Cladistics and Phylogenetic Analyses of the Grasshopper Genus *Chorthippus* Fieber (Orthoptera: Acrididae)[1]

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Abstract Cladistic and phylogenetic analyses were conducted for the grasshopper genus *Chorthippus* Fieber. Forty-two species were analyzed, including nine belonging to the subgenus *Megaulacobothrus,* three to the subgenus *Chorthippus*, 11 to the subgenus *Glyptobothrus* and 19 to the subgenus *Altichorthippus*. In total, 50 equally parsimonious trees were constructed, with length = 176 steps, ci = 34% and ri = 77%. A strict consensus tree was constructed. All nine species of the subgenus *Megaulacobothrus* formed a clade, which is corroborated by five transformations. This clade is paraphyletic and near the root of the cladogram containing other *Chorthippus* species. In the latter clade, subclade Altichorthippus is on the base, subclade Glyptobothrus on top with subclade Chorthippus nested in it. We, therefore, suggest that the current grasshopper genus *Chorthippus* is paraphyletic. The subgenus *Megaulacobothrus* Caudell should be removed from *Chorthippus* and treated as a genus. The subgenus *Altichorthippus* contains the most ancient species of the grasshopper genus *Chorthippus.* The subgenus *Glyptobothrus* is derived from *Altichorthippus* and contains some species that should be referred to as *Altichorthippus.* The subgenus *Chorthippus* is a recent evolutionary group, descended from *Glyptobothrus.*

Key Words Phylogeny, Acrididae, *Chorthippus*

The grasshopper genus *Chorthippus* Fieber (1852) is a large genus within Orthoptera consisting of more than 250 species (Zheng 1994, Zheng and Xia 1998, Otte 1994). Most species of the genus are distributed in the Palaearctic Region, but a few species are reported from Africa and only one (*Chorthippus curtipennis* Harris) from America (Pfadt 2002). There is morphological variation in these species, including body color, wing length, shape of lateral carina, wings (forewing and hindwing) and postocular band (Ingrisch 1995). Some subgenus divisions have been suggested. Caudell (1921) established the subgenus *Megaulacobothrus* Caudell with the type species *Chorthippus fuscipennis* (Caudell). This subgenus is characterized by long and black hindwing. Chopard (1951) erected the subgenus *Glyptobothrus*, based on the characters of long wings and curved lateral carina. Jago (1971) established the subgenus *Altichorthippus*, based on the characters of short wings and curved lateral carina. In the same paper, he merged the genera *Dasyhippus* Uvarov and *Gomphocerippus* Roberts into *Chorthippus* as two subgenera. Because both of these genera

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Table 1. List of the species included in the cladistic analysis

Subgenus *Megaulacobothrus*
Chorthippus aethalinus (Zub.)
C. latipennis (I. Bol.)
C. longisonus Li et Yin
C. chinensis Tarb.
C. humanensis Yin et Wei
C. fuscipennis (Caudell)
C. yuanshanensis Zheng
C. flexivenus Liu
C. rufitibis Zheng
Subgenus *Chorthippus*
C. albomarginatus (De Geer)
C. qingzangensis Yin
C. dichrous (Eversmann)
Subgenus *Glyptobothrus*
C. apricarius (L.)
C. huchengensis Xia et Jin
C. zhengi Ma et Guo
C. changbaishanensis Liu
C. brunneus huabeiensis Xia et Jin
C. biguttulus (L.)
C. shantungensis Chang
C. hsiai Cheng et Tu
C. albonemus Cheng et Tu
C. dubiz Zubovsky
C. rubensabdomenis Liu
Subgenus *Altichorthippus*
C. hammarstroenci (Miram)
C. conicaudatus Xia et Jin
C. genheesis Li et Yin
C. changtunensis Yin
C. louguanensis Cheng et Tu
C. flavabdomensis Liu
C. fallax (Zub.)

Table 1. Continued.

