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# **PATHWAYS OF APHIDS AND GRASSHOPPERS TO RADIATE FROM STRESS TO NEW SPECIES**

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## **Abstract**

Environmental stress can evolve new insect species by epigenetic inheritance and changes in their morphology and physiology. Recent phylogenetic research has emphasized that the adaptation of insects to feed on plants increased their diversity. Discovery of many fossil aphid species trapped in tree resins proved that they started with sexual or holocyclic life cycles by overwintering in the egg stage during the winter. Adelgidae and Phylloxeridae appeared about 200 Mya after Coccoidea. They were rapidly adapted to feed on trees and herbaceous plants after the acquisition of cyclical parthenogenesis life cycle 140 Mya. The economic importance of aphids and grasshoppers and aphid relation to their host is by direct damage or carrying viral plant diseases. Phylogenetic research indicates that Orthoptera radiated 300 Mya and grasshoppers radiated in the Pliocene of the Cenozoic period about 59.3 Mya. The radiation of 40 Orthopteran orders representing 15 super-families of monophyletic insect group is composed of Ensifera and Caelifera suborders. In this article, the possible route for speciation in aphids and Chorthippus grasshoppers is discussed. Two articles in the appendix describe specific information about Gomphocerinae and Chorthippus species of Iran.

## INTRODUCTION

First, the short history of aphid historical evolution and the possibility of their genetic changes to surpass plant resistance preventing aphids from feeding on them is described. An example is given by the difficulties in *Aphis* species identification. Then Orthoptera phylogenetic and radiation by reference to Gomphocerinae radiation by female choice of copulation and the appearance of various plasticity and traits in their population is described. Taxonomic identification of *Chorthippus* is associated with female choice of copulation with special acoustic characteristics. Difficulties of *Chorthippus* of Iran identification are explained in attached articles.

The variation in aphid life cycles and their diversification on various host plants increased their number of species (Jousselin and Elias, 2019; Dohlen and Moran, 1995). Aphids of Europe are composed of about 1600 species and subspecies with mostly holocyclic life cycles producing sexual morphs in autumn and females lay eggs on trees to overwinter cold winter conditions. They spend summers on trees and reproduce parthenogenetically on herbaceous summer hosts or on crops. They are adapted to the environmental stressful conditions and hymenopteran parasitoid wasps that have some effects to reduce their population. Many aphid species are attended by ants that are attracted to their sweet secretions or they are crop pests and resistant to insecticide. Their winged parthenogenetic forms spread on crops and affect them by viral diseases (Loxdale and Balog, 2018). In Iran a list of 324 aphid species with short descriptions of their biology, host plants and distribution or migration in the summer is described (Hodjat, 1993). Aphids' host plant change occurs by increased temperatures and lack of rainfalls.

Stress-induced changes in the biology of aphids and grasshoppers on crops are evolutionary processes for agricultural insect pests (AIPs) causing outbreaks or escaping the stressors during their life period. Resistance to pesticides, diapause, acclimatization, migration, and the number of their generations are adaptations to increase the insect pest fitness on crops. The rapid evolution of AIP increases their damage to

crops. The following processes give extra chances to AIP that by genetic evolution and insect radiation increase their damage to crops:

- Stress induces variation to specific genomic sites to increase insect population and adapt them to farm conditions.
- Genomic change linked to AIP increasing fitness.
- AIPs exposed to various stressors show homothetic physiological response to heritable DNA methylation by histone modification.
- Transposable elements (TE) regulation and mobilization effects on morphogen (Gum et al., 2024).

Genotypes of *A. gossypii* by mutation or recombination can produce genetic variable strains by asexual reproduction. Variable genotypes by mutation or recombination have different potentials in viral pathogen transmission to plants. Viral transmission genes produce plant responses for defense called gene-for-gene interaction. Interspecific genetic and phenotypic variability in *A. gossypii* was measured in 49 clonal lineages against plant defense genes or gene-for-gene interaction. It was found that the level of genetic melon aphid polymorphism in various clones is associated with the phenotypic variability of aphid genotypes responding to plant defense. It is concluded that environmental stress in aphid can shape plant resistance to viral infestation by aphids (Lombaert et al., 2009).

## **I-APHIDS**

### **Phylogeny and history of evolution**

Protein complex that is active in mitochondria and functions as riboproteins are intercellular structures made of both RNA and protein for protein synthesis in the cell ribosome or nucleosome. The ribosome reads the messenger RNA (mRNA) sequence and translates the genetic code into a specified string of amino acids. Post-transcriptional diversity in riboproteins highlights similarities and differences of proteins. Hillis and Dixon (1991) studied molecular evolution and phylogenetic inference in Precambrian divergence by ribosomal DNA (rDNA) sequences in a number of living organisms. Pairs of primers were selected to facilitate the analysis of rRNA. Analysis was carried out and aligned for sequences of four nuclear rDNA

and two mitochondrial ribosomal (rRNA) genes. Identified regions of test genes are likely to give information to identify closely related species of organisms in relation to food or their distribution. rDNA array in 15 sections by use of PCR (Polymerase Chain Reaction) are primers that can be selected in relation to the analysis of divergence of the rRNA genes to answer systematic problems in the hierarchy of food and geographic distribution (Hillis and Dixon 1991). By using allozyme and microsatellite markers it is found that *Acyrtosiphon pisum* collected from pea, clover, and alfalfa plants were genetically divergent. Therefore, there are some host-associated genetic differences between biotypes (Khanal et al., 2023).

### **Aphid biotypes and pathway to radiation**

The main aphid radiation is recorded about 80 MYA when they selected a holocyclic life cycle producing sexual morphs on trees and, in the spring, fundatrix produced parthenogenesis morphs of winged and wingless and migrated to herbaceous plants. These aphids, if faced with stressful conditions, migrate to new hosts. Adaptation to new hosts sometimes produces new species, which is radiation with phylogenetic branching for speciation. Host changing usually produces similar aphids called biotypes. Biotypes with similar morphology are also called biological species with different traits. They may have different genetic compositions with little morphological and physiological differences from the main population. The detailed lists of aphid biotypes are published (Khanal, Vitek, and Kariat, 2023).

