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Phylogenetic analyses of some genera in Oedipodidae (Orthoptera: Acridoidea) based on 16S mitochondrial partial gene sequences

Xiang-Chu Yin[1,2,4], Xin-Jiang Li[1], Wen-Qiang Wang[3], Hong Yin[1], Cheng-Quan Cao[4], Bao-Hua Ye[4] and Zhan Yin[4]

[1]*College of Life Sciences, Hebei University, Baoding, Hebei Province,* [2]*Northwest Plateau Institute of Biology, Chinese Academy of Sciences, Xining,* [3]*College of Life Sciences, Yan'an University, Yan'an, Shaanxi Province, and* [4]*College of Plant Protection, Shandong Agricultural University, Taian, Shandong Province, China*

Abstract Based on the 16S mitochondrial partial gene sequences of 29 genera, containing 26 from Oedipodidae and one each from Tanaoceridae, Pyrgomorphidae and Tetrigidae (as outgroups), the homologus sequences were compared and phylogenetic analyses were performed. A phylogenetic tree was inferred by neighbor-joining (NJ). The results of sequences compared show that: (i) in a total of 574 bp of Oedipodidae, the number of substituted nucleotides was 265 bp and the average percentages of T, C, A and G were 38.3%, 11.4%, 31.8% and 18.5%, respectively, and the content of A+T (70.1%) was distinctly richer than that of C+G (29.9%); and (ii) the average nucleotide divergence of 16S rDNA sequences among genera of Oedipodidae were 9.0%, among families of Acridoidea were 17.0%, and between superfamilies (Tetrigoidea and Acridoidea) were 23.9%, respectively. The phylogenetic tree indicated: (i) the Oedipodidae was a monophyletic group, which suggested that the taxonomic status of this family was confirmed; (ii) the genus *Heteropternis* separated from the other Oedipodids first and had another unique sound-producing structure in morphology, which is the type-genus of subfamily Heteropterninae; and (iii) the relative intergeneric relationship within the same continent was closer than that of different continents, and between the Eurasian genera and the African genera, was closer than that between Eurasians and Americans.

Key words Oedipodidae, Acridoidea, Orthoptera, 16S rDNA, phylogenetic analyses

Introduction

Oedipodid (band-winged grasshopper) is a very important group of grasshoppers, which is distributed in all zoogeographical regions. Since the group being first established as a family by Walker (1870), it was treated as part of the family Oedipodidae (Yin, 1982, 1984; Zheng & Xia, 1998), subfamily Oedipodinae (Bey-Bienko & Mishchenko, 1963; Otte & Naskrecki, 2004) or tribe Oedipidini (Dirsh, 1961; Harz, 1975) depending on different taxonomic systems.

So far, there are 124 genera described in this group (Yin *et al*., 1996; Otte & Naskrecki, 2004). Some of the species are world-important pests to agriculture and grazing, for example, *Locusta migratoria* (Linnaeus, 1758), *Oedaleus decorus* (Germar, 1826), and so on. Thus, it is important to study the taxonomy of the group, including the phylogenetic analysis of them at the molecular level, which will help us in pest control.

The mitochondrial 16S ribosomal DNA (rDNA) has been used as a molecular marker to explain the phylogenic relationship of Acridoidea (Flook *et al*., 1995, 1997a, b,

Correspondence: Xiang-Chu Yin, College of Life Sciences, Hebei University, Baoding, Hebei 071002, China. Tel: +86 312 5079707; fax: +86 312 5079707; email: yxch34@yahoo.com, yxch@sdau.edu.cn

1999, 2000; Walton, 1997, Chapco *et al*., 1997, 1999; Guljaeva *et al*., 2001; Yin *et al*., 2003; Zhang *et al*., 2005). There are several reports on Oedipodids phylogeny at the molecular level (Chapco *et al*., 1997; Guljaeva *et al*., 2001). However, reports regarding on molecular phylogeny of Oedipodidae from Eurasian groups has not yet been undertaken. In this study, we used mitochondrial ribosomal DNA sequences to clarify phylogenic relationships of some genera of Oedipodidae from China.

