

10

Biodiversity of Orthoptera*Hojun Song**Department of Entomology, Texas A&M University, College Station, Texas, USA*

With more than 26,000 extant species, the Orthoptera are the most diverse order among the polyneopteran insect lineages (Grimaldi and Engel 2005, Eades et al. 2015). The order includes familiar singing insects, such as crickets and katydids, as well as often-devastating pests, such as grasshoppers and locusts (Gangwere et al. 1997). Orthopteran insects have diversified into numerous lineages that occupy every conceivable terrestrial habitat outside the polar regions and play integral roles in their ecosystems (Uvarov 1966, Kevan 1982). Such diversity in form and function has attracted researchers who use these insects as model systems for studying anatomy, bioacoustics, chemical ecology, evolutionary ecology, life-history traits, neurobiology, physiology, and speciation (Uvarov 1966, 1977; Baccetti 1987a; Chapman and Joern 1990; Gangwere et al. 1997; Pener and Simpson 2009).

In this chapter, I present a general overview of the systematics of the Orthoptera, as well as diversity in form and function in the order, and provide a brief synopsis of each of the known families. A number of excellent reviews have been informative in compiling this chapter: Uvarov (1966, 1977) and Chapman and Joern (1990) on general biology, especially of grasshoppers; and Kevan (1982), Vickery (1997), and Grimaldi and Engel (2005) on taxonomic diversity.

10.1 Taxonomic Classification and Phylogeny

The monophyly of the Orthoptera has been supported by morphological and molecular data (Chopard 1949, Sharov 1968, Kevan 1982, Flook et al. 1999). Among many morphological and physiological characters that define the Orthoptera (Chopard 1920; Slifer 1939; Judd 1947; Ragge 1955; Dirsh 1957, 1973; Blackith and Blackith 1968; Baccetti 1987b; Eades 2000), the presence of a cryptopleuron, developed from the lateral extension of the pronotum over the pleural sclerites (Grimaldi and Engel 2005), and the jumping hind legs are major diagnostic characters (Kevan 1982). Molecular phylogenetic studies based on ribosomal RNA genes and mitochondrial genes have supported the monophyly of the order (Flook et al. 1999), and, most recently, a phylogenetic study based on complete mitochondrial genome data and four nuclear genes (Song et al. 2015) also strongly supports monophyly. However, the phylogenetic position of the Orthoptera within the Polyneoptera is still not fully resolved. Based on extensive fossil data, the Paleozoic Orthoptera were thought to be closely related to the Phasmatodea (Sharov 1968). Wheeler et al. (2001) presented a cladistics analysis based on morphology and ribosomal RNA data and also found a

sister relationship between the Orthoptera and Phasmatodea. However, the most recent phylogenomic study by Misof et al. (2014) found the Orthoptera to be sister to a clade consisting of the Mantophasmatodea, Grylloblattodea, Embiodea, Phasmatodea, and Dictyoptera. A more comprehensive phylogenetic study of the Polyneoptera is required to fully resolve the position of the Orthoptera relative to other members.

The taxonomic classification of the Orthoptera has a tumultuous and complex history, as different taxonomists proposed conflicting classification schemes based on different character sets, such as fossil wing venation (Zeuner 1942, Sharov 1968, Gorochov 1995a), internal organs (Slifer 1939, Judd 1947, Dirsh 1957, Baccetti 1987b), external morphology (Blackith and Blackith 1968), and the male phallic complex (Chopard 1920, Ander 1939, Roberts 1941, Dirsh 1973, Amédégnato 1974, Eades 2000). Based on the early application of numerical taxonomy, Blackith and Blackith (1968) suggested that the phenetic differences between the Ensifera and Caelifera were greater than among other orthopteroid (polyneopteran) orders and raised the possibility of treating them as two distinct orders. Kevan (1973) went one step further and elevated the Ensifera as a separate order and called it the Grylloptera, while redefining the Caelifera as Orthoptera *sensu stricto*. In 1975, the higher classification of the Orthoptera reached its most chaotic state when Dirsh (1975) proposed a superorder Orthopteroidea with 10 new orders. However, most taxonomists today agree that the Orthoptera should be treated as a single order.

These different classification schemes were pre-cladistic and mostly based on the taxonomists' interpretations of the characters and relationships. From the late 1990s, a series of modern cladistic studies using morphological or molecular data were published, which objectively tested the previous classification schemes (Gwynne 1995; Flook and Rowell 1997; Chapco et al. 1999, 2001; Flook et al. 1999, 2000; Desutter-Grandcolas 2003; Jost and Shaw 2006; Matt et al. 2008; Legendre et al. 2010; Zhou et al. 2010; Chintauan-Marquier et al. 2011; Leavitt et al.

2013; Mugleston et al. 2013; Zhang et al. 2013; Chintauan-Marquier et al. 2016; Song et al. 2015). The most notable study was by Flook et al. (1999), who produced the first modern phylogeny of the Orthoptera, based on 31 in-group taxa representing all major lineages and three ribosomal loci; they also reclassified some superfamilies. In 2015, Song et al. published a large-scale molecular phylogeny based on complete mitochondrial genome data and four nuclear loci to thoroughly test the previous classification schemes, and proposed a new phylogeny-based natural classification, which is adopted in this chapter. According to this new classification scheme, the Orthoptera consists of two monophyletic suborders, the Ensifera and Caelifera. The Ensifera consist of two infraorders, the Gryllidea and Tettigoniidea, and are characterized by long, flagellate antennae that are often longer than the length of the body, and a sword-like or needle-like female ovipositor. The Gryllidea include the superfamilies Grylloidea and Gryllotalpoidea, whereas the Tettigoniidea include the Schizodactyloidea, Rhaphidophoroidea, Hagloidea, Stenopelmatoidea, and Tettigoniidea. Collectively, the Ensifera include about 14,000 described species. The Caelifera also consist of two infraorders, the Tridactylidea and Acrididea, and are characterized by shorter antennae and a female ovipositor with only two valvular pairs. The Tridactylidea include the Tridactyloidea, whereas the Acrididea include eight superfamilies: Tegtrigoidea, Eumastacoidea, Proscopioidea, Tanaoceroidea, Pneumoroidea, Trigonopterygoidea, Pyrgomorphoidea, and Acridoidea. The Caelifera include more than 11,000 described species. The higher-level relationships among different superfamilies in the Orthoptera are now well resolved (Fig. 10.1).

10.2 Diversity and Distribution

When establishing a robust classification scheme, a comprehensive synonymic catalog is

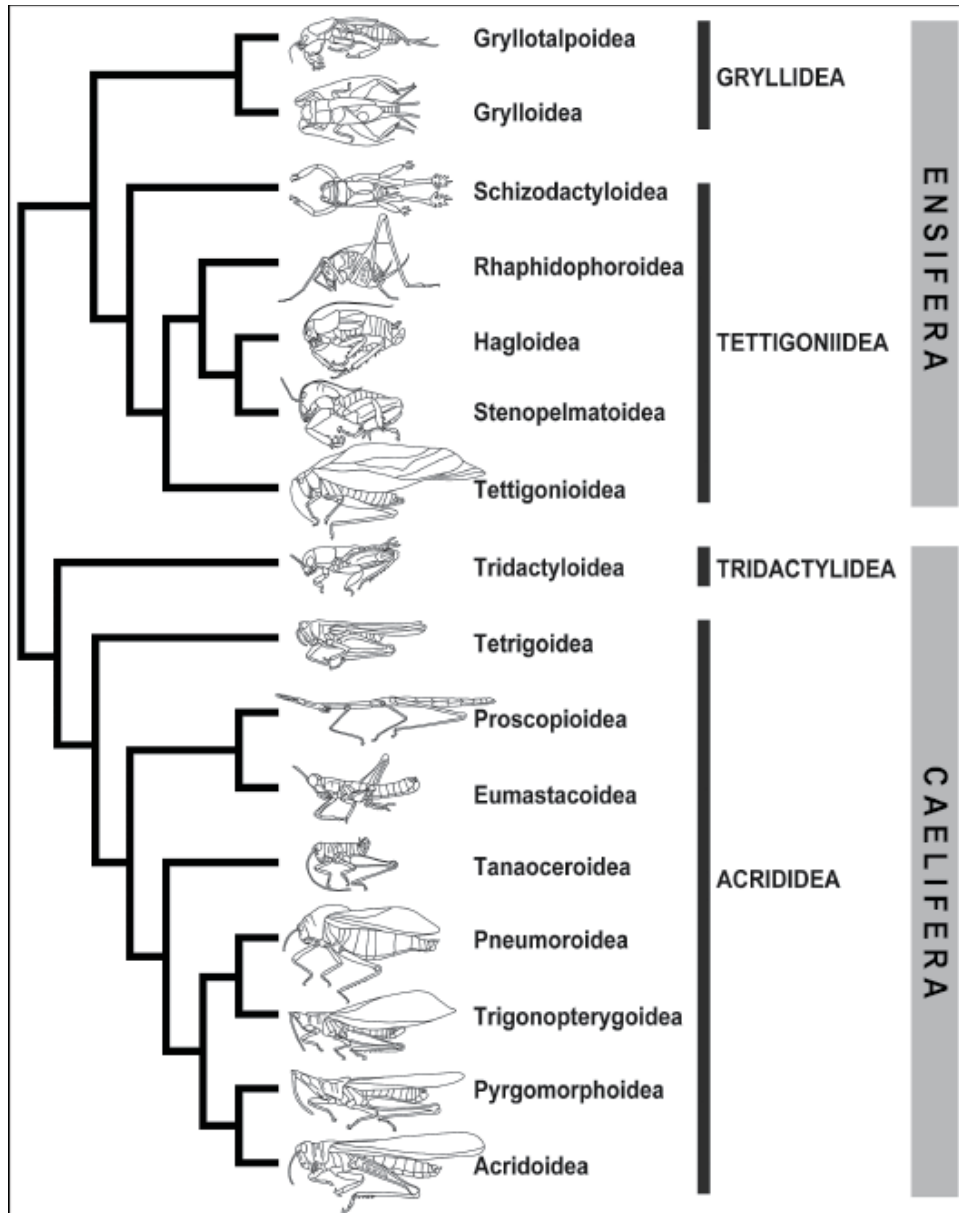


Figure 10.1 Phylogenetic relationships among major superfamilies of Orthoptera. The topology is based on that of Song et al. (2015).

an invaluable tool. For the Orthoptera, the Orthoptera Species File (OSF) (Eades et al. 2015) is the most definitive catalog available today. The concept of the OSF, a collection of all taxonomic and synonymic information for the Orthoptera, was developed by Daniel Otte, one of the most important and prolific orthopteran taxonomists of the 20th century (Song 2010). Otte published the first paper volume of OSF in 1994 to cover

the Grylloidea, and, subsequently, a total of eight volumes to cover all the Orthoptera were published by 2000. In 1997, Otte and Piotr Naskrecki, an expert in Tettigoniidae systematics, developed the first online version of the OSF. Then in 2001, David Eades, an expert in Acrididae systematics, joined and further developed it using a relational database, which ultimately led to the current version of the OSF – available to the

public at <http://orthoptera.speciesfile.org/>. For all known species of orthopterans, the OSF online contains as complete as possible synonymic and taxonomic information, citations and references, images and sound recordings, maps, specimen collecting records, and identification keys. As of March 2015, the OSF online contains full information on 26,690 valid species (including fossils), 43,970 scientific names, 192,500 citations leading to 13,000 references, 81,300 images, 1300 sound recordings, 89,500 specimen records, and keys to 2800 taxa. The underlying software for the OSF is the Species File Software (SFS), which relies on a powerful relational model database server (Microsoft SQL Server). The contents are continuously being updated as taxonomic studies are published.

Because of the abundance of data in the OSF, it can be used to perform meta-analyses. For example, Song (2010) used OSF data to describe the trends in descriptive taxonomy in grasshopper systematics over the past 250 years and to identify geographical regions that needed urgent taxonomic expertise. Because the OSF contains information regarding the geographical distribution of every orthopteran species described to date, it is possible to estimate how many species have been described from each geographical region. It is important to realize the limitation of this type of analysis, because it will be based on some inherent assumptions. First, it assumes that sampling efforts have been similar across geographical regions. This assumption is certainly not true because regions such as central Africa and southeastern Asia have not been thoroughly explored relative to North America. Second, large areas generally harbor more species than do small areas, and this analysis does not take the size of the region into account. Third, regions near the tropics naturally have more productivity and can harbor more species, which can bias the analysis. Even with these caveats, however, this analysis reveals patterns about the species richness of the Orthoptera.

The OSF currently identifies a total of nine geographic regions: Africa, North America

(including Mexico), Central and South America, Temperate Asia, Tropical Asia, Australia, Europe, Pacific, and Antarctica. In each region there are additional layers of finer details, such as countries and states. For instance, using a complex search, one can find how many species have been recorded from North America or the North Central United States (10 US states). When such an analysis is performed for the Orthoptera and each of the suborders, patterns begin to emerge (Fig. 10.2). When the Orthoptera as a whole are considered, Central and South America harbor 22% of the entire known diversity, followed by Tropical Asia (21%), Africa (20%), and Temperate Asia (17%). For Central and South America, the bulk of recorded diversity is from Brazil and western South America, which includes Bolivia, Colombia, Ecuador, and Peru. North America has comparatively poor species richness, representing only 8% of the described species, despite the fact that the size of the continent is comparable to other, more species-rich regions. Ironically, only 3% of the entire diversity is found in Europe, where most influential orthopteran taxonomists were based in the 18th to 20th centuries (Song 2010). Perhaps, the paucity of orthopteran diversity in Europe prompted those early taxonomists to explore other regions.

