Phylogeny of the leafhopper subfamily Deltocephalinae (Hemiptera: Cicadellidae) based on molecular and morphological data with a revised family-group classification

JAMES N. ZAHNISER and CHRISTOPHER H. DIETRICH
Illinois Natural History Survey, Institute for Natural Resource Sustainability, University of Illinois at Urbana-Champaign, IL, U.S.A.

Abstract. Deltocephalinae, a highly diverse and economically important subfamily of leafhoppers, contains over 6200 species and 36 tribes distributed worldwide in habitats ranging from xeric grasslands and shrublands to tropical rainforests. Recent morphological and molecular phylogenetic analyses of Cicadellidae and a morphology-based analysis of Deltocephalinae and related subfamilies indicated that several previously recognized cicadellid subfamilies are closely related to or derived from within Deltocephalinae, but these analyses did not provide a comprehensive or well-supported hypothesis of the phylogeny of Deltocephalinae s.l. due to either low taxon sampling or low branch support. Here, taxon sampling was increased to include members of most family-group taxa of Deltocephalinae and molecular data (~2800 bp 28S rDNA and ~350 bp histone H3) were added to improve the phylogenetic estimate. Five putative outgroup taxa were included, and parsimony and Bayesian analyses of the combined molecular and morphological (119 characters) data and maximum likelihood analyses of the 28S data showed strong support for the monophyly of Deltocephalinae as defined here. Branches near the base of the tree and towards the tips were longer and better supported than many of the shorter internal branches. Similar to a previous morphological phylogenetic analysis of Deltocephalinae, all of the grass- and sedge-specializing tribes were recovered in one common clade, with a few apparent reversals to nongrass feeding. Although support for this clade was low and requires further testing, the results suggest that grass/sedge specialization is a phylogenetically conservative trait within Deltocephalinae. The history of the classification of Deltocephalinae and related subfamilies is reviewed, and based on the results of the phylogenetic analyses presented here, a revised family-group taxonomic classification is proposed. In addition to subfamilies that were recently included in Deltocephalinae, the following are considered junior synonyms of Deltocephalinae: Acostemminae syn.n., Arrugadinae syn.n., Drakensbergeninae syn.n., Mukariinae syn.n. and Stegelytrinae syn.n. The morphological characters supporting this interpretation of Deltocephalinae are provided and discussed, and a description of the subfamily is provided. A new tribe, Faltalini tribe n. (11 genera, 31 species) is described, and Magnentiini placement n. and Paraphrodini placement n. are transferred to Deltocephalinae from Nioniinae and Aphrodinae, respectively. New placements of genera include: Twiningia Ball and Eusama Oman.
Based on morphological evidence, some of these groups, which were previously recognized as separate subfamilies because of their highly exaggerated or apomorphic external characters (e.g. the highly modified head structure of Eupelcinae; the robust beetle-like appearance of Penthiminae), possess some synapomorphies of the deltocephaline lineage (e.g. of the male genitalia), thus reinforcing the findings from molecular analyses. Some other subfamilies sensu Oman et al. (1990), i.e. Acostemminae, Arrugadinae, Drakensberginae and Mukarini, have been suggested to be related to Deltocephalinae based on morphology (Dietrich, 1999; Zahniser & Dietrich, 2008), but these hypotheses were not tested with molecular data.

Other previous phylogenetic studies of deltocephalines have focused on the relationships among genera in tribes (Knight & Webb, 1993; Fang et al., 1993, 1995; Kamitani, 1999; Zahniser, 2008) or among species within genera (Ross, 1968; Knight, 1974; Blocker, 1983; Blocker & Johnson, 1988a, b, 1990a, b, c; Whitcomb & Hicks, 1988; Dietrich et al., 1997, 1998; Zahniser & Hicks, 2007). These studies provided important insights and have influenced subsequent studies, including those presented here.

Among the phylogenetic studies of the group, the taxon and character sampling in the morphological analysis of Deltocephalinae and related subfamilies by Zahniser & Dietrich (2008) is the most comprehensive to date. The results and conclusions of that analysis were limited by low branch support and other analyses were limited by low taxon sampling. In the analyses presented here, taxon sampling was increased significantly over previous analyses and molecular data (28S rDNA and histone H3 regions) were combined with morphological data to infer the phylogeny of the deltocephaline lineage based on all available evidence. The resulting phylogeny has been used to revise the classification and provide a framework in which to understand diversification patterns and the evolution of host use in Deltocephalinae. It is hoped that a comprehensive and well-supported phylogenetic estimate of the group will help to stabilize the classification.

Classification

In part because of its size (~6200 described species) and morphological diversity, Deltocephalinae and related subfamilies have eluded a stable classification. Attempts to characterize the group morphologically have not succeeded because

Introduction

Deltocephalinae as proposed here (see Classification below) contains over 6200 described species placed in over 850 genera (McKamey, in press), making it the largest subfamily of Cicadellidae based on the number of described species. Deltocephalines feed on the phloem sap of a wide variety of vascular plants, and species range from monophagous to polyphagous. Deltocephalines are diverse and abundant components of tropical, subtropical and temperate forest ecosystems, but they are possibly best known for their diversification patterns and host use in Deltocephalinae. It is hoped that a comprehensive and well-supported phylogenetic estimate of the group will help to stabilize the classification.

Phylogeny

Recently, phylogenetic analyses of Cicadellidae based on morphological and molecular data (Dietrich, 1999; Dietrich et al., 2001) and of Deltocephalinae based on morphological data (Zahniser & Dietrich, 2008) resolved a well-supported lineage including Deltocephalinae and several other subfamilies sensu Oman et al. (1990). These analyses showed that Deltocephalinae sensu Oman et al. (1990) is paraphyletic with respect to most of these other leafhopper subfamilies, and in recent taxonomic works, Eupelcinia, Koebelinina, Paraboloponinae, Penthiminae and Selenoccephalinae were treated as synonyms of Deltocephalinae (Dietrich & Rakitov, 2002; Dietrich & Dmitriev, 2003). Additionally, the tribes Occinirvanini (Nirvanininae) and Anoterostemmini (Cicadellinae) have been placed in Deltocephalinae (Dmitriev, 2000; Dietrich, 2004) based on morphological evidence. Some of these groups, which

(Athysanini: Platymetopiina), placement n.; Cerrillus Oman (Athysanini), placement n.; Scaphotettix Matsumura and Agrica Strand (Mukarini), placement n.; Loralia Evans and Phlogotettix Ribaut (Deltocephalinae, unplaced to tribe), placement n. The recognition of Scaphioideini Oman 1943 as a nomen nudum results in

...
Table 1. A summary of six classifications of the past 60 years.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Acinopterus</td>
<td>2*Euscelini</td>
<td>4*Acinopterini</td>
<td>7*Acinopterini</td>
<td>10*Platymetohipina</td>
<td>–</td>
<td>18*Acinopterini</td>
</tr>
<tr>
<td>Acostemma</td>
<td>1*Krisnini</td>
<td>–</td>
<td>–</td>
<td>12*Krisnini</td>
<td>16*Acostemminae</td>
<td>21*Adamin</td>
</tr>
<tr>
<td>Adama</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>9*Anoterostemmina</td>
<td>–</td>
<td>18*Anoterostemminae</td>
</tr>
<tr>
<td>Anoterostemma</td>
<td>1*Anotrophi</td>
<td>–</td>
<td>–</td>
<td>9*Anoterostemmina</td>
<td>–</td>
<td>18*Anoterostemminae</td>
</tr>
<tr>
<td>Athysanida</td>
<td>4*Euscelini</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Athysanina</td>
<td>–</td>
<td>18*Athysaninia</td>
</tr>
<tr>
<td>Balclutha</td>
<td>2*Balcluthini</td>
<td>6*Balcluthini</td>
<td>7*Macrostellini</td>
<td>10*Macrostelina</td>
<td>–</td>
<td>18*Balkluthini</td>
</tr>
<tr>
<td>Cerrillus</td>
<td>1*Hecalini</td>
<td>–</td>
<td>7*Hecalini</td>
<td>–</td>
<td>–</td>
<td>18*Cerrillini</td>
</tr>
<tr>
<td>Chiasmus</td>
<td>1*Anotrophi</td>
<td>–</td>
<td>–</td>
<td>11*Eupelici</td>
<td>–</td>
<td>18*Chiasmusina</td>
</tr>
<tr>
<td>Cidacula</td>
<td>2*Euscelini</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Cicadulina</td>
<td>–</td>
<td>18*Cicadulina</td>
</tr>
<tr>
<td>Cochilorhës</td>
<td>1*Anotrophi</td>
<td>6*Cochlorhinë</td>
<td>–</td>
<td>10*Cochlorhinë</td>
<td>–</td>
<td>18*Cochlorhinë</td>
</tr>
<tr>
<td>Coryphaelus</td>
<td>3*Euscelini</td>
<td>–</td>
<td>–</td>
<td>10*Athysanina</td>
<td>–</td>
<td>18*Coryphaelina</td>
</tr>
<tr>
<td>Deltocoephalus</td>
<td>5*Euscelini</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Deltocephalinë</td>
<td>–</td>
<td>14*Deltocoephalinae</td>
</tr>
<tr>
<td>Doratura</td>
<td>1*Anotrophi</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>9*Eupelicanë</td>
<td>14*Deltocoephalinae</td>
<td>18*Doraturina</td>
</tr>
<tr>
<td>Dorycephales</td>
<td>1*Dorycephe</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Eupelicanë</td>
<td>–</td>
<td>18*Dorycephales</td>
</tr>
<tr>
<td>Drabescus</td>
<td>2*Euscelini</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Athysanina</td>
<td>–</td>
<td>21*Drabescina</td>
</tr>
<tr>
<td>Drakensbergena</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>19*Drakensbergena</td>
</tr>
<tr>
<td>Dwightia</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>19*Dwighti</td>
</tr>
<tr>
<td>Eupelix</td>
<td>2*Eupelici</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Athysanina</td>
<td>–</td>
<td>19*Eupelicia</td>
</tr>
<tr>
<td>Euscelis</td>
<td>1*Euscelini</td>
<td>6*Deltocephali</td>
<td>7*Euscelini</td>
<td>–</td>
<td>–</td>
<td>19*Euscelina</td>
</tr>
<tr>
<td>Faltala</td>
<td>2*Euscelini</td>
<td>–</td>
<td>7*Euscelini</td>
<td>–</td>
<td>–</td>
<td>19*Faltala</td>
</tr>
<tr>
<td>Fieberiella</td>
<td>1*Euscelini</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Platymetohipina</td>
<td>14*Fieberiellina</td>
<td>18*Fieberiellina</td>
</tr>
<tr>
<td>Goniagnathus</td>
<td>1*Euscelini</td>
<td>–</td>
<td>–</td>
<td>10*Goniagnathë</td>
<td>18*Goniagnathë</td>
<td>18*Goniagnathë</td>
</tr>
<tr>
<td>Grypotes</td>
<td>2*Euscelini</td>
<td>–</td>
<td>–</td>
<td>10*Athysanina</td>
<td>–</td>
<td>18*Grypote</td>
</tr>
<tr>
<td>Hecalus</td>
<td>1*Hecalina</td>
<td>6*Hecalina</td>
<td>7*Hecalini</td>
<td>–</td>
<td>18*Hecalini</td>
<td>18*Hecalini</td>
</tr>
<tr>
<td>Hypacostemma</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>18*Hypacostrëmìnë</td>
</tr>
<tr>
<td>Ianeira</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>21*Ianeirina</td>
</tr>
<tr>
<td>Jassus</td>
<td>4*Jassina</td>
<td>1*Jassina</td>
<td>6*Jassina</td>
<td>–</td>
<td>15*Jassina</td>
<td>18*Jassina</td>
</tr>
<tr>
<td>Koebelia</td>
<td>2*Koebelini</td>
<td>1*Koebelina</td>
<td>6*Koebelina</td>
<td>–</td>
<td>15*Koebelina</td>
<td>18*Koebelina</td>
</tr>
<tr>
<td>Krisina</td>
<td>3*Krisnini</td>
<td>–</td>
<td>1*Krisnini</td>
<td>6*Krisnini</td>
<td>–</td>
<td>15*Krisnini</td>
</tr>
<tr>
<td>Ledra</td>
<td>3*Ledrina</td>
<td>1*Ledrinë</td>
<td>6*Ledrinë</td>
<td>–</td>
<td>15*Ledrina</td>
<td>18*Ledrina</td>
</tr>
<tr>
<td>Limotettix</td>
<td>1*Euscelini</td>
<td>6*Deltocephali</td>
<td>7*Euscelini</td>
<td>–</td>
<td>–</td>
<td>15*Limotettix</td>
</tr>
<tr>
<td>Luheria</td>
<td>2*Euscelini</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Athysanina</td>
<td>–</td>
<td>15*Luheria</td>
</tr>
<tr>
<td>Magnentities</td>
<td>1*Macrosteli</td>
<td>6*Macrosteli</td>
<td>7*Macrosteli</td>
<td>–</td>
<td>15*Macrosteli</td>
<td>18*Macrosteli</td>
</tr>
<tr>
<td>Magnusentia</td>
<td>1*Macropsina</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>15*Magnusentia</td>
</tr>
<tr>
<td>Mukaria</td>
<td>5*Nirvanina</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>18*Mukaria</td>
</tr>
<tr>
<td>Neobala</td>
<td>2*Euscelini</td>
<td>–</td>
<td>Neoballina [sic]</td>
<td>7*Neobalina</td>
<td>–</td>
<td>18*Neobala</td>
</tr>
<tr>
<td>Occinivarna</td>
<td>2*Nirvanina</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>18*Occinivarna</td>
</tr>
<tr>
<td>Opsiis</td>
<td>2*Euscelini</td>
<td>6*Deltocephali</td>
<td>7*Euscelini</td>
<td>10*Platymetohipina</td>
<td>16*Bhatiinë</td>
<td>18*Opsiis</td>
</tr>
<tr>
<td>Parabolopona</td>
<td>4*Selonocephali</td>
<td>–</td>
<td>–</td>
<td>10*Paraboloponina</td>
<td>–</td>
<td>18*Paraboloponina</td>
</tr>
<tr>
<td>Paralimnus</td>
<td>1*Parodylii</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Deltocephalinë</td>
<td>–</td>
<td>18*Paralimninen</td>
</tr>
<tr>
<td>Paraprophës</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>21*Paraprophës</td>
</tr>
<tr>
<td>Penthimmia</td>
<td>1*Penthimmë</td>
<td>6*Penthimmë</td>
<td>7*Penthimmë</td>
<td>–</td>
<td>18*Penthimmë</td>
<td>21*Penthimmë</td>
</tr>
<tr>
<td>Platymetohipina</td>
<td>4*Platymetohipina</td>
<td>–</td>
<td>–</td>
<td>10*Platymetohipina</td>
<td>–</td>
<td>18*Platymetohipina</td>
</tr>
<tr>
<td>Portanina</td>
<td>2*Portanini</td>
<td>–</td>
<td>8*Portanini</td>
<td>–</td>
<td>–</td>
<td>22*Portanini</td>
</tr>
<tr>
<td>Scaphoidiens</td>
<td>4*Scaphoidi</td>
<td>–</td>
<td>–</td>
<td>10*Scaphoidi</td>
<td>–</td>
<td>18*Scaphoidiens</td>
</tr>
<tr>
<td>Scaphytopiens</td>
<td>4*Scaphytopi</td>
<td>–</td>
<td>–</td>
<td>10*Scaphytopi</td>
<td>–</td>
<td>18*Scaphytopiens</td>
</tr>
<tr>
<td>Selenocephalinae</td>
<td>1*Selenocephali</td>
<td>–</td>
<td>–</td>
<td>10*Selenocephalinae</td>
<td>–</td>
<td>18*Selenocephalinae</td>
</tr>
<tr>
<td>Stirellus</td>
<td>2*Euscelini</td>
<td>6*Deltocephali</td>
<td>–</td>
<td>10*Stirellina</td>
<td>–</td>
<td>18*Stirellina</td>
</tr>
<tr>
<td>Stenometopius</td>
<td>Nirvanina</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>18*Stenometopius</td>
</tr>
<tr>
<td>Steglytra</td>
<td>Coelidiinae</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>18*Steglytra</td>
</tr>
</tbody>
</table>