Subgenus *Altichorthippus*
C. intermedius (B.-Bienko)
C. unicubitus Xia et Jin
C. charpini Chang
C. chayuensis Yin
C. dahinganlingensis Lian et Zheng
C. deqinensis Liu
C. nemus Liu
C. brevipterus Yin
C. brevicornis Wang et Zheng
C. squamopennis Zheng
C. curtipennis Harris
C. parallelus Zetterstedt
Outgroup *Omocestus haemorhoidalis* (Charp.)

have clavate antennae, most orthopterologists did not accept this opinion. Synthesizing all these opinions, Xia and Jin (1982) suggested a four-subgenus division of the genus, which excluded species of *Dasyhippus* Uvarov and *Gomphocerippus* Roberts. Those four subgenera are: (1) *Megaulacobothrus* (type species *Chorthippus fuscipennis* Caudell) characterized by long and black hindwing; (2) *Chorthippus* (type species *Chorthippus albomarginatus* (De Geer)) with all the species of this subgenus sharing the characters of straight lateral carina and long wings; (3) *Glyptobothrus* Chopard (1951), characterized by curved lateral carina and long wings, and; (4) *Altichorthippus* Jago with shared characters of curved lateral carina and short wings.

These divisions are based on only a few morphological characters and do not consider the phylogeny of the species. None have, therefore, been well accepted. Many scientists refuse to accept *Megaulacobothrus* as a subgenus of *Chorthippus*, regarding it as a genus. Some proof is needed that these subgenera are monophyletic, only then, can the phylogenetic relationship among them be established.

The objective of this study was to determine the phylogenetic relationships among the 42 grasshopper species of *Chorthippus* based upon cladistic analysis.

Materials and Methods

Forty-two species of *Chorthippus* were selected for the cladistic analysis (Table 1). Of them, nine species belonged to the subgenus *Megaulacobothrus*, three to *Chorthippus*, eleven to *Glyptobothrus* and 19 to *Altichorthippus*. The species selection was

Table 2. Characters and character states used in the cladistic analyses of *Chorthippus*

Characters	Character states
0. Length/width of a segment in the middle antennae	0 = ≥2.5; 1 = <2.5.
1. Shape of lateral foveola	0 = oblong; 1 = not oblong.
2. Length/width of lateral foveola	0 = ≥3; 1 = <3.
3. Longitudinal groove on the frontal ridge of male	0 = obvious in the whole length; 1 = obvious on part of the frontal ridge.
4. Shape of fastigium (male)	0 = obtuse angle; 1 = right-angle; 2 = acute-angle.
5. Post ocular band	0 = absent; 1 = present.
6. Body size	0 = small; 1 = bigger.
7. Length of prozona and length of metazona	0 = equal; 1 = prozona longer; 2 = metazona longer.
8. Shape of lateral carina in prozona (male and female)	0 = cambered; 1 = constricted in the mid-length; 2 = straight.
9. Widest of lateral carina/narrowest in prozona	0 = ≤2; 1 = >2.
10. Lateral carina of pronotum	0 = distinct in the whole length of pronotum; 1 = distinct in part length of pronotum.
11. "X" band on the pronotum	0 = absent; 1 = present.
12. Shape of post margin of pronotum	0 = cambered; 1 = obtuse angle.
13. Shape of tympanal organ	0 = wide-slot shape; 1 = semicircle, 2 = narrow-slot shape; 3 = oviform.
14. Color of abdominal sternum	0 = red; 1 = brown; 2 = yellow.
15. Middle groove on male epiproct	0 = obvious in the whole length; 1 = obvious on basal half; 2 = obvious in more than half of length but not whole length.
16. Ridge in the middle male epiproct	0 = absent; 1 = present.
17. Number of stridulatory pegs on the inner side of post femur	0 = ≥150; 1 = <150.
18. Color on lower side of post femur	0 = tan; 1 = orange; 2 = reddish.
19. Band in the inner margin of post femur	0 = absent; 1 = present.
20. Knees	0 = not black; 1 = black.
21. Hind-tibia color	0 = tan; 1 = yellowish; 2 = reddish.

Table 2. Continued.

