Grasshopper Systematics: Past, Present and Future

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Grasshopper systematics: past, present and future

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Abstract

For the past 250 y, tremendous advances have been made in the field of grasshopper systematics. There have been several breakthroughs that have pushed the field forward, and behind these breakthroughs were numerous visionary taxonomists. This article is a celebration of those taxonomists and their achievements. In this review, I provide a general overview of the field and describe major advances that have shaped our understanding of grasshopper systematics. Specifically, I review the pattern of species description in Acridomorpha (Orthoptera: Caelifera) since Linnaeus, and highlight the achievements of important taxonomists. Finally, I end with some of the problems that we grasshopper taxonomists are facing today and challenge the field as a whole to move forward.

Key words

Acridomorpha, taxonomy, taxonomic impediment

What is Acridomorpha?

The classification of Caelifera has a convoluted history (Dirsh 1961, 1975, Kevan 1976, Key 1976a). It is beyond the scope of this paper to review all the classification schemes proposed by various authors, and a concise summary can be found in Flook & Rowell (1997a: 89-91). Based on the latest classification scheme adopted by the Orthoptera Species File Online (Eades & Otte 2009), the orthopteran suborder Caelifera consists of two infraorders Tridactylidea and Acrididea. Tridactylidea contains a single extant superfamily Tridactyloidea, which consists of three families: Cylindrachetidae, Ripipterygidae and Tridactylidae. Acrididea consists of seven extant superfamilies: Acridoidea, Eumastacoidea, Pneumoroidea, Pyrgomorphoidea, Tanaoceroidea, Trigonopterygoidea and Tetrigoidea. The first six superfamilies are grasshopper-like in morphology and therefore grouped in a monophyletic superfamily group Acridomorpha. Tetrigoidea contains a single family Tetrigidae. The focus of this paper is on Acridomorpha, which contains about 24 families as a whole (Fig. 1).

Acridoidea is the largest superfamily within Orthoptera and contains about 11 extant families and about 7680 species, defined by the morphology of the male phallic complex and the lack of basioccipital slit, among other characters (Roberts 1941, Amédégnato 1974, Kevan 1982).

Most species in this group are familar and easy to recognize as typical grasshoppers. Eumastacoidea consists of about 8 extant families and about 1269 species, commonly known as the monkey grasshoppers. This group is defined by antennal tubercles and no auditory organ (Flook & Rowell 1997a).

A recent molecular phylogenetic study (Matt *et al.* 2008) suggests a possibility of the stick insect-like Proscopiidae being its own superfamily (Proscopioidea), sister to Eumastacoidea, because the family was never placed within any of the existing branches of Eumastacoidea. However, Proscopiidae has always been shown to have a close affinity to Eumastacoidea (Roberts 1941, Blackith & Blackith 1968, Dirsh 1975) and therefore I tentatively include it in this superfamily.

Pyrgomorphoidea contains some of the most colorful grasshopper species and consists of a single family, Pyrgomorphidae, having about 476 species, characterized by the presence of a groove in the fastigium (Kevan & Akbar 1964).

The remaining three superfamilies are small in number, highly unusual and mostly endemic. Pneumoroidea contains one family, Pneumoridae, and 17 species, mostly found in South Africa, and is known for its unique femoro-abdominal stridulatory mechanism (Dirsh 1965). Males have a swollen abdomen that can amplify their calls for a long distance signal (van Staaden & Römer 1997) and they are commonly known as bladder grasshoppers. Tanaoceroidea contains one family and 3 known species endemic to the southwestern U.S. and is characterized by extremely long antennae and a rudimentary male phallic complex (Rehn 1948, Dirsh 1975).

Finally, Trigonopterygoidea consists of two rather divergent families, Trigonopterygidae and Xyronotidae. The former is endemic to the Southeast Asia and contains about 16 species and is characterized by reversed male genitalia and foliaceous tegmina (Dirsh 1952, 1975). The latter contains four species endemic to central Mexico and can be characterized by rudimentary male genitalia and a stridulatory ridge on third abdominal tergites (Dirsh 1955). These two families form a monophyletic group based on molecular phylogeny (Flook *et al.* 2000).

Major advances in grasshopper systematics

The field of grasshopper systematics has been shaped by numerous taxonomists who spent their lifetimes documenting biodiversity and understanding the relationships among lineages. I consider that three major breakthroughs have been particularly crucial in propelling the field forward. They are the use of male genitalia in taxonomy, the use of molecular characters in resolving higher-level relationships, and the development of the Orthoptera Species File. Below I review and elaborate on each topic.

Male genitalia.—In insect systematics, male genitalia are arguably the most important of taxonomic characters. Their utility for species identification as well as higher-level classification has been shown in most groups of insects (Tuxen 1970). Species-specificity of male

