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Review Article

Variation, plasticity and possible epigenetic influences in species belonging to the tribe Gomphocerini (Orthoptera; Gomphocerinae): A review

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Abstract: Environmental conditions can cause variation in morphology, behavior, and possibly epigenetic in the numerous species of the Gomphocerinae, especially in mountain habitats. Plasticity and changes in morphology in many of the species in this subfamily is caused by character segregation through the female choice of copulation that has produced various clines, sub-species or species groups. The variation and plasticity, as a result of environmental stress, besides morphology, affect physiology and epigenetics of many insect species. Environmental stress and female assortative mating might be accompanied by hybridization in populations, resulting in character divergence and speciation after a long period of time. Contemporary evolution and/or epigenetic inheritance may be a reason for their variation in acoustic and morphology of Gomphocerinae and the main factor in the present situation of difficulty in their classification. We review possible effects of environmental stress on plasticity, hybridization, and speciation by the appearance of endemic species. About half of the insect pest species have reduced their impacts as pests under global warming. The present insect pest situation in Iran is discussed.

Keywords: Classification, Hybridization, Groups, Gomphocerini, Phenotype, Song

1. Introduction

Geographical distribution of Gomphocerinae species is the source for variation, plasticity, and hybridization by environmental effects. Many endemic species and subspecies are created by acoustic divergence and sympatric speciation. The degree and direction of a trait is related to sexual dimorphism and female choice for copulation in insects (Robinson and Hall, 2002; Mol *et al.*, 2003; Tishechkin and Bukhvalova, 2009; Vedenina and Helversen, 2009; Şirin *et al.*, 2010, 2014; Stillwell *et al.*, 2010; Vedenina and Mugue, 2011). Therefore morphology alone is not enough to define many species of Gomphocerini and taxonomists are using sound characteristics for identification. Biodiversity studies of Gomphocerinae species are difficult due to a lack of knowledge for accurately identifying them in Iran without recording their songs and considering other factors causing variation in their populations (Sultana *et al.*, 2013; Hodjat *et al.*, 2019).

More than 81 species of Gomphocerini grasshoppers are widely distributed in the world (Sergeev, 2011). In other words, Gomphocerini

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is an assemblage of several similar grasshopper genera including *Gomphocerus*, *Myrmeleotettix*, *Chorthippus*, *Pseudochorthippus*, *Stauroderus*, and *Aeropedellus* (Jago, 1971; Defaut, 2011, 2012, 2017). The genus *Chorthippus* has 229 species and is divided into 2 or 3 subgenera *Chorthippus* (*Altichorthippus*) (20 species), *Chorthippus* (*Chorthippus*) (32 species), and for various authors (including orthoptera species file OSF), *Chorthippus* (*Glyptobothrus*) (57 species). The other species of *Chorthippus* are not classified into any subgenera. The *Chorthippus* (*Glyptobothrus*) *biguttulus* group has 12 species and *C. binotatus* group has two species. The genus *Pseudochorthippus* Defaut, 2012 with four species and two sub-species is closely related to *Stenobothrus* Fischer and *Omocestus* Fieber (subtribe Stenobothrina).

Character changes in Gomphocerini species are a reaction to environmental factors that its stress may have influenced their genetics, epigenetics and external morphology (Laiolo *et al.* 2013). Neurohormones regulate all life processes in Gomphocerinae and insects in general (Perica-mataruaga *et al*., 2006; Hodjat, 2006). Juvenile hormones (JHs) and the neurosecretory neurons (NSNs) secretions of *corpora cardiac* (CC), *corpora allata* (CA) and the brain (CNS) release methylsulfonylmethane (MSM) into the haemolymph. The gene expression is involved in *C. biguttulus* (L.) biogenic amines and chitin-binding. Transcriptomic methods of profiling show differential expression pattern in various stages of *C. biguttulus* life cycle and are described by Berdan *et al.* (2017), and Tatsuta and Butlin (2001). Gene expression pattern in *C. albonemus* change when pastures have been overgrazed in cases of food shortage (Qin *et al*., 2017). The increased activity in locust is initiated after adipokinetic neurohormones are secreted (Hodjat, 2016). The reaction to acoustic communication in response to environmental conditions has been studied in *C. biguttulus* (Klappert and Reinhold, 2003). Species in the *Chorthippus* (*Glyptopothrus*) group communicate by special male songs to fend off competitors from the female, a behavior regulated by *corpora cardiac* secretion (Heinrich *et al*., 2012).

