

Phylogeny of the South African species of restioid leafhoppers, tribe Cephalelini (Homoptera: Cicadellidae, Ulopinae)

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A cladistic analysis of the twenty-one South African species of restioid leafhoppers (Cicadellidae: Ulopinae: Cephalelini) is presented, based on fifty characters of the adult morphology. The results are largely congruent with Davies' (1986) subjective hypothesis. Monophyly of the genera *Cephalelus* Evans and *Duospina* Davies is supported. Two major clades are evident within the genus *Cephalelus*.

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Introduction

The tribe Cephalelini Evans, 1947a is a group of austral leafhoppers (family Cicadellidae: subfamily Ulopinae), associated exclusively with plants of the monocotyledonous family Restionaceae (Davies 1986, 1988). These leafhoppers date from Mesozoic times (Linnavuori 1972; Evans 1977) and display a typical Gondwana distribution pattern, similar to their host plants, in the southwestern and eastern Cape Province of South Africa, southwestern and eastern Australia, Tasmania and the North Island of New Zealand (Evans 1947b, 1977; Davies 1986, 1988). The Australian and New Zealand Cephalelini, which are closely related, differ from the South African Cephalelini in several respects (Davies 1986, 1988), demonstrating a well-known biogeographic pattern attributed to the earlier separation of Africa from the post-Gondwana landmass including Australia and New Zealand (Brundin 1965).

Evans (1977) retained the four South African species of the tribe in the genus *Cephalelus* Percheron, 1832 and transferred the fourteen Australo-New Zealand species to seven new genera. Subsequently, Davies (1986, 1988) revised the South African Cephalelini, describing thirteen new species of *Cephalelus* and a new genus,

Duospina, with two new species, to which *Cephalelus capensis* Evans, 1947a was also transferred. Although Davies (1986, 1988) did not undertake a cladistic analysis of the South African species of Cephalelini, he did present a 'probable' phylogeny (Davies 1986: 47): a subjective evaluation based on his personal knowledge of the group (Fig. 1).

In a recent study of host-plant associations between the Cephalelini and their host Restionaceae, Prendini (1997) discovered two additional species of *Cephalelus*. This provided an opportunity to re-evaluate phylogenetic relationships among the South African species of Cephalelini by cladistic analysis, the results of which are presented here.

Methods

An investigation of adult morphology was undertaken for the cladistic analysis, in which fifty characters were scored across the twenty-one species. Thirty-nine of these relate to the male genitalia which have long been recognised as providing extremely valuable, definitive characters throughout the Auchenorrhyncha (Linnavuori 1972; Blocker et al. 1995; Fang et al. 1995). Most

