas in the United States with descriptions of new species. N.Y. Ent. Soc. Jour. 38: 53-72.

Davis, William Thompson

1932. Additional records of North American cicadas with descriptions of new species. N.Y. Ent. Soc. Jour. 40:241-264.

Davis, William Thompson

1934. New cicadas from North America. N.Y. Ent. Soc. Jour. 42:37-62.

Davis, William Thompson

1936. A remarkable cicada from Mexico and other North American species. N.Y. Ent. Soc. Jour. 44:101-122.

Davis, William Thompson

1938. New North American cicadas with notes on described species. N.Y. Ent. Soc. Jour. 46:291-310.

Davis, William Thompson

1942. American Cicadas. A collection of papers published, with a single exception, in the Journal of the New York Entomological Society. Volume 2 from 1922 to 1942. Staten Island, N.Y., 1942. Vol. 2 (each article paged separately).

Davis, William Thompson

1943. Two ways of song communication among our North American cicadas. N.Y. Ent. Soc. Jour. 51:185-190.

Davis, William Thompson

1944. The remarkable distribution of an American Cicada; a new genus, and other Cicada notes. N.Y. Ent. Soc. Jour. 52: 213-222.

Distant, William Lucas

1881. Rhynchota:Homoptera. Biologia Centrali-Americana; contributions to the knowledge of the fauna and flora of Mexico and Central America 1:1-16.

Distant, William Lucas

1889. A monograph of Oriental Cicadidae, Parts 1 and 2:1-48.

Distant, William Lucas

- 1904a. Rhynchotal notes. XXVI. Ann. and Mag. Nat. Hist. (7)14: 293-303.

Distant, William Lucas

- 1904b. Rhynchotal notes. XXVIII. Ann. and Mag. Nat. Hist. (7)15:304-319.

Distant, William Lucas

- 1905a. Rhynchotal notes. XXX. Ann. and Mag. Nat. Hist. (7)15: 304-319.

Distant, William Lucas

- 1905b. Rhynchotal notes. XXXII. Ann. and Mag. Nat. Hist. (7)15: 478-486.

Distant, William Lucas

- 1905c. Rhynchotal notes. XXXIII. Ann. and Mag. Nat. Hist. (7)16: 22-35.

Distant, William Lucas

- 1905d. Rhynchotal notes. XXXIII. Ann. and Mag. Nat. Hist. (7)16: 22-35.

Distant, William Lucas

1906. A synonymic catalog of Homoptera. Part 1. Cicadidae 1906:1-207.

Distant, William Lucas

1912. Homoptera Fam. Cicadidae, Subfam. Cicadinae. Gen. Insect. 142:1-64.

Distant, William Lucas

1914. On a few undescribed Cicadidae from California. Ann. and Mag. Nat. Hist. (8)14:165-167.

- Dugdale, J.S. and C.A. Fleming
1969. Two New Zealand Cicadas collected on Cook's Endeavor voyage with description of a new genus. New Zealand Jour. Sci. 12:929-957.
- DuPorte, E. Melville
1962. The anterior tentorial arms in instecs and their significance in interpreting the morphology of the cranium of the Cicadas. Can. Jour. Zool. 40:137-144.
- DuPorte, E. Melville
1977. Manual of Insect Morphology 1977:vii-xi, 1-224.
- Dybas, Henry S. and D. Dwight Davis
1962. A population census of seventeen-year periodical cicadas (Homoptera:Cicadidae:Magicicada). Ecology 43:432-444.
- Dybas, Henry S. and Monte Lloyd
1962. Isolation by habitat in two synchronized species of periodical cicadas (Homoptera:Cicadidae: *Magicicada*). Ecology 43:44-459.
- Edwards, James
1896. The Hemiptera-Homoptera (Cicadina and Psyllina) of the British Islands 1896:vi-xii, 1-271.
- Essig, Edward Oliver
1942. College entomology 1942:i-vi, 1-900.
- Fabre, J.H.
1897. La fable de la cigale et la fourmi. Souvenirs entomologiques. Etudes sur l'instinct et les moeurs des insects. Cinquieme série 1897:1-355.
- Fabricius, Johann Christian
1775. Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus 1775:1-816.
- Fautin, Reed W.
1946. Biotic communities of the northern desert shrub biome in Western Utah. Ecol. Monog. 16:253-310.
- Froeschner, Richard C.
1952. A synopsis of the Cicadidae of Missouri (Homoptera). N.Y. Ent. Soc. Jour. 60:1-13.
- Handlirsch, Anton
1925. Systematische Übersicht, in Schröder, Christoph, Handbuch der Entomologie 3:1102-1126.
- Heath, James Edward
1967. Temperature responses of the periodical "17-year" Cicada, *Magicicada cassini* (Homoptera, Cicadidae). Amer. Midland Nat. 77:64-76.

