Phylogeny and classification of the Catantopidae at the tribal level (Orthoptera, Acridoidea)

Baoping Li¹, Zhiwei Liu², Zhe-Min Zheng³

¹ Department of Entomology, Nanjing Agricultural University, Nanjing, Jiangsu, China ² Department of Biological Sciences, Eastern Illinois University, Charleston, IL61920, USA ³ Department of Biology, Shaanxi-Normal University, Xi’an, Shaanxi, China

Corresponding author: Zhiwei Liu (zliu@eiu.edu)

Academic editor: M. Engel | Received 13 September 2011 | Accepted 24 October 2011 | Published 21 November 2011

Citation: Li B, Liu Z, Zheng ZM (2011) Phylogeny and classification of the Catantopidae at the tribal level (Orthoptera, Acridoidea). In: Engel MS (Ed) Contributions Celebrating Kumar Krishna. ZooKeys 148: 209–255. doi: 10.3897/zookeys.148.2081

Abstract

The grasshopper family Catantopidae is a well-known group, whose members include some of the most notorious agricultural pests. The existing classifications of the family are mostly utilitarian rather than being based on phylogenetic analysis and therefore unable to provide the stability desired for such an economically important group. In the present study, we present the first comprehensive phylogenetic analysis of the family based on morphology. By extensively sampling from the Chinese fauna, we included in the present analysis multiple representatives of each of the previously recognized tribes in the family. In total, we examined 94 genera represented by 240 species and evaluated 116 characters, including 84 for external morphology and 32 for male genitalia. The final matrix consists of 86 ingroup taxa and 88 characters. Our phylogenetic analyses resulted in a high resolution of the basal relationships of the family while showed considerable uncertainty about the relationships among some crown taxa. We further evaluated the usefulness of morphological characters in phylogeny reconstruction of the catantopids by examining character fit to the shortest trees found, and contrary to previous suggestions, our results suggest that genitalia characters are not as informative as external morphology in inferring higher-level relationship. We further suggest that earlier classification systems of grasshoppers in general and Catantopidae in particular most probably consist of many groups that are not natural due the heavy reliance on genitalia features and need to be revised in the light of future phylogenetic studies. Finally, we outlined a tentative classification scheme based on the results of our phylogenetic analysis.

Keywords

Orthoptera, Acridoidea, Catantopidae, China, Phylogeny, Morphology, Systematics, Male Genitalia
Zhiwei Liu would like to dedicate this paper to the honor of Professor Kumar Krishna for his friendship, kindness, professional encouragement, and the good times at the AMNH.

Introduction

Catantopidae (Acridoidea, Orthoptera) is a well-known grasshopper family; its members include some of the most notorious pests in agriculture, including *Schistocerca gregaria* (Forsköl), *Oxya* spp, and *Melanoplus* spp (Hill 1987). The family is by far the largest and the most diverse acridoid family, consisting of over 3000 species in about 640 genera mainly distributed in the tropical and subtropical areas of the world (Vickery and Kevan 1983).

The previous classifications of Acridoidea (Orthoptera) have been predominantly utilitarian; existing classifications of the superfamily almost entirely ignored phylogenetic relationships among taxa. Among the various classification systems or schemes of acridoids (Dirsh 1961, 1975, Harz 1975, Otte 1981, Yin 1982, Xia 1994, Li and Xia 2002) and several other classifications specifically proposed for the Catantopidae (Tinkham 1940, Mistshenko 1952, Harz 1975), there exist a great deal of disagreement concerning the classification within the family (Table 1), which cannot be easily settled because of the lack of phylogenetic studies. The most influential classification systems of Acridoidea at the present are still the one established by Dirsh (1956) and its modified versions (Dirsh 1961, 1975). The classifications by Dirsh are based on extensive comparative studies of the genitalia morphology of both sexes as well as other morphological characters, emphasizing especially the importance of the morphology of phallic complex and epiphallus in defining higher taxa. Several other authors also proposed their own classification for the Acridoidea (Rehn and Grant 1960, Uvarov 1966, Jago 1971, Vickery and Kevan 1983, Liu 1991). Otte (1981, 1984) adopted a compromised version of the various systems in his monographic treatment of North American grasshoppers. These classifications, although different, have one thing in common: all are entirely based on overall similarity and make little, if any, reference to phylogenetic relationship.

The need for a classification of the grasshoppers and locusts based on phylogeny, rather than based on overall similarity, is obvious. Yin (1982) pointed out the importance of distinguishing between plesiomorphic and derived features in the classification of the acridoids and paid special attention to the transformation series of antennae, wings, and stridulating apparatuses and tympanum. However, Yin's classification of Acridoidea based on his studies of the Chinese members of the group was not based on phylogenetic analysis and his circumscriptions of higher-rank taxa were often based on characters that obviously have been obtained through convergent evolution. Key and Colless (1993) attempted to conduct a cladistic (and phenetic) analysis of the subfamily Catantopinae from Australia. They coded 104 male external characters for 166 genera and conducted a series of analyses from typical phenetic approaches to cladistic
| Classification systems of the Catantopid fauna from China |
|----------------------------------------------------------|
| Tinkham (1940) Mistshenko (1952)                         |
| Dirsh (1961), Uvarov (1966)                              |
| Harz (1975)                                              |
| Dirsh (1975)                                              |
| Yin (1982)                                               |
| Xia (1994)                                               |
| Otte (1981), Eades et al (2011)                          |
| **Cyrtacanthacrinae**                                    |
| Catantopinae                                             |
| Acrididae                                                |
| Catantopidae                                             |
| Hemicaridida                                             |
| Oedipodidae                                              |
| Catantopidae                                             |
| Acrididae                                                |
| Conophymatini                                            |
| Hemiacaridinae                                           |
| Conophyminae                                             |
| Conophyminae                                             |
| Conophyminae                                             |
| **Spathosternini**                                       |
| Spathosterninae                                          |
| Spathosterninae                                          |
| Spathosterninae                                          |
| **Leptacri**                                             |
| Leptacrinae                                              |
| Leptacrinae                                              |
| **Caryandae**                                            |
| Dericorythini                                            |
| Dericorythinae                                           |
| Dericorythinae                                           |
| Dericorythinae                                           |
| **Oxyae**                                                |
| Oxyini                                                   |
| Oxyinae                                                  |
| Oxyinae                                                  |
| Oxyinae                                                  |
| **Catantopini**                                          |
| Catantopini                                              |
| Catantopinae                                             |
| Catantopinae                                             |
| Catantopinae                                             |
| Catantopinae                                             |
| **Calliptamini**                                         |
| Calliptaminae                                            |
| Calliptaminae                                            |
| Calliptaminae                                            |
| Calliptaminae                                            |
| Calliptaminae                                            |
| **Eyprepocnemini**                                       |
| Eyprepocnemidini                                         |
| Eyprepocneminae                                          |
| Eyprepocneminae                                          |
| Eyprepocneminae                                          |
| Eyprepocneminae                                          |
| Eyprepocneminae                                          |
| **Cyrtacanthacridini**                                   |
| Cyrtacanthacridini                                       |
| Cyrtacanthacridina                                       |
| Cyrtacanthacridina                                       |
| Cyrtacanthacridina                                       |
| Cyrtacanthacridina                                       |
| **Coptacrae**                                            |
| Coptacrina                                               |
| Coptacrina                                               |
| Coptacrina                                               |
| Coptacrina                                               |
| **Podisinae**                                            |
| Podisinae                                                 |
| Podisinae                                                 |
| Podisinae                                                 |
| Podisinae                                                 |
| **Tropidopolini**                                        |
| Tropidopolinae                                           |
| Tropidopolinae                                           |
| Tropidopolinae                                           |
| **Tristrini**                                            |
| Tristrini                                                |
| **Hieroglyphini**                                        |
| **Tauliae**                                              |
| Tauliini                                                 |
| **Oxyrrhepini**                                          |
| Habrocneminae                                            |
| Habrocneminae                                            |
| Habrocneminae                                            |
| **Xenacanthippi**                                        |
| Melanoplinae                                             |
| Melanoplodinae                                           |
| **Tauchirae**                                            |
| Acridae                                                  |
| **Incolacri**                                            |
| Leptacrinae                                              |
| **Egnatiinae**                                           |
| Egnatiidae                                               |
| Egnatiinae                                               |
| Egnatiinae                                               |
| Egnatiinae                                               |

1. Additional subfamilies of Acrididae: Cpiocerinae, Eremogryllinae, Euryphyminae, Leptysminae, Marellinae, Oedipodinae, Ommatolampinae, Pauliniinae, Protolabinae, Rhytidochrotinae, Teratodinae
methods as implemented in PAUP (version not mentioned). The results of this particular study showed almost no resolution of relationships or useful clustering except for a few 'low-level groups'. The authors consequently did not even bother to present the cladograms and resolved to 'develop a classification by traditional non-quantitative methods'.

There has been an increased interest in recent years in the phylogenetic relationship of orthopteroid insects in general (Flook and Rowell 1997a, 1997b, 1998, 1999; Flook et al 2000, Rowell and Flook 1998, Yin et al. 2003) and the acridoids in particular (Amedegnato et al. 2003, Chapco et al 2001, Litzenberger and Chapco 2001, 2003, Ren et al. 2002, Xi and Zheng 1997, Xu et al. 2003, Xu and Zheng 1999, 2002; Zheng and Qiao 1998). Most of these recent studies are based on molecular data with relatively limited taxon sampling: the few morphology-based studies either targeted at lower level relationship (e.g., within genus, Xu et al. 2003, but see Song and Wenzel 2007) or are characterized by sporadic taxon sampling (Ren et. al 2002, Xu and Zheng 1999, 2002; Zheng and Qiao 1998). Therefore, the potential of morphology in resolving higher-level phylogeny within Orthoptera and Acridoidea has not been fully explored.

This lack of higher-level phylogenetic study of Catantopidae leads to a lack of stability in the classification within the family (Table 1), which is unusual for such a well-known and economically important group. In this paper, we present the first comprehensive phylogenetic analysis of the family Catantopidae based on morphology by sampling extensively from the Chinese fauna. Our purpose is to (1) conduct an exploratory phylogenetic analysis of the phylogenetic relationship within the family represented by the Chinese members, (2) provide an objective evaluation of the usefulness of morphological characters in phylogeny reconstruction of the acridoids in general and the catantopids in particular, and (3) provide a general framework for taxon sampling in future studies of acridoid phylogeny on a global basis.

**Materials and methods**

I. Monophyly

The name Catantopidae, or its original form Catantopinae as subfamily, has had a long history of divergent usages (Key and Colles 1993). The modern definition of Catantopidae took after the name of Cyrtacanthacrinae (Tinkham 1940, Roberts 1941) and was subsequently assigned subfamily status as Catantopinae by Mistshenko (1952). The latter author further assigned the members of the subfamily in the fauna of the former Soviet Union and adjacent countries into thirteen tribes, and considered Egnatiiinae as a separate group from the Catantopinae. Mistshenko (1952) was mostly accepted by later authors, including Dirsh (1961), Uvarov (1966), and Harz (1975). Dirsh (1975) later divided Mistshenko's Catantopinae into two families, Hemiacrididae and Catantopidae, and included Egnatiinae in the family Catantopidae. Yin (1982) also
divided Mistshenko’s Catantopinae into two families, Acrididae and Oedipodidae, but treated Egnatiidae as a separate family. Xia (1994) included in the family Catantopidae some of the subfamilies of Oedipodidae in Yin’s system and raised most of the tribes in Mistshenko’s system to subfamilies. The Xia System has been adopted for the recent monographic treatment of the Chinese fauna of Catantopidae (Li and Xia 2002). The classification scheme used by Otte (1981, 1984) in his monographic treatments of the grasshoppers of North America north of the Gulf of Panama, although unexplained, is obviously completely utilitarian without reference to phylogenetic relationship among groups. The Otte classification was later expanded and adopted by the author in his multi-volume catalog of the orthopteran insects of the world (Otte 1994a, 1994b, 1994c, 1995a, 1995b), which in turn has been eventually published as a searchable online database, the Orthoptera Species File (Eades et al 2011). While the Orthoptera Species File database is tremendously useful for taxonomic purposes, species groups defined by earlier classification systems were often used in phylogenetic studies on Acrididae / Acridoidea at levels of tribe and above (Litzenberger and Chapco 2003; Song and Wenzel 2007). A comparison of catantopid classification systems by various authors is given in Table 1.