Morphological differences between *Hyalopterus pruni* (Geoffroy, 1762) and *H. amgdali* (Blanchard, 1840) are in the length-width ratio of the cornicle (Siphunculi) of the wingless parthenogenesis forms. The ratio is less in *H. amgdali* than *H. pruni*. The morphology alone is not a suitable character for the separation of the two aphid species. The differences in the two species are clearly seen after sexual morph production on their different host plants with different sexual morphs on each host (Basky and Szalay-Marsze, 1985). In Iran, *H. pruni* is collected from apricots, peaches, prunes, and almonds. Both aphid species are using *Prunus* as a primary host and *Poaceae* species as summer hosts in central and northern parts

of Iran (Hodjat, 1993). There are many factors such as insect-host plant relationships and various stressors that cause phenotypic plasticity in insects (Hodjat, 2021). Stress can produce continuous, discrete, and fixed variation in morphology and cause a systematic problem for their identification. The main point for radiation of aphid separation by choosing another host is by sexual morphs that usually appear on trees. The host-related species are called peach and plum aphids. Sycamore aphid *Drepanosiphum platanoides* survival depends on the trait in reproducing at the onset of warm conditions in the spring. Early spring heat increases the mortality of their second generation. Therefore, the first generation increases their reproduction of nymphs, but in the second generation, a longer living adult in winged parthenogenesis form has less reproduction (Wellings, 1985). Therefore, biotypes of fundatrix from first or second generation aphids are likely to produce species adapted to the time of warm weather onset in the spring. Speciation and parthenogenesis of aphids by changing summer hosts throughout the year without sexual reproduction in mild winter temperatures is common in *Myzus persicae*, *Aphis gossypii*, and *A. craccivora*. They are likely to have less variation compared to holocyclic species (Hodjat, 1992; 1985).

Following are suggestions by the perplexity site and other sources to show a possible route of aphid biotypes to change into new species.

Holocyclic aphids choose a new winter host for fundatrix appearance in spring. An example is *Hyalopterus pruni* and *H. amigdali*.

Aphid symbiotic relationships play a crucial role in *Acyrtosiphon pisum* adaptation to use *Vicia villosa* as a new host (Lu et al., 2020).

*Myzus cerasi*, or black cherry aphid, overwinters on cherry and their summer hosts with low survival is *Gallium aparine*. Transitioning to a new host plant resulted in low survival rates due to the need for significant transcription changes, particularly in genes related to detoxification and metabolic processes (Thorpe et al., 2020).

Clones of *Myzus persicae* were collected from *Prunus persicae* and secondary hosts; *Nicotiana tabacum*, *Brassica oleracea*, *Beta vulgaris*, and

*Capsicum annuum* from various regions of Greece. In the northern regions, they were holocyclic, producing sexuals, but in the south, they lived parthenogenetically predominantly. All clones were reared in the laboratory on potato and their color or morphological differences were measured. It is concluded that 89% of 1723 specimens studied could be classified into two groups (Margaritopoulos et al., 2000).

The preference of aphids feeding on cultivated sweet lupine compared to wild bitter plants. Many aphid species such as *Acyrtosiphon pisum* (Ap), *Aphis craccivora* (Ac), *Aphis fabae* (Af), *Macrosiphum albifrons* (Ma), *M. euphorbiae* (Me), *Myzus persicae* (Mp), and *M. ornatus* (Mo) feed on lupines. It was found that only lupines with reduced alkaloids were preferred by these aphids for feeding on lupines. The difference in acceptance of aphids to feed on sweet or wild bitter lupines was related to their alkaloid contents. It was interesting to find that previously resistant cultivars to aphid infestation needed only five generations of *Macrosiphum albifrons* to become adapted for feeding on resistant cultivars with increased alkaloid contents (Thieme et al., 2014).

### **Speciation in Aphids**

Aphids have evolved diverse strategies for host plant association and have developed the ability to change their host plants in evolutionary time. New species described as a result of genetic variability, phenotypic plasticity, and their symbiotic relationships often means that they rapidly evolved various routes of escaping plant secondary metabolites. There is evidence that metabolic and other stressors can induce evolution by DNA epigenetic modifications and genomic variation in agricultural insect pest (AIP) aphids. Adaptive reaction to stress by DNA methylation in CpG, and histone modification is the first step for producing resistance to stress. Mutagenesis and variation in genome structure are factors for inducing new characters into increasing genotypes (Gunn et al., 2024). Stress can only increase individual resistance to stressors by differential performances. Insects have individual responses to stress by metabolic signaling pathways. Adapted individuals to stress can resist or decrease the harmful stress effects of sub-lethal doses of insecticides or resist starvation and heat stress. Epigenetic changes can pass the resistance to the next generations by

genetic DNA modifications after a few generations of bisulfite sequencing (WGB-seq). Gene regulation by DNA methylation in an experiment design can obtain multi-omic data on AIP to assess the mechanism of adaptive evolution in morphology and physiological variations (Gunn et al., 2024). The morphological distinction between *Aphis* L. species in Iran was only possible by comparing identified species in the British Museum (Hodjat, 1985).

## **II-GRASSHOPPERS**

Orthoptera radiated 300 mya and Acrididae originated in the Paleocene era of the Cenozoic period about 59.3 mya. There are more than 25,700 known Orthoptera species that contain crickets, katydids, locusts, and grasshoppers. Acrididae is divided into Ensifera with long antennae and Caelifera with shorter antennae. The phylogeny of Orthoptera after mitogenomic gene sequences divided the order into the following five superorders (Song et al., 2017):

- Tridactyloides
- Tetrigoidea
- Eumastacoidea
- Pneumoroidea
- Acridoidea

Acridoidea is divided into eight subfamilies:

- Cyrtacanthacridina
- Calliptaminae
- Catantopinae
- Oxyinae
- Melanopinae
- Acridina
- Oedipodinae
- Gomphocerinae

Bei-Bienko and Mishchenko published keys to the fauna of the USSR and adjacent countries in two parts translated to English in 1963. A list of aphid



species in Iran and Afghanistan was published by Shumakov (1963). Extinction of many aphids is reported when Shumakov's list of Iranian Orthoptera in 1963 is compared with Garai's list in 2010 (Hodjat et al., 1992; 2019). The identification of Gomphocerinae, especially Chorthippus spp., needs careful comparison of female attraction to male song and requires careful acoustic studies. The attached article shows the putative efforts of Hodjat (Appendix 2) to separate Chorthippus species by morphological keys.