Materials and methods

We sequenced the mitochondrial 16S rDNA partial sequences of 11 genera of Oedipodidae grasshoppers from China, and indexed 18 sequences of relative genera (including 15 genera of Oedipodidae and one each of Tanaoceridae, Pyrgomorphidae and Tetrigidae) from the GenBank database (Table 1). These homologous sequences were compared, the used frequencies of nucleotide were calculated and a molecular phylogenetic tree was constructed from this study.

Research materials

Representative species of each genus in Oedipodidae were selected (Table 1). Distinguished and differentiated species are based on descriptions of Yin (1984) and on comparisons with type material in the Museum of Hebei University (MHU), China.

Adult insects were preserved in 75% alcohol for DNA investigation or were dried and pricked with a needle for morphological study.

Table 1 List of species together with the higher taxa adopted and the sequences data used in this study.

No.	Superfamilies	Families	Species	Distributions	References	GenBank accession
1	Acridoidea	Tanaoceridae	*Tanaocerus koebeli* Bruner, 1906	North America	Flook *et al*., 1997	Z97621
2		Pyrgomorphidae	*Pyrgomorpha conica* (Oliver, 1791)	Eurasia	Flook *et al*., 1997	Z97616
3		Oedipodidae	*Epacromius coerulipes* (Ivan, 1888)	Eurasia	Present study	AY627643
4			*Aiolopus tamulus* (Fabricius, 1798)	Eurasia	Present study	AY627644
5			*Chortophaga viridisfasciata* (De Geer, 1773)	North America	Favret *et al*., 2000	AF212057
6			*Encoptolophus costalis* (Scudder, 1862)	North America	Chapco *et al*., 1997	U18064
7			*Bryodemella holdereri* (Krauss, 1901)	Eurasia	Present study	AY604598
8			*Compsorhips davidium* (Saussure, 1888)	Eurasia	Present study	AY627645
9			*Bryodema luctuosum* (Stoll, 1813)	Eurasia	Present study	AY627646
10			*Angaracris rhodopa* (F.-W., 1836)	Eurasia	Present study	AY627647
11			*Helioscirtus moseri* Saussure, 1884	Eurasia	Present study	AY627648
12			*Leptopternis gracilis* (Eversm, 1848)	Eurasia	Present study	AY627649
13			*Sphingonotus haitensis* (Saussure, 1861)	North America	Rowell *et al*., 2003	AY352436
14			*Trachyrhachis kiowa* (Thomas, 1872)	North America	Chapco *et al*., 1997	U18074
15			*Celes akitanus* (Shiraki, 1910)	Eurasia	Present study	AY627650
16			*Metator pardalinus* (Saussure, 1884)	North America	Chapco *et al*., 1997	U18072
17			*Dissosteira carolina* (Linnaeus, 1758)	North America	Chapco *et al*., 1997	U18076
18			*Camnula pellucida* (Scudder, 1862)	North America	Chapco *et al*., 1997	U18073
19			*Arphia conspersa* Scudder, 1875	North America	Flook *et al*., 2003	Z93295
20			*Spharagemon campestris* (McNeill, 1900)	North America	Chapco *et al*., 1997	U18070
21			*Trimerotropis pistrinaria* Saussure, 1884	North America	Chapco *et al*., 1997	U18069
22			*Circotettix carlinianus* (Thomas, 1870)	North America	Chapco *et al*., 1997	U18068
23			*Oedipoda coerulescens* (Linnaeus, 1758)	Eurasia	Flook *et al*., 1999	Z93793
24			*Oedaleus asiaticus* Bei-Bienko, 1941	Eurasia	Yin *et al*., 2003	AY379747
25			*Locusta migratoria* (Linnaeus, 1758)	Eurasia	Flook *et al*., 1997	Z93294
26			*Gastrimargus marmoratus* (Thunberg, 1815)	Eurasia	Present study	AY627651
27			*Morphacris fasciata* (Thunberg, 1815)	Africa	Rowell *et al*., 2003	AY352430
28			*Heteropternis respondens* Bei-Bienko, 1951	Eurasia	Present study	AY627652
29	Tetrigoidea	Tetrigidae	*Tetrix tuerki* (Krauss, 1876)	Eurasia	Flook *et al*., 1997	Z93310