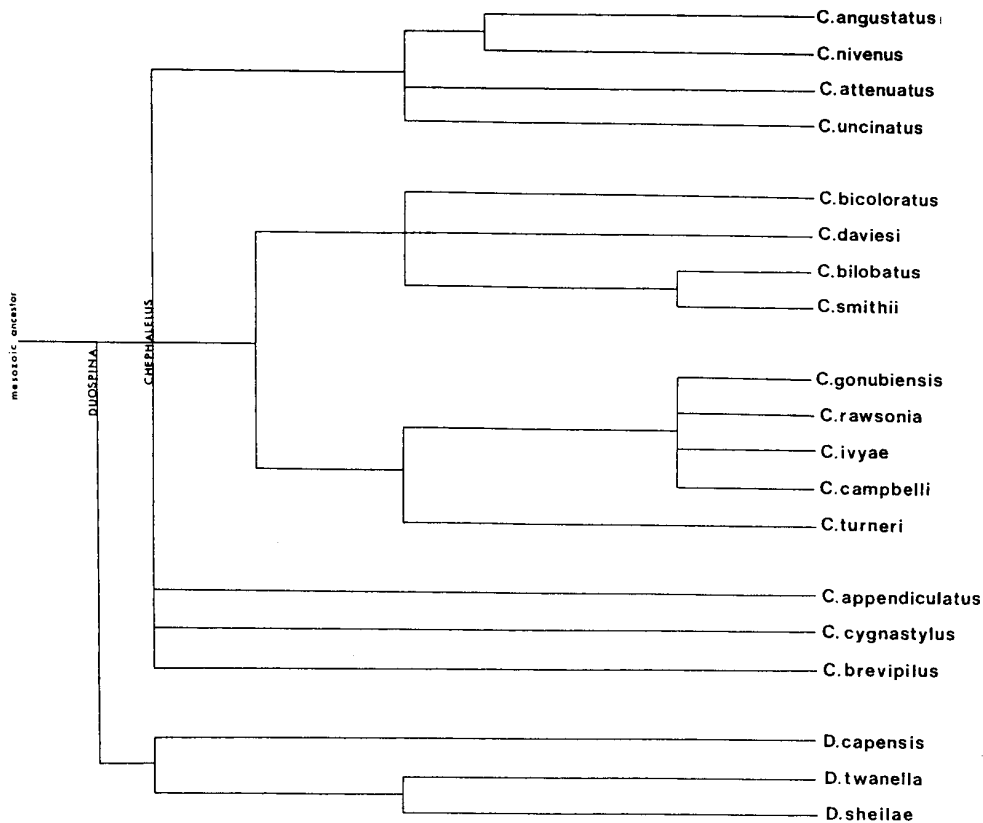


Fig. 1. Davies' (1986: 47) 'probable' phylogeny of the South African species of Cephalelini Evans.

of the characters, particularly those pertaining to male genitalia, female pregenital sternites and crown features, were adopted from Davies' (1986, 1988) comprehensive taxonomic treatment of the group. Additional characters were obtained by examination of freshly-collected material (lodged with the South African Museum, Cape Town) and Davies' collection housed at the Department of Entomology, University of Stellenbosch. Terminology follows Evans (1977), Davies (1986, 1988) and other recent taxonomic treatments of Cicadellidae (Blocker et al. 1995; Fang et al. 1995; Hamilton 1995). The characters used in the analysis are given in Appendix 1 and the character distribution among the taxa in Table 1.

Characters were polarised using the outgroup

method (Nixon & Carpenter 1993). Two Australian species of Cephalelini were included as an outgroup. Characters were not weighted *a priori*. Thirty-three characters were coded into binary states and seventeen were coded into multistates. Ten multistate characters were arranged in hypothesised transformation series (Farris 1970). The remainder, for which transformation series could not be inferred, were treated as unordered (Fitch 1971).

The data were edited in the data manager DADA, version 0.87 (Nixon 1992). The Cephalelini cladograms were prepared using CLADOS, version 1.4 (Nixon 1993). Most parsimonious trees were calculated using Hennig86, version 1.5 (Farris 1988) and PAUP, version 3.1 (Swofford

Table 1. Character distribution used to infer a cladogram for the South African species of Cephalelini Evans*