© 2010 The Authors
Journal compilation © 2010 The Royal Entomological Society, Systematic Entomology, 35, 489–511
of a lack of stable morphological characters, apparently high
degrees of homoplasy, some highly derived or exaggerated
morphologies and because different authors historically empha-
sized the importance of a different, limited number of char-
acters. Also, most workers have focused on regional faunas,
which do not provide the broad perspective needed for a com-
prehensive classification. What follows is a historical account
of the classification of Deltocephalinae and related subfam-
ilies over the last 60 years, highlighting some of the major
groupings proposed by different authors and some of the mor-
phological characters upon which they were based.

Table 1 summarizes six of the most comprehensive clas-
sifications of the past 60 years. Because of its inclusiveness
and for the purposes of this discussion, Evans’ (1947)
classification of world Jassoida (sic = Cicadellidae), based pri-
marily on characters of the head and wings, provided a frame-
work upon which subsequent classifications have been based.
He placed genera that were more recently considered delto-
cephalines into five subfamilies. One of these, Aphrodiinae,
included four tribes, of which the most relevant to this study
is Aphrodisini. This tribe, characterized mainly on the position
of the ocelli near the anterior margin of the head and dis-
tant from the eyes, contained genera now widely believed not
to be closely related (see Linnavuori, 1979a). Among them are
Anoterostemma Löw, Aphrodes Curtis, Arrugada Oman,
Cochlorhinus Uhler, Doratura Sahiberg and Luheria Osborn,
of which all but Aphrodes were all subsequently placed in
other subfamilies and tribes. Hamilton’s (1975) tribe Aphro-
dini bears a resemblance to Evans’ interpretation. Hamilton
placed Aphrodes, Anoterostemma, Doratra, Neobala Oman
and Xestocephalus Van Duzee as nominate genera of subtribes
of Aphrodisini, which was placed within his broad circumscrip-
tion of Aphrodiinae (= Deltocephalinae). However, the degree
of variability in the characters purported to distinguish the
group did not exclude many other groups, and few taxonomists
have followed this and other aspects of Hamilton’s classifi-
cation. Aphrodisinae was recognized in a more strict sense as
a subfamily separate from Deltocephalinae by Oman (1949),
Linnavuori (1979a) and Oman et al. (1990). The other three
tribes in Evans’ Aphrodiinae (Errhomenellini, Evacanthini and
Signorettini) are not related to any deltocephaline lineages
(Dietrich, 1999; Dietrich et al., 2001).

Evans’ Euscelinae closely approximates the interpretation
of Deltocephalinae sensu Oman et al. (1990). Exceptions are
the inclusion of Neobala, placed in its own subfamily by
Linnavuori (1959) and Oman et al. (1990) and Xestocephali,
usually considered as its own subfamily. Tribes of Evans’
Euscelinae that were retained in subsequent classifications are
Balcluthini and Macrostellini (synonymized by Knight & Webb,
1993) and Platymetopini (although in a restricted sense).
Oman (1949) also recognized the tribes Acinopterini, which
was included in Evans’ Euscelini; Scaptopytini, which was
included in Evans’ Platymetopini; and Cochlohrhini, which
was included in Evans’ Aphrodisini. Evans also retained the
tribe Euscelini (relatively large, robust leafhoppers, clypellus
expanded apically, Y-shaped connective, two closed subapical
cells), which was later called Athysanina by Hamilton
(1975) and Athysanini by Oman et al. (1990). Oman (1949)
did not recognize Platymetopini, and included many of
Evans’ platymetopine genera in his broad circumscription of
Deltocephalini, parts of which Oman et al. (1990) included
in other tribes. Linnavuori (1959) considered Deltocephalini
in a more restricted sense, including only genera with a
tapered clypellus, usually three closed forewing subapical
cells and linear connective [= Deltocephalini+Paralimmini
sensu Oman et al. (1990)]. The classification of genera
into Deltocephalini and Paralimmini has not been consistent
among workers with respect to genital characters. European
workers [e.g. Emeljanov, 1962, 1999; Ossianilsson, 1983; see
discussion in Webb & Heller (1990)] placed genera with a
linear connective articulated with the aedeagus in Paralimmini
and genera with a linear connective fused to the aedeagus
in Deltocephalini, but this was not followed by Oman et al.
(1990), as several genera with an articulated connective and
aedeagus were placed in Deltocephalini. Kamitani (1999)
reassigned many of the genera placed in Deltocephalini by
Oman et al. (1990) to Paralimmini, and the issue was discussed
recently by Webb & Viraktamath (2009).

In the subfamily Hecalinae, Evans included Hecalin,
Dorycephalin, Eupelicini and Paradorydiini [the last three are
in Eupelcini sensu Oman et al. (1990)], based on the shared

Table 1. Continued

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Tetartostylus</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>18Platymetopini</td>
<td>14Tetartostylini</td>
<td>18Tetartostylini</td>
</tr>
<tr>
<td>Xestocephalus</td>
<td>2Xestocephalini Xestocephalina</td>
<td>8Xestocephalina</td>
<td>17Xestocephalina</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a Genera that have been treated as the type genus for a subtribe, tribe or subfamily.
b Included in tribe Nionini.
c Mentioned as a separate subfamily, and not included in Aphrodinae.
d Treated as a tribe of Cicadellinae.
e Treated as a tribe of Nirvaninae.
– Not treated in the author’s classification.

Subfamilies are in bold and with a superscript number. For each author, tribes with the same superscript number belong to the correspondingly numbered subfamily in bold except Hamilton (1975), where all groups treated are in the subfamily Aphrodinae (except two marked subfamilies), tribes are in bold and with a superscript number; subtribes with the same number belong to the correspondingly numbered tribe.
characters of an elongate head and genae strongly emarginate below the eyes. In contrast, Oman (1949) recognized two subfamilies for these groups, Hecalini and Dorycephealinae, based on differences in the appearance of the proepisternum (small and concealed in Hecalini). Subsequent authors classified Hecalini sensu Oman 1949 as a tribe of Deltocephalinae (Linnatuori, 1959; Oman et al., 1990) or of Aphrodesinae (Hamilton, 1975), and Oman et al. (1990) retained Eupelcinini as a separate subfamily. Hamilton (1975, 1983) recognized the tribes Eupelcini and Paradorydiini in Aphrodesinae, but did not consider Dorycephealini to be closely related. Subsequently, Hamilton (2000) defined the distinction between Hecalini and discussed characters shared by Hecalini and Dorycephealini.