DNA preparation

Specimens were washed in sterile deionized, distilled water before DNA extraction. Total genomic DNA was extracted from the hind leg of each individual specimen. The muscular tissue was briefly rehydrated in Tris-EDTA (TE) buffer, cut into pieces. Smashed tissue was resuspended in STE (400 μL TE [pH 8.0], 80 μL ddH_2O, 25 μL 1.0% sodium dodecyl sulfate [SDS], 5 μL proteinase K [5 mg/mL]) and incubated at 56°C for 12−15 h. The DNA was extracted with phenol and chloroform, and ethanol-precipitated, and resuspended in TE buffer, and stored at 4°C until use.

DNA amplification

A partial region of the mitochondrial 16S rDNA was amplified using the primers: LR-J (5' -CCGGTCTGAA CTCAGATCAC G-3') and LR-N (5' -CGCCTGTTTAA CAAAAACAT- 3') (Yin *et al*., 2003). The amplifications (50 μL) contained 5 μL (5 μmol/L) primer, 5 μL (2.5 mmol/L, respectively) dNTP, 5 μL (5 U/μL) *Taq* DNA polymerase, 5 μL (100 μg/mL) template DNA, 5 μL buffer, 25 μL ddH_2O, for 10 sec at 94°C, 30 sec at 50°C and 40 sec at 72 °C for 40 cycles with an initial denaturing step at 94°C for 8 min and a final extension step at 72°C for 10 min. Amplification product was loaded directly onto 1.5% agarose gel for detection.

DNA purification and sequencing

Polymerase chain reaction (PCR) product was purified using the Agarose Gel DNA Purification Kit (TaKaRa Biltechnology Co., Ltd., Dalian, China) after the appropriate band was excised from agarose gel, and resuspended in H_2O to a final volume of 25 μL. A no-DNA control went through the entire DNA extraction procedure, as well as purification and rounds of PCR. Automated sequencing was performed using the amplification primer at the Mendel DNA Center Co., Ltd., Shanghai, China. Sequences have been deposited in the Genbank database with the accession numbers of AY604598 and AY627643-AY627652, respectively (for details see Table 1).

Sequence analyses

The sequence data were aligned and compared using the ClustalX (1.81) computer program (Thompson *et al*., 1997). Phylogenetic analyses were performed using neighbor-joining (NJ), available in the software package MEGA 2.1 (Kumar *et al*., 2001). Estimation of substitution rate, nucleotide composition, and sequence variability was performed at the same time. The robustness of support for the tree was estimated by performing 1 000 bootstrap replicates (Fig. 1). In all the above analyses, gaps were treated as missing characters with pair-wise deletion option and used 16s rDNA sequences from *Tetrix* (Tetrigoidea, Tetrigidae), *Tanaocerus* (Acridoidea: Tanaoceridae) and *Pyrgomorpha* (Acridoidea: Pyrgomorphidae) as outgroups to root the tree.

Results

We have aligned the mitochondrial 16S rDNA partial sequences of a total 29 species, representing two superfamilies, four families and 29 genera (including 26 genera of Oedipodidae) (Table 1). The number of nucleotide substitutions and the percentage of differences for each pair-wise comparison of the sequences are shown in Table 2. In analysis and comparison of the sequences data, a total of 574 bp, 265 variable sites (46.2%) and 159 parsimony informative sites (27.7%) of the sequence divergence were observed. The average percentages of T, C, A and G within all taxa were 39.0%, 11.5%, 32.0% and 17.5%, respectively. The average percentages of T, C, A and G within Oedipodidae were 38.3%, 11.4%, 31.8% and 18.5%, respectively. As shown in Table 2, the ranges of 16S rDNA nucleotide substitutions between two superfamilies (Tetrigoidea and Acridoidea) were 88−121 bp (mean 106.6 bp), among three families (Tanaoceridae, Pyrgomorpidae