<i>Alocephaleus ianthe</i> Evans †	100-4100110--00-000-----0----10--001000100000
<i>Anacephaleus minutus</i> Evans †	10024100010--00-000-----0----10--000000200000
<i>Duospina capensis</i> (Evans)	110252001002-010000-----10000101-000000001310
<i>Duospina sheilae</i> Davies	110240001002-011110-----0-00010000201-001020101311
<i>Duospina twanella</i> Davies	110240001002-011110-----0-00010000101-000210211311
<i>Cephaleus angustatus</i> Evans	000010001100120-00120---0-1010----101-012001000120
<i>Cephaleus appendiculatus</i> Davies	000001001101-00-00100---2-0100----2001012110001000
<i>Cephaleus attenuatus</i> Davies	000010010100120-000-----0----101-022001000120
<i>Cephaleus bicoloratus</i> Evans	000120000011-00-000-----11201212-111000101110
<i>Cephaleus bilobatus</i> Davies	000130101001-00-000-----11000212-011120201210
<i>Cephaleus brevipilus</i> Davies	000021001100110-00100---0-0000----1000012111001000
<i>Cephaleus campbelli</i> Davies	000121000011-00-00102001100000---202-111110001110
<i>Cephaleus cygnastylus</i> Davies	00100100100--10-00100---110000----1000012110001000
<i>Cephaleus daviesi</i> Davies	000120000011-00-000-----11110212-111000101110
<i>Cephaleus gonubiensis</i> Davies	000121000011-00-00102011100000---202-112100001110
<i>Cephaleus ivyae</i> Davies	000121000011-00-001020101100011000202-112110211110
<i>Cephaleus linderi</i> Prendini	000121000011-00-00102200110000---202-111110001110
<i>Cephaleus nivenus</i> Davies	000010003100010-00110---0-1000----1001012001000120
<i>Cephaleus pickeri</i> Prendini	000010003100010-00120---0-1010----1000012001000120
<i>Cephaleus rawsonia</i> Davies	000121000011-00-001021001100011000202-112120211110
<i>Cephaleus smithi</i> Davies	000120101001-00-000-----11000312-011120201210
<i>Cephaleus turneri</i> Evans	00012011100--00-00101000110000---012-010000101210
<i>Cephaleus uncinatus</i> Davies	000011002100010-000-----0----103-012001000120

*Characters and character states correspond to Appendix 1. Inapplicable characters are denoted by -.

†Outgroup taxa.

1991). The implicit enumeration (ie*) option of Hennig86, which obtains the complete set of shortest tree(s), proved too time consuming, hence the heuristic branch breaking routine (command sequence 'mh*'; bb*;) was used instead. This algorithm generates multiple trees and then applies branch swapping to them to select the complete set of multiple equally parsimonious tree(s) (Platnick 1989). Successive approximations weighting (command sequence 'xs w; mh*'; bb*;) was applied to find the topologies supported by the most consistent characters (Farris 1969; Carpenter 1988). In PAUP, the heuristic TBR option was employed, again because the exhaustive Branch-and-Bound option was too computer-intensive. This algorithm generates an initial tree(s) by stepwise addition and then subjects this tree to trial re-arrangements to obtain the complete set of multiple equally parsimonious tree(s) (Platnick, 1989), a process referred to as tree-bisection-reconnection (TBR) branch-swapping (Swofford 1991).

The relative degree of support for each node in the resultant tree was assessed by 500 bootstrap replicates (Felsenstein 1985; Sanderson 1989) determined with the TBR option in PAUP. The

bootstrap percentage for each node reflects the frequency with which that node is retrieved from randomly sampled data sets with replacement and thus provides an assessment of the robustness of each node relative to the other nodes in the cladogram (Linder 1991). Although there is widespread debate regarding the value of bootstraps as a statistical test of the robustness of a cladogram (Sanderson 1989; Hillis & Bull 1993; Kluge & Wolf 1993; Carpenter 1996), the values returned provide some indication of the degree of robustness of each node relative to the other nodes on the tree.

Results

The parsimony analysis located a single tree with a length of 125 steps, a consistency index (ci) of 0.57 and a retention index (ri) of 0.78, with the autapomorphies removed (Fig. 2). The successive weighting routine located the same topology, with a ci of 0.79 and an ri of 0.90. The bootstrap percentiles for each node, calculated from 500 replicates, are shown in Fig. 3. Six nodes occurred in fewer than 50 % of the bootstrap replicates.