Evans' subfamily Jasmini included three tribes that other authors cited as closely related to Deltocephalinae: Selenocephalini, Krisnini and Penthimini. The other four tribes that Evans included are now regarded as members of Iassinae (as well as Krisna Kirkaldy). Evans' Selenocephalini mostly included members of Linnatuori & Al-Ne'amy's (1983) selenocephaline tribes Drabescini (= Bhatini, Paraboloponini), Janeirini and Selenocephalini. Linnatuori & Al-Ne'amy (1983) also recognized the tribes Adamini, Dwightlini (now named Dwightlini McKamey, 2003) and Hypacostemmini in Selenocephalinae, and they cited the following diagnostic characters for the subfamily: anterior tentorial branches falcate, first valvulae with striate sculpturing pattern, anterior margin of head with transverse sulci, antennal pits close to upper margin of face, antennal ledge strong and epistomal suture keeled. However, Zhang & Webb (1996) reviewed these characters and pointed out that not all occur in all selenocephaline tribes, and that many of them are also shared with members of Acostemminae, Penthimini and some Deltocephalinae. They concluded that Selenocephalinae was not defined by any universally shared derived characters, and that even its distinction from Deltocephalinae, also a morphologically poorly defined group, was insufficient.

In Krisnini, Evans included Krisna and Acostemma Signoret [and related genera in Acostemminae sensu Oman et al. (1990) and Evans (1972b)]. Linnatuori & Quatuau (1975) restricted this tribe to include only Krisna, placed it in Iassinae and recognized the subfamily Acroponinae for Acostemma and related genera. Evans (1972b) had first recognized a separate subfamily for this group, Acostemminae. However, Hamilton (1975) retained Krisnini as a tribe of Aphrodesinae, and considered Acostemminae to be a synonym of Krisnini. In contrast to the other taxa included in Krisnini by Hamilton (1975), Acostemminae have the distinctive characters of the anterior margin of the head with a single carina, the forewing without an appendix, the male valve fused to the pygofer, the subgenital plates fused and the aedeagus fused to the connective.

Subsequent to Evans (1947), Penthimini has fluctuated in status between a tribe of Deltocephalinae (Wagner, 1951; Lindberg, 1954; Linnatuori, 1959, 1960; Dietrich & Rakitov, 2002) and its own subfamily (Oman, 1949; Evans, 1972a; Hamilton, 1975; Linnatuori, 1977; Linnatuori & Al-Ne'amy, 1983; Oman et al., 1990). Penthimines have deltocephaline-like male genitalia (broadly bilobed style base, Y-shaped connective, basolateral membranous cleft on pygofer, valve with single point of articulation with pygofer, valve triangular or posteriorly produced, style broadly bilobed basally and triangular plates), but differ from typical deltocephalines in possessing some of the selenocephaline characters mentioned above and also in the dorsal position of the ocelli and the flattened and carinate dorsal surface of the prothorax (which also occurs in some Drabescini). Dietrich & Rakitov (2002) provided an expanded classification of Deltocephalinae and considered Penthimini, Eupelcininae, Paraboloponini and Selenocephalinae synonyms of Deltocephalinae. Dietrich (2005) and Zahniser & Dietrich (2008) pointed out that Penthimini Kirschbaum 1868 is an older name than Deltocephalinae Dallas 1870, but the latter name was retained according to their interpretation of Articles 23.9.1 and 35.5 in the International Code of Zoological Nomenclature (1999) (see Zahniser & Dietrich, 2008).

Evans (1947) placed Koebelia Baker in a tribe of its own in the subfamily Lethrini, whereas Oman (1949), Hamilton (1975) and Oman et al. (1990) recognized Koebelini as a separate subfamily. Recent phylogenetic analyses of Cicadelidae (Dietrich, 1999; Dietrich et al., 2001) placed Koebelia in the deltocephaline lineage, and Dietrich & Dmitrev (2003) synonymized its monobasic tribe with the deltocephaline tribe Grynotini, citing the position of the ocelli (distant from eye), length of the clypellus and the peg-like setae on the first hind tarsomere as synapomorphies. The phylogeny of Dietrich (1999) also suggested that the little-known tribe Occinirvanini [listed in Nirvaninae by Oman et al. (1990)] is related to Grynotini Fieber and Dietrich (2004) placed it in Deltocephalinae.

Materials and methods

Taxon sampling

In total, 114 taxa were included in the analyses (Table S1). Putative outgroup taxa included members of Aphrodes, Xestocephalinae, Euchelidae, Portanus and Chinaia. Previous phylogenetic analyses (Dietrich et al., 2001; Zahniser & Dietrich, 2008) showed moderate to strong support for Deltocephalinae s.l., and members of this group were considered the putative ingroup. Representatives of all family-group taxa (subfamilies or tribes) of Deltocephalinae s.l. were included except for Dwightlini, Listrophorini, Magnentiini, Occinirvanini and Paraphrodini, which were not available for DNA extraction. Effort was made to include representatives from all areas of the world and to include multiple representatives from large tribes (e.g. Athysanini, Deltocephalini and Paralimnini).

Morphological data

One hundred and nineteen adult morphological characters were scored for all included taxa except one of two exemplars of Chlorotettix. In a few instances, one gender was not
available for study, and missing data were scored with ‘?’). For 13 taxa, females were not available and thus required missing data values for 13 female-specific characters; for two taxa, males were not available, thus requiring missing data values for 20 male-specific characters. The characters used in this analysis are provided in Table S2, and these are identical to those used by Zahniser & Dietrich (2008), where illustrations can be found. Table S3 provides the data matrix for the taxa included in this analysis. Usually, characters were scored based on examination of the specimen from which DNA was extracted and of other specimens from the same locality. In instances when other specimens from the same locality were not available, morphological data were scored from museum holdings when other specimens from the same locality were not available for study, and missing data were scored with ‘?’). In some instances when the body of the leafhopper was sacrificed for DNA extraction or when morphological data scored for another congeneric species in a previous study (Zahniser & Dietrich, 2008) could be utilized, molecular data were taken from a different congeneric species than the morphological data, and these instances are noted in Table S1.

**DNA extraction**

Field-collected leafhoppers were preserved in 95% ethanol. Upon processing, the ethanol was replaced with fresh 95%, and the samples were stored at −20 °C. DNA was extracted from entire leafhoppers minus the abdomen, which was usually removed and dissected prior to DNA extraction. DNA extraction was performed with a DNeasy Tissue Kit (Qiagen, Valencia, CA) or using ethanol precipitation/resuspension (Coen et al., 1982). Occasionally, DNA was also extracted from the abdomens to include their symbiont DNA. For some very large specimens, only the hind legs and metathoracic segment were used for DNA extraction. DNA was extracted from dried and pinned specimens, some as old as 13 years, of *Hypacostemma, Korana* and *Loralia*. Entire DNEasy-extracted specimens (completely cleared leafhoppers) and the dissected abdomens from ethanol precipitation/resuspension-extracted leafhoppers are stored in glycerin in microvials and labelled in a voucher collection housed at the Illinois Natural History Survey. The specimen of *Idiocerominus* is housed at the Cole Entomol a Prof. Jos Ifredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro, Brazil.

**Polymerase chain reaction (PCR) amplification and sequencing**

A list of primers used for amplification of five overlapping fragments, referred to as fragments I–V, of 28S rDNA regions can be found in Dietrich et al. (2001). 28S primers were modified from Hillis & Dixon (1991). Fragments III and IV or IV and V were sometimes amplified together using the forward primer of the former and the reverse primer of the latter. Some 28S sequences were taken from a previous study (Dietrich et al., 2001) and some unpublished sequences were generously provided by R. Rakitov. Histone H3 primers are: HEX-AF (forward) 5’-ATGGCTCGTACAAAGCCACACGGC-3’ and HEX-AR (reverse) 5’-ATATCCTTGGGATGTTGAC-3’ (Ogden & Whiting, 2003). All PCR products were amplified in a 25 μL total reaction volume using Taq polymerase (Promega, Madison, WI), held first for 3 min at 94 °C, then 30 cycles of 94 °C for 1 min, 55 °C for 1 min and 72 °C for 2 min, then a final elongation step at 72 °C for 7 min, and held at 10 °C before being removed from the cycler. Double-stranded PCR products were checked for quality by running 5 μL of the product on a 1% agarose gel, stained with ethidium bromide, and imaged under ultraviolet light. Gel images, raw DNA sequence files, laboratory notebook procedures and notes are deposited in the library of the University of Illinois at Urbana-Champaign (Zahniser, 2008). Successfully amplified products were purified using a Qiapquick PCR purification kit (Qiagen) or with a GeneClean III kit. Both strands were sequenced using ABI Prism BigDye Terminator Kit version 3 (PE Applied Biosystems, Foster City, CA). Sequencing products were run on an ABI 3730XL capillary sequencer. Preliminary analyses suggested that 28S fragments I, III, IV and V were more phylogenetically informative than fragment II, and these regions were sequenced for most taxa. Fragment II was sequenced for some taxa, but was not included in the analyses. GenBank accession numbers for all sequences are given in Table S1.

**Alignment and phylogenetic analyses**

Chromatograms were visualized in SEQENCIER 4.7 (Gene Codes, Ann Arbor, MI) and forward and reverse sequences were checked and annotated. Full 28S contigs were constructed by aligning fragments sequenced in this study to previously published 28S rDNA leafhopper sequences (Dietrich et al., 2001) and inserting missing data values for fragment II (from aligned position ~750 to ~1300 of the entire ~3300 bp region), which was not amplified for most taxa in this study. Annotated sequences were imported into bioedit 7.0.9.0 (Hall, 1999), aligned with the CLUSTAL W accessory application; the alignment was later adjusted by hand to correct what appeared to be obviously misaligned regions. The sequence alignment and all data matrices are available from Treebase (www.treebase.org, study accession number S2530, matrix accession number M4836; also available from the authors upon request). Gaps were treated as a fifth base in parsimony analyses, and to include information from insertions and deletions (indels) in the Bayesian analysis they were coded using the program SEQSTATE (Müller, 2005) according to the simple indel coding (SIC) method. Other methods of treating indels were explored in a parsimony framework, but the resulting trees did not significantly differ from those treating gaps as a fifth base. Alignment of histone H3 sequences required no gaps.

 Parsimony analyses were run in PAUP*4.0b10 (Swoford, 1998). All characters were treated as unordered except for four morphological characters – characters 24, 25 and 115 were treated as ordered and character 27 had a user-defined step...
matrix (Zahniser & Dietrich, 2008). Analyses were run with the following search commands: ‘hssearch enforce = no start = stepwiseaddseq = random nreps = 10000 nchuck = 5 chuck-score = 1; hsearch enforce = no start = current chuck-score = no;’. Parsimony bootstrap analyses were run with the commands: ‘default hsearch addseq = randomnchuck = 10 chuck-score = 1 nreps = 10; bootstrap nreps = 1000;’. Total and partitioned Bremer support values (Bremer, 1988) for the resulting strict consensus tree from the combined analysis were calculated with the aid of command files generated in t reeroot v2 (Sorensen, 1999), which were modified to include search commands similar to the parsimony analyses above, with 2000 repetitions for each tree search with a constrained node. Separate parsimony analyses were also run including the 28S data only, 28S and H3 datasets only, histone H3 only and morphological data only (with some taxa excluded due to some missing data values that caused unacceptably long search times).

Maximum likelihood analyses of the 28S data (excluding segment II; 2818 aligned positions) were performed with garli 0.96. The primary search included 100 tree searches using the default settings, except for ten of these searches in which the threshold for the number of generations without significant change was set to 200 000 (from the default of 20 000) to examine the effect of longer searches on the ability to find trees with higher likelihood scores. The maximum likelihood bootstrap analysis included 100 bootstrap replicates with five searches per replicate.