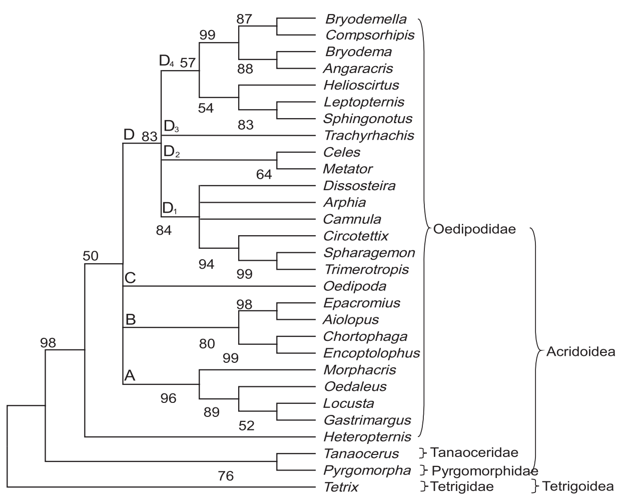

Fig. 1 Molecular phylogenetic tree of Oedipodidae. Numbers at the branches are bootstrap confidence values (%) inferred with neighbor-joining (single integer). Test of inferred phylogeny were used 1 000 bootstrap replications and 64 238 random seed. *Tetrix* is as an outgroup rooted to the tree.