Populations in various species of Gomphocerini may change their characteristics by choosing different selection routes. Differentially fixation of various characters on the population of a species may increase their adaptation and survival chance. The process of divergence in colour, morphology, and song in *Pseudochorthippus parallelus* (Zetterstedt) produces different traits by genetic polymorphism (Kohler *et al*., 2017). A long separation of their population increases their genetic distance, colour and morphological or acoustic diversification (Tregenza *et al*., 2000; Butlin and Hewitt, 2008; Vedenina and Mugue, 2011; Monge, 2017). Subspecies and species group formations are the results of genetic or epigenetic changes in Gomphocerini (Smith and Ritchie, 2013; Noguerales *et al*., 2016), through assortative mating and environmental conditions (Klapper and Reinhold, 2003; Burggren, 2017).

Rapid character divergence of grasshoppers in response to the male songs for copulation and other environmental factors are influencing taxonomists to clarify their classification. A new line of research on sound production, epigenetic, and stress has proved its influence on the Gomphocerinae species radiation (Franzke and Reinhold, 2012). We refer to some publications of research on species radiations creating endemic forms by phylogenetic, taxonomic, stress and genetic or epigenetic investigations (Pravdin, 1969; Mark, 1983; Hodjat *et al*., 2018; Burggren, 2018; Riede, 2018).

2. Phylogeny and classification difficulties

Orthoptera Species File (OSF) has provided a list of 20 tribes classified in the Gomphocerinae subfamily. Gomphocerini Fieber, 1853 or Chorthippini Shumakov, 1963 with 16 genera is among the largest group of grasshoppers (Cigliano *et al*., 2018). Some investigations have placed Gomphocerini, Chrysochraontini, Dociostaurini, and Arcypterini in the phylogenetic structures of Gomphocerinae and included

Omocestus, *Myrmeleotettix, Stenobothrus*, *Chorthippus* and *Arcyptera* in their phylogenetic tree (Vedenina and Mugue, 2011; Garcia-Navas *et al*., 2017; Rohde *et al*., 2017).

Considerable phenotypic plasticity is a major source of difficulty in developing a unique phylogenetic classification for Gomphocerini (Song, 2005; Zhang *et al*., 2013; Şirin *et al*., 2014; Defaut, 2017). Morphological characters of a few species in Chrysochraontini, Arcypterini, Locustinae, Acridinae, Melanoplinae, Calliptaminae and Cyrtacanthacridinae tribes or subfamilies are close to Gomphocerinae or overlapping in some morphological characters (Defaut, 2017). The most common phylogenetic method of their separation is by the NADH (nicotine amid adenindinuclrotide phosphate) mitochondrial analysis. Yet, with this method, the relative time of appearance of Ramburiellini, Dociostaurini, and Arcypterini could not be determined. However, it was estimated that the Gomphocerini and species in *Stenobothrus*, *Myrmeleotettix*, *Omocestus, Stenobothrus,* and *Stauroderus* genera are closely related (Defaut, 2017). The acoustic and phylogenetic relations of various polyphyletic taxa in Gomphocerinae are comparable (Nattier *et al*., 2011; Vedenina and Mugue, 2011).

Integrating genomic and phylogenetic data with molecular studies might result in species delimitation and find how various traits produced the evolutionary radiation in grasshoppers (Contreras and Chapco, 2006; Nattier *et al*., 2011; Via, 2012; Noguerales *et al*., 2018). The common species of Gomphocerini in Europe and the Middle East are *C. albomarginatus, C. apricarius, C. maritimus, C. brunneus, C. biguttulus* and *Pseudochorthippus parallelus* (Harris, 1835), the latter is classified as one of the *P. parallelus* subgroups (Sergeev, 2011).

Morphologically similar groups of Gomphocerini species are as follows:

2. 1. *Chorthippus albomarginatus* species group

Sound changes in this group of species is studied by Vedenina (2015); Vedenina and Helversen (2003, 2009); Vedenina and Shestakov (2014); Vedenina *et al.* (2001, 2007b). Hybridization of *C. albomarginatus* and *C. oschei* produces asymmetric populations and reduces the hybrid viability (Vedenina *et al*., 2007a). The founder effect of the population with different songs can establish sibling species and new cline (Helversen and Helversen, 1997). The main driving force of speciation in this group of species is sexual selection by the female choice of courtship.

2. 2. *Chorthippus* (*Glyptobothrus*) *biguttulus* species group and subgroup

Habitat segregation, character diversification by the female choice of copulation, and hybridization are known to have established many similar species in this group or subgroup of species (Saldamando *et al*., 2005; Gottsberger 2007; Şirin *et al*., 2010; Gomez and Dyck, 2012). The complex *C. biguttulus* group is formed by a mixture of macropterous and brachypterous forms in occidental and central Europe (Ingrisch, 1995). Many species in this group share habitat with *C. binotatus binotatus* (Charpentier) and are similar to *C. jacobsi* (Harz), *C. bornhalmi* (Harz), *C. ilkazi* (Uvarov), *C. miramae* (Ramme) and *C. rubratibialis* (Schmidt). Hybridization is reported between these species in this group (Stumpner and Helversen, 1994; Klapper and Reinhold, 2003; Helversen *et al*., 2004; Saldamando *et al*., 2005; Gottsberger, 2007; Franzke and Reinhold, 2012b).