A slightly different pattern emerges when the same analysis is conducted but the search is constrained to the suborders. For the Ensifera, the most species-rich region is Tropical Asia (25%) followed by Central and South America (24%). Specifically, the highest species richness of the Ensifera is found in the tropical regions. The most diverse lineages in the Ensifera are the Grylloidea and Tettigonioidea, which seem to have diversified in the early Mesozoic when the global climate was hot and humid (Song et al. 2015). Possibly, the ecological and physiological traits that evolved in the ancestral ensiferans in the tropical climate resulted in exaptations that allowed these insects to thrive in modern tropical regions. For the Caelifera, the most species-rich region is Africa (25%) followed by Temperate Asia (23%). The most diverse lineage within the

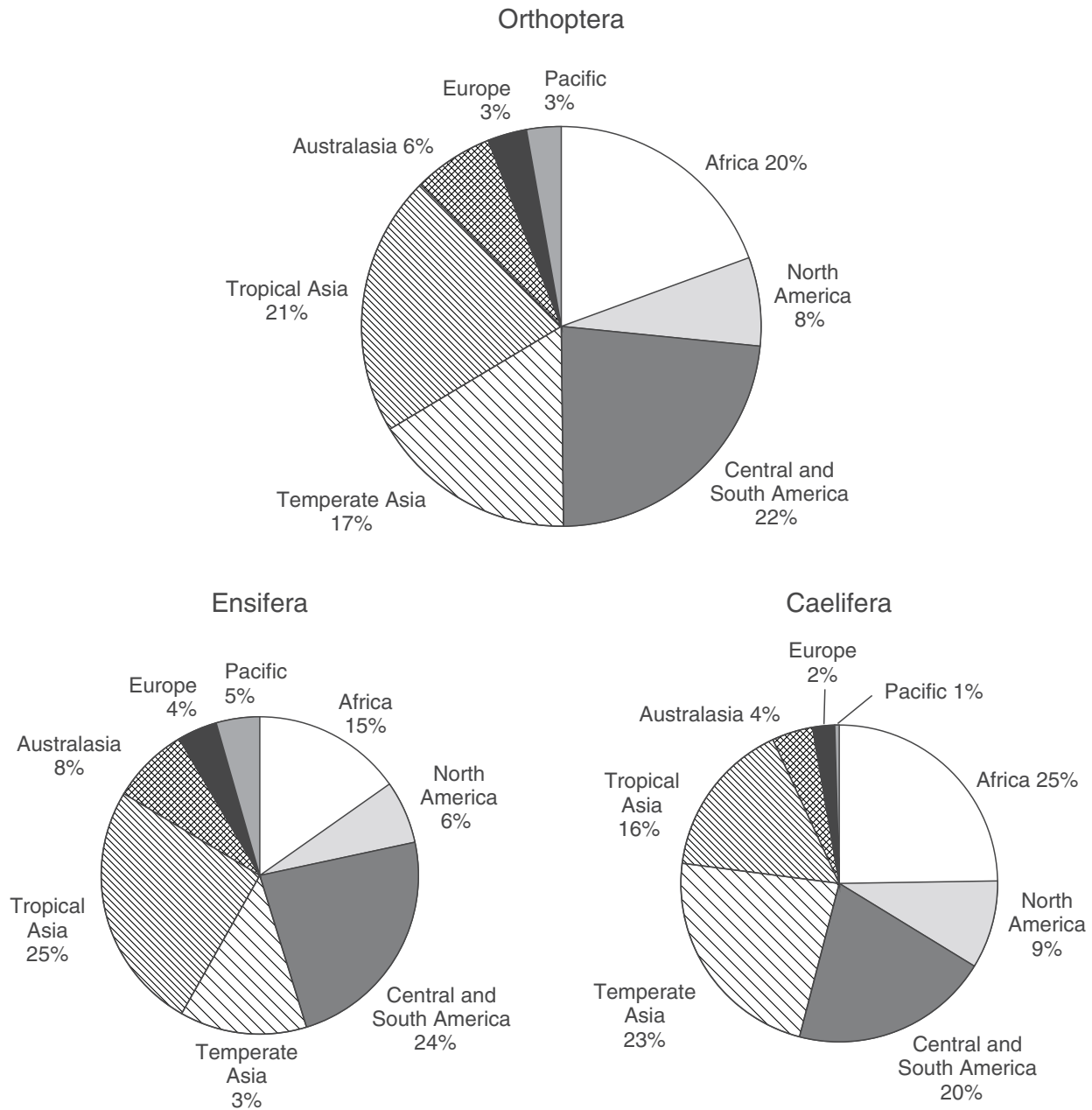


Figure 10.2 Regional diversity of Orthoptera as a whole and its suborders Ensifera and Caelifera based on the number of described species from each geographical region. The data were generated from the Orthoptera Species File (Eades et al. 2015).

Caelifera is the Acridoidea, which diverged in the Cenozoic when the global climate cooled down (Song et al. 2015). The highest diversity of grasshoppers is found mostly in the temperate regions, where grasslands dominate. Similarly to the ensiferans, the modern diversity of the Caelifera

in temperate regions might be due to exaptations to the temperate climate when the lineage originated. Although these scenarios are speculative, it is clear that the Ensifera and Caelifera show different patterns of diversity in terms of their geographical distributions.

10.3 Morphological and Biological Diversity

The Orthoptera are the most species-rich group among the lower neopterans, and there is a tremendous amount of diversity in biology, ecology, and morphology in the order. For those who are familiar only with common crickets, grasshoppers, and katydids, the rich diversity of the Orthoptera might be surprising. But given that the order has successfully diversified for 300 million years, such incredible diversity is to be expected and appreciated.

Orthopterans can be found in almost every conceivable habitat. Besides some of the obvious ones, such as temperate grasslands and tropical rainforests, many orthopterans thrive in unusual and unexpected habitats. Numerous orthopterans are adapted to xeric environments, such as the numerous and often-flightless Melanoplinae (Caelifera: Acrididae) inhabiting scrubby habitats across North America, particularly in the southeastern United States and especially in Florida, but some of the most extreme examples are found in the open desert (Deyrup 1996). For instance, species in the caeliferan family Lathiceridae are found in the Namib Desert, where they presumably burrow in sandy desert soil to avoid the heat (Dirsh 1954, Kevan 1982). Their bodies are squat and depressed, with an almost pebble-like texture and well-camouflaged sandy coloration. In the Australian outback, a catantopine grasshopper, *Urnisiella rubropunctata*, is highly adapted to the sandy habitat, where it can withstand high temperatures. Colored in earthy red, this species uses its long middle legs to sweep sand over its body to bury itself when it is threatened (Rentz 1996).

Although orthopterans are typically associated with the terrestrial environment, several species are adapted to aquatic habitats. Most members of the Tetrigidae (Caelifera) are found near water, where they feed on algae and mosses (Bastow et al. 2002). The species in the subfamily Scelimeninae are semiaquatic and can swim vigorously under water (Kevan 1982, Amédégno

and Devriese 2008). Similarly, many species of the Ripipterygidae and Tridactylidae are associated with aquatic habitats, and some of the smaller species can even walk on the surface of water (Günther 1969, 1979). A South American grasshopper, *Marellia remipes* (Acrididae), lives on broad, floating leaves of aquatic plants, and its hind tibiae are modified and expanded to be oar-like to help the grasshopper swim underwater (Carbonell 1957). Although most female grasshoppers lay eggs in soil, *M. remipes*, along with several other aquatic species in the acridid subfamilies Pauliniinae and Oxyinae, have modified ovipositors that allow them to lay eggs in plants or on the surface of plants (Amédégno and Devriese 2008).

Although many crickets can burrow, some orthopterans have adapted to a true subterranean lifestyle. The most familiar subterranean orthopteran is the family Gryllotalpidae (Ensifera), commonly known as mole crickets. Their legs, particularly their fossorial forelegs, are modified for burrowing, and mole crickets create tunnels and galleries underground where they spend most of their life (Frank and Parkman 1999). Commonly known as sandgropers, the Cylindrachetidae (Caelifera) are worm-like, entirely subterranean, and found in Australia and Argentina. Like the mole crickets, they, too, possess the ability to create tunnels and galleries underground using their powerful digging front legs (Günther 1992).

Additionally, some orthopterans have taken up cave-dwelling habits. A number of species in the Rhabdiphoridae (Ensifera) are highly adapted to cave environments, where they prey on other cave-dwellers (Allegrucci et al. 2010). Some species of cave crickets are considered keystone species in cave communities. For example, many cave systems in central Texas are home to federally endangered karst invertebrates. Unlike typical cave systems that can harbor large numbers of roosting bats, which provide energy for cave-dwelling organisms, many of the caves in central Texas lack bats (Elliott and Veni 1994). In these caves, cave crickets provide a functionally equivalent role to bats in that they forage outside the caves and

bring a source of potential energy into the cave ecosystem, which karst invertebrates can access and use in the form of feces (guano), eggs, and dead or live bodies (Lavoie et al. 2007). Recently, a katydid species (*Cedarbergeniana imperfecta*) was found in a cave in the Cederberg area of South Africa; so far, it is the only known katydid species that is adapted to life in caves (Bazelet and Naskrecki 2014).

Many specialized grasshopper species live in the canopy of tropical rainforests in the Amazon (Descamps 1976a, 1976b, 1976c). As these species do not come down to the forest floor, the existence of this fauna was not known until the 1970s. So far, members of the acridid subfamilies Proctolabinae and Ommatolampidinae, and a romaleid subfamily, Bactrophorinae, have been found to be particularly adapted to canopy-dwelling (Descamps 1976a, 1976c, 1978). Although canopy orthopterans have been studied extensively in Amazonian rainforests, the existence of such a fauna in Africa and Southeast Asia is completely unknown at this time.

Some orthopterans are adapted to alpine habitats. These insects are typically short-winged and have limited dispersal abilities. A number of melanopline grasshoppers are found in so-called “sky islands” in the Rocky Mountains of the United States, and major adaptive radiation is presumed to have occurred during the Pleistocene (Knowles 2001, Knowles and Richards 2005). In the Australian alps, grasshopper species in the genus *Kosciuscola* are distributed along elevational gradients, with different species adapted to specific elevations (Tatarnic et al. 2013).

Just as orthopterans have used a wide array of habitats, they also have diversified in their dietary breadth. All caeliferans are virtually phytophagous in a broad sense (Kevan 1982), although different groups show specific feeding preferences that seem to be phylogenetically conserved (Chapman and Sword 1997). For example, the Tetrigidae feed on algae and mosses (Amédégno and Devriese 2008), and many eumastacoids feed on ferns (Descamps 1973). Within the Acrididae, the Acridinae, Gomphocerinae, and Oxyinae prefer grasses,

whereas other subfamilies feed on a wide variety of herbaceous plants (Uvarov 1977, Chapman and Sword 1997). Most grasshoppers are polyphagous, although many species can be narrowly oligophagous (Chapman and Sword 1997). At least two grasshopper species are strictly monophagous: *Schistocerca ceratiola*, endemic to Central Florida in the United States, feeds only on Florida rosemary (*Ceratiola ericoides*) (Hubbell and Walker 1928, Smith and Capinera 2005), and *Boottetix argentatus* from Arizona in the United States feeds exclusively on creosote bush (*Larrea tridentata*) (Otte and Joern 1977, Chapman et al. 1988).

Unlike caeliferans, ensiferans demonstrate incredible variety in their diet. Most crickets are omnivorous, feeding on detritus, dead insects, and plants (Kevan 1982). Many basal ensiferans, including the Anostomatidae, Gryllacrididae, Rhaphidophoridae, and Stenopelmatidae, are scavengers or are predatory on small insects (Field 2001a). In the Tettigoniidae, several subfamilies, including the Listroselidinae and Saginae, are predatory, with spined tibiae modified for capturing prey (Bailey and Rentz 1990). Other subfamilies are mostly herbivorous, but some groups show more specialized diets. For example, in Australia, the Phasmodinae feed solely on flowers, whereas the Zaprochilinae feed on pollen and nectar (Rentz 1996). Some orthopterans have even evolved to feed on toxic plants to use secondary plant compounds for their own defense (Whitman 1991). The most well-known example is the grasshopper family Pyrgomorphidae, which feeds on plants rich in alkaloids and cardenolides and then secretes toxic chemicals through the midabdominal gland (Qureshi and Ahmad 1970). As a possible warning to other organisms, many of these insects are aposematically colored.

Acoustic communication is one of the most well-known behavioral traits of the Orthoptera. Numerous studies have used crickets and katydids as model systems to understand the evolution of sound production and reception (Greenfield 1997). Male crickets and katydids stridulate (produce sound) by rubbing together

their tegmina, which have a scraper on the upper edge of one wing and a stridulatory file with numerous ridges on the underside of the other wing. As both tegmina rub against each other, sound is produced and resonates through a structure called the harp, which is an area of thick sclerotized wing membrane (Kevan 1982, Greenfield 1997, Desutter-Grandcolas 2003). The physical differences in these sound-producing structures, as well as the speed of rubbing, determine the song characteristics (Greenfield 1997).

Although tegminal stridulation is by far the most common mechanism of acoustic communication in the Orthoptera, other mechanisms are found in other lineages. New Zealand wetas (Ensifera: Anostostomatidae), for instance, use a femoro-abdominal mechanism, in which patches of spines, pegs, or a file of ridges on each side of the abdomen are rubbed against opposing pegs on the inner surface of the hind femur (Field 2001b). These structures are found in both sexes, and unlike crickets and katydids, the sound is not used for sexual courtship, but apparently for aggression (Field 2001b). Conversely, the Stenopelmatidae (Ensifera) do not have any sound-producing structures, but they are known to drum their abdomen against a substrate in a stereotypical and species-specific way, producing ground impulses that can be detected by other individuals (Weissman 2001a). Both sexes produce drumming. In the Caelifera, femoro-tegminal stridulation is a primary mechanism for acoustic communication in the acridid subfamily Gomphocerinae and the Pamphagidae (Kevan 1954). Males of these insects rub a row of pegs found along the inner side of the hind femur against a stridulatory file on the tegmen to produce sound, which is used in the context of courtship. Many species of the acridid subfamily Oedipodinae can produce sound from wings during flight, through a phenomenon known as crepitation. The mechanism of crepitation is still not well understood, but it has been suggested that the membranes between the anal veins of the hind wings produce a snapping sound when they suddenly become taut (Otte 1970). Femoro-abdominal stridulation is also found in

the Pneumoridae (van Staaden and Römer 1997) and Xyronotidae (Kevan 1953). South American romaleids have a tegmino-alar mechanism in which the first vannal area of the hindwing has a series of serrate veinlets that rub against the strongly raised scraper veins on the underside of the tegmen (Uvarov 1966). Male pneumorids, in particular, have enlarged abdomens for resonating the sound produced from this form of stridulation (Dirsh 1965, van Staaden and Römer 1997). Other methods of sound production in orthopterans abound, involving the abdominal tergites, hind wings, mandibles, pronotum, and even tibiae (Kevan 1954, Otte 1970), but the exact functions and mechanics of these other types are not yet clearly understood.

Sexual dimorphism is prominent in the Orthoptera. Similar to many other insect groups, many orthopterans display sexual size dimorphism (SSD) in which females are larger than males. Hochkirch and Gröning (2008) reviewed SSD in more than 1500 species of Orthoptera and showed that SSD is uniform in the Ensifera, with the females being about 9% larger than the males, whereas SSD is much stronger and more variable in the Caelifera. SSD in the Orthoptera is often associated with a higher number of nymphal instars in females, leading to an earlier emergence of adult males, a phenomenon known as protandry (Hochkirch and Gröning 2008). Sexual dimorphism in wings is also common in the Orthoptera, especially in the Caelifera. In the Pneumoridae, males are macropterous (fully winged) and have inflated abdomens, whereas females are apterous and have normal, uninflated abdomens (Dirsh 1965). In *Bullacris membracioides*, alternative males without wings and inflated abdomens co-occur with the primary males (Donelson and van Staaden 2005). These alternative males eavesdrop on the duets of inflated males and females to exploit the acoustic mate-location system. In the pamphagid subfamily Porthetinae, females are usually apterous and males are winged with a specially modified stridulatory area (Uvarov 1966). Some species of wetas and king crickets in the family

Anostomatidae show a unique sexual dimorphism in that males have modified and enlarged mandibles, commonly referred to as tusks, whereas females have normal mandibles. In the New Zealand tree weta (*Hemideina maori*), males defend harems of females from rival males by using their enlarged mandibles, and Gwynne and Jamieson (1998) showed that sexual dimorphism is a result of sexual selection for male defense of the harems and that mandible sizes and harem sizes were positively correlated.

Many orthopterans show spectacular mimicry. Katydid (Tettigoniidae) are probably the most well-known examples of leaf mimicry among insects. This mimicry has evolved as a defense mechanism against diurnal predators (Nickle and Castner 1995). The species in the Neotropical genus *Typophyllum* (Pterochrozinae) have tegmina that perfectly resemble brown dead leaves with veins and even feeding damage. Leaf mimicry in the Tettigoniidae seems to be a convergent trait that has independently evolved in at least six lineages (Mugleston et al. 2013). Some katydids (such as *Markia* or *Lichenodraculus*) remarkably resemble lichen, on which they also feed. Some species mimic other insects, and one of the most impressive examples is in the genus *Aganacris* (Phaneropterinae), which mimics pompilid wasps (Nickle and Castner 1995). Among the Caelifera, grass-feeding species in the acridid subfamilies Acridinae, Gomphocerinae, Hemiaceridinae, and Leptysminae have elongated heads and bodies that appear to mimic grasses. Similar grass-mimic ecomorphs have convergently evolved in the Morabidae (Eumastacoidea), Pyrgomorphidae (Pyrgomorphae), and Lentulidae (Acridoidea) (Uvarov 1977). Some ground-dwelling pamphagids and romaleids even resemble inanimate objects such as small rocks and pebbles.