- Heath, James Edward
1968. Thermal synchronization of emergence in periodical "17-year" cicadas (Homoptera, Cicadidae, *Magicicada*). Amer. Midland Nat. 80(2):440-447.
- Heath, James Edward
1978. Personal communication.
- Heath, James Edward and P.A. Adams
1969. Temperature regulation and heat production in insects. In G.S. Kerkut, ed. Experiments in physiology and biochemistry. 1969. 2:275-294.
- Heath, James Edward, J.L. Hanegan, P.J. Wilkin, and M.S. Heath
1971. Adaptation of the thermal responses of insects. Am. Zool. 11:145-156.
- Heath, James Edward and Peter Julian Wilkin
1970. Temperature responses of the desert cicada, *Diceroprocta apache* (Homoptera, Cicadidae). Physiol. Zool. 43:145-154.
- Heath, James Edward, Peter Julian Wilkin, and Maxine Shoemaker Heath
1972. Temperature responses of the Cactus Dodger *Cacama valvata* (Homoptera, Cicadidae). Physiol. Zool. 45(3):238-246.
- Heath, Maxine Shoemaker
1972. Temperature requirements of the Cicada, *Okanagana striatipes beameri*: A study from Flagstaff, Arizona. Plateau 45: 31-40.
- Heath, Maxine Shoemaker
1976. Arizona cicadas of the genus *Okanagana*. M.S. Thesis. Univ. Florida. 1976:iii-vi, 1-177.
- International Commission on Zoological Nomenclature
1961. International code of zoological nomenclature adopted by the XV international congress of zoology 1961:ii-xvii, 1-176.
- Jacobi, Arnold
1907. Ein Schrillapparat bei Singcicaden. Zool. Anz. 32:67-61.
- Kato, Masayo
1932. Monograph of Cicadidae 1932:1-450.
- Kato, Masayo
1961. Cicadidae. Fauna Japonica 1961:v-xiv, 1-72.
- Kolenati, Friedrich
1857. Meletemata Entomologica Fasc. VII. Soc. Nat. de Moscou, Sect. Biol. Bul. 30:399-444.
- Kolner, Martin
1976. Personal communication.

Kramer, Sol

1950. The morphology and phylogeny of Auchenorhynchous Homoptera (Insecta). Ill. Biol. Monog. 20(4):1-109.

de Lamarck, Jean Baptiste Pierre Antoine de Monet

1801. Système des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres de ces animaux; présentant leurs caractères essentiels et leur distribution, d'après la considération de leurs rapports naturels et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Hist. Naturelle, parmi leurs dépouilles conservées; précédé du discours d'ouverture du cours de zoologie donné dans le Muséum National d'Histoire Naturelle l'an de la République 1801:i-viii, 1-432.

Latreille, Pierre André

1802. Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs Sociétés savantes 3:i-xii, 13-467.

Latreille, Pierre André

1825. Familles naturelles du règne animal, exposée succinctement et dans un ordre analytique, avec l'indication de leurs genres 1825:1-570.

Lawson, Paul Bowen

1920. The Cicadidae of Kansas. Kans. Univ. Sci. Bul. 12:309-376.

Leach, William Elford

1832. Entomology, in Brewster, David, the Edinburgh Encyclopaedia. 1st American edition. Vol. 8:646-714 (reprint of Leach, 1815).

Linné, Carl

1758. II. Hemiptera. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata 1:1-824.

Lloyd, Monte and Henry S. Dybas

- 1966a. The periodical cicada problem. I. Population ecology. Evolution 20:133-149.

Lloyd, Monte and Henry S. Dybas

- 1966b. The periodical cicada problem. II. Evolution. Evolution 20(4):465-505.

Mead, Frank

1978. Personal communication.

Merriam, C. Hart

1890. Results of a biological survey of the San Francisco mountain region and desert of the Little Colorado, Arizona. North American Fauna, No. 3. Wash. U.S. Govt. Print. Off. 1-136 p.

- Metcalf, Zeno Payne
1946. The center of origin theory. Elisha Mitchell Sci. Soc. Jour. 62:149-175.
- Metcalf, Zeno Payne
1951. Phylogeny of the Homoptera Auchenorrhyncha. Comm. Biol. 12(1):1-14.
- Metcalf, Zeno Payne
1962. A bibliography of the Cicadoidea (Homoptera:Auchenorrhyncha) 1962:iii-iv, 1-229.
- Metcalf, Zeno Payne
1963. General catalog of the Homoptera, Fascicle VIII, Cicadoidea. Raleigh, N.C. 1963:4v.
- Moore, Thomas E.
1966. The Cicadas of Michigan (Homoptera:Cicadidae). Papers of the Mich. Acad. of Sci., Arts, and Letters 51:75-96.
- Moore, Thomas E.
1975. Personal communication.
- Moore, Thomas E.
1977. Personal communication.
- Moore, Thomas E. and John W. Kausch
1975. 17-Year Cicadas (*Magicicada septendecim*). 1975:Film, 16 mm. 29 min. color, sound.
- Myers, John G.
1928. The morphology of the Cicadidae (Homoptera). [London] Zool. Soc. Proc. 1928:365-472.
- Myers, John G.
1929. Insect singers, a natural history of the Cicadas 1929:i-xix, 1-304.
- Ortega, Juan Gomez-Menor
1957. Monografía de cicádidos (Homoptera) de España 1957:1-87.
- Ossiannilsson, Frej
1949. Insect drummers. A study on the morphology and function of the sound-producing organ of Swedish Homoptera Auchenorrhyncha with notes on their sound production. Opuscula Entomologica Sup. 10:1-145.
- Pringle, J.W.S.
1954. A physiological analysis of cicada song. Jour. Exp. Biol. 31:525-560.