Catantopidae in our view is readily defined by the unmistakable synapomorphy of having a distinct prosternal process between the forecoxae. Although some species of Pamphagidae and Pyrgomorphidae have a lamellate process on the pro sternum, the process in these species is on the anterior margin of the pro sternum and is obviously an independently evolved feature not homologous to the prosternal process between the forecoxae observed in Catantopidae. Nonetheless, as shown in Table 1, there was considerable disagreement among earlier authors about the definition of Catantopidae, which obviously arose from the fact that earlier acridologists defined higher-level taxa on basis of overall similarities, instead of on synapomorphies. Our interpretation of Catantopidae in the present paper, as defined by the presence of prosternal process between the forecoxae, is in accordance with Catantopinae of Roberts (1941) and Mistshenko (1952) and Catantopidae of Harz (1975) and is equivalent to the “Spine-breasted Acrididae” as keyed out in Otte (1981). Throughout the paper, we consistently use the name Catantopidae except when discussing its treatment by various previous authors. In the latter case, they were referred to as were originally treated by these authors, such as Catantopinae or Catantopini. The same rule is also consistently applied to other taxa, e.g. Egnatiidae.

II. Taxa Sampling and Sources of Specimens

About 327 species in 96 genera of Catantopidae (sensu Mistshenko 1952) are known from China, with representatives from both the Palearctic (21.44%) and the Oriental regions (79.56%) (adjusted according to Huang and Chen (1999)). The Chinese fauna of catantopids represents 15% of world genera of the family (data from Vickery and Kevan, 1983) and all of the tribes recognized by Mistshenko (1952) or subfamilies by
Dirsh (1975). In this study, we examined a total of 2,536 specimens representing 240 species in 94 genera, accounting for 73% and 98% of the total number of species and genera known from the country, respectively. Of the 94 examined genera, 84 genera were included in our phylogenetic analysis while the other eight were excluded (Appendix 1). The reasons for the exclusion are: 1) type specimens were not available for examination and no other specimen of these genera had been collected since the original publications, such as Tzacris Tinkham and Chapacris Tinkham; 2) only females were then discovered, such as Liaopodisma Zheng. In addition, we also left out several genera that were described after the data collection stage of this study, such as Caryandoides (Liu and Li 1995, Özdikmen 2009) and Tectiacris (Wei and Zheng 2005). The final inclusion of taxa represented all of the tribes recognized by Mistshenko (1952) and subfamilies by Dirsh (1975).

The majority of the study materials of the present project were provided by the following institutions (curators in parentheses):

Entomological Museum, Shaanxi Normal University, Xi’an, Shaanxi Province (Shengquan Xu)
Entomological Museum, Zhongshan University, Guangzhou, Guangdong (Geqiao Liang)
Entomological Museum, Research Institute of Entomology, Chinese Academy of Sciences, Shanghai (Kailing Xia)
Entomological Museum, Beijing Institute of Zoology, Chinese Academy of Sciences, Beijing (Chunmei Huang)
Zoological Museum, Northwest Plateau Institute of Biology, Chinese Academy of Sciences, Xining, Qinghai (Xiangchu Yin)

III. Selection of outgroups

Because of the lack of phylogenetic analysis of Acridoidea at levels above subfamily, we had to rely on previous systematic studies on Acridoidea for outgroup selection. All existing classifications of Acridoidea treated Catantopinae, Egnatiiinae, Acridinae, and Oedipodinae as being closer to each other than they are to Pyrmorphinae and Pamphaginae (Roberts 1941, Mistshenko 1952, Dirsh 1956, 1961, 1975; Yin 1982, Xia 1994). Dirsh (1961, 1975) suggested that Egnatiiinae was closer to Catantopinae than any other subfamily of his Catantopidae because Egnatiiinae possesses a Comstock-Kellogg gland, which is otherwise believed to occur only in Catantopinae. Furthermore, Egnatiiinae and Catantopinae share similar folds and sculpture in the internal surface of foregut, which are different from those of Oedipodinae. Stebaev et al. (1984) also agreed on a close relationship between Egnatiiinae and Catantopinae on basis of cytogenetical, taxonomical and ecological data, but considered the Egnatiiinae as a tribe within Catantopinae. Many contemporary acridologists are in agreement about a close relationship between Egnatiiinae and Catantopinae (e.g., David Hollis, pers. comm.). Because of the close relationship
between Egnatiidae and Catantopidae, very likely as sister clades, and the lack in Egnatiidae of the obvious catantopid synapomorphy of having a prosternal process between the forecoxae, the family Egnatiidae represented by the two genera *Egnatius* Stal and *Egnatioides* Voss, was used as outgroup for the phylogenetic analysis of Catantopidae relationships.

IV. Specimen study and character coding

Terms and abbreviations used in the present study followed B.-Bienko and Mistshenko (1952) for external morphology and Dirsh (1956, 1961, 1975) for genitalia structures.

Specimens for the study were selected in the following order of priority: 1) type specimens, 2) specimens determined by the author of the taxon, and 3) specimens determined by experts of the taxon. All characters were coded from direct observation of specimens, except in a few instances where characters of a species were coded based on illustrations and descriptions from monographs or reviews (Willemse 1956, 1957; B.-Bienko and Mistshenko 1951, Mistshenko 1952, Hollis 1975).

External morphology was surveyed before specimens were dissected for examination of genitalia characters. When available, multiple individuals were examined for each species and multiple species for each genus. For polymorphism at species level, we took an approach similar to, but much more restricted than, the “majority state rule” proposed by Wiens (1995). We generally avoided characters that are polymorphic at species level, and only in very few cases, coded species in question as the predominant state when the other state(s) was rare (presence rate < 15%). In a few cases when character polymorphism occurred at generic level, the characters in question were initially coded as missing for the genus, but were eventually abandoned and not included in the analysis. Some of the characters with three or more states were treated prior to the cladistic analysis as ordered or additive characters, *i.e.*, the transformation series was hypothesized to be 0-1-2 and so on. This was done only when it was possible to order the states unambiguously, e.g., for measurement ratios, and ordered characters are indicated in Appendix 1. In a few cases, one of the states of a main character was more finely subdivided into one or two subsidiary character(s). Taxa with other states of the main character were coded as having state unknown (character not applicable) in the subsidiary character. This commonly used method has been referred to as ‘state-unknown coding’ (Nordlander et al. 1996). The method may give incorrect lengths for some trees when there is homoplasy in the main character and different subsidiary states are ancestral for the different clades having the subdivided state of the main character (Maddison 1993). It has been suggested to use step matrices to represent main/subsidiary character systems exactly (Maddison and Maddison 1992), but this will slow down calculations considerably and is especially impractical for relatively large matrixes like ours. In the present study, therefore, we consistently used state-unknown coding for main/subsidiary character systems and weighted all main and subsidiary
characters equally. More detailed discussion about the application of the method is found in Nordlander et al. (1996).

The final matrix contained 87 terminals, including outgroup and 86 catantopid genera in the ingroup, and 88 characters, of which 79 were phylogeny-informative and the other nine were autapomorphies (Appendix 2-3). The autapomorphic characters were excluded from the final cladistic analyses and not counted when calculating tree length, CI, or RI. Nonetheless, they were kept in the matrix for their taxonomic values and potential use in future phylogenetic studies involving the included taxa.

V. Phylogenetic Analysis

PAUP version 4.0 beta10 (Swofford 2003) was used for phylogenetic analyses. The large number of taxa and characters included in this study did not allow the use of exact searching algorithms. Therefore, we used a combination of several ‘shortcut’ approaches. We first used PAUPRat (Sikes and Lewis 2001) to generate batch files for maximum parsimony analysis within PAUP using the Parsimony Ratchet method described by Nixon (1999). We performed 30 repetitions of the Parsimony Ratchet analysis, with 200 iterations per run as suggested by Sikes and Lewis (2001), giving a total of 6,000 iterations. The single shortest tree from each of the 6,000 iterations were then loaded into computer memory for comparison and only the shortest trees over all iterations were kept and duplicates of trees were removed. Because these overall shortest trees were each only the single best tree retained from a particular iteration, they each were probably one of the many possible equally most parsimonious trees or one of the less than most parsimonious trees that actually exist for the dataset. Therefore, these trees were further subjected to TBR branch swapping in order to find out all possible trees of equal or shorter length. To ensure that we find the best trees, we also analyzed our dataset in NONA 2.0 (Goloboff 1999a), a program said to be much faster than competitors like PAUP (Goloboff 1999b). For NONA analyses, we started with MULT*50 (randomize order of taxa, create a weighted Wagner tree, swap using TBR, and with 50 replications) and then swapped the shortest trees from MULT analysis using Max*, which is equal to PAUP’s TBR swapping. NONA was also used for calculation of Bremer Support values (decay index) for branches (Bremer 1994) while PAUP was used for diagnosis of apomorphic characters supporting each branch. TNT (Goloboff et al. 2011), a program that implemented the tree search methods of NONA as well as additional search methods, including sectorial search, tree drifting, and tree fusing (Goloboff 1999b), was also used for Parsimony Ratchet analysis of the dataset with options comparable to afore-described NONA analysis. The other so-called “New Technology” searching techniques were also used with default options of the software, but were not extensively explored because our dataset was not too large and thus further aggressive approximation was not considered necessary.
Results

I. Character Analysis

We examined a total of 116 characters, including 84 characters of external morphology and 32 characters of male genitalia morphology. Twenty-eight characters were excluded from our analysis either because they were too variable across examined species of a genus to reach a generic consensus or because they were continuous and discrete coding of character states was impossible. In addition, characters of body color patterns, although important for identification of some species of the family, were found to be too variable, both among individuals of species and among species of genera, to be of much use in resolving phylogenetic relationships within Catantopidae and were therefore excluded from the present study. The eighty-eight characters included in the final character matrix consist of 71 external morphological characters and 17 genitalia characters (Appendix 2). Character fit on the shortest trees, as expressed by the consistency index (CI) and retention index (RI), was lower for characters of male genitalia morphology in comparison to characters of external morphology (Table 2).

II. Phylogenetic Analyses

Using maximum parsimony analysis with Nixon's ratchet method, we found in thirteen of our 30 replications and 218 of the 6,000 iterations a tree with the shortest length of 688 steps (L=688, CI = 0.17, RI = 0.55). With duplicate trees deleted, the final number of the shortest trees was 204; subsequent swapping of these optimal trees using TBR did not find shorter trees, but found a total of 22,354 equally most parsimonious trees. Figs. 1–2 and Fig. 3 show the strict consensus tree with Bremer Support for completely resolved branches and the 50% majority consensus tree with percentage of branches appearing in all shortest trees summarized, respectively.

Searching with NONA 2.0 (Hold=10,000–30,000, Mult*50, and Max*) did not find trees shorter than those found with PAUP 4.0 using parsimony ratchet method. Although we were always able to find trees of the shortest length in a few minutes with NONA, our searches invariably resulted in only about 50 trees with MAX*, even when we increased the number of trees to be held in memory to 30,000. Further swapping using SSWAP*2 and MSWAP*2 apparently would take a long time (3.2GHZ CPU frequency and 1G RAM) and were terminated after a few hours. Comparison of the NONA trees with PAUP trees showed that they were a (small) subset of the trees we found using ratchet method in PAUP. Searching with TNT, either ratchet method or other new technology methods, did not resulted in shorter trees.
**Table 2.** Fit on shortest trees of different categories of characters, as expressed by the consistency index (CI) and retention index (RI) (n = number of characters; autapomorphis excluded).

| Character Category      | n  | CI  | RI  |
|-------------------------|----|-----|-----|
| External Morphology     | 63 | 0.19| 0.58|
| Body shape              | 1  | 0.25| 0.63|
| Head                    | 10 | 0.17| 0.54|
| Mesosoma                | 29 | 0.20| 0.66|
| Metasoma                | 23 | 0.20| 0.45|
| Male Genitalia          | 16 | 0.12| 0.49|

**Figure 1.** Strict consensus tree of the 22,355 found shortest trees using Parsimony Ratchet method in PAUP 4.0 beta10 (30 repetitions and 200 iterations per run, followed by TBR swapping). Above each resolved branch is the Bremer Support value (/decay index) for the branch estimated using NONA2.0. Only the completely resolved basal part is shown.
Figure 2. Strict consensus tree of the 22,355 found shortest trees using Parsimony Ratchet method in PAUP 4.0 beta10 (30 repetitions and 200 iterations per run, followed by TBR swapping). Shown in the figure is the expansion of Clade A of Figure 1. Several completely resolved clades are further expanded as A1, A2, A3, A4 and A5 respectively.
III. Phylogenetic Relationship

Although the number of shortest trees found by our cladistic analyses is huge, the phylogenetic relationship among genera at the base of the cladogram was well resolved, and all basal clades were also relatively well supported with Bremer Support values ranging mostly from 3 to 8 (Fig. 1). The majority of genera, 71 out of 88, fell into the monophyletic Clade A (Fig. 1), which is a polytomy consisting of several relatively well-supported monophyletic clades (Fig. 2: A, A1–5; clade A3 is only supported by a Bremer Support value of 1) as well as a number of unresolved genera / pairs of genera (Fig. 2: A). When a 50% majority consensus tree was calculated, better resolution within Clade A is achieved (Fig. 3, A, B2–B6). In comparison to the strict consensus tree, a sister relationship between A1 and the rest of the clade is supported by 99% of all shortest trees (Fig. 3: A), and A5 (Fig. 2: A5) is supported as the sister clade of the clade consisting of the rest of the genera with improved within-clade resolution (Fig. 3: B5), and (Fruhstorferiola + Tonkinacris) becomes the sister clade to the clade including all members of Clade A except clade A1 and B5 (Fig. 3:A). This terminal clade, while supported by 59% of all shortest trees, form a polytomy consisting of several monophyletic, relatively well resolved clades, 12 distinct genera, and three genera pairs. In addition, there is also an increased resolution at the base of Clade A -- B2 consists of A2 and (Dericorys + Spathosternum) (Fig. 3: B2), B3 includes A3 and Bannacris, and an additional clade is resolved (Fig. 3: B6).

