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REVIEW ARTICLE

# Patterns in Orthoptera biodiversity. I. Adaptations in ecological and evolutionary contexts

**Claudio J. Bidau**[1]

*[1]Paraná y Los Claveles, 3304 Garupá, Misiones, Argentina. E-mail: bidau47@yahoo.com*

**Abstract:** The Orthoptera have inhabited the Earth for ca 300 million years and today include about 25,000 described species. Although orthopterans are mainly known to the general public by their most conspicuous species such as rangeland grasshoppers, locusts, katydids and crickets, they include an amazing diversity of forms and life-styles. In this review, I bring together a series of facts about orthopteran biology that demonstrate their enormous biodiversity, concentrating on ecological and evolutionary characteristics such as habitat variation, modes of feeding, defense mechanisms and phase transformation. In a second part of this review I will consider subjects of more direct human interest as their use as food, their importance in folk medicine and their role as entertainment.

**Key words:** Anti-predator defenses; cricket; feeding habits; grasshopper; habitat; katydid; locust; phase polyphenism; weta.

> *“The poetry of earth is never dead:*
> *When all the birds are faint with the hot sun,*
> *And hide in cooling trees, a voice will run*
> *From hedge to hedge about the new-mown mead;*
> *That is the Grasshopper's--he takes the lead*
> *In summer luxury,--he has never done*
> *With his delights; for when tired out with fun*
> *He rests at ease beneath some pleasant weed.*
> *The poetry of earth is ceasing never:*
> *On a lone winter evening, when the frost*
> *Has wrought a silence, from the stove there shrills*
> *The Cricket's song, in warmth increasing ever,*
> *And seems to one in drowsiness half lost,*
> *The Grasshopper's among some grassy hills.”*
>
> John Keats, On the Grasshopper and Cricket, December 1816

## Introduction

Insects are small animals and many species pass unnoticed to most humans; however, their stunning diversity – recognised since ancient times – is unrivaled on Earth (Capinera

2008a; Resh &Cardé 2009; Gullan & Cranston 2010). About one million species are extant and certainly many more await discovery and description, especially in the tropics. The class includes 30 orders with variable number of species: the less diverse include the Mantophasmatodea (gladiators, 24 spp.) (Zompro *et al.* 2002; Damgaard *et al.* 2008), Grylloblattodea (icecrawlers, 32 spp.) (Wipfler *et al*. 2014), and Zoraptera (angel insects, 30 spp.) (Mashimo *et al.* 2014); whereas the more diverse comprise the Diptera (flies, 100,000 spp.), Hemiptera (bugs, 100,000 spp.), Hymenoptera (wasps, bees, ants, and sawflies; 120,000 spp.), Lepidoptera (butterflies and moths, 150,000 spp.) and, of course, the Coleoptera (beetles, 370,000 spp.) (Capinera 2008a). The Orthoptera *sensu stricto* is somewhat in the middle regarding number of species (ca 25,000) although this figure may be doubled with new species from poorly surveyed or unexplored regions. The order includes well-known insects such as grasshoppers, locusts, katydids and crickets but also, bush-crickets, wetas, mole-crickets, ant-inquiline crickets etc (Table 1).

Orthopterans (and most insects) and humans have had a "love-hate" relationship for millenia (Grimaldi & Engel 2005; Rehling 2013). These insects have been artistically represented in most cultures since the Paleolithic, and are present in mytholgy, folklore, and all aspects of culture. Orthoptera is an order of the Neoptera group of winged insects which appeared in the earliest Late Carboniferous and are briefly defined by the possession of special muscles attached to the third axillary sclerite which allows wing flexion, other wing novelties, and the apparition of the ovipositor gonoplac. The Neoptera has been an extraordinarily successful insect group with representatives in every possible aquatic or terrestrial environment. The stem group is probably the Carboniferous family Paoliidae. Within the Neoptera, the Polyneoptera (or Orthopteroid-Plecopteroid assemblage of Neoptera) includes about 11 orders: Isoptera, Blattodea, Mantodea, Dermaptera, Grylloblattodea, Plecoptera, Orthoptera, Phasmatodea, Embioptera, Zoraptera and Mantophasmatodea. Orthoptera originated about 300 million years ago in the Upper Carboniferous-Permian period from the late Paleozoic, which is well represented by an extensive geological record. The Polyneopteran group "Protorthoptera", is a polyphyletic assemblage used as a "container" for all Paleozoic or Early Mesozoic insects which cannot be assigned to any of the extant orders. Protorthopterans retain many primitive traits not only of Polyneoptera but of Neoptera as a whole. The Orthoptera probably underwent an early split that led to the two recognised monophyletic suborders: Ensifera (Fig. 1) and Caelifera (Fig. 2) although the former are considered more primitive. However, it has been suggested that Ensifera and Caelifera could have evolved independently from different protorthopteran ancestors, and the appearance of enlarged hind legs for leaping could have been the result of convergent evolution. However, this characteristic first appeared in the Paleozoic Oedischiidae (classically assigned to Ensifera) that could in fact be the stem group from which both suborders evolved. It is worth noting that both suborders differ radically in the mechanisms of sound-production: the fossil record shows that stridulatory organs on wings seem to have first appeared in the Triassic in Ensiferan families, such as Haglidae and Gryllidae. Nevertheless, the general consensus is that Ensifera and Caelifera constitute a monophyletic clade. The first definitive fossil evidence of the existence of both Orthopteran suborders comes from the end of the Permian and early Triassic periods (see Bethoux *et al.* 2002; Legendre *et al.* 2010; Bethoux 2012 for Ensifera, and Jarzembowski 1999 and references therein, for Caelifera; also, Gwynne & DeSutter 1999; Rowell & Flook 2001; Rasnitsyn & Quicke 2002).

Orthopterans have a long and distinguished history as subjects of biological investigations. The first written account of Orthoptera is 5,000 years old. The Babylonian Urra = Hubullu (or Harra = Hubullu) is the first known “dictionary” or “encyclopedia” which belongs to the Sumerian (2900-2334 B.C.) and Akkadian periods (2334-2154 B.C.) (Watson & Horowitz

**Table 1.** Number of species in all recognised families of Orthoptera.

| Suborder | Superfamily | Family | Common name | Number of species |
|---|---|---|---|---|
| Ensifera | Grylloidea | Gryllidae | True crickets | 1115 |
| | | Gryllotalpidae | Mole crickets | 111 |
| | | Mogoplistidae | Scaly crickets | 372 |
| | | Myrmecophilidae | Ant crickets | 71 |
| | Hagloidea | Prophalangopsidae | Grigs | 8 |
| | Raphidiophoroidea | Raphidiophoridae | Camel crickets, Cave crickets, Cave wetas | 627 |
| | Schizodactyloidea | Schizodactylidae | Dune crickets | 16 |
| | Stenopelmatoidea | Anostostomatidae | Wetas, King crickets | 206 |
| | | Cooloolidae | Cooloola monsters | 4 |
| | | Gryllacrididae | Leaf-rolling crickets, Raspy crickets | 756 |
| | | Stenopelmatidae | Jerusalem crickets | 39 |
| | Tettigonioidea | Tettigoniidae | Katydids, Bush crickets | >6,400 |
| Caelifera | Acridoidea | Acrididae | Grasshoppers, Locusts | >10,000 |
| | | Dericorythidae | * | 181 |
| | | Lathiceridae | Desert gravel-hoppers | 4 |
| | | Lentulidae | Wingless or nymph-like grasshoppers | 104 |
| | | Lithidiidae | * | 13 |
| | | Ommexechidae | South American toad-hoppers | 33 |
| | | Pamphagidae | Toad grasshoppers | 511 |
| | | Pamphagodidae | Tween-keeled grasshoppers | 5 |
| | | Pyrgacrididae | * | 2 |
| | | Romaleidae | Lubber grasshoppers | 468 |
| | | Tristiridae | Andean wingless grasshoppers | 20 |
| | Eumastacoidea | Chlorotypidae | *. | 150 |
| | | Episactidae | * | 63 |
| | | Eumastacidae | Monkey grasshoppers | 224 |
| | | Euschmidtiidae | * | 240 |
| | | Mastacideidae | * | 10 |
| | | Morabidae | Matchstick grasshoppers | 87 |
| | | Thericleidae | Bush grasshoppers | 128 |
| | Proscopoidea | Proscopiidae | Stick grasshoppers, Jumping sticks | 215 |
| | Pneumoroidea | Pneumoridae | Bladder grasshoppers | 17 |
| | Pyrgomorphoidea | Pyrgomorphidae | Gaudy grasshoppers | 463 |
| | Tanaoceroidea | Tanaoceridae | Desert long-horned grasshoppers | 3 |
| | Trigonopterygoidea | Trigonopterydae | Broad-leaf bushhoppers | 17 |
| | | Xyronotidae | Razor-backed bushhoppers | 4 |
| | Tetrigoidea | Tetrigidae | Pygmy grasshoppers, groundhoppers, grouse locusts | 1623 |
| | Tridactyloidea | Cylindrachetidae | Sandgropers | 16 |
| | | Ripipterygidae | Mud crickets | 69 |
| | | Tridactylidae | Pygmy mole crickets | 135 |

*No common name is known.