10.4 Societal Importance

In the Book of Exodus, a plague of locusts covered the land of Egypt as one of 10 miraculous signs from God to warn and dishearten the

Pharaoh. Swarming locusts of biblical scale have affected us since humans began cultivating crops, and they are still a source of great fear and devastation across the world. Locusts are grasshoppers (Orthoptera: Acrididae) that are capable of expressing an extreme form of density-dependent phenotypic plasticity that can lead to migrating swarms (Pener 1983, Pener and Simpson 2009, Simpson and Sword 2009, Sword et al. 2010). Under low population densities, locusts exist in the solitary phase, which is characterized by cryptic coloration, infrequent social interactions, and generally sedentary behavior. When crowded, locusts develop into the gregarious phase, which is characterized by often striking, contrasting black and orange coloration, and formation of cohesive nymphal bands and adult swarms capable of concerted, long-distance marching and flying (Uvarov 1921, 1966). Under certain favorable conditions, locusts can produce devastating plagues and become a major threat to crop production and global food security (Latchininsky et al. 2011). Locust outbreaks have occurred on all continents except Antarctica, and they can affect the livelihood and well-being of one in 10 people on Earth (Latchininsky 2010). About 15 species of locusts belonging to at least four acridid subfamilies (Cyrtacanthacridinae, Oedipodinae, Gomphocerinae, and Calliptaminae) can develop into plagues (Song 2011).

The economic importance of locusts is not limited merely to direct crop and pasture damage. During outbreaks, which can expand to a transcontinental scale, tremendous effort is applied to control these pests. For example, in 2003–2005, an outbreak of the desert locust *Schistocerca gregaria* in Africa affected 8 million people, with an estimated 80 to 100% loss of crops in afflicted regions (Brader et al. 2005). To curtail this outbreak, 13 million hectares (approximately the area of the state of New York) were treated with broad-spectrum neurotoxic insecticides in 26 countries. Such transcontinental operations, together with food aid for affected populations, cost over half a billion US dollars to

the world community, not to mention the human and environmental health costs (Belayneh 2005). Because many locusts inhabit developing countries, management of these pests depends largely on the geopolitical interests of donors, availability of funds, stakeholder inputs, and numerous other socioeconomic aspects (Peveling 2005). Locusts produce outbreaks (and thus require control) at irregular intervals, which makes the sustainability of management infrastructure (e.g., survey programs and logistical expertise) even more challenging (Lockwood et al. 2001). Simultaneous consideration of environmental, social, and economic systems is fundamental for shifting toward a preventive and sustainable locust-management system (Lecoq 2005).

Orthopterans represent one of the major insect groups that are consumed by humans, and at least 267 species are known to be used in human diets (Raubenheimer and Rothman 2013). Many cultures from Asia, Africa, and Central and South America have used crickets, grasshoppers, and katydids as a major source of nutrients because these insects are often abundantly and easy to collect (Gahukar 2011). Orthopterans are rich in protein content, ranging from 23 to 91% protein (Raubenheimer and Rothman 2013). The United Nations Food and Agriculture Organization (FAO) recently endorsed entomophagy as a potential solution for the global food-security problem, and highlighted orthopterans as a suitable source of human food (FAO 2013).

Grasshoppers and locusts can be collected in large quantities, and there are many ways people consume these insects. They can be boiled, stir-fried, deep-fried, smoked, roasted, or sun-dried, and consumed with or without seasoning, depending on the country (Gahukar 2011). Most of the grasshoppers and locusts consumed by humans are collected in the wild or in crop fields (Gahukar 2011). For regions that are affected by locust plagues, people can harvest a large number of locusts easily. However, because of their pest status, locusts are often exposed to chemical pesticides, and there are reports of relatively high concentrations of organophosphate pesticide residues in locusts collected for

human consumption (FAO 2013). Because grasshoppers require fresh vegetation for proper survival and development, large-scale farming for human consumption is not practical. Conversely, crickets are farmed commercially, although only two species (*Acheta domestica* and *Gryllus bimaculatus*) are currently being farmed, mostly for the pet-food industry (FAO 2013).

One of the most well-known orthopterans for human consumption is found in Mexico, and is commonly known as “chapulines.” In the states of Tlaxcala, Puebla, and Oaxaca, chapulines refers to a pyrgomorph species, *Sphenarium purpurascens*, which is one of the most abundant species of grasshoppers in Mexico (Ramos-Elorduy et al. 1997). It is considered a plague in northern areas of central Mexico. The typical method of preparing chapulines after collecting in the field is to leave them without food for one or two days to clean the digestive tract. Afterwards, they are boiled, sun-dried, and seasoned with salt, lemon, and garlic juice. Finally, they can be fried or grilled and are sold in markets, especially in the state of Oaxaca.

10.5 Overview of Taxa

10.5.1 Suborder Ensifera

The Ensifera are one of the two monophyletic suborders in the Orthoptera and include familiar insects, such as crickets, katydids, wetas, and their relatives (Fig. 10.3). The ensiferans are characterized by long and thread-like antennae that are usually longer than the body, symmetrical mandibles, thoracic pleura concealed by lateral pronotal lobes, three or four tarsal segments, and tympana often present on the front tibia. Many ensiferans communicate acoustically by tegminal stridulation or by rubbing their tegmina together, and there are many modifications of the tegmina for sound production and crypsis. Female ovi-positors are often sword-shaped. Currently, two infraorders are recognized within the Ensifera: Gryllidea and Tettigoniidea. The Gryllidea include

the Grylloidea (true crickets) and Gryllotalpoidea, whereas the Tettigoniidea include the Hagloidea, Stenopelmatoidea, Tettigoniidea, Rhabdophoroidea, and Schizodactyloidea. Collectively, the Ensifera include 11 families, 2111 genera, and 14,313 species (Eades et al. 2015) (Table 10.1). The phylogenetic relationships among the basal ensiferans are still not well understood.

10.5.1.1 Superfamily Grylloidea

The Grylloidea are the second largest superfamily in the Ensifera, and include a single family, the Gryllidae. This superfamily represents one of the earliest branching lineages in the Orthoptera, and a recent molecular study suggests that it diverged from other ensiferans in the Triassic period (Song et al. 2015). Some authors historically considered the Mogoplistidae and Myrmecophilidae as members of the Grylloidea (Rehn and Hebard 1912), but a recent phylogenetic study (Song et al. 2015) grouped these two families with the Gryllotalpidae. Another recent study by Chintauan-Marquier et al. (2016) found the Mogoplistidae to be sister to the Gryllidae, but did not recover a monophyletic Myrmecophilidae. I consider that Grylloidea consist solely of one family, the Gryllidae. The Grylloidea are sister to the Gryllotalpoidea, and these two superfamilies collectively form the infraorder Gryllidea.

Gryllidae This family (Fig. 10.3a,b) is highly diverse and includes 21 subfamilies with 605 genera and 4900 species distributed worldwide (Eades et al. 2015). Commonly known as crickets, the Gryllidae are characterized by long antennae, a generally quadrate pronotum, tegmina positioned flat across the dorsum, long cerci, and a needle-like ovipositor. In many species, males produce melodic songs by rubbing scrapers on the left tegmen against stridulatory files on the right tegmen. Cricket wings have modified veins that form the mirror and harp, which function as resonators when stridulation takes place. Virtually all crickets stridulate by passing the right tegmen over the left (Kevan

1982). Crickets are omnivorous scavengers and typically nocturnal.

The taxonomic diversity in the Gryllidae is great, and many authors have divided the Gryllidae into several families in the past (Desutter 1987). Given the antiquity of the family and the distinct morphological differences among different subfamilies, such a taxonomic action might be warranted. Of the 21 currently recognized subfamilies, four are highly cosmopolitan and are found in temperate, subtropical, and tropical regions on all continents. These are the Gryllinae (field crickets, 1121 spp.), Nemobiinae (ground crickets, 327 spp.), Oecanthinae (tree crickets, 169 spp.), and Trigonidiinae (trigs or sword-tail crickets, 635 spp.). Some subfamilies are found both in the Old World and the New World, but are restricted to subtropical and tropical regions. These are the Landrevinae (141 spp.), Pentacentrinae (silent litter crickets, 70 spp.), Podoscirtinae (802 spp.), Luzarinae (280 spp.), Paragryllinae (121 spp.), Phalangopsinae (spider crickets, 958 spp.), and Eneopterinae (bush crickets, 340 spp.) Subfamilies exclusive to the Old World include the Gryllomiminae, Gryllomorphinae, Itarinae, Sclerogryllinae, Euscyrntinae, Phaloriinae, and Pteroplistinae, whereas the only subfamily exclusive to the New World is the Hapithinae. A new molecular phylogeny of the Gryllidae (Chintauan-Marquier et al. 2016) shows many of the subfamilies to be paraphyletic, which indicates that reclassification of the Gryllidae is urgently needed.

10.5.1.2 Superfamily Gryllotalpoidea

This superfamily is recognized here as a result of a recent molecular phylogenetic study by Song et al. (2015). The close relationship between the Gryllidae and Gryllotalpidae has been supported by previous studies (Ander 1939, Zeuner 1939, Sharov 1968, Vickery 1977), but their relationship with respect to the Mogoplistidae and Myrmecophilidae has not been resolved because they have sometimes been included as subfamilies of the Gryllidae (Rehn and Hebard 1912). Song et al. (2015) suggested that the Mogoplistidae and Myrmecophilidae form a clade, which is, in turn,

Table 10.1 Summary of the known number of orthopteran subfamilies, genera, and species for each family.

Suborder	Infraorder	Superfamily group	Superfamily	Family	No. of subfamilies	No. of genera	No. of species		
ENSIFERA	Grylloidea		Grylloidea	Gryllidae	21	605	4,900		
			Gryllotalpoidea	Gryllotalpidae	2	6	107		
				Mogoplistidae	2	30	375		
					Myrmecophilidae	1	5	71	
	Tettigoniidea			Schizodactyloidea	Schizodactylidae	2	2	15	
				Rhaphidophoroidea	Rhaphidophoridae	9	81	646	
				Hagloidea	Prophalangopsidae	2	5	8	
				Stenopelmatoidea	Anostomatidae	7	43	217	
					Gryllacrididae	2	100	772	
					Stenopelmatidae	3	6	39	
					Tettigoniidae	23	1,228	7,163	
	CAELIFERA	Tridactylidea		Tridactyloidea	Ripterygidae	1	2	70	
					Tridactylidae	2	9	134	
Cylindrachetidae					1	3	16		
Acrididea		Acridomorpha		Tetrigoidea	Tetrigidae	9	260	1,823	
					Eumastacoidea	Chorotypidae	6	43	162
						Episactidae	4	18	67
						Eumastacidae	9	46	228
						Euschmidtidae	3	60	241
						Mastacideidae	1	2	8
						Morabidae	2	42	119
						Thericleidae	6	57	220
					Proscopioidea	3	32	214	
					Tanaoceroidea	1	2	3	

Suborder	Infraorder	Superfamily group	Superfamily	Family	No. of subfamilies	No. of genera	No. of species
			Trigonopterygoidea	Trigonopterygidae	2	5	17
				Xyronotidae	1	2	4
			Pneumoroidea	Pneumoridae	1	9	17
			Pyrgomorphoidea	Pyrgomorphidae	2	149	477
			Acridoidea	Acrididae	25	1,429	6,679
				Dericorythidae	3	22	183
				Lathiceridae	1	3	4
				Lentulidae	2	36	103
				Lithidiidae	1	4	13
				Ommexechidae	3	13	33
				Pamphagidae	5	96	456
				Pamphagodidae	1	4	5
				Pyrgacrididae	1	1	2
				Romaleidae	2	110	471
				Tristiridae	2	18	25

Data are from the Orthoptera Species File, and the classification used here follows that of Song et al. (2015).



Figure 10.3 Representative families of Ensifera. (a) Grylloidea: Gryllidae: Gryllinae. (b) Grylloidea: Gryllidae: Phalangopsinae. (c) Gryllotalpoidea: Gryllotalpidae. (d) Schizodactyloidea: Schizodactylidae: Comicinae. (e) Stenopelmatoidea: Stenopelmatidae. (f) Stenopelmatoidea: Anostomatidae. (g) Stenopelmatoidea: Gryllacrididae. (h) Rhaphidophoroidea: Rhaphidophoridae. (i) Hagloidea: Prophalangopsidae: Cyphoderrinae. (j) Tettigonioidea: Tettigoniidae: Conocephalinae. (k) Tettigonioidea: Tettigoniidae: Pseudophyllinae. (l) Tettigonioidea: Tettigoniidae: Pterochrozinae. (Photographs: Piotr Naskrecki). (See color plate section for the color representation of this figure.)

sister to the Gryllotalpidae. The clade formed by these three families is quite divergent from the Gryllidae. Compared to the Grylloidea, the Gryllotalpoidea is a small superfamily with 553 known species (Eades et al. 2015).

Gryllotalpidae Commonly known as mole crickets, the Gryllotalpidae (Fig. 10.3c) are characterized by a small and conical head, legs modified for digging and burrowing, hind legs not modified for jumping, tegmina of males lacking a mirror, and a highly reduced ovipositor in females. The Gryllotalpidae consist of two extant subfamilies (Gryllotalpinae and Scapteriscinae) and include six genera and 107 species distributed worldwide (Eades et al. 2015). Mole crickets spend most of their lives creating tunnels and galleries underground. They use the galleries to amplify their songs for sexual communication (Kevan 1982). In the United States, some mole cricket species are urban pests of lawn and turf grass (Frank and Parkman 1999).

Mogoplistidae Commonly known as scaly crickets, this family is characterized by a small body size (typically less than 1.5 cm) and the presence of scales that cover the entire body. Hind wings are completely absent and males have reduced tegmina concealed by the pronotum. This group is the most diverse in the Gryllotalpoidea, with two subfamilies (Malgasiinae and Mogoplistinae), 30 genera, and 375 species (Eades et al. 2015). The Malgasiinae are represented by a single genus, *Malgasia*, which is endemic to Madagascar, whereas the Mogoplistinae have a worldwide distribution.

Myrmecophilidae Commonly known as ant-loving crickets, this peculiar family is characterized by an oval body shape, small eyes, and lack of wings, as well as sound-producing structures. The Myrmecophilidae have a worldwide distribution, with five genera and 71 species (Eades et al. 2015). They are found mostly in temperate regions, and not many are known

from tropical regions. As the common name suggests, myrmecophilids are obligate inquilines in ant nests (Henderson and Akre 1986, Komatsu et al. 2008). They steal food from ants or feed on what is left in the nests. These insects acquire cuticular hydrocarbons from the ants to be able to live in the nests undetected (Komatsu et al. 2008).

10.5.1.3 Superfamily Schizodactyloidea

This superfamily includes a single family, the Schizodactylidae, which includes 15 species. Heads and Leuzinger (2011) placed a fossil schizodactylid from the early Cretaceous into an extant genus, *Schizodactylus*, suggesting that this group is a relict that has changed little for the past 100 million years. The fossil was from the Crato Formation of Brazil, whereas the extant members of the family are known only from the Middle East and southern Africa, suggesting the presence of the family in the Atlantic rift zone of South America before its separation from Africa (Heads and Leuzinger 2011). The phylogenetic placement of this superfamily has always been questioned, but Song et al. (2015) placed the Schizodactyloidea as the basal lineage of the Tettigoniidea.

