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Molecular Phylogeny of the Higher Category of Acrididae (Orthoptera: Acridoidea)

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Abstract: The phylogenetic relationships among all taxa within the Acrididae (Orthoptera: Acridoidea) were largely unknown until now. In this study, to further investigations, 24 species of Acrididae from China were used as sample taxa. The sequence constitutions and variations were analyzed and the molecular phylogenetic trees were reconstructed based on the combined sequence data (795 bp length in total) of 12S rDNA and 16S rDNA, using the grasshopper *Pyrgomorpha conica* of Pyrgomorphidae as the outgroup. The results showed that the rates of the two kinds of transitions are obviously much higher than that of the four kinds of transversions in these combined 12S+16S rDNA sequence data. The saturation of nucleotide substitutions happened in 12S and 16S rDNA sequence data. The molecular phylogenetic trees indicated that Oedipodinae is a monophyletic group and this subfamily is a natural one, but Catantopinae and Acridinae are non-monophyletic. Oedipodnae is a relatively primitive group within the Acrididae, whereas the Oxyinae may have diverged later than Oedipodinae, but earlier than most other species of Acridide.

Key words: Phylogeny; Acrididae; 16S rDNA; 12S rDNA

蝗科高级阶元的分子系统发育

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摘要：迄今，蝗科内各分类阶元之间的系统发生关系大部分是未知的。本文用来自中国 24 种蝗科昆虫的 12S rDNA 和 16S rDNA 2 个基因的联合序列(共 795 bp)数据，以锥头蝗科的锥头蝗(*Pyrgomorpha conica*)为外群，重建了分子系统树。研究结果表明，在 12S rDNA 与 16S rDNA 组成的联合数据中，转换的替代速率明显比颠换的替代速率高得多，核酸的替代已经发生了饱和。分子系统树表明：斑翅蝗亚科是一单系群，该亚科是一个合法的亚科，但斑腿蝗亚科和蝗亚科都不是单系群；斑翅蝗亚科在蝗科内是一个相对原始的类群，而稻蝗亚科比斑翅蝗亚科相对进化，比蝗科的其他亚科的种类相对原始。

关键词：系统发育；蝗科；16S rDNA；12S rDNA
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The Acrididae belongs to the superfamily Acridoidea of Orthoptera and is the largest family in the Acridoidea. So far, more than 800 species of Acrididae have been described in China（Xia, 1994）and Chinese taxonomists have widely adopted Xia's taxonomic system of Acridoidea. In this system, Acridoidea was divided into eight families: Pamphagidae, Chrotogonidae, Pyrgomorphidae, Catantopidae, Oedipodidae, Arcypteridae, Gomphoceridae and Acrididae (Zheng, 1993; Xia, 1994). However, this system is very different from the

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international taxonomic system, the Orthoptera Species File (OSF) (http://osf2.orthoptera.org/HomePage.aspx), in which the superfamily Pyrgomorphoidea includes only one family Pyrgomorphidae, and the superfamily Acridoidea was divided into 11 families, including the Acrididae,Charilaidae, Dericorythidae, Lathiceridae, Lentulidae, Lithidiidae, Ommexechidae, Pamphagidae, Pyrgacrididae, Romaleidae and Tristiridae. The members of the Catantopidae, Oedipodidae, Arcypteridae, Gomphoceridae and Acrididae in Xia's system belong to the same family as the Acrididae in the international system (Kevan, 1982; Flook & Rowell, 1997; Eades, 2007; Xia, 1994). In addition, it had been proven by 18*S* rDNA (Liu & Jiang, 2005) and 16*S* rDNA (Liu et al, 2005; Sun et al, 2006) that Catantopidae, Arcypteridae, Gomphoceridae and Acrididae were non-monophyletic. At the molecular level, Liu & Jiang (2005) proposed that the above five families should be grouped into the family Acrididae in accordance with the international system.