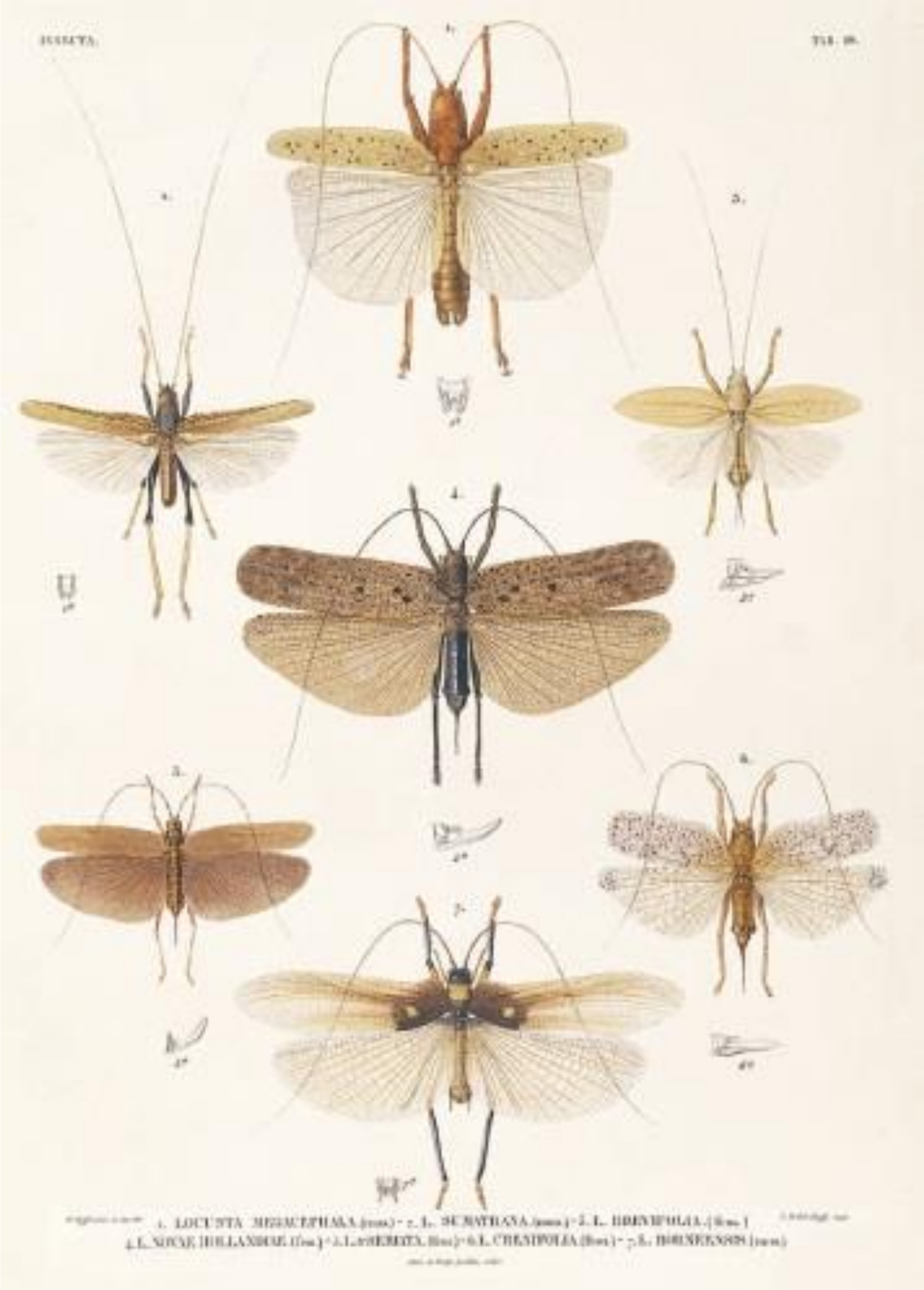

**Figure 1.** Ensiferan species (Tettigoniidae and Gryllacrididae) from Haan (1842-1844) (Plate 19). 1. *Salomona megacephala* (Haan, 1842); 2. *Macroxiphus sumatranus* (Haan, 1842); 3. *Mioacris brevifolia* (Haan, 1842); 4. *Tegra novaehollandiae* (Haan, 1842); 5. *Poecilopsyra octoseriata* (Haan, 1842); 6. *Olcinia crenifolia* (Haan, 1842); 7. *Borneogryllacris borneoensis* (Haan, 1842), 1,2. Conocephalinae, 3,4,6. Pseudophyllinae, 5. Phaneropterinae, 7. Gryllacridinae. Present-day binomials from the Orthoptera Species File (Eades *et al*. 2014).

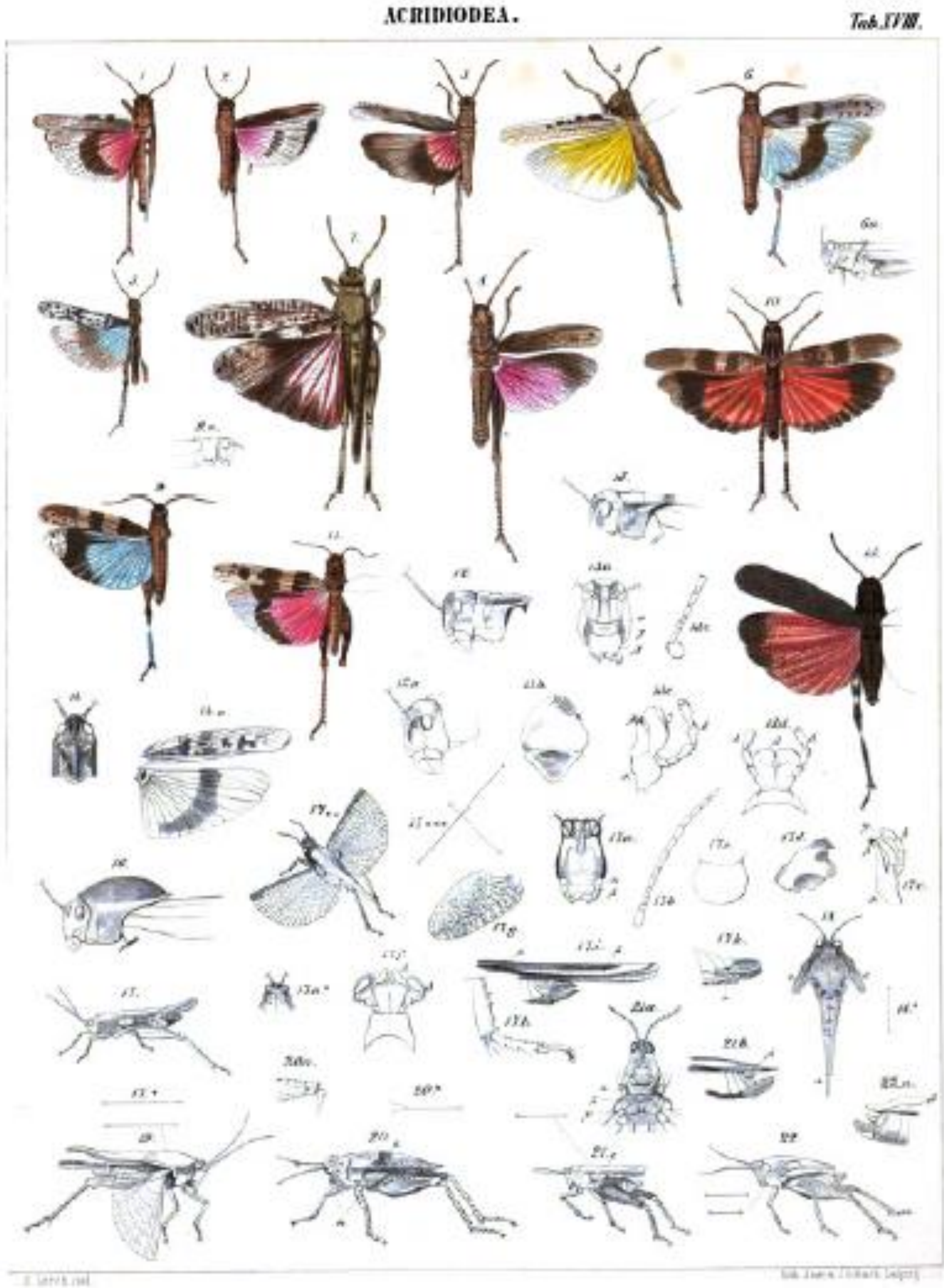

**Figure 2.** Caeliferan species (Acrididae and Tetrigidae) from Fischer (1853) (Plate XVIII) 1.2.3. *Acrotylus insubricus* (Scopoli, 1786); 4. *Acrotylus longipes* (Charpentier, 1845); 5. 6, 6a. *Sphingonotus caerulanscyanopterus* (Charpentier, 1825); 7. *Bryodemella tuberculata* (Fabricius, 1775); 8. *Celes variabilis* (Pallas, 1771); 9. 9a.10.11. *Oedipoda caerulescens* (Linnaeus, 1758); 12. *Locusta migratoria* (Linnaeus, 1758); 13. *Locusta migratoria* (Linnaeus, 1758); 14. *Oedalus nigrofasciatus* (De Geer, 1773); 15. *Psophus stridulus* (Linnaeus, 1758); 16. *Pyrgodera armata* Fischer von Waldheim, 1846. 17, 18, 19. *Tetrix subulata* (Linneaeus, 1758); 20. *Depressotetrix depressa* (Brisout de Barneville, 1848); 21. *Tetrix bipunctata* (Linnaeus, 1758); 22. *Tetrix bipunctata* (Linnaeus, 1758). 1-11, 14-16, Oedipodinae, 12-13, Cyrthacanthacridinae, 17-22, Tetriginae. Present-day binomials from the Orthoptera Species File (Eades *et al*. 2014).

2011). It consists of Sumerian and Akkadian lexica ordered by topic ranging from lists of vehicles to compendia of animals, plants and stars. The canonical version consists of 24 clay tablets the first of which was discovered in the library of Assur.Bani-Pal (7th century B.C.) in Mesopotamia (Bodenheimer 1947). Tablets nos. 13, 14 and 15 are zoological lists of domestic and wild animals. Of these, tablet no 14 translated by Landsberger (1934) lists the names of 410 terrestrial animals including 120 insect species of which several are orthopterans (grasshoppers, locusts, crickets) although identification of Linnean species is rather difficult (Abivardi 2005) (however, see section on plague locusts). The first serious orthopterologist (and entomologist) was undoubtly Aristotle who did a great number of important observations (many of them fairly accurate) on all aspects of the anatomy, natural history and behaviour of grasshoppers and locusts (Aristotle 1856, 1882, 1887, 1943). For an example, in Chapter XXIII of Book V of "The History of Animals", he writes: "*1. Locusts copulate in the same manner as all other insects, the smaller mounting upon the larger, for the male is the smaller. They oviposit by fixing the organ which is attached to their tail (the ovipositor) in the ground. The males do not possess this organ. Many of them deposit their ova in one spot, so as to make it appear like a honeycomb. As soon as they have deposited their ova, egg-like maggots are formed, which are covered with a thin coating of earth like a membrane, and in this they are matured.*" (Aristotle 1887).

In writing this review, my aim was to bring together a number of important, curious, and little-known facts about Orthoptera which are usually not found in a single paper. However, I did not pretend to be absolutely comprehensive and some relevant subjects which are well-known such as anatomy (see Fig. 3 and Fischer (1853) for wonderful illustrations of orthopteran anatomy) or have been recently thoroughly reviewed, have not been treated. These include acoustic communication (Robillard & Desutter-Grandcolas 2004; Himmelman 2011; Nattier *et al*. 2011; Montealegre-Z. *et al.* 2012), body size (Whitman 2008), sexual size dimorphism (Hochkirk & Gröning 2008; Bidau *et al*. 2013), cytogenetics (Bidau & Martí 2010), and sex chromosomes (Castillo *et al*. 2010). Also, no profound systematic treatment of the Orthoptera is presented although a number of classical and modern taxonomic and systematic sources have been included in the reference list (e.g. Harz 1969, 1975; etc.). Furthermore, for an exhaustive bibliography of the orthopteran systematic publications from 1750 to 2000, the reader is referred to the excellent compilation by Ingrisch & Willemse (2004). In this paper and in its second part, a comprehensive bibliography is provided including publications of historic interest as well as the latest research on the subjects treated in this review for the benefit of those readers interested in this fascinating group of organisms.

## A Diversity of Adaptations

"*It is, however, in the insect world that this principle of the adaptation of animals to their environment is most fully and strikingly developed*." Alfred Russel Wallace, 1871 (p.56)

Adaptation through natural selection was, and still is the essential nature of the evolutionary process (Williams 1966; Shanahan 2004), despite a number of other mechanisms that can promote evolution. As any other highly diversified group of living organisms, orthopterans display myriad life-styles and adaptations to their habitats, food resources, defense against predators and parasites, reproduction and many other characteristics. In the following sections, I review some aspects of orthopteran biology relating to their adaptation to different habitats, their diversity of feeding modes, the mechanisms evolved as predators' defense, and the extraordinary phenomenon of phase polymorphism.