Schizodactylidae Commonly known as splay-footed crickets, the Schizodactylidae (Fig. 10.3d) are characterized by long hind wings that coil into a tight spiral (in winged species), tarsal segments that are broadly expanded with a finger-like process, a large head with strong mandibles, four tarsal segments, and a lack of tympana in the front tibia. This unusual and relict family includes two subfamilies (Comicinae and Schizodactylinae) with two genera and 15 species (Eades et al. 2015). The Comicinae are confined to southern Africa and the Schizodactylinae are in southwestern Asia, India, and Turkey. Members of this family are active predators and demonstrate subsocial behavior (Aydin and Khomutov 2008).

10.5.1.4 Superfamily

Rhaphidophoroidea

This superfamily features a single family, the Rhaphidophoridae, which includes 646 species distributed throughout temperate regions around the world (Eades et al. 2015). The majority of this apterous lineage inhabits woodlands, caves, crevices, or burrows in sand. Song et al. (2015) placed it as sister to the clade formed by the Hagloidea and Stenopelmatoidea.

Rhaphidophoridae Commonly known as camel crickets or cave crickets, this apterous family (Fig. 10.3h) is characterized by the lack of hearing organs, elongated hind legs, and laterally compressed tarsi without pulvilli. The family currently includes nine subfamilies, 81 genera, and 646 species (Eades et al. 2015). Despite the relatively high species diversity, not much is known about this group, mainly due to their secretive habits. The taxonomy and classification of this group also needs a major revision because no comprehensive work has been published since Hubbell's (1936) monograph on *Ceuthophilus*. The subfamilies of the Rhaphidophoridae are characterized by limited geographic distributions. There is no cosmopolitan lineage. The Aemodogryllinae (165 spp.) and Anoplophilinae (28 spp.) are known only from Asia and the Dolichopodainae (52 spp.) and Troglophilinae (21 spp.) are known only from Europe. The Ceuthophilinae (149 spp.) are confined to North America and the Gammarotettiginae (6 spp.) and Tropidischinae (1 spp.) are endemic to the western United States. The Rhaphidophorinae (129 spp.) are widely distributed in Southeast Asia, the Indo-Pacific, and Australia. The Macropathinae (95 spp.), which were considered a distinct family at one point (Kevan 1982), show a classic Gondwanan distribution, with representatives in South America, southern Africa, Australia, and New Zealand.

10.5.1.5 Superfamily Hagloidea

This superfamily is the smallest group in the Ensifera, with a single extant family, the

Prophalangopsidae, which includes eight species (Eades et al. 2015). However, this group has a rich fossil record, with 133 genera and 204 species ranging from the late Permian to the early Cretaceous, and, thus, this lineage is often considered to be a "living fossil" for the Orthoptera. The Hagloidea are characterized by the primitive male tegminal stridulatory organs, which lack a mirror and function ambidextrously (Morris and Gwynne 1978).

Prophalangopsidae All modern hagloids belong to the Prophalangopsidae (Fig. 10.3i), which include two subfamilies (Cyphoderrinae and Prophalangopsinae) with five genera and eight species (Eades et al. 2015). The Cyphoderrinae include two brachypterous genera: *Cyphoderris* is found in western North America, and *Parachyphoderris* is found in the Russian Far East. The Prophalangopsinae include three macropterous genera (*Aboilomimus*, *Prophalangopsis*, and *Tarragoilus*) found in India and China. Commonly known as ambidextrous crickets, hump-winged crickets, or grigs, prophalangopsids have a functional file on the underside of each tegmen and often switch wings when stridulating (Morris and Gwynne 1978). In *Cyphoderris*, mating behavior is peculiar in that the female mounts the male and feeds on his fleshy hind wings during the initial phase of copulation (Johnson et al. 1999). During this time, the male uses a pinching organ on his abdomen to hold the female in place while he copulates.

10.5.1.6 Superfamily Stenopelmatoidea

This superfamily includes three families (Anostomatidae, Gryllacrididae, and Stenopelmatidae) and is sister to the Hagloidea (Song et al. 2015). With 1028 described species, this group is largely characterized by small and widely separated eyes, four-segmented tarsi, and long and flexible cerci. The superfamily includes fully winged insects and completely apterous ones. The members of this group do not have stridulatory organs on the tegmina, but some do have femoro-abdominal stridulatory

organs, and almost all have hearing organs on the front tibia.

Anostomatidae Commonly known as wetas and king crickets, this family (Fig. 10.3f) is found mostly in the Southern Hemisphere, including Australia, New Zealand, and southern Africa (Field 2001a). The family is generally characterized by large body size, a large head, greatly enlarged male mandibles, and anterior coxae with spines, although there are some small-bodied anostomatids without enlarged mandibles in southern Africa (Brettschneider et al. 2007). Sound production is achieved primarily by rubbing pegs on the inner surface of the hind femur against the stridulatory files on the abdomen (Field 2001b). Other known methods of sound production include the use of mandibulo-mandibular, pleuro-coxal, and tergo-tergal structures, as well as substrate-based vibration (Field 2001b). Male wetas form harems with multiple females, which will brood eggs and young larvae in isolated chambers (Field and Jarman 2001). The Anostomatidae now include the Cooloolidae, unusual subterranean insects endemic to northern Australia, commonly known as Cooloola monsters (Rentz 1986). The phylogenetic position of the Cooloolidae was not clearly understood, but Song et al. (2015) found that the Anostomatidae were paraphyletic with respect to the Cooloolidae and argued that the Cooloolidae are actually aberrant Anostomatidae. This view was also expressed by Gorochov (2001). With this change, the Anostomatidae includes seven subfamilies, 43 genera, and 217 species.

Gryllacrididae This family is the most diverse lineage in the Stenopelmatoidea, with two subfamilies (Gryllacridinae and Lezininae), 100 genera, and 772 species (Eades et al. 2015). The Gryllacrididae (Fig. 10.3g) are distributed mostly in tropical and subtropical regions worldwide, although a few species occur in temperate regions. The family is characterized by a lack of hearing organs on the front tibia, the anal veins parallel to the corresponding wing

margin in the tegmina, the presence of a “scrotum” in the posterior abdominal segments in males, and a long and narrow ovipositor in females (Kevan 1982). Commonly known as raspy crickets or leaf-rolling crickets, gryllacridids are arboreal and make chambers by rolling leaves and sewing them closed using silk produced from their mouthparts (Walker et al. 2012). Many species are scavengers or are predators of smaller arthropods.

Stenopelmidae Commonly known as Jerusalem crickets or potato bugs, the Stenopelmidae (Fig. 10.3e) are characterized by a disproportionately large head, a pronotum that widens anteriorly, and tibiae that are all flattened with spines for digging. Some groups in this family are completely apterous, whereas others are winged. With three subfamilies (Oryctopinae, Siinae, and Stenopelmatinae), this family includes six genera and 39 species (Eades et al. 2015), and shows a disjunct distribution. All members of the Stenopelmatinae are found in North America to Central America, whereas the Oryctopinae are restricted to India, and the Siinae are found in southern Africa and Malaysia. Although the number of described species is small, there is evidence for cryptic species diversity. North American stenopelmatids are associated with sand dunes, and they dig burrows (Weissman 2001b). Other than the insect order Phasmida (stick insects), this family contains the only known insects that are capable of regenerating legs during nymphal development (Weissman 2001b).

10.5.1.7 Superfamily Tettigonioidae

The Tettigonioidae are the largest and most diverse lineage in the Ensifera. Represented by a single family, the Tettigoniidae, this cosmopolitan superfamily is widely distributed throughout the world. Song et al. (2015) suggested that the Tettigonioidae are sister to a clade consisting of the Rhabdophoroidea, Hagloidea, and Stenopelmatoidea, and they seem to have diversified into major lineages during the Cretaceous period.

Tettigoniidae Commonly known as katydids or bush crickets, the Tettigoniidae (Fig. 10.3j,k,l) are characterized by tegmina that are held roof-like over the abdomen, a male subgenital plate with a pair of styles, a sword-like ovipositor in females, and four-segmented tarsi. Stridulation is achieved by rubbing the left tegmen over the right. The Tettigoniidae are the most species-rich family in the Orthoptera, including 23 subfamilies with 1228 genera and 7163 species distributed throughout the world (Eades et al. 2015). Although the family has always been considered a monophyletic group, some authors have divided it into several families, owing to its great diversity in morphology and ecology. Heller et al. (2014) elevated the tettigoniid subfamily Phaneropterinae to full family status (Phaneropteridae). Based on a recent molecular study by Mugleston et al. (2013) and a previous hypothesis by Gorochov (1995b), the Phaneropteridae have been divided into four plant-feeding subfamilies, the Phaneropterinae, Pseudophyllinae, Mecopodinae, and Phyllophorinae. This taxonomic change implies that the Phaneropteridae as a whole are a monophyletic group, but Mugleston et al. (2013) found that one of the pseudophylline tribes, the Pterochrozini, did not group with other pseudophyllines, and was placed at the base of the katydid phylogeny, rendering the concept of Phaneropteridae paraphyletic. Moreover, Gorochov (2012) elevated several tribes in the Pseudophyllinae to subfamilies and created five additional subfamilies. This example serves to demonstrate that katydid classification is currently in a state of flux, and a major revision of the family will be required once a definitive phylogeny of Tettigoniidae becomes available. In this work, the Tettigoniidae are treated as a single family.

Of the 23 subfamilies, only the Conocephalinae (1197 spp.) and Phaneropterinae (2471 spp.) show truly cosmopolitan distributions throughout temperate, tropical, and subtropical regions. Four other subfamilies are globally distributed, but the Meconematinae (811 spp.) are found throughout tropical and subtropical regions, the Hexacentrinae (48 spp.) and Mecopodinae (150 spp.) are confined

to the tropics, and the Tettigoniinae (893 spp.) are distributed only in temperate regions. Five subfamilies (Austrosaginae, Microtettigoniinae, Phasmodinae, Tympanophorinae, and Zaprochilinae) are endemic to Australia. Only two subfamilies are confined to the New World (Polyancistrinae and Pterochrozinae), and most subfamilies are distributed throughout the Old World.

Many tettigoniids have tegmina that resemble leaves, and a recent study (Mugleston et al. 2013) showed that this crypsis has evolved multiple times in this family. Song et al. (2015) showed that the Tettigoniidae diversified in the Cretaceous period, which is when angiosperms also diversified. This finding then leads to the speculation that the leaf-resembling katydids are the product of close interactions between these insects and plants. Katydid also have diverse feeding habits. Many are herbivorous on forbs and grasses, but there are several predatory lineages, such as the Bradyporinae, Hexacentrinae, Listrosclidinae, and Saginae (Bailey and Rentz 1990), as well as specialists on flowers, nectar, and pollen, such as the Phasmodinae and Zaprochilinae (Rentz 1996).

Perhaps the most well-known aspect about katydid biology, other than their acoustic behavior, is their mating behavior, in which males produce protein-rich spermatophylaxes during copulation as a nuptial gift to ensure the complete transfer of their spermatophores (Gwynne 2001). This phenomenon can be explained in the context of sexual selection in which females choose males with the “best” nuptial gift. However, in some cases, the production of the spermatophylax is too costly for males, and a reverse phenomenon has been observed wherein the males are the ones that choose the females; the latter then compete for this protein-rich meal (Gwynne 1993).

10.5.2 Suborder Caelifera

The Caelifera are one of the two monophyletic suborders in the Orthoptera. Although commonly referred to as “short-horn grasshoppers”

because included taxa often have short antennae relative to other orthopterans, the suborder includes highly diverse lineages with various body forms and life-history traits. Some of the familiar members of the Caelifera include grasshoppers, locusts, and their relatives (Fig. 10.4). The main morphological traits defining this suborder include robust antennae with fewer than 30 flagellomeres, asymmetrical mandibles each with a heavy molar, mostly exposed thoracic pleura, three or fewer tarsal segments, and abdominal tympana. With more than 11,700 described species (Eades et al. 2015) (Table 10.1), the Caelifera, as a whole, show a cosmopolitan distribution, although some groups have more limited distributions. The Caelifera consist of two infraorders, the Tridactylidea and Acrididea, which seem to have diverged in the late Permian (Sharov 1968, Song et al. 2015). The Tridactylidea include a single superfamily, the Tridactyloidea, which consist of three families: Tridactylidae, Ripterygidae, and Cylindrachetidae. The Acrididea consist of the Tetrigoidea (pygmy grasshoppers) and seven superfamilies collectively known as the Acridomorpha, named for their grasshopper-like body form (Dirsh 1975).

10.5.2.1 Superfamily Tridactyloidea

The Tridactyloidea represent the earliest diverging branch in the Caelifera (Song et al. 2015) and include three extant families. The members of this superfamily differ from other, more grasshopper-like relatives in that they possess forelegs adapted for digging. The group includes two closely related families (Tridactylidae and Ripterygidae) that are commonly referred to as pygmy mole crickets, and an aberrant family that is completely subterranean and apterous (Cylindrachetidae).

Ripterygidae This Neotropical family is similar to the more well-known Tridactylidae, but differs in that it is generally larger (4.0 mm to 1.5 cm), has large eyes, hypognathous mouthparts, and forelegs less modified for digging (Kevan 1982).

This family includes two genera and 70 species (Eades et al. 2015).

Tridactylidae Commonly known as pygmy mole crickets, this family (Fig. 10.4a) is generally small (less than 1 cm) and has small eyes, prognathous mouthparts, and forelegs well-modified for digging. Nine genera and 134 species are included (Eades et al. 2015). Two genera are cosmopolitan (mostly tropical and subtropical), two are restricted to the New World, and five are widespread across the Old World. Tridactylids are often associated with habitats near water, and many species can swim or move across the water's surface (Kevan 1982).

Cylindrachetidae Commonly known as sandgropers, this subterranean family has little resemblance to the Orthoptera as it lacks jumping hind legs and wings. Sandgropers have forelegs strongly modified and sclerotized for digging, a relatively long prothorax, and an elongated and tube-like abdomen (Günther 1992). Known only from three genera and 16 species (Eades et al. 2015), the Cylindrachetidae display a Gondwanan distribution in that one monotypic genus is known from South America (Patagonia), whereas the other two genera are known from Australia and Papua New Guinea (Günther 1992).

10.5.2.2 Superfamily Tetrigoidea

The Tetrigoidea are the second most species-rich group in the Caelifera. A single family, the Tetrigidae, is included, although some authors have considered its subfamily, the Batrachideinae, to be a separate family (Kevan 1982). The superfamily represents the earliest branching lineage in the Acrididea, probably diverging in the Triassic period (Song et al. 2015). The group, as a whole, has a cosmopolitan distribution, whereas some subfamilies have more restricted distributions.