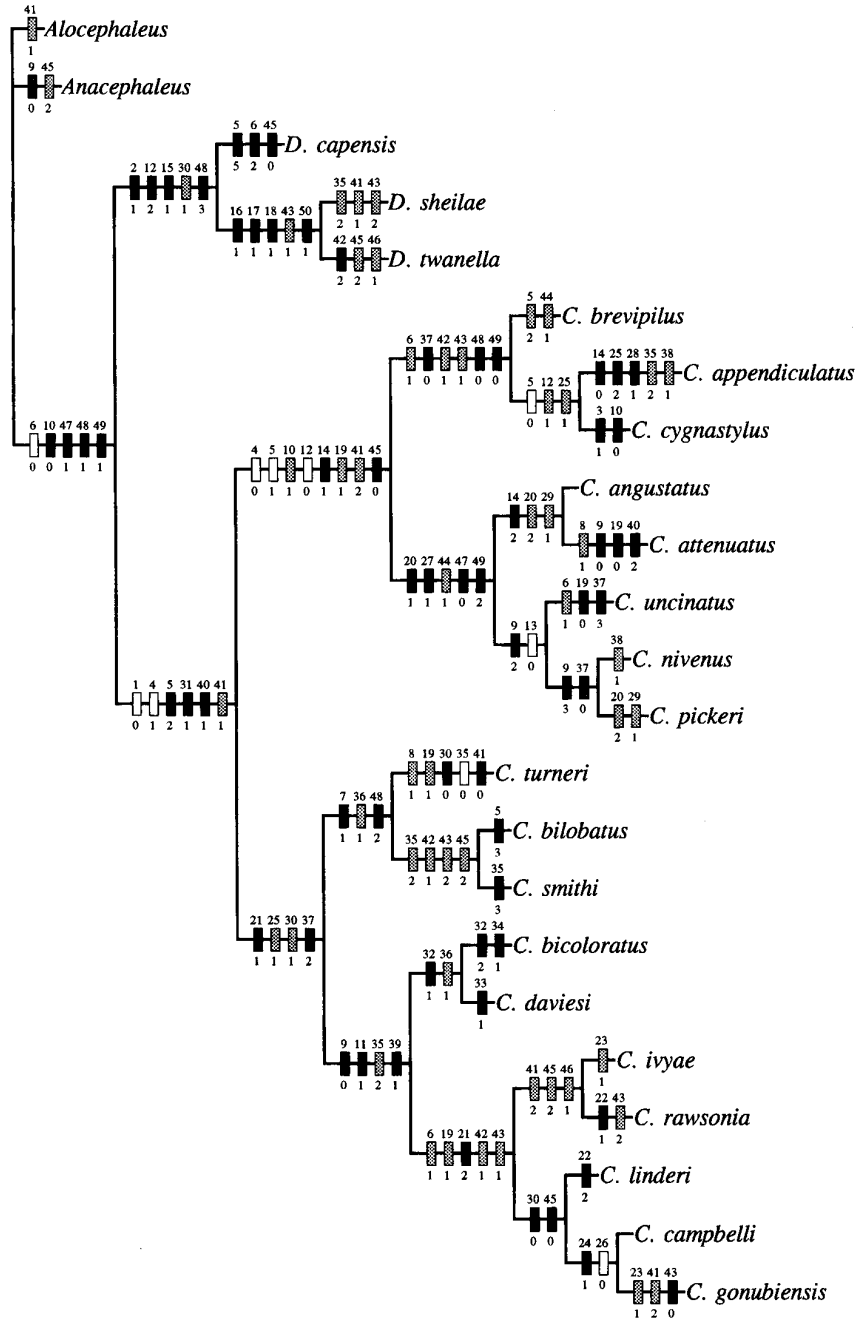


Fig. 2. Cladogram for the South African species of Cepheleini Evans, derived from the character matrix in Table 1. Synapomorphies are indicated by solid bars, parallelisms by empty bars and reversals by shaded bars. The top figure on each character bar gives the character number, whereas the bottom figure gives the character state.