Combined Bayesian analyses were performed with mrbayes v3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) and with a parallel version (Altekar et al., 2004) run on a supercomputing cluster available through the National Center for Supercomputing Applications at University of Illinois at Urbana-Champaign. Separate data partitions were defined for the 28S rDNA data, SIC indel dataset, each of three codon positions for histone H3 and morphology. The model for all molecular data partitions corresponded to GTR + I + Γ (the most complex currently available) as suggested by Huelsenbeck & Rannala (2004), and parameter values were estimated by mrbayes. The indel and morphology datasets were run under the standard discrete model. A user tree from a previous analysis was defined to speed up the search. All priors were left at default settings. The temperature setting was adjusted to 0.15 (from the default of 0.20) due to low rates of chain swapping in preliminary runs. Preliminary analyses showed strong support for the putative ingroup and early branching patterns, and most outgroup taxa were on long branches. Therefore, in the final Bayesian analyses, the outgroup taxa were excluded to allow the sequence model rate parameters to be estimated without the very long outgroup taxon branches and to allow the analyses to run faster. Four runs of four chains each were run for 10 million generations, which is near the maximum number possible given this dataset and the time constraints on the supercomputing cluster (100 h running 16 processors). Trees were sampled every 1000 generations. Convergence between runs was examined with tracer (Rambaut & Drummond, 2007).

Results

PCR amplification and sequence alignment

PCR products of all fragments were easily obtained for most taxa. However, some fragments for some taxa could not be amplified or sequenced. Fragment I was not sequenced for Bonaspeia, Gcaleka, Luheria, Renosteria and Scaphoideus (specimen from South Africa); fragment III was not sequenced for Korana; fragment IV was not sequenced for Aflesia, Chlorotettix, Eutettix, Flexania, Kinonia, Parmodes, Penthiomila and Tropicanus; and fragment V was not sequenced for Hypacostemma, Luheria, Paralimnus, Penthiomila and Tenoucetaphus.

The complete aligned 28S dataset included 3379 positions. With segment II excluded, the dataset included 2818 positions. With gaps considered a fifth base, 1768 characters were constant, 543 variable characters were parsimony uninformative and 507 characters were parsimony informative. With gaps considered ‘missing’ (for Bayesian analyses with SIC indel dataset), 1975 characters of the 28S dataset were constant, 376 variable characters were parsimony uninformative and 467 variable characters were parsimony informative. The SIC indel dataset included 191 binary characters (excluding 11 scored from segment II).

Amplification of histone H3 was successful in most cases. Histone sequences were not included for some taxa for which 28S sequences were obtained from previous studies: Chinaia, Chlorotettix unicolor, Placidellus and Portanus. Histone was not amplified from Eryapus and both species of Scaphoideus apparently due to primer mismatch and was not amplified from Oxyccephalotettix probably due to low DNA concentration. Alignment of histone H3 sequences required no gaps and included 353 positions. In total, 228 characters were constant, 14 variable characters were parsimony uninformative and 111 variable characters were parsimony informative.

Phylogenetic analyses

The strict consensus from the combined parsimony analysis is shown in Fig. 1 and is used as a reference for comparison with other trees. Parsimony bootstrap, total Bremer support and partitioned Bremer support values are provided on this tree. Parsimony trees were rooted with Aphrodes. Ninety-five per cent confidence intervals of average total Bremer support values per node for the entire tree for the 28S, histone H3 and morphological datasets are given in Table S4. Fifty of the 100 nodes in the tree in Fig. 1 received bootstrap support > 50%.

Parsimony analysis of the histone H3 data alone failed because the search reached the limit of the number of trees able to be stored in the memory on the computer (446 800 trees). Initial parsimony analysis of the morphological data alone also reached the memory capacity, so taxa with some missing data were then excluded for further analyses of morphological data alone.
Fig. 1. Strict consensus of 28 most parsimonious trees resulting from parsimony analysis of combined data. The numbers above the branches are parsimony bootstrap percentage(combined Bremer support and the numbers below the branches are partitioned Bremer support values for 28S/histone H3/morphology datasets. The clades discussed in the text are numbered and the revised classification is given to the right.

© 2010 The Authors
Journal compilation © 2010 The Royal Entomological Society, Systematic Entomology, 35, 489–511
The maximum likelihood analysis of the 28S data yielded trees with likelihood scores between -22029 and -22003, with the highest score of -22003.752. Extended search times did not appear on average to yield trees with higher likelihood scores, although this was not examined statistically. Maximum likelihood bootstrap scores are provided in Fig. 2. Forty-three nodes received maximum likelihood bootstrap scores > 50%.

Two of the four runs in the Bayesian analysis converged, as determined with TRACER v1.4 (Rambaut & Drummond, 2007) and these runs were used to compute Bayesian posterior probability values. Trees from the first 2 million generations (20% of the total) were discarded as burnin. The tree with the highest likelihood score is shown in Fig. 2 annotated with posterior probability values and maximum likelihood bootstrap values for branches that co-occurred in Bayesian and maximum likelihood bootstrap analyses. The tree was rooted with Placidellus, a member of Stegelytrini, which was found in previous analyses with high support to be the sister lineage to the remainder of Deltocephalinae as defined here.

Discussion

Phylogenetic signal in 28S, histone H3 and morphology datasets

Overall, the 28S rDNA dataset provided higher branch support and was more influential on the overall tree topologies than the histone H3 and morphology datasets. Although the histone H3 and morphology datasets influenced some relationships and branch support in the combined analyses, they did not provide much resolution for the overall structure of the trees. The stronger signal in the 28S dataset was probably due in part to its size (507 parsimony informative characters versus 111 for histone H3 and 118 for morphology). The weaker signal in the histone dataset, in which most of the parsimony informative characters were in third codon positions, was probably also partly due to homoplasy. The morphology dataset also exhibited a high amount of homoplasy and was sensitive to small amounts of missing data, as found by comparing analyses with and without taxa with missing data and different taxon sampling compared with an analysis of the same morphological characters in a previous study (Zahniser & Dietrich, 2008). The tree based on morphology alone (not shown) resolves some relationships found in combined analyses (e.g. Deltocephalinae s.l. and Deltocephalini + Paralimmini), but many of the groupings suggested by this tree are at odds with some well-supported branches suggested by combined analyses and therefore seem dubious.

Despite the shortcomings of the histone H3 and morphology datasets for resolving most higher-level relationships on their own, they provided very useful data for resolving some relationships towards the tips of the trees and seem to become more useful when combined with the 28S data, which provide a well-supported framework. For example, Eupelicini (as delimited here; Eupelix, Paradoryodium and Chloropelix sampled in analyses) was not recovered in some analyses of only the 28S data, but was monophyletic in the combined analyses with high support (parsimony bootstrap = 97%, partitioned Bremer support values for 28S/histone H3/morphology = −1.2/4/8.2; Bayesian posterior probability = 1.0). The increased resolution over trees based on 28S data alone and increased branch support from these datasets helped to provide a better overall picture of the phylogeny of Deltocephalinae, and the inclusion of morphological data was useful for tracing the characters onto the tree, which helped to define lineages of the subfamily and for the included tribes.

Strong conflicts between datasets where partitioned Bremer support values were lower than -5 for a particular data partition were not common, but did occur on some branches. Five of six of these instances were on branches towards the tips of the tree and the conflict was between the 28S and morphology datasets. One internal node (branch number 5, Fig. 1) was very highly supported by 28S data (partitioned Bremer = 17.9) but was opposed by histone H3 and morphology (partitioned Bremer = −2.3, −8.6, respectively).

There was strong branch support for relationships near the base of the tree and for some relationships near the tips, but many of the internal branches were not resolved in the strict consensus trees of some maximum parsimony analyses and received low branch support in the combined analysis parsimony analysis. This pattern of branch support was also reflected in the branch lengths found in Bayesian and maximum likelihood analyses: longer branches towards the base and tips were well supported and shorter internal branches were poorly supported. As suggested by the partitioned Bremer support values, this does not appear to be due to strong conflict among datasets, but rather varying levels of phylogenetic signal for different levels of the phylogeny. Additional data from other sources, such as nuclear protein coding genes, may help to clarify whether the short internal branches are due to idiosyncrasies of the 28S data or if they are due to an ancient rapid radiation of these leafhopper lineages, wherein little time was available for DNA base pair substitutions to have accumulated (Whitfield & Lockhart, 2007).

Analyses based on only the 28S data yielded some consistent differences from combined analyses, which suggest the influence of the histone and morphology datasets. For instance, in the tribe Chiasmini, Chiasmus and Doratura were always found sister to each other, but ‘Brazil sp’. was always found sister to them in parsimony analyses of the 28S data only, contrary to combined parsimony analyses, and the position of Nephotettix was ambiguous in the 28S-only analyses, whereas it grouped with Chiasmini in combined analyses. Interestingly, analysis of the 28S plus histone H3 datasets (without morphology) resolved Chiasmus and Doratura as sister taxa and Nephotettix and ‘Brazil sp.’, as sister taxa, but with both branches separate from each other. Female genitalia characters of Chiasmini are quite distinctive and probably influenced the resolution of Nephotettix with other chiasmines in combined analyses, but were not scored for ‘Brazil sp.’, and this may have influenced its tree position in those analyses.
Fig. 2. Tree from the combined Bayesian analysis with the highest likelihood score. The numbers above or below the branches are Bayesian posterior probability (combined data)/maximum likelihood bootstrap scores (28S data only). Unlabelled nodes did not occur in the Bayesian consensus tree. The revised classification is given to the right. The terminal branches for *Attenuipyga*, *Balclutha* and *Chiasmus* were truncated to allow them to fit into the figure. Their actual branch lengths are approximately twice those shown. Pictured to the lower left are the branching patterns for the outgroup taxa and the deltocephaline branch recovered in maximum likelihood analyses of the 28S data. Maximum likelihood bootstrap scores are given below the branches; branch lengths not to scale with the Bayesian tree.

© 2010 The Authors
Maximum likelihood analysis of the 28S data yielded a nearly completely resolved tree. Overall, this tree was similar to the majority-rule consensus trees of MP analyses of the 28S data. One exception involves the two members of Penthimini included here, of which Penthimiola was resolved as sister to Fiebriella and Penthimia was resolved in a distant clade in the Bahita group, sister to Menosoma in the maximum likelihood analyses, contrary to MP analyses, which placed the two penthimines as sister taxa. Another example was observed in Chiasmini (discussed in MP analyses above).

A maximum likelihood analysis of only the 28S data resolved Nephotettix with the other two chiasmines in a monophyletic group (along with ‘Brazil sp.’), suggesting that the evolutionary model improved the phylogenetic estimate, because with this model, this relationship, which reflects some convincing morphological characters (e.g. hinged aedeagus; distinctive shape of teeth of second valvula), is resolved. This group was also supported as monophyletic in the combined Bayesian analysis (Fig. 2), which both implemented an evolutionary model for the 28S data and included morphology.