### **The ER role in Spreading Depression (SD) of locust**

At high temperature or anoxia stress temporarily shuts down the neural-muscular system of the locust that by stressing depression-like (SD) events become motionless for short periods of time. The detailed function of SD is similar to mammalian pathogenesis of stress by affecting the cortical tissue in the cerebral cortex. The endoplasmic reticulum (ER) potassium channels are vital in maintaining K<sup>+</sup> homeostasis in locusts. Studies have identified ATP-sensitive cationic channels in the ER that are involved in the regulation of intercellular or intracellular ion concentration of K<sup>+</sup>. These channels influence the overall ionic balance of locust cells. SD in locusts is the phenomenon that has a relation to stress response with ER interaction. A wave of cellular depolarization followed by a period of suppressed neural activity in locusts under environmental stress can serve an adaptive function by conserving energy and terminating neural network operation during stressful conditions. The detailed function of SD stress in locusts and ER affecting cell physiology in response to stress is described in reviews by various authors (Rodgers et al., 2010; Hodjat, 2024).

*Schistocerca gregaria* (Forsk.) under low density is green and in cryptic form. At high densities, they produce conspicuous yellow and black markings with morphological, physiological, and behavioral changes (Wilson and Cotter, 2009; Harrison et al., 2010; Showler, 2013; Cornell and Hawkins, 2003). Insect hormones are involved in activating anti-oxidative enzymes (Bendarova, 2013). Adipokinetic hormones (AKHs) regulate insect metabolism and provide flight energy in *Locusta migratoria* (L.). Three peptide structures: two octapeptides and one decapeptide are

involved in the onset of flight. They regulate flight energy by metabolic neurohormones that are released from the corpora cardiacum (CC) (Van der Horst et al., 1999; Bednarova, 2013; Peric-Mataruga, et al., 2006). Free radicals are quickly converted to water and oxygen to prevent damage to cells. They can have a beneficial effect in destroying or damaging cells or detoxifying poisons (Dean, 2013; Wu et al., 2012; Lanz-Mendoza et al., 2002; Komarov et al., 2005; Even et al., 2012; Peric-Mataruga, et al., 2006; Zhao and Jones, 2012). For example, free radicals are produced in *Anopheles albimana* Petrocchi for killing its parasite, *Plasmodium* (Lanz-Mendoza et al., 2002).

**Stridulation and Chorthippus species complex.** Refer to appendix 1.

## DISCUSSION

It is clear that the morphology and physiology of insect species in different ecological conditions will change, and if they succeed in surpassing environmental stressors, they are adapted to their niche by some changes in their morphology and physiology. The subject of adaptation, plasticity, and variation in insects is basically discussed for defining species. The author is faced with many problems in identifying Iranian species of *Aphis* and *Chorthippus*. Molecular phylogeny of insect identification by barcoding, genomics, and other -omics suggest ways for accurate insect identification. Studying evolution is underway by scientists to explain achievements of *Aphis* and *Chorthippus*' possible routes of speciation. Attached articles explain examples of difficulties in identifying aphids and *Chorthippus* species by morphological keys.

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**Appendix 1:****Why identifying Gomphocerinae (Orthoptera, Acrididae) is not easy?**

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**Key words:** Systematics, Acoustics, Phenotypic Plasticity, *Chorthippus*, Species group, epigenetics, type specimen.

**Abstract**

Five species groups of Gomphocerini are; *Chorthippus albomarginatus*, *Gomphocerippus biguttulus* plus *G. Brunneus* sub group, *G. Saulcyi*, and *Pseudochorthippus parallelus*. Revision is made to factors of morphological variability in main species of these groups and difficulties associated with their identification. We briefly discuss windows of research in acoustic, plasticity, variation, and epigenetic as further attempts to define the closely related species in each group. The morphological changes of species in reaction to their environment and frequent presence of hybrid forms underline the static shape of type specimen.

**INTRODUCTION**

Gomphocerinae characters are close to Chrysochraontini, Arcypterini, Locustinae, Acridinae, Melanoplinae, Calliptaminae and Cyrtacanthacridinae in phylogenetic dendograms (Table 1; Defaut, 2017). Nattier et al,(2011) introduced Gomphocerini, Chrysochraontini, Dociostaurini and Arcypterini in the phylogenetic structures of Gomphocerinae and defined Stenobothrini, *Omocestus*, *Myrmeleotettix*, *Stenobothrus*, *Chorthippus* and *Arcyptera* in the dendogram. Phylogenetic reaction of *Pseudochorthippus montanus* is in very variable shape at various mountain regions. Its molecular analysis was obtained by sequence analysis in a portion of mitochondrial gene and coding for

cytochrome oxidase (Vedenina and Mugue, 2011; Rohde, 2017; Garcia-Navas et al, 2017). Only Phylogenetic studies accurately identify species group (Song, 2005; Defaut, 2017; Nattier et al, 2011; Vedenina and Mugue, 2011, Hodjat, 2015; Hodjat et al, 2018). Therefore the problem of Gomphocerinae identification is rooted in morphological similarity between species. Environmental factors can affect the differential population survival. In other words variation and plasticity produces morphological forms different from the type specimen. Female choice for matting a particular male sound are known as another factor in production of various forms different from the type specimen. To avoid confusion taxonomist divided various similarly shaped species into different groups of species. Research on acoustic, variation, plasticity, phylogenetic, population genetic and recently epigenetics is used for solving identification problem. The results on Gomphocerini species identification is arrangements differently by various authors. Table (1) is a few of the various classification scheme introduced for Gomphocerinae classification followed by short description about its groups and subgroups.

**Table 1:** Taxa arrangement from the Phylograms of Gomphocerinae. Names are arranged from the top of the author's clade, some of them are omitted.