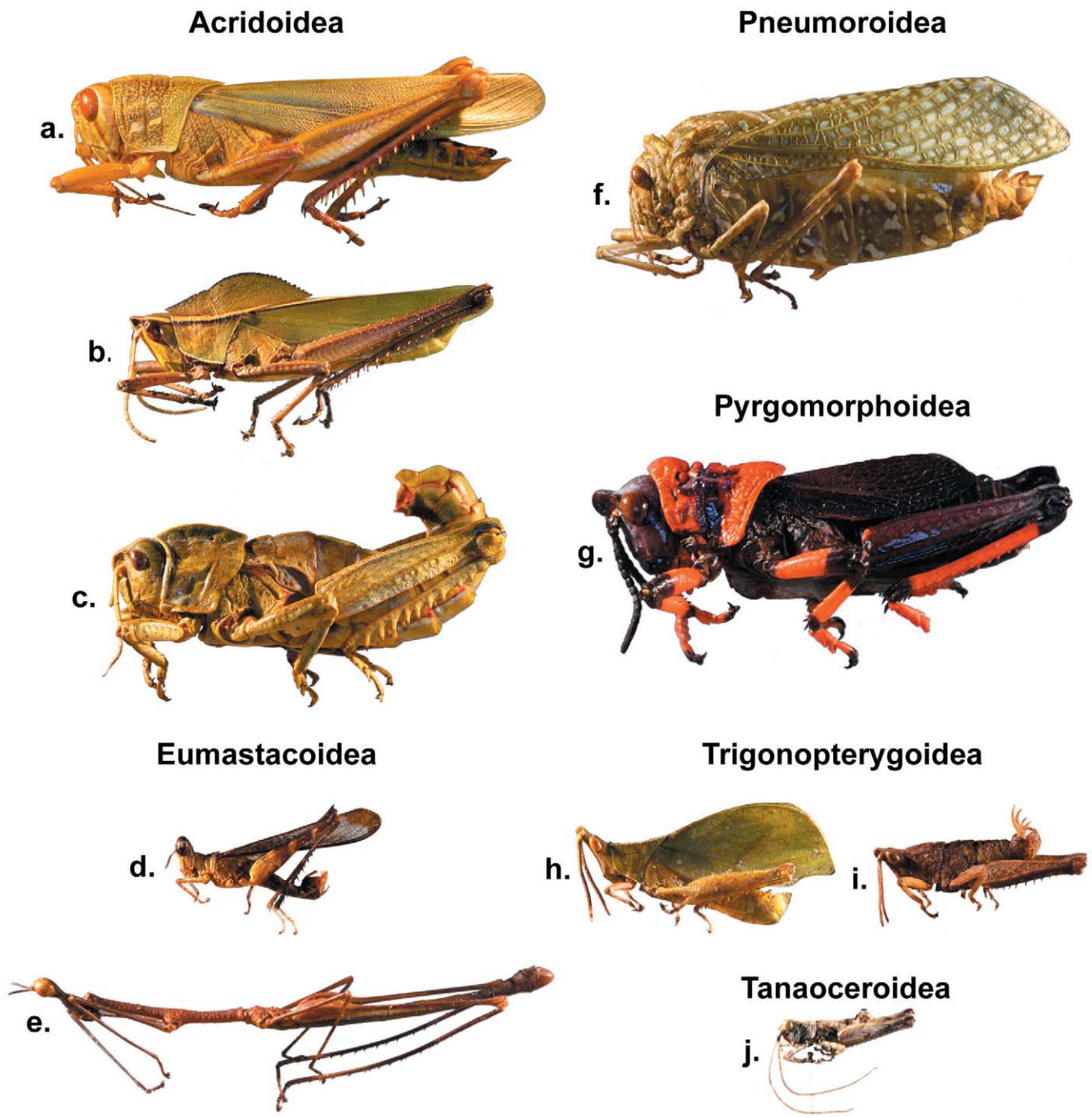

Fig. 1. Representatives of superfamilies within Acridomorpha. a, *Chondracris rosea* (De Geer, 1773) [Acrididae]; b, *Prionolopha serrata* (Linnaeus, 1758) [Romaleidae]; c, *Pamphagus elephas* (Linnaeus, 1758) [Pamphagidae]; d, *Erucius bifasciatus* Stål, 1877 [Chorotypidae]; e, *Apioscelis bulbosa* (Scudder, 1869) [Proscopiidae]; f, *Physemacris variolosa* (Linnaeus, 1758) [Pneumoridae]; g, *Dictyophorus spumans* (Thunberg, 1787) [Pyrgomorphidae]; h, *Systella philippensis* (Walker, 1870) [Trigonopterygidae]; i, *Xyronotus aztecus* Saussure, 1884 [Xyronotidae]; j, *Tanaocerus koebelei* Bruner, 1906 [Tanaoceridae].

genitalia is often considered to be one of the most general trends in biology (Eberhard 1985).

In Orthoptera, the taxonomic value of male phallic structures was not realized until the early 20th century; most species were being described based on coloration and external morphology, rather than internal structures. Crampton (1918), Chopard (1918) and E.M. Walker (1922) were among the first morphologists who used internal structures to infer phylogenetic relationships among orthopteroid orders. Walker's (1922) contribution was particularly valuable because he proposed homologies of different parts of male genitalia among different orders. Snodgrass (1935) published a detailed anatomical study of a grasshopper abdomen, in which he described many parts of male genitalia and then (1937) brought his understanding of male terminal structures to other orthopteroid insects.

Hubbell (1932) was the first grasshopper taxonomist to use

male genitalia for species-level analysis. He discovered that the phallic structure of *Melanoplus* was highly species-specific even among externally similar species. Since Hubbell (1932), almost all taxonomic publications on Acrididae have included discussion and illustration of male genitalia (Dirsh 1961).

Roberts (1941) was one of the first taxonomists who realized the value of the male phallic complex in higher-level classification and divided grasshoppers into two groups, Chasmosacci and Cryptosacci, based on the form of the ejaculatory sac and associated phallic structures. He argued that male genital characters provide excellent phylogenetic signal, unlike the external morphological traits that are easily influenced by environmental variation.

Dirsh (1956) published a very detailed study of male genitalia based on 778 genera in Acridomorpha, and argued that male genitalia are the single most important character for interpreting phylogenetic relationships. He also suggested that primitive groups have simpler and less differentiated phallic structures than more advanced groups. He found that the taxonomic utility of male genitalia actually varies according to groups. For example, he found that male genitalia are mostly uniform among closely related species in Acridinae and Truxalinae. This trend was also found in Oedipodinae by Barnum (1959) who studied 123 species in 45 genera of Oedipodinae. Barnum found the amount of variation in this subfamily was small compared to other groups such as Melanoplinae, and this finding was corroborated in later work by Otte (1984).

Kevan *et al.* (1969a, 1969b, 1969c, 1969d, 1972) studied the male genitalia of Pyrgomorphidae and found that the structures were very useful at all taxonomic levels. Amédégnato (1974) found male genitalia to be very useful in distinguishing different groups of the Neotropical Acridoidea and reclassified the South American grasshoppers. Descamps (1973) and Key (1976b), working on the classification of Eumastacidae and Morabidae respectively, found that male genitalia were very informative in higher-level classification within Eumastacoidea.

Based on a thorough comparative study, Amédégnato (1976) demonstrated that the male phallic complex consists of three concentric layers (epiphallic, ectophallic, and endophallic structures) and becomes progressively elaborate through the evolutionary history of Acridomorpha, with the Acridoidea representing the most advanced evolutionary genital form.