2. 3. *Pseudochorthippus parallelus* species group

Pseudochorthippus montanus (Charpentier), *P. curtipennis* (Harris), *P. tatrae* (Harz), *P. parallelus erythropus* (Fieber, 1858), *P. p. serbicus* (Karanian, 1953), and *P. p. tenuis* (Brulle, 1832) are classified in this group. Hybrids between the last two subspecies are formed because of cytoplasmic incompatibility as a result of *Wolbachiella* infection (Bella *et al*., 2010). The differences in song and the hypothetical change of flight activity in separating flightless and winged forms have been studied in this group (Ritchie, 1990; Tregenza *et al.* 2000; Butlin and Hewitt, 2008; Kohler *et al*., 2017) Morphological variations in *P. parallelus* from samples at 450-2500 m elevation indicate that tegmina and body length of samples was decreased by ascending the mountain but morphology of pronotum is unchanged.

2. 4. *Chorthippus (C.) dorsatus* species group

Chorthippus loratus (Fischer von Waldheim) and *C. dorsatus* are *s*ibling species in this group of species. Songs in *C. albomarginatus* group represent an advanced development of the *C. dorsatus* group (Stumpner and Helversen 1994). The complexity of the calling songs in these two groups of grasshoppers is comparable (V. Vedenina personal communication).

2. 5. *Chorthippus* (*Glyptobothrus*) *binotatus* species group

Three subspecies of *C. binotatus* and three subspecies of *Chorthippus* (*G.*) *saulcyi* (Krsuss) are classified in separate groups of species. The two groups are very similar and are usually classified into one group. The genetic lineages between populations in this group of species living in the mountainous region of the border between France and Spain were studied by Defaut (2011) and Noguerales *et al.* (2016, 2018). Isolation of populations living in different mountain habitats may have been the cause for species separation in this group (Noguerales *et al*., 2016).

3. Factors affecting classification of the Gomphocerinae

3. 1. Variation and Plasticity

The definitions of phenotypic plasticity and its relation to selection, coevolution, ecological speciation, genetic drift, phylogenetic inference, pleiotropy, reinforcement, sexual dimorphism and size constraints have been explicitly described with examples of Gomphocerini species (Whitman and Agrawal, 2009; Feng *et al*., 2015; Zinna *et al*., 2018). Plasticity is more liable to fix characters after insects acquire a new trait. Variations are temporary morphological character dissociation that may fix on a part of a population for several generations. Plasticity and variation may cause speciation or contemporary evolution i.e. the evolution of traits over a short period of time (e.g. centuries rather than eons; Górür, 2005; Whitman and Agrawal, 2009). Plasticity can change individual, population or species epigenetic by environmental stress in insects (Hoffmann and Parsons, 1991; Oxford Research Group, 2015; Augustyniak *et al*., 2016; Burggren, 2018).

Phenotypic plasticity reflects the “reaction norm” of individuals to climate and other environmental conditions (Laiolo *et al*., 2013). Reception of environmental stressful conditions by CNS can cause variation and plasticity in parts of species population (Ronacher, 1989; Romer, 1993; Skinner, 2014). The genotype of an organism in the reaction norm may also be affected by life incidents. That is, plasticity confers the capability of producing changes in phenotype in response to environmental changes (Sgro *et al*., 2016). Final decision for direction of movement towards a stimuli such as attraction to the opposite sex in *C. biguttulus, Gomphocerus sibiricus* (L.), *Omocestus viridulus* (L.) and *Stenobothrus lineatus* (Panzer, 1796) is taken by the brain signals that are involved to activate the appropriate muscles (Helversen and Helversen, 1997; Klapper and Reinhold, 2003). Therefore plasticity is a broad term that can apply to the genetic, epigenetic and contemporary evolution of Gomphocerini response to the environment.

3. 1. 1. Plasticity and variation on insect pests

Increasing plant defense against herbivores and pathogens is related to DNA methylation and histone modification by the transgenerational defense. Changes in the phenotypic traits of grasshoppers are also linked to their performance and gene profile. Genes in *C. albonemus* change expression pattern when pastures are overgrazed and in cases of food shortage (Qin *et al*., 2017). The effects of ambient and optimal temperatures on 31 species of insect pests have been compared by Lehmann *et al*., (2018). North Europe, South America, and Australia had fewer outbreaks of these pests compared to Asia and Africa. Aridity is an important factor in locust and grasshoppers to reach the outbreak point (Uvarov, 1957). Repeated insecticide treatments without considering the importance of natural enemies can cause pest outbreaks (Hodjat, 1967). A pest control project using modeling to consider the efficiency of pest control methods for Iran is suggested by Hodjat (1974). Modares-Awal's (2012) list of Orthoptera pests in Iran indicated that most species do not seriously damage crops and hardly reach to outbreak position. Caution for not using repeated insecticide treatments without pest management strategies has reduced pest damage to crops (Hodjat, 1967).