Characters	Character states
22. Length/width of male tegmen	0 = <4; 1 = ≤4.
23. Tegmen and hindwing	0 = equally long; 1 = tegmen longer.
24. Length of procostal area of female tegmen	0 = exceeding middle of tegmen; 1 = not exceeding middle of termen.
25. Intercalary vein in the medial area and cubital area of female tegmen	0 = both absent; 1 = present in cubital area, absent in medial area; 2 = present in medial area, absent in cubital area; 3 = both present.
26. Color of tegmen and hindwings of male and female	0 = not dark; 1 = dark.
27. Length of tegmem	0 = exceeding tip of post femur; 1 = reaching end of abdomen; 2 = not reaching tip of post femur.
28. Precostal area of male tegmen	0 = reaching middle of tegmen; 1 = not reaching middle of termen.
29. Width of subcostal area and radial area (male tegmen)	0 = equal; 1 = subcostal area wider; 2 = subcostal area narrower.
30. Width of subcostal area and costal area (male tegmen)	0 = subcostal area narrow; 1 = equal; 2 = subcostal area wider.
31. Costa and subcosta of male tegmen	0 = curved; 1 = straight.
32. Media of male	0 = straight; 1 = curved.
33. Medial area and radial area of male tegmen	0 = medial area wider; 1 = equally wide; 2 = radial area wider.
34. Shape of female tegmen	0 = scale-like; 1 = not scale-like.
35. Whitish band on the costal area of male tegmen	0 = absent; 1 = present.
36. Intercalary vein in the precostal area of male tegmen	0 = absent; 1 = present.

determined by specimens available in the collection housed in our laboratory at Institute of Zoology, Shaanxi Normal University. The number of species in the analysis represents about 1/6 of >250 described members of the genus *Chorthippus*. Examination of all the original descriptions for the species of *Chorthippus* shows that the 42 species in the analysis are representative of the diversity of the group. The species *Omocestus haemorhoidalis* was used as an out-group specimen in the analysis.

Characters and character states. After examining all the 42 grasshopper species of *Chorthippus* preserved in our collection, we selected 37 potentially informative

Table 3. The data matrix for the cladistic analysis of *Chorthippus*

Taxa	Character states* 1111111111222222222233333333 01234567890123456789012345678901234567890123456
Omocestus	?00100000000100???0000?00000000000000
aethalinus	00100100110010110011111010101210100001
latipennis	00100110010010110011111010101110100001
longisonus	00101002000010010?20120000101100000001
chinensis	00112110100000 2?10111110031002000000 1
hunanensis	00112012110010010021?2000310020000001
fuscipennis	01111112010000010020111100101200000001
yuanshanensis	11112102110002000011120100100200010000
flexivenus	?00??0020?00?2?00??1?2010011101000000
rufitibis	11012102010002000021120000101000000001
albormarginatus	?1????01200001?00?100?100000020110010
qingzangensis	????2000200001?00?1000100000020111010
dichrous	11002000200001?00110001000001201000001
apricarius	?1????0?100003?00?1100001000120110001
huchengensis	10101000000013?001?00?101000120100001
zhengi	10101000000131???00100010011201000001
changbaishanensis	10111100000000100?0010?11000120100001
brunneus	11100102110002220101001010001201100 01
biguttulus	?11020001100102 00?0100000000100111001
shantungensis	1101110011001?200?2002?00001120110001
hsiai	1???2102211012200111001001011221000 00
albonemus	1???2100110112200111011002011201100 00
dubis	?1??2000111112200101001000011201000 00
rubensabdomenis	?11?20000?0012000?2102?00002120100001
hammarstroenci	?1???1010000130010101100000112011000 0
conicaudatus	1110100200000320000010111001120110000
genheensis	1010110000001 3?0000011?1100112011?000
changtunensis	00?0?1000000112 11?0110011001120110001
louguanensis	10??2102000011011021120110021201000 00
flavabdomensis	0101000000000112?0?1011011001120110000
fallax	1000110010001122010001010002120100101

Table 3. Continued.

Taxa	Character states* 1111111111222222222233333333 01234567890123456789012345678901234567
intermedius	11002100000011210111110103011201100 01
unicubitus	11010000000013220100110100021201 1?001
charpini	00012100010011 2?0100110110020??10?100
chayuensis	?0102100000011?11121020103020?0100101
dahinganlingensis	01000001000013?10101110100111201001 00
deqinensis	11000000001003?00?0012?10002010100101

* The two digit lines under Character states is the character number. The numbers (0, 1, 2, and 3) after each taxon are character states, ? means the missing character.

characters of adult external and internal morphology for cladistic analysis. The multistate characters were treated as nonadditive. The characters, character states and codes are listed in Table 2. The data matrix is presented in Table 3.