IV. Discussion

Male genital morphology received special attention from Dirsh (1956, 1961, and 1975) when the author established his classification of acridoids. In fact, the various versions of Dirsh classification depended heavily on the male genitalia morphology, and the practice has greatly influenced later systematists of grasshoppers and other orthopteran insects (Hollis 1975, Yin 1982, Ronderos and Cigliano 1991, Xia 1994, Zheng and Xia 1998). Our result showed that character fit on the shortest trees, as expressed by the consistency index (CI) and retention index (RI), was actually lower for characters of male genitalia morphology in comparison to external morphology characters (Table 2), suggesting that genital characters are not as phylogeny informative as previously thought, at least at higher level, and earlier classification systems of grasshoppers in general and Catantopidae in particular probably include many groups that are not natural due to the heavy reliance on genital features. Eberhard (1985) argued that the species-specific diagnostibility of male genitalia is a reflection of both the rate and extent to which they diverge, and any structure so useful taxonomically must have evolved rapidly. In fact, a recent study showed that morphologically very similar species of Melanoplus grasshoppers differ in the shape of the male genitalia and this is probably due to extremely rapid speciation caused by glacial cycles during the Pleistocene glaciations (Knowles and Otte 2000). The rapid evolution of male genitalia morphology is considered to be caused by strong sexual selection on the male imposed by the females (Eberhard 19985, Knowles
Figure 3. Majority (50% and above) consensus tree of the 22,355 found shortest trees using Parsimony Ratchet method in PAUP 4.0 beta10. The basal part of the majority consensus tree is completely resolved and is the same as in Figure 1, and the figure shows only the phylogenetic relationship within Clade A as resolved by MJ consensus tree. The clades better resolved in comparison with strict consensus tree are further expanded as B2, B3, and B5. B5 is the same as A5 of Figure 2, but with better internal resolution. B2 is A2 plus (Dericorys, Spathosternum) at the base, and B3 is A3 plus Bannacris added at base and has higher internal resolution. B6 consists of several pairs of genera unresolved in the strict consensus tree. A1 and A4 are each completely resolved and remain the same as in Figure 1, and are thus not expanded here in. More differences between strict and MJ consensus trees are found in the basal part of Clade A (cf. Figure 2: A). Number above each branch is frequency of occurrence of a particular branch among all 22,354 found shortest trees, and branches not indicated with a number have 100% occurrence.
Regardless of the mechanism, male genital features, while very useful in species identification, show high degree of homoplasy and are therefore of limited value in phylogenetic studies, especially at higher levels. Consequently earlier classifications of acridoids as well as Catantopidae need to be revised critically in the light of phylogenetic analyses based on a broad range of characters.

An earlier attempt to study the phylogenetic relation within Catantopidae from Australia found almost no resolution, especially at the base (Key and Colless 1993), which is strikingly different from the results of our study where the phylogenetic relationship was reasonably resolved, especially at the base. Key and Colless (1993) was able to assemble an impressive dataset consisted of 166 terminals and 104 characters, but unfortunately provided otherwise very limited information about their dataset, which prevents us from interpreting exactly why there is such a big difference between their results and ours. Several factors might have contributed to this. For example, their study is based on males only. While male characteristics are frequently the only useful features for species identification, especially for closely related species, males of different grasshopper species may have been subjected to sexual selection and developed convergent similarities similar to what we have discussed earlier about male genital characteristics. In addition, the authors only used Neighbor-joining and Wagner parsimony without further branch swapping in their analyses, and it is thus very unlikely that what the authors found were the shortest trees. It would be of interest to request from the authors their dataset and reanalyze it using the currently available computation power that is far more superior than it was almost two decades ago. Computation power is especially relevant for analyzing dataset of their size.

Rowell and Flook (1998) presented a phylogenetic tree for the Acridoidea based on the mitochondrial DNA sequences 12S and 16S. They found support for several catantopid clades, i.e., Oxyinae, Podisminae+Melanoplinae, and Coptacridinae. In addition, their study also supported as monophyletic the clade consisting of Cyrtacanthacridinae, Calliptaminae, Catantopinae s. str., and Eyprepocnemidinae. These clades are mostly supported by the present study except the monophyly of (Cyrtacanthacridinae + Calliptaminae + Catantopinae s.s. + Eyprepocnemidinae). While a sister relationship between Cyrtacanthacridinae and Calliptaminae is supported by the present study, Catantopinae is supported as a monophyletic basal clade in the family cladogram and Eyprepocnemis as a member of Calliptaminae (Fig. 4).

Rowell and Flook (1998) also suggested that the Acridoidea ‘seems to be the product of a single explosive radiation’ because they were unable to find a resolution at the subfamily level for the basal acridoids. However, this conclusion, according to the authors, is based on a ‘preliminary analysis’, for which the method was not described, and therefore has to be treated with caution. Meanwhile, the result of the study may be biased simply because of the used genes being inadequate with regard to the divergence level and evolution rate of the study group. According to Simon et al. (1994), the mitochondrial rRNA genes of 12S and 16S are considered to be mostly useful at the population level where highly variable sites have not yet experienced multiple substitutions and at deep levels of divergence where the more conserved sites of these genes supply useful phylogenetic
Figure 4. A possible scheme classification of Catantopidae from China based on parsimony phylogenetic analysis of 86 genera and 79 phylogeny–informative morphological characters. Details of Coptacridae and Oxynae are found in Figure 2 (Clade A1 Coptacridae and A5 Oxynae) and Figure 3 (B5 Oxynae). Podisminae is further divided into six tribes, of which five are supported as monophyletic by the 50% majority consensus tree of all shortest trees found while the other ‘tribe’ Melanoplini is suggested as a ‘sink’ to temporarily keep the genera that do not belong to any of the supported clades. The Fruhstorferiolini is the most basal tribe consisting of Fruhstorferiola and Tonkinacris, while details of Melanoplini are found in Figure 2 (A4: Promeosternini) and Figure 3 (B2 Dericorythini, B3 Traulini, B6 Podismini).
information. At intermediate levels of divergence, however, the relatively variable sites probably have experienced multiple substitutions that may obscure phylogenetic signals. In addition, the rates and patterns of evolution of mitochondrial rRNA genes can vary greatly among taxa (Simon et al. 1994, and references therein). The particular analysis of Rowell and Flook (1998) of Acridoidea based on these two genes might just deal with this ‘intermediate level of divergence’ for the Orthoptera. It would be interesting to reanalyze their dataset to resolve the phylogenetic relationship at various levels with in the superfamily, e.g., to include all their major lineages, but include only a few of their sampled species for each of these lineages, or alternatively, analyze each of these major lineages with all their sampled species included. Unfortunately, the article provided neither the sequences nor genbank accession numbers for the sequences.

To our knowledge, the present study is the most comprehensive of its kind to study the higher level phylogeny of orthopteran insects in terms of the number of taxa sampled and characters examined and coded. Through this study we were able to demonstrate that the external morphology of orthopteran insects can be a very useful source for assessing higher-level phylogeny. For example, the study provided complete resolution for the basal relationships of the Catantopidae (Fig. 1). Nonetheless, our dataset were unable to provide an unambiguous solution for the relationships within the largest terminal clade that comprise 80% of all sampled genera in this study (Figs. 2, 3). It is generally accepted that phylogenetic hypotheses basing on as many independent lines of evidence as possible have the highest explanation value (Nixon and Carpenter 1996a). Combining morphological and molecular data should be the direction for future phylogenetic studies of orthopteran insects including Catantopidae. In addition, our study sampled only taxa from China, which was necessary due to the lack of resources, and future phylogenetic studies of Catantopidae should include representative taxa from other areas of the world.

V. Classification of Chinese Catantopidae

Based on the strict consensus tree and the 50% Majority-rule consensus of the 22,355 shortest trees, we hereby outline a scheme for the classification for the family Catantopidae from China. As we discussed above, a comprehensive phylogenetic study based on a more inclusive taxon sampling from all regions of the world and including both morphology and molecular sequences is needed for highly resolving the phylogenetic relationship within the family, especially with regard to the relationship between and within the subfamilies Coptacridinae, Oxyinae, and especially Podisminae (see below). Therefore, the purpose of our outline is to serve as a basis for further studies, rather than as formal classification.

According to this scheme, the Chinese Catantopidae can be classified into seven subfamilies: Habrocneminae, Catantopinae, Cyrtacanthacrinae, Calliptaminae, Coptacridinae, Oxyinae, and Podisminae (Fig. 4). Among the seven recognized subfamilies, Habrocneminae, Catantopinae, Cyrtacanthacrinae, and Calliptaminae are unambiguously supported as monophyletic clades, and the relationship of each to the rest
of the family are completely resolved (Fig. 1, Fig. 4). Coptacridinae and Oxyinae, although each relatively well supported as monophyletic clade, are part of a crown clade that is highly unresolved in terms of within clade relationship (Clade A, Fig. 2). The monophyly of Podisminae, and the resolution of its relationship with Coptacridinae and Oxyinae are only supported by the 50% Majority-rule consensus, which is considered as a compromised solution in phylogenetic systematics (Nixon and Carpenter 1996b). Our analyses also identified within the subfamily Podisminae five monophyletic clades (Fig. 4), which may be treated as tribes: Fruhstorferiolini, Promesthessternini, Dericorythini, Traulini, and Podismini. Finally, the rest of the genera within Podisminae are temporarily lumped together in the tribe ‘Melanoplini’ for convenience until further phylogenetic information becomes available.

Acknowledgements

We wish to thank Geqiao Liang, Chunmei Huang, Kailing Xia, and Xiangchu Yin for their generous support in arranging the specimen loans for the project. We also wish to thank David Hollis, Xinbao Jing, Zhibing Liu, Tieqiao Zhao for discussions and/or comments on earlier versions of the manuscript. Jim Carpenter, Gordon Tucker, and several anonymous reviewers have kindly provided valuable comments / criticisms on the final drafts of the manuscript. BL wishes to thank Shengquan Xu, XiaoHong Ou, Zhenghui Xu, Jun Chen, Wei Zhang, Fuming Shi, and other former colleagues at the Institute of Zoology, Shaanxi Normal University for their generous help and friendship. Part of the work was completed when ZL was a research associate under Richard Brusca of Arizona-Sonora Desert Museum and Terry Markow of the Center for Insect Science, University of Arizona. The work was funded in part by a National Science Foundation of China Grant to BL (#30370237), NIH Training Grant (#1 K12 Gm00708) in the form of fellowship to ZL through the Center for Insect Science, University of Arizona, and a Summer Research and Creative Activity Award to ZL from the EIU Council on Faculty Research.

References

Amedegnato C, Chapco W, Litzenberger G (2003) Out of South America? Additional evidence for a southern origin of Melanoplinae grasshoppers. Molecular Phylogenetics and Evolution 29, 115–119. doi: 10.1016/S1055-7903(03)00074-5

B.–Bienko GR, Mistshenko LL (1951) Acridoidea of the fauna of USSR and neighboring countries. [In Russian] Moscow, Akad. Nauk. CCCR. Part 1, 378 pp. doi: 10.1111/j.1096-0031.1994.tb00179.x

Bremer K (1994) Branch support and tree stability. Cladistics 10: 295–304.