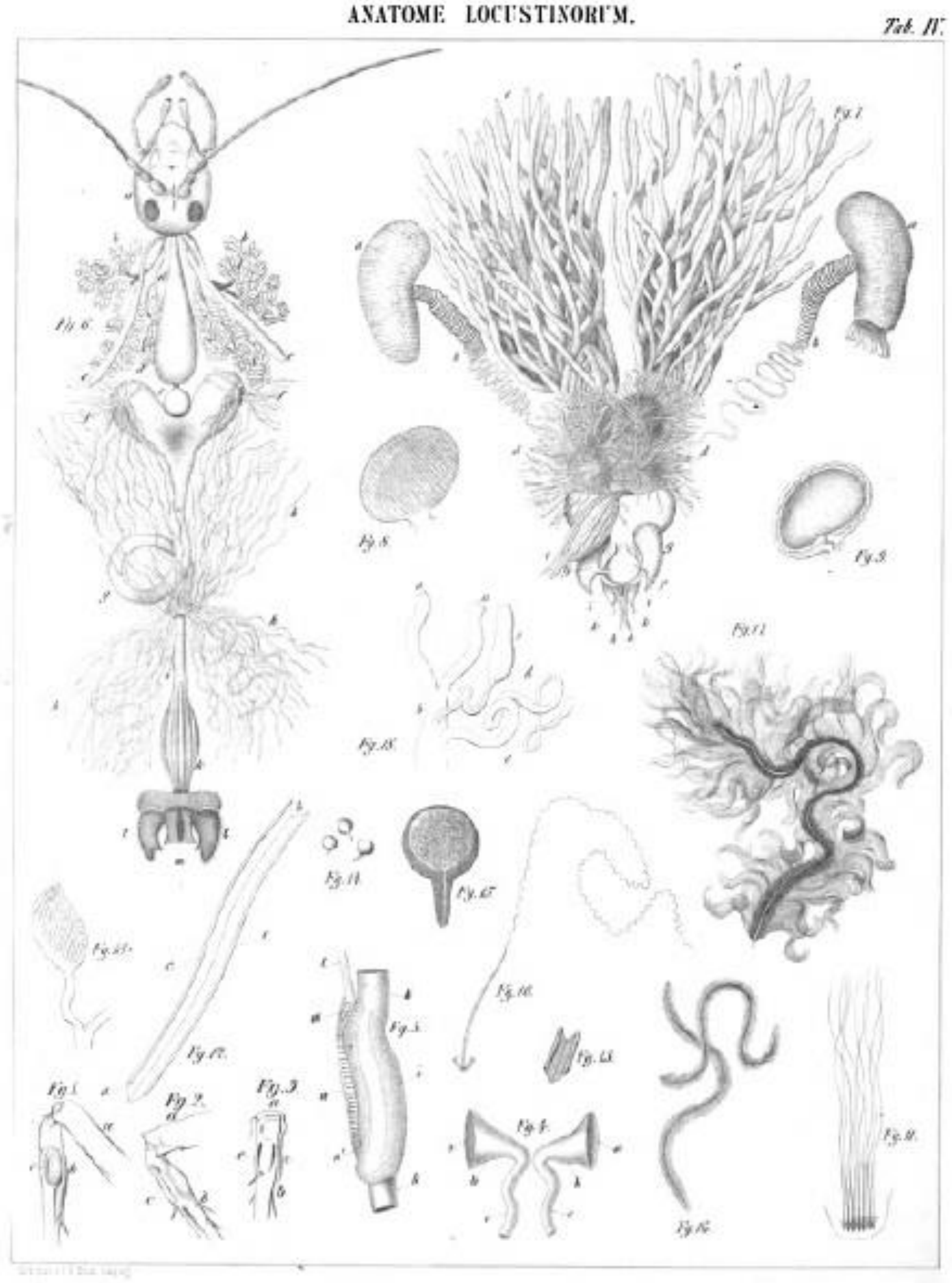

**Figure 3.** Anatomical details of several tettigoniids from Fischer (1853) (Plate IV). 1. *Meconema thalassinum* (De Geer, 1773). 2. *Tettigonia viridissima* (Linaneus, 1758). 6. *Ephippiger ephippiger* (Fieber, 1785). 7. *Uromenus rugosicollis* (Serville, 1838). 11. *Pholidoptera griseoaptera* (De Geer, 1773). 12-14. *Decticus verrucivorus* (Linnaeus, 1758). 1, Meconematinae, 2, 11, 12, 14 Tettigoniinae, 6, 7, Bradyporinae, Present-day binomials from the Orthoptera Species File (Eades *et al*. 2014).

## Home on the range?

*"Home is where my habits have a habitat"* Fiona Apple

Orthopterans are found in all terrestrial habitats in almost all continents, except for Antarctica. They tend to be considered inhabitants of open habitats such as grasslands, pampas and savannas where grasshoppers, crickets and katydids are abundant and conspicuous because of their size, movements, singing, and in many cases, brilliant colours.However, orthopterans have colonised practically all available terrestrial habitats and a few have become truly semiaquatic. Notably, a considerable number of orthopteran species belonging to separate evolutionary lineages have conquered the subterranean environment with radically different adaptations (Fig. 4). These groups include truly subterranean (endogean) species, cavernicolus (hypogean) species, and tiny crickets that live as guests of ants in their nests. All these species have idiosyncratic adaptations and specialisations that accompany their life strategies.

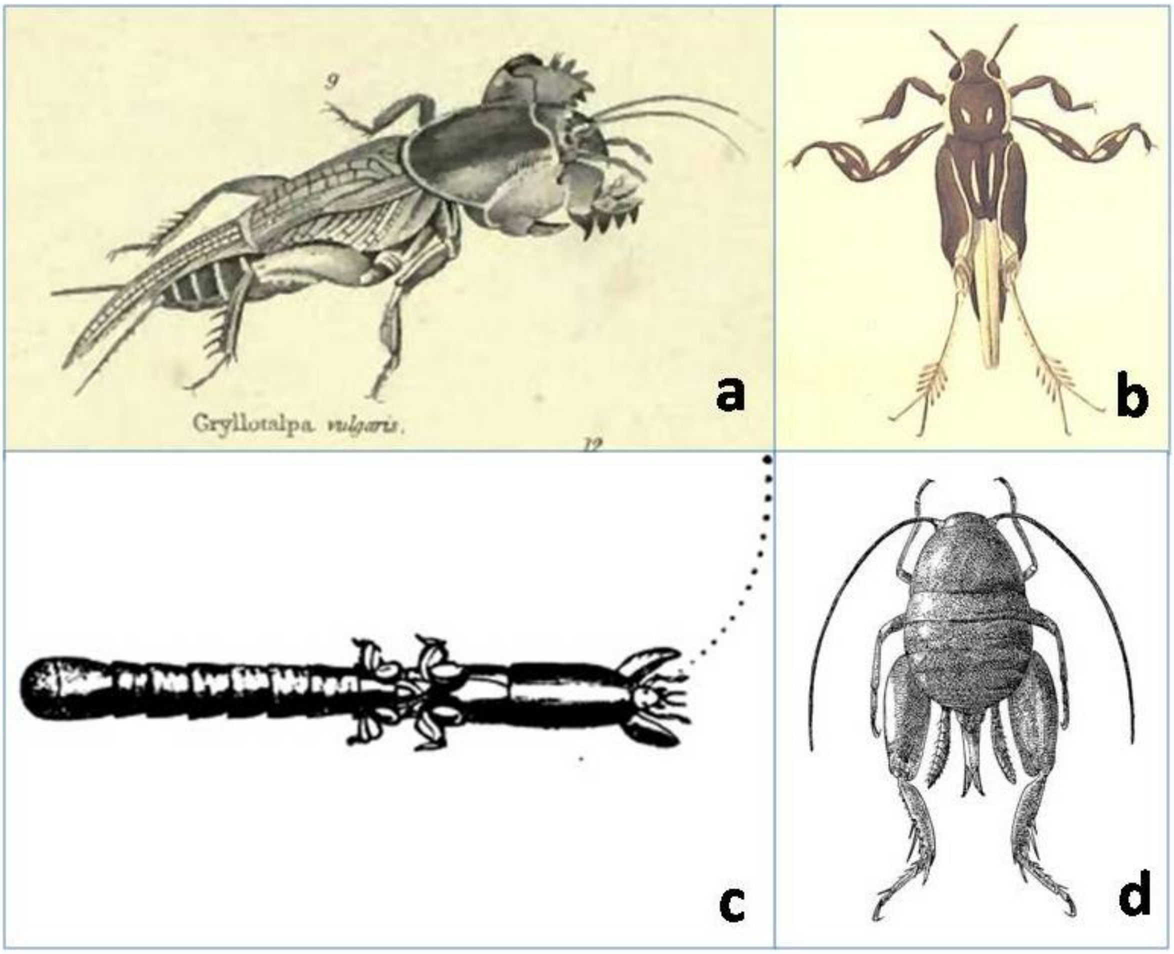

**Figure 4.** Examples of endogean and hypogean orthopterans. a. Mole cricket, *Gryllotalpa gryllotalpa* (Linnaeus, 1758) Gryllotalpidae). b. Pygmy mole cricket, *Xya variegata* (Latreille, 1809) (Tridactylidae). c. *Cylindracheta campbellii* (Gray, 1837) (Cylindrachetidae). d. Ant-cricket, *Myrmecophilus acervorum* (Panzer, 1799). (Myrmecophilidae). Illustrations from: a., Rothschild, 1878, b. Charpentier (1825), c. Gray (1837), d. Chopard (1943) Present-day binomials from the Orthoptera Species File (Eades *et al*. 2014).

The best known of the endogean orthopterans, even for non-specialist observers and despite their subterranean and nocturnal habits, are mole crickets because many species may become serious agricultural pests. The Gryllotalpidae (Ensifera) include 111 species distributed in several genera and are found in all continents, excepting Antarctica. The family displays extraordinary adaptations to the subterranean life-style (despite many species being, occasionally, very strong fliers) such as compact cylindrical bodies, short appendices, reduced eyes and especially, forelegs transformed into efficient digging tools that resemble in detail those of true mammalian moles, a notable case of evolutionary convergence (Capinera 2008b; Frank & Leppla 2008; Ingrisch & Rentz 2009). The other ensiferan group of fossorial insects is represented by the endemic Australian family Cooloolidae described by D.F.C. Rentz in 1980 and presently including 4 species (Rentz 1980, 1986; John & Rentz 1987). These “Cooloola monsters” are highly specialised cricket-like orthopterans with adaptations for digging, and according to Rentz (1980), constitute and aberrant family of the Gryllacridoidea with morphological aphinities with the Stenopelmatidae.

Another family of fully endogean orthopterans belongs to the Tridactyloidea superfamily of Caelifera: the Cylindrachetidae or sandgropers. This is a small family of only 16 described species included in three genera which show a restricted and disjunct geographic distribution: *Cylindracheta* Kirby (2 spp.) and *Cylindraustralia* Günther (13 spp.) are found in Australia with the second also present in Papua-New Guinea. The third genus, *Cylindroryctes* Tindale with just one species, *C. spegazzini* (Giglio-Tos 1914) is found in the Argentinean Patagonia (southern South America). Sandgropers look even more adapted to a subterranean lifestyle: they are wingless, with very short legs (including the third pair), antennae, and cerci, streamlined cylindrical bodies, compound eyes replaced by ocelli, and a pair of strongly modified digging forelegs convergent with those of the mole crickets. Australian sandgropers inhabit a wide variety of sandy soils including calcareous and siliceous sands and sandy loams (Richards 1980; Houston 2007a,b, 2011).