Finally, Eades (2000) presented a synthesis of classification based on male genitalia and proposed a scenario regarding the evolution of the endophallus in Acridomorpha. He clearly demonstrated that the male phallic complex is very informative in understanding the

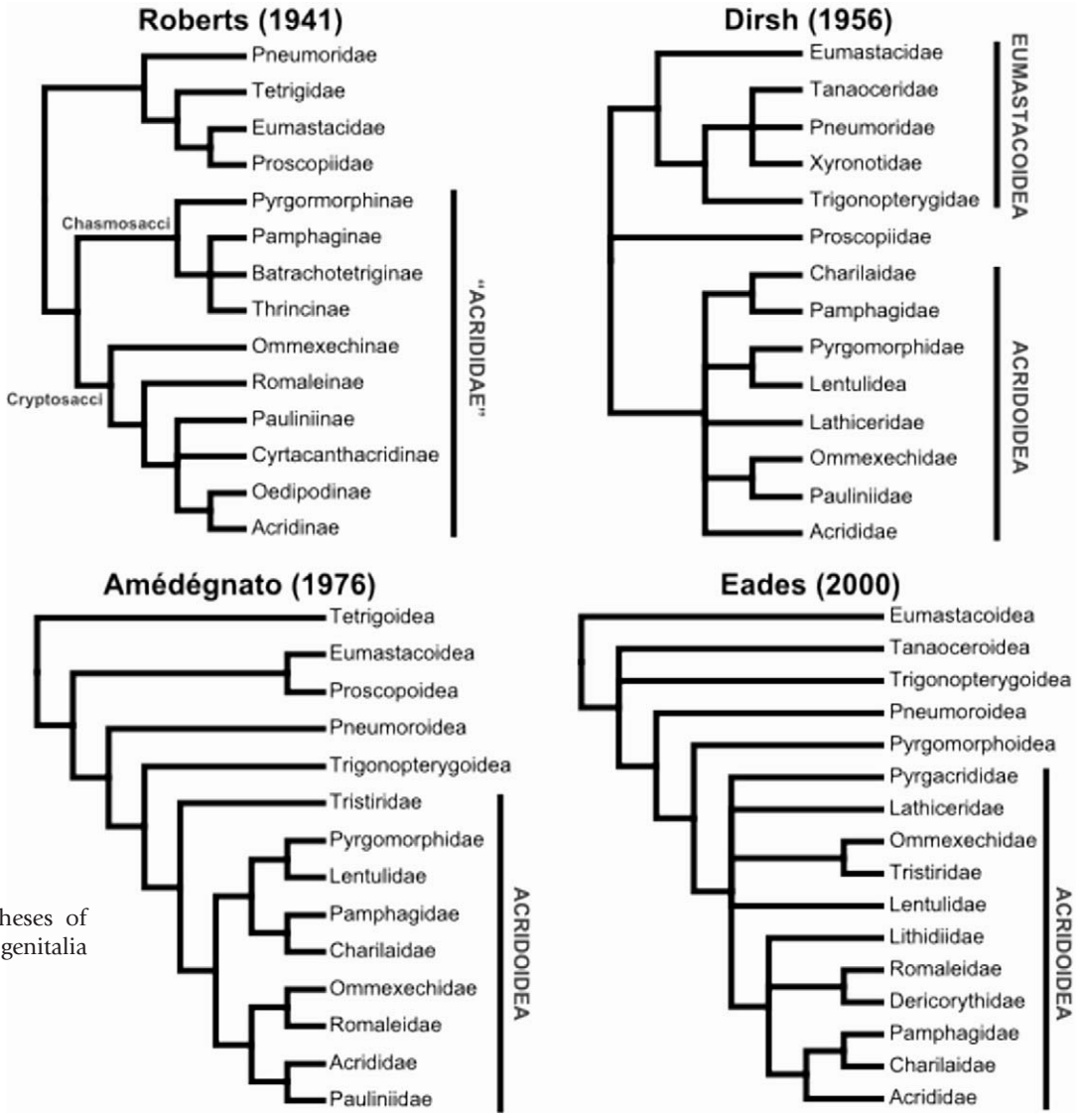

Fig. 2. Phylogenetic hypotheses of Acridomorpha based on male genitalia by various taxonomists.

higher-level classification of Acridomorpha and that each superfamily and many families can be characterized by the shape and position of phallic structures.

Because different taxonomists had different understanding of genital morphology, which led to quite different homology statements, the classification schemes changed continuously (Fig. 2); but this change represents increased knowledge and every subsequent proposal should be taken as a step toward understanding the phylogeny of Acridomorpha.

Molecular systematics.—Over the past few decades, an exponential growth in our ability to generate DNA sequence data has brought about a revolution in systematics. Previously unanswered questions arising from a lack of morphological characters, or convergence have been effectively addressed using molecular characters. Of course, molecular characters have many intrinsic problems that can complicate inferences, but it is more than fair to say that grasshopper systematics has benefited from this revolution and our understanding of the phylogenetic relationships within Acridomorpha has advanced tremendously. An excellent review by Chapco (1997) provides an overview of how molecular data were used in understanding the evolution of Orthoptera between 1970 and mid-1990. Since then, a number of important studies focusing on the phylogeny of Orthoptera, especially Acridomorpha, have been published.

The first breakthrough in grasshopper molecular systematics was the sequencing of the complete mitochondrial genome (mtgenome) of the migratory locust, *Locusta migratoria* by Flook *et al.* (1995). At that time, complete mtgenome sequences of insects were available only from four species (3 dipteran and 1 hymenopteran) and the findings of Flook *et al.* therefore represented the first nonholometabolous insect mtgenome and provided a valuable resource for comparative genomics.