Bryantseva IB (1953) Peculiarities in the structure of the foregut of Acridids of the subfamily Egnatiinae (Orthoptera, Acrididae). Rev. Entomol. USSR 33.
Chapco W, Litzenberger G, Kuperus WR (2001) A molecular biogeographic analysis of the relationship between North American Melanopline grasshoppers and their Eurasian and South American relatives. Molecular Phylogenetics and Evolution 18: 460–466. doi: 10.1006/mpev.2000.0902

Dirsh VM (1956) The phalic complex in Acridoidea (Orthopetra) in relationship to taxonomy. Transactions of the Royal Entomological Society of London 108: 223–356. doi: 10.1111/j.1365-2311.1956.tb02270.x

Dirsh VM (1961) A preliminary review of the family and subfamilies of Acridoidea (Orthoptera, Insecta). Bulletin of British Museum of Natural History (Entomology) 109

Dirsh VM (1975) Classification of the Acridomorphoid insects. E.W. Classey LTD, Oxford. 170pp.

Eades DC, Otte D, Cigliano MM, and Braun H (2011) Orthoptera Species File Online. Version 2.0/4.0. [retrieved on June 14, 2011]. <http://Orthoptera.SpeciesFile.org>.

Eberhard WG (1985) Sexual selection and animal genitalia. Harvard Univ. Press, Cambridge, MA.

Flook PK, Rowell CHF (1997) The Phylogeny of the Caelifera (Insecta,Orthoptera) as Deduced from mrTRNA Gene Sequences. Molecular Phylogenetics and Evolution 8: 89–103. doi: 10.1006/mpev.1997.0412

Flook PK, Rowell CHF (1997) The Effectiveness of Mitochondrial rRNA Gene Sequences for the Reconstruction of the Phylogeny of an Insect Order (Orthoptera). Molecular Phylogenetics and Evolution 8, 177–192. doi: 10.1006/mpev.1997.0425

Flook PK, Rowell CHF (1998) Inferences about Orthopteroid phylogeny and molecular evolution from small subunit nuclear ribosomal DNA sequences. Insect Molecular Biology 7: 163–178. doi: 10.1046/j.1365-2583.1998.72060.x

Flook PK, Klee S, Rowell CHF (1999) Combined Molecular phylogenetic Analysis of the Orthoptera (Orthopteroid, Insecta) and Implications for their higher Systematics. Systematic Biology 48, 233–253. doi: 10.1080/106351599260274

Flook PK, Klee S, Rowell CHF (2000) Molecular Phylogenetic Analysis of the Pneumoroidea (Orthoptera, Caelifera): Molecular Data Resolve Morphological Character Conflicts in the Basal Acridomorpha. Molecular Phylogenetics and Evolution 15: 345–354. doi: 10.1006/mpev.1999.0759

Goloboff P (1999a) NONA (NO NAME) ver. 2, published by the author, Tucumán, Argentina. (free download from www.zmuc.dk/public/phylogeny/Nona–PeeWee/)

Goloboff P (1999b) Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15: 415–428. doi: 10.1111/j.1096-0031.1999.tb00278.x

Goloboff P, Farris F, Nixon KC (2011) TNT (Tree analysis using New Technology) ver. 1.1. Published by the authors, Tucumán, Argentina. (free download from http://www.zmuc.dk/public/phylogeny/TNT/)

Harz K (1975) Die Orthopteren Europas (Unterordnung Caelifera). The Orthoptera of Europe. – Vol. 2. Dr. W. Junk N.V., The Hague. 939pp. doi: 10.1007/978-94-010-1947-7

Hills DS (1987) Agricultural insect pests of temperate regions and their control. Cambridge University Press, London.

Hollis D (1975) A review of the dubfamily Oxyinae (Orthoptera, Acridoidea). Bulletin of British Museum of Natural History (Entomology) 31:191–234.
Huang C, Chen X (1999) The fauna of Catantopidae and its origin in China and adjacent region. Acta Entomologica Sinica 42, 184–198.

Jago ND (1971) A review of the Gomphocerinae of the world with a key to the genera (Orthoptera: Acrididae). Proceedings of the Academy of Natural Sciences of Philadelphia 123: 205–243.

Key KHL, Colless DH (1993) A higher classification of the Australian Acridoidea (Orthoptera). II. Subfamily Catantopinae. Invertebrate Taxonomy 7, 89–111. doi: 10.1071/IT9930089

Knowles LL, Otte D (2000) Phylogenetic analysis of montane grasshoppers from western North America (genus Melanoplus, Acrididae: Melanoplinae). Annals of the Entomological Society of America 93: 421–431. doi: 10.1603/0013-8746(2000)093[0421:PAOMGF]2.0.CO;2

Li H, Xia KL (Ed.) (2002) Fauna Sinica Insecta Vol.43 Orthoptera: Acridoidea: Catantopidae. Science Press, Beijing, China.

Litzenberger G, Chapco W (2001) Molecular phylogeny of selected Eurasian podismine grasshoppers (Orthoptera: Acrididae). Annals of the Entomological Society of America 94: 505–511. doi: 10.1603/0013-8746(2001)094[0505:MPOSEP]2.0.CO;2

Litzenberger G, Chapco G (2003) The North American Melanoplinae (Orthoptera: Acrididae): A molecular phylogenetic study of their origins and taxonomic relationships. Annals of Entomological Society of America 96: 491–497. doi: 10.1603/0013-8746(2003)096[0491:TNAMOA]2.0.CO;2

Liu J (1991) A preliminary study on morphology of eggs of grasshoppers and its application in phylogenetic classification of grasshoppers from China. Proceedings of Systematic Zoology, Beijing, China Science and Technology Press, 89–94.

Liu Z, Li B (1995) A new genus and two new species of Catantopidae from Hunan Province, China (Orthoptera: Acridoidea). Entomologia Sinica 2: 104–109.

Ma EB, Bai GR, Guo YP, Ren ZM (2001) A study on taxonomic value of follicles in Catantopidae (Orthoptera: Acridoidea). Acta Zoologica Sinica 47: 30–36.

Maddison WP (1993) Missing data versus missing characters in phylogenetic analysis. Systematic Biology 42, 576–581. doi: 10.1093/sysbio/42.4.576

Maddison DR, Maddison WP (1992) Manual for MacClade: Analysis of phylogeny and character evolution, Version 3. Sinauer Associates, Sunderland, Massachusetts.

Maddison DR, Maddison WP (2001) MacClade 4: Analysis of phylogeny and character evolution. Version 4.0.2. Sinauer Associates, Sunderland, Massachusetts.

Mistshenko LL (1952) Catantopinae. Fauna USSR, Leningrad, 611 pp. [In Russian]

Nixon KC (1999) The Parsimony Ratchet, a New Method for Rapid Parsimony Analysis. Cladistics 15: 4 407.

Nixon KC, Carpenter JM (1996a) On simultaneous analysis. Cladistics 12: 221–242. doi: 10.1111/j.1096-0031.1996.tb00010.x

Nixon KC, Carpenter JM (1996b) On consensus, collapsibility and clade concordance. Cladistics 12: 305–321. doi: 10.1111/j.1096-0031.1996.tb00017.x

Nordlander G, Liu Z, Ronquist F (1996) Phylogeny and Biogeography of the family Ibaliidae (Hymenoptera: Cynipoidea). Systematic Entomology 21: 151–166. doi: 10.1046/j.1365-3113.1996.d01-4.x

Otte D (1981) The North American Grasshoppers. Vol.I (Acrididae, Gomphocerinae, Acridinae). Harvard University Press, 273pp.
Otte D (1984) The North American Grasshoppers. Vol. 2. Oedipodinae. Harvard University Press, 366 pp.
Otte D (1994a) Orthoptera Species File. 1. Crickets (Grylloidea) [of the World]. Academy of Natural Sciences, 120 pp.
Otte D (1994b) Orthoptera Species File. 2. Grasshoppers (Acridomorpha) A. Eumastacoidea, Trigonopterygoidea, Pneumoroidea. Academy of Natural Sciences, 162 pp.
Otte D (1994c) Orthoptera Species File. 3. Grasshoppers (Acridomorpha) B. Pamphagoidea. Academy of Natural Sciences, 241 pp.
Otte D (1995a) Orthoptera Species File. 4. Grasshoppers (Acridomorpha) C. Acridoidea (part). Academy of Natural Sciences, 518 pp.
Otte D (1995b) Orthoptera Species File. 5. Grasshoppers (Acridomorpha) D. Acridoidea (part). Academy of Natural Sciences, 630 pp.
Özdikmen H (2009) Substitute names for two preoccupied genera (Orthoptera: Acrididae and Tettigoniidae). Munis Entomology & Zoology 4 (2): 606-607
Ren ZM, Ma EB and Guo YP (2002) The Studies of the Phylogeny of Acridoidea Based on mtDNA Sequences. Acta Genetica Sinica 29: 314–321.
Rehn RAG, Grant H (1960) A Monograph of the Orthoptera of North America. Monographs of Acad. Nat. Sci. Philad. 12: 1–225
Roberts HR (1941) A comparative study of the subfamilies of the Acrididae (Orthoptera) primarily on the base of their phallic structures. Proceedings of the Academy of Natural Sciences of Philadelphia 93: 201–246.
Ronderos R, Cigliano MM (1991) The Andean Dichroplini: Cladistic analysis with description of Keyacris n. gen. And Ponderacris n. gen. (Orthoptera: Acrididae: Melanoplinae). Transactions of the American Entomological Society 117: 167–191.
Rowell CHF, Flook PK (1998) Phylogeny of the Caelifera and the Orthoptera as derived from ribosomal gene sequences. Journal of Orthoptera Research 7: 139–146.
Sikes DS, Lewis PO (2001) PAUPRat: PAUP* implementation of the parsimony ratchet, beta software, version 1. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, USA.
Simon C, Frati F, Beckenbach A, Crespi B, Liu H, and Flook PK (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the Entomological Society of America 87: 651–701.
Song H, Wenzel JW (2007) Phylogeny of bird–grasshopper subfamily Cyrtacanthacridinae (Orthoptera: Acrididae) and the evolution of locust phase polyphenism. Cladistics 23: 1–28.
Song H, Buchelibr SR (2010) Comparison of phylogenetic signal between male genitalia and non–genital characters in insect systematics. Cladistics 26: 23–35. doi: 10.1111/j.1096-0031.2009.00273.x
Stebaev IV, Bugrov AG and Vysotzkava LV (1984) An analysis of phylogenetic relations in the Eumastacoidea and Acridoidea (Orthoptera, caelifera) of the fauna of the USSR on the basis of cytogenetical, taxonomical and ecological data. Zh. Obshch. Biol. 45: 456–471 [In Russian].
Swofford DL (2003) PAUP* Beta10. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
Tinkham ER (1940) Taxonomic and Biological Studies on the Cyrtacanthacrinae of South China. Lingnan Science Journal 19: 269–364 (plus 4 plates)

Uvarov BP (1966) Grasshoppers and Locusts. Cambridge University Press. Vol. 1:1–475.

Vickery VR, Kevan DKM (1983) A monograph of the orthopteroid insects of Canada and adjacent regions. Memorials Lyman entomological museum and research laboratory 13: 681–707.

Watrous LE, Wheeler QD (1981) The outgroup comparison method of character analysis. Systematic Zoology 30: 1–11. doi: 10.2307/2992297

Wei SZ, Zheng ZM (2005) New genus and new species of grasshoppers from Yunnan and Guangxi (Orthoptera, Acridoidea). Acta Zootaxonomica Sinica. 30(2): 368–373.

Wiens JJ (1995) Polymorphic characters in phylogenetic systematics. Systematic Biology 44: 482–450.

Willemse C (1956) Synopsis of the Acridoidea of the Indo–Malayan and adjacent regions (Insecta, Orthoptera). Part II, fam. Acrididae, subfam. Catantopinae. part 1. Publ. Natuurh. Genoot. Limburg 8: 1–225

Willemse C (1957) Synopsis of the Acridoidea of the Indo–Malayan and adjacent regions (Insecta, Orthoptera). Part II, fam. Acrididae, subfam. Catantopinae. Part 2. Publ. Natuurh. Genoot. Limburg 10: 227–500.

Xi GS, Zheng ZM (1997) A comparison of Acridoidea sperm and its important signification in taxonomy. Entomotaxonomia 19: 1–9.

Xia KL (ed.) 1994. Fauna Sinica, Insecta Vol.4 Orthoptera. Science Press, Beijing, China. 340 pp.

Xu S, Zheng ZM (1999) The study of the phylogenetic relationship of Acridoidea (Orthoptera) based on the female subgenital plate. Entomotaxonomia 21: 79–83.