Another Caeliferan family, the Tridactylidae, considered the most basal of true grasshoppers (Flook *et al.* 1999), includes 135 species, distributed almost worldwide, with subterranean habits. Interestingly, although superficially resembling mole crickets (hence their common name, pygmy mole crickets), they are related to grasshoppers and not to crickets; in some old literature, they were considered as part of the Gryllidae. For example, Comstock (1888) places the genus *Tridactylus* Olivier alongside with *Gryllotalpa* Latreille under the heading "fossorial crickets". Pygmy mole crickets are very small insects, most species are less than 10 mm long and never exceed 20 mm. Typically, Tridactylidae occupy moist, sandy soil near water, such as lakes, streams, and even the sea, where they dig superficial tunnels, in which they live, sometimes gregariously and together with other insects; an interesting case is that of the tridactylids *Ellipes gurneyi* Gunther, 1977 and *Neotridactylus apicialis* (Say, 1825) in which burrows they coexist with the sundry beetle *Damphius collaris* (Kiesenwetter, 1851) (Heteroceridae) in eastern North America (Folkerts 1989). Accompanying their subterranean habits, tridactylids show a number of adaptations for digging in moist sandy soil, most notably the hind tibiae bear articulated spines near their tips, and spurs longer than the hind tarsi (usually absent or vestigial with a single segment). The insect uses its hind tibial spurs for digging, which is unusual for an insect's hind leg and differentiates pygmy mole crickets from sandgropers and true mole crickets. Tegmina are vestigial and wings, although present, are not an indication of the insect's flying ability. However, the most notable adaptations of these small orthopterans relate to their swimming abilities. Hind legs are also characteristic because of their enlarged femora indicative of powerful jumping ability (Burrows & Picker 2010). Furthermore, hind tibiae have movable plates, called natatory lamellae, at their distal ends that can be fanned for swimming, and even diving. Surprisingly, these insects not only do swim and walk on water: they can jump off the water surface aided by these plates (Burrows & Sutton 2012).

Besides the above described examples, a few single species may show burrowing behaviour while belonging to otherwise non-subterranean orthopteran groups (Alexander 1961). One of these cases is that of *Anurogryllus muticus* (DeGeer, 1773) (Gryllidae), the short-tailed burrowing cricket studied by West & Alexander (1963). Females of this species hide themselves in a burrow after mating remaining there, first with their eggs, then with the hatchlings, until their death. Meanwhile, the female lays trophic eggs to feed her offspring, accumulates other kinds of food, and defends the burrow against intruders. This has been interpreted by West & Alexander (1963) as sub-social behaviour.

A number of orthopterans live underground but are not burrowers, and comprise a number of cavernicolous or hypogean species (Vandel 1965). All truly cavernicolous orthopterans belong to Ensifera and are included in two families: Raphidophoridae and Gryllidae. The first family, of wide but patchy distribution, includes most of the hypogean forms (many described by Lucien Chopard) all being apterous, hygrophylic and omnivorous scavengers (Vandel 1965). Many species show elongated appendages and eyes may be reduced or normal. In some cases, such as *Diestrammena cuenoti* (Chopard, 1929) different degrees of eye reduction are found in different individuals. All these species are troglophiles which occasionally leave their caves during the night. The only completely anophtalmic and truly troglobious species seem to be two species of *Eutachycynes* Storozhenko (Vandel 1965; Richards 1968): *E. caecus* (Chopard, 1924) and *E. cassani* (Chopard, 1954), from Assam and Laos respectively. Representative genera in Asia and Indonesia are *Raphidophora* Serville (Rhaphidophorinae) and *Diestrammena* and *Paradiestramenna* Chopard (Aemodogryllinae); in Australia and New Zealand live *Pachyrhamma* Brunner von Wattenwyl, *Pleioplectron* Hutton, *Neonetus* Brunner von Wattenwyl and *Speleotettix* Chopard, all belonging to the Macropathinae. Only one species occurs in Africa, *Spelaeiacris tabulae* Péringuey, 1916, found only in caves and crevices in Table Mountain and the mountains around Kalk Bay in the Cape Peninsula, South Africa. At least four Holarctic genera of cavernicolous and endogean rhaphidophorids are known (i.e. *Troglophilus* Krauss, Troglophilinae). Cave and camel crickets are of little economic importance except as a nuisance in buildings and homes, especially basements which sometimes they invade if conditions resemble those of the natural caves they normally inhabit.

Regarding the cavernicolan Gryllidae, almost all known cavernicoles belong to genera included in subfamilies of the Phalangopsinae Group such as *Dyscophogryllus* Rehn (Luzarinae, South America), *Uvaroviella* Chopard (Phalangopsinae, Jamaica), *Amphiacusta* Saussure (Luzarinae, Central America), *Arachnomimus* (Phalangopsinae, Indonesia), *Malgasia* Uvarov (Mogoplistinae, Madagascar) and *Phaeophilacris* Walker, Cachoplistinae, South Africa). Cavernicolous Gryllidae show a number of modifications: body colour is usually pale, eyes and ocelli are reduced, wings and tegmina are short or absent. The most modified species which tends towards the troglobious type is *Arachnomimus microphthalmus* Chopard, 1929 from the Batu Caves (Selangor, Malaysia). It is a depigmented form with reduced eyes and with greatly elongated appendages (Vandel 1965). Also of great scientific interest are the cave-dwelling, presumably troglobytic crickets that inhabit lava tunnels in Hawaii and were discovered as recently as 1972 (Howarth 1972). These flightless species belong to the endemic genera *Thaumatogryllus* Perkins (Oecanthinae) and *Caconemobius* Kirby (Nemobiinae) (Gurney & Rentz 1978).

Other orthopterans are not subterranean but also have seclusive lives. New Zealand tree wetas (*Hemideina* Walker spp., Anostostomatidae) are large, flightless orthopterans which commonly live in vacated tunnels made by other insects in branches and trunks of trees (Miller 1984; Field & Sandlandt 2001). Wetas are nocturnal insects, and probably occupy the tunnels in the daytime to escape predation by visual predators, such as birds. However, the wetas also seem to centre much of their nocturnal activity around these refuges and often individuals occupy specific tunnels for extended periods of time (Ordish 1992). A study of two species, *Hemideina femorata* Hutton, 1896 (Canterbury tree weta) and *H. crassidens* (Blanchard, 1851) (Wellington tree weta) has shown that wetas enlarge and groom the tunnels (Field & Sandlandt 2001). Therefore, the authors designated the tunnels as galleries, implying that these serve as relatively “stable homes” from which the nightly activity cycle of wetas is based.

A most unusual habitat in which orthopterans are expected to be found is within ant nests. However, a whole family of very small crickets, the Myrmecophilidae does exactly this. Its 71 recognised species are known as ant, ant-loving or ant-inquiline crickets, most of them included in the genus *Myrmecophilus* Berthold. Ant crickets are tiny (1.5-4 mm; ~2 mg; Whitman 2008) wingless insects symbiotic with ants and living in and around ant nests. They cannot live independently from the ants and apparently are taken for ants by their hosts (Capinera 2008b). *Myrmecophilus* crickets are kleptoparasitic on their host ants: they feed on food resources in the ant nests and also induce the ants to regurgitate liquid food (Wetterer & Hugel 2008). While most *Myrmecophilu*s species are not species-specific in their association with host ants, a study of *M. americanus* Saussure, 1877 that reviewed all published records of the species around the world, showed that in all cases except one, the ant cricket was associated with a single ant species, the Longhorn Crazy Ant, *Paratrechina longicornis* (Latreille, 1802) (Formicidae) suggesting adaptations to this species-specific association (e.g. adult crickets resemble the gaster of *P. longicornis* queens in size and shape) (Wetterer & Hugel 2008). Conversely, *M. acervorum* (Panzer, 1799) has been reported to be an inquiline of at least 20 different ant species (Bellman 1988).

Differently from other insect orders such as Coleoptera and Hemiptera in which whole families have evolved toward a completely aquatic lifestyle, the Orthoptera have not followed this evolutionary path. However, I have already described the extraordinary behaviour of pygmy mole crickets, and there are other cases of strong relationship between some orthopteran species and fresh water. Pflüger & Burrows (1978) have analysed and discussed the swimming abilities of locusts and other Orthoptera when by accident or necessity fall into water. Furthermore, some Neotropical Acrididae live a semi-aquatic life on leaves of broad aquatic plants (e.g. water hyacinth *Eichhornia crassipes* (*Pontederiaceae*)). These species include the Acridids *Paulinia acuminata* (De Geer, 1773) (Paulininae), *Marellia remipes* Uvarov, 1929 (Marellinae), and *Cornops aquaticum* (Bruner, 1906) (Acrididae, Leptysminae) (Amedegnato & Devriese 2008). The tibiae and tarsi of their hind legs are oar-like, enabling them to swim on the surface of the water, walk on the ground under water or climb upon submerged water plants (Carbonell 1959). In fact, these species are seriously considered as biological controllers of aquatic plants. Some crickets seem to be able to skate on water as is the case of *Hydropedeticus vitiensis* Miall & Gibson, 1902 (Trigonidiinae) from Fiji (Miall & Gilson 1902). Although Orthoptera have not conquered the sea, at least one apterous cricket species, *Marinemobius asahinai* (Yamasaki, 1979) (Nemobiine), inhabits mangrove swamps (Cheng 2009).

Finally, a curious example deserves mentioning. Edwards (1952) described a strange behaviour in what he termed a stream side weta of New Zealand. In fact, the organism belonged to an undescribed species of *Paraneonetus* Salmon and the author observed that individuals of this species, when disturbed, resort to the expeditious means of throwing themselves into the stream and stay underwater at least for 23 min. Although this problem was not studied further, more recent findings suggest that this type of behaviour is possibly more common than previously thought. For example, similar behaviour is displayed by the tusked weta *Motuweta riparia* Gibbs, 2002, the Australian king cricket *Transaevum laudatum* Johns, 1997 and many pygmy grasshoppers (Tetrigidae) (Monteith & Field 2001). A more recent example of semi-aquatic defensive behaviour has been observed in South American representatives of the Lutosinae Gorochov (synonym Lutosini Gorochov). This group belongs to the Gondwanaland Anostostomatidae, the family that includes wetas and king crickets (Johns, 1997). The genus *Hydrolutos* Issa & Jaffe includes six species of apterous, troglophilic, medium-sized crickets which are found in quartzite caves of tepuis or tafelbergs of the Roraima Formation of Venezuela (Issa & Jaffe, 1999; Šmida *et al.* 2005; Derka & Fedor, 2010; Derka *et al.* 2013). These species live in perpetual darkness associated with freshwater pools and streams flowing through the caverns. These insects are highly adapted to move easily, and even swim against strong currents in this semi-aquatic environment showing the same defensive behaviour previously described above, of staying underwater when disturbed (Šmida *et al.* 2005; Derka & Fedor 2010). Despite being cavernicolous these species cannot be considered true troglobionts because they lack adaptations such as reduced eyes or lack of body pigmentation. For this reason, they are expected to inhabit streams outside caves on the tepui (Derka & Fedor 2010).

Orthopterans, as other insects, have adapted to and are successful in a number of extreme environments which require special adaptations such as deserts, arctic and subarctic environments, and high altitude (Mani 1968; Cloudsley-Thompson 1988; Vickery 1997; Punzo 2000; Bell 2012). In the case of high altitude, orthopterans show an enormous amplitude. The old idea that holometabolous insects predominate at high elevations whereas the 'warmth-loving' Orthoptera are less adapted to cold (i.e. Hesse 1937) is erroneous and based on observations of conspicuous and not abundant forms (Alexander 1951). Some species inhabit a wide range of elevations with extremely different ambient conditions such as the Neotropical grasshoppers *Dichroplus pratensis* Bruner, 1900 and *D. vittatus* Bruner, 1900 (Melanoplinae) which can be found between 0 and 2,500 masl in Argentina (Bidau *et al.* 2012). Grasshoppers, which have normally diurnal habits, are much more frequent at high altitudes than nocturnal crickets or katydids. Already in 1925, Major R.W.H. Hingston, a member of the 1924 British expedition to Mt. Everest, reported the finding of nymphs of an unnamed acridid at 18,000 ft (5,500 m) (Hingston 1925), which the famed orthopterologist, Sir Boris Uvarov could not identify nor describe (Uvarov 1925). However, in the same paper, Uvarov described two new grasshoppers from Mt. Everest in the subfamily Gomphocerinae: *Dysanema irvinei* Uvarov, 1925 (15,000 ft= 4,600 m) and *D. malloryi* Uvarov, 1925 (16,000 ft= 4,900 m) (anecdotically, the specific names of both species honour A.C. Irvine and G. Mallory, who lost their lives during the final assault to the summit). In a previous paper, Uvarov (1922) had described another Everest gomphocerine, *Hypernephia everesti* Uvarov, 1922 which probably helds the altitudinal record for orhopterans: 18,500 ft (5,640 m). Grasshoppers are evidently not intimidated by heights.