Building upon these findings, Paul Flook and Hugh Rowell spearheaded grasshopper molecular systematic research for the next 10 years. They presented the first molecular phylogeny of Orthoptera (Flook & Rowell 1997b) and a more complete phylogeny of Caelifera (Flook & Rowell 1997a, Rowell & Flook 1998) based on mitochondrial ribosomal RNA genes (16S and 12S). They also explored the phylogenetic utility of nuclear ribosomal gene (18S) in resolving orthopteran phylogeny (Flook & Rowell 1998). Combining both mitochondrial and nuclear ribosomal genes, they presented the most comprehensive molecular phylogeny of Orthoptera to date (Flook *et al.* 1999). Their sampling (31 orthopteran ingroup and three ribosomal genes) was very small by today's standards, but it was a state-of-art study at the time of publication. Using the same markers, they published a series of taxon-specific phylogenies on Pneumoroidea (Flook *et al.* 2000), a grasshopper subfamily Proctolabinae (Rowell & Flook 2004), and Eumastacoidea (Matt *et al.* 2008). Their findings and previous understanding of morphology collectively form a basis for our current classification of Acridomorpha.

In Canada, William Chapco and his colleagues focused on understanding the phylogeny of a grasshopper subfamily Melanoplinae, using mitochondrial genes and published a series of papers (Chapco 1997; Chapco *et al.* 1997; Chapco *et al.* 1999; Chapco *et al.* 2001; Chapco & Litzenberger 2002a, 2002b; Amédégnato *et al.* 2003; Litzenberger & Chapco 2003; Chapco & Litzenberger 2004; Chapco 2006). Chapco was successful in generating sequence data from dried museum specimens and a highlight of his work was the investigation of the phylogenetic position of the now extinct Rocky Mountain locust, *Melanoplus spretus*, which he sequenced using DNA from 400-year-old specimens frozen in a glacier in Wyoming (Chapco & Litzenberger 2004). He also worked on the molecular phylogenetics of other grasshopper groups including Gomphocerinae (Contreras & Chapco 2006) and Oedipodinae (Fries *et al.* 2007).

Besides studies by these two research groups, little work has been done to clarify the higher-level classification, except for a few isolated studies by Asian researchers (Maekawa *et al.* 1999, Zhang *et al.* 2005, Bugrov *et al.* 2006, Huo *et al.* 2007, Liu *et al.* 2008, Yin *et al.* 2008); these were often based on small-taxon and character sampling.

In 2008, Fenn *et al.* (2008) published a preliminary molecular phylogeny based on complete mtgenome sequences and showed that mtgenome data could help resolve relationships over a broad time scale. However, their study only included three caeliferan taxa, all Acrididae, so not much could be inferred of the relationships within Acridomorpha.

Over the past several years, there has been considerable growth in the number of complete caeliferan mtgenomes in Genbank, including six acridid subfamilies (Flook *et al.* 1995, Fenn *et al.* 2008, Liu & Huang 2008, Zhang & Huang 2008, Ma *et al.* 2009) and one pyrgomorphid (Ding *et al.* 2007), and this number is expected to increase. Soon it will be possible to test the previous phylogenetic hypotheses using much larger taxon and character sampling, which may challenge the currently accepted classification scheme.

Since this paper focuses on higher-level systematics of Acridomorpha, I do not review any of the population-level studies. However, one research program deserves particular mention. Also working on the genus *Melanoplus*, Lacey Knowles studied the effect of the Pleistocene glaciations on speciation in a phylogeographic framework (Knowles 2000, 2001). She used a variety of molecular markers, including mitochondrial loci (Knowles 2000), AFLP (Knowles & Richards 2005), and single-copy nuclear polymorphic sequences (Carstens & Knowles 2006), to estimate phylogeny using population genetic approaches. Currently, Knowles is the leading figure in the field of statistical phylogeography, a demographic inference that takes into account the stochasticity of genetic processes (Knowles 2004, 2009).

While molecular data have clearly enriched our understanding of grasshopper systematics, it is important to understand that they are just another source of characters that can be affected by past evolutionary phenomena, phenomena which may cause incorrect phylogenetic inferences. It is beyond the scope of this paper to review all the possible issues of molecular characters, but it should be emphasized that a thorough and careful analysis of molecular characters is imperative in molecular systematics, because these characters can be easily affected by base compositional heterogeneity (Lake 1994, Lockhart *et al.* 1994, Galtier & Gouy 1995, Jermiin *et al.* 2004), among-site rate variation (Yang 1996, Felsenstein 2001, Mayrose *et al.* 2005), and heterotachy (Kolaczkowski & Thorton 2004, Philippe *et al.* 2005).

Grasshoppers are peculiar among animals in having some of the largest known nuclear genomes: 5950-20600 Mb (Bensasson *et al.* 2001a). To give perspective, most insect genomes are between 98 and 8900 Mb in size and the human genome is about 3400 Mb. It is hypothesized that a major proportion of the grasshopper genome is noncoding (Bensasson *et al.* 2001b). At the same time, grasshoppers are known to harbor the largest amount of nuclear mitochondrial pseudogenes (numts), which are nonfunctional fragments of mtDNA integrated into the nuclear genome (Lopez *et al.* 1994). These two observations led to a hypothesis that a large nuclear genome size is

correlated with an increased number of numts, because fragments of mtDNA keep on accumulating in the noncoding region of the nuclear genome (Bensasson *et al.* 2000).

The first case of numts in Metazoa was reported from *Locusta migratoria* (Gellissen *et al.* 1983), in which a copy of a mitochondrial ribosomal RNA gene was found in the nuclear genome. Since then, grasshoppers have become model organisms in studying the evolution of numts (Zhang & Hewitt 1996a, 1996b; Bensasson *et al.* 2000; Bensasson *et al.* 2001b; Sword *et al.* 2007; Song *et al.* 2008).

The presence of numts poses a serious problem in PCR-based mitochondrial systematics. One of the main reasons why mtDNA has been so widely used is the ease of generating sequence data using conserved primers (Folmer *et al.* 1994, Simon *et al.* 1994, Simon *et al.* 2006). However, studies have consistently shown that numts are very easy to co-amplify with the orthologous mtDNA, using conserved primers (Collura & Stewart 1995, Zhang & Hewitt 1996b, Sorenson & Quinn 1998, Bensasson *et al.* 2001a, Benesh *et al.* 2006, Song *et al.* 2008). It is also possible to preferentially amplify numts if the nuclear integration of numts was an ancient and sufficient sequence divergence accumulated in the orthologous mtDNA (Bensasson *et al.* 2001a, Song *et al.* 2008). In 2008, I empirically showed that the coamplification of numts can lead to incorrect inferences in DNA barcoding studies (Song *et al.* 2008), and this finding is applicable to other types of molecular studies utilizing mtDNA as well. Therefore, it is always important to control against numts when using mtDNA as a phylogenetically informative marker and this is especially true for Acridomorpha.