Phylogenetic relationships

Unless otherwise noted, the tree referred to is Fig. 1. The putative ingroup, Deltocephalinae as defined here, was resolved as monophyletic and received high branch support (branch number 2, Fig. 1; parsimony bootstrap = 100%, combined Bremer = 23, maximum likelihood bootstrap = 100%; see Fig. 2). Stegelytrini sensu Webb (1999) and Acostemmini were found to be sequential sister lineages to the rest of Deltocephalinae. Other early diverging tribes of Deltocephalinae were Acinopterini, Goniagnathini, Luheriini and Fieberiellini. Their relative positions in the phylogeny were independently supported by separate morphological (Zahniser & Dietrich, 2008) and molecular analyses reflecting their lack of some apomorphic deltocephaline male genitalia structures, such as triangular subgenital plates, connective Y-shaped or with anterior arms appressed, and style broadly bilobed at base. Luheria was on a very long terminal branch due to its highly divergent 28S sequence, which included several large insertions, and it was supported as sister to Fiebriella in MP but not in maximum likelihood or Bayesian analyses. Orientus (Athysanini) and, depending on the analysis, one or two exemplars of Penthimini were also within this region of the phylogeny in varying arrangements with respect to other taxa. Loraliia, from Australia, is rather distinct both morphologically and genetically, being placed on a relatively long terminal branch in Bayesian and maximum likelihood analyses. It is removed here from Deltocephalini and is not assigned to any currently described tribe of Deltocephalinae, placement n. It appears to represent a distinct lineage potentially related to the other tribes in this region of the tree. Further sampling and discovery of the highly unique Australian fauna (e.g. Euleimonios Kirkaldy, Occiplanocephalus Evans) may reveal other relatives and how they are related to the rest of Deltocephalinae.

The first branch diverging distad of Loraliia contains some genera unplaced to tribe (Bonapaseia, Cerus and Gcaleka), two members of Athysanini (Dagama and Renosteria) and some of the sampled exemplars that were placed in Selenocephalineae by Linnavuori & Al-Ne’amy (1983). The unplaced genera are Ethiopian, as are the other tribes in this branch (Selenocephalus extends into the Palearctic region), but along with Hypacostemma, which was found with high support to be sister to this branch in Bayesian analyses (Fig. 2), lack the distinctive carinae on the anterior margin of the head that are characteristic of most other tribes in this branch. This finding suggests that this lineage is more diverse than was previously recognized, and includes many genera and species described from South Africa (e.g. Theron, 1975; Stiller, 1986). Further studies of this group should improve the classification and morphological characterization of these tribes and may yield insights into their diversification.

Two other groups were found to be closely related to the Selenocephalus clade in analyses of the 28S data alone or as the sister lineage to the rest of Deltocephalinae – one containing Korana, Phlepsius and Excultatus (= the ‘Phlepsius group’, Athysanini) and the other containing genera previously placed in ‘Scaphoidei’ (Scaphoideini Oman 1943 is considered a nomen nudum in the revised classification; see below for details) and Drabescini. The Phlepsius group was strongly supported and appears to represent a distinct, relatively early lineage of Athysanini, a polyphyletic tribe. Phlogotettix was found to be closely related to Scaphoideus and Osborniella, a position quite distant from the Platymetopiina group, and is therefore removed from Platymetopiina and left unplaced in Deltocephalinae, placement n., along with the other genera previously placed in ‘Scaphoidei’. The genera of Athysanini and related tribes, including those related to Scaphoideus, are currently being reviewed and the classification of these groups will be revised in the near future. Drabescini sensu Dmitriev (= Paraboloponini) was supported as a monophyletic group. Its phylogenetic position apart from the selenocephaline branch described above and its relationship to other Deltocephalinae reflect Zhang & Webb’s (1996) observation that Selenocephalineae sensu Linnavuori & Al-Ne’amy (1983) was not supported by any universally shared derived characters and that it was not distinguishable from some tribes of Deltocephalinae.

Moving further from the root of the phylogeny, the next region of the tree contains many of the genera sampled from Athysanini. Some generic groups were found and were relatively well supported, and these relationships may be used and explored further in future classification efforts to break Athysanini, the largest tribe of Deltocephalinae, into more natural groups. MP and Bayesian analyses recovered a monophyletic group of genera corresponding to the Neotropical Bahita group (Linnavuori & DeLong, 1978) of Athysanini. This branch includes two exemplars of Bahita and one each of Menosoma, Taperinha and Oxycephalotettix. One well-supported branch included Platymetriopus, Twingia, Eusama, Brazosa and Colladonus. Another consistently resolved branch included some New World genera: Chlorotettix, Copididonus, Bandarominus, Paraphlepsius and Dorydiella. Scaphytopius,
the type genus of its tribe, was not found to be closely related to the other scaphytopiines included here, *Nesothisanus* and *Stymphalus*. Rather, it was found to be closely related to *Tropicanus* (Athysanini) with high branch support, suggesting that Scaphytopiini needs to be redefined.

A relatively large clade containing all of the grass/sedge-specializing tribes plus some other taxa (branch number 7, Fig. 1) was resolved with a slightly different makeup between different analyses. Opsini (three exemplars), a nongrass-specializing tribe, was sometimes placed in this clade, but was not always monophyletic, as *Neoaltitrus* did not always group with *Opsius* and *Hishimonus*. Cicadulini (two exemplars), Macrostelini (three exemplars), Koebeliiini (two exemplars), Stenometopiini (two exemplars), Chiasmini (three exemplars), Paralimmini (four exemplars) and Deltocephalini (four exemplars) were found to be monophyletic, and some relationships between these tribes and other taxa were well supported.

One well-supported grouping of other genera is a branch containing *Kramerana*, *Heculus* and *Tenuephalus*. *Kramerana* was suggested to be in the *Falta* group of genera (DeLong & Thambimuttu, 1973); Zahniser & Webb (2004) found similarities in the ovipositors of the *Falta* group and *Heculus*; but the finding of their relationship to *Tenuephalus* is new and is also reflected in some characters of the female genitalia. This group is recognized here as a new tribe, Faltalini, tribe n. The phylogenetic analyses suggest that it is related to a group of three tribes, Tetartostylini, Paralimmini and Deltoccephalini, although support for this relationship was not strong.

The sister-group relationship between Deltocephalini and Paralimmini, two of the most speciose tribes in Deltocephalinae, was suggested earlier by Whitcomb et al. (1987) and was recovered in other analyses (Fang et al., 1995; Zahniser & Dietrich, 2008); the relationship of these two tribes to Tetartostylini was suggested by Wagner (1951). These three tribes share a similarly shaped connective – with the anterior arms closely appressed.

Members of two of the four tribes placed in Eupelicinae by Oman et al. (1990), Eupelicia and Paradorydini, were resolved as sister groups in the large grass/sedge-feeding clade, and *Drakensbergena* was suggested to be sister to this group. Despite the many shared morphological characters of Dorycephalini and other eupelcines, the former was found to be more closely related to Hecalinini on a relatively long branch that was usually placed in the large grass/sedge-feeding clade. The strong support from the 28S data for the *Attenuiopyga* (Dorycephalini)/*Heculus* (Hecalinini) relationship apparently overwhelmed the nearly equally strong evidence from morphology for an *Attenuiopyga*/eupelicine relationship [as found by Zahniser & Dietrich (2008)], and this is reflected in the conflicting 28S and morphological partitioned Bremer support values for the *Hecali/Attenuuiopyga* branch. *Attenuiopyga* and *Heculus* share some unique morphological characters of the male and female genitalia (Hamilton, 2000), which support this relationship. In the MP and Bayesian analyses, *Glossocratus* (Hecalinini) and *Arrugada* (Arrugadinini) were found in a branch with *Heculus* and *Attenuiopyga* (recovered in the Bayesian consensus tree, but not in the tree in Fig. 2). *Drakensbergena* and *Arrugada*, each previously placed in its own separate subfamily, are nested well within Deltocephalinae. The structures of their male genitalia, which are typical of Deltocephalinae, provide a compelling argument to include them in Deltocephalinae, and this was observed here. The relationships of these taxa were similar to those found by Zahniser & Dietrich (2008), except *Koebelia* was excluded from this clade in these analyses, and branch support was higher in these analyses.

Representatives of a third former subfamily, Mukariniae, were also nested well within this grass/sedge-feeding clade, justifying inclusion of the group in Deltocephalinae. In all analyses, the sister genus to *Mukaria* was *Agrica* Strand (= *Horvathiella* Matsumura), which was previously placed in Anoterostemminia. This pair was found to be closely related to *Scaphotettix* and *Stymphalus* in MP and Bayesian analyses. *Mukaria*, *Agrica* and *Scaphotettix* have the upper part of the frontoclypeus somewhat inflated, all are recorded from bamboo hosts and *Scaphotettix* and *Agrica* have a similar forewing venation and colour pattern. These relationships support the interpretation of Mukariini by Li & Chen (1998) and Chen et al. (2007), who included the *Mohunia* group of genera, which in turn shares some unique characters of the head, forewing and male genitalia with *Scaphotettix* (Zahniser, 2007; Dai et al., 2009). On the basis of these results and these morphological characters, *Scaphotettix* sensu Dai et al. (2009) and *Agrica* Strand are transferred to Mukariini, placement n., the former from Athysanini and the latter from Anoterostemminia [considered a subtribe of Limotettigini by Dmitriev (2002); also observed here]. *Stymphalus* has a foliaceous median longitudinal carina on the upper part of the frontoclypeus, and resembles other Scaphytopiini in some external characters, but a relationship to *Scaphytopius* was not recovered here. Its relationship to Mukariini was not well supported and deserves further investigation. The African genera currently placed in Mukariini, *Pseudobalbillus* Jacobi and *Neobassareus* Kocak, were not included in these analyses, and their placement in this tribe should be tested with molecular data in the future. Mukariini was sometimes resolved in a clade together with Cochliorhinini, Koebelini and some Athysanini. Further phylogenetic studies of these groups may provide insights on the origins of the western North American groups Cochliorhinini and Koebeliana and their biogeographical relationships to possible ancestors in the Oriental region.

**Evolution of host plant use and grass specialization**

For many species of leafhoppers, host plants are unfortunately not known. Despite this setback, some broad trends in host use are apparent. The known hosts of Deltocephalinae reveal a pattern wherein nearly all the members of 14 of the 36 tribes feed on grasses or sedges. Feeding on grasses or sedges is known in other tribes, but its occurrence is sporadic and is not nearly as ubiquitous as in these grass/sedge-specializing tribes whose members require grasses or sedges as both feeding...
and oviposition hosts. Similar to the findings in a previous analysis (Zahniser & Dietrich, 2008), all of the grass/sedge-specializing tribes were found within one clade (Fig. 1, branch number 7). Within this branch, there are several taxa (Opsiini, Koebelini, Macrosteles, Ballana, Thannmotettix and Euscelis) that do not specialize on grasses, suggesting that grass/sedge specialization is a reversible trait. Within this clade, hosts are unknown for Arrugadini, Idioceromimus, ‘Brazil sp.’ and Tenucephalus, and within Limotettix some species feed on grasses or sedges whereas others feed on dicots. Dmitriev (2002) found a similar pattern of relationships based on nymphal morphology wherein the grass/sedge-feeding tribes were most closely related, and Tisheckkin (2001) observed similarities in the acoustical calling behaviours of some grass-feeding tribes (Chi-asmini, Hecalini, Eupelicini and Dorycephalini) and suggested that this group may be related to a group including Deltocephalini, Paralimnini, Macrostelini and Aphrodini.

One other grass/sedge-feeding branch was found outside of this group, and included Chlorotettix, Copididoncus, Dorydiella, Paraphlepsius and Bandaromimus (Fig. 1, branch number 8). Hosts are unknown for Bandaromimus, and not all species of Paraphlepsius feed on grasses. Some species feed on pines or herbaceous dicots. As is the case for Limotettix, a genus with similar host association patterns and found within the large grass-feeding lineage, many species of Paraphlepsius are known from open woodland or forest edge grasses, prairies or wetland areas.