Chapco & Contreras (2011)	Zhang (2013)	Nattier et al (2011)	Vedenina & Mugue (2011)	Hodjat & al., list of species (2018)
<i>Acrotylus</i>	Gomphocerini	<i>Gomphocerippus</i>	Gomphocerini	Arcypterini
<i>Locusta</i>	Chrysochraontini	<i>Gomphocerus</i>	<i>Chorthippus</i>	<i>Arcyptera</i>
<i>Oedaleus</i>	Arcypterini	<i>Stauroderus</i>	<i>Gomphocerippus</i>	Chrysochraontini
<i>Oedipoda</i>	LOCUSTINAE	<i>Chorthippus</i>	<i>Stauroderus</i>	<i>Euchorthippus</i>
<i>Celesia</i>	Acridinae	<i>Omocestus</i>	Stenobothrini	Dociostaurini
<i>Sphingonotus</i>	Melanopiinae	<i>Stenobothrus</i>	<i>Stenobothrus</i>	<i>Dociostaurus</i>
<i>Aiolopus</i>	Calliptaminae	<i>Dociostaurus</i>	<i>Myrmeleotettix</i>	<i>Stauroderus</i>
<i>Paracinema</i>	Cyrtacanthacridi	<i>Ramburiella</i>	<i>Omocestus</i>	<i>Leva</i>

	nae			
<i>Acrida</i>	Pamphagidae	<i>Chrysochraon</i>	<i>Ch. parallelus</i>	<i>Notostaurus</i>
<i>Duroniella</i>	Pyrgomorphidae	<i>Euchorthippus</i>	<i>Euchorthippus</i>	<i>Mizonocara</i>
<i>Holopercna</i>	Tetrigidae	<i>Stenobothrus</i>	Chrysochraont ini	<i>Eremippus</i>
<i>Cannula</i>	Tridactylidae	<i>Arcyptera</i>	<i>Podismopsis</i>	Hypernephini
<i>Duroniella</i>	Tettigoniidae	LOCUSTINAE	<i>Chrysochraon</i>	<i>Grigorija</i>
<i>Sherifuria</i>	Gryllidae		Arcypterini	Gomphocerinae
<i>Pyrgomorph a</i>	Phasmida		<i>Arcyptera</i>	<i>Gomphoceripp us</i>
	Mantophasmode a		<i>Ramburiellini</i>	<i>Chorthippus</i>
			<i>Ramburiella</i>	<i>Stauroderus</i>
			Dociostaurini	Ochrilidini
			<i>Dociostaurus</i>	Ramburiellini

## 1. Phylogeny and taxonomy of Gomphocerinae

phylogenetic classification has indicated the presence of many other taxa resembling *Chorthippus* or their species groups. More than 81 species of grasshoppers belong to Gomphoceriniare widely distributed in the world (Latchinsky, 2011). Gomphocerini is an assemblage of several similar grasshopper genera including *Gomphocerippus*, *Gomphocerus*, *Stenobothrus*, *Myrmeleotettix*, *Omocestus*, *Chorthippus*, *Pseudochorthippus*, *Stauroderus*, *Aeropedellus*, *Glyptobothrus* (Jago, 1971; Defaut, 2011, 2012, 2017). Species such as *Chorthippus albomarginatus*, *Gomphocerippus apicarius*, *G. maritimus*, *G. brunneus*, *G. biguttulus*, and *Pseudochorthippus curtipennis* are commonly found in Europe (Latchinsky, 2011). Many specialists use the sound characteristics to solve the identification problem of Gomphocerinae species (Benediktov, 2005). Geographical variation in song production is the source of plasticity and hybridization or speciation. This review intends to investigate the sources of the variability explained by various authors. In phylograms *Chorthippus* (Type species; *C. albomarginatus*), *Gomphocerippus* (type species : *G. sibiricus*), *Stauroderus* (type species: *S. scalaris*) and *Althichorthippus* (type species *A. uvarovi*) are in one clade while *Pseudochorthippus* type species; *P. parallelus* is in other clade (Table, 1). The morphologically similar groups of Gomphocerini species and species group or their subgroups are in orthoptera species file (OSF).

In the following list we mention factors affecting their trait and various routes to their speciation.

## **2. Attempts to define species groups**

The following species groups are sharing many common morphological characters. Species or subspecies in the groups have shown character bifurcation as a result of variable environmental stressors that may affect female choice of mate selection. The genetic, epigenetic and other factors, responsible for character variations in each specie groups, are indicated by references to research publications.

### **2.1 Species group *Chorthippus (Chorthippus) albomarginatus* (De Geer, 1773)**

Stable populations of *C. albomarginatus* may change characters by refuge in other places and staying isolated for a long period of time. The new population with different song characteristics may establish a new cline or a sibling species (Vedenina and Helversen, 1997; Helversen 1997). Therefore founder effect is the initial factor for population bifurcating characters in sympatric speciation. The process is thoroughly studied for populations of *C. palbomarginatus* from central Europe. Although Peg numbers inside the hind femur are inherited in *C. albomsrginatus* group but there is selection pressure for changing the position of their hind femur to produce different songs. In each position of the hind femur the density of pegs varies and for *albomarginatus* they are more condense in proximal parts (Vedenina et al, 2006). In each population song element characteristics or a chirp sound might be a reason for forming a new species in the group (Vedenina, 2015; Vedenina et al, 2007). Variation in the hybrid zone produces two clines in the population of *C. albomarginatus*. Frequency of leg strokes and consequently the song elements recorded is changed and selected in founder population (Vedenina, 2014). Vedenina and Helversen (2003) recorded specimen from *Ch. albomarginatus* in 17 localities in Germany, Hungary, Ukraine and Maldawi. The species in this group were easily distinguishable by recording their songs. Intermediate songs of hybrids between *albomarginatus* and *oschei* were also recorded in the laboratory.



Another cause of variation in this group is oxidative stress. Stressed species in this group were different in the structure of pegs and can be regarded as distinct species. Radiation in Chernobyl on *Chorthippus albomarginatus* caused genetic damage and mutation. Exposure to radiation also damaged the DNA of their offspring (Bonisoli-Alquati, 2018).

## **2.2 Species group *Gomphocerippus biguttulus* (Linnaeus, 1758)**

Various publications indicate that *G. jacobsi*, *G. bornhalmi*, *G. ilkazi*, *G. Bornhalmi bornhalmi*, *G. miramae*, and *G. rubratibialis* produce hybrids (Stumpner and von Helversen, 1994; Klappert and Reinhold, 2003; Helversen et al 2004). Gotsberger (2007) published a list of hybrid populations of Gomphocerini sketching difference in their songs with the main species. Morphological differences of *G. biguttulus*, *G. mollis*, and *G. brunneus* are described by Defaut (2001). Hybrid zones, distribution and song variation of this species group is also studied by Butlin and Hewitt (1985; 2008). The complexity of *G. biguttulus* (Charpentier 1825) identification is sharing habitat with *G. binotatus binotatus* (Charpentier 1825). They live in occidental and central Europe and aberrant form of this group may have evolved by hybridization with *G. biguttulus* (Ingrisch, 1995).