Table 2 Percentages of differences based on the nucleotide *p*-distance (above diagonal) and numbers of nucleotide substitutions (below diagonal) for 16S rDNA sequences. Numbers 1–29 in the first lines correspond to those in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1		15.6	15.4	15.8	14.4	13.8	16.4	16.2	17.4	15.9	15.7	15.8	14.6	16.0	17.5	17.1	16.1	16.3	17.0	14.7	14.0	15.0	15.8	16.5	15.6	17.5	16.4	16.2	25.6
2	78		17.7	17.3	17.5	16.3	19.1	18.5	20.3	18.6	17.6	17.3	17.4	19.0	20.3	18.8	19.3	18.5	18.8	17.8	17.0	17.7	16.6	18.8	17.2	19.3	17.9	19.3	24.9
3	75	87		5.9	8.8	6.0	9.9	8.5	10.7	8.8	8.2	9.2	8.7	7.3	11.8	8.6	8.6	9.4	11.1	8.6	7.3	8.6	9.6	13.3	9.7	10.7	12.4	12.6	24.4
4	78	86	30		10.4	8.1	11.6	10.1	12.2	10.6	10.5	11.4	11.4	9.6	12.0	11.5	10.5	11.2	11.6	10.0	9.7	10.2	10.5	13.7	10.8	11.5	13.2	12.7	24.4
5	71	87	45	53		1.6	10.9	9.5	12.1	9.6	9.5	8.5	8.4	7.9	12.7	9.2	10.0	9.5	11.5	10.3	9.5	9.7	10.4	12.2	11.0	12.1	11.8	12.6	23.7
6	52	62	23	31	6		8.9	8.4	9.7	8.1	7.6	8.1	8.9	8.9	8.9	10.0	11.1	10.5	10.1	11.9	10.6	10.8	10.2	11.0	11.0	10.0	11.8	13.1	23.4
7	81	95	50	59	55	34		1.4	3.6	2.4	5.1	6.2	5.8	5.5	8.0	7.3	7.6	7.6	9.3	8.6	7.6	8.6	10.1	12.0	9.7	11.1	10.8	12.1	23.3
8	79	91	42	50	47	32	7		4.2	2.6	4.6	5.8	5.1	4.9	6.2	6.8	7.1	7.0	8.6	8.1	7.1	8.1	9.6	11.9	9.0	10.5	10.1	11.8	23.0
9	85	100	53	61	60	37	18	21		2.4	5.6	7.3	6.9	6.2	8.8	7.5	7.6	7.5	10.2	9.4	8.3	9.4	10.6	13.7	11.2	12.9	11.3	14.4	24.5
10	78	92	44	53	48	31	12	13	12		4.2	5.6	4.8	4.7	6.8	6.0	6.3	6.3	8.4	8.4	7.1	8.1	9.0	11.9	9.5	10.8	10.1	12.2	22.7
11	77	87	41	53	48	29	26	23	28	21		3.9	3.6	4.4	7.7	5.2	6.8	6.8	9.2	8.3	7.0	8.6	8.3	11.9	9.3	10.4	10.3	11.0	23.6
12	76	84	44	55	41	31	30	28	35	27	19		2.9	4.7	6.4	5.5	7.0	6.5	8.3	9.1	7.8	8.6	9.4	10.2	9.7	10.6	10.7	11.7	23.0
13	73	88	43	57	42	34	29	25	34	24	18	14		3.6	6.8	5.5	6.0	6.5	8.0	8.3	7.0	8.1	10.1	10.4	9.9	10.5	10.3	10.6	24.1
14	61	73	28	37	30	34	21	19	24	18	17	18	14		4.7	4.9	5.2	6.0	6.0	7.3	6.0	7.0	8.8	9.6	10.1	9.4	9.6	10.1	23.2
15	86	101	60	61	65	34	41	31	44	34	39	31	34	18		4.9	5.5	6.8	8.9	7.1	6.3	7.3	8.3	12.1	9.0	12.3	10.8	13.5	24.2
16	65	72	33	44	35	38	28	26	29	23	20	21	21	19	19		7.6	7.6	7.4	8.9	7.6	9.4	8.6	10.7	9.9	9.7	10.9	12.2	24.0
17	61	74	33	40	38	42	29	27	29	24	26	27	23	20	21	29		4.4	5.2	5.5	4.7	5.7	9.9	11.2	10.4	9.7	9.7	13.6	23.6
18	62	71	36	43	36	40	29	27	29	24	26	25	25	23	26	29	17		5.7	7.0	6.2	6.5	11.2	11.2	9.9	10.5	8.9	13.5	23.5
19	84	94	54	57	57	38	46	42	50	41	45	40	40	23	44	28	20	22		6.8	6.0	6.8	12.2	12.0	10.9	12.5	10.2	14.8	23.8
20	56	68	33	38	39	45	33	31	36	32	32	35	32	28	27	34	21	27	26		1.3	4.9	10.4	12.3	10.7	10.7	9.9	13.6	23.6
21	53	65	28	37	36	40	29	27	32	27	27	38	27	23	24	29	18	24	23	5		3.6	9.7	11.8	10.7	10.2	9.9	12.8	23.0
22	57	68	33	39	37	41	33	31	36	31	33	33	31	27	28	36	22	25	26	19	14		12.0	11.7	12.0	11.5	10.9	14.1	23.8
23	70	74	43	47	46	39	45	43	47	40	37	42	45	34	37	33	38	43	54	40	37	46		12.4	10.5	10.7	10.2	13.2	23.6
24	78	90	62	65	58	42	57	56	64	56	56	48	50	37	57	41	43	43	57	47	45	45	55		5.4	7.0	8.1	13.1	24.2
25	70	78	44	49	50	42	44	41	51	43	42	44	45	39	41	38	40	38	49	41	41	46	47	24		4.4	6.1	11.2	23.1
26	86	95	54	58	61	38	56	52	64	54	52	51	52	36	62	37	37	40	61	41	39	44	48	33	20		8.2	11.1	25.0
27	82	90	61	66	59	45	54	50	56	50	51	52	52	37	54	42	37	34	51	38	38	42	46	39	28	41		12.4	25.1
28	79	95	63	63	62	50	60	58	71	60	54	56	52	39	67	47	52	52	72	52	49	54	59	61	51	55	61		24.8
29	121	119	116	116	112	89	111	109	116	108	112	107	115	89	115	92	90	90	112	90	88	91	105	110	105	119	120	118	

and Oedipodidae) of Acridoidea were 52−101 bp (mean 77.7 bp), and among 26 genera of Oedipodidae were 5−72 bp (mean 42.6 bp). The percentages of differences between two superfamilies were 22.7%−25.5% (mean 23.9%), among three families of Acridoidea were 13.8%−20.3% (mean 17.0%), and among 26 genera of Oedipodidae were 1.3%−14.8% (mean 9.0%), respectively.