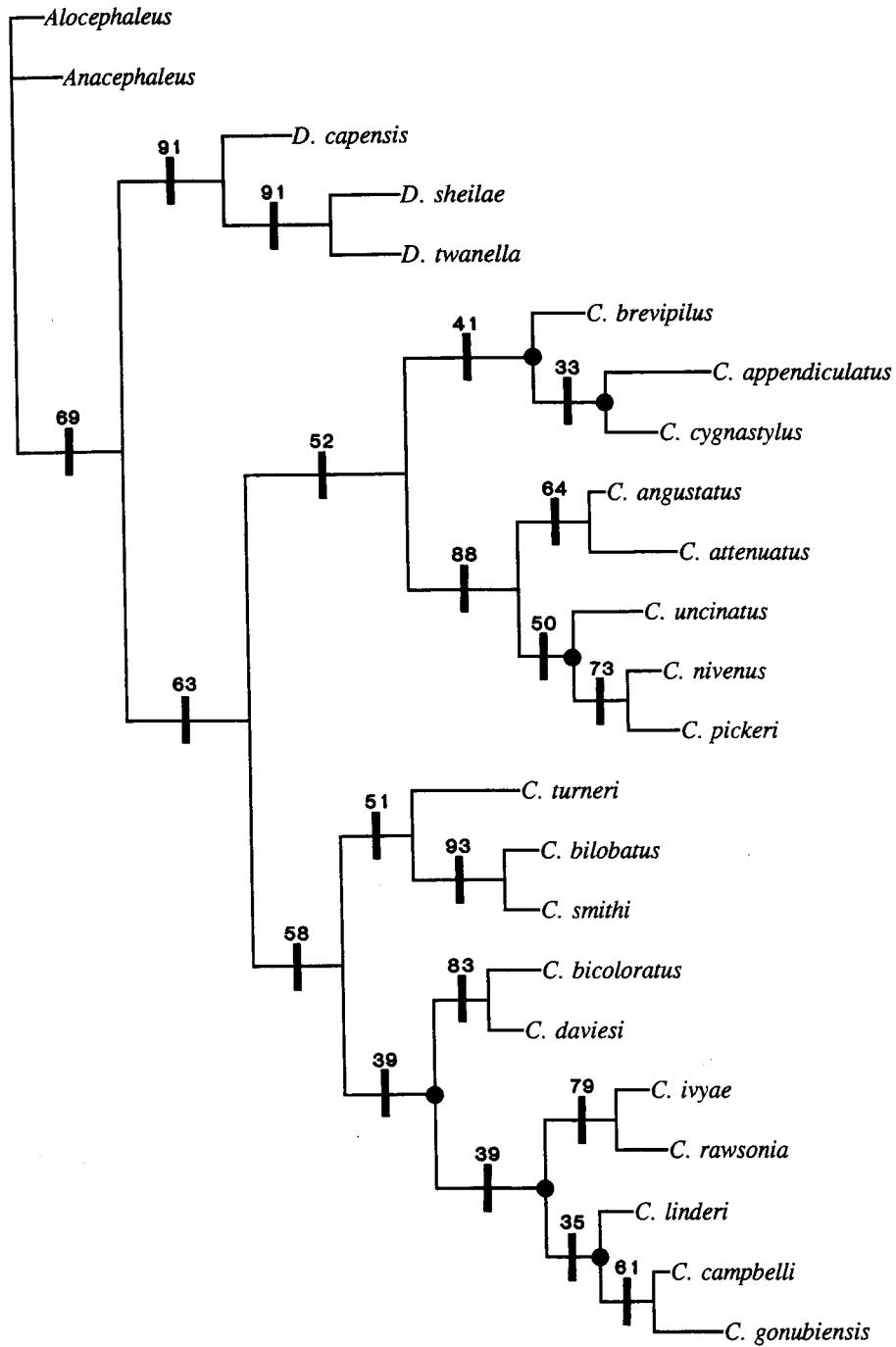


Fig. 3. The tree topology from Fig. 2, showing bootstrap percentiles and nodes that occurred in fewer than 50% of the bootstrap replicates (marked with solid circles).

Discussion

The results of the cladistic analysis are largely congruent with the groupings suggested in Davies' (1986: 47) estimate of the phylogeny of the Cephalelini, although several differences do exist.