At present, the locust outbreaks are occasionally reported only after a rainy winter and revival of natural pastures in Iran. Some pest species such as *Eurygaster integriceps* Puton*, Bemisia tabaci* (Gennadius, 1889), *Chilo suppressalis* (Walker) and occasionally other insect pests of crops and fruit trees need a continuous survey (Davatchi, 1954). However, locust phase polymorphism, phenotypic plasticity, including various mechanisms responsible for the insurgence of aggressive biotypes, or resistance to insecticides are the main factors behind the pest control problems (Song, 2011; Augustyniak, 2016; Hodjat, 2016; Sgro *et al.*, 2016; Lehmann *et al.*, 2018).

3. 2. Epigenetic and stress influences

Various stressors trigger epigenetic modifications in animals and plants. Modifications allow gene transcription and remain in genome memory. Transgenerational epigenetic memory ensures plasticity and genetic variation (Tricher, 2015). Gomphocerini species may change colour, size, and activity in response to climatic conditions, and these changes are epigenetically inheritable (Rohde *et al.* 2017). In fact, such polymorphisms are common in Orthoptera (Wall, 1987; Mol *et al.*, 2003; Laws and Belovsky, 2010; Stillwell *et al.*, 2010; Gomez *et al.*, 2012; Nettle and Bateson, 2015; Valverde and Schielzeth, 2015; Lonsdale, 2018). Adaptive mutations by stress in locust are non-directional but they may cause new traits in populations (Whitman and Agrawal, 2009). Such rapid phenotypic adaptation to new environmental conditions reduces the strength of divergent selection (Sword, 2002, 2003; Smadja and Butlin, 2011).

Methylation of DNA through epigenetic regulation of the neural transcriptome occurs in response to the stress of insects that become resistant to various toxins and escape unsuitable environmental conditions such as drought, heat and food restriction. In *C. biguttulus* DNA breaking and its repair with new arrangements of amino acids is the result of environmental stress effects (Bijlsma and Loeschke, 2005; Augustyniak *et al.*, 2006; Burggren, 2017; Lonsdale, 2018). Environmental stress and epigenetic inheritance are closely related to the physiological change of organisms in reaction to the inhabiting conditions that affect individual traits in the population (Skinner, 2014). Methylation of DNA through epigenetic regulation of the neural transcriptome occurs in response to environmental stress in insects. Most insects become resistant to various environmental toxins and escape unsuitable living conditions such as drought, heat and food restriction. Food shortages in crowded conditions of locust may increase cyclooxygenase, or COX stress enzymes. The enzyme affects the metabolism of locust for a few generations and the gregarious phase of the locust is produced (Rogers *et al.*, 2003; Hodjat, 2006, 2016; Song, 2011). DNA breaking and its repair with new arrangements of amino acids in *C. biguttulus* are the results of environmental stress effects (Bijlsma and Loeschke, 2005; Augustyniak *et al.*, 2006; Burggren, 2017; Lonsdale, 2018).

The genes responsible for oxidative stress are expressed by superoxide dismutase (SOD) (Bijlsma and Loeschcke, 2005; Glastad *et al.*, 2011; O'Grady and Markow, 2012; Skinner, 2014; Burggren, 2017, 2018). Transgenerational morphological and genetic characters are modified by stress-related levels of cytochrome oxidase. The toxin stress effects on mitochondria and metabolism as a result of aging and zinc toxicity in insects are studied in detail (Augustyniak *et al.*, 2008, 2011, 2016;

Skinner, 2014; Bultman, 2015; Lonsdale, 2018). Food shortages in crowded conditions of locust may also increase COX stress enzymes. After a few generations of crowding, metabolic enzymes change appears in locust and may change them to the gregarious phase (Rogers *et al.*, 2003; Hodjat, 2006; Song, 2011). To maintain plasticity, stress-induced epigenetic modifications buffer against DNA sequence-based evolution (Tricker, 2015).