Erwin (1983) called the tropical forest canopy '*The last biotic frontier*' and quoted William Beebe (1917): '*Yet another continent of life remains to be discovered, not upon the earth, but one to two hundred feet above it, extending over thousands of square miles of South America*.' In fact, the tremendous amount of arthropod biodiversity in the tropical forest canopy has only recently began to be surveyed and described since new sampling techniques were developed (Erwin 1982, 1983; Stork *et al.*1997; Basset 2001; Floren & Schmidl 2006). Again, orthopterans are proving to be a fundamental component of this extraordinary biota not essentially in abundance as other arthropod groups (i.e. ants) but in species diversity of both Ensifera and Caelifera with some taxa being notably frequent (e.g. the acridoid Proctolabinae and the leaf-mimicking katydids of the Pseudophyllinae subfamily (Roberts 1973; Descamps 1976; Nickle & Cstner 1995; Amedegnato 1997, 2003; Floren *et al.* 2001; Rowell & Flook 2004; Mugleston *et al.* 2013; Tan 2013).

## Not just plant eaters

"*Part of the secret of success in life is to eat what you like and let the food fight it out inside*." Mark Twain

Insect-plant interactions have a long co-evolutionary history: already in the Carboniferous (300 million years ago), almost all of major insect orders including the Orthoptera, had evolved (Hassell & Southwood 1978; Chaloner *et al.* 1991; Mitter *et al.* 1991; Bernays 1998). It is recognised that omnivory preceded herbivory (Dethier 1954) and that the passage to plant feeding implied important physiological adaptations (Berembaum & Isman 1989). Although orthopterans are considered essentially herbivorous insects, many species are in fact omnivorous, consuming a variety of living and dead organic food items other than living vascular plants including among others fungi, lichens, algae, mosses, feces, paper, wood, and wool of living sheep (Whitman & Richardson 2010). They may also feed on other living or dead arthropods, including conspecifics (cannibalism or intraspecific predation) and dead vertebrates. Few orthopteran groups are fully carnivorous.

While most orthopterans of both suborders are herbivorous (Snodgrass 1930; Parker 1952; Gangwere 1961; Uvarov 1966, 1977; Joern 1979; le Gall 1989), feeding habits assume a great diversity of forms, ranging from extreme generalists to strict specialists (Joern 1979). Regarding the consumption of vascular plants orthopterans are usually classified as graminivorous, forbivorous, or omnivorous each class showing special adaptations of their mouthparts (Gangwere 1961). However, orthopterans may feed on different plant structures such as leaves, flowers, fruits, pollen, etc. (Gangwere 1961). For example, eaters of *Classopollis* Pflug-like pollen (from a primitive *Cheirolepidaceae*, a conifer) date back to the Jurassic as represented by the large genus *Aboilus* Martynov (Prophalangopsidae) (Labandeira 1997; Krassilov *et al.* 2007). The relationship between orthopteran feeding habits and pollen has an interesting derivation. Since Darwin (1862) it has been considered that Orthoptera are not capable of regular pollination. Recently however, a new species of raspy cricket (Gryllacrididae), *Glomeremus orchidophilus* Hugel *et al*. 2010, endemic of Réunion island (Mascarenes, Indian Ocean) has been reported as the sole pollinator of the orchid *Angraecum cadetti* Bosser, 1987 (Micheneau *et al*. 2009, 2010; Hugel *et al.* 2010). Gryllacridids may be carnivorous, herbivorous, florivorous, granivorous and opportunistically omnivorous (Hale & Rentz 2001). Gut content analyses of *G. orchidophilus* revealed mainly plant material including pollen and seeds (Michenau *et al*. 2010; Hugel *et al*. 2010). However, these insects regularly visit flowers of *A. cadetii* probably for nectar (food reward) and carry pollen from flower to flower (pollinaria are stuck to the insect's head when they retreat from the flower): *A. cadetii* seems to rely exclusively on the raspy cricket for achieving fruit set (Hugel *et al.* 2010). Although specialised tettigoniid subfamilies such as the Australian Zaprochilinae and Phasmodinae feed on nectar, pollen and even full flowers (Rentz 2010), *G. orchidophilus* represents the first scientifically supported case of orthopteran mediated pollination in angiosperms.

Other unusual vegetable diets occur in a number of orthopteran clades. For example, the pygmy grasshoppers (or groundhoppers) (Tetrigidae) are terricolous and inhabit marshy places, some are even semi-aquatic (see section "Home on range?") and are known to feed variously on algae, lichens, mosses, small plants and detritus although few studies report the diet of individual species. *Tetrix ceperoi* (Bolivar, 1887) has been reported to feed essentially on mosses (Kočárek *et al*. 2008). While the riparian groundhoppers *Paratettix aztecus* (Saussure, 1861) and *P. mexicanus* (Saussure, 1861) are algal feeders mainly consuming beached *Cladophora glomerata* (Linnaeus) Kützing, 1843 (Cladophoraceae) (Bastow *et al.* 2002). Other algal feeders include pygmy mole-crickets (Tridactylidae) (Deyrup 2005).

Regarding carnivory (essentially the consumption of insects and other arthropods), it is common in some tettigoniid subfamilies such as Decticinae and Saginae (Isely 1941; Cantrall 1972) (Fig. 5). Studying caged specimens in laboratory, Isely (1941) found that the shield-backed katydids (Decticinae) *Pediodectes nigromarginatus* (Caudell, 1902) and *P. haldemanni* (Girard, 1854) are predatory, night-prowling insects, although these may eat plant food when deprived of animal prey. These species accepted as prey various species of pentatomid bugs, nymphal and adult grasshoppers, hoverflies (Syrphidae) and woodlice (*Oniscus*). The Saginae are also very efficient predators; the matriarchal or predatory katydid, *Saga pedo* (Pallas, 1771) is a large (ca 90-100 mm) Old World parthenogenetic katydid recently introduced in northeastern United States (Cantrall 1972). Matriarchal katydids are ferocious predators: a single individual in captivity was observed to eat up to six adult large grasshoppers (ca 25 mm) daily (*Melanoplus sanguinipes* (Fabricius, 1798)). Carnivory also may appear in single species within otherwise herbivorous groups. Mole crickets (Gryllotalpidae) are well-known pests of turfgrass and a number of crops world-wide (Brandenburg *et al.* 2002). For example, *Gryllotalpa africana* Palisot de Beauvois, 1805 is a world-wide pest (Sithole 1986) which damages plants including wheat, maize, rice, sorghum, millet, barley, oats, potatoes, cassava, groundnuts, strawberries, turnips, tobacco, and vegetables in Africa, Asia, and Europe. However, the southern mole cricket of North America *Scapteriscus vicinus* Scudder, 1869 is completely carnivorous while the sympatric tawny mole cricket, *S. borellii* Giglio Tos, 1894 is herbivorous (Matheny 1981; Fowler *et al.* 1985; Brandenburg *et al.* 2002).

Although it was suspected for long that herbivorous orthopterans supplemented their diets with cadavers of other arthropods, this was considered as an aberrant feeding behaviour (Isely & Alexander 1949). It was not until the beginning of studies of crop contents that the role of orthopterans as scavengers came to be considered as a normal behaviour (Isely & Alexander 1949; Gangwere 1961; Lavigne & Pfadt 1964). In their pioneering study of 30 species of rangeland grasshoppers from Wyoming, USA, during a 3-year period, Lavigne & Pfadt (1964) found that 14 species from 9 genera (*Ageneotettix* McNeill, *Aulocara* Scudder [Acridinae], *Brachystola* Scudder [Romaleidae], *Hesperotettix* Scudder, *Melanoplus* Stål [Melanoplinae], *Hadrotettix* Scudder, *Spharagemon* Scudder, *Trachyrhachys* Scudder, and *Trimerotropis* Stål [Oedipodinae]) included arthropod material among their gut contents indicating that scavenging is a rather normal behaviour of grasshoppers. This is reinforced by observations that different species compete aggressively for carrion as shown by O´Neill *et al.* (1993). However, necrophagy is not limited to other arthropods. The aposematic western lubber grasshopper *Taeniopoda eques* is a desert species inhabiting northern Mexico and southwestern United States. Whitman & Richardson (2010) observed adult individuals of the species (mostly females) scavenging on the cadaver of a coyote (*Canis latrans* Say, 1823). Grasshoppers consumed hair, dried hide and dried tissues adhering to bones. Since the majority of scavengers were females, the authors hypothesised that egg production requires nutrients that may make vertebrate carrion complement to an herbivorous diet (Whitman & Richardson 2010).

Cannibalism, defined as intraspecific predation, is by no means rare in insects, even in non-carnivorous groups: in fact it is widespread in certain orders, such as Coleoptera and Lepidoptera (Fox 1975; Elgar & Crespi 1992; Capinera 2008i; Mathews & Mathews, 2010; Richardson *et al.* 2010; Santana *et al.* 2012). Although the Orthoptera are no exception, regular cannibalism is not common: Richardson *et al.* (2010) reported 7 cases (species) in Acrididae, one in Tettigoniidae and one in Gryllotalpidae. Cannibalism is often regarded as a