**Subgroup of *Gomphocerippus brunneus*** Linkage dendogram for the male and female songs can separate *G. antecessor*, *G. bornhalmi*, *C. brunneus* and *G. relicticus* from the song of *G. brunneus*. The variation in morphology of these subgroups and their distribution in Turkey and European relation to species group formation are described by Sirin et al (2010). *G. biguttulus*, *G. mollis*, *G. ilkazi*, *G. eisentrauti* and *G. jacobsi* are also common hybridizing populations in this subgroup. Occasionally *G. rubratibialis* and *G. jacobsi* form hybrid in the laboratory (Gottsberger, 2007). Saldamando et al, (1995) found polygenic inheritance of peg numbers on the hind femur of *G. brunneus* species group. The peg number divergence produces hybrids between *G. brunneus* and *G. jacobsi* and have produced hybrid population.

Genetic basis of divergence is described in three song components between *G. brunneus* and *G. Jacobsi*. These two species are living as hybrids in northern Spain and the genetic differences between them are based on the number of pegs on

hind femur and the sound components (Saldamando et al, 2005). Acoustic preference of female *G. biguttulus* for male songs can also change from the stabilizing selection to directional selection in accordance to female choice (Klappert and Reinhold, 2003). The directional, stabilizing and disruptive selections are acting on male song properties of *G. biguttulus* and can produce various traits (Klappert and Reinhold, 2003). DNA breaking and its repair with new arrangements of amino acids are the result of environmental stress effects on *G. brunneus* (Augustyniak et al, 2006; Burggren, 2017). Zinc as poison has long term effect during oogenesis and their oxidative stress effects are transferred to embryonic DNA of *G. brunneus* (Augustyniak et al, 2006, 2016).

### **2.3 Species group *Pseudochorthippus parallelus* (Zetterstedt, 1821)**

The process of evolution in flightless *P. parallelus* to morphologically similar but winged *P. montanus* is tested in various experiments by Tregenza et al (2000). They measured changes in morphology, acoustic and cuticular pheromones by samples taken from Greece, Italy, Spain, France, Switzerland, Germany and England. The purpose of this study is to determine what causes divergence between populations of *P. Parallelus* to change to *P. Montanus*. The incompatible mutational evolution or incidental effects of environmental changes (pleiotropic) can increase sexual selection by founder effects. The major hypothesis tested by Tregenza et al (2000) studies enhancement of genetic drift between the population and produce variation in morphology or acoustic characteristics. Polymorphism and morphological difference between populations at various localities in Europe show pattern of traits in populations from various countries. The authors indicate that geographic variation between populations living in various habitats increase genetic distance and may initiate speciation. They conclude that a sympatric species is formed by substantial pre-mating isolation followed by strong selection. It is difficult to prove that by these variations winged *P. montanus* changed to *P. parallelus erythropus* in Iberian mountains by changing the male calling signal. The differences in evolving *P. parallelus erythropus* subspecies are based on DNA sequence alteration. The genetic divergence between the similar species of this group might be mutational by creating new forms due to contemporary evolution (Butlin and Hewitt, 2008).

Natural hybridization in *P. parallelus* and *P. montanus* caused quasi-unidirectional gene flow to produce hybrid forms in small populations for choosy females (Rohde et al, 2015). By increasing the female development time in *P. montanus* at lower temperatures their body size increased. In contrast the male body size decreased with increasing density (Rhode et al, 2015).

The evolution of head shape for conical and up-directed head as compared to globular or normal head shape in some species of Gomphocerinae, Locustinae and Calliptaminae is compared between ground and tree perching species. There is disparity between species. The morphological group of hoppers and their ecological adaptation but is not quite related to the principal component of head shape (Garcia-Navas, 2017). *P. parallelus* group such as *P. parallelus parallelus* and *P. p. erythropus* are subspecies or geographic races differing only by song characteristics (Ritchie et al, 1990).

#### **2.4 Species group *Ch. (Glyptobothrus) (binotatus)* (Charpentier, 1825) =*Gomphocerippus saulcyi* (Kraus, 1888).**

The *G. saulcyi* (Krauss, 1888) lineage with the species or subspecies *daimei* (Azam 1898) in French Alps is *moralesi* (Uvarov, 1959) in Spanish and French Pyrenees and *algoaldensis* (Chopard 1952) in Central France and *vicdessossi* Defaut, 2011 in the French Pyrenees. The other genetic lineages *G. binotatus* is *G. armoricanus* (Defaut, 2015) in French plains and *G. atlasi* (Defaut, 1987) in North African mountains. *Chorthippus saulcyi moralesi* in mountain region of Pyrenean in Spain and French border have neutral genetic variation. The *saulcyi* species group and endemic subspecies are selected by mountain microhabitats (Noguerales et al, 2016) Hybridization and molecular evolution by mDNA sequencing can create new routes to investigate epigenetic of speciation and factors affecting phylogenetic divergence in Gomphocerinae (Hewitt, 2001; Smith and Ritchie, 2013).

*Chorthippus saulcyi moralesi* in mountain region of Pyrenean in Spain and French border show neutral genetic variation. The *saulcyi* species group and endemic subspecies are selected by mountain microhabitats (Noguerales et al, 2016) Hybridization and molecular evolution by mDNA sequencing can create new routes to investigate epigenetic of speciation and factors affecting phylogenetic divergence in Gomphocerinae (Hewitt, 2001; Smith and Ritchie, 2013).

## 2.5 Species group of *Chorthippus (Chorthippus) (dorsatus)* (Zettersted. 1821)

The species of this group are *C. loratus*, *C. dichrous* and *C. dorsatus* and all are distributed in Europe. Except for difference in song characters it is difficult to separate them by morphology. The song in females and males in the three species are similar. *C. Loratus* song is produced by synchronous movement of hind leg while *Ch. dichorous* move their hind-legs alternatively. *Ch. Dorsatus* hind leg movement are equally alternative and simultaneous (Stumper and Helversen, 1994).