Cladistic analysis. The software Hennig 86 1.5 (Farris 1988) was used for the cladistic analysis. The command line *mh;bb*; was* used to construct trees, and *xs w;* was used to do successive weighting. The command line *xs w;mh;bb**; was repeated till three indices (Length, ci, ri) did not change to find out the most parsimonious tree. The command *nelsen;* was used to construct the strict consensus tree from multiple parsimonious trees (Lipscomb 1994). The tree obtained was imported into Winclada (Nixon 1999) along with the data matrix to plot the cladogram (Lipscomb 2000).

Results

Trees obtained. Fifty parsimonious trees were constructed using the data and characters selected, with length = 176 steps, ci = 34%, ri = 77%. Because the objective of this study was to identify major groupings within the diverse assemblage of species in the analysis, strict consensus trees were constructed (Fig. 1). To facilitate the analysis, we mapped the current taxonomic status of every group in the cladogram and developed three well-supported clades (Fig. 1). The three clades, from largest to smallest, are Megaulacobothrus, Glyptobothrus and Chorthippus. All the species of *Altichorthippus* are located in the middle of cladogram and this clade is named Altichorthippus. The root of this clade is weakly supported.

Discussion

Taxonomic status of *Megaulacobothrus*. All nine species of *Megaulacobothrus* examined in the cladistic analysis formed a single clade. This clade is at the base of cladogram, and is supported by five transformations: shape of fastigium (male) is acute-angle 4.2; metazona is longer than prozona 7.2, lower side of post femur is reddish 18.2; hind-tibia is reddish 21.2; tegmen and hindwings of male and female are