Xu SQ, Zheng ZM (2002) Morphology of female subgenital plates and evolution of some Chinese genera of Acrididae (Orthoptera: Acridoidea). Acta Entomologica Sinica 2002 45: 700–703.

Xu SQ, Li HH, Zheng ZM (2003) Cladistic study on Chrotogonidae and Pyrgomorphidae from China. Acta Zootaxonomica Sinica 28: 381–384.

Yacobson GG and Bianka VA (1905) Locusts and Grasshoppers. In Orthoptera and Pseudoneuroptera of Russian Empire. St. Petersburg. 72–79, 162–320 [In Russian].

Yin H, Zhang D, Bi Z, Yin Z, Liu Y, Yin X (2003) Molecular phylogeny of some species of the Acridoidea based on 16SrDNA. Acta Genetica Sinica 30: 766–772

Yin X (1982) On the taxonomic system of Acridoidea from China. Acta Biologica Plateau Sinica 1: 69–99.

Yin X (1984) Grasshoppers and Locusts from Qinghai–Xizang Plateau of China. Scientific Press, Beijing, China.

Yin X, Liu Z (1987) A new subfamily of Catantopidae with a new genus and new species from China (Orthoptera: Acridoidea). Acta Zootaxonomica Sinica 12: 66–72.

Zheng ZM (1993) Classification of Grasshoppers and Locusts from China. Xi’an, Shaannxi. Shaanxin Normal University Press.

Zheng ZM, Qiao GX (1998) Cladistic Analysis of the Phylogenetic Relationships among the Families of Acridoidea (Orthoptera: Acrodomorpha). Acta Zootaxonomica Sinica 23: 276–280.

Zheng ZM, Xia KL (Eds) (1998) Fauna Sinica. Insecta, Vol. 10. (Orthoptera: Acridoidea: Oedipodidae and Arcypteridae). Science Press, Beijing, China.
### Appendix 1.

**List of sampled taxa** († outgroups. *indicates genus not included in the final analysis. All ingroup genera are listed alphabetically).

| Genus                  | Species                  | Examined specimens |
|------------------------|--------------------------|--------------------|
| *Egnatius* Voss.†      | *apicalis* Stål          | 10 5               |
| *Egnatioides* Liu†     | *xinjiangensis* Liu      | 6 4                |
| *Arcyptera* Serv. †*  | *coreona* Shiraki        | 4 4                |
|                       | *fusca fusca* (Pall.)    | 4 4                |
| *Epacromius* Uv. †*   | *tergestinus* (Charp.)   |                    |
| *Alulacris* Zheng      | *shilingensis* (Cheng)   | 11 8               |
| *Anapodisma* Dov.-Zap.| *miramae* Dov.-Zap.      | 10 8               |
|                       | *rufipenna* Zheng        | 2                  |
| *Anepipodisma* Huang   | *punctata* Huang         | 1 1                |
| *Apalacris* Walker     | *hyaline* Walker         | 6 5                |
|                       | *nigrogeniculata* Bi     | 5 5                |
|                       | *tonkinensis* Ramme      |                    |
|                       | *varicornis* Walker      | 5 5                |
|                       | *viridis* Huang et Xia   | 1                  |
|                       | *xizangensis* Bi         | 14 11              |
| *Armatacris* Yin       | *xishanensis* Yin        | 1 5                |
| *Assamacris* Uv.       | *curticerca* (Huang)     | 1                  |
|                       | *longicerca* (Huang)     | 6 12               |
| *Bannacris* Zheng      | *punctonotus* Zheng      | 2 2                |
| *Calliptamus* Serv.    | *abbreviatus* Ikonn.     | 15 10              |
|                       | *barbarus* (Costa.)      | 15 10              |
| Genus            | Species                  | Examined specimens |
|------------------|--------------------------|--------------------|
|                  |                          | ♂                  | ♀                  |
| **coelesyriensis** (G.-T.) |                          | 7                  | 2                  |
| **italicus** (L.)       |                          | 15                 | 10                 |
| **turranicus** Tarb.    |                          | 7                  | 15                 |
| **Carsula** Stal        |                          |                    |                    |
|                  | **brachycerca** Huang et Xia |                    | 1                  |
|                  | **brachyptera** Huang et Xia |                    | 2                  |
|                  | **yunnana** Zheng       |                    | 1                  |
| **Caryanda** Stal       |                          |                    |                    |
|                  | **bambusa** Liu et Yin  | 3                  | 3                  |
|                  | **bidentata** Zheng et Liang |                    | 1                  |
|                  | **elegans** Bol.         | 15                 | 15                 |
|                  | **glauca** You           | 6                  | 5                  |
|                  | **gracilis** Liu et Yin | 2                  | 10                 |
|                  | **hunana** Liu et Yin   | 2                  | 3                  |
|                  | **methiola** Chang      |                    | 1                  |
|                  | **nigrovittata** Lian et Zheng |          | 4                  |
|                  | **omeiensis** Cheng     |                    | 1                  |
|                  | **pieli** Chang         | 4                  | 5                  |
|                  | **quadrata** Bi et Jin | 1                  | 1                  |
|                  | **vittata** Li et Jin   | 4                  | 5                  |
| **Catantops** Schaum   |                          |                    |                    |
|                  | **pinguis** (Stal)       | 10                 | 7                  |
|                  | **simlae** Dirsh        | 2                  | 2                  |
| **Chondracris** Uv.    |                          |                    |                    |
|                  | **rosea brunneri** Uv.  | 6                  | 8                  |
|                  | **rosea** (De Geer)     | 10                 | 10                 |
| **Choroedocus** I. Bol.|                          |                    |                    |
|                  | **capensis** (Thunb.)   | 11                 | 10                 |
|                  | **robusta** (Serv.)     | 13                 | 10                 |
|                  | **violaceipes** Miller  | 15                 | 10                 |
| **Conophyma** Zub.     |                          |                    |                    |
|                  | **almasyi almasyi** Kuthy |                    | 10                 |
|                  | **zhaosuensis** Uv.     | 2                  | 1                  |
| **Conophymacris** Will.|                          |                    |                    |
|                  | **chinensis** Chang     | 10                 | 10                 |
|                  | **szechwanensis** Chang | 10                 | 10                 |
|                  | **viridis** Zheng       | 10                 | 10                 |
|                  | **yunnanensis** Zheng  | 2                  | 2                  |
| Genus                     | Species            | Examined specimens |
|--------------------------|--------------------|--------------------|
| *Conophymopsis* Huang    | labrispinus Huang  | 10                 |
|                          | linguspinus Huang  | 6                  |
| *Coptacra* Stal          | hainanensis Tink.  | 1                  |
|                          | tonkinensis Will.  | 2                  |
| *Cuvipennis* Huang       | wixiensis Huang    | 10                 |
| *Cyrtacanthacris* Walk   | tatarica L.        | 10                 |
| *Dericorys* Serv.        | annulata roseipennis (Redt.) | 1 |
|                          | tibialis (Pall.)   |                    |
| *Dimeacris* Niu et Zheng| prasina Niu et Zheng | 2     |
| *Ecphanthacris* Tink.    | mirabilis Tink.    | 4                  |
| *Ecphymacris* Bi         | lofaoshana (Tink.) | 2                  |
| *Eirenephilus* Ikonn.    | longipennis (Shir.)| 10                 |
| *Epistaurus* I. Bol.     | aberrans r.-W.     | 10                 |
|                          | meridionalis Bi    | 15                 |
| *Eucoptacra* I. Bol.     | binghami Uv.       | 4                  |
|                          | kwangtungensis Tink.| 10            |
|                          | motuoensis Yin     | 5                  |
|                          | praemorsa Stal     | 5                  |
| *Eyprepocnemis* Fieb.    | hoktuensis Shiraki | 2                  |
|                          | perbrevipennis Bi et Xia | 2 |
| *Fer* I. Bol.            | bimaculatus You et Li | 4        |
|                          | nonmaculatus Zheng | 1                  |
|                          | yunnensis Huang et Xia | 2      |
| Genus             | Species                  | Examined specimens |
|------------------|--------------------------|--------------------|
|                  |                          | ♂   | ♀   |
| Fruhstorferiola Will. | huangshanensis Bi et Xia | 6   | 11  |
|                  | huayinensis Bi et Xia    | 3   | 3   |
|                  | kulinga (Chang)          | 10  | 10  |
|                  | omei (Rehn et Rehn)      | 1   | 5   |
|                  | tonkinensis Will.        | 10  | 10  |
|                  | viridifemorata (Caud.)   | 12  | 8   |
| Genimen I.-Bol.  | burmanum Ramme          |     | 1   |
|                  | yunnanensis Zheng        | 7   | 4   |
| Gerenia Stal     | intermedia Br.-W.        | 1   | 1   |
| Geronula Uv.     | mundataszemaensis Cheng  | 3   | 3   |
|                  | punctifrons Stal         | 8   | 6   |
| Habrocnemis Uv.  | sinensis Uv.             | 1   | 4   |
| Hieroglyphus Krauss. | annuliconis (Shir.)     | 10  | 5   |
|                  | banian (Fabr.)           | 13  | 7   |
|                  | concolor (Walk.)         | 1   |     |
|                  | tonkinensis I.-Bol.      | 10  | 3   |
| Indopodisma Dov.-Zap. | kingdoni (Uv.)         | 7   | 10  |
| Kingdonella Uv.  | hanburyi Uv.             | 15  | 3   |
|                  | kozlovii Mistsh.         | 14  | 13  |
|                  | nigrofemora Yin          | 2   | 2   |
|                  | nigrotibia Zheng         |     | 1   |
|                  | parvula Yin              | 5   | 8   |
|                  | pienbaensis zheng        | 1   | 1   |
|                  | qinghaiensis Zheng       | 2   |     |
|                  | rivuna Huang             | 3   | 1   |
| Lemba Huang      | bituberculata Yin et Liu| 2   | 7   |
|                  | daguanensis Huang        | 1   |     |
|                  | viridatibia Niu et Zheng| 2   | 2   |
| Genus       | Species                      | Examined specimens |
|-------------|------------------------------|--------------------|
|             | ♀ yunnana Ma et Zheng        | 1                  |
|             | ♀ zhashi Li                  | 2                  |
| Leptacris   | ♀ taeniata (Stal)            | 3                  |
|             | ♀ vittata (Fabr.)            | 4                  |
| Liaoacris   | ♀ ochropteris Zheng          | 2                  |
| Zheng       |                             | 4                  |
| Longgenacris| ♀ maculacorina You et Li     | 2                  |
| You et Li   |                             | 2                  |
| Longzhouacris| ♀ hainanensis Zheng et Liang| 4                  |
| You et Bi   |                             | 5                  |
| Melanoplus  | ♀ frigidus (Boh.)            | 4                  |
| Stal        |                             | 7                  |
| Miramella   | ♀ sinensis Chang             | 2                  |
| Dov.-Zap.   |                             | 1                  |
| Niitakacris | ♀ goganzanensis Tink.        | 4                  |
| Tinkham     |                             | 5                  |
| Emeiacris   | ♀ rosaeceanum (Shir)         | 8                  |
| Zheng       |                             | 1                  |
| Ognevia     | ♀ maculata Zheng             | 2                  |
| Ikonn.      |                             | 2                  |
| Oxya        | ♀ adentata Will.             | 10                 |
| Saerv.      |                             | 10                 |
|             | ♀ agavisa Tsai               | 14                 |
|             |                             | 10                 |
|             | ♀ anagavisa Bi               | 11                 |
|             |                             | 9                  |
|             | ♀ chinensis (Thunb.)         | 12                 |
|             |                             | 10                 |
|             | ♀ hainanensis Bi             | 11                 |
|             |                             | 10                 |
|             | ♀ intricata (Stål)          | 10                 |
|             |                             | 10                 |
|             | ♀ ningpoensis Chang          | 13                 |
|             |                             | 13                 |
|             | ♀ tinkhami Uv.               | 13                 |
|             |                             | 12                 |
|             | ♀ velox (Fabr.)              | 6                  |
|             |                             | 3                  |
|             | ♀ yunnana Bi                 | 8                  |
|             |                             | 10                 |
## Phylogeny and classification of the Catantopidae at the tribal level (Orthoptera, Acridoidea)