Orthoptera Species File.—Perhaps the single most important milestone in grasshopper systematics (and in orthopteran systematics in general) is the development of the Orthoptera Species File Online. This concept, a collection of all taxonomic information for a single taxonomic group, was the brainchild of Daniel Otte. Otte published the first paper volume of OSF in 1994 to cover Grylloidea and subsequently a total of eight volumes to cover all Orthoptera were published by 2000. In 1997, Otte and Piotr Naskrecki developed the first online version of the OSF and in 2001 David Eades joined and further developed it using a relational database, which ultimately led to the current version of the OSF. An excellent summary on the history of the OSF can be found in the OSF website.

The OSF online contains complete synonymic and taxonomic information, citations and references, images and sound recordings, maps, specimen collecting records and identification keys. As of December 2009, the OSF online contains full information on 29,464 valid species, 41,425 scientific names, 160,586 citations to 12,333 references, 65,764 images, 188 sound recordings, 74,111 specimen records, and keys to 2,867 taxa. The OSF online uses a powerful relational model database server (Microsoft SQL Server) and most of the programming is done in Visual Basic. It extensively implements the TDWG geographic classification and the Bishop Museum system for specimen depositories. It is also capable of allowing others to import hierarchy and nomenclatural data. The contents are continuously being updated as new taxonomic studies are published. Another initiative developed from the OSF online was the Species File Software, which serves as a foundation for taxonomic database development for researchers who want to create their own taxonomic databases. So far, researchers working on other taxonomic groups, such as Plecoptera, Blattodea, Mantodea, Phasmida, Aphidomorpha, Psocodea, and Coreoidea, are extensively using the software.

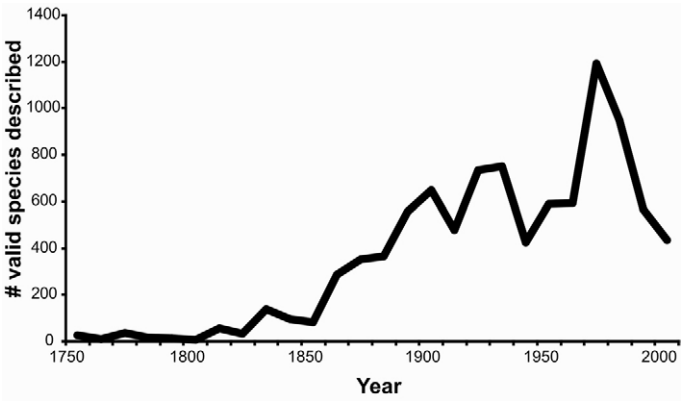

Fig. 3. A trend in species description in Acridomorpha for the last 250 years. y-axis shows the number of valid species described and x-axis shows the year of species description.

One of the exciting features of the current version of the OSF online is the ability to generate a subset of a species file for the private use of someone working on a taxonomic revision. This gives a greater flexibility to the taxonomist who can make sure of the most up-to-date taxonomic and synonymic information and utilize many available multimedia tools such as high-resolution digital images and interactive maps of species distribution. Once the taxonomic work is published, this private copy can be merged back into the OSF online and becomes available to the public immediately. I expect to see many taxonomists utilizing this feature soon. There is no taxonomic database quite like the OSF online in terms of its breadth, capacity and interactivity, and it sets itself as a benchmark for excellence.

Trends in grasshopper systematics for the last 250 years

Since Linnaeus described *Gryllus* (*Acrida*) *turritus* [= *Acrida turrita*] along with 26 other grasshopper species in the 10th edition of Systema Naturae in 1785, more than 9400 valid species of grasshoppers have been described by numerous taxonomists. Who were these taxonomists and what was the pattern of species description during the last 250 years? Taxonomy is a unique field of science in which one needs to completely evaluate all past works, both bad and good, since first description. Therefore, it is important to know how the field of grasshopper systematics has been shaped and by which taxonomists.

In order to address this, I performed a complex search on the OSF online, first by constraining the scope of search to valid names only in Acridomorpha, by the year of publication using the "between" option so that species described per decades can be counted, and by specifying the rank to only include species. The search found a total of 9443 valid species of Acridomorpha described between 1785 and 2009 and the results are shown as a graph in Fig. 3. The overall trend in species description can be described as a slow start and a rapid increase, followed by a sharp decline.

Naturalists in the 18th century, such as Linnaeus, Fabricius, and Thunberg, were beginning to realize the diversity of organisms in nature, but mostly relied on specimens brought back by explorers. Only a small number of species were described by the end of 18th century and the descriptions were mostly superficial. The 19th century was a period of exponential growth in number of species described. Taxonomists affiliated with museums began to develop insect collections based on the specimens collected by explorers in

Table 1. A list of taxonomists who have significantly contributed to the field of grasshopper systematics over the last 250 y. For each information is given on the number of valid species described, active publication dates, and the region of interest. The region of interest follows the scheme used by the OSF. Besides the obvious categories such as Africa and Europe, North America includes the USA., Canada, Mexico, and subarctic America; South America includes the whole of Central America except Mexico, the whole of South America, and the Caribbean; Temperate Asia includes the Arabian Peninsula, Caucasus, China, Mongolia, Russia and Siberia; Tropical Asia includes the Indian Subcontinent, Indo-China, Malasia and Papuasia; and Australasia includes Australia and New Zealand. The data presented here are up-to-date as of December 2009.