## DISCUSSION

Gomphocerinae are classified differently in some publications (Defaut, 2017; Hodjat & all, 2018; Table 1). Zhang, et. al. (2013) described various difficulties in finding appropriate molecular markers to construct their phylogenetic tree. The most usual method is by the NADH mitochondrial gene. With this method the relative period of Ramburiellini, Dociostaurini and Arcypterini appearance could not be estimated. However, it was estimated that Gomphocerinae is very close to *Stenobothrus*, *Myrmeleotettix*, *Omocestus*, *Stenobothrus* and *Stauroderus* genera (Table 1-Defaut, 2017). Researchers describe variation in forms and the effect of female choice for mating males with certain song characteristics as the main cause of phenotypic plasticity (Nattier et al, 2011; Vedenina and Mugue, 2011). Acoustic niche of calling signals and the variability in relation to grasshopper communities in South Siberia and appearance of 25 species is giving the indication for ecological effects in formation of species group. Genetic, epigenetic and additive genetic factors are some of the topics extensively studied to define acoustic changes influenced by environment to produce hybrids and plastic forms (Vedenina and Helversen, 2003; Saldamando et al, 2005; Burggren, 2017, 2018).

Recent biodiversity studies have suggested the automatic identification of animals and specially *Chorthippus* species by sound recognition via A-matrices using an artificial neural network (ANN) system (Chesmore, 2004). This investigation is on its initial steps but further research may help to realize the plastic changes in species and type specimen (Riede, 1993; Schwenker et al, 2003; Chesmore, 2004; refer to appendix 2).

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## A ppendix 2:



## IRANIAN SPECIES OF GOMPHOCERINI FIEBER 1853 (ORTHOPTERA; CAELIFERA) CLASSIFIED FROM IN THE OLD GENUS “*CHORTHIPPUS*”

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### SUMMARY

A list of pamphagidae species of Iran and a view on historic compared to contemporary species of Iran Orthoptera indicate that it is important to identify and provide new list of Iranian Orthoptera. Difficulty of changes of insect morphology of specially some insect groups such as aphids and grasshoppers indicate the importance of achieving this task (Hojat, 2012; Hodjat et al, 2019). The present article is an effort to identify fourteen species and subspecies of *Chorthippus* Fieber, 1852 recorded in Iran that are classified in three genera (1) *Chorthippus* Fieber 1852 with parallel lateral carinae. *Glyptobothrus* Chopard 1952, which was a subgenus of *Chorthippus*, is now a junior synonym of *Gomphocerippus* Roberts, 1941. (2) *Gomphocerippus* Roberts, 1941 with lateral carinae of pronotum approaching in prozona. (3) *Pseudochorthippus* Defaut, 2012, with straight or slightly curved lateral carina but mostly with short wings. *Chorthippus davatchi* Descamps, 1967 recorded from Fars region in Iran is classified in this genus. *Chorthippus savalanicus* Uvarov, 1931, and *Chorthippus macrocerus* (Fischer-Waldheim, 1846) with angled lateral carinae approaching in prozona are now classified in *Gomphocerippus* Roberts, 1941. *Chorthippus giganteus* Mistshenko 1951 have many common morphological characters with *Chorthippus loratus* (Fischer von Waldeheim, 1846 ). Seven species of *Chorthippus*, six species of *Gomphocerippus* plus *Pseudochorthippus davatchi* are recorded from Iran.

### INTRODUCTION

The taxonomy of Gomphocerinae is not completely worked out. Three different phyllograms indicate that the taxa do not have fixed position in phylogenetic trees of various authors. Variation in Iranian Dicoelostaurini (Gomphocerinae) species and its plasticity is described by (Hodjat and Saboori, 2016). Vedenina and Mugue (2011) placed *C. dichrous* in the lowest position close to *C. dorsatus* (Defaut, 2017). *Chorthippus* Fieber 1852 in Iran are classified in; (1) *Gomphocerippus*, Robert, 1941 with angled pronotal lateral carinae in some species of previously classified as *Chorthippus*. (2) *Chorthippus* species with

parallel lateral carinae (3) *Pseudochorthippus* species mostly with very short wings and with parallel or slightly curved lateral carina (Defaut, 2012). In general identifying “*Chorthippus*” species in France (Defaut, 1988), Greece (Willemse et al, 2009) or Iran are not easy by only morphological characters. *Gomphocerippus brunneus brunneus* (Thunberg, 1815) is difficult to separate from *G. mollis* (Charpentier, 1825), and other species in *G. biguttulus* (L.) species group (Defaut, 2008).

*Chorthippus* species are mainly separated by their song characteristics. For accurately identifying some of the Iranian specimen knowledge of their acoustic and biology is required (Hodjat and Saboori, ). The distribution and the classification of Acridoidea in Iran are given by Descamps (1967), Popov (1951), Mirzayanse (1959), Shumakov (1963), Garai (2010) and Hodjat et al (2018). Some of the Gomphocerinae species of Iran are very similar and variable in morphology in different localities that cannot be identified accurately by morphological keys alone. The morphology of *Stenohippus*, *Eremippus*, *Dociostaurus*, *Notostaurus*, *Mizonocaria*, *Stenobothrus*, *Omocestus*, *Stauroderus*, *Euchorthippus*, *Xenocheila* and *Pseudochorthippus* need careful examination in order to accurately identify *Chorthippus* species. The old genus “*Chorthippus*” is characterized by the presence of a notch on the margin of tegmina. Lobule or projection is seen on their labium. Foveola is present but spurious vein is mostly absent except in *G. brunneus* and *Chorthippus giganteus* Mistsenko, 1951 recorded from Kordestan (Hosseini and Neyestanek, 2014). *Chorthippus davatchi* Descamps 1967 is classified in *Pseudochorthippus*. *Chorthippus savalanicus* Uvarov, 1931, and *Chorthippus macrocerus* (Fischer-Waldheim, 1846) are now classified in *Gomphocerippus*. *Gomphocerippus* Roberts, 1941 with six species in Iran is closely related to *Glyptobothrus* Chopard, 1852 subgenus. In this revision of *Chorthippus* taxonomy in Iran the main purpose is to identify limited Iranian species morphologically.