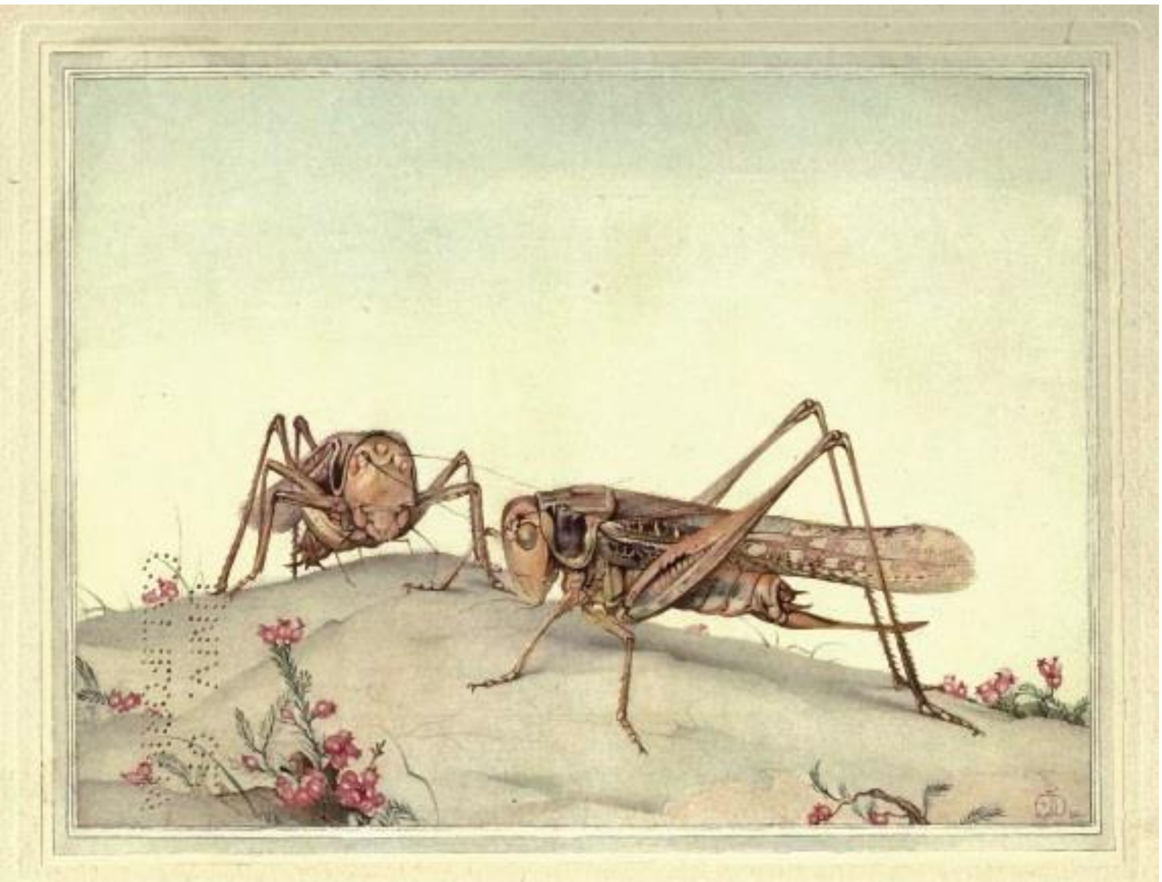

**Figure 5.** A carnivorous katydid, *Decticus albifrons* (Fabricius, 1775) (from Stawell, 1935 "Fabre's Book of Insects). "*I find, when the Decticus is imprisoned in my menagerie, that any fresh meat tasting of Locust or Grasshopper suits his needs*." (Jean-Henri Fabre).

density-dependent mechanism that acts on the population only under intense environmental pressure (Richardson *et al*. 2010; Santana *et al*. 2012) such as that encountered in species that undergo phase polymorphism (locusts, mormon crickets; see section "Days of the locust") (Simpson *et al*. 2006; Srygley *et al*. 2009; Bazazi *et al*. 2011; Hansen *et al*. 2011). However, other non-density dependent mechanisms may trigger cannibalism (Fox 1975; Santana *et al*. 2012).

Sexual cannibalism in which the female attacks and consumes her male mate at some stage during courtship or mating, occurs in several invertebrate taxa, most notoriously in mantids and spiders (Elgar & Schneider 2004). True sexual cannibalism has not been observed in Orthoptera although a number of feeding interactions between male and female during courtship and mating do occur. These interactions are usually included in such categories as "courtship feeding" or "nuptial gifts" (Gwynne 1988, 2008; Boggs 1995; Gullan & Cranston 2010). Nuptial gifts may take the form of some food ("oral gift") item offered by the male during courtship, for example, a dead insect (Thornhill 1976; Gwynne 2008). In ensiferan insects such as katydids and crickets, a special form of gift involving the spermatophore is produced by courting males (Gwynne 1990; Wedell 1994; Will & Sakaluk 1994). The insect spermatophore is commonly regarded as a container which serves to protect the semen during the transfer from the male to the female (Davey 1960) but in fact, is a complex structure that may serve important additional functions (Khalifa 1949a, b; Davey 1960). The two hypotheses concerning nuptial gifts involving the spermatophore indicate that the nuptial gift may serve the function of increasing male mating success by protecting the ejaculate during copulation, or/and to enhance female fecundity and offspring fitness fathered by the donating male (Wedell 1994; Gwynne 2008). These models apply to the "spermatophylax" (Boldyrev 1915; Richards 1927) of Ensifera. The spermatophore consists of two parts: the ampullae containing sperm that is attached to the female's genital opening, and the sperm-free spermatophylax which is fed upon by the female during and after copulation (Gwynne 1990; Wedell 1994). It has been hypothesised that this mechanism has evolved through sensory exploitation and some experimental evidence supports this idea (Sakaluk 2000). A number of experimental investigations in different species have demonstrated that both previously mentioned functions occur in nature either separately or jointly (Reinhold & Heller 1993; Wedell 1994; Will & Sakaluk 1994; Gwynne 2008) and that at least in one species, *Gryllodes sigillatus* (Walker, 1869), aminoacid content of the spermatophylax is under sexual selection (Gershman *et al.* 2012).This form of oral gifts is not exclusive of katydids, bush crickets and crickets, but also occurs in wetas and king crickets (Field & Jarman 2001; Monteith & Field 2001).

Finally, a certain form of limited sexual cannibalism does occur in Orthoptera. For example, in the flightless sagebrush cricket, *Cyphoderris strepitans* Morris & Gwynne, 1978 (Prophalangopsidae) receptive females approach singing males, mount them dorsally and start chewing on the unusually fleshy male's hind wings while the male deposits a spermatophore at the female´s genital opening (Eggert & Sakaluk 1994). It has been experimentally shown that the removal of the male´s hind wing significantly reduced the chances of successful spermatophore transfer (Eggert & Sakaluk 1994) while sexual cannibalism influences the chances of female remating (Johnson *et al.* 1999). Other body parts may serve similar functions as oral nuptial gifts as in the gryllids *Hapithus agitator* Ulher, 1864 (tegmina; Alexander & Otte 1967) or *Allonemobius socius* Scudder, 1877) (specialised hind tibia spurs; Fedorka & Mousseau 2002a, b). In all these cases, eating by females of the male's body parts gives them access to their partner haemolymph, which probably contains important nutritional substances (Fedorka & Mousseau 2002a).

## Masters of disguise and deception

"*In the other orders of insects, the Orthoptera (locusts, grasshoppers, &c.) will be found to include the most beautiful examples of Protective Resemblance.The tropical 'leaf insects' and 'walking-stick insects' belong to this order.*" Edward Bagnall Poulton, The Colours of Animals, 1890, p. 58

"*The commonest use of colour is for concealment (Cryptic), enabling an animal to escape its enemies, or to approach its prey. In these Protective (Procryptic) or Aggressive (Anticryptic) resemblances, animals are concealed by a likeness to some object which is of no interest to enemies or prey respectively. Similar effects may be produced by the use of foreign objects with which the animal covers itself to a greater or lesser extent (Allocryptic).*" Edward Bagnall Poulton, Essays on Evolution 1889-1907, 1908, p. 297

All insects, and orthopterans are no exception, are subject to intense predation by an enormous variety of animal species, including other insects. Thus, evolution has produced a vast array of adaptations to allow insects to escape predators and this has been the subject of an enormous amount of studies in all insect groups since long ago (Darwin 1859; Bates 1862a; Müller 1876; Semper 1881; Tylor 1886; Poulton 1890; Wallace 1879a,b; 1891; Beddard 1892; Thayer 1896; Sykes 1904; Thayer 1909; Carpenter 1921; Cott 1940; Blum 1981; Evans & Schmidt 1990; Blaisdell 1992; Ruxton *et al.* 2004a; Eisner *et al.* 2005; Joron 2009a,b; Wilsdon 2009; Mathews & Mathews 2010; Stevens & Merilaita 2009, 2011; Waldbauer 2012). Capinera (2010) classified these protective strategies in a number of non-mutually exclusive categories: crypsis, aposematism, mimicry, flight, startle behaviour and attack, chemical defenses, group actions, and nocturnal activities. The Orthoptera, in their impressive diversity, have produced many examples in most of these categories, which will be treated individually.

**Crypsis** refers to the biological situation in which an organism comes close to perfectly matching its surroundings so as to make detection by predators difficult (Ruxton *et al.* 2004a; Bond 2007). Robinson (1969) made a useful distinction between *eucrypsis*- animals have adaptations that prevent their presence be detected by predators-, and *special protective resemblance*- the protective devices are background-independent. Orthopterans offer a vast number of cases of visual crypsis: from the desert grasshoppers that blend with the sandy soil (Dearn 1990), to spectacular cases such as the Pseudophyllinae (leaf-mimicking or false-leaf katydids) which, as implied in the subfamily denomination, resemble leafs, even dead ones,sometimes uncannily (Robinson 1969; Nickle & Castner 1995). However, a recent study suggests that the leaf-mimicking adaptations may have appeared independently several times during the group's phylogeny (Mugleston *et al.* 2013). Another noteworthy case is that of the Proscopiidae, a family of endemic South American Caelifera related to the Eumastacidae (Liana 1972; Bentos-Pereira 2003). Proscopiidae are wingless grasshoppers (although with winged ancestors, ca. 110 myr, Heads 2008) that resemble sticks much more than the phasmatid classic examples.It is erroneous to think that crypsis is just a visual phenomenon, since predators often detect their prey using other sensory means than vision. Thus, animals have evolved different mechanisms of acoustic, olfactory, and chemical crypsis (see recent review by Ruxton 2009). An interesting example was reported by Zuk *et al.* (1998, 2001) in the cricket *Teleogryllus oceanicus* (Le Guillou, 1841) (Gryllinae). This species inhabits Pacific islands, Northeastern coastal Australia, and has recently been introduced to Hawaii (Kevan 1990). In their first paper, Zuk *et al.* (1998) discovered that males whose calling songs consisted of longer pulses were more efficiently detected by an acoustically oriented parasitoid, the tachynid fly *Ormia ochracea* (Bigot, 1889). However, crickets living in the Pacific islands have longer pulses than those of mainland Australia, which was interpreted by Zuk *et al.* (2001) as a response to a low intensity of predation in the island populations.

**Countershading.** Many terrestrial and aquatic animals show a distinctive pattern of pigmentation in which bodily parts that are more lighted (i.e. the *dorsa*) tend to be darker than those less exposed to light (the *ventra*). This idea was put forward by the painter-naturalist Abbott Handerson Thayer (1849-1921) (Thayer 1896) who called the phenomenon “obliterative shading”, now called “countershading” and sometimes “Thayer’s Law” (Behrens 2009). When animals are illuminated from above, they cast shadows on their undersides so that they appear lighter on their dorsal than on their ventral sides (Thayer 1909; Rowland 2009); this would, in principle, reduce detectability by visually-oriented predators. It is worth noting that this idea was somewhat anticipated by the British evolutionary biologist Edward Bagnall Poulton (1856-1943) (Poulton 1888). Many gasshoppers are ventrally lighter (e.g. pale green) than dorsally (dark green) thus, when resting on the substrate they appear uniformly green when lighted from above (Edmunds 1990, 2008). However, this century-old problem has been controversial and the protective properties of countershading, despite the proposal of several models is until now poorly understood (Kiltie 1988, 1989; Edmunds & Dewhirst 1994; Ruxton *et al.* 2004b; Stevens *et al.* 2006; Rowland 2009; Allen *et al.* 2012).