Tetrigidae The Tetrigidae (Fig. 10.4b) are characterized by the shape of the pronotum, which projects posteriorly to the end of the

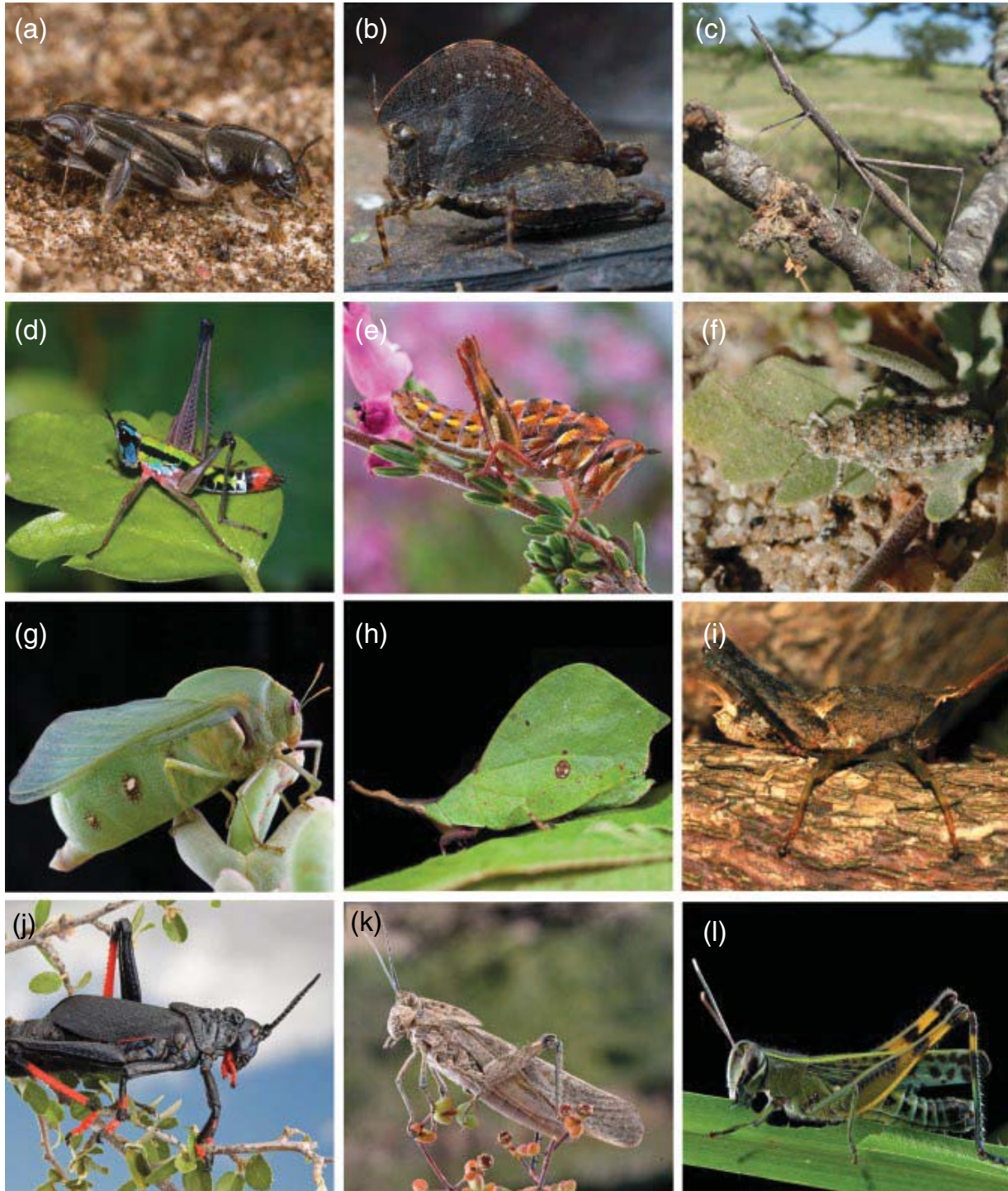


Figure 10.4 Representative families of Caelifera. (a) Tridactyloidea: Tridactylidae. (b) Tetrigoidea: Tetrigidae. (c) Proscopioidea: Proscopiidae. (d) Eumastacoidea: Episactidae. (e) Eumastacoidea: Thericleidae. (f) Tanaoceroidea: Tanaoceridae. (g) Pneumoroidea: Pneumoridae. (h) Trigonopterygoidea: Trigonopterygidae. (i) Trigonopterygoidea: Xyronotidae. (j) Pyrgomorpoidea: Pyrgomorphidae. (k) Acridoidea: Pamphagidae. (l) Acridoidea: Acrididae. (Photographs: Piotr Naskrecki (a,b,e,g,j–l), Paul Lenhart (c), Robert A. Behrstock (d), Hartmut Wisch (f), Chien C. Lee (h), and Paolo Fontana (i)). (See color plate section for the color representation of this figure.)

abdomen. Some of the tetrigids have an elaborate pronotum, resembling those of the Membracidae, but not much is known about the function of this fascinating trait. Commonly known as pygmy grasshoppers, pygmy locusts, or grouse hoppers, tetrigids are often associated with habitats near water, and they feed on algae and mosses (Amédégno and Devriese 2008). Currently, nine subfamilies with 260 genera and 1823 species are recognized (Eades et al. 2015). Of these subfamilies, the Batrachideinae, Cladonotinae, Metrodorinae, and Tetrigininae are found in the Old and the New Worlds, although only the Tetrigininae occur in the temperate region. Other subfamilies are found near the tropics. The Lophotettigininae are the only group restricted to the New World, whereas the other subfamilies are found in the Old World. Despite the diversity of the group, there is a critical shortage of taxonomic expertise for the Tetrigidae.

10.5.2.3 Superfamily Eumastacoidea

Members of the Eumastacoidea are commonly referred to as monkey grasshoppers because of the characteristic shape of their heads and their peculiar stance, in which they spread their hind legs when sitting. Eumastacoids are relatively small in size (less than 4.5 cm) and can be recognized by their short antennae; lack of a basioccipital slit in the head; spined, serrulate, or dorsally tuberculate metatarsi; the lack of an abdominal tympanum; and highly complex male phallic structures. Currently, seven families (Chorotypidae, Episactidae, Eumastacidae, Euschmidtidae, Mastacideidae, Morabidae, and Thericleidae) with 268 genera and 1045 species are recognized (Eades et al. 2015), most of which are known from the tropics. The most recent classification of the Eumastacoidea was established by Descamps (1973) who categorized the superfamily into four groups based on the male phallic structures: Cryptophalli, Stenophalli, Euphalli, and Disclerophalli. Matt et al. (2008) attempted to test this classification, using a small molecular data set, and found support for the Stenophalli and Disclerophalli, but not for the

Cryptophalli. Their taxon sampling was too restricted to fully test the classification. According to Song et al. (2015), the Eumastacoidea seem to have diversified in the Jurassic period and are sister to the Proscopioidea. Despite their diversity, there is currently little or no taxonomic expertise for this group, and the superfamily is in desperate need of a revision.

Chorotypidae This family is characterized by a compressed body form, foliaceous crest on the pronotum, and leaf-like tegmina. The Chorotypidae are widely distributed throughout Southeast Asia with a few African representatives. Six subfamilies are included (Chininae, Chorotypinae, Erianthinae, Eruciinae, Mnesicleinae, and Prioacanthinae) with 43 genera and 162 species (Eades et al. 2015). The Chorotypidae are currently classified as a member of the Cryptophalli *sensu* Descamps (1973).

Episactidae This family (Fig. 10.4d) is characterized by an elongate and subcylindrical body, a distinct frontal ridge on the head, a long hind femur, and four apical spines on the hind tibia. The Episactidae currently include four subfamilies (Episactinae, Espagnolinae, Miraculinae, and Teicophryinae) with 18 genera and 67 species (Eades et al. 2015). Except for the Miraculinae, which are endemic to Madagascar (and a Chinese genus, *Pielomastax*, the taxonomic position of which is not clear at this time), Episactidae is restricted to Central America and, thus, some authors have considered Miraculinae as a separate group from the Episactidae. The Episactidae are currently classified as members of the Cryptophalli *sensu* Descamps (1973).

Eumastacidae This family is characterized by a slender body, long and slender hind legs, and four well-developed apical spurs on the hind tibia. The Eumastacidae currently contain nine subfamilies with 46 genera and 228 species, and the majority are found in the New World (Eades et al. 2015). The only Old World subfamily is the Gomphomastacinae, which are completely

apterous, and have been considered a separate family from the Eumastacidae by some authors, based on geographic disjunction and a unique set of morphological features (Dirsh 1975, Kevan 1982). Matt et al. (2008) found that the position of the Gomphomastacinae was highly unstable within the phylogeny of the Eumastacoidea, so a separate family status for this group might be warranted in the future. Although eumastacids are typically found in the tropics, three genera of the subfamily Moreseinae (*Eumorsea*, *Morsea*, and *Psychomastax*) are found in the United States. The Eumastacidae are currently classified as a member of the Stenophalli *sensu* Descamps (1973).

Euschmidtidae This family is characterized by an elongate and cylindrical body, the rostrum of the head projecting in front of the eyes with an apical furrow, a saddle-shaped pronotum, and three well-developed apical spurs on the hind tibia. The family is the most diverse group in the Eumastacoidea and includes three subfamilies (Euschmidtinae, Pseudoschmidtinae, and Stenoschmidtinae) with 60 genera and 241 species (Eades et al. 2015). This family is restricted to Africa and Madagascar. The Euschmidtidae are currently classified as member of the Disclerophalli *sensu* Descamps (1973).

Mastacideidae This family is characterized by the presence of reduced, flap-like wings and a long aedeagus in the phallic complex. Only eight known species exist (Eades et al. 2015) and all are restricted to the subcontinent of India, making this family the least diverse group in the Eumastacoidea. The Mastacideidae are currently classified as the only members of the Euphalli *sensu* Descamps (1973).

Morabidae This apterous family is characterized by a stem-like body; long, pointed head with a long rostrum; ensiform antennae; and hind tibia with only one inner and one outer spur. Restricted to Australia and Papua New Guinea, the Morabidae include two subfamilies (Biroellinae and Morabinae) with 42 genera and 119 species (Eades et al. 2015). As the only eumastacoids in

Australia, the Morabidae seem to have speciated extensively (Key 1976, 1981). The Morabidae are currently classified as members of the Stenophalli *sensu* Descamps (1973).

Thericleidae This family (Fig. 10.4e) is characterized by a short and stout body, short rostrum of the head with a furrowed apex, short hind femur with heavy dorsal spines, and hind tibia with four well-developed apical spurs. Consisting of six subfamilies with 57 genera and 220 species (Eades et al. 2015), thericleids can be found mostly on shrubs or bushes in dry habitats south of the Sahara in Africa (Descamps 1977). The Thericleidae are currently classified as members of the Disclerophalli *sensu* Descamps (1973).

10.5.2.4 Superfamily Proscopioidea

The Proscopioidea consist of a single Neotropical family, the Proscopiidae. This superfamily has always been considered closely related to the Eumastacoidea. Matt et al. (2008) showed that the Proscopioidea are a separate lineage from the Eumastacoidea, and Song et al. (2015) supported the sister relationship to the Eumastacoidea, the superfamilies probably having diverged during the Jurassic period.

Proscopiidae Commonly known as false stick insects or stick grasshoppers, the Proscopiidae (Fig. 10.4c) can be characterized by their elongate and twig-like body shape, long and pointed head, and short antennae. Members of this family are mostly apterous and live on bushes and trees in South America (Jago 1989). Currently, three subfamilies (Hybusinae, Proscopiinae, and Xeninae) are recognized with 32 genera and 214 species (Eades et al. 2015).

10.5.3.5 Superfamily Tanaoceroidea

The Tanaoceroidea are an unusual and relict lineage, represented by two genera and three known species restricted to the southwestern United States and northern Mexico. A single family is included, the Tanaoceridae. Although once considered to be closely related to the Xyronotidae

(Trigonopterygoidea) because of the stridulatory organ on the abdomen (Dirsh 1955, 1975; Grant and Rentz 1967), Song et al. (2015) suggested that the Tanaoceroidea are a more ancient lineage than the Xyronotidae.

Tanaoceridae The Tanaoceridae (Fig. 10.4f) are small, apterous, and characterized by unusually long and filiform antennae. Males have a stridulatory organ on the third abdominal segment (Dirsh 1955), which is presumably used for acoustic communication, but the biology of the group is not currently well known. Tanaocerids are quite rare and known only from desert habitats in the southwestern United States and Baja California (Grant and Rentz 1967).

10.5.3.6 Superfamily Trigonopterygoidea

The Trigonopterygoidea include two very different families that show a wide geographical disjunction. The Trigonopterygidae are found in Southeast Asia (Kevan 1966), whereas the Xyronotidae are endemic to central Mexico (Dirsh 1955). Morphologically, they are quite different from each other, but molecular data have consistently recovered a sister relationship (Flook et al. 1999, 2000; Song et al. 2015).

Trigonopterygidae This family (Fig. 10.4h) is endemic to Southeast Asia and found in Indonesia, the Philippines, and Myanmar, and is characterized by ensiform antennae, leaf-resembling tegmina, lack of a tympanum, and having the phallic complex reversed relative to other known grasshoppers (Kevan 1966, Dirsh 1975). Two subfamilies (Borneacridinae and Trigonopteryginae) are currently recognized with five genera and 17 species (Eades et al. 2015).

Xyronotidae This family (Fig. 10.4i) is found only in Mexico (Veracruz and Oaxaca) (Fontana et al. 2008). Xyronotids are characterized by a laterally compressed body, lack of wings, lack of tympanum, trifurcate male cerci, and the presence of a crescent-shaped row of stridulatory ridges on the abdomen (Kevan 1953, Dirsh

1955, Dirsh and Mason 1979). This family contains two genera and four species (Eades et al. 2015).

10.5.3.7 Superfamily Pneumoroidea

This superfamily includes a single family, the Pneumoridae, which is endemic to South Africa and known only from 17 species (Eades et al. 2015). The Pneumoroidea are characterized by undifferentiated phallic structures and, thus, have been considered primitive by many authors (Dirsh 1965). But Song and Mariño-Pérez (2013) suggested that the level of sclerotization of male phallic structures of the Pneumoridae might have diminished because sexual selection has worked strongly on the pre-copulatory acoustic courtship mechanism, thereby lifting selective pressure off of the male genitalia.

Pneumoridae Commonly known as bladder grasshoppers or flying gooseberries, the Pneumoridae (Fig. 10.4g) are a small family that includes nine genera and 17 species (Eades et al. 2015), distributed mainly in South Africa. The family is well known for its unique femoro-abdominal stridulatory mechanism (Dirsh 1965), and males have a swollen abdomen that can amplify their calls for a long-distance signal (van Staaden and Römer 1997). Despite the fact that they rely on acoustic communication, pneumorids do not have external tympana. Instead, they have a series of abdominal chordotonal organs that are tuned to different frequencies, and collectively these abdominal ears function as an effective and continuous hearing organ (van Staaden and Römer 1998). Sexual dimorphism is often dramatic, and females are often short-winged and large (Dirsh 1965).

10.5.3.8 Superfamily Pyrgomorpoidea

This superfamily includes a single family, the Pyrgomorphidae, which is widely distributed throughout the Old World with a few representatives in the New World. The exact phylogenetic position of the Pyrgomorpoidea has been debated, but recent molecular studies (Flook and

Rowell 1997, Flook et al. 1999, Leavitt et al. 2013, Song et al. 2015) have consistently found it to be sister to the Acridoidea, having possibly diverged in the early Cretaceous (Song et al. 2015).