| Genus                   | Species                  | Examined specimens |
|-------------------------|--------------------------|--------------------|
| Oxyina Hollis           | *sinobidentata* (Hollis) | ♂ 13 ♀ 14          |
| Oxyrrhepes Srtal        | *cantonensis* Tink.      | ♂ 5 ♀ 11           |
|                         | *obtusae* (De Haan)      |                    |
|                         | *quadripunctata* Will.   |                    |
| Oxytauchira Ramme       | *brachyptera zheng*      | ♂ 1 ♀ 1            |
|                         | *elegans* Zheng et Liang| ♂ 2                |
| Pachyacris Uv.          | *vinosa* (Walk.)         | ♂ 3 ♀ 3            |
| Paratoacris Li et Jin   | *reticulipennis* Li et Jin| ♂ 4 ♀ 3          |
| Patanga Uv.             | *apicerca* Huang         | ♂ 1 ♀ 1            |
|                         | *humilis* Bi             | ♂ 12 ♀ 10          |
|                         | *japonica* (I.-Bol.)    | ♂ 10 ♀ 7           |
|                         | *succincta* (Johan.)     | ♂ 6 ♀ 5            |
| Pedopodisma Zheng       | *emeiensis* (Yin)        | ♂ 3 ♀ 3            |
|                         | *huangshana* Huang       | ♂ 1 ♀ 1            |
|                         | *protrucula* Zheng       | ♂ 4 ♀ 4            |
|                         | *shennongjiana* Huang    | ♂ 1 ♀ 1            |
|                         | *tsinlingensis* (Chang)  | ♂ 2 ♀ 2            |
| Podisma Berthold        | *aberrans* Ikonn.        | ♂ 4 ♀ 3            |
|                         | *pedestris* (L.)         | ♂ 3 ♀ 5            |
| Prumna Motschulsky      | *arctica* Zhang et Jin   | ♂ 10 ♀ 12          |
|                         | *cavicercia* Zhang       | ♂ 3 ♀ 3            |
|                         | *jingpohu* Huang         | ♂ 1 ♀ 3            |
|                         | *primnoa* F.-W.          | ♂ 10 ♀ 10          |
|                         | *primnoides* (Ikon.)     | ♂ 3 ♀ 3            |
|                         | *wuchangensis* Huang     | ♂ 1 ♀ 1            |
| Promesosternus Yin      | *himalayicus* Yin        | ♂ 1 ♀ 1            |
|                         | *vittatus* Yin           | ♂ 1 ♀ 1            |
| Genus                              | Species                | Examined specimens |
|-----------------------------------|------------------------|--------------------|
| *Pseudoptygonotus* Zheng          | *gunshensis* Zheng et al | 1                  |
| *Pseudoxya* Yin et Liu            | *kunmingensis* Cheng   | 7                  |
| *Pyramisternum* Huang             | *diminuta* (Walk.)     | 15                 |
| *Qinlingacris* Yin et Chou        | *herbaceum* Huang      | 1                  |
| *Quilta* Stal                     | *oryzae* Uv.           | 7                  |
| *Shirakiacris* Dirsh              | *brachyptera* Zheng    | 13                 |
|                                   | *shiraki* (I.-Bol.)    | 15                 |
|                                   | *yunkweiensis* (Chang) | 9                  |
| *Sinacris* Tinkham                | *longipennis* Liang    | 1                  |
|                                   | *oreophilus* Tink.     | 1                  |
| *Sinopodisma* Chang               | *bidenta* Liang        | 1                  |
|                                   | *formosana* (Shir.)    | 5                  |
|                                   | *houshana* Huang       | 2                  |
|                                   | *huangshana* Huang     | 1                  |
|                                   | *jiulianshana* Huang   | 2                  |
|                                   | *kawakamii* (Shir.)    | 1                  |
|                                   | *kellogii* (Chang)     | 10                 |
|                                   | *kodamae* (Shir.)      | 1                  |
|                                   | *lofaoshana* (Tink.)   | 11                 |
|                                   | *pieli* (Chang)        | 10                 |
|                                   | *quizhouensis* Zheng   | 10                 |
|                                   | *rostellcerca* Zheng et Liang | 8     |
|                                   | *shiraki* (Tink.)      | 3                  |
|                                   | *spinocerca* Zheng et Liang | 1   |
|                                   | *splendida* (Tink.)    | 2                  |
|                                   | *tsai* (Chang)         | 13                 |
|                                   | *yingdensis* Liang     | 7                  |
| Genus                  | Species               | Examined specimens |
|-----------------------|-----------------------|--------------------|
| **Sinstauchira Zheng** |                       |                    |
|                       | *gressitti* (Tink.)   | 1                  |
|                       | *pui* Liang et Zheng  | 11                 |
|                       | *ruficornis* Huang     | 10                 |
|                       | *yunnansis* Zheng     | 1                  |
| **Spathosternum Krauss** |                       |                    |
|                       | *prasiniferum* (Walk.)| 15                 |
| **Squaroplatacris Liang et Zheng** |                       |                    |
|                       | *elegans* Zheng et Cao| 4                  |
|                       | *violatibialis* Liang | 1                  |
| **Stenocatantops Dirsh** |                       |                    |
|                       | *splendens* (Thunb.)  | 15                 |
| **Stolzia Will.**     |                       |                    |
|                       | *hainanensis* (Tink.) | 1                  |
|                       | *jianfengensis* Zheng et Liang | 1          |
| **Tauchira Stal**     |                       |                    |
|                       | *damingshana* Zheng   | 1                  |
| **Toacris Tink.**     |                       |                    |
|                       | *shaloshanensis* Tink. | 1                |
|                       | *yaoshanensis* Tink.  | 1                  |
| **Tonkinacris Carl.** |                       |                    |
|                       | *decoratus* Carl.     | 1                  |
|                       | *meridionalis* Li     | 4                  |
|                       | *sinensis* Chang      | 10                 |
| **Traulia Stal**      |                       |                    |
|                       | *lofaoshana* Tink.    | 4                  |
|                       | *minuta* Huang et Xia | 5                  |
|                       | *nigrotibialis* Bi    | 3                  |
|                       | *orientalis* Ramme    | 4                  |
|                       | *szetshuanensis* Ramme.| 7                  |
|                       | *orchotibialis* Liang et Zheng | 1         |
|                       | *ornate* Shir.        | 4                  |
|                       | *tonknensis* C. Bol.  | 3                  |
| **Tristria Stal**     |                       |                    |
|                       | *palvinata* Uv.       | 1                  |
|                       | *pisciform* (Serv.)   | 1                  |
| Genus                | Species                           | Examined specimens |
|---------------------|-----------------------------------|--------------------|
|                     |                                   | ♂                   | ♀                   |
| *Tylotropidius* Stal| sp.                               | 2                   | 3                   |
|                     | *yunnanensis* Zheng et Liang Ge-qiu| 2                   | 5                   |
| *Xenacanthippus* Mill. | *hainanensis* Tink.               | 4                   | 1                   |
| *Xenocatantops* Dirsh | *brachycerus* (Will.)             | 10                  | 8                   |
|                     | *humilis* (Serv.)                 | 15                  | 10                  |
| *Yunnanacris* Chang | *yunnaneus* (Ramme)              | 10                  | 10                  |
| *Yupodisma* Zhang et Xia | *rufipennis* Zhang et Xia       | 2                   | 2                   |
| *Zubovskia* Dov.-Zap. | *koeppeni* (Zub.)               | 4                   | 3                   |
|                     | *parvula* (Ikonn.)               | 8                   | 10                  |
|                     | *planicaudata* Zhang et Jin      | 5                   | 3                   |
|                     | *striata* Huang                  | 10                  | 10                  |
Appendix 2.

Character list

1. Shape of body: (0) stout, ratio of body length to width equal at most 4; (1) moderate; ratio of body length to width is between 4–8; (2) elongated and cylindrical, ratio of body length to width is at least 8. (ordered)

I. Head

2. Obliquity of frons in profile: (0) not oblique, forming with vertex an right angle; (1) oblique, forming with vertex an acute angle of over 40º; (2) strongly oblique, forming with vertex an very acute angle less than 40º. (ordered)

3. Shape of fastigium in dorsal view: (0) normal, not strongly projected anteriorly, the distance from anterior margin of eyes to the apex of fastigium equal or less than the horizontal diameter of eye; (1) strongly projected anteriorly, the distance from anterior margin of eyes to the apex of fastigium obviously greater than the horizontal diameter of eye (Fig. 5).

4. Transverse groove at base of fastigium: (0) absent; (1) present and fine, not interrupting lateral carinae of vertex. (2) present and distinct, cutting through lateral carinae of vertex (Fig. 6). (ordered)

5. Interorbital distance of vertex: (0) obviously wider than the width of the frontal costa between antennae; (1) almost as broad as the frontal costa between antennae; (2) obviously narrower than the frontal costa between antennae. (ordered)

6. Foveola: (0) distinct; (1) absent or not perceptible.

7. Frontal costa between antennae: (0) not obviously projected; (1) obviously projected forward.

8. Shape of eye: (0) long oval, vertical diameter of eye greater than 1.3 times its horizontal diameter; (1) oval, vertical diameter of eye equal to or less than its horizontal diameter.

9. Size of eye: (0) large, vertical height greater than 1.3 times length of subocular groove; (1) small, vertical height less than 1.2 times length of subocular groove.

10. Shape of antennae: (0) filiform; (1) sward-shaped, width of basal segments greater than length.

11. Length of male antennae: (0) short, tip distinctly not reaching to base of hind femur; (1) long, tip distinctly reaching to or beyond base of hind femur.

II. Mesosoma

12. Convexity of median posterior margin of pronotum: (0) smoothly round or broadly angular; (1) projected into a right or acute angle.

13. Concavity of median posterior margin of pronotum: (0) not concave; (1) broadly concave (Fig. 12); (2) distinctly concave, forming a triangle (Fig. 11). (ordered)

14. Longitudinal margins of dorsal surface of pronotum: (0) constricted in the middle; (1) parallel.

15. Surface of pronotum: (0) smooth to finely sculptured; (1) coarsely granulate, irregularly carinulate, or tuberculate (Fig. 8).

16. Median carina on prozona of pronotum: (0) flat; (1) distinctly elevated and roundly pectinate (Fig. 9).
Figures 5–9. Head and pronotum: 5–6 *Carsula brachyptera* Huang et Xia, female: head and pronotum, dorsal view and lateral view, respectively; 7 *Yunnanacris yunaeus* (Ramme), pronotum, lateral view; 8 *Ecphanthacris mirabilis* Tinkham, male, pronotum, lateral view; 9 *Dericorys roseipennis* (Redt.), male, pronotum, lateral view.
17. Distinctness of median carina on pronotum: (0) distinct, from almost complete to complete; (1) barely discernible to absent.
18. Median carina on pronotum in lateral view: (0) straight; (1) strongly elevated medially, forming a distinct round ridge (Fig. 10).
19. Incision on median carina of pronotum by principal sulcus: (0) shallow to indistinct; (1) very deep (Fig. 8).
20. Presence of additional incisions of median carina of pronotum by minor transverse carina(e): (0) absent; (1) present.
21. Ratio of length of prozona to length of metazona of pronotum measured along median carina: (0) 1.0–1.2; (1) 1.5–2.0; (2) more than 2.3. (ordered)
22. Lateral carinae on pronotum: (0) absent or slightly elevated, distinctly not reaching to posterior margin of pronotum; (1) distinctly elevated, complete or nearly so.
23. Ventral posterior angle of lateral lob of pronotum: (0) broadly round (Fig. 7); (1) roundly angular to angular (Fig. 6, 10).
24. Posterior margin of lateral lob of pronotum: (0) not concave to slightly arched; (1) strongly concave.
25. Shape of prosternal process: (0) conical (Fig. 16); (1) cylindrical (Fig. 17); (2) transverse and lobular (Fig. 20, 21); (3) mushroom-shaped (Fig. 18, 19).
26. (25:0) Apical part of cone-shaped prosternal process: (0) straight; (1) strongly bent posteriorly.
27. (25:1) Apical part of cylindrical prosternal process: 0 straight or slightly bent posteriorly; (1) strongly bent posteriorly, almost reaching anterior margin of mesosternum, (2) compressed laterally and flat apically.
28. (25:2) Ventral margin of lobular prosternal process: (0) truncate or slightly serrated (Fig. 21); (1) with 2–3 apically rounded, triangular processes (Fig. 20); (2) medially projected into a large triangle; (3) triangular as state 2 and turned anteriorly (Fig. 22, 23).
29. Anterior border of mesosternum: (0) straight or slightly arched; (1) broadly projected in the middle (Fig. 13).
30. Shape of mesosternal interspace: (0) wide, as long as or less than width; (1) elongate, length at least 1.3 times its narrowest width; (2) very reduced, lateral margins partly or completely contiguous. (ordered)
31. Contact of lateral lobes of metasternum medially: (0) separated; (1) contiguous.
32. Inner posterior corners of lateral lobes of mesosternum: (0) obtusely round or angularly round; (1) right angular to acutely angular.
33. Relative length of dorsal and ventral basal lobe of hind femur: (0) dorsal lobe as long as ventral lobe; (1) dorsal lobe longer than ventral lobe.
34. Shape of ventral genicular lobe of hind femur: (0) round or roundly angular distally; (1) spined distally.
35. Shape of dorsal genicular lobe of hind femur: (0) round distally; (1) spined distally.
36. Serration of dorsal carina of hind femur: (0) absent, smooth; (1) present, finely serrated.
Figures 10–14. Thorax: 10 *Chondracris rosae rosae* (De Geer), male, pronotum, lateral view; 11 *Caryanda elegans* Bol., male, pronotum, dorsal view; 12 *Niitakacris rosaceanum* Shiraki, male, pronotum, dorsal view; 13 *Longzhouacris hainanensis* Zheng et Liang, male, mesosternum and metasternum, ventral view; 14 *Tauchira damingshana* Zheng, female, elytron.
37. Shape of distal end of dorsal carina of hind femur: (0) round or slightly broadly angular; (1) spined, acutely pointed, or narrowly obtuse-angular.
38. Outer apical spine on hind tibia: (0) absent; (1) present.
39. Number of spines on outer margin of hind tibia: (0) 5–6; (1) 8–10; (2) over 12. (ordered)
40. Distance between 1st and 2nd spines of inner spine series on hind tibia: (0) as long as any other inter-spine distance; (1) longer than any other inter-spine distance.
41. Distal half of hind tibia: (0) not obviously broaden toward apex, without obvious edges running through the spines; (1) broadened toward apex, with distinct outer and inner edges running through the spines; (2) strongly broadened toward apex, with sharp outer and inner edges running through the spines. (ordered)
42. Size of male tegmina: (0) developed, at least in contact with each other above abdomen; (1) abbreviated, lobate, and lateral, not in contact above abdomen, but reaching to posterior margin of metanotum; (2) rudimentary, not reaching to posterior margin of metanotum; (3) absent. (ordered)
43. Distal margin of tegmina: (0) round; (1) obliquely truncated.
44. Cells of distal part of tegmina: (0) rectangular or irregular; (1) oblique.
45. Radial cells in the middle of tegmina: (0) with irregular cross-veins; (1) with parallel cross-veins (Fig. 14).