Era	Taxonomists	# valid species described	Active publication dates	Regional Interest
18C	Linnaeus C.	33	1758-1771	World
	Fabricius J.C.	26	1775-1798	World
	Thunberg C.P.	49	1787-1824	World
19C	Serville J.G.A.	63	1831-1838	World
	Stål C.	198	1855-1878	Africa, South America, Tropical Asia
	Walker F.	202	1859-1871	Africa, Tropical Asia
	Saussure H.	201	1859-1903	Africa, North America, South America
	Brunner von Wattenwyl C.	95	1861-1900	South America, Asia
	Scudder S.H.	200	1862-1902	North America, South America
	Thomas C.	40	1865-1876	North America
	Gerstaecker A.	63	1869-1889	Africa, South America
	Bolivar I.	434	1876-1922	Africa, Tropical Asia, Europe
	Krauss H.A.	53	1877-1909	Africa
	Bruner L.	284	1885-1920	North America, South America
	Karsch F.A.F.	141	1888-1900	Africa
	Giglio-Tos E.	71	1894-1907	South America
20C	Rehn J.A.G.	309	1900-1964	Africa, North America, South America, Australia
	Hebard M.	165	1906-1938	North America, South America
	Karny H.H.	57	1907-1915	Africa
	Sjöstedt Y.	232	1909-1936	Africa, Australia
	Uvarov B.P.	500	1910-1962	Africa, Temperate Asia, Tropical Asia
	Ramme W.	307	1911-1941	Africa, Temperate Asia, Tropical Asia, Europe
	Bolivar C.	105	1914-1944	Tropical Asia
	Willemse C.J.M.	204	1921-1962	Tropical Asia
	Miller N.C.E.	66	1925-1953	Africa, Tropical Asia
	Bei-Bienko G.Y.	121	1926-1968	Temperate Asia
	Dirsh V.M.	191	1927-1979	Africa
	Hubbell T.H.	10	1928-1932	North America
	Mishchenko L.L.	200	1936-1990	Temperate Asia
	Roberts H.R.	54	1937-1992	North America, South America
	Key K.H.L.	92	1937-1994	Australia
	Storohecker H.F.	36	1939-1963	North America
	Gurney A.B.	25	1940-1971	North America
	Piza Jr. S de T.	50	1946-1984	South America
	Kevan D.K.McE.	137	1948-1990	Africa, Tropical Asia
	La Greca M.	32	1948-present	Africa, Europe
	Popov G.B.	50	1951-1996	Africa, Temperate Asia
	Baccetti B.P.	26	1954-present	Africa
	Jago N.D.	157	1962-1996	Africa, South America
	Willemse F.M.H.	80	1963-2009	Tropical Asia
	Zheng Z.	373	1963-present	China
	Rentz D.C.F.	28	1964-1984	North America
	Descamps M.	1050	1964-1989	Africa, South America, Tropical Asia
	Ronderos R.A.	142	1964-1994	South America
	Wintrebert D.	89	1965-1972	Africa
	Carbonell C.S.	92	1967-present	South America
	Amedegnato C.	177	1970-present	South America
	Johnsen P.	30	1973-1991	Africa
	Yin X.	118	1974-present	China
	Cohn T.J.	11	1974-present	Mexico
	Massa B.	12	1975-present	Africa

Table 1. Continued.

Era	Taxonomists	# valid species described	Active publication dates	Regional Interest
	Otte D.	115	1979-present	North America, South America
	Weissman D.B.	14	1981-present	North America
	Ritchie J.M.	12	1981-1992	Africa
	Ingrisch S.	35	1983-present	Tropical Asia
	Storozhenko S.Y.	27	1983-present	Temperate Asia, Tropical Asia
	Usmani M.K.	8	1983-present	India, Libya
	Poulain S.	48	1986-present	South America
	Grunshaw J.P.	18	1986-1996	Africa
	Cigliano M.M.	39	1989-present	South America
	Baehr M.	22	1992	Australia

the European colonies, as well as the specimens collected by the taxonomists themselves. The early taxonomists were specialists of insects and described species belonging to many different insect orders, but some focused on Orthoptera more than others. Among the notable taxonomists of 19th century were Swiss entomologists Henri Louis Frédéric de Saussure and Carl Brunner von Wattenwyl, a Spanish entomologist Ignacio Bolívar, a Swedish entomologist Carl Stål, an Italian entomologist Ermanno Giglio-Tos, and American entomologists Samuel Hubbard Scudder and Lawrence Bruner. By the end of the 19th century, over 2000 valid species of Acridomorpha (or over 3100 names, which were later synonymized) were described.

The 20th century was a time of specialization and systematic exploration of fauna and the majority of our taxonomic knowledge on Acridomorpha comes from the taxonomists of this period. These taxonomists began to specialize on more narrow taxonomic groups (such as Acrididae, rather than Orthoptera) and on specific geographic regions. Therefore it is possible to name several taxonomists who were influential in describing grasshopper species from each continent. James A. G. Rehn, Morgan Hebard, H. Radclyffe Roberts, and Daniel Otte, all associated with the Academy of Natural Sciences at Philadelphia, significantly contributed to our understanding of the Nearctic grasshopper fauna mostly from North America.

These taxonomists also worked extensively on the Neotropic fauna, but there are a goodly number of taxonomists who worked exclusively on Neotropic grasshoppers. In particular, Marius Descamps, Ricardo A. Ronderos, Carlos S. Carbonell, Christiane Amédégnato, C. Hugh Fraser Rowell, María Marta Cigliano, and Alba Bentos-Pereira all contributed significantly to our understanding of the grasshoppers in this region, especially in the latter half of the 20th century. Among them, Descamps stands out as the most prolific taxonomist, describing over 1000 species belonging to Acridomorpha during his tenure at the Muséum National d'Histoire Naturelle in France.

African grasshopper fauna was studied by many taxonomists already mentioned, as well as other European taxonomists, importantly, Yngve Sjöstedt, Sir Boris P. Uvarov, Willy Ramme, Vitaly M. Dirsh, D. Keith McE. Kevan, and Nicholas D. Jago. Uvarov's two-volume book *Grasshopper and Locusts* published in 1966 and 1977 is still considered one of the best syntheses of research on Acridomorpha, and Dirsh's comprehensive taxonomic review, *The African Genera of Acridoidea*, is the most useful resource on the taxonomy of African grasshoppers.