Pyrgomorphidae Commonly known as gaudy grasshoppers or bush hoppers, the Pyrgomorphidae (Fig. 10.4j) are widely distributed in the tropics and subtropics around the world. Although morphologically diverse, they are characterized by the presence of a fastigial groove in the head and the capsule-like ectophallus in the phallic complex. The Pyrgomorphidae are currently divided into two subfamilies (Orthacridinae and Pyrgomorphinae) and about 30 tribes, but the subfamily designations seem to be artificial at best, and the phylogenetic relationships among the tribes are not well understood owing to the extreme morphological variation among species (Kevan and Akbar 1964). Currently, 149 genera and 477 species are recognized (Eades et al. 2015). Many pyrgomorphids are aposematically colored and feed on toxic plants (Rowell 1967, Chapman et al. 1986, Whitman 1991). Some species have specialized abdominal glands to eject distasteful chemicals at approaching predators (Qureshi and Ahmad 1970). Some species demonstrate gregarious behaviors, especially as juveniles, and can cause serious crop damage (Chapman et al. 1986).

10.5.3.9 Superfamily Acridoidea

The Acridoidea are the largest superfamily in the Caelifera, consisting of 11 families (Acrididae, Dericorythidae, Lathiceridae, Lentulidae, Lithidiidae, Ommexechidae, Pamphagidae, Pamphagodidae, Pyrgacrididae, Romaleidae, and Tristiridae) (Song 2010). Historically, the Pyrgomorphidae were considered members of the Acridoidea, but molecular data (Flook and Rowell 1997, Flook et al. 1999, Leavitt et al. 2013, Song et al. 2015) have consistently recovered a sister relationship between the Pyrgomorphidae and Acridoidea as a whole, and therefore the Pyrgomorphidae are treated here as a separate superfamily, the Pyrgomorphoidea. Within the Acridoidea,

the most basal lineage is the Pyrgacrididae, which has been considered an intermediate form between the Pyrgomorphidae and Acridoidea. Molecular and morphological data strongly support sister relationships between the Pamphagodidae and Pamphagidae, and the Lentulidae and Lithidiidae. The Tristiridae are closely related to the clade consisting of the Ommexechidae, Romaleidae, and Acrididae. Higher-level relationships among families are now relatively well understood (Leavitt et al. 2013, Song et al. 2015), but the relationships among subfamilies and tribes in each family are still unclear.

Acrididae This family (Fig. 10.4l) is the largest and the most diverse in the Caelifera. The Acrididae have a worldwide distribution, although some subfamilies are restricted to certain geographical regions. Members of this family are extremely variable in terms of size, body shape, biology, ecology, and life-history traits (Uvarov 1977, Chapman and Joern 1990). Because of this, the Acrididae have been used as a taxonomic dumping ground for unrelated taxa when authors did not know where to place them (Eades 2000). Eades (2000) proposed that all members of this family have a strongly developed arch sclerite in the male phallic complex – such a structure is not found in other families in the Acridoidea except the Pamphagodidae, which apparently evolved a similar structure independently.

The Acrididae include 25 subfamilies, 1429 genera, and 6679 validly described, extant species (Eades et al. 2015). Of the 25 subfamilies, certain subfamilies have a cosmopolitan distribution, whereas others have more restricted distributions. The Acridinae, Cyrtacanthacridinae, Gomphocerinae, Melanoplinae, and Oedipodinae are found widely in the Old and New Worlds. Of these, the center of origin for the Acridinae, Cyrtacanthacridinae, Gomphocerinae, and Oedipodinae is considered to be the Old World (probably Africa), whereas it is South America for the Melanoplinae (Amédégno et al. 2003). The Calliptaminae, Catantopinae, Coptacridinae, Egnatiinae, Eremogryllinae,

Euryphyminae, Eyprepocnemidinae, Habrocneminae, Hemiacridinae, Oxyinae, Spathosterninae, Teratodinae, and Tropidopolinae are found exclusively in the Old World. The Copiocerinae, Marelliinae, Ommatolampidinae, Pauliniinae, Proctolabinae, and Rhytidochrotinae are restricted to Central and South America. The Leptysmiinae are found in both North and South America.

In terms of species diversity, the Gomphocerinae include the largest number of described species (1252 spp.), followed by the Catantopinae (1194 spp.) and Melanoplinae (1112 spp.). Most gomphocerines are graminivorous and have mouthparts adapted for grass-feeding (Isley 1944). Gomphocerines have a row of stridulatory pegs on the inner face of the hind legs, which they use for acoustic communication (Otte 1981). Members of the Catantopinae are highly diverse in terms of morphology, a fact that is evident from the number of described genera (380 genera), which is nearly double the number of that of the Gomphocerinae (192 genera). Additionally, the Catantopinae in particular seem to have undergone explosive adaptive radiation in Australia, representing more than 85% (~600 species) of all grasshoppers in the region, all of which are endemic (Rentz 1996). The Melanoplinae include *Melanoplus*, the largest grasshopper genus of all with more than 330 described species, most of which are only distinguishable by differences in male phallic structures (Hubbell 1932, Deyrup 1996).

Many acridids are agriculturally important pests, but the most dramatic examples include plague locusts that are capable of forming enormous migrating swarms (COPR 1982, Sword and Simpson 2008). There are about 15 species of locust known, which collectively belong to the Calliptaminae, Cyrtacanthacridinae, Gomphocerinae, and Oedipodinae (Song 2011).

Dericorythidae Represented by three subfamilies (Conophyminae, Dericorythinae, and Iranellinae), the Dericorythidae was once treated as a subfamily within the Acrididae, but Eades (2000) elevated it to the family level on the basis of the presence of

a deep groove in the endophallic sclerite and the presence of a pseudoarch in the phallic structures, both of which make members of this family distinct from species of the Acrididae. This family is restricted to the Palearctic Region, including North Africa, the Middle East, and China, and there are currently 22 genera and 183 species described (Eades et al. 2015). At least one species, *Dericorys albidula*, is an economically important pest in Saudi Arabia and Central Asia (COPR 1982).

Lathiceridae Members of this family are apterous, with a prognathous to opisthognathous head, and lack ocelli, a stridulatory mechanism, and a tympanum (Uvarov 1966). The depressed and rugose body form suggests that the family is highly adapted to a desert environment. The family includes three genera and four species (Eades et al. 2015), all endemic to the Namib Desert (Dirsh 1954). Members of this family are rarely collected and are seldom represented in museums.

Lentulidae This family is characterized by the absence of a fastigial furrow in the head, complete lack of wings, the absence of an abdominal tympanum, and a strongly developed capsule-like cingulum in the phallic complex. The body form can be quite variable, from robust and stout to elongated, and some species can be colorful. Lentulids are restricted to south of the Sahara in Africa, with most of the diversity in South Africa and East Africa (Brown 1961). Currently, there are two subfamilies (Lentulinae and Shelforditinae), 36 genera, and 103 species reported (Eades et al. 2015), but there are probably many more species to be described (Daniel Otte, personal communication).

Lithidiidae This family is characterized by typically being small, with a stout and depressed body form, an absence of a tympanum, and a wide mesosternal interspace in the thorax. This small family is restricted to the desert regions of South Africa and Namibia (Brown 1962),

and is known from four genera and 13 species (Eades et al. 2015). In the past, it has been treated as a subfamily of the Acrididae, but Eades (2000) elevated it to family level based on the unique shape of the phallic complex. A recent phylogenetic study placed it as being most closely related to the Lentulidae (Song et al. 2015).

Ommexechidae This family is characterized by often being dorsoventrally flattened, with protruding eyes and rugose integument. The Ommexechidae are restricted to South America and include three subfamilies (Ommexechinae, Aucaridinae, and Illapeliinae), with 13 genera and 33 species (Eades et al. 2015). The placement of the Aucaridinae and Illapeliinae in the Ommexechidae has been questioned several times because of different interpretations of male phallic structures (Eades 2000). A recent phylogenetic work based on morphology (Domenico 2012) found this family to be paraphyletic with the Tristiridae, but this situation needs further investigation. Not much is known about the biology of the family, but some species in *Clarazella* and *Ommexecha* feed on tobacco (COPR 1982).

Pamphagidae This family (Fig. 10.4k) is characterized by the lack of antennal grooves, the absence of apical fastigial areolae in the head, and a shield-like epiphallus in the phallic complex. The Pamphagidae are widely distributed in the Old World from Africa to Asia and include five subfamilies (Akicerinae, Echinotropinae, Pamphaginae, Porthetinae, and Thrinchinae) with 96 genera and 456 species (Eades et al. 2015). Many pamphagids are large and are weak jumpers and fliers (Kevan 1982). Sexual dimorphism is often dramatic in this group because males are fully winged (in those species that have wings), whereas females are flightless. Acoustic communication is well developed in this family, and males have specialized veins on the forewings that can stridulate against the abdomen or femur to produce sound (Kevan 1954, Johnsen 1972). Some species can be minor agricultural pests (COPR 1982). *Prionotropis*

hystrix rhodanica is endemic to the Crau Steppe in France (Foucart and Lecoq 1998) and, in 2012, was listed as critically endangered by the International Union for Conservation of Nature (IUCN) owing to a 2009 oil spill in that region (Hochkirch 2012).

Pamphagodidae This family is closely related to the Pamphagidae, but can be distinguished by the presence of two parallel median carinae in the pronotum (Dirsh 1953). The Pamphagodidae are represented by four genera and five species (three genera are monotypic) and are distributed across arid regions in Morocco (*Pamphagodes riffensis*) and South Africa (the other four species) (Eades et al. 2015). In past treatments, this family has been more commonly known as Charilaidae (Eades and Deem 2008), which is now a junior synonym of Pamphagodidae (ICZN 2012).

Pyrgacrididae This small family is only known from the Mascarene Islands (Mauritius and Réunion) in the Indian Ocean, east of Madagascar, and includes two apterous species (Hugel 2005). Its taxonomic placement has been questionable because its members have male phallic structures that are similar to those of the Acrididae (Eades 2000, Eades and Kevan 1974), but have a groove in the fastigium, which is diagnostic for the Pyrgomorphae. A recent molecular phylogenetic study (Song et al. 2015) found it to be the most basal lineage in the Acridoidea. The two known species (*Pyrgacris relictus* and *Pyrgacris descampsi*) feed exclusively on *Acanthophoenix* palms, which are endemic to the islands (Hugel 2005). Due to exotic palms and recent urban development, suitable habitats for the grasshoppers are rapidly diminishing and both species were listed as critically endangered by the IUCN in 2015 (Hugel 2014a, 2014b).

Romaleidae Commonly known as lubber grasshoppers, romaleids can be distinguished from the Acrididae by the presence of an external apical spur on the hind tibia. The tegmina are often

densely reticulated, and the hind wings are often brightly colored. Also, the valves of the cingulum in the phallic complex are often reduced or absent. This family is widely distributed in Central and South America, with a few representatives in North America, and consists of two subfamilies (Romaleinae and Bactrophorinae) with 110 genera and 471 species (Eades et al. 2015). The Romaleidae occur in various habitats from the tropics to the desert and feed on a variety of herbaceous plants. Many species, especially in the Romaleinae, possess what can be considered aposematic coloration, and some species exude distasteful chemicals through spiracles (Whitman 1991). Some species can be large (*Tropidacris* or *Titanacris*) and have the ability to defoliate entire trees (COPR 1982). Many species in the Bactrophorinae were not discovered until the 1970s because of their habit of dwelling in the canopies of Amazonian rainforests (Descamps 1978).

Tristiridae All members of this family are apterous and cryptically colored, and are often associated with arid habitats. This family is endemic to South America (Cigliano 1989) and includes two subfamilies (Atacamacridinae and Tristirinae), 18 genera and 25 species. Due to the similarity of male phallic structures to those of the Lentulidae and Pyrgomorphidae (Eades 2000, Eades and Kevan 1974), the phylogenetic position of the Tristiridae in the Acridoidea has always been questionable, but Song et al. (2015) suggested that this family is sister to a clade consisting of the Ommexechidae, Romaleidae, and Acrididae, indicating that the Tristiridae diverged prior to the evolution of modern grasshoppers.

Acknowledgments

I thank Peter Adler for inviting me to write this chapter. During the course of writing, I was constantly reminded of numerous orthopterists who have positively influenced me over the years, and I would like to express my gratitude to these mentors: the late Ted Cohn, the late Christiane

Amédégnato, Daniel Otte, Maria Marta Cigliano, Laure Desutter-Grandcolas, Dave Rentz, Dave Eades, the late Reg Chapman, Stephen Simpson, and Greg Sword. Derek A. Woller provided a critical review of an earlier version. Comments from two anonymous reviewers helped improve the clarity of this chapter. I thank Piotr Naskrecki, Hartmut Wisch, Robert A. Behrstock, Paolo Fontana, and Paul Lenhart for allowing me to use their fabulous photographs in the figures.

References

- Allegrucci, G., S. A. Trewick, A. Fortunato, G. Carchini and V. Sbordoni. 2010. Cave crickets and cave weta (Orthoptera, Rhabdophoridae) from the southern end of the world: a molecular phylogeny test of biogeographical hypotheses. *Journal of Orthoptera Research* 19: 121–130.
- Amédégnato, C. 1974. Les genres d'acridiens neotropicaux, leur classification par familles, sous-familles et tribus. *Acrida* 3: 193–203.
- Amédégnato, C., W. Chapco and G. Litzenberger. 2003. Out of South America? Additional evidence for a southern origin of melanopline grasshoppers. *Molecular Phylogenetics and Evolution* 29: 115–119.
- Amédégnato, C. and H. Devriese. 2008. Global diversity of true and pygmy grasshoppers (Acridomorpha, Orthoptera) in freshwater. *Hydrobiologia* 595: 535–543.
- Ander, K. 1939. Vergleichend-Anatomische und Phylogenetische Studien über die Ensifera (Saltatoria). *Opuscula Entomologica, Supplementum* 2: 1–306.
- Aydin, G. and A. Khomutov. 2008. The biology, nymphal stages, and life habits of the endemic sand dune cricket *Schizodactylus inexpectatus* (Werner, 1901) (Orthoptera: Schizodactylidae). *Turkish Journal of Zoology* 32: 427–432.
- Baccetti, B. M. 1987a. *Evolutionary Biology of Orthopteroid Insects*. Ellis Horwood Limited, Chichester, UK. 612 pp.
- Baccetti, B. M. 1987b. Spermatozoa and phylogeny in orthopteroid insects. Pp. 12–112.