## METHODS AND GENERA RECORDED IN IRAN

Iranian species of Gomphocerini Fieber 1853 available in Professor Afshar museum of Agricultural College in Karaj, was compared with morphological keys published by Bey-Bienko, and Mishchenko, 1951, Defaut, 2008, Jago, 1971, Willemse et al, 2009. All of the *Chorthippus* species recorded in Iran are classified in three genera;

***Gomphocerippus* Roberts, 1941;** Type species of this genus is *G. rufus* (L.) which is widely distributed in Europe and North Caucasus. Morphologically species are

near to *Myrmeleotettix* which is a subgenus of *Omocestus* Bolivar, 1878. They have distinct lateral carinae on pronotum with projecting posterior margin (Bey-Bienko and Mishchenko, 1951). *Glyptobothrus* Chopard, 1952 subgenus of *Chorthippus* is a junior synonym of *Gomphocerippus* Roberts, 1941. Iranian species of *Gomphocerippus* are; *G. apricarius*, *G. brunneus*, *G. mollis*, *G. elbursianus*, *G. macrocerus* and *G. savalanicus*. They have lateral carinae with an angle in prozona of pronotum. Therefore the original *Chorthippus* species in Iran can be divided into *Gomphocerippus* Roberts, 1941, *Pseudochorthippus* Defaut, 2012 and *Chorthippus* Fieber 1852 genera. *Stenobothrus* and *Omocestus* are morphologically close to *Chorthippus*.

***Chorthippus* Fieber, 1852;** *C. dichrous*, *C. albomarginatus* (De Geer, 1773), *C. karelina*, *C. dorsatus*, *C. dichrous*, *C. hyrcanus*, *C. giganteus* are recorded in this genus in Iran. In these species tegmina and wings are well developed. Subcostal field of wings not widened. Foveola is long and narrow. Pronotum is with parallel lateral carinae or slightly curved in the middle (*C. hyrcanus*).

***Pseudochorthippus* Defaut, 2012.** The main morphological characters in this genus are; 1- Dilation or projection at the base of tegmina. 2-Lateral carinae of pronotum are almost parallel, or weakly inflexed in the prozona (non-angular). 3- Flight organs shortened, at least the hind wings. *Chorthippus parallelus* species group is classified in this genus (Defaut, 2012). The genus has the general character of *Stenobothrina* sub-tribe. Their Pronotum is with a narrow posterior part (*montanus*) or they have very short wings (*parallelus* and *davatchi*).

***Euchorthippus transcaucasicus* Tarbinsky, 1925**

Writing precise keys for identifying Iranian species of Gomphocerini require basic knowledge by examining all available specimen and species in the museums. We need to study phylogeny, biometric and acoustic of Iranian species. We gathered morphological description of the species from various publications to construct the following keys. Therefore our knowledge is limited to studies of specimen available in the University of Tehrean Afshar museum. With this method we identified *Euchorthippus transcaucasicus* (Chryochraontini). *Euchorthippus* differ from *Chorthippus* by having elongated subgenital plate in male and asymmetrical claws. It was collected from Alborz province (figures 2 & 3).

**KEY TO GOMPHOCERINI GENERA RECORDED IN IRAN**

- 1- With angled lateral carinae on pronotum. The tympanal opening is narrow or slit-shaped. Male tegmina with wide costal field or tegmina narrow....  
.....**Gomphocerippus Roberts, 1941**
- The lateral carinae of pronotum parallel. ....2
2. The transverse groove of pronotum in the middle. The tympanal opening wide or semicircular.....**Chorthippus Fieber, 1852**
- The transverse groove of pronotum posteriorly located. Frontal margin of pronotum dilated in small lobule at their base. Male subgenital plate is apically straight or truncate. Flight organs usually short, especially in females.  
.....**Pseudochorthippus Defaut, 2012**

#### KEY TO GOMPHOCERINAE GENERA CLOSE TO *CHORTHIPPUS*

- 1- Lateral carinae of pronotum parallel or slightly incurved.  
Tympanal organ is with wide or semicircular opening.  
Antennae are usually about equal to the length of head plus pronotum.  
Transverse groove of pronotum is in the middle of the pronotum.  
Foveolae quadrangular short and wide (*C. loratus*) or long and narrow (*C. dorsatus*). If median field of tegmina widened, antennae longer than the length of head plus pronotum. Subgenital plate of the female with projecting posterior margin.....**Chorthippus Fieber 1852**
- If lateral carina of pronotum is parallel, then either hind tibia with a long spur or radial vein of the wing is thick in the middle. ....2
2. Hind tibia with a long spur. Its length is more than the second tarsal segment.  
Mesosternum with narrow interspace equal to its length. Metasternum with contiguous lobes. Transversgroove of pronotum postritory located  
Hind wings with curved and slightly thickened costal and subcostal vein.  
.....**Stenohippus Uvarov, 1926**
- Hind tibia with shorter spur than the second tarsal segment  
Radial vein of the wing thickened in the apical third.  
Antennae are slender and longer than head plus pronotum.

The subcostal field of the wing widened in the middle.

.....***Stauroderus* Bolivar 1897**

## KEY TO SPECIES GROUPS OF GOMPHOCERINAE RECORDED IN IRANIAN

1. Tegmina wider or with a notch at its frontal border.  
With angled pronotal lateral carinae (Fig. 1.)  
.....***Gomphocerippus biguttulus* species group**
- Lateral carina of pronotum not angular in prozona. ....2
- 2-. Transvers groove of pronotum are posteriorly located.  
Front margin of the tegmina dilated in lobule at the base  
Females wings not covering all abdominal segments (Fig. 4).  
.....***Pseudochorthippus* species group**
- Transverse groove of pronotum in the middle.....3
3. Median field on tegmina wider than the cubital field.  
White band exist on the margin of tegmina.  
The length of a median antennal segment 2.3-2.5 times its basal width.  
.....***C. albomarginatus* species group**
- Median field of tegmina is narrower than the costal field.  
White band is not seen on the margin of tegmina.  
Foveolae are long and narrow. .... ***C. dorsatus/loratus* species group**

**Table 1:** Important distinguishing morphological character of *G. biguttulus* (Linnaeus, 1758), *G. mollis* Charpentier, 1825; *G. brunneus* (Thunberg, 1815) and *G. mollis elbursianus* Mistshenko, 1959 (Bey-Bienko, G. Y. & Mishchenko, 1951). Variation between the morphological characters in *C. biguttulus* group of species is the main difficulty in morphological identification of the species (Ingrisch, 1995).