What are the phylogenetic relationships of some taxa within the Acrididae? Is each subfamily within the Acrididae a monophyletic group? In this study, using *Pyrgomorpha conica* of Pyrgomorphidae as the outgroup, the molecular phylogenetic trees were reconstructed based upon the combined data of the 12*S* rDNA of 17 species (newly determined), the homologous sequences of 8 species (downloaded from GenBank) and 16*S* rDNA of 25 species (downloaded from GenBank) in Acrididae grasshoppers to reassess their phylogenetic relationships, so as to further clarify these unresolved issues.

1 Materials and methods

1.1 Samples and DNA extraction

Seventeen species of grasshoppers from the Acrididae were collected from China (Tab. 1) and the samples were stored in absolute ethanol at −20℃. Total genomic DNA was extracted from the legs of single grasshoppers by using a simple proteinase K/SDS method. Tissue was ground and incubated in 0.02 mol/L Tris-HCl (pH8), 0.01 mol/L EDTA, 0.5% SDS, and 50 mg/mL of Proteinase K overnight at 50℃.This mixture was extracted with phenol/chloroform and DNA was precipitated with ethanol.

1.2 PCR

The primers, which were used for amplification in this study, were designed according to Simon et al (1994). The two primers used for the 12S rDNA fragment and the sequences were: SR-J-14233: 5'-AAGAGCGAC-GGGCGATGTGT-3' and SR-N-14588: 5'-AAACTAGG-ATTAGATACCCTATTAT-3'.

PCR reactions were performed in 30 μL volume containing 10 mmol/L Tris (pH8.3), 50 mmol/L KCl, 0.01% TritonX-100, 1.5 mmol/L $MgCl_2$, 0.2 mmol/L each dNTP, 0.4 mmol/L primers, 1 unit of Taq-polymerase and 1 μL template DNA (10−25 ng). Amplifications were performed under the following protocols: an initial denaturation of 5 min at 94℃; 30 s at 94℃, 40 s at 48℃, 30 s at 72℃, 30 cycles; a final extension at 72℃ for 10 min.

Products of successful PCR amplifications were purified using a GeneClean III kit (Anachem), following the protocol in the manual. Purified amplified product was sequenced by Shanghai United Gene Company.

1.2 Data and phylogenetic analysis

Tab. 1 List of specimens sampled and voucher numbers

Subfamily	Species	Locality	Voucher number
Spathosterninae	*Spathosternum prasiniferum sinense*	Fangchenggang, Guangxi	H4232
	Spathosternum prasiniferum prasiniferum	Longzhou, Guangxi	H4231
Cytacanthacridinae	*Chondracris rosea rosea*	Nanning, Guangxi	H4651
	Patanga succincta	Fangchenggang, Guangxi	H4681
Oxyinae	*Oxya chinensis*	Tianlin, Guangxi	H4132
	Pseudoxya diminuta	Fangchenggang, Guangxi	H4161
	Hieroglyphus banian	Longzhou, Guangxi	H4222
Melanoplinae	*Tonkinacris sinensis*	Tianlin, Guangxi	H4362
Catantopinae	*Xenocatantops brachycerus*	Tianlin, Guangxi	H4811
	Xenocatantops humilis	Jinxiu, Guangxi	H4822
	Apalacris varicornis	Longzhou, Guangxi	H4751
	Traulia szetechuanensis	Tianlin, Guangxi	H4691
Oedipodinae	*Pternoscirta sauteri*	Tian'e, Guangxi	H5011
	Oedaleus manjius	Juesui, Guangxi	H5191
	Trilophidia annulata	Longzhou, Guangxi	H5281
Acridinae	*Acrida willemsei*	Chongzuo, Guangxi	H8271
	Phlaeoba antennata	Chongzuo, Guangxi	H8221

The 12*S* rDNA fragments of 17 species from the Acrididae were sequenced in this study, and the 12S rDNA fragments of 8 grasshoppers and 16S rDNA of 25 grasshoppers were downloaded from GenBank (Tab. 2). All species of the ingroup belonged to Acrididae and their samples were collected from China, and their sequences of both 12S and 16*S* rDNA were submitted by Chinese researchers. The outgroup, *Pyrgomorpha conica*, from Swissland, belongs to the Pyrgomorphidae of the Pyrgomorphoidea, whose sequences of both 12*S* and 16*S* rDNA were sequenced by Flook et al (1999). In this paper, the classification of the Acridoidea was based on the Orthoptera Species File (OSF) (http://osf2.orthoptera.org/HomePage.aspx).