- In B. M. Baccetti (ed). *Evolutionary Biology of Orthopteroid Insects*. Ellis Horwood Limited, Chichester, UK.
- Bailey, W. J. and D. C. F. Rentz. 1990. *The Tettigoniidae: Biology, Systematics and Evolution*. Crawford House, Bathurst, Australia. 395 pp.
- Bastow, J. L., J. L. Sabo, J. C. Finlay and M. E. Power. 2002. A basal aquatic–terrestrial trophic link in rivers: algal subsidies via shore-dwelling grasshoppers. *Oecologia* 131: 261–268.
- Bazelet, C. and P. Naskrecki. 2014. *Cedarbergeniana imperfecta*. The IUCN Red List of Threatened Species. Version 2014.3. <http://www.iucnredlist.org/details/20641422/0> [Accessed 1 March 2015].
- Belayneh, Y. T. 2005. Acridid pest management in the developing world: a challenge to the rural population, a dilemma to the international community. *Journal of Orthoptera Research* 14: 187–195.
- Blackith, R. E. and R. M. Blackith. 1968. A numerical taxonomy of orthopteroid insects. *Australian Journal of Zoology* 16: 111–131.
- Brader, L., H. Djibo and F. G. Faye. 2005. *Towards a More Effective Response to Desert Locusts and Their Impacts on Food Insecurity, Livelihoods and Poverty*. Independent Multilateral Evaluation of the 2003–2005 Desert Locust Campaign. Food and Agriculture Organization (FAO) of the United Nations, Rome, Italy.
- Brettschneider, H., C. T. Chimimba, C. H. Scholtz and P. W. Bateman. 2007. Review of southern African Anostomatidae (Orthoptera: Ensifera), with a key to genera. *African Entomology* 15: 103–119.
- Brown, H. D. 1961. A remarkable new genus of the family Lentulidae (Orthoptera: Acridoidea). *Journal of the Entomological Society of Southern Africa* 24: 253–258.
- Brown, H. D. 1962. New and interesting grasshoppers from Southern Africa – 2 (Orthoptera: Acridoidea). *Journal of the Entomological Society of Southern Africa* 25: 3–19.
- Carbonell, C. S. 1957. The external anatomy of the South American semiaquatic grasshopper *Marellia remipes* Uvarov (Acridoidea, Pauliniidae). *Smithsonian Miscellaneous Collections* 137: 61–97.
- Chapco, W., W. R. Kuperus and G. S. Litzenberger. 1999. Molecular phylogeny of melanopline grasshoppers (Orthoptera: Acrididae). The genus *Melanoplus*. *Annals of the Entomological Society of America* 92: 617–623.
- Chapco, W., G. Litzenberger and W. R. Kuperus. 2001. A molecular biogeographic analysis of the relationship between North American melanoploid grasshoppers and their Eurasian and South American relatives. *Molecular Phylogenetics and Evolution* 18: 460–466.
- Chapman, R. F., E. A. Bernays and T. Wyatt. 1988. Chemical aspects of host-plant specificity in three *Larrea*-feeding grasshoppers. *Journal of Chemical Ecology* 14: 557–575.
- Chapman, R. F. and A. Joern. 1990. *Biology of Grasshoppers*. John Wiley & Sons, New York, New York. 576 pp.
- Chapman, R. F. W. W. Page and A. R. McCaffery. 1986. Bionomics of the variegated grasshopper (*Zonocerus variegatus*) in West and Central Africa. *Annual Review of Entomology* 31: 479–505.
- Chapman, R. F. and G. A. Sword. 1997. Polyphagy in the Acridomorpha. Pp. 183–196. In S. K. Gangwere, M. C. Muralirangan, M. Muralirangan (eds). *The Bionomics of Grasshoppers, Katydid and Their Kin*. CAB International, Wallingford, UK.
- Chintauan-Marquier, I. C., S. Jordan, P. Berthier, C. Amédégnato and F. Pompanon. 2011. Evolutionary history and taxonomy of a short-horned grasshopper subfamily: the Melanoplineae (Orthoptera: Acrididae). *Molecular Phylogenetics and Evolution* 58: 22–32.
- Chintauan-Marquier, I. C., F. Legendre, S. Hugel, T. Robillard, P. Grandcolas, A. Nel, D. Zuccon and L. Desutter-Grandcolas. 2016. Laying the foundations of evolutionary and systematic studies in crickets (Insecta, Orthoptera): a multilocus phylogenetic analysis. *Cladistics* 32: 54–81.

- Chopard, L. 1920. *Recherches sur la conformation et le développement des derniers segments abdominaux chez les Orthoptères*. Thèse de la Faculté des Sciences de Paris. Imprimerie Oberthur, Rennes, France.
- Chopard, L. 1949. Ordres des Orthoptères. Pp. 617–722. In P. P. Grassé (ed). *Traité de Zoologie*. Masson, Paris, France.
- Cigliano, M. M. 1989. A cladistic analysis of the family Tristiridae (Orthoptera, Acridoidea). *Cladistics* 5: 379–393.
- COPR. 1982. *The Locust and Grasshopper Agricultural Manual*. Centre for Overseas Pest Research, London, UK. 690 pp.
- Descamps, M. 1973. Révision des Eumastacoidea (Orthoptera) aux échelons des familles et des sous-familles (genitalia, répartition, phylogénie). *Acrida* 2: 161–298.
- Descamps, M. 1976a. La faune dendrophile néotropicale I. Revue des Proctolabinae (Orth. Acrididae). *Acrida* 5: 63–167.
- Descamps, M. 1976b. Le peuplement acridien d'un périmètre d'Amazonie Colombienne. *Annales de la Société Entomologique de France* 12: 291–318.
- Descamps, M. 1976c. Les Nicarchi, Ommatolampini dendrosclérophiles de la forêt néotropicale [Acridomorpha, Ommatolampinae]. *Annales de la Société Entomologique de France* 12: 509–526.
- Descamps, M. 1977. Monographie des Thericleidae (Orthoptera Acridomorpha Eumastacoidea). *Annales du Musée royal de l'Afrique centrale* 8: 1–475.
- Descamps, M. 1978. La faune dendrophile néotropicale II. Revue des Taeniophorini et Ophthalmolampini (Orth. Romaleidae). *Bulletin du Muséum National d'Histoire Naturelle, 3e série, no 517, Zoologie* 355: 371–476.
- Desutter, L. 1987. Structure et évolution du complexe phallique des Gryllidea (Orthoptera) et classification des genres néotropicaux de Grylloidea. 1ère partie. *Annales de la Société Entomologique de France* 23: 213–239.
- Desutter-Grandcolas, L. 2003. Phylogeny and the evolution of acoustic communication in extant Ensifera (Insecta, Orthoptera). *Zoologica Scripta* 32: 525–561.
- Deyrup, M. 1996. Two new grasshoppers from relict uplands of Florida (Orthoptera: Acrididae). *Transactions of the American Entomological Society* 122: 199–211.
- Dirsh, V. M. 1953. Charilainae, a new subfamily of Acrididae (Orthoptera). *Annals and Magazine of Natural History* 6: 161–173.
- Dirsh, V. M. 1954. Lathicerinae, a new subfamily of Acrididae (Orthoptera). *Annals and Magazine of Natural History* 7: 670–672.
- Dirsh, V. M. 1955. Tanaoceridae and Xyronotidae: two new families of Acridoidea (Orthoptera). *Annals and Magazine of Natural History* 8: 285–288.
- Dirsh, V. M. 1957. The spermatheca as a taxonomic character in Acridoidea (Orthoptera). *Proceedings of the Royal Entomological Society of London Series A General Entomology* 32: 107–114.
- Dirsh, V. M. 1965. Revision of the family Pneumoridae (Orthoptera: Acridoidea). *Bulletin of the British Museum (Natural History) Entomology* 15: 325–396.
- Dirsh, V. M. 1973. Genital organs in Acridomorpha (Insecta) as taxonomic character. *Zeitschrift für die Zoologische Systematik und Evolutionsforschung* 11: 133–154.
- Dirsh, V. M. 1975. *Classification of the Acridomorphoid Insects*. E.W. Classey Ltd., Faringdon, UK.
- Dirsh, V. M. and J. B. Mason. 1979. Systematic and phylogenetic position of the family Xyronotidae (Acridomorpha, Insecta). *Zeitschrift für die Zoologische Systematik und Evolutionsforschung* 17: 201–210.
- Domenico, F. C. 2012. *Estudo filogenético da família Ommexechidae (Orthoptera, Caelifera, Acridomorpha)*. Doctoral thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil.
- Donelson, N. C. and M. J. van Staaden. 2005. Alternate tactics in male bladder grasshoppers *Bullacris membracioides* (Orthoptera: Pneumoridae). *Behaviour* 142: 761–778.

- Eades, D. C. 2000. Evolutionary relationships of phallic structures of Acridomorpha (Orthoptera). *Journal of Orthoptera Research* 9: 181–210.
- Eades, D. C. and L. S. Deem. 2008. CHARILAIIDAE Dirsh, 1953 (Insecta, Orthoptera): proposed precedence over PAMPHAGODIDAE I. Bolivar, 1916. *Bulletin of Zoological Nomenclature* 65: 20–23.
- Eades, D. C. and D. K. M. Kevan. 1974. The phallic musculature of Pyrgomorphidae, with particular reference to *Atractomorpha sinensis sinensis* Bolivar, and notes on the family Tristiridae and the subfamily Pyrgacridinae, nov. (Orthoptera: Acridoidea). *Acrida* 3: 247–265.
- Eades, D. C., D. Otte, M. M. Cigliano and H. Braun. 2015. Orthoptera Species File. Version 5.0/5.0. [3/1/2015]. <http://Orthoptera.SpeciesFile.org> [Accessed 1 March 2015].
- Elliott, W. R. and G. Veni. 1994. *The Caves and Karst of Texas (1994 National Speleological Society Convention Guidebook)*. National Speleological Society, Huntsville, AL. 342 pp.
- FAO. 2013. *Edible Insects: Future Prospects for Food and Feed Security*. Food and Agriculture Organization (FAO) of the United Nations, Rome, Italy. 187 pp.
- Field, L. H. 2001a. *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, UK. 540 pp.
- Field, L. H. 2001b. Stridulatory mechanisms and associated behaviour in New Zealand wetas. Pp. 271–296. In L. H. Field (ed). *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, UK.
- Field, L. H. and T. H. Jarman. 2001. Mating behaviour. Pp. 317–332. In L. H. Field (ed). *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, UK.
- Flook, P. K. and C. H. F. Rowell. 1997. The phylogeny of the Caelifera (Insecta, Orthoptera) as deduced from mtrRNA gene sequences. *Molecular Phylogenetics and Evolution* 8: 89–103.
- Flook, P. K., S. Klee and C. H. F. Rowell. 1999. Combined molecular phylogenetic analysis of the Orthoptera (Arthropoda, Insecta) and implications for their higher systematics. *Systematic Biology* 48: 233–253.
- Flook, P. K., S. Klee and C. H. F. Rowell. 2000. Molecular phylogenetic analysis of the Pneumoroidea (Orthoptera, Caelifera): molecular data resolve morphological character conflicts in the basal Acridomorpha. *Molecular Phylogenetics and Evolution* 15: 345–354.
- Fontana, P., F. M. Buzzetti and R. Mariño-Pérez. 2008. *Chapulines, Langostas, Grillos y Esperanzas de México. Guía fotográfica—Grasshoppers, Locusts, Crickets & Katydid of Mexico. Photographic Guide*. World Biodiversity Association, Verona, Italy. 272 pp.
- Foucart, A. and M. Lecoq. 1998. Major threats to a protected grasshopper, *Prionotropis hystrix rhodanica* (Orthoptera, Pamphagidae, Akicerinae), endemic to southern France. *Journal of Insect Conservation* 2: 187–193.
- Frank, J. H. and J. P. Parkman. 1999. Integrated pest management of pest mole crickets with emphasis on the southeastern USA. *Integrated Pest Management Review* 4: 39–52.
- Gahukar, R. T. 2011. Entomophagy and human food security. *International Journal of Tropical Insect Science* 31: 129–144.
- Gangwere, S. K., M. C. Muralirangan and M. Muralirangan. 1997. *The Bionomics of Grasshoppers, Katydid, and Their Kin*. CAB International, New York, New York. 529 pp.
- Gorochov, A. V. 1995a. Contribution to the system and evolution of the order Orthoptera. *Zoologicheskii Zhurnal* 74: 39–45.
- Gorochov, A. V. 1995b. System and evolution of the suborder Ensifera (Orthoptera). Part 1. *Trudy Zoologicheskogo Instituta* 260: 1–224.
- Gorochov, A. V. 2001. The higher classification, phylogeny and evolution of the superfamily Stenopelmatoidea. In L. H. Field (ed). Pp. 3–33. *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Cambridge, Massachusetts.
- Gorochov, A. V. 2012. Systematics of the American katydids (Orthoptera: Tettigoniidae). Communication 1. *Proceedings of the Zoological Institute RAS* 316: 3–21.

- Grant, H. J., Jr. and D. C. F. Rentz. 1967. A biosystematic review of the family Tanaoceridae including a comparative study of the proventriculus. *Pan-Pacific Entomologist* 43: 65–74.
- Greenfield, M. D. 1997. Acoustic communication in Orthoptera. Pp. 197–230. In S. K. Gangwere, M. C. Muralirangan and M. Muralirangan (eds). *The Bionomics of Grasshoppers, Katydid and Their Kin*. CAB International, Wallingford, UK.
- Grimaldi, D. and M. S. Engel. 2005. *Evolution of the Insects*. Cambridge University Press, New York, New York. 772 pp.
- Günther, K. K. 1969. Revision der familie Rhipipterygidae Chopard, 1949 (Saltatoria, Insecta). *Mitteilungen aus dem Zoologischen Museum in Berlin* 45: 259–425.
- Günther, K. K. 1979. Einige Bemerkungen über die Gattungen der Familie Tridactylidae Brunner und zur Klassifikation der Tridactyloidea. *Deutsche entomologische Zeitschrift, N.F.* 26: 255–264.
- Günther, K. K. 1992. Revision der Familie Cylindrachetidae Giglio-Tos, 1914. *Deutsche entomologische Zeitschrift, N.F.* 39: 233–291.
- Gwynne, D. T. 1993. Food quality controls—sexual selection in Mormon crickets by altering male mating investment. *Ecology* 74: 1406–1413.
- Gwynne, D. T. 1995. Phylogeny of the Ensifera (Orthoptera): a hypothesis supporting multiple origins of acoustical signalling, complex spermatophores and maternal care in crickets, katydids, and weta. *Journal of Orthoptera Research* 4: 203–218.
- Gwynne, D. T. 2001. *Katydid and Bush-crickets: Reproductive Behavior and Evolution of the Tettigoniidae*. Cornell University Press, Ithaca, New York. 317 pp.
- Gwynne, D. T. and I. Jamieson. 1998. Sexual selection and sexual dimorphism in a harem-polygynous insect, the alpine weta (*Hemideina maori*, Orthoptera Stenopelmatidae). *Ethology Ecology & Evolution* 10: 393–402.
- Heads, S. W. and L. Leuzinger. 2011. On the placement of the Cretaceous orthopteran *Brauckmannia groeningae* from Brazil, with notes on the relationships of Schizodactylidae (Orthoptera, Ensifera). *ZooKeys* 77: 17–30.
- Heller, K.-G., C. Hemp, C. Liu and M. Volleth. 2014. Taxonomic, bioacoustic and faunistic data on a collection of Tettigonioidae from Eastern Congo (Insecta: Orthoptera). *Zootaxa* 3785: 343–376.
- Henderson, G. and R. D. Akre. 1986. Biology of the myrmecophilous cricket, *Myrmecophila manni* (Orthoptera: Gryllidae). *Journal of the Kansas Entomological Society* 59: 454–467.
- Hochkirch, A. and J. Gröning. 2008. Sexual size dimorphism in Orthoptera (*sens. str.*)—a review. *Journal of Orthoptera Research* 17: 189–196.
- Hochkirch, A. 2012. *Prionotropis hystrix ssp. rhodanica*. The IUCN Red List of Threatened Species. Version 2014.3. <http://www.iucnredlist.org/details/15038481/0> [Accessed 1 March 2015].
- Hubbell, T. H. 1932. A revision of the Puer group of the North American genus *Melanoplus*, with remarks on the taxonomic value of the concealed male genitalia in the Cyrtacanthacridinae (Orthoptera, Acrididae). *Miscellaneous Publications, Museum of Zoology, University of Michigan* 23: 1–64.
- Hubbell, T. H. 1936. A monographic revision of the genus *Ceuthophilus* (Orthoptera, Gryllacrididae, Rhabdophorinae). *University of Florida Publication, Biological Science Series* 2: 1–551.
- Hubbell, T. H. and F. W. Walker. 1928. A new shrub-inhabiting species of *Schistocerca* from Central Florida. *Occasional Papers of the Museum of Zoology, University of Michigan* 197: 1–10.
- Hugel, S. 2005. Redécouverte du genre *Pygacris* à l'île de la Réunion: description du mâle de *P. descampsi* Kevan, 1975 (Orthoptera, Caelifera). *Bulletin de la Société Entomologique de France* 110: 153–159.
- Hugel, S. 2014a. *Pygacris descampsi*. The IUCN Red List of Threatened Species. Version 2014.3. <http://www.iucnredlist.org/details/62148098/0> [Accessed 1 March 2015].
- Hugel, S. 2014b. *Pygacris relictus*. The IUCN Red List of Threatened Species. Version 2014.3.