The epigenetic regulatory system of neurosecretions allows reaction against stress effects (Smith and Ritchie, 2013; Tetreau, 2018). Stressors with different intensity influence the insect nervous secretions and hormones such as biogenic amines controlling carbohydrate or lipid metabolism and causing variation in insect behavior and morphology (Perić-Mataruga *et al.*, 2006). Insect pricking by injection wound produced antimicrobial phenoloxidase that masked the effect of lipopolysaccharide (LPS) immune challenge (Monge, 2017).The embryogenesis in *C. biguttulus* by transcriptomic profiling at various stages of development shows that genes are upregulated in the imago of *C. biguttulus* and are mostly involved in aging and immunity (Berdan *et al.*, 2017). In stressed insects, changes in NF-kB (nuclear factor kapper-light chain of activated B-cells) of proteins that bind to DNA can decrease the antioxidant activities in the Gluthathion redox system. Molecular and physiological effects of stress can impose novel trade-offs and character changes (Isaksson *et al.*, 2011). Stress can produce asymmetric forms in insect populations (Parsons, 1991, 1992; Møller and Swaddle, 1997; Jentzsch *et al.,* 2003; Hodjat, 2016) or asymmetric mate choice in grasshoppers (Hochkirch and Lemke, 2011). Multigenerational environmental stressors on insects may last for a few generations by epigenetic effects but after the disappearance of stress, populations can obtain the previous phenotypic form (Burggren, 2016).

3. 3. Phenotypic plasticity in a noisy and toxic environment

Environment and stressful conditions can change the phenotype of grasshoppers by changing their song loudness, resisting the toxins in their surroundings or competing with other males in copulation with females. Males of *C. biguttulus* resist the road noise by increasing the loudness of their song. Female selection of these males for copulation will increase the chance of progeny survival (Einhaupl *et al.*, 2011; Lampe *et al.*, 2012, 2014). A male of *Omocestus viridulus* sings shorter songs when other males are close by (Eiriksson, 1992). Various morphological forms of *Glyptobothrus pullus* (Philippi) appear as a result of feeding on different host plants in Switzerland (Steiner, 2006). In *C. biguttulus* DNA breaking and its repair with new arrangements of amino acids are the results of environmental stress effects (Bijlsma and Loeschke, 2005; Augustyniak *et al.*, 2006; Burggren, 2017; Lonsdale, 2018).

In unfavorable environmental conditions, DNA damage or its partial modification may cause phenotypic plasticity (Steiner, 2006; Gottsberger, 2007; Dowle *et al.*, 2014; Rohde *et al.*, 2015a). The genetic modification in the beet armyworm, *Spodoptera exigua* (Hübner) is taking place after about 120 generations in multigenerational microevolution. DNA damage by zinc treatment disrupted the development of *C. brunneus*, during diapause or induced embryonic disorders (Augustyniak *et al.*, 2011). In stressed insects, Glutathione S-transferase (GSTs) and catalase (CAT) enzymes, important for metal defense against intoxication, were reduced. The cycle of protein digestion inside the cell and its effects on synthesizing antioxidant is reviewed by Isaksson *et al.*, (2011). Common field grasshoppers usually can adapt to metal-polluted habitats (Augustyniak *et al.*, 2008, 2011). Zinc-induced effects are transferred to the embryonic DNA of *C. brunneus* (Augustyniak *et al.,* 2006, 2016). Chernobyl radiation caused genetic damage and mutation on *C. albomarginatus*, as well as oxidative stress (Bonisoli-Alquati *et al.*, 2018).

3. 4. Epigenetic modifications

So far the epigenetic influence on morphological changes or character divergence of *Chorthippus* species is not known.

Transgenerational defense induction and epigenetic inheritance are cued by methylation signaling in the parental generation. The changes in the offspring genotype caused by gene imprinting and neural fingerprints transcribe experiences of insects by affecting maternal and paternal DNA methylation (Norouzitallab *et al*., 2019; Ernst *et al*., 2015; Burggren, 2017). Epigenetic modification is known to cause phenotypic changes by DNA methylation across insects (Bewick *et al*., 2017). DNA methylation can regulate genome at CG -sets on chromosomes. They can also regulate transcription at the CpG islands (Deaton and Bird, 2011). The epigenetic mechanisms can cause polymorphism, change the locust phase, and act on caste formation of social insects (Weiner, 2012; Ernst, *et al.,* 2015; Mallon *et al*., 2016; Burggren, 2017; Lonsdale, 2018). Environmental epigenetic modification is closely related to the stress effects by stimuli-response effects for defense on living organisms.

4. Hybridization and endemism

Basic factors responsible for hybridization are genomically influenced by genetics and epigenetics. They influence cell division by cytoplasmic and genetic incompatibility resulting in the presence of different genomes (Ishikawa and Kinoshita, 2009). Hybrid and endemic species of Gomphocerinae are described in relation to asymmetry in female preferences of male songs. Geographical distribution of Gomphocerinae species is the source for variation, plasticity, and endemism by environmental stress. Many endemic species and subspecies are created by acoustic divergence and sympatric speciation in mountain regions. Hybridization and molecular evolution by mDNA sequencing are creating new routes for investigating trait divergence in Gomphocerinae. Trans-generational defense induction and epigenetic inheritance are cued by environmental signaling in the parental generation. The changes in the offspring genotype caused by gene imprinting and neural fingerprints transcribe experiences of insects by affecting maternal and paternal DNA methylation (Ernst *et al*., 2015; Burggren, 2017). Some of the Gomphocerinae hybrid species are produced after females choose to copulate with preferable males songs (Gottersberg, 2007).