Monophyly of the genera *Duospina* and *Cephalelus*, suggested by Davies' scheme, is supported by the cladistic analysis. The three species of *Duospina* form a distinct clade, defined by a pair of stylar appendages, an elongated, curved aedeagal apex with a midventral ridge and a U-shaped female pregenital sternite. The *D. sheilae-D. twanella* sister group, suggested by Davies, is also supported, based on the presence of a single aedeagal appendage, connected to the aedeagal shaft with a membrane, a barbed midventral ridge on the aedeagal apex and a pair of pits on the pronotum. *Duospina* forms a sister clade to the remaining species of Cephalelini, grouped into the genus *Cephalelus*, which is defined by the absence of a stylar apophysis, a posterodorsally rounded pygofer, a pair of teeth located at the mid-length of the aedeagus and a cylindrical crown. However, *Cephalelus* has only 63 % bootstrap support.

Two major clades are evident within the genus *Cephalelus*. The first clade, also recognised by Davies, comprising the species *C. turneri* to *C. bicoloratus*, including *C. linderi* (Prendini 1997) is characterised by a pair of small horn-like aedeagal appendages and an apically situated gonopore. This clade contains three distinct subclades. The subclade containing *C. ivyae* to *C. gonubiensis*, defined by the presence of a pair of large, horn-like aedeagal appendages, appears in Davies' scheme, although the relationships of its component species are unspecified. However, contrary to Davies' suggestion, *C. turneri* forms a sister species to Davies' *C. bilobatus-C. smithi* sister group, in a subclade defined by a dorsally concave aedeagal shaft and a V-shaped female pregenital sternite. The third subclade, viz. the *C. bicoloratus-C. daviesi* sister group, was placed in a polytomy with the *C. bilobatus-C. smithi* sister group by Davies. In the present analysis it is defined by the intermediate position of the aedeagal teeth on the shaft.

The second major clade, comprising *C. brevipilus* to *C. nivenus*, including *C. pickeri* (Prendini 1997), represented as a polytomy in Davies'

scheme, is defined in the present analysis by a shovel-shaped or arrow-shaped aedeagal apex, with short subapical teeth and the pygofer sloping posterodorsally, with a beak-like extension posteroventrally. Although the affinities of the polytymous species (*C. appendiculatus*, *C. brevipilus* and *C. cygnastylus*) are resolved, with *C. brevipilus* forming a sister species to the *C. appendiculatus-C. cygnastylus* sister group, the support for this subclade is weak. Its sister subclade, including *C. angustatus*, *C. attenuatus*, *C. nivenus* and *C. uncinatus*, that was recognised by Davies, is defined by lyre-shaped aedeagal appendages, addressed to aedeagal shaft and the ovipositor extending far beyond the edge of the tegmina. However, Davies' putative *C. angustatus-C. nivenus* sister group is not supported.

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Appendix 1. Characters and character states used to infer a cladogram for the South African species of Cephalelini Evans.

Multistate characters were coded additively, unless otherwise indicated. Characters indicated with an asterisk are autapomorphies that were excluded from the analysis.

Styles

- 1 Stylar apophysis is absent (0) or present (1).
- 2 Pair of stylar appendages are absent (0) or present (1).
- 3 Stylar tip is hook-shaped (0) or swan-shaped (1).*

Pygofer

- 4 Posterodorsally, pygofer is sloping (0), rounded (1), or square (2). [nonadditive]
- 5 Posteroventrally, pygofer is without lobes or extensions (0), with beak-like extension (1), with one rounded lobe (2), with two rounded lobes (3), with triangular extension (4), or with rectangular extension (5). [nonadditive]

Aedeagal shaft

- 6 In cross-section, shaft is dorsoventrally flattened (0), cylindrical (1), or laterally flattened (2).
- 7 Dorsal surface of shaft is concave: no (0); yes (1).
- 8 Shaft is expanded subapically: no (0); yes (1).
- 9 In lateral aspect, shaft is straight (0), curved (1), uncinately (2), or sinuate (3).
- 10 Shaft is relatively short (0) or relatively long (1).