III. Metasoma
46. Development of tympanal organ: (0) developed, distinct; (1) vestigial with just discernible opening, or absent.
47. Presence of tubercle on sides of apical field of male supra-anal plate: (0) absent, (1) present.
48. Presence of transverse groove on apical field of male supra-anal plate: (0) absent, (1) present.
49. Presence of transverse ridge on middle field of male supra-anal plate: (0) absent, (1) present (Fig. 25).
50. Presence of tubercle on sides of middle field of male supra-anal plate: (0) absent, (1) present.
51. Presence of transverse groove on middle field of male supra-anal plate in male: (0) absent, (1) present.
52. Presence of hair tufts on last sternum of abdomen: (0) absent; (1) present.
53. Presence and size of furcula: (0) absent; (1) present and small (Fig. 26); (2) present, and large and long (Fig. 28–30). (ordered)
54. Basal field of male supra-anal plate: (0) smooth without tubercles near lateral margins; (1) with two digitiform tubercles near lateral margins (Fig. 28).
55. Shape of male supra-anal plate: (0) triangular; (1) rectangular or trapezoid; (2) scutate.
56. Shape of male cerci: (0) conical; (1) compressed laterally.
57. (55:0) Length of conical cerci in male: (0) short; (1) long.
Figures 15–23. Prosternal process: 15 *Cyrtacanthacris tatarica* L., male lateral view; 16 *Caryanda elegans* L–Bol., male lateral view; 17 *Calliptamus barbarus* (Costa), male lateral view; 18–19 *Tristria pulvinata* Uv., male lateral view and ventral view respectively; 20 *Sinstauchira yunnana* Zheng, male rear view; 21 *Spathosternum prasiniferum* (Walk), male front view; 22–23 *Conophymopsis labrispinus* Huang, male ventral view, and lateral view respectively (from Huang 1983).

58. Curvature of male cerci: (0) straight; (1) curved inward posteriorly (Fig. 28); (2) curved upward posteriorly; (3) curved downward posteriorly.

59. Apex of cerci in males: (0) pointed; (1) round (Fig. 34); (2) truncated (Fig. 31); (3) bifurcated (Fig. 29); (4) dentate (Fig. 35). (ordered)

60. Shape of male cerci in lateral view: (0) strongly tapering toward apex, width at apical part less than at middle; (1) broadened toward apex, width at apical part slightly greater than at middle (Fig. 32, 33); (2) strongly broadened toward apex, width at apical part much greater than at middle (Fig. 35). (ordered)
Figures 24–28. 24 Dericorys roseipennis (Redt.), male, hind femur, lateral view; 25–28 End of male abdomen in dorsal view: 25 Dericorys roseipennis (Redt.); 26 Ecphanthacris mirabiis Tinkham; 27 Spathosternum prasiniferum (Walk); 28 Anapodisma miramæ Dov.–Zap.
Figures 29–35. 29–30 End of male abdomen in dorsal view: 29 Niitakacris rosaceanum (Shiraki); 30 Indopodisma kingdoni (Uv.); 31–34 Cercus in lateral view: 31 Indopodisma kingdoni (Uv.); 32 Squaroplatacris elegans Zheng et Cao; 33 Sinopodisma tsaii (Chang); 34 Fruhstorferiola omei (Rehn et Rehn); 35 Calliptamus barbarus (Costa).
61. Shape of male subgenital plate in ventral view: (0) very short, length equal to or less than basal width; (1) long, length greater than basal width, but not more than 1.5 times; (2) strongly elongated, more than twice basal width (Fig. 38). (ordered)

62. Shape of posterior part of male subgenital plate in ventral view: (0) conical; (1) trapezoid.

63. (61:0) Compression of posteriorly conical subgenital plate in males in ventral view: (0) not compressed; (1) compressed laterally.

64. Shape of male subgenital plate in dorsal view: (0) strongly tapering toward apex, end pointed or blunt; (1) gradually tapering toward apex, end round or concave; (2) not tapering, sometimes even slightly broaden, toward the apex, end truncated. (ordered)

65. Presence of tubercle at apex of male subgenital plate: (0) absent; (1) present and short (Fig. 29, 30); (2) present and much prolonged, forming prominent pointed projection. (ordered)

66. Posterior margin of female subgenital plate in ventral view: (0) triangularly projected posteriorly in the middle; (1) straight or broadly rounded.

67. Presence of lateral teeth on posterior margin of female subgenital plate in ventral view: (0) absent; (1) present.

68. Shape of dorsal valves of ovipositors in profile: (0) stout, less than 3 times as long as broad when in a position coalesced with ventral valves; (1) slender, more than 3.5 times as long as broad when in a position coalesced with ventral valves.

69. Serration of dorsal external margin of dorsal ovipositor valves: (0) smooth or weakly serrated; (1) distinctly serrated.

70. Presence of a notch on apex of dorsal external margin of dorsal valves of ovipositor: (0) absent; (1) distinctly present.

71. Apex of dorsal valves of ovipositor: (0) not bidentate; (1) bidentate.

IV. Male genitalia

Details of the male genitalia morphology are explained in Figures 43-53. Terminology for genital structures follow Dirsh (1956). Acronyms used in description of the listed genital characters are:

Ac: arc of cingulum (of phallic complex)
A: ancora (of epiphallus)
Ap: apical valves of penis (of phallic complex)
Anp: anterior projection (of epiphallus)
Apd: apodeme (phallic complex)
B: bridge (of epiphallus)
Bp: basal valves of penis (of phallic complex)
Cv: valves of cingulum (of phallic complex)
L: lophus (of epiphallus)
Rm: rami of cingulum (of phallic complex).

72. Rami of cingulum (Rm) of phallic complex: (0) undeveloped, narrowly sclerotized; (1) developed, broadly sclerotized (Fig. 45).
Figures 36–42. 36. *Assamacris longicerca* (Huang), cercus, male, lateral view; 37 *Anapodisma miramae* Dov.–Zap., upper ovipositor valve of female, dorsal view; 38 *Leptacris vittata* (Fabr.), subgenital plate of male, lateral view; 39 *Longzhouacris hainanensis* Zheng et Liang, ovipositor, lateral view. 40–42 *Egnatus apicalis* Stål 40: phallic organ of male, dorsal view 41 epiphallus dorsal view and 42 phallic organ, lateral view.
Figures 43–47. General morphology of phallic complex. Terminology and abbreviations used in the figures follow Dirsh (1956). 43 Whole phallic complex, dorsal view; 44 Phallic organ (phallic complex with epiphallus removed) dorsal view; 45. Phallic organ lateral view; 46 Penis and cingulum of simple form lateral view; 47 Phallic organ with zygoma apodems and rami removed ventral view. Abbreviations: 

Ap – apical valves of penis, Apd – apodemes, Bp – basal valves of penis, Cv – valves of cinglum and Rm – rami of cinglum Zyg – zygoma. Additional abbreviations for characters not coded: Ect – ectophalus Ejd – ejaculatory duct, Ejs – ejaculatory sac, Eph – epiphallus, Gpr – gonopore process, Os – oval sclerite of epiphallus, Sps – spermatophore sac.
73. Length of the apodemes (Apd): (0) far from reaching to apex of the basal valves of penis (Bp); (1) reaching to apex of basal valves of penis; (2) reaching beyond apex of the basal valves of penis. (ordered)

74. Shape of apodemes (Apd) (dorsal view): (0) slender, more than 7 times as long as broad; (1) stout, less than 6 times as long as broad.

75. Prominence of arc of cingulum (Ac): (0) well developed and large; (1) weak, but perceptible; (2) absent. (ordered)

76. Bp and apical valves of penis (Ap): (0) connected by strongly sclerotized flexure (Fx) (Fig. 53); (1) separated, being connected by membrane.

77. Apex of Ap (in profile): (0) distinctly bent upward (Figs. 42); (1) straight; (2) distinctly bent sideward.

78. Length of the valves of cingulum (Cv): (0) very long, apex distinctly reaching beyond apex of Ap (Fig. 42); (1) long, apex reaching to or almost to apex of Ap; (2) reduced, apex reaching at most to middle of Ap; (3) completely absent. (ordered)

79. Shape of epiphallus: (0) bridge-shaped (Fig. 41); (1) shield-shaped (Fig. 49).

80. Integrity of epiphallus: (0) complete, not divided (Fig. 41); (1) longitudinally divided into two parts along midline, connected by membrane (Figs. 49).

81. Bridge of epiphallus in dorsal view in relation to width of lateral plate (width of plate refers to its width at ancora without including the latter): (0) broad; width in the middle broader than 1/2 of, but narrower than width of lateral plate (Fig. 49); (1) narrow; width in the middle narrower than half of the width of lateral plate (Fig. 41); (2) absent (Fig. 50). (ordered)

82. Presence of ancorae (A) and its size in relation to width of bridge of epiphallus: (0) developed, distinctly projected, longer than 1/2 of width of bridge (Fig. 41); (1) small, obviously less than 1/2 of width of bridge; (2) absent. (Ordered)

83. Development of lophi (L): (0) well developed, large; (1) undeveloped, small but perceptible; (2) absent. (ordered)

84. Shape of lophi: (0) lobiform with 2 or 3 lobes (Fig. 41); (1) lobiform with only one lobe.

85. Shape of anterior projections of epiphallus (Anp): (0) distinctly projected (Fig. 41); (1) slightly projected.

86. Posterior projections of epiphallus (Pp): (0) not or slightly projected; (1) distinctly projected.

87. Apex of ancorae: (0) pointed, (1) bluntly round; (2) truncated.

88. Length of Bp relative to Ap: (0) Bp more than 1.5 times length of Ap; (1) Bp as long as Ap (Fig. 42); (2) Bp less than 0.8 times length of Ap. (ordered).
Figures 48–53. Variations of phallic complex: 48–50 Variation of epiphallus in dorsal view; 51. Penis with sheath formed from cingulum and exposed apex of penis; 52. Penis with arch of cingulum and valve derived from it; 53. Valve of penis with flexure. Abbreviations: A – ancora of epiphallus, Ac – arc of cingulum of phallic complex, Anp – anterior projections of epiphallus, Ap – apical valves of penis of phallic complex, Apd – apodeme of phallic complex, B – bridge of epiphallus, Bp – basal valves of penis of phallic complex, Cv – valves of cingulum of phallic complex, Fx – flexure, L – lophi of epiphallus, Ms – median slit of epiphallus, Pp – posterior projections of epiphallus, Rm – rami of cingulum and Sh – sheath
### Appendix 3.