4. 1. Hybridization

Hybridization and factors responsible for character diversification may ultimately result in evolution and sympatric speciation. Many publications investigate factors responsible for the separation of population characters in Gomphocerinae and their hybrids (Pravdin, 1969; Gottsberger, 2007; Vedenina *et al*., 2007a; Smadja and Butlin, 2011; Frank and Reinhold, 2012b; Rhode, 2015; Job *et al*., 2016). Positive selection in favor of increasing flight ability is involved in some grasshopper populations at high altitudes in the mountains of China (Li *et al*., 2018). The relative abundance of *C. montanus* and *C. parallelus* as specialist and generalist also produce hybrids that can trigger speciation (Rhode *et al*., 2015). Crosses of the following species can produce hybrids in Gomphocerinae species (Gottesberg, 2007; Bella *et al*., 2010; Rhode, 2015; Vedenina, 2015):

C. brunneus X C. jacobsi; *C. bigutulus X C. brunneus*; *C.eisentrauti X C. brunneus*;
C. biguttulus X C. mollis; C. albomarginatus X C. oschei; *C. albomarginatus X;*
C. karelini; *P. montanus X P. parallelus; Stenobothrus clavatus X S. rubicundus*;
P. parallelus parallelus X P. parallelus erythropus.

In northeastern Ukraine, *C. albomarginatus* and *C. oschei* produce hybrid offspring. The two crossing species are morphologically very similar except for their songs and organs for song production. The differences in the song are caused by leg movements and the type of pegs involved on femur after hoppers change the angle of their body (Vedenina *et al*., 2007b; Sardnick *et al.* 2016). Courting males can produce more complex sounds and are preferentially selected by the female's inheritance. Duplicate loci controlled the homologous elements in the songs of the two copulating species of *C. oschei* from *C. albomarginatus* (Vedenina and Helversen, 2003; Vedenina *et al*., 2007b). *C. karelini* produced a song with two short elements alternating with a longer element. Even courtship songs of two males of *C. karelini* recorded from two different localities in Ukraine produced different songs. The songs from these localities had hybrid characteristics of the two populations (Vedenina, 2015). In the Picos district in the north Spain hybridization between *C. brunneus* and *C. jacobsi* produced offspring with different numbers of stridulatory pegs in different localities. Various peg numbers produced different cline in the Picos region. The changes were significant from populations approximately 30 km south of Picos de Alps. The differences for wingless meadow grasshoppers, *P. parallelus* were measured by the nested model for geographic variation. Mark and recapture methods for measuring the elation of stridulatory pegs differences in various habitats have been applied to measure the extent of differences (Bridle *et al*., 2001). Investigation of hybridization and molecular evolution by mDNA sequencing is creating new routes for finding genetic or phylogeographic trait divergence in Gomphocerinae (Hewitt, 2001). Asymmetric mate choice between the two closely related populations of Gomphocerini in the same locality is presumed to produce hybrid forms (Hochkirch and Limke, 2011; Hochkirch, 2013). Asymmetry is recorded in female preferences between two closely related *Stenobothrus clavatus* and *S. rubicundus* (Vedenina *et al*., 2014; Sardnick *et al*., 2016). Song of *C. biguttulus* changes characteristics in relation to male robustness and the attractiveness to females. The loudness of songs also changes to neutralize noisy surroundings (Gottsberger, 2007; Einhaupl *et al*., 2011; Lampe *et al*., 2014).

Hybrid sterility and mate preferences between two closely related species of Gomphocerini are related to many factors such as genetic incompatibility, gene flow between sympatric species, attractiveness to intermediate phenotypes and plasticity (Gootsberger, 2007; Hochkirch, 2013; Sgro *et al*., 2016). Courting males can produce more complex sounds and are preferentially selected by the females. Inheritance implying duplicate loci that control the homologous elements in the song of two closely related species are involved in hybridization between them such as hybrids between *C. oschei and C. albomarginatus* (Vedenina and Helversen, 2003; Vedenina *et al*., 2007b).

Even courtship songs of two males of *C. karelini* recorded from two different localities in Ukraine produced different songs. The songs from these localities had a hybrid characteristic of the two populations (Vedenina, 2015). Asymmetry is observed in female preferences between two closely related *Stenobothrus clavatus* and *S. rubicundus* (Vedenina *et al*., 2014; Sardnick *et al*., 2016). In the Picos district of north Spain, hybridization between *C. brunneus* and *C. jacobsi has* produced offspring with a different numbers of stridulatory pegs in different localities. Various peg numbers produced different clines in the Picos region. The changes were significant from populations approximately 30 km south of Picos de Europa Mountains.