Overall, this pattern suggests that grass/sedge specialization is phylogenetically conservative. However, as in the previous analysis (Zahniser & Dietrich, 2008), the large grass-feeding branch received low support, so further data are needed to test this topology. Some of the grass-specializing groups (e.g. Deltocephalini and Paralimmini) are among the most speciose groups of Deltocephalinae, and further studies might shed light on the role of grass/sedge feeding on the diversification of these lineages. The grass/sedge-specializing clade also contains some morphologically extreme taxa (e.g. greatly elongated and flattened head in Dorycephalini, similar in Eupelicini), suggesting that this switch in host preference may have promoted morphological radiation as well. Because many of the relationships between tribes within this group were poorly supported and varied among phylogenetic analyses, we refrained from conducting more rigorous comparative analyses regarding these hypotheses. Further phylogenetic resolution and documentation of hosts of some groups, especially genera currently in Athysanini, will help to understand the roles of host plants in the diversification of these leafhoppers. The timing of the evolution of this clade is also of interest, as it would allow a comparison with the timing of the origin of grasses and sedges (76–88 mya; Janssen & Bremer, 2004) and of the origin and spread of grasslands (15–30 mya; Jacobs et al., 1999; Strömberg, 2005). However, no reliably identified fossils of Deltocephalinae are known because those described are either placed incorrectly to subfamily or contain so few diagnostic characters that their assignment to subfamily is dubious. Thus, phylogenetic dating with deltocephaline fossils is not possible at this time.

Conclusions

The results of these analyses are generally congruent with previous phylogenetic studies of Cicadellidae (Dietrich, 1999; Dietrich et al. 2001) and Deltocephalinae and related subfamilies (Zahniser & Dietrich, 2008), but the wider taxon sampling and increased amount of data over the previous analyses provide a more detailed and better supported hypothesis of relationships within the lineage. The consistent support for the monophyly of Deltocephalinae as defined here (Fig. 1, branch number 2) in all analyses of only the 28S and the high partitioned Bremer support for Deltocephalinae from the 28S data (−15.4) in the combined analysis show that this gene region contains useful characters for delimiting the subfamily as such. This branch was also very well supported by morphological data, which contributed a partitioned Bremer support value of 6.6. The 28S rDNA regions used here are informative at various levels in the history of Deltocephalinae, and will probably be useful for further studies on the group, and possibly for other leafhoppers. The histone H3 and morphology datasets have limited ability to resolve higher relationships on their own, but in combination with the 28S data were informative for some higher- and lower-level relationships. Branch support was high near the base of the tree and near the tips, but was low for some intermediate-level relationships. Further datasets are needed to test the relationships found in these analyses and to test whether the short internal branches are due to idiosyncrasies in the 28S data or to a rapid diversification of these deltocephaline lineages. Because representatives of most deltocephaline family-group taxa were included and because there was strong branch support near the base of the tree, for Deltocephalinae as defined here, and for a number of other branches, some revisions to the classification of the subfamily are justified at this time. Below, we outline a revised classification that suggests changes strongly supported by these phylogenetic analyses. Namely, we consider five subfamilies sensu Oman et al. (1990) to be junior synonyms of Deltocephalinae, describe one new tribe (Faltalini, previously recognized as a ‘generic group’), include two tribes previously placed in other subfamilies, transfer some genera to different tribes and describe characters that define Deltocephalinae. This classification is conservative in that it only recognizes changes that are strongly suggested by phylogenetic analyses and retains the family-group status of all synonymized subfamilies, as they are treated as tribes of Deltocephalinae. Because this is such a diverse group of leafhoppers, and because the scope of these analyses was necessarily limited to a subset of the deltocephaline genera, this is probably not the final revision to the higher-level classification. However, in making changes that are strongly supported by both molecular and morphological data, we hope that this classification will represent a consensus of the current state of knowledge of the group that can be updated in the future when more detailed studies of particular lineages may suggest further changes (i.e. synonymies or descriptions of tribes and subtribes and their generic composition).
Classification

Circumscription of Deltocephalinae

The best-supported branch in the phylogenetic analyses presented here that includes the family-group taxa recently placed in Deltocephalinae is branch number 2 (Fig. 1) (see phylogeny and classification sections for a history of the classification of the subfamily). A similar clade was found with moderate to high branch support in molecular analyses of Membracoidea (Dietrich et al., 2001) and of Deltocephalinae and related subfamilies (Zahniser & Dietrich, 2005). This group is very strongly supported by molecular data and moderately supported by morphological data. Thus, overall, the data suggest that this is a well-defined lineage. On the basis of these results, in addition to the subfamilies recently included in Deltocephalinae, Acostemminae, Arrugadinae, Drakensberginae, Mukariinae and Stegelytrinae are considered to be junior synonyms of Deltocephalinae, and are proposed as tribes of Deltocephalinae in the revised classification presented below.

As with any large and morphologically diverse lineage, Deltocephalinae as circumscribed here is difficult to define precisely based on a few diagnostic morphological features, due in part to a lack of completely stable morphological characters and high rates of homoplasy. Nevertheless, almost all deltocephalines have some very characteristic structures of the male genitalia, including: pygofer with basolateral membranous lateral cleft; valve produced medially and posteriorly; valve articulated with pygofer at a single point; subgenital plates triangular and relatively dorsoventrally flattened; subgenital plate with a dorsolateral fold articulating closely with style; style broadly bilobed basally, with median anterior lobe pronounced; connective Y-shaped or with anterior arms closely appressed; connective without median anterior or ventral lobe. Outside of the deltocephaline lineage, some of these features also occur in Cicadellinae sensu Young 1968, and most are in plesiomorphic states or other conditions in Aphroditinae (Aphrodiini, Portanini and Xestocephalini), Euacanthellinae, Neocoelidiinae and early diverging tribes of Deltocephalinae (Stegelytrini, Acostemmini, Acinopterini, Gonignathini, Fieberiellini and Luherini).

Character state reconstruction on the phylogeny in Fig. 1, analysis of the characters supporting these branches and examination of these characters in related taxa not included in these analyses yielded the following suite of characters that can be used to define this lineage, although not all characters are consistent within the entire lineage, and known departures from these characters are noted.

The traits defining Deltocephalinae as defined here (Fig. 1, branch number 2) are:

1 Gena with a single fine erect seta near lateral frontal suture (character 9); reconstructed on branch number 1 under ACCTRAN optimization and branch number 2 under DELTRAN. This character is lost in Eupelicini and Dorycephalini and is recorded as present in Calliscarta (Neobalinae) and Chinaia (Neocoelidiinae), although this may not be homologous because Chinaia has several other fine erect setae on the face, and the one considered present is very distant from the lateral frontal suture. A similar seta has also been observed in Coelidiinae. This seta was first noticed in Deltocephalinae by D. Novikov (personal communication).

2 Ocelli close to eyes (character 34); reconstructed unambiguously on branch number 2. This state also occurs in Calliscarta and some leafhopper subfamilies not included in these analyses (e.g. some Typhlocybinae, Evacanthinae and Coelidiinae), and is reversed in several deltocephalines, but helps to differentiate Deltocephalinae from Aphroditinae, Xestocephalinae, Euacanthellinae and Neocoelidiinae. Within Deltocephalinae, the ocelli are relatively distant from the eyes in Arrugadini, some Adysanini, some Chiasmini, some Cicadulini, Cochlorhinini, Drabescina, Drakensbergiini, Eupeliciini, most Faltulini, Koebellini, Paraphrodini and Penthimini.

3 Ocelli on anterior margin of head (character 33); reconstructed unambiguously on branch number 1. This also occurs in Xestocephalus and Portanus, and the position of the ocelli is different in several deltocephaline groups, including Drakensbergiini, Janeirini, Koebelina, some Mukariini, Occincirvanini, Penthimini, Anoterostemma, Chiasmus, Eupelix and Evinus.

4 Profemur anteroventral row with a single row of stout setae along basal two-thirds; setae usually short, sometimes longer (character 52); unambiguously reconstructed on branch number 2. This distinctive row of setae is reduced in several deltocephalines, including some Adysanini, some Cicadulini, Drabescini, some Macrostelini, Mukariini, some Penthimini, many Scaphoideus and related genera, Tetartostylini, Grypotes, Idiocerominus, Paradorydium and Tenacephalus. Some lassoineae have a similar condition for this row of setae.

5 Male pygofer with basolateral membranous cleft (character 103); reconstructed on branch number 1 in ACCTRAN and branch number 3 in DELTRAN optimization. This was recorded as present in Portanus, but its homology to that of Deltocephalinae is questionable. When present in Portanus, it appears not membranous, but as a fold or thickening of the pygofer. It is not present in Portanus elegans Kramer. Within Deltocephalinae, it is absent in Acostemminae, some Stegelytrini and Paradorydiina and is not membranous or absent in some Chiasmini and Stenometopiini.

6 Valve articulated with pygofer at a single point (character 102); unambiguously reconstructed on branch number 2. This is variable in Stegelytrini, in which some genera have a longer area of articulation between the valve and pygofer; the valve is fused to the pygofer in Acostemmini and Paradorydium.

7 Subgenital plate more or less dorsoventrally flattened and more or less triangular (character 105); this is a combination of states 1–4 in the character list and differentiates Deltocephalinae from the other subfamilies in the analysis that have the subgenital plates more or less elongate, lobate and expanded laterally and/or apically.

8 Subgenital plate with dorsolateral fold closely articulating with style (character 107); reconstructed on branch number 2 in ACCTRAN and branch number 4 in DELTRAN optimization.

© 2010 The Authors
Journal compilation © 2010 The Royal Entomological Society, Systematic Entomology, 35, 489–511
It was mistakenly coded as absent in *Fieberiella*, but is present in all of Deltocephalinae except some Acostemmini and Goniagnathini, which have modified fused subgenital plates. This fold is less obvious in Acinopterini and Fieberiellini, but is interpreted to be present in those taxa. A similar structure occurs in Cicadellinae and Tartessinae.

9 Connective anteromedial or anteroventral lobe or process absent (character 116); unambiguously reconstructed on branch number 2. This lobe is also absent in *Aphrodes*, and is present in some Stegelytrini.

10 In addition to the morphological characters listed above, the 28S rDNA data show very high support for Deltocephalinae as defined here (Fig. 1, branch number 2). If membership to Deltocephalinae is ever in doubt, this region of the genome can be sequenced for the taxon in question and analysed with a subset of the taxa included here for which sequences are publicly available in GenBank (accession numbers in Table S1). One particular position is diagnostic for nearly all Deltocephalinae: in aligned position 1699 (alignment available from www.treebase.org, study accession number S2530, matrix accession number M4836, or from authors by request), all deltocephalines, with the possible exceptions of *Attenuipyga* and *Hecalus* whose alignments are somewhat ambiguous in this region, contain a base pair (a one base insertion), and all sampled outgroups have an inferred gap at this position.

Features 5–9 listed above also occur in Cicadellinae sensu Young 1968 to some degree. Most Cicadellini have a basolateral cleft on the pygofer, the valve is usually articulated to the pygofer at a single point, and the subgenital plates are usually more or less triangular, depressed and sometimes have a dorsolateral fold or other modified structure that articulates with the style. The styles are usually not as broad basally as in typical deltocephalines, but the connective is usually U- or Y-shaped. Cicadellines are easily distinguished by their inflated frontoclypeus, ocelli located on the crown distant from the margins, forewing inner apical cell elongate and parallel sided, and hind femoral setal formula never 2+2+1 (usually 2+1+1); previous analyses of the entire family have not provided evidence of a close relationship to Deltocephalinae.