**Aposematism** is the correlation between conspicuous signals, such as bright colouration, and prey unprofitability (Joron 2009a). The Romaleidae or lubber grasshoppers, is a subfamily of Acridoidea of South American stock with representatives in Central and North America, which tend to be large-bodied and frequently show bright wing and body colours. *Chromacris speciosa* (Thunberg, 1824) is a South American species with an enormous geographic distribution (Roberts & Carbonell 1982). Nymphs of *C. speciosa* are jet-black with red and some white markings, and are highly gregarious, forming large groups upon their food plants (Roberts & Carbonell 1982; Turk & Barrera 1976). Their shiny and contrasting black coloration suggests they are unpalatable or poisonous to predators, being thus a case of aposematism produced through natural selection as originally proposed by Alfred Russel Wallace (Wallace 1879a; Poulton 1890; Joron 2009a). Turk & Barrera (1976) reported that *C. speciosa* feeds on at least six species of *Solanaceae*, which are known to produce compounds toxic to most herbivores; but grasshoppers such as *Chromacris* probably accumulate them,becoming unpalatable (Naskrecki 2004). A similar situation occurs in another romaleid, *Taeniopoda eques* (Bumeister, 1838) (Whitman *et al.* 1985).

**Mimicry** is the adaptive resemblance in signal between several species in a locality (Joron 2009b). It may be classified as 1) Batesian, which is the evolutionary convergence of appearance among palatable species to resemble an unrelated unpalatable species; 2) Mullerian, or the evolutionary convergence of unrelated unpalatable species to resemble one another; 3) Aggressive, which occurs when a predator mimics something that another species considers desirable or attractive, and 4) Wasmannian, which occurs among non-ant insects that live within ant nests (Wasmann 1913; Pasteur 1982; Joron 2009b; Capinera 2010).

A noteworthy case of orthopteran Batesian mimicry involves katydidis and wasps. New world wasps of the genus *Pepsis* Fabricius, 1804 (Pompilidae), known as Tarantula hawks, include at least 133 solitary fierce predators of tarantulas (Theratopsidae) (Vardy 2000). Several species of Phaneropterinae katydids (Tettigoniidae) are Batesian mimics of *Pepsis* wasps, the models. A well studied species is the harmless *Scaphura nigra* (Thunberg, 1824) which uncannily resemble the dangerous wasps. Furthermore, *S. nigra* is a polymorphic mimic of wasps. Del Claro (1991) demonstrated that three morphs of *S. nigra* mimicked three different wasp species in Brazil. This author identified in laboratory–bred *S. nigra* nymphs, three morphs (also found in the field) that mimic wasps of three different species. The "Pepsis" morph is a mimic of *Pepsis* wasps (Pompilidae); two other morphs resemble, *Polistes* Latreille (Vespidae) and *Entypus* Dahlbom (Pompilidae) wasps, respectively. This exceptional polymorphism is probably maintained by density-dependent selection (Del Claro 1991).

With respect to aggressive mimicry, a very interesting case involves the Australian katydid *Chlorobalius leucoviridis* Tepper, 1896 (Litroscelidinae) and cicadas of the tribe Cicadettini (Marshall & Hill 2009). The predator lures male cicadas mimicking specific reply clicks of sexually willing females. The most extraordinary aspect of this type of aggressive mimicry is that the katydid is able to attract males of different cicada species (including species from other continents), even though each species possesses unique species-specific mating signals. This versatility may have resulted from the exploitation of general design elements which are common to the acoustic signals of many insects that use duets in mating (Marshall & Hill 2009).

Wassmanian mimicry occurs in the gryllid family Myrmecophilidae (see section “Home on the range?”). As known, no cases of Mullerian mimicry have been described in Orthoptera.

**Flight and startle behaviour**: a startle stereotyped response in which, when discovered, insects usually rise their spinylegs and, in winged forms, open their tegmina and wings, showing flash coloration, appendage extension and other means (Capinera, 2010; Mathews & Mathews, 2010). Having startled the intruder, insects probably can escape before the predator reacts. Examples of Orthopterans having this response are: the New Zealand weta *Deinacrida heteracantha* White, 1842, the tettigoniids *Neobarrettia spinosa* (Caudell,

1907) (Litroscelidinae) from Mexico, the predatory *Clonia multispina* Uvarov, 1942 (Saginae) from eastern Africa, and *Balboana tibialis* (Brunner von Wattenwyl, 1895) from Central America and Colombia (Robinson 1968; Kaltenbach 1990; Mathews & Mathews 2010).

In other cases, orthopterans may use flash colouration, as is the case of *Acripeza reticulata* Guérin-Méneville, 1832, an Australian katydid (Phaneropterinae) which is erroneously called 'Mountain Grasshopper' (Rentz 2010). The species lives in leaf litter and it has a grayish exterior appearance that makes it cryptic to predators. However, if disturbed, females raise their wings and show a brilliant black, blue and red colour pattern (Mathews & Mathews 2010). Flash colouration in reverse also occurs in some cryptic grasshoppers [e. g., lubber grasshoppers (Romaleidae) and band-winged grasshoppers (Acrididae, Oedipodinae)] which while on flight display colourful wings but when they settle their exterior matches the ground colour (Mathews & Mathews 2010).

**Chemical defenses**. This kind of secondary defenses, show an extremely complex ecology and may involve venoms, toxins, and irritants that can act before, during, and after attacks to raise the inclusive fitness of a prey animal (Happ 1974; Pasteels *et al.* 1983; Blum 1981; Ruxton *et al.* 2004a).These secondary defensive compounds are sometimes synthesised by the animal, or merely appropriated intact from its food (Brown *et al.* 1970; Whitman *et al.* 1990; Berembaum 1995), are called *allomones* a term coined by Brown (1968) to signify "*a chemical substance produced or acquired by an organism which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral or developmental reaction adaptively favorable to the transmitter*". A number of different chemical defense mechanisms are known in the Orthoptera (Whitman *et al.* 1990). For example, grasshoppers are popularly known to "spit tobacco" because when grabbed by a predator (or an entomologist) they regurgitate their gut contents (enteric discharge) which are irritant or toxic. Some species fortify their blood cells or internal organs with distasteful or toxic allomones. Furthermore, *Eugaster* Serville katydids autohemorrhage in response to visual stimuli and can accurately eject blood 40 cm. Other orthopterans also produce defensive secretions containing blood cells.

Some lubber grasshoppers (Romaleidae) have been particularly well studied respect to their chemical defenses. These include *T. eques* and *Romalea guttata* (Stoll, 1813) (= *R. microptera*). Both species discharge a defensive secretion from paired metathoracic spiracles. Whose effectiveness depends on the amount of stored secretion (which is lost at every moult and has to be renewed at each stage). This amount is strongly dependent on age, sex, diet, and discharge frequency (Whitman *et al.* 1992). The defensive role of this secretion has been tested in *T. eques*: grasshopper mice *Onychomys torridus* (Coues, 1874) selectively avoid eating *T. eques* when another, palatable species (*Brachystola magna* (Girard, 1854)) is present, but they also reject the latter when individuals are coated with *T. eques* secretion (Whitman *et al.* 1985). However, at least in *R. guttata*, this secretion is not a universal defense against predators: two lizards, *Anolis carolinensis* Voigt, 1832 and *Sceloporus undulates* (Bosc & Daudin, 1801) are not deterred by the secretion from attacking and eating the grasshoppers, and do not develop an aversion to the secretion (Hatle & Townsend 1996).

**Group actions** involve coordinate behaviour of several individuals that can compensate for their small size and may involve *mobbing*, the simultaneous attack of hymenopterans mediated by pheromones, or *predator satiation*, the sudden and simultaneous emergence of large numbers of insects (e.g., termites). Group defensive behaviour is common in aposematic insects (see above) (Capinera 2010).

**Nocturnal activity** helps insects to avoid most visually-oriented predators. The distribution of diurnal and nocturnal activity across the order Orthoptera is very variable:

while the Acrididae are predominantly diurnal (with few exceptions, e. g. *Paulinia*), some taxa are almost completely nocturnal (e. g., Stenopelmatoidea, Tanaoceroidea) while others, such as the Tettigoniidae, include diurnal and nocturnal species and a few that perform their activities both diurnally and at night (Ingrisch & Rentz 2009). A most interesting adaptation to life at night has been reported for *Motuweta isolata* Johns, 1997 in New Zealand: these insects emerge from the soil only in the dark spells before moonrise and after moonset. Their activity is probably completely suppressed in full moon, and it is considered that this lunar effect has been evolutionarily driven by the predation by tuatara, *Sphenodon punctatus* (Gray, 1842), a nocturnal predator with great visual acuity (McIntyre 2001).

## Days of the locusts

"*If you refuse to let them go, I will bring locusts into your country tomorrow.***5***They will cover the face of the ground so that it cannot be seen. They will devour what little you have left after the hail, including every tree that is growing in your fields*." Exodus 10: 4, 5.

Plague locusts are first mentioned in the Urra = Hubullu (see Introduction) where they are referred to with the Akkadian word *senu* or *sennu* which means “evil” (Landsberger, 1934; Abivardi, 2000). Furthermore, a grasshopper translated as “Meeresheuschrecke” meaning “marine locust” probably corresponds to *Schistocerca gregaria* Forskål, 1775 because this locust bears the same name in modern Persian (*Malakh-e Daryai*= marine locust) (Abivardi 2000). The common name reflects the fact that swarms of *S. gregaria* usually come from the Persian Gulf region. King Solomon (ca 1000 B.C.) allegedly stated, “*The locusts have no king, yet go they forth all of them by bands*” (Prov. 30, 27), while Samuel Purchas (1619) expressed it as: “*Though they be sine rege, sine lege,* [without king, without law] *yet they have a conspiring agreement to do mischief*”. Most insect orders have representatives that are pests of range and cultivated plants and usually cause damage directly proportional to their size. Orthoptera are not an exception: numerous herbivorous or omnivorous species of Caelifera and Ensifera may cause serious destruction of vegetation depending on their abundance and their study has interested entomologists since long ago (Harris 1841, 1852, 1862; Arthurs 2008; Capinera 2008a,b,c). In the case of Caelifera the main pests are species of grasshoppers and locusts (mainly Acrididae and Romaleidae), and the ensiferan crop-feeding species are usually tettigoniids. The distinction of grasshoppers and locusts is relevant because their identification as one or the other responds to radical differences in life histories. Locusts are grasshoppers that exhibit a form of phenotypic plasticity called "phase change" or, more correctly, "density-dependent phase polyphenism" (Evans & Wheeler 2001; Simpson & Sword 2008). Solitary insects are stimulated to enter a gregarious phase by the increased contact caused by high population densities which in turn may be the consequence of two concurrent factors: very high precipitations during rainy seasons with resulting high levels of reproduction, followed by very dry periods reducing the normal habitat, limiting available resources, and stimulating the insects to group-migrate, at the nymphal stage in the form of bands, and, when flying adults, as swarms. A locust species may behave for many years as a "normal" grasshopper limited to its usual breeding grounds until the phase change is induced by the environment (Froeba 2008; Simpson & Sword 2008; Chapman 2009). In *Schistocerca gregaria* (Forskål, 1775) contact with other individuals at the level of touch receptors in the hind legs, has been shown as a powerful stimulus for gregarisation (Simpson *et al.* 2001). Recently, the neurotransmitter serotonin has been implicated in the process of gregarisation (Anstey *et al.* 2009). Only about 20 grasshopper species within different lineages worldwide are considered locusts (Table 2). Solitary and gregarious individuals of a locust species differ in many characteristics, from colouration to immune response (Simpson & Sword 2008). In *Locusta migratoria* (Linnaeus, 1758) differences are so great that Carl Linnaeus identified both phases as different species. Only in 1921, Sir Boris Uvarov (1889-1970) demonstrated that not only both phases belong to the same species but that their genotypes are the same: the genes that codify the characteristics of both phases are contained in the same genome and activated differentially under different conditions (Uvarov 1921; Simpson & Sword 2008).