Tab. 2 Sequence data used in this study and GenBank accession numbers

Subfamily	Species	16S		12S	
		Accession No	Reference	Accession No	Reference
Spathosterninae	*Spathosternum prasiniferum sinense*	DQ366828	Lu and Huang, 2006	AY247167	This paper
	Spathosternum prasiniferum prasiniferum	AY566259	Liu et al, 2005	AY247166	This paper
Cytacanthacridinae	*Chondracris rosea rosea*	AY566262	Liu et al, 2005	AY247184	This paper
	Patanga succincta	AY804006	Liu et al, 2005	AY247185	This paper
Oxyinae	*Oxya chinensis*	AY804002	Liu et al, 2005	AY247182	This paper
	Pseudoxya diminuta	AY566254	Liu et al, 2005	AY247170	This paper
	Hieroglyphus banian	AY804005	Liu et al, 2005	AY247173	This paper
Melanoplinae	*Tonkinacris sinensis*	AY566261	Liu et al, 2005	AY247186	This paper
Catantopinae	*Xenocatantops brachycerus*	AY804007	Liu et al, 2005	AY247177	This paper
	Xenocatantops humilis	AY566258	Liu et al, 2005	AY247178	This paper
	Apalacris varicornis	AY804000	Liu et al, 2005	AY247192	This paper
	Traulia szetechuanensis	AY803999	Liu et al, 2005	AY247174	This paper
Oedipodinae	*Pternoscirta sauteri*	AY856118	Jiang and Liu, 2005	AY247195	This paper
	Locusta migratoria manilensis	AY856117	Jiang and Liu, 2005	AY324452	Ye et al, 2003
	Oedaleus asiaticus	AY856122	Jiang and Liu, 2005	AY560523	Ye et al, 2004
	Oedaleus manjius	AY952313	Lu and Huang, 2006	AY247196	This paper
	Trilophidia annulata	AY856120	Jiang and Liu, 2005	AY247194	This paper
Acridinae	*Ceracris fasciata szemaoensis*	AY995328	Jiang and Liu, 2006	AY995320	Jiang and Liu, 2006
	Ceracris fasciata fasciata	AY995327	Jiang and Liu, 2006	AY995319	Jiang and Liu, 2006
	Ceracris nigricornis laeta	AY995325	Jiang and Liu, 2006	AY995322	Jiang and Liu, 2006
	Rammeacris kiangsu	AY995330	Jiang and Liu, 2006	AY995316	Jiang and Liu, 2006
	Acrida willemsei	DQ077181	Sun et al, 2006	AY247188	This paper
	Phlaeoba antennata	DQ077179	Sun et al, 2006	AY247187	This paper
Gomphocerinae	*Chorthippus albonemus*	AY995332	Jiang and Liu, 2006	AY995323	Jiang and Liu, 2006
Pyrgormorphinae	*Pyrgomorpha conica*	Z97616	Flook et al, 1999	Z97600	Flook et al, 1999

All sequences were aligned using Clustal X1.83 (Thompson et al, 1997) with parameters set to default. Alignments were improved by comparison to the secondary structures and regions of uncertain alignment were omitted from subsequent analyses. Bases composition and sequence variability were examined using the software package MEGA4.0（Tamura et al, 2007）. Two different types of phylogenetic analyses were performed as below: the minimum evolution (ME) and the Bayesian inference. The former analyses were conducted using MEGA4.0 and the later inference was conducted using MrBayes3_0b4 (Huelsenbeck & Ronquist, 2001). Trees saved below the burn-in generations were discarded, and a majority-rule consensus tree of the remains were calculated in Mrbayes3_0b4, providing posterior probabilities for each clade.