Temperate Asia was studied by Russian taxonomists Grigory Y. Bei-Bienko and Leo L. Mishchenko, and Chinese taxonomists Zhemin Zheng and Xiangchu Yin. Particularly, the two-volume book, *Locusts and Grasshoppers of the U.S.S.R. and Adjacent Countries*, co-authored by Bei-Bienko and Mishchenko, provides a comprehensive review on grasshoppers in temperate Asia. Tropical Asia received relatively little attention by comparison and was partly studied by Sjöstedt, Uvarov, Ramme, Candido Bolivar, Cornelis J. M. Willemse and Fer M. H. Willemse, Kevan, Descamps, Sigfrid Ingrisch, and Sergei Y. Storozhenko. Australia was originally studied by Sjöstedt and Rehn, but most of what we know came from a life-long study by Kenneth H. L. Key at the CSIRO, Australian National Insect Collection. Finally, European grasshoppers have been described by many taxonomists already mentioned above. Complete data on important grasshopper taxonomists are presented in Table 1.

Unfortunately, however, the pattern of species description turns sharply in an opposite direction near the end of the 20th century. The decline does not mean we have described every single grasshopper species in the world, given the fact that only about 10% of the world's biodiversity has been described (Wheeler & Cracraft 1996). Rather, it represents a lack of taxonomic expertise to continue the enormous task of identifying and describing biodiversity; I refer to this here as the 'taxonomic impediment'. When examined in more depth, by different geographic regions, it is clear that the sharp decline is ubiquitous across all continents (Fig. 4).

Taxonomic impediments and the need for biodiversity

We are presently living in an age of biodiversity crisis. Species are rapidly going extinct due to destruction of habitat, introduced exotic species, pollution, and climate change (Wilson 1992). At the same time, there is an enormous shortage of taxonomists who can identify and describe species (Wheeler 2004). The loss of biodiversity coupled with the taxonomic impediment is one of the most challenging issues we biologists face today.

It is a serious issue for all taxonomic groups, but the prospect is particularly bleak for the field of grasshopper systematics. Unlike the glorious days of the 20th century, when numerous taxonomists debated taxonomic concepts and classifications, there are now only a handful of active grasshopper specialists around the world, many of whom are retired or near retirement.

For other major groups of insects, there are research programs that systematically train young students in taxonomy (such as the U.S. National Science Foundation-sponsored PEET program), but no such program is yet available for grasshoppers. Globally, it has become very difficult to secure funding for basic descriptive taxonomy. This coincides with the proliferation of molecular systematics and with fewer students being trained in morphology. The fact that training in taxonomy takes a much longer time than training in molecular studies and that taxonomic studies are often only publishable in taxon-specific journals with low impact factors, probably contributes to the decline of descriptive taxonomy as well.

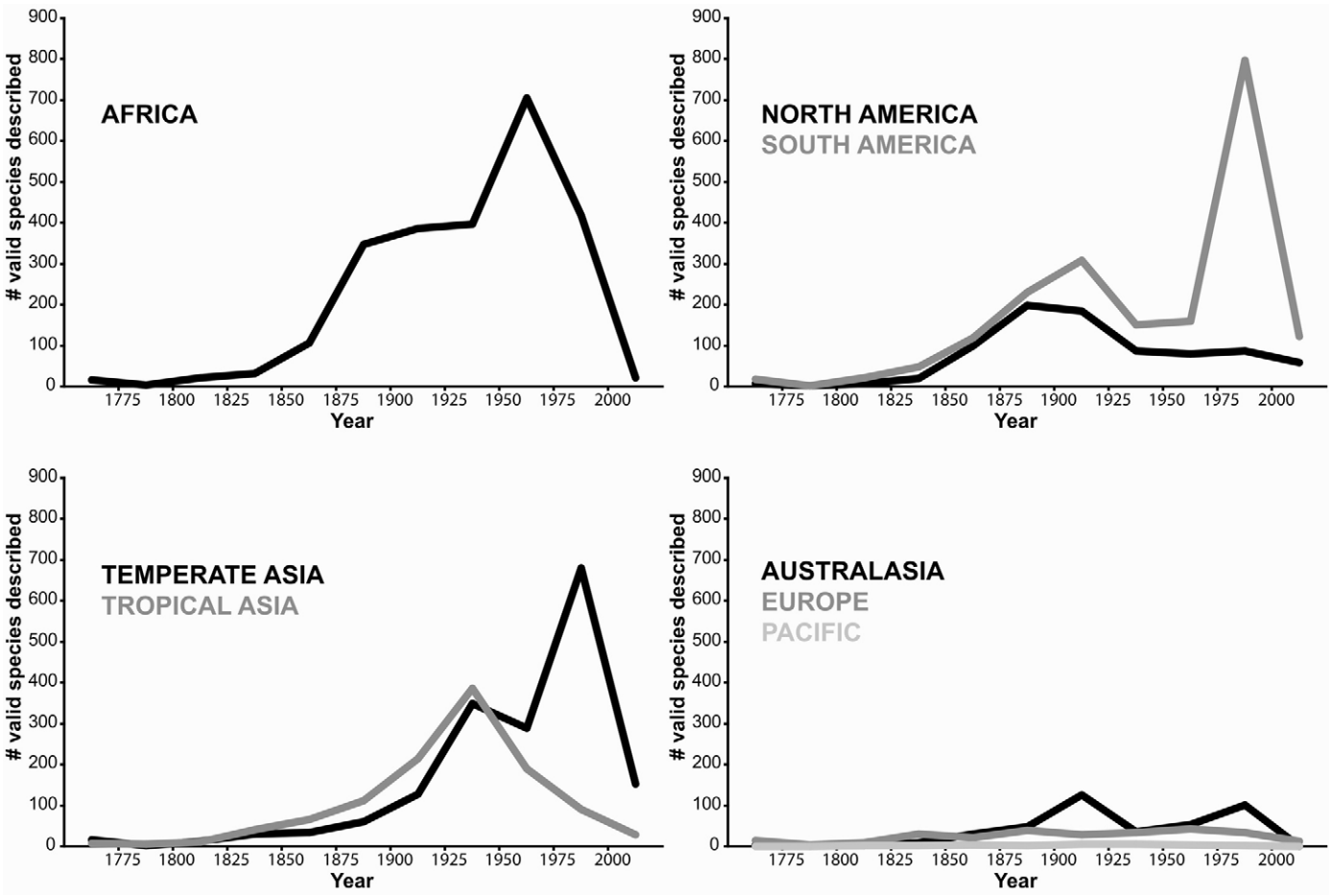

Fig. 4. Trends in species description in Acridomorpha examined according to different geographic regions.