<i>G. biguttulus</i>	<i>G. brunneus</i>	<i>G. mollis</i>	<i>G. elbursianus</i>
Male tegmina	Male tegmina	Male tegmina	Tegmina in the

wider at preapical part.	with a narrow, tegmina and costal field.	with a wider tegmina and the costal field.	male 3.5-4.2 times its greatest width.
Tegmina extends beyond the distal end of hind femur.	Tegmina with narrow median and cubital veins.	Tegmina long and narrow, 4.5-5.5 times its greatest width.	Tegmina just reaching to the distal end of hind femur.
Foveolae are thin and narrow	Foveolae short rectangular. Eyes in males usually small.	Foveolae long and narrow.	Foveolae short and wide.
Body length: Male 12-17 mm Female 15-22mm	Body length: Male 14-18mm Female 20-24 mm	Body length: Male 13-17mm Female 17.5-19.5mm	Body length: Male 11-14mm Female 16-21mm

**Table 2;** Some of the prominent morphological differences between *C. loratus* and *C. dorsatus* (Bey-Bienko, G. Y. & Mishchenko, 1951). *C. dorsatus* species group share some morphological features with *C. albomarginatus*. In *C. albomarginatus* tegmina is with a narrower median field than *C. dorsatus*. In *C. dichrous* hind femur is long and narrow, 5-6 times longer than its widest parts. It is also classified as subgenus of *dorsatus*. *C. brauneri* Znojko, 1928 is synonym of *C. loratus* (Cigliano et al, OSF, 2018).

<b><i>C. loratus</i> (Fischer von Waldheim,</b>	<b><i>C. dorsatus/dichrous</i> Zetterstedt, 1821</b>
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<b>1846)</b>	
<ul style="list-style-type: none"> <li>• Foveolae short and wide</li> <li>• Eyes large, the vertical diameter in male 2.5-3 times in female 2 times the subocular groove.</li> </ul> <p>Cerci in males 2.5-3 times longer than width.</p> <p>In <i>C. dorsatus dichroust</i> tegmina is with weakly curved median vein.</p> <p>Body length: Male 12-16mm Female 18-21 mm</p>	<ul style="list-style-type: none"> <li>• Foveolae long and narrow, 3.5-4 times longer than width.</li> <li>• Eyes vertical diameter less than 2 times the length of subocular groove.</li> </ul> <p>Cerci in males less than 2 times the width.</p> <p>In <i>C. dorsatus dorsatus</i> tegmina is with sharply curved median vein.</p> <p>Body length: male 13-16 mm Female 17-20mm</p>

### KEY TO GOMPHOCERIPPUS SPECIES

1. Wings short exposing 4-6 terminal abdominal segments.  
Hind femur long, its length about four times its greatest width.  
.....**savalanicus Uvarov, 1933**
- Wings covering all abdominal segments. ....2
2. Cubital field of tegmina in female with spurious vein or with its traces in median field. Male eyes small, its longer diameter 1.5 times subocular groove.  
.....**brunneus brunneus (Thunberg, 1815)**
- Cubital field of tegmina in females without spurious vein. ....3
3. Male tegmina long and 3.5-5 times longer than its width. ....4
- Male tegmina less than four times its width. ....5
4. Foveolae small quadrate or short rectangle. Male tegmina about 3.5-4.2 times longer than the widest parts.....**elbursianus Mistshenko, 1951**

- Foveolae long and narrow. The length of foveolae is about three times longer than its width. Tegmina is about five times longer than wide, extending beyond the distal end of the hind femur. .... ***mollis* (Charpentier, 1825)**
- 5. Mesosternal interspace equal to side grooves. Tegmina with wide median field and with parallel cross veins. .... ***apricarius* (Linnaeus, 1758)**
- Mesosternal interspace wider than the side grooves. Tegmina with narrow Median field. Hind femur four times longer than its widest parts. .... ***macrocerus* (Fischer-Waldheim, 1846)**

### KEY TO *CHORTHIPPUS* SPECIES

1. Male tegmina are without spurious vein and usually narrow. ....
- Spurious vein usually present on wider precostal field of tegmina.  
Male genital plate long and conical. .... ***giganteus* Mischenko, 1951**
2. The narrow precostal field extends beyond the middle of hind femur.  
Stridulatory pegs inside hind femora 130-135. .... ***albomarginatus* and *ssp karelina* (Uvarov, 1910)**
- The precostal field not reaching the middle of hind femur. .... 3
3. Wings short and exposing the terminal abdominal segment. .... ***hyrcanus* Bey-Bienko, 1960**
- Wings covering all abdominal segments. .... 4
4. Foveolae long, cerci shorter. .... ***dorsatus* (Zetterstedt, 1821)**
- Median vein on male tegmina weakly curved near the apex. .... ***dorsatus dichrous* (Eversmann, 1859)**
- Foveola short, cerci longer. Eyes large, the vertical diameter 2.5-3 times the length of subocular groove. .... ***loratus* (Fischer von Waldheim, 1846)**

### DISCUSSION

*C. albomarginatus*, *C. bicolor* (Charpentier, 1825), *C. brunneus*, *C. dorsatus*, *C. macrocerus* and *C. mollis mollis* are recorded in rice fields of Iran (Ghahari et al, 2009). In new classification the position and names of these species are changed. *C. bicolor* is synonym of *G. brunneus brunneus* (Thunberg, 1815), which is



classified in subgenus *Glyptobothrus* Chopard 1952 (OSF). Recently *C. brunneus* is classified in *Gomphocerippus* Roberts, 1941 genus and placed in *G. biggutulus* species group (Fig.1).

*Chorthippus davatchi* is classified in *Pseudochorthippus* Defaut 2012 genus. It bears all description for this genus and can be classified in Sternobothrina subtribe (Defaut, 2012). European and American species of *Chorthippus* such as *Chorthippus montanus*, *C. curtipes* and *C. parallelus* are also classified in *Pseudochorthippus*. *C. savalanicus*, and *C. macrocerus* are with angled lateral carina on pronotum and classified in *Gomphocerippus* genus (Roberts, 1941). *C. macrocerus* is also classified in *Gomphocerippus*. *C. giganteus* Mistshenko 1951 with spurious vein on tegmina is classified in *C. dorsatus* species group.

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1-*Gomphicerippus biguttulus* Species group 2- *Euchorthippus transcaucasicus*



3- *Euchorthippus transcaucasicus*  
*davatchi*

4-*Pseudochorthippus*