Aedeagal apex

- 11 Tip of apex is obtuse (0) or acute (1).
- 12 Apex is shovel-shaped or arrow-shaped (0), wedge-shaped (1), or elongated and curved in lateral aspect (2). [nonadditive]
- 13 If shovel-shaped or arrow-shaped, apex is small (0) or large (1).

- 14 Subapical teeth are absent (0), short (1), or long (2).
 15 Midventral ridge on apical third is absent (0) or present (1).*
 16 If present, midventral ridge with barb at tip absent (0) or present (1).

Aedeagal appendages

- 17 Single appendage is absent (0) or present (1).
 18 Membrane connecting appendage to aedeagal shaft is absent (0) or present (1).
 19 Paired appendages are absent (0) or present (1).
 20 If paired, appendages are not lyre-shaped (0), small and lyre-shaped (1), large and lyre-shaped (2). [nonadditive]
 21 If paired, appendages are not horn-like (0), small and horn-like (1), large and horn-like (2). [nonadditive]
 22 If paired and horn-like, appendages are distally parallel (0), diverging slightly (1), or diverging markedly (2).
 23 If paired and horn-like, appendages are tapering (0), or claviform (1).
 24 If paired and horn-like, appendages are strongly elbowed: no (0); yes (1).
 25 If present, appendages arise from socle (0), shaft (1), or subapically (2). [nonadditive]
 26 If appendages arising from shaft, arising ventrally (0), or laterally (1).
 27 If present, appendages are adpressed to aedeagal shaft: no (0); yes (1).
 28 If present, appendages are hinged: no (0); yes (1).*
 29 If present, appendages with outer edges smooth (0) or serrated (1).

Aedeagal teeth

- 30 Teeth are absent (0) or present (1).
 31 If present, vertical position of teeth on aedeagal shaft is near base (0) or at mid-length (1).
 32 If present, lateral position of teeth on aedeagal shaft is dorsally-angled (0), midway between dorsal and ventral surfaces (1), or ventrally-angled (2).
 33 If present, teeth are small (0) or large (1).*
 34 If present, number of pairs of teeth: one (0); two (1).*

Gonopore

- 35 Gonopore is square (0), round (1), teardrop-shaped (2), or elongate (3). [nonadditive]
 36 Gonopore is small (0) or large (1).
 37 Gonopore is located *ca.* two-thirds along length of aedeagal shaft (0), subapically on aedeagal shaft (1), apically (2), at tip of aedeagal apex (3).
 38 If gonopore is located *ca.* two-thirds along length of aedeagal shaft, groove connecting gonopore to aedeagal apex is absent (0) or present (1).
 39 Subapical teeth of gonopore are absent (0) or present (1).

Crown

- 40 In cross-section, crown is dorsoventrally flattened (0); cylindrical (1), or laterally flattened (2).
 41 Crown is extremely short (0), medium in length (1), or extremely long (2).
 42 In dorsal aspect, crown tapers towards apex (0), expands towards apex (1), or tapers rapidly and expands subsequently (2).
 43 Crown apex is unmodified (0), swollen (1), or spatulate (2).
 44 Crown apex is attenuated: no (0); yes (1).
 45 Mid-dorsal ridge of crown is absent (0), weakly-developed (1), or strongly-developed (2).
 46 Mid-ventral ridge of crown is absent (0) or weakly-developed (1).

Tegmina

- 47 Tegminal venation is obscure (0) or distinct (1).

Pregenital sternite of female

- 48 Margin entire (0), with groove or incision (1), with V-shaped indentation (2), or with U-shaped indentation (3).

Ovipositor

- 49 Ovipositor extends to edge of tegmina, or stops short thereof (0), extends just beyond edge of tegmina (1), or extends far beyond edge of tegmina (2).

Pronotum

- 50 Pronotum with a pair of pits absent (0) or present (1).