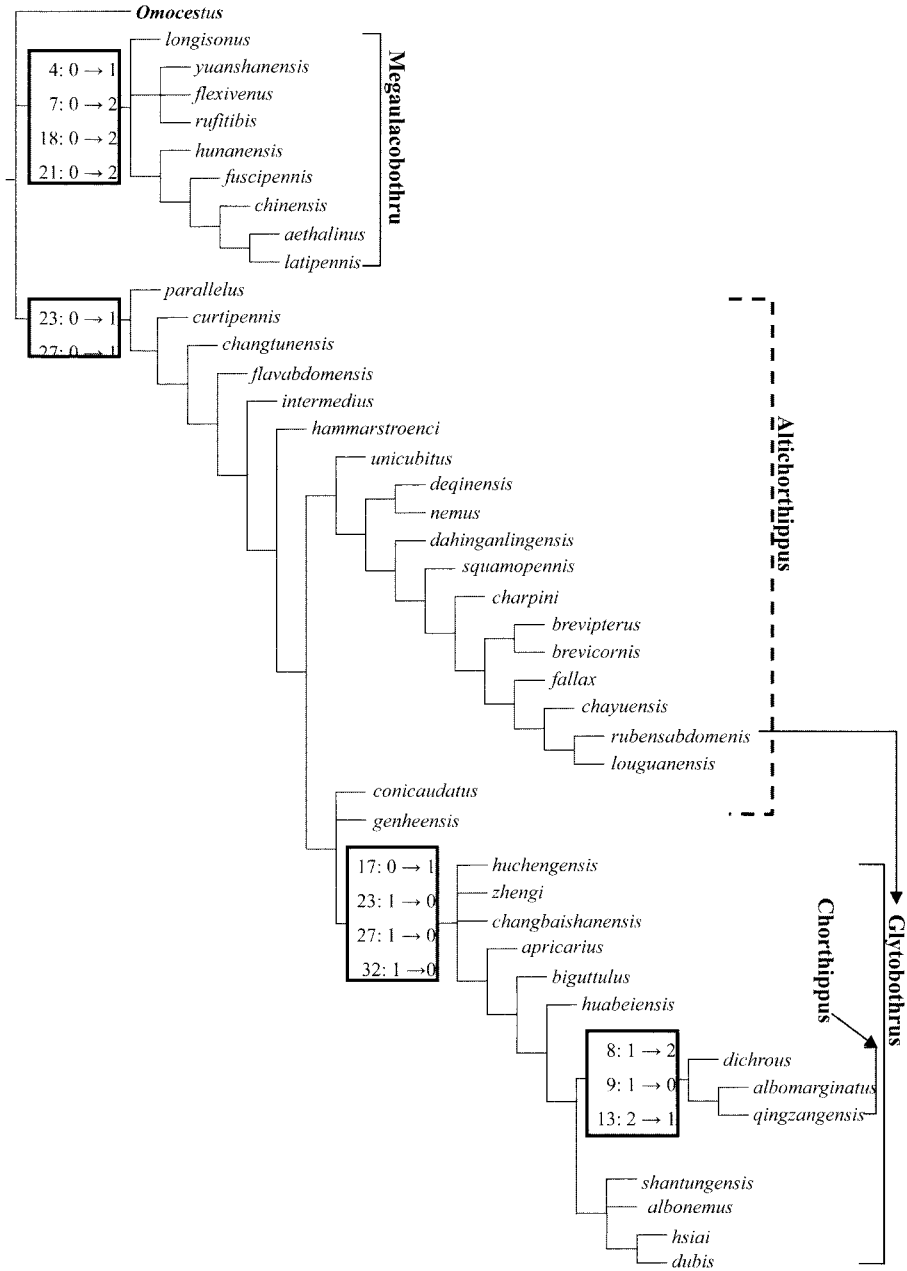

Fig. 1. The strict consensus tree from 50 parsimonious trees showing the transformations are common to all the most-parsimonious trees. The squares show the character transformations on the node, which support the cluster divisions. The numbers in front of ":" are the character number, the letters after ":" are the character changes.

dark 26.1. Besides the character state 26.1, which was used as a subgenus character state by Caudell, there are four other character states that support the clade. This clade and the clade containing other *Chorthippus* species form a paraphyly at the base of the cladogram. Therefore, it appears the current grasshopper genus *Chorthippus* is paraphyletic whereas the current subgenus *Megaulacobothrus* should be removed from *Chorthippus* and be treated as a separate genus with the five character states described above defining the genus.

***Relationships among subgenera* Chorthippus, Glyptobothrus *and* Altichorthippus.** Based on the strict consensus tree, three clades form a large clade at the base of the cladogram. The larger clade is paraphyletic with the Megaulacobothrus clade. The Altichorthippus clade is at the base of the larger clade. The Glyptobothrus clade is located above the larger clade, with the Chorthippus clade nested within it. The larger clade, Altichorthippus, is weakly supported by two character states: tegmen is longer than hind-wing 23.1 and tegmen reaches the end of abdomen 27.1. The location of the Glyptobothrus clade above the larger clade is supported by 5 character states: the stridulatory pegs on the inner side of the post femur are less than 150 17.1; tegmen and hind-wing are equally long 23.0; male tegmen exceeds the tip of post femur 27.0; media of male is straight 32.0, and; the intercalary vein in the precostal area of the male tegmen is present 36.1. These five transformations indicate that the Glyptobothrus clade is a highly diversified group. Of the species selected for this analysis, one *Chorthippus* species used in our study, *C. rubensabdonensis*, should be relocated from the subgenus *Glyptobothrus*, to the *Altichorthippus* clade. This suggests that, although most species of *Glyptobothrus* were assembled in the clade Glyptobothrus, the subgenus that is paraphyletic with some species should be referred to as *Altichorthippus*. The Chorthippus clade is nested in the Glyptobothrus clade, but four transformations show that it is a highly-diversified group. These include: lateral carina in prozona (male and female) is straight 8.2; widest of lateral carina/narrowest in prozona is not more than 2 9.0; tympanal organ is semicircular 13.1, and the post femur has a band in the inner margin 19.0. This larger clade suggests that the subgenus *Altichorthippus* might contain the most ancient species in the genus *Chorthippus*. The *Glyptobothrus* subgenus is derived from *Altichorthippus* and contains some species that should be moved to *Altichorthippus*. The *Chorthippus* subgenus is a more recently evolved group, descending from *Glyptobothrus*. Identification of key subgenus character states of *Glyptobothrus* and those species that should be moved to *Altichorthippus* will depend on a cladistic analysis of all the species in the subgenus.

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