**Table 2.** Locust and locust-like species.*

| | **Subfamily** | **Species** | **Authority** | **Common Name** | **Geographic Distribution** |
|---|---|---|---|---|---|
| True Locusts | Calliptaminae | *Calliptamus italicus* | (Linnaeus, 1758) | Italian locust | Europe, Eastern and central Asia |
| | Cyrtacanthacridinae | *Anacridium aegyptium* | (Linnaeus, 1764) | Egyptian tree locust | Northern Africa, europe, central and southern Asia |
| | | *Anacridium melanorhodon* | (Walker, 1870) | Sahelian tree locust | Sahel, eastern Africa, southwestern Arabia |
| | | *Anacridium wernerellum* | (Karny, 1907) | Sudanese tree locust | Sahel, eastern Africa |
| | | *Austracris guttulosa* | (Walker, 1870) | Spur-throated locust | Australia |
| | | *Nomadacris septemfasciata* | (Serville, 1838) | Red locust | Southern Africa |
| | | *Patanga succincta* | (Johannson, 1763) | Bombay locust | Southwest Asia |
| | | *Schistocerca cancellata* | (Serville, 1838) | South American locust | South America |
| | | *Schistocerca gregaria* | (Forskål, 1775) | Deseert locust | Northern Africa, Arabia, India |
| | | *Schistocerca piceifrons* | (Walker, 1870) | Central American locust | Central America |
| | Gomphocerinae | *Dociostaurus maroccanus* | (Thunberg, 1815) | Moroccan locust | Mediterranean countries, Middle East |
| | Melanoplinae | †*Melanoplus spretus* | (Walsh, 1866) | Rocky Mountain locust | Western and central North America |
| | Oedipodinae | *Chortoicetes terminifera* | (Walker, 1870) | Australian plague locust | Australia |
| | | *Locusta migratoria* | (Linnaeus, 1758) | Migratory locust | Southern Europe, Africa south of the Sahara, Madagascar, southern Russia, China, Japan, Philippines, Australia |
| | | *Locustana pardalina* | (Walker, 1870) | Brown locust | South Africa, Mozambique |
| Borderline Species | Oedipodinae | *Oedaleus senegalensi #* | (Krauss, 1877) | Senegalese grasshopper | Northern Africa, southern Arabia,India |
| | | *Aiolopus simulatrix§* | (Walker, 1870) | Sudanese plague locust | Northern Africa, Arabia,Middle Easte, India |

*Data from Steedman 1990 and Chapman 2009; †Extinct; # Often displays locust-like behaviour in the Sahel region; § Occasionally behaves like a locust in eastern Sudan.

The literature on locusts is enormous, evidently deriving from the magnitude of outbreaks (swarms may contain billions of insects), their devastating effects on crops and the usually catastrophic economic and social consequences (Krall 1995). The magnitude of the effects of locust outbreaks can be simply evaluated considering that for millenia locust plagues were regarded a manifestation of God's wrath (Frazer 1890; León Vegas 2012) leading to downright preposterous situations such as the criminal prosecution of a swarm of locusts (Evans 1906). Since it is not possible to review all the subject properly within the limits of this paper, I refer the reader to a number on important works: Wilson 2000; Lomer *et al.* 2001; Capinera 2008d,e,f; Froeba 2008; Showler 2008; Buhl *et al.* 2011; Raffles 2011; Liedvogel *et al.* 2011; Pérez Romagnoli 2011; Alberola Roma 2012; Campos Goenaga 2012; Garcia Quintanilla 2012; Gurr *et al.* 2012; Más Galván 2012; Spinage 2012; Viruell 2012 and Yu *et al.* 2013). Nevertheless, I will elaborate on two cases which are unique for very different reasons (despite the parallel destructive abilities of both species): the Rocky Mountain locust *Melanoplus spretus* (Walsh, 1866) (Acrididae, Melanoplinae), and the Mormon cricket *Anabrus simplex* Haldeman, 1852 (Tettigoniinae, Tettigoniidae).

The Rocky Mountain locust of North America is exceptional because *M. spretus* belongs to the Melanoplinae subfamily while all other locust species are included in the Cyrtacanthacridinae or Oedipodinae (Table 2)., although other *Melanoplus* species, such as the migratory grasshopper *M. sanguinipes* (Fabricius, 1798), may qualify as locusts according to certain criteria (Capinera 2008f). The most notable aspect of this pest insect is that, after an epidemic migration from the foothills of the Rockies to the Mississippi valley between 1874 and 1876, which caused tremendous ravage that led to a national crisis, it declined precipitously, reaching complete extinction in the beginnings of the twentieth century. The story of the Rocky Mountain locust has been excellently summarised by Lockwood (2001, 2004). The contemporaneous reports are quite clear about the devastating power of the hordes of minute devils (Snow 1875; Riley 1877; Whitman 1877; Riley *et al.* 1880). Even serious scientists studying the problem could not avoid referring to this locust as an 'evil' (Whitman 1877) or stating that "*For no part of the duties pertaining to this office have I felt less favorably inclined than that of collecting and recording the statistics of the damages inflicted by this insect. To make record of dead losses such as these, out of which no possible compensating good can arise, is necessarily an ungrateful task*." (J. B. Phillips in Whitman 1877). An idea of the magnitude of the outbreak is given by Lockwood (2001) based in the report of A. L. Child transcribed in Riley *et al.* (1880): Child calculated that a swarm of locusts passing over Nebraska in 1875 had a length of 1,800 miles (2,900 km) and a width of 110 miles (180 km). This implies an area of 198,000 square miles (513,000 square kilometers) (Lockwood 2004); density data from swarms of African locusts (which are larger than *M. spretus*) estimated that Child's swarm may have contained 3.5 trillion individuals. The life cycle and migration of the Rocky Mountain locust has been summarised in Chapter 2 of Lockwood (2004). The mystery is then, how this species disappeared from the face of the earth in less than 30 years (the last living *M. spretus* was captured in 1902)? A series of important studies by Lockwood and colleagues (Lockwood & De Brey 1990; Lockwood 2001, 2004) concluded that a natural population crash combined with habitat destruction and introduced species possibly led the Rocky Mountain grasshopper to extinction.

The other outstanding quite different story is that of the Mormon cricket (war cricket, western cricket, buffalo cricket etc., of early authors). In addition to locusts, some tettigoniids may constitute fearful pests and it has been suggested that phase polyphenism also occurs in these species that can reach extraordinarily high population densities and migrate in bands (Cowan 1929; Cowan & Shipman 1943; La Rivers 1947; Wakeland & Parker 1952; Wakeland 1959; Bailey *et al.* 2005; Sword 2008; Capinera 2008g). *Anabrus simplex* is a shield-backed flightless black katydid (not a cricket) that inhabits Western North America

(Capinera 2008d). The genus contains three additional extant species, two of which, *A. cerciata* Caudell, 1907 and *A. longipes* Caudell, 1907, are sometimes given the same common name (Wakeland 1959). The coulee cricket, *Peranabrus scabricollis* (Thomas, 1872) is in a distinct but closely related genus. Some African tettigoniids also show band-forming behaviour and cause considerable damage to crops in periods of outbreak (i.e. *Ruspolia differens* (Serville, 1838) and *Decticoides brevipennis* Ragge, 1977) (Matojo & Njan 2010a,b). *Anabrus simplex* is however, the best studied species. The earliest recorded reports of Mormon cricket attacks date back to 1848 when bands of this insect damaged the crops of the first Mormon pioneers in Salt Lake County (USA), as described by Bancroft (1889); "*...vast swarms of crickets, black and baleful as the locust of the Dead Sea*" (p. 279). Tradition tells that total destruction of the crops was impeded by the "Miracle of the gulls", whence myriad of these birds appeared to feed on the Mormon crickets (Bancroft, 1899; pp. 280-281). Nevertheless, bands of *A. simplex* can be really destructive: in 1938, at the peak of an outbreak, 19,000,000 acres (7,700,000 hectares= 77,000 km2) were known to be infested in 11 western states (Wakeland 1959). The first study to investigate the behavioural mechanisms that control the movement of migratory band-forming *A. simplex* was that of Sword (2005) who concluded that "*interindividual interactions play a greater role in inducing the movement of migratory band-forming Mormon crickets than do endogenous behavioural-phase changes mediated by high local rearing density*." Swarming and migration have been hypotesised to result from actual or anticipated scarcity of food in conditions of high density. In a field study of Mormon crickets, Simpson *et al.* (2006) showed that large migratory bands were deprived of essential food resources: protein, and salt. One of the consequences of such situation was the high incidence of cannibalism which intensity was reduced in conditions of salt and protein satiation. Marching band formations would then represent a trade-off between costs (cannibalism) and benefits (protection from predators) of group living (Simpson *et al.* 2006; Bazazi *et al.* 2008, 2010).

Finally, the association of the periodic swarms of *Locusta migratoria manilensis* (Meyen, 1835) (synonym of *L. m. migratorioides* (Reiche & Fairmaire, 1849) with climatic factors in China has been recently analysed using a historical approach and powerful statistical treatment (Stige *et al.* 2007; Zhang *et al.* 2009). The authors analysed annual abundance of locusts for a 1000-year period (957-1956) compiled by Chinese officials and obtained from ancient Chinese literature. Correlating these data with temperature and precipitation estimates for this period, the authors were able to determine that cold and wet periods are positively correlated with locust abundance coinciding with abnormally high frequencies of floods and droughts of the lower Yangtze River.

# Conclusion

*“Others there are who capture and breed insects with the object of ascertaining what may be learnt of their habits, of discovering the life-history both of the individual and of its race, of tracing the relationships that exist, or have existed, between insect-races extant or extinct, or with some other scientific purpose in view. To the notice of these our Orthoptera may with confidence be presented.”* W.J. Lucas, 1919, (p.2)

Almost a century has elapsed since the words of entomologist William John Lucas (1858-1932) were printed. Then, less than 10,000 orthopteran species were scientifically known which included many species nowadays considered to belong to other insect orders (Mantodea, Phasmatodea, Blattodea, Dermaptera, etc.). Today, more than 25,000 species of Orthoptera *sensu stricto* have been named and the number increases continuously and steadily. Lucas´s statement was justified: orthopterans have proved excellent models for countless scientific studies on areas of biology as diverse as evolutionary biology, genetics and cytogenetics, physiology, behaviour, ecology, macroecology, pest management, and many others. To cite just one illustrious example, acridid grasshoppers were one of the cytological foundations of the Chromosome Theory of Heredity which gave birth to the modern science of cytogenetics (Sutton 1903; Bidau & Martí 2010). The contributions of grasshoppers, katydids and their allies to biology has been enormous. Even a superficial survey of the more recent literature reveals many wonderful, exciting and surprising discoveries and new hypotheses in acoustic communication (Montealegre-Z *et al.* 2012; Sarria 2014), convergent evolution, speciation, and hybrid zones (Kawakami *et al*. 2009; Bella *et al*. 2010; Pascoal *et al*. 2014), dynamics of neo-sex chromosomes (Veltsos *et al*. 2008; Bidau *et al.* 2011), macro- and microgeographic patterns of life-history traits (Miño *et al.* 2011; Parsons & Joern 2014), molecular cytogenetics (Viera *et al*. 2010), DNA damage (Gosálvez *et al.* 2010), effects of supernumerary chromosomes (Bakkali *et al.* 2010), and many more. I wrote this review with the hope that scientific and popular interest in orthopterans will be acknowledged and increased in future years and thus keep contributing to Darwin´s splendid idea of Descent with Modification.

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*Correspondence*: Claudio J. Bidau, e-mail*:* *bidau47@yahoo.com*

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