Mark and recapture method is used for measuring the relation of stridulatory peg numbers of *C. brunneus* living in different habitats in Santander mountain regions of north Spain. The principal component analysis for mean peg scores against the distance from the fitted cline center shows that *C. brunneus* can be easily distinguished from *G. jacobsi* by their peg numbers. The hybrid forms are found within 30 km distance (Bridle *et al*., 2001). Similar studies of female choice of male song for copulation have been conducted in other grasshopper species (Ritchie, 1989, 1990; Helversen and Helversen, 1997; Bridle *et al*., 2001; Benediktov, 2005, 2014; Einhaupl *et al*., 2011; Heinrich *et al*., 2012; Job *et al*., 2016; Kohler *et al*., 2017).

4. 2. Endemism

Endemism is produced by divergence in morphology and the song of *Pseudochorthippus parallelus* (Zetterstedt) populations in mountains. Their populations by genetic polymorphism have chosen various traits. A long separation of population traits increased their genetic distance and caused morphological or acoustic diversification in various directions. The variability in characters are signs for forming an endemic or sympatric species (Tregenza *et al*., 2000; Butlin and Hewitt, 2008; Stillwell *et al*., 2010; Vedenina and Mugue, 2011; Monge, 2017).

Chorthippus pullus by feeding on various host plants produced plastic forms in Switzerland (Steiner, 2006). Procedures for the appearance of endemic species in *Chorthippus* in Turkey (Mol *et al*., 2003) and the list of Acrididae endemic species of Iran (Hodjat *et al*., 2018) show the reality of having endemic forms of grasshoppers. The *Euloryma* Spearman, 2013 (Hemiacridinae; Acridinae) of the Cape Floristi region in South Africa produce endemic species in their narrow distribution area. *Euloryma larsinorom* and *E. lapollei* are congeneric flightless hoppers distributed in natural shrub and heath vegetation. *E. umoja* and *E. ottei* can tolerate vineyard and agricultural environment (Adu-Acheampong *et al*., 2017). DNA methylation leading to epigenetic inheritance of the modified phenotype in endemic species of grasshoppers requires further investigation (Nettle and Bateson, 2015).

5. Song and phenotypic variation

Sound in Gomphocerinae is produced by rubbing the hind femora with a row of the stridulatory pegs, up and down against the radial vein of the tegmina, which is more prominent than the other veins and is called the *plectrum*. The song of males in *C. dorsatus, C. dichrous*and *C. loratus* is also produced by movements of the hind femur against the tegmina but differs in various localities. The song character may change by the position of their upward body direction or the speed of rubbing the set of pegs. Detailed registration of song characters differs between *Chorthippus* (*Glyptobothrus*) *bozdaghi* (Uvarov), *Chorthippus* (*Glyptobothrus*) *ilkazi* (Uvarov) and *Chorthippus* (*Glyptobothrus*) *helverseni* (Mol *et al*., 2003). Temporal features of the song in *C. brunneus* and *C. jacobsi* depend on the neurological pattern that controls leg movement. The neuromuscular activity during stridulation of *C. biguttulus, Gomphocerus sibiricus*, *Omocestus viridulus* (L.) and *Stenobothrus lineatus* (Panzer, 1796) is not related to the number of pegs (Elsner, 1974; Saldamando *et al*., 2005; Perić-Mataruga *et al*., 2006).

Mating of female grasshoppers with a preferable male is because of their particular song characteristics and can initiate sympatric species for adapting to the prevailing conditions. Consequently, in large parts of central Europe, hybrid populations and sympatric species have originated (Hochkirch and Limke, 2011; Hochkirch, 2013; Rohde *et al*., 2015b, 2017).

Chortoicetes terminifera song is changed by crowding conditions (Song, 2005, 2011; Chapuis *et al*., 2010; Ernst *et al*., 2015). The internal reaction to resist the road noise in males of *C. biguttulus* is causing an increase in the loudness of their song. Female selection of these males for copulation will also increase the chance of progeny survival (Klappert and Reinhold, 2003; Einhaupl *et al*., 2011; Heinrich *et al*., 2012; Lampe *et al*., 2012).