Other characters that were reconstructed on branches subsequent to branch number 2 that are diagnostic for most of the rest of Deltocephalinae are:

1 Crossvein between A1 and claval suture present (character 41); reconstructed unambiguously on branch number 4. This crossvein is lost in many deltocephalines, but is listed here because it is a unique character of the subfamily.

2 Style broadly bilobed basally, with median anterior lobe pronounced (character 108); reconstructed unambiguously on branch number 4. This character state is present in all deltocephalines included in this clade.

3 Anterior arms of connective somewhat divergent (Y-shaped) to closely appressed anteriorly (linear) (not widely divergent) (character 115); unambiguously on branch number 4. All deltocephalines in this clade have one of these conditions of the connective except *Phlogotettix* and some Mukariini, which have the anterior arms widely divergent.

Some other characters that help to separate Deltocephalinae from other leafhopper subfamilies are:

1 Lateral frontal sutures extending to ocelli (character 18); unambiguously reconstructed on branch number 1, reversed in many deltocephalines (19 exemplars in the analyses have the lateral frontal sutures not reaching the ocelli).

2 Antennal nodes absent (character 25); the ancestral state for this character was reconstructed to be ‘weakly developed or weakly carinate’, which is present through many of the early diverging lineages of Deltocephalinae with an unambiguous change to ‘absent’ on branch number 6. Some other leafhopper subfamilies have a well-developed antennal node, as do some deltocephalines (e.g. *Adama* [*Krisnella*], *Drabescus*, *Penthimini*, *Mukaria* and *Eryapus*).

3 Hind femur setal formula 2+2+1 with penultimate pair close together. This is a combination of characters 67–69. In some deltocephalines, this group of setae is reduced to 2+1+1, 2+1+0, or 2+0+0. If the penultimate pair is present, they are always close set, which differs from some other leafhopper subfamilies.

Overall, this is a broader circumscription of Deltocephalinae than most authors have recognized previously, but is narrower than that of Hamilton (1975), which also included Neobalini, Aphrodoni, Xestocephalini, Portanini and Krisnini. Deltocephalinae can be separated from other leafhopper subfamilies, including Euacanthellinae, Neocoelidiinae and Aphrodoniidae s.s. (including Aphrodoni, Portanini and Xestocephalini) in the key provided by Dietrich (2005), with the exception of Magentiini, which keys out earlier. The diagnostic characters provided above, the ability for Deltocephalinae to be keyed out in relation to other leafhopper subfamilies and the strong support from molecular and morphological data provide justification for recognizing this group as circumscribed here. Alternatives to this circumscription seem less desirable due to low branch support for less (or more) inclusive clades in the phylogenetic analyses presented here and in others on Cicadellidae to date and subsequent low confidence in their monophyly, few diagnostic morphological characters for potentially smaller circumscriptions and difficulties in treating other groups that would be excluded from a narrower version of Deltocephalinae.

Classification of tribes

The revised classification is conservative in that changes that were well supported by the phylogenetic analyses have been incorporated. Tribes of Selenoccephalinae sensu Oman *et al.* (1990) are treated as tribes of Deltocephalinae, and tribes of Eupelcicini sensu Oman *et al.* (1990) are considered subtribes of Eupelicini, following McKamey (in press), except for Dorycephalini, which is considered distinct here because it was not recovered as closely related to the other eupelicine tribes and is instead apparently more closely related to Hecalini, as suggested by Hamilton (2000). Other taxa previously considered separate subfamilies are treated as tribes of Deltocephalinae (Acostemmini, Arrugadini, Drakensbergenini, Mukariini and Stegelytrini).
The largest tribe of Deltocephalinae, Athysanini, contains over 250 genera and nearly 2000 described species. It is poorly defined morphologically; its members do not share any unique morphological characters and, in most cases, lack the synapomorphies that define other tribes. The phylogenetic analyses confirm that Athysanini is polyphyletic. Many of the sampled genera were resolved on short branches in the middle portion of the phylogenetic tree, and some monophyletic groups of athysanine genera were recovered by the present analyses. These groupings may form the basis for recognition of additional tribes or subtribes of Athysanini, but until more detailed morphological and molecular analyses of this group are performed, the tribe is retained as a polyphyletic assemblage with many of the genera unplaced to subtribe, and the remaining genera placed to the subtribes recognized by recent authors (see below). Further exploration of nontraditional morphological character sets, e.g. the female genitalia, may prove to be useful in future classification considerations of this large tribe.

In considering portions of the European and Asian faunas, Emeljanov (1999) and Dmitriev (2006) considered Platymetopiina s.s. [not sensu Hamilton (1975)] and Athysanina s.s. as subtribes of Athysanini, and Dmitriev (2006) further considered Cicadulina and Allygidiina as subtribes. This system is followed here with the exception that Cicadulina is considered a tribe, following Oman et al. (1990) and McKamey (in press). Emeljanov’s (1999) and Dmitriev’s (2006) classifications are largely congruent, but some differences between them in the placement of genera are noted here and compared with their placement in the phylogenetic analyses presented here. Thamnotettix Zetterstedt was placed in Athysanina by Emeljanov (1999) who did not explicitly provide morphological characters for the subtribes, but was placed in Platymetopiina by Dmitriev (2006) who used nymphal characters (some of which are the same or similar in the adults, e.g. shape of clypellus). Despite the recent work, Platymetopiina still remains to be adequately described by adult morphological characters and circumscribed considering genera from all geographical regions. In the phylogenetic analyses given here, Thamnotettix was found with good branch support to be related to Euscelis Brullé, which both Emeljanov (1999) and Dmitriev (2006) included in Athysanina s.s. Unfortunately, the present analyses did not recover a strongly supported placement of Athysanus Burmeister. Emeljanov (1999) and Dmitriev (2006) placed Phlepsius Fieber in Platymetopiina. This genus was found with moderate branch support to be related to Excultanus Oman and Korana Distant, possibly forming, with other related genera, a group that may eventually warrant recognition as a distinct subtribe of Athysanini. Future studies of these subtribes should review the adult characters that support them and should consider the rest of the world genera of Athysanini and their proper placement to subtribe. The phylogenetic analyses suggest that Eusama Oman and Twiningia Ball are closely related to Platymetopius, and are thus placed in Athysanini: Platymetopiina (sensu Emeljanov, 1999; Dmitriev, 2006), here placement n. The former genus was previously placed in Athysanini (unplaced to subtribe) and the latter in ‘Scaphoideini’ by Oman et al. (1990).

Cerrillini, containing only the type genus, is considered a junior synonym of Athysanini because it is phylogenetically nested within a clade of other athysanines, and although it has some unique features (carinate anterior margin of head, rugose texture of frontal clypeus), a similar statement can be made for many other genera of Athysanini, and it serves little purpose to recognize distinct tribes for them.

One group previously placed in Athysanini is recognized here as a new tribe. The Faltalala Oman group has been recognized as an informal group of Athysanini, but has not previously been recognized as a separate tribe. It is separated from Athysanini because it is recognizable with morphological characters and is phylogenetically distinct from other athysanines. The circumscription of Faltalalini here includes 11 genera, six of which have not previously been considered part of this group.

These phylogenetic analyses suggest that the circumscriptions of some tribes by Oman et al. (1990) do not reflect relationships among genera. For example, it was found that Phlogotettix, placed in Platymetopiini by Oman et al. (1990), is most closely related to Scaphoideus and Osborniellus. Conversely, ‘Scaphoideini’ sensu Oman et al. (1990) (recognized as a nomen nudum here) contains genera that are not closely related to Scaphoideus. For example, Twiningia, placed in Scaphoideini by Oman et al. (1990) was found to be closely related to Platymetopius. Scaphytopiini was also found not to be monophyletic based on the current classification (Webb & Godoy, 1993). The only sampled taxon found to be closely related to Scaphytopius was Tropicanus (Athysanini), which does not possess the single diagnostic character for the tribe, gena not incised laterally and visible behind eye in dorsal view. Two other sampled genera that do possess this character, Nesothamnus and Symphilus, were not found to be closely related to Scaphytopius. Thus, the circumscription and morphological characterization of Scaphytopiini should be reconsidered in the future. The phylogenetic analyses support characterizing Paralimmini with: connective linear or triangular, with anterior arms closely appressed anteriorly and usually articulated with the aedeagus; and characterizing Deltocephalini with: connective with anterior arms closely appressed, fused with the aedeagus.

Magnentiini (Nioniniinae) and Paraphrodini (Aphrodininae) were not included in these phylogenetic analyses, but are placed in Deltocephalinae here based on possessing structures of the male genitalia that are characteristic of the subfamily. Their inclusion in the subfamily should be tested in the future with molecular data. Magnentiini contains two genera and four species from the Ethiopian and Oriental (India) regions. The structure of the head is very different from the rest of Deltocephalinae. The specimens examined had damaged legs, so the chaetotaxy could not be observed. The New World tribe Nioniini is not placed in Deltocephalinae based on: gena without fine erect seta near lateral frontal suture; forewing r2+3 – r3+5 crossovein absent; hind wing m-cu crossovein long, meeting CuA obliquely; profemur anteroventral row without stout setae on basal two-thirds; profemur intercalary row with scattered setae
or with more than one row; hind femur macrosetal formula 2 + 1; valve fused to pygofer; pygofer without basolateral membranous cleft; connective with anteromedial lobe; style base not broadly bilobed. Paraphrodini contains one genus and species widely distributed in equatorial Africa. It is included in Deltocephalinae here based on features of the male genitalia diagnostic for most Deltocephalinae, ocelli on the anterior margin of the head (but distant from eyes) and gena with a fine erect seta near lateral frontal suture.

Several family-group taxa were created by Oman (1943). The names published in this paper, a summary of a doctoral thesis, are not considered available because, as required by the ICZN, Article 13, they are not accompanied by descriptions stating characters that differentiate the taxa or by a bibliographic reference to such published statements. The dissertation referred to is not considered to be a published work under ICZN Article 8. Thus, these names are considered nona nuda. Some of these names became available when Oman (1949) provided the first formal descriptions.

Deltocephalinae Dallas 1870

Head

Head usually as wide as or wider than pronotum, sometimes narrower than pronotum; anterior margin shagreen with crown rounded to face or angulate, transversely striate, with one or more carinae, or foliaceous. Ocelli on anterior margin of head, usually close to eyes, sometimes on crown (Penthimini, Occinirvanini, Drakensbergenini, Eupelicina, some Chiasmini) or on face (Ianeirini, Koebeliini, Magnentiini), and sometimes relatively distant from eyes. Antennal ledges absent or reduced (weakly carinate) (distinct ledges only in Drabescini, Penthimini and some Stegelytrini). Lateral frontal sutures usually extending to ocelli. Frontoclypeus usually not tumid (tumid anteriorly in most Penthimini and Mukarini; entire frontoclypeus somewhat tumid in Anoterostemma). Frontoclypeus extending onto crown laterally. Antennal pits near middle or lower corner of eye, more rarely near upper corner of eye (Drabescini, Drakensbergenini, Dwightlini, Eupelicina, Mukarini). Gena broad and largely concealing proepisternum (proepisternum exposed in Dorycephalini and Paradorydiini). Gena with distinct fine seta near lateral frontal suture (absent in Dorycephalini, Eupelicini), usually very close to lateral frontal suture, sometimes relatively distant.

Thorax

Pronotum with or without lateral carina; usually transversely striate.