It also has to do with economic rationalisms and changing directions and attitudes of universities and government agencies. It is therefore extremely urgent to rejuvenate grasshopper systematics by training more students through creative and innovative approaches.

Although taxonomists have described more than 9400 valid species of Acridomorpha from all corners of the world, there is still great need for exploration. To illustrate this point more clearly, I performed a complex search using the OSF online, first by constraining the scope of search to valid names only in Acridomorpha and then by specifying the locality down to geographic level 3 (country). The result is shown graphically on the map of the world, coded by how well-studied each fauna is (Fig. 5).

Most of the regions, Nearctic, Neotropic and Palearctic, as well as temperate Asia (except China) and southern Africa, have been extensively studied and we have a good understanding of what grasshopper species occur in these regions. In Central America, however, we have little understanding of the grasshopper fauna in Guatemala, Belize, El Salvador, Honduras, and Nicaragua. The Hispaniola fauna has recently received much attention by Daniel Perez-Gelabert and there are still more species to discover. Some parts of South America still need to be explored despite concentrated efforts by a number of taxonomists including Descamps, Ronderos, Carbonell, Amédégnato, Cigliano, and Bentos-Pereira. Specifically, Venezuela, Guyana, Surinam, Bolivia and Chile deserve to be explored more in depth.

Africa has been studied by numerous taxonomists over the last 250 y, but western Tropical Africa still remains one of the least studied fauna. Only the orthopteran fauna of East Africa, especially near Mt Kilimanjaro has been systematically studied by Claudia Hemp.

India is also poorly studied, and recently it has become particularly challenging to work on the Indian fauna due to logistical and political problems.

China presents a different challenge. Two leading Chinese taxonomists, Zheng and Yin, and their numerous students have described a large number of species from different parts of China, but unfortunately they have adopted a taxonomic scheme of their own (Yin 1984, Zheng & Lian 1988) which elevated some tribes and subfamilies to families. For example, Chinese authors recognize "Acrypteridae" as a separate family which is a junior synonym of the gomphocerine tribe Arcypterini and "Hieroglyphinae" as a separate subfamily of "Catantopidae", which is a junior synonym of hemiacridine tribe Hieroglyphini. Hundreds of species described from China under the Chinese classification scheme will need to be reclassified under a phylogenetically sound classification system and this error is being recognized by the Chinese researchers themselves (Huo *et al.* 2007).

Southeast Asia and the islands in the Central Indo-Pacific are uncharted territories for grasshopper taxonomy. Early taxonomists such as Sjöstedt and Willemse provided a basic foundation for future studies, but the fauna has never been systematically explored. Virtually nothing is known about the grasshopper fauna of countries like Vietnam, Laos, and Cambodia and these places need desperately to be explored.

Finally, Australia presents yet another problem. Of some 225

Fig. 5. The current status of taxonomic knowledge in grasshopper systematics in terms of countries explored. White color represents a country that is reasonably well-studied, light gray represents a country where some work has been done but is still needed to be explored, dark gray represents a country that is poorly explored, and black represents a country that has not been systematically explored at all.

identified genera of grasshoppers, of which 85 are yet to be described, 93% are endemic to Australia (Key 1992). Although Australia harbors only three Acridomorpha families (Pyrgomorphidae, Morabidae, and Acrididae), these (especially Catantopinae) have undergone explosive radiation, giving rise to a current high diversity of Australian grasshoppers. Although Key's lifelong investigation tremendously advanced our knowledge of the Australian fauna, there are still numerous species and genera to be described and this is particularly evident in the latest field guide on the Australian grasshoppers *A Guide to Australian Grasshoppers and Locusts* by Rentz *et al.* (2003) which included numerous unnamed species and genera.

Biodiversity exploration is not a thing of the past, but the way of the future. There are still many regions of the world that need to be explored and there are still many, many grasshoppers to describe. A well-planned biodiversity survey can result in an enormous increase in knowledge. For example, a comprehensive survey of the Neotropical grasshoppers by the Muséum National d'Histoire Naturelle in the 1970s, based on a series of expeditions to Colombia, French Guiana, Peru and Brazil, led to a realization that an amazing diversity of highly specialized grasshoppers dwells in canopies. The result was the publication of an excellent taxonomic study by Amedegnato and Descamps (1979) which revealed the diversity and convergence occuring in dendrophilous grasshoppers. Compared to the 1970s, there are many more tools and technological advances available for exploratory studies and it is imperative to take advantage of these resources to understand the true diversity of grasshoppers.

A challenge

Over the last 250 y, taxonomists in the field of grasshopper systematics have created a rich legacy upon which future generations can build. It is unfortunate that the field today is suffering from the impediment to taxonomy, but it is not too late to begin to rejuvenate and revitalize grasshopper systematics.

The most important area of improvement is the recruitment of young students to taxonomy. Working grasshopper taxonomists around the world need to collaborate and share resources in order to pass on their enormous body of knowledge to the next generation. Grasshoppers represent a wonderful system to address all sorts of interesting evolutionary questions, and it is certainly possible to attract enthusiastic students to grasshopper systematics, rather than losing them to the already saturated fields of major holometabolous insects.

Another area of encouragement is to realize that taxonomy is evolving. The development of technology in digital imaging, databasing, and cyberinfrastructure has merged with taxonomy to result in what is commonly referred to as cybertaxonomy (Wheeler 2004). The goal of cybertaxonomy is to explore and describe biodiversity rapidly and effectively, using these technological advances and so to remove the impediments to taxonomy. In this sense, grasshopper taxonomists are in a very good position because of the OSF online, which is capable of performing all the tasks related to conducting a solid cybertaxonomic study. To move forward, the field of grasshopper systematics as a whole needs to adapt to the changing environment of taxonomy and to become a leader in exploring biodiversity.

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