- <http://www.iucnredlist.org/details/full/55929685/0> [Accessed 1 March 2015].
- ICZN. 2012. Opinion 2309 (Case 3429) Charilaidae Dirsh, 1953 (Insecta, Orthoptera): proposed precedence over Pamphagodidae I. Bolívar, 1916 not granted. *Bulletin of Zoological Nomenclature* 69: 297–299.
- Isley, F. B. 1944. Correlation between mandibular morphology and food specificity in grasshoppers. *Annals of the Entomological Society of America* 37: 47–67.
- Jago, N. D. 1989. The genera of the Central and South American grasshopper family Proscopiidae (Orthoptera: Acridomorpha). *Eos* 65: 249–307.
- Johnsen, P. 1972. Alar-notal and tegmino-alar sound production in the African *Glaudia* and *Acinipe* (Acridoidea: Pamphagidae), with notes on other behavior. *Natura Jutlandica* 16: 61–80.
- Johnson, J. C., T. M. Ivy and S. K. Sakaluk. 1999. Female remating propensity contingent on sexual cannibalism in sagebrush crickets, *Cyphoderris strepitans*: a mechanism of cryptic female choice. *Behavioral Ecology* 10: 227–233.
- Jost, M. C. and K. L. Shaw. 2006. Phylogeny of Ensifera (Hexapoda: Orthoptera) using three ribosomal loci, with implications for the evolution of acoustic communication. *Molecular Phylogenetics and Evolution* 38: 510–530.
- Judd, W. W. 1947. A comparative study of the proventriculus of orthopteroid insects with reference to its use in taxonomy. *Canadian Journal of Research* 26: 93–159.
- Kevan, D. K. M. 1953. An unusual stridulatory mechanism in *Xyronotus aztecus* Sauss. (Orth., Acrididae). *Entomologist's Monthly Magazine* 139: 169–170.
- Kevan, D. K. M. 1954. "Unorthodox" methods of sound-production in Orthoptera. *Special Papers of the University of Nottingham School of Agriculture Zoology Section* 2: 1–22.
- Kevan, D. K. M. 1966. A new genus of Trigonopterygidae (Orthoptera: Acridoidea) from Sabah (North Borneo). *Pacific Insects* 8: 389–396.
- Kevan, D. K. M. 1973. The place of classical taxonomy in modern systematic entomology, with particular reference to orthopteroid insects. *Canadian Entomologist* 105: 1211–1222.
- Kevan, D. K. M. 1982. Orthoptera. Pp. 352–383. In S. P. Parker (ed). *Synopsis and Classification of Living Organisms*. McGraw-Hill Book Company, New York, New York.
- Kevan, D. K. M. and S. S. Akbar. 1964. The Pyrgomorphidae (Orthoptera: Acridoidea): their systematics, tribal divisions and distribution. *Canadian Entomologist* 96: 1505–1536.
- Key, K. H. L. 1976. A generic and suprageneric classification of the Morabinae (Orthoptera: Eumastacidae), with description of the type species and a bibliography of the subfamily. *Australian Journal of Zoology Supplementary Series* 37: 1–185.
- Key, K. H. L. 1981. Species, parapatry, and the morabine grasshoppers. *Systematic Zoology* 30: 425–458.
- Knowles, L. L. 2001. Genealogical portraits of speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of the Rocky Mountains. *Proceedings of the Royal Society of London B* 268: 319–324.
- Knowles, L. L. and C. L. Richards. 2005. Importance of genetic drift during Pleistocene divergence as revealed by analyses of genomic variation. *Molecular Ecology* 14: 4023–4032.
- Komatsu, T., M. Maruyama, S. Ueda and T. Itino. 2008. mtDNA phylogeny of Japanese ant crickets (Orthoptera: Myrmecophilidae): diversification in host specificity and habitat use. *Sociobiology* 52: 1–12.
- Latchininsky, A. V. 2010. Locusts. Pp. 288–297. In M. D. Breed and J. Moore (eds). *Encyclopedia of Animal Behavior*. Volume 2. Academic Press, Oxford, UK.
- Latchininsky, A. V., G. A. Sword, M. G. Sergeev, M. M. Cigliano and M. Lecoq. 2011. Locusts and grasshoppers: behavior, ecology and biogeography. *Psyche* 2011: 578327.
- Lavoie, K.H., K. L. Helf and T. L. Poulson. 2007. The biology and ecology of North American

- cave crickets. *Journal of Cave and Karst Studies* 69: 114–134.
- Leavitt, J. R., K. D. Hiatt, M. F. Whiting and H. Song. 2013. Searching for the optimal data partitioning strategy in mitochondrial phylogenomics: a phylogeny of Acridoidea (Insecta: Orthoptera: Caelifera) as a case study. *Molecular Phylogenetics and Evolution* 67: 494–508.
- Lecoq, M. 2005. Desert locust management: from ecology to anthropology. *Journal of Orthoptera Research* 14: 179–186.
- Legendre, F., T. Robillard, H. Song, M. F. Whiting and L. Desutter-Grandcolas. 2010. One hundred years of instability in ensiferan relationships. *Systematic Entomology* 35: 475–488.
- Lockwood, J. A., A. T. Showler and A. V. Latchininsky. 2001. Can we make locust and grasshopper management sustainable? *Journal of Orthoptera Research* 10: 315–329.
- Matt, S., P. K. Flook and C. H. F. Rowell. 2008. A partial molecular phylogeny of the Eumastacoidea *s. lat.* (Orthoptera, Caelifera). *Journal of Orthoptera Research* 17: 43–55.
- Misof, B., S. Liu, K. Meusemann, R. S. Peters, A. Donath, C. Mayer et al. [95 additional authors]. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science* 346: 763–767.
- Morris, G. K. and D. T. Gwynne. 1978. Geographical distribution and biological observations of *Cyphoderris* (Orthoptera: Haglidae) with a description of a new species. *Psyche* 85: 147–167.
- Mugleston, J. D., H. Song and M. F. Whiting. 2013. A century of paraphyly: a molecular phylogeny of katydids (Orthoptera: Tettigoniidae) supports multiple origins of leaf-like wings. *Molecular Phylogenetics and Evolution* 69: 1120–1134.
- Nickle, D. A. and J. L. Castner. 1995. Strategies utilized by katydids (Orthoptera: Tettigoniidae) against diurnal predators in rainforests of northeastern Peru. *Journal of Orthoptera Research* 4: 75–88.
- Otte, D. 1970. A comparative study of communicative behavior in grasshoppers. *Miscellaneous Publications Museum of Zoology, University of Michigan* 141: 1–168.
- Otte, D. 1981. *The North American Grasshoppers Volume 1. Acrididae: Gomphocerinae and Acridinae*. Harvard University Press, Cambridge, Massachusetts. 304 pp.
- Otte, D. and A. Joern. 1977. On feeding patterns in desert grasshoppers and the evolution of specialized diets. *Proceedings of the Academy of Natural Sciences of Philadelphia* 128: 89–126.
- Pener, M. P. 1983. Endocrine aspects of phase polymorphism in locusts. Pp. 379–394. In R. G. H. Downer and H. Laufer (eds). *Invertebrate Endocrinology*. Volume 1. Endocrinology of Insects. Alan R. Liss Inc., New York, New York.
- Pener, M. P. and S. J. Simpson. 2009. Locust phase polyphenism: an update. *Advances in Insect Physiology* 36: 1–286.
- Peveling, R. 2005. We believe what we see—and vice versa: evidence versus perception in locust control. *Journal of Orthoptera Research* 14: 207–212.
- Qureshi, S. A. and I. Ahmad. 1970. Studies on the functional anatomy and histology of the repellent gland of *Poeciloceris pictus* (F.) (Orthoptera: Pyrgomorphidae). *Proceedings of the Royal Entomological Society of London A* 45: 149–155.
- Ragge, D. R. 1955. *The Wing-venation of the Orthoptera Saltatoria, with Notes on Dictyopteran Wing-venation*. British Museum of Natural History, London, UK. 159 pp.
- Ramos-Elorduy, J., J. M. P. Moreno, E. E. Prado, M. A. Perez, J. L. Otero and O. L. De Guevara. 1997. Nutritional value of edible insects from the state of Oaxaca, Mexico. *Journal of Food Composition and Analysis* 10: 142–157.
- Raubenheimer, D. and J. M. Rothman. 2013. Nutritional ecology of entomophagy in humans and other primates. *Annual Review of Entomology* 58: 141–160.
- Rehn, J. A. G. and M. Hebard. 1912. A revision of the genera and species of the group *Mogoplistii* (Orthoptera: Gryllidae) found in North America north of the Isthmus of Panama. *Proceedings of the Academy of Natural Sciences of Philadelphia* 64: 184–234.

- Rentz, D. C. F. 1986. The Orthoptera family Cooloolidae, including description of two new species and observations on biology and food preferences. *Systematic Entomology* 11: 231–246.
- Rentz, D. C. F. 1996. *Grasshopper Country: The Abundant Orthopteroid Insects of Australia*. University of New South Wales Press, Sydney, Australia. 284 pp.
- Roberts, H. R. 1941. A comparative study of the subfamilies of the Acrididae (Orthoptera) primarily on the bases of their phallic structures. *Proceedings of the Academy of Natural Sciences of Philadelphia* 93: 201–246.
- Rowell, C. H. F. 1967. Experiments on aggregations of *Phymateus purpurascens* (Orthoptera, Acrididae, Pyrgomorphidae). *Journal of Zoology (London)* 152: 179–193.
- Sharov, A. G. 1968. Phylogeny of the Orthopteroidea. *Akademiya Nauk SSSR Trudy Paleontologicheskogo Instituta* 118: 1–216.
- Simpson, S. J. and G. A. Sword. 2009. Phase polyphenism in locusts: mechanisms, population consequences, adaptive significance and evolution. Pp. 147–190. In D. W. Whitman and T. N. Ananthakrishnan (eds). *Phenotypic Plasticity of Insects: Mechanisms and Consequences*. Science Publishers, Enfield, New Hampshire.
- Slifer, E. H. 1939. The internal genitalia of female Acridinae, Oedipodinae and Pauliniinae (Orthoptera, Acrididae). *Journal of Morphology* 65: 437–469.
- Smith, T. R. and J. L. Capinera. 2005. Host preferences and habitat associations of some Florida grasshoppers (Orthoptera: Acrididae). *Environmental Entomology* 34: 210–224.
- Song, H. 2010. Grasshopper systematics: past, present and future. *Journal of Orthoptera Research* 19: 57–68.
- Song, H. 2011. Density-dependent phase polyphenism in nonmodel locusts: a minireview. *Psyche* 2011: 741769.
- Song, H., C. Amédégno, M. M. Cigliano, L. Desutter-Grandcolas, S. W. Heads, Y. Huang, D. Otte and M. F. Whiting. 2015. 300 million years of diversification: elucidating the patterns of orthopteran evolution based on comprehensive taxon and gene sampling. *Cladistics* 31: 621–651.
- Song, H. and R. Mariño-Pérez. 2013. Re-evaluation of taxonomic utility of male phallic complex in higher-level classification of Acridomorpha (Orthoptera: Caelifera). *Insect Systematics & Evolution* 44: 241–260.
- Sword, G. A., M. Lecoq and S. J. Simpson. 2010. Phase polyphenism and preventative locust management. *Journal of Insect Physiology* 56: 949–957.
- Sword, G. A. and S. J. Simpson. 2008. Locusts. *Current Biology* 18: 364–366.
- Tatarnic, N. J., K. D. L. Umbers and H. Song. 2013. Molecular phylogeny of the *Kosciuscola* grasshoppers endemic to the Australian alpine and montane regions. *Invertebrate Systematics* 27: 307–316.
- Uvarov, B. P. 1921. A revision of the genus *Locusta*, L. (= *Pachytylus*, Fieb.), with a new theory as to the periodicity and migrations of locusts. *Bulletin of Entomological Research* 12: 135–163.
- Uvarov, B. P. 1966. *Grasshoppers and Locusts*. Volume 1. Cambridge University Press, Cambridge, UK.
- Uvarov, B. P. 1977. *Grasshoppers and Locusts*. Volume 2. Centre for Overseas Pest Research, London, UK.
- van Staaden, M. J. and H. Römer. 1997. Sexual signalling in bladder grasshoppers: tactical design for maximizing calling range. *Journal of Experimental Biology* 200: 2597–2608.
- van Staaden, M. J. and H. Römer. 1998. Evolutionary transition from stretch to hearing organs in ancient grasshoppers. *Nature* 394: 773–776.
- Vickery, V. R. 1977. Taxon ranking in Grylloidea and Gryllotalpoidea. *Lyman Entomological Museum and Research Laboratory Memoir* 4: 1–31.
- Vickery, V. R. 1997. Classification of the Orthoptera (*sensu stricto*) or Caelifera. Pp. 5–40. In S. K. Gangwere, M. C. Muralirangan and M. Muralirangan (eds). *The Bionomics of Grasshoppers, Katydid and Their Kin*. CAB International, Wallingford, UK.

- Walker, A. A., S. Weisman, J. S. Church, D. J. Merritt, S. T. Mudie and T. D. Sutherland. 2012. Silk from crickets: a new twist on spinning. *PLoS One* 7: e30408.
- Weissman, D. B. 2001a. Communication and reproductive behaviour in North American Jerusalem crickets (*Stenopelmatus*) (Orthoptera: Stenopelmatidae). Pp. 351–373. In L. H. Field (ed). *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, UK.
- Weissman, D. B. 2001b. North and Central American Jerusalem crickets (Orthoptera: Stenopelmatidae): taxonomy, distribution, life cycle, ecology and related biology of the American species. Pp. 57–72. In L. H. Field (ed). *The Biology of Wetas, King Crickets and Their Allies*. CABI Publishing, Wallingford, UK.
- Wheeler, W. C., M. Whiting, Q. D. Wheeler and J. M. Carpenter. 2001. The phylogeny of the extant hexapod orders. *Cladistics* 17: 113–169.
- Whitman, D. W. 1991. Grasshopper chemical communication. Pp. 357–391. In R. F. Chapman and A. Joern (eds). *Biology of Grasshoppers*. John Wiley & Sons, New York, New York.
- Zeuner, F. E. 1939. *Fossil Orthoptera Ensifera*. [2 volumes] British Museum (Natural History), London, UK.
- Zeuner, F. E. 1942. The Locustopsidae and the phylogeny of the Acridodea (Orthoptera). *Proceedings of the Royal Entomological Society of London B* 11: 1–18.
- Zhang, H., Y. Huang, L. Lin, X. Wang and Z. Zheng. 2013. The phylogeny of the Orthoptera (Insecta) as deduced from mitogenomic gene sequences. *Zoological Studies* 52: 37.
- Zhou, Z., H. Ye, Y. Huang and F. Shi. 2010. The phylogeny of Orthoptera inferred from mtDNA and description of *Elimaea cheni* (Tettigoniidae: Phaneropterinae) mitogenome. *Journal of Genetics and Genomics* 37: 315–324.