Wings

Forewing in macropterous individuals usually with apices overlapping at rest (not overlapping in Acinopterini, Acostemmini, Fieberiellini, Eupelicini, Hypacostemmini, Luherini, Paradorydiini, some Stegelytrini); appendix usually developed but not extending around wing apex (reduced in Acinopterini, Acostemmini, Fieberiellini, Luherini and Stegelytrini; extending around wing apex in Chiasmini, Eupelicini, Goniagnathini, Penthimini and Drabescini); usually with three antecapital cells (Macrostelini with two antecapital cells); usually with crossvein r-m1 (central antecapital cell closed); often with crossvein connecting A1 and claval suture; with or without A1-A2 crossvein; inner apical cell tapered distally, usually not extended to apical margin. Hind wing crossvein m-cu, when present, usually very short and perpendicular to CuA.

Legs

Profemur AM1 seta usually distinct, sometimes with extra setae based on AM1 (some Acinopterini, some Acostemmini, Adamini, few Athysanini, Dwightlini, Fieberiellini, Ianeirini, Luherini, few Penthimini, Selenoccephalini and Stegelytrini); anteroventrally row extending from base to one-half to two-thirds length of femur, usually consisting of short stout setae (somewhat longer in several tribes), or reduced or absent (some Athysanini, some Drabescini, Macrostelini, Mukarini, some Paradorydiini, Penthimini); intercalary row usually with four to 15 thin setae arranged in one row, rarely reduced or absent (some Chiasmini, Dorycephalini, Eupelicini, Koebeliina, Tetartostylini) or rarely with extra scattered setae. Metafemur macrosetal formula usually 2 + 2 + 1 with penultimate pair close set, rarely 2 + 0, 2 + 1, 2 + 1 + 1, 2 + 2 + 1 + 1 or with numerous additional macrosetae. Metatibia usually anteriorly–posteriorly compressed, ventral side with median ridge. Metatibia posterdorsal row usually with alternating long and short setae. Metatibia anterdorsal row with numerous macrosetae interspersed by one to four small stout setae. Metatarsomere 1 usually with dorsal pair of macrosetae distally and two rows of stout setae on planar surface, rarely with plantar plateae (Cochlorhinini, Koebeliina, Occinirvanini); with apical row of three or more plateae; usually relatively straight, sometimes expanded apically (some Athysanini, Eupelicini, Dorycephalini, some Hecalini); usually longer than apical two tarsomeres combined (shorter in some Athysanini, Eupelicini, Dorycephalini, some Hecalini).

Male genitalia

Pygofer usually with oblique basolateral membranous cleft (without cleft in some Chiasmini, Paradorydiini, some Stegelytrini, some Stenometopiini); usually with macrosetae. Valve (sternite IX) articulated to pygofer at a single point (fused to pygofer in Acostemmini, Paradorydiini, some Stegelytrini); somewhat to largely produced posteriorly; articulated with subgenital plates (fused to subgenital plates in Goniagnathini, some Scaphytophiini, few Athysanini, few Deltocephalini, some Opsiini). Subgenital plates dorsoventrally compressed; usually more or less triangular; often with macrosetae laterally; with dorsal fold articulating with style; rarely fused to each other (Acostemmini, Goniagnathini, some Scaphytophiini). Connective without anterior median lobe (except some Stegelytrini);
Y-, U- or V-shaped (with anterior arms divergent), or with anterior arms closely appressed anteriorly: Deltocephalini, Paralimmini, Tetartostylini, some Chiasmini, few Athysanini, or with anterior arms widely divergent (Acinopterini, Acostemmini, Fieberiellini, Luheriini, some Mukarii, Phlogotetrix, Stegelytrini); usually articulated to aedeagus (fused to aedeagus in Acostemmini, some Athysanini, Deltocephalini, Cochlorhinini, Goniagnathini, some Ianeirini, some Mukarii, some Scaphytopiini). Style broadly bilobed anteriorly (with anterior median lobe produced) (linear or median anterior lobe not produced in Acinopterini, Fieberiellini, Luheriini, Stegelytrini); apophysis short and falcate, slightly to strongly incrassate, or somewhat elongate, usually not very elongate.

Female genitalia

Pygofer with or without macrosetae. Ovipositor usually not extending far beyond pygofer (extending far beyond in Chiasmini, Dorycephalini, Hecalini, Koebeliina, Paradorydiina, Stenometopiini, rarely in other tribes). First valvula usually broad; relatively straight to strongly arched, as indicated by shape of ramus. First valvula dorsal sculpturing strigate, concatenate, reticulate, imbricate, maculose or granulose; reaching dorsal margin or submarginal; ventroapical sculpturing absent or indistinctly delimited or sometimes distinctly delimited with semi-triangular shaped patch (Arrugadini, Dorycephalini, Faltalinii, Hecalini, some Macrostelini, Stenometopiini, Tetartostylini). Second valvulae usually with basal fused section as long as or longer than distal paired blades; with or without median dorsal tooth; usually with small to large, regularly or irregularly shaped dorsoapical teeth on apical one-third or more; teeth sometimes restricted to apical one-quarter (Acostemmini, Adamini, Dwightlini and Koebeliina) or absent (Arrugadini, Hecalini, Dorycephalini, Paradorydiina, Stenometopiini, some Macrostelini, rarely in other tribes).

Deltocephalinae Dallas 1870

= Acostemminae Evans 1972 syn.n.
= Arrugadinae Linnauvori 1965 syn.n.
= Drakensbergeninae Linnauvori 1979 syn.n.
= Eupelicinae Sahlberg 1871
= Koebeliinae Baker 1897
= Mukariinae Distant 1908 syn.n.
= Paraboloponina Ishihara 1953
= Penthimiinae Kirkaldy 1906
= Selenocephalinae Fieber 1872
= Stegelytrinae Baker 1915 syn.n.

Included tribes:
Acinopterini Oman 1949
Acostemmini Evans 1972
Adamini Linnauvori & Al-Ne’amy 1983
Arrugadini Linnauvori 1965
Athysanini Van Duzez 1892
= Bobacellini Kusnezov 1929
= Cerrillini Linnauvori 1975 syn.n.
= Colladonini Bliven 1955
= Euscelini Van Duzez 1917
= Phrynomorphini Kirkaldy 1907
= Platymetopiini Haupt 1929
= Thamnotettigini Distant 1908

Included subtribes:
Allygidiina Dmitriev 2006
Athysanina Van Duzez 1892
Platymetopiina Haupt 1929

Chiasmini Distant 1908
= Doraturini Emeljanov 1962
Cicadulini Van Duzez 1892
Cochlorhinini Oman 1949
Deltocephalini Dallas 1870
Dorycephalini Oman 1949
Drabescini Ishihara 1953

Included subtribes:
Drabescina Ishihara 1953
Paraboloponina Ishihara 1953
= Bhatiini Linnauvori & Al-Ne’amy 1983

Drakensbergenini Linnauvori 1979
Dwightlini McKamey 2003
Eupelcici Sahlberg 1871

Included subtribes:
Eupelcicina Sahlberg 1871
Listrophorina Bouard 1971
Paradorydiina Evans 1962
= Doridiini Fieber 1872

Faltalini Zahniser & Dietrich tribe n.

Fieberiellini Wagner 1951
= Synophropsini Ribaut 1952
Goniagnathini Wagner 1951
Hecalini Distant 1908
= Reuteriellini Evans 1947

Included subtribes:
Glossocratina Dmitriev 2002
Hecalina Distant 1908

Hypacostemmini Linnauvori & Al-Ne’amy 1983
Ianeirini Linnauvori 1978
Koebeliini Baker 1897

Included subtribes:
Grypotina Haupt 1929
Koebeliina Baker 1897

Limotettigini Baker 1915

Included subtribes:
Anoterostemmina Haupt 1929
Limotettigina Baker 1915

Luheriini Linnauvori 1959
Macrostelini Kirkaldy 1906
= Balcluthini Baker 1915
= Coryphaeini Nast 1972 (= Coryphaeini Emeljanov 1962)
= Gnathodini Baker 1915

Magnentiini Linnauvori 1978 placement n., transferred from Nioniinae
Mukariiini Distant 1908
Occinirvanini Evans 1966
Opsiini Emeljanov 1962

© 2010 The Authors
Included subtribes:
- Achaeticina Emeljanov 1962
- Circuliferina Emeljanov 1962
- Eremophlepsiina Dmitriev 2002
- Opsiina Emeljanov 1962
- Paralimnini Distant 1908
  = Jassargini Emeljanov 1962
- Paraphrodini Linnavuori 1979 placement n., transferred from Aphrodiinae
- Penthimini Kirschbaum 1868
  = Thaumatoscopini Baker 1923
- Scaphytopini Oman 1949
- Selenocephalini Fieber 1872
- Stegelytrini Baker 1915
- Stenometopini Baker 1923
  = Streillini Emeljanov 1966
- Tetartostylini Wagner 1951

‘Scaphoideini’ Oman 1943 is a nomen nudum and an unavailable tribal name. However, the phylogenetic analyses showed relatively high support for a group of genera including Scaphoideus, and the group is related to Drabescini. Preliminary searches of the literature and an examination of specimens suggest that there are at least 40 genera that are quite similar to Scaphoideus, whereas several of the genera placed in ‘Scaphoideini’ by Oman et al. (1990) do not appear to be related to Scaphoideus. Further research and characterization of this group may allow recognition of a tribe for this speciose group of deltocephalines. For now, with the exception of Twiningia Ball, the genera placed in ‘Scaphoideini’ by Oman et al. (1990) or listed by McKamey (in press) are considered unplaced to tribe in Deltocephalinae: Acunasus DeLong, Cantura Oman, Danbara Oman, Osbornellus Ball, Prescottia Ball, Scaphodhora Viraktamath & Mohan, Scaphoideus Uhler, Scaphoidophyes Kirkaldy, Sincholata DeLong, Sobara Oman and Soleatus DeLong, placement n.

Note: The new tribe Pendarini Dmitriev 2009 was described while this publication was in proof.

Faltalini Zahnisr & Dietrich tribe n.

Type genus: Faltala Oman 1938

Small to large sized, somewhat dorsoventrally flattened, ivory, ochraceous, fuscous, yellowish, or brown leafhoppers; sometimes sexually dimorphic. Dorsal side sometimes with five to six or less developed longitudinal ochraceous stripes bordered with fuscous or darker colouring; stripes may be present on head, pronotum, wings and/or abdomen.

Head

Head nearly as wide as or wider than pronotum; anterior margin shagreen and crown rounded to face, or angled, subfoliaceous, foliaceous, or carinate. Crown somewhat to strongly produced. Frontoclypeus shagreen or glabrous. Fine erect seta on gena close to lateral frontal suture. Clypellus parallel sided or slightly tapering apically. Lorum as wide as or narrower than clypellus at base. Antennal bases near middle or posteroventral (lower) corners of eyes or near anterodorsal (upper) corners of eyes (some Tenucephalus, Bonanus). Antennal ledge absent. Antennae short or long (Tenucephalus, Bonanus). Ocelli small, distant from eye (close to eye in Tenucephalus), sometimes absent. Lateral frontal suture meeting ocellus, closer to eye than ocellus, or obscure apically and not reaching ocellus.

Thorax

Lateral margins of pronotum long and carinate laterally, usually as long as width of eye at base.

Wings

Both sexes with forewings brachypterous, quadrate, coriaceous, venation indistinct to reticulate; or males submacropterous or macropterous and females brachypterous (Acrolithus