The tree (Fig. 1) shows that the outgroup taxa (*Tetrix*, *Tanaocerus* and *Pyrgomorpha*) separated first from Oedipodidae taxa with high confidence values (⩾ 98%) at the base of the tree. All Oedipodidae taxa in this study are confirmed as forming a monophyletic group. Of these Oedipodidae taxa, an interesting and unexpected phenomenon is the genus *Heteropternis* definitely separating from other taxa first. The remaining taxa are divided into four clades (A−D) and the clade D subdivided into four branches (D1−D4), and their branching orders are not clearly resolved.

Discussion

The result of composition of mitochondrial 16S rDNA partial sequences within Oedipodidae taxa in this study show that the average percentage of A+T was 70.1% and C+G was only 29.9%, which is consistent with previous results that show the content of A+T was richer than that of C+G in the 16S rDNA sequence of insects (Yin *et al.*, 2003). There were distinct differences between the ranges of the 16S rDNA nucleotide divergence within different taxonomic ranks. As in the above-mentioned, the average nucleotide differences between two superfamilies (Tetrigoidea and Acridoidea), three families (Pyrgomorphidae, Tanaoceridae and Oedipodidae) of Acridoidea, and 26 genera of Oedipodidae were 23.9%, 17.0% and 9.0%, respectively. These are in accordance with the results of a morphological study, which considered the increase of morphological difference along with heightening of the taxon rank. It is suggested that the different scales of 16S rDNA nucleotide divergence should be better reference indices for distinguishing different taxa.

The independent taxonomic situation of Oedipodidae within the Acridoidea has been widely accepted by most current grasshopper taxonomists based on morphological data, although some of them consider it as a subfamily (Oedipodinae) or tribe (Oedipodini) (Bey-Bienko & Mishchenko,1963; Harz, 1975; Yin, 1984; Zheng & Xia, 1998; Otte & Naskrecki, 2004) based on the molecular evidence of the phylogenetic relations of some holarctic acridids (Guljaeva *et al.*, 2001). However, there are some reverse opinions. Chapco (1997) suggested that the taxonomic status of the subfamily itself is uncertain according to a molecular phylogenetic study on North American band-winged grasshoppers. Our analyses indicated that the Oedipodidae are a monophyletic group, which supports the idea that Oedipodidae are an independent taxonomic situation within the Acridoidea.

In this study, the result of phylogenetic reconstruction shows that the genus *Heteropternis* was separated solely from the other Oedipodids first at the base of the molecular phylogenetic tree. This is an interesting result, because current taxonomists place the genus within either subfamily Oedipodinae (Bey-Bienko & Mishchenko, 1963; Yin, 1984; Zheng & Xia, 1998) or tribe Aiolopini (Otte & Naskrecki, 2004) based on morphology, or consider the genus relatively close to *Epacromius* Uvarov, 1942. However, we found that all *Heteropternis* species have unique characters and differ from other Oedipidids, such as "elytron with parallel transverse veinlets in anterior part of intercalary vein of medial area, both intervalary vein and veinlets finely serrated; lower spur on inner side of hind tibia evidently longer than upper spur (Zheng & Xia, 1998)". Thus, the *Heteropternis* probably possesses another unique sound-producing mechanism, which is the type-genus of subfamily Heteropterninae, Oedipodidae (Yin & Wang, 2005c). This viewpoint was strongly supported by our molecular phylogenetic analyses in this study.

Although the tree (Fig. 1) did not resolve the relationships among either the four main clades A−D or four second branches D_1−D_4, there is still some significant information that may be gained from our phylogenetic analyses. For example, the North American species of six genera (i.e. *Trimerotropis*, *Spharagemon*, *Circotettix*, *Camnula*, *Arphia*, and *Dissosteira*) are clustered together independently and form a clade D_1 in which the six genera are closely related, and another two genera (*Encoptolophus* and *Chortophaga*) clustered together forming a sister relation. However, the African genus *Morphacris* is clustered together with the Eurasian genera and forms clade A. As a whole, the relative intergeneric relationship in the same continent is closer than that of different continents, and the relative intergeneric relationship between the Eurasian genera and the African is closer than that between the Eurasian genera and the American.

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