For the ME analysis, the Tamura-Nei's nucleotide substitution model was selected with pair-wise deletion of gaps, meanwhile, the interior branch test with 1000 replicates was used to assess the confidence that could be attached to the individual nodes. The MrBayes3_0b4 was run with the following specifications: The analysis was performed using GTR model including estimation site's invariants with a gamma distribution (invgamma). The Markov's chains were started from a random tree for 400,000 generations, sampling the Markov chains at intervals of 100 generations. Four chains were run simultaneously, 3 hot and one cold, with the initial 200 cycles discarded as burn-in.

2 Results

2.1 Description of data

After aligning, using Clustal X1.83, the lengths of 12*S* and 16*S* rDNA sequences including gaps were about 332 bp and 463 bp respectively, 795 bp in total. The sequence data set of 12S rDNA contained 159 variables and 100 parsimony-informative sites, and the sequence data set of 16*S* rDNA contained 181 variables and 124 parsimony-informative sites. Across the two gene fragments, 340 sites were variable and 224 sites were parsimony-informative. The average values of intraspecific pair-wise sequence divergence was 0.118 in 12*S* data set, 0.112 in 16*S* data set and 0.113 in combined data set, respectively.

Nucleotide variation and substitution patterns were examined using the software package MEGA 4.0. The average value T_S/T_V was 1.415 in 12*S* rDNA sequence data, 0.876 in 16*S* rDNA sequence data, and 1.046 in combined sequence data set. T_V was almost identical to T_S in combined data. The nucleotide compositions of the sequences were similar, and had a high A+T content both in 12*S* and 16*S* sequences. The A+T contents was 71.4% and the G+C contents was 28.6% in the combined data set. Due to the existence of many differences in base composition, the Tamura-Nei's substitution model, which considers not only T_S/T_V but also base composition, was selected in this analysis.

The nucleotide substitution model parameter from Bayesian analysis is shown in Tab. 3. Bayesian analysis indicated that two kinds of transition rates were much higher than transvertions.

2.2 Phylogenetic relationships

Fig.1-2 present the phylogenies recovered under minimum evolution and Bayesian analysis, respectively. The values of interior branch test for some nodes in minimum evolution trees and the posterior probability values for some nodes in Bayesian tree were low. However, the topologies of the two trees were identical or very similar in most clusters. In ME and Bayesian trees, the species studied could be clearly classified into four clades as follows: Clade I included six species: *Ac. willemsei* (Acridinae), *T. annulata* (Oedipodinae), *P. sauteri* (Oedipodinae), *Lo. migratoria manilensis* (Oedipodinae), *O. manjius* (Oedipodinae) and *O. asiaticus* (Oedipodinae). Clade II contained three species: *Ps. diminuta* (Oxyinae), *H. banian* (Oxyinae) and *Oxya chinensis* (Oxyinae). Clade III consisted of only one species: *Ap. varicornis* (Catantopinae). Clade IV contained other species from this study. The relations between clusters were identical for Clade I, Clade II, and Clade III in ME and Bayesian trees, but topologies of Clade IV were different in the two trees. However, it was same between the two trees that *S. prasiniferum sinense* (Spathosterninae), *S. prasiniferum prasiniferum* (Spathosterninae) and *To. sinensis* (Melanoplinae) were clustered into one cluster, *Xe. brachycerus* (Catantopinae) and *Xe. humilis* (Catantopinae) were clustered into one cluster, *Ch. rosea rosea* (Cytacanthacridinae) and *Pa. succincta* (Cytacanthacridinae) clustered into one cluster, and *Ce. fasciata szemaoensis* (Acridinae) and *Ce. fasciata fasciata* (Acridinae) clustered into one cluster. Moreover, these nodes were supported by high values of interior branch test (Fig. 1) or posterior probability values (Fig.2).