Limited condition dependence of male body condition is likely to be correlated with male acoustic signals in *C. biguttulus* (Franzke and Reinhold, 2012a). The embryogenesis in *G. bigutullus* by transcriptomic profiling at various stages of development shows that gene expression at various stages of the life cycle ranged from synthetic biogenic amines to chitin-binding. Genes upregulated in the imago of *C. biguttulus* were mostly involved in aging and immunity (Berdan *et al*., 2017). In stressed insects, changes in NF-kB (nuclear factor kapper-light chain of activated B-cells) of proteins that bind to DNA can decrease the antioxidant activities in the Gluthathion redox system. Molecular and physiological effects of stress can impose novel trade-offs and character changes (Isaksson *et al*., 2011). Stress can produce asymmetric forms in insect populations (Parsons, 1991, 1992; Møller and Swaddle, 1997; Jentzsch *et al.,* 2003; Hodjat, 2016) or asymmetric mate choice in grasshoppers (Hochkirch and Lemke, 2011). Multigenerational environmental stress on insects may last for a few generations by epigenetic effects but in some cases after the disappearance of stress populations can show phenotypic modification (Burggren, 2018). Pharmacologically induced stridulation had little effect on the courtship song and only changed one or two of the sound elements (Vedenina *et al.*, 2001).

6. Conclusion

Environmental and genetic factors have produced various endemic populations with new characters that may create endemic hybrid and sympatric species of grasshoppers (Hodjat *et al.*, 2018). The problem for taxonomists is to classify Orthoptera by considering their phylogenetic or ancestral relationship. In taxonomy, mainly morphological abrupt changes between taxa are the measure for defining them but variation in morphological characters is the gradual results of gene flow into the population. Morphological differentiation despite gene flow is based on a selection of phenotypes in the survived population as a result of the environmental stress (Dowle *et al.*, 2014). It is difficult to find the degree of morphological character changes in each taxon. The physiological trade-offs and diversifying characters of populations are known to affect the taxonomy and life history at various localities in animals (Zera and Harshman, 2001). In stressed insects, changes in NF-kB (nuclear factor kapper-light chain of activated B-cells) proteins that bind to DNA can decrease the antioxidant activities in the Gluthathion redox system. Molecular and physiological effects of stress can impose novel trade-offs and character displacements (Isaksson *et al.*, 2011).

Phase polymorphism and variation in locust morphometrics appear to be the result of environmental stress effects on their physiology (Hodjat, 2016). Epigenetics in contemporary evolution separates the characters of the migratory phase for several generations from the solitary phase (Mallon *et al.*, 2016). This phenomenon can also affect other Gomphocerini species and produce variation in their morphological characters in response to environmental stress (Parsons, 1992; Chapuis *et al.*, 2010; Ketmaier *et al.*, 2010; Murren *et al.*, 2015). Hormones and physiological changes, affecting insects due to environmental conditions, are capable of being epigenetically inherited through methylation. A new line of research is proposed for investigating the relation of epigenetic changes to stress in insects (Merritt and Bewick, 2017).

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مروری بر تأثیرات تغییر، انعطاف‌پذیری و اپی‌ژنتیک احتمالی در گونه‌های قبیله Gomphocerini (Orthoptera; Gomphocerinae)

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چکیده: شرایط محیطی موجب تغییر در ریخت‌شناسی، رفتار و احتمالاً اپی‌ژنتیک در بسیاری از گونه‌های زیرخانواده Gomphocerinae به‌ویژه در زیستگاه‌های کوهستانی می‌شود. انعطاف‌پذیری و تغییرات در ریخت‌شناسی بسیاری از گونه‌ها در این زیرخانواده در اثر جدایی ویژگی‌ها در طی انتخاب ماده برای جفت‌گیری ایجاد می‌شود که کشانه‌های مختلف، گروه‌های زیرگونه‌ای یا گونه‌ای تشکیل می‌دهد. تغییرات و انعطاف‌پذیری در اثر استرس‌های محیطی افزون بر ریخت‌شناسی، بر فیزیولوژی و اپی‌ژنتیک بسیاری از گونه‌های حشرات تأثیر می‌گذارد. استرس‌های محیطی و جفت‌گیری با ماده مناسب ممکن است با تولید دورگ در جمعیت همراه شده و منجر به جدایی صفات و گونه‌زایی در درازمدت شود. تکامل معاصر و یا وراثت اپی‌ژنتیک ممکن است دلیل بر تغییرات در آوازخوانی و ریخت‌شناسی Gomphocerinae بوده و عامل اصلی در مشکلات کنونی در رده‌بندی آنهاست. در این مقاله، اثرات احتمالی استرس‌های محیطی، دورگ‌گیری و گونه‌زایی با ظهور گونه‌های بومی مرور می‌شود. تأثیر حدود نیمی از گونه‌های حشرات به‌عنوان آفت در اثر تغییر در شرایط محیطی کنونی کم‌رنگ شده است. وضعیت کنونی حشرات آفت در ایران مورد بحث قرار گرفته است.

واژگان کلیدی: رده‌بندی، دورگ‌گیری، Gomphocerini، فنوتایپ، آواز