- Pringle, J.W.S.
1957. The structure and evolution of the organs of sound-production in cicadas. Proc. Linn. Soc. London 167:144-159.
- Reamur
1740. Mémoires pour servir à l'Histoire des Insectes. Quatrième Mémoire. Sur les Cigales; et sur quelques mouches de genres approchant du leur. Tom. V:145-206. Paris.
- Ross, Herbert H.
1974. Biological systematics 1974:1-345.
- Samouelle, George
1819. The entomologist's useful compendium; or an introduction to the knowledge of British insects, comprising the best means of obtaining and preserving them, and a description of the apparatus generally used; together with the genera of Linné and the modern method of arranging the classes Crustacea, Myriapoda, spiders, mites and insects from their affinities and structures according to the views of Dr. Leach 1819: 1-496.
- Schaefer, C.W.
1976. The reality of the higher taxonomic categories. 2. Zool. Syst. Evolut.-forsch. 14(1976):1-10.
- Simons, John Norton
1953. New California cicadas with taxonomic notes on other species (Homoptera:Cicadidae). Pan-Pacific Ent. 30:191-198.
- Simons, John Norton
1954. The cicadas of California Homoptera:Cicadidae. Calif. Ins. Surv. Bul. 2:153-192.
- Smith, John B. and John A. Grossbeck
1907. Studies in certain Cicada species. Ent. News 1907:116-129.
- Snodgrass, Robert Evans
1935. Principles of Insect Morphology 1935:v-ix, 1-667.
- Soper, R.S.
1963. *Massospora levispora*, a new species of fungus pathogenic to the cicada, *Okanagana rimosa*. Can. J. Bot. 41:875-878.
- Soper, R.S., G.E. Shewell, and D. Tyrrell
1976. *Colcondomyia auditrix* nov. sp. (Diptera:Sarcophagidae), a parasite which is attracted by the mating song of its host, *Okanagana rimosa* (Homoptera:Cicadidae). Can. Ent. 108:61-68.
- Stål, Carl
1870. Hemiptera insularum Philippinarum. Bidrag till Philippinska öarnes Hemipter-fauna. Öfversigt of Svenska Vetensk. Akad. Förhandl. 27:607-776.

- Torre-Bueno, J.R. de la
1962. A glossary of entomology. Smith's "An explanation of terms used in entomology" completely revised and rewritten by J.R. de la Torre-Bueno and Supplement A edited by George S. Tulloch. Brooklyn, N.Y., Brooklyn Entomological Soc. 1962: 1-336, 1-36.
- Tuxen, S.L. ed.
1970. Taxonomist's glossary of genitalia in insects 1970:1-359.
- Uhler, Philip Reese
1888a. Preliminary survey of the Cicadaea of the United States. Ent. Americana 4:21-23.
- Uhler, Philip Reese
1888b. Preliminary survey of the Cicadaea of the United States, Antilles, and Mexico. Ent. Americana 4:81-85.
- Uhler, Philip Reese
1892. Preliminary survey of the Cicadidae of the of the United States, Antilles and Mexico. Trans. Maryland Acad. Science 1892:147-175.
- Van Duzee, Edward Payson
1912. Hemipterological gleanings. Buffalo Soc. Nat. Sci. Bul. 10:477-512.
- Van Duzee, Edward Payson
1914. Nomenclatural and critical notes on Hemiptera. Canad. Ent. 46:377-389.
- Van Duzee, Edward Payson
1915. A preliminary review of the West Coast Cicadidae. N.Y. Ent. Soc. Jour. 23:21-44.
- Van Duzee, Edward Payson
1916. Check list of Hemiptera (excepting the Aphididae, Aleurodidae and Coccidae) of America north of Mexico 1916:i-xi, 1-111.
- Van Duzee, Edward Payson
1917. Catalogue of the Hemiptera of America north of Mexico excepting the Aphididae, Coccidae and Aleurodidae. Calif. Agr. Expt. Sta. Ent. Techn. Bul. 2:i-xiv, 1-902.
- Vasvary, Louis M.
1966. Musculature and nervous system of the thorax, of the sound mechanism, and of a typical pregenital abdominal segment of the male of the annual Cicada, *Tibicen chloromera* (Walker) (Homoptera:Cicadidae). N.Y. Ent. Soc. Jour. 74:2-55.
- Walker, Thomas J.
1976. Personal communication.

Westwood, John Obadiah

1840. An introduction to the modern classification of insects; founded on the natural habits and corresponding organization of the different families. 2 vol.

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