3 Discussion

3.1 The saturation of sequence data and the reason for lower credibility on some nodes

The results of the Bayesian analysis showed that the

Tab. 3 Nucleotide substitution model parameter estimates for Bayesian analysis

Parameter	Mean	Variance	95% Credible Interval	
			Lower	Upper
TL	2.057086	0.043160	1.777000	2.361000
r(G<->T)	1.000000	0.000000	1.000000	1.000000
r(C<->T)	4.255614	0.983908	2.701429	6.483768
r(C<->G)	0.057406	0.005037	0.010603	0.236028
r(A<->T)	2.542484	0.327689	1.610336	3.805997
r(A<->G)	8.291493	2.880768	5.536824	11.794261
r(A<->C)	0.117518	0.008359	0.013451	0.317179
pi(A)	0.338327	0.000207	0.312000	0.366404
pi(C)	0.088537	0.000089	0.072088	0.105061
pi(G)	0.149924	0.000118	0.130286	0.171227
pi(T)	0.423212	0.000268	0.391838	0.452411
alpha	0.636878	0.023375	0.390973	0.976867
pinvar	0.310891	0.004560	0.153007	0.423776

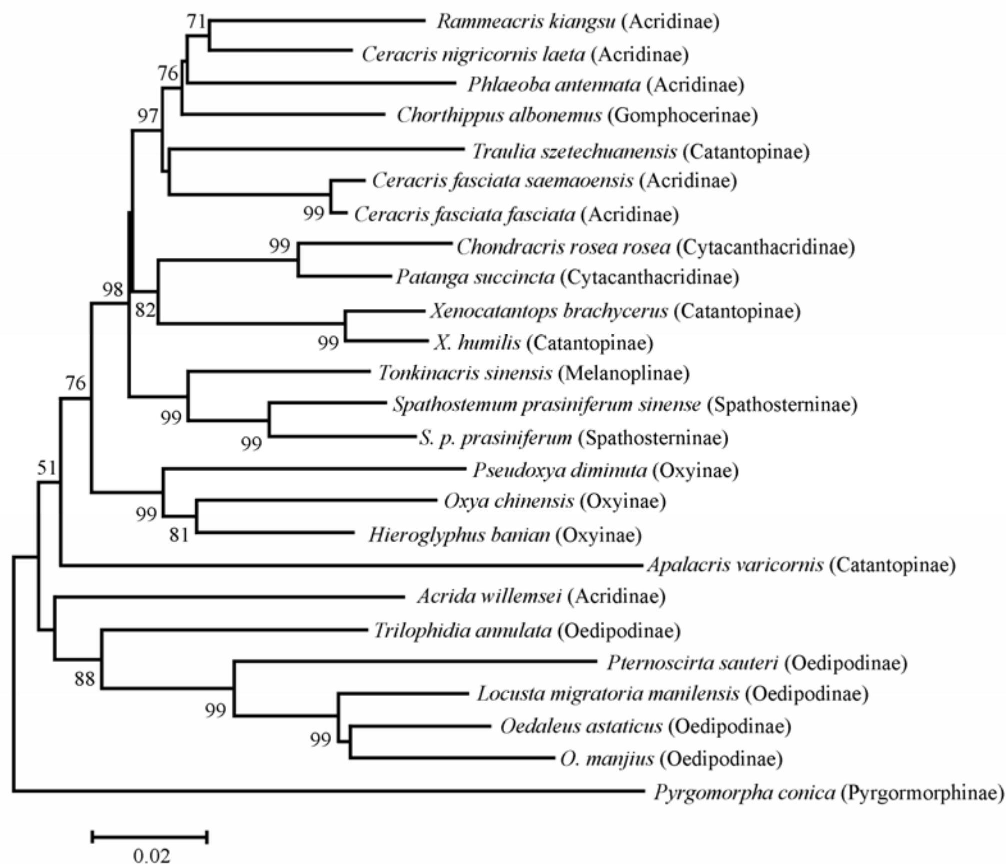

Fig. 1 Phylogram of ME tree reconstructed from combined 12*S*+16*S* data set

Numbers on nodes correspond to values of interior branch test for 1000 replicates.

ratios of the two kinds of transitions were obviously much higher than the four kinds of transversions. However, the results from MEGA4.0 indicated that the average value of T_S/T_V was 1.415 in 12*S* rDNA sequence data, 0.876 in 16S rDNA sequence data, and 1.046 in combined sequence data sets. The average value of T_S was close to that of T_V in the combined data set. We assume that the phenomenon results from two specifics. One is that saturation of nucleotide substitutions occur in 12S and 16S rDNA sequence data. Many scholars think that when the average value T_S/T_V is smaller than 2, saturation of nucleotide substitutions happen in sequences (Knight & Mindell, 1993; Chen, 2003; Liu & Jiang, 2005). The other reason is that the nucleotide compositions of the sequences have a high A+T content both in 12S and 16S sequences. The high A+T content increases the frequency of transversion A-T, which leads to the average value of T_S/T_V decreasing (Desalle, 1997; Liu & Jiang, 2005).