Character Matrix (Taxa in bold are outgroups).

| TAXA            | CHARACTERS                                                                 |
|-----------------|-----------------------------------------------------------------------------|
| *Egnatius*      | 1100000002 0000000001 0000----00 0000000010 0000000000 0000000000 0000000000 001000100 100000000 |
| *Egnatiuides*   | 1100000002 0000000001 0000----00 0000000010 0000000000 0000000000 0000000000 001000100 100000000 |
| *Avulacris*     | 0000110100 0101001000 -01000--11 0100001010 1010010010 1000001010 1000000000 010001010 100000000 |
| *Anapodisma*    | 0000110100 1011001000 20000--11 0000001010 0100000000 1010000000 0000000000 010001010 100000000 |
| *Anepipodisma*  | 0000000000 0111010000 20000--11 0000000000 03----1000 1010001000 0000000000 011001010 010001001 |
| *Apulacris*     | 0000110000 0100001000 0101000000 1000000010 0000000000 0000000000 0000000000 000010001 100000000 |
| *Armatacris*    | 0000111000 0100000000 010001--11 0100001010 0000000000 0000000000 0000000000 000010001 010001001 |
| *Aseratus*      | 0000001000 0001000100 0010001010 0100010010 0000000000 0000000000 0000000000 000000000 000000000 |
| *Assamacris*    | 0000001100 1101100000 101000--11 0000000000 0000000000 0000000000 0000000000 000010001 010001001 |
| *Bannacris*     | 0000210000 1101000000 101000--11 0000000000 0000000000 0000000000 0000000000 000010001 100000000 |
| *Calliptamus*   | 1100110000 0100000000 0101001010 1100000000 1000000010 1000000010 0000000000 01100010 000000000 |
| *Carsula*       | 2212000011 0101000000 10103---12 1000000120 1000100000 1110000000 0000000000 01100101 000000000 |
| *Caryanda*      | 0001010000 ---100-00 010000--00 1001001110 1100000000 1110000000 0000000000 01100010 010001001 |
| *Catantops*     | 0000210000 0100000000 0010001010 0100010000 0000000000 0000000000 0000000000 01100010 000000000 |
| *Chondracris*   | 0000000000 0211001000 0100011010 0100001010 0000001000 0000001000 0000001000 01100010 000000000 |
| *Choroedocus*   | 0000010000 0100100000 1010111010 0000000000 0000000000 0000000000 0000000000 01100010 000000000 |
| *Conophyma*     | 0000001000 0021100000 0100011010 0100010010 0000001000 0000001000 0000001000 01100010 000000000 |
| *Conophymacris* | 0000110000 0101000000 1011000000 1100000000 0000000000 0000000000 0000000000 01100010 000000000 |
| *Conophymopsis* | 0000010110 0001000000 211000--11 0000000110 03-----00 03-----00 03-----00 01100010 000000000 |
| *Coptacra*      | 0002100000 0021100000 0100001010 0100010010 0000001000 0000001000 0000001000 01100010 000000000 |
| *Curripennis*   | 0001010000 0101000000 1100000000 0000001010 0100000000 1000010010 0000000000 01000101 000000000 |
| *Cyrtacanthacris*| 0000010000 0001000000 20102--311 0000000110 03-----100 1020100000 0000000000 01000101 000000000 |
| *Dimeacris*     | 0002010000 1001000000 20000--11 1000000000 0100000000 1110101010 0000000000 00101010 000010010 |
| *Dericorys*     | 0100000000 0100000000 0100000000 0100001010 0000000000 0000000000 0000000000 01100110 000001001 |
| TAXA              | 1   | 11  | 21  | 31  | 41  | 51  | 61  | 71  | 81   |
|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|------|
| Ecphanthacris     | 010 | 200 | 001 | 010 | 000 | 100 | 000 | 010 | 000  |
| Ecphyacris        | 010 | 021 | 000 | 021 | 000 | 100 | 000 | 010 | 000  |
| Eirenephilus      | 000 | 000 | 101 | 011 | 000 | 000 | 100 | 000 | 000  |
| Emeliacris        | 000 | 000 | 100 | 101 | 000 | 000 | 000 | 010 | 000  |
| Eokingdonella     | 000 | 001 | 100 | 111 | 000 | 003 | 000 | 100 | 000  |
| Epistaurus        | 010 | 020 | 000 | 010 | 000 | 100 | 000 | 110 | 000  |
| Eucoptacra        | 010 | 021 | 000 | 010 | 000 | 100 | 000 | 010 | 000  |
| Eyprepocnemis     | 000 | 000 | 100 | 010 | 000 | 100 | 000 | 010 | 000  |
| Fer               | 000 | 101 | 000 | 100 | 000 | 100 | 000 | 101 | 000  |
| Fruhstorferiola   | 000 | 011 | 000 | 010 | 100 | 010 | 000 | 100 | 000  |
| Genimen           | 000 | 021 | 010 | 010 | 000 | 100 | 000 | 100 | 000  |
| Gerenia           | 100 | 000 | 000 | 021 | 000 | 010 | 000 | 110 | 000  |
| Gesonula          | 000 | 100 | 000 | 010 | 010 | 000 | 100 | 110 | 000  |
| Habrocnemis       | 100 | 000 | 000 | 011 | 000 | 100 | 100 | 010 | 000  |
| Hieroglyphus      | 000 | 010 | 010 | 110 | 000 | 100 | 000 | 100 | 000  |
| Indopodisma       | 000 | 002 | 000 | 010 | 100 | 000 | 100 | 001 | 000  |
| Kingdonella       | 110 | 000 | 010 | 010 | 000 | 110 | 000 | 010 | 000  |
| Lemba             | 000 | 010 | 000 | 010 | 000 | 110 | 000 | 110 | 000  |
| Leptacris         | 220 | 020 | 000 | 010 | 000 | 100 | 000 | 110 | 000  |
| Liaoacris         | 000 | 001 | 010 | 010 | 010 | 000 | 000 | 100 | 000  |
| Longenacris       | 000 | 001 | 100 | 001 | 000 | 100 | 000 | 101 | 000  |
| Longzhouacris     | 000 | 101 | 110 | 100 | 000 | 010 | 100 | 000 | 110  |
| Melanoplus        | 000 | 001 | 010 | 010 | 000 | 100 | 000 | 101 | 000  |
| Minamella         | 000 | 000 | 111 | 001 | 000 | 100 | 000 | 110 | 000  |
| Niitakacris       | 000 | 001 | 100 | 010 | 000 | 100 | 000 | 110 | 000  |
| Ognevia           | 000 | 000 | 101 | 010 | 000 | 100 | 000 | 110 | 000  |
| Oxya              | 000 | 011 | 100 | 010 | 000 | 110 | 000 | 101 | 000  |
| TAXA               | CHARACTERS                                                                 |
|-------------------|---------------------------------------------------------------------------|
| Oxyna             | 0001110000 0101001000 101000--10 1001001110 2000000000 1100000000 0000000010 0---0--0 0000000-          |
| Oxyrrhepes        | 2000000000 0101000000 001000--12 0000010120 0000000001 01000--10 1000000000 0---11100 010-10-01          |
| Oxytauchira       | 0000010000 010100--00 01012--110 0001001110 1000000000 0110000000 0000101010 010001101 00000100       |
| Pachyacris        | 000000-0000 0101101010 001000--10 1100011010 0001010000 1000000000 0111000100 11010011          |
| Paratoacris       | 0001010000 0101001000 101000--10 1001001010 1000000000 1110000000 0000000010 0100000011 00000000    |
| Paratonkinacris   | 0000010010 110100100- 101000--11 0000000010 0000000001 0010000310 0001000100 00000000          |
| Patanga           | 0000110000 0100000000 0010111-10 110010010 0000100000 1000010000 0100010000 011100101 01010011    |
| Pedopodisma       | 0000011000 0001001000 001000--12 0000010120 0000000001 0110011112 0010001000 0100010000 01000010 |
| Podisma           | 0000021011 0010000000 001000--1- 0000000010 0-0-0-0000 1020201000 0000000010 0121110100 01000100 |
| Primnoa           | 0000110110 -011001000 201000--11 000000-010 01000--00 1010--0-0 01-2000-0 021014200 11010102    |
| Promoeosternus    | 0001010000 1101110100 1010100000 1000010000 010-000001 0021001111 0000010100 00011110          |
| Pseudoxya         | 0000021000 0101001000 101000--10 0111001110 2000000000 1110000000 0000000010 0100001111 01000100 |
| Pseudoxytagonotus | 0000010000 0000010000 0010000000 201000--10 0000000010 1101000000 1102000000 0000--1010 0100010101 00000011 |
| Pynamisternum     | 0001110000 0101001000 10102--210 0010000110 1000000000 1100000000 0000000110 0101100110 001000010          |
| Quita             | 2000001000 0101000100 1011101010 0011101010 2000000010 0110000000 1010010000 0111001000 0210100-0          |
| Qinlingacris      | 0000001011 0001000000 0100001110 0100001111 0000000010 03--0-0000 1020010000 0000000010 02000-0100 01000100       |
| Ranacris          | 0000000000 0001100000 0010000000 0100100100 0000000110 1010000000 0000011110 0100010000 0100100110          |
| Shinkokecris      | 0000000000 0101100100 10102--110 0010011110 1000000000 1100000000 0000000010 0101001101 01010100 |
| Sinacris          | 0000001000 0101001000 10102--110 0010011110 1000000000 1100000000 0000000010 0100011011 01010100       |
| Sinopodisma       | 0000000000 0101001000 10102--110 0010000110 0100000000 1100000000 0000000010 0101010010 0100101000          |
| Sinstauchina      | 0002-10000 0101001000 10102--010 1000011110 1000100000 11-000000 0000000010 010000011 00010100          |
| Spathosternum     | 0000010000 0101000001 01002--010 1000000110 0000101000 1010001000 0000000000 0110011000 01101121          |
| Squaroplataciris  | 0000001000 0101000000 01101-0-10 1000001020 0000000000 1010111-11 1000010000 0110100110 00010100       |
| Stenocatantops    | 0000210000 0101000000 00011-0-10 1000011010 0000000000 1000000110 1000000000 0100001010 10000000          |
| Stolzia           | 0000021000 -101101000 001000--11 0010011110 0000010000 1110000000 0000000110 0---0--0 0100000-          |
| Tauchina          | 0001011000 0101001000 10102--110 0010010110 1000100000 1110000000 0000000010 0100001101 01010100          |
| Toacris           | 0002010000 0101001000 1010100-10 1010010110 1000100000 1110000000 0000000010 0101000101 00000100          |
### CHARACTERS

| TAXA             | 1     | 11    | 21    | 31    | 41    | 51    | 61    | 71    | 81    |
|------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| *Tonkinacris*    | 0000210000 | 1101001000 | -01000--10 | 000001010 | 0000000000 | 10100----0 | 0000100010 | 0100101000 | 00001000 |
| *Traulia*        | 0000010000 | -101000000 | 101000--1- | 0000011010 | 0-00000000 | 10-00000-- | 000000000-0 | 01--000001 | 00000010 |
| *Tristria*       | 2000010000 | 0101000000 | 11103--12 | 0000000120 | 0000000000 | 1020000100 | 1001000000 | 0101001100 | 00000000 |
| *Traulitonkinacris* | 0000011000 | 1101001000 | 101000--10 | 0000011010 | 1000000010 | 0102103101 | 0000000010 | 0100001000 | 00001001 |
| *Tylotropidius*  | 0000010000 | 0101000000 | 01101-2-10 | 1000011020 | 0000000000 | 1010200000 | 0000000000 | 0011000100 | 10001001 |
| *Xenacanthippus* | 2212010001 | 0101001000 | 20101-0-12 | 1000000110 | 000000010 | 0010000000 | 2010000100 | 0011210200 | 120100-2 |
| *Xenocatantops*  | 0000210100 | 0100000000 | 00101-0-10 | 0000011010 | 0000000000 | 1010000100 | 0000000000 | 0110000000 | 100000-0 |
| *Yupodisma*      | 0000010110 | 0001001000 | 100000--11 | 000001010 | 0000000000 | 1010000100 | 0000010010 | 0000111100 | 01000101 |
| *Yunnanacris*    | 0000210000 | 0001001000 | 100000--11 | 000001010 | 0100000000 | 1010000100 | 0000010010 | 0000111100 | 01000101 |
| *Zubovskia*      | 0000110000 | 0001001000 | 20-000--11 | 0000000010 | 03-1--0--0 | 10-0000010 | 000-00010 | 1000111100 | 01000100 |