The values of interior branch test on some of nodes of the minimum evolution tree were weak, and the posterior probability values for some nodes of the Bayesian tree were also relatively low. This result may be due to the high sequence divergence of 12*S* and 16*S* rDNA for some species studied. Cognato & Sperling (2000) suggested that clades of closely related species (<10% sequence divergence) commonly have high bootstrap values (>90%), while clades with >10% sequence divergence generally have lower bootstrap values (<90%). In this study, the average value of intraspecific pair-wise sequence divergence is 11.8 % in 12S data set, 11.2% in 16S and 11.3% in the combined data set, respectively, and these sequence divergences all are higher than 10%.

3.2 Taxonomic status of the Oedipodinae

Most species of the Oedipodinae, as may be deduced from their common name, have brightly colored hind wings with a marginal or sub-marginal band, while a few species of this subfamily have clear hind wings. In this group of grasshoppers, the peg is absent between the front legs, and there is a median keel on pronotum. They make a crackling sound (crepitate) when they fly. The

Fig. 2 Phylogram of Bayesian tree reconstructed from combined 12S+16S data set

Numbers on nodes correspond to posterior probability values.

taxonomic status of Oedipodinae has changed several times. The synonym of this subfamily was Locustidae by Kirby (1825), and Oedipodidae by Walker (1871). In Xia's system (Xia, 1994), Oedipodinae is also upgraded to the taxonomic status of family. The Chinese scholars widely adopt Xia's taxonomy system about the Acridoidea. But in the OSF and NCBI taxonomy database, the group is classified as a subfamily in the Acrididae. Recently, based on the phylogenetic results of 18*S* rDNA, Liu & Jiang (2005) proposed that it was unreasonable to classify this group as a family and that the group should be placed as one of the subfamilies within Acrididae.

A taxon in a good taxonomic system should be a natural and monophyletic group. In our ME and Bayesian trees, *T. annulata*, *P. sauteri*, *Lo. migratoria manilensis*, *O. manjius* and *O. asiaticus* of the Oedipodinae were clustered into one clade. The results indicated that the subfamily is a monophyletic group, supporting Rowell & Flook's (1998) view. Thus we suggest that the Oedipodnae should be taken as a legal subfamily.

3.3 Monophylies of the subfamilies Catantopinae and Acridinae

According to the OSF, the four species of grasshoppers, *Xe. brachycerus*, *Xe. humilis*, *Apalacris*

varicornis and *Tr. szetechuanensis*, all belong to the subfamily Catantopinae. In this study, however, the four species of grasshoppers were not clustered together in the ME and Bayesian trees. The result agrees with the opinion of Rowell & Flook (1998), from which Catantopinae is not a monophyletic but a polyphyletic group.

The Acridinae are silent and characterized by a slanted face and distinct hind wings (Yin & Xia, 2003), usually found around marshes and wet meadows in small numbers and do little damage to vegetation. In our trees, the species of the subfamily Acridinae were not clustered as one clade, with the *Acrida willemsei* clustered together with the species of Oedipodinae. The results show that current Acridinae is non-monophyletic.

3.4 Phylogenetic relationships of the subfamilies of the Acrididae

The fact that the Oedipodinae was at the base of phylogenetic trees (Figs.1-2), indicated that Oedipodnae is a relatively primitive group within the Acrididae. The subfamily Oxyinae is basal to the remaining subfamilies of Acrididae, and this result shows that the Oxyinae may have diverged later than Oedipodinae, but earlier than most other species of Acridide. Because of the differences in relationships among the Cytacanthacridinae, Catantopinae, Spathoterninae, Melanoplinae and Acridinae in both of the ME and Bayesian trees, their phylogenetic relationships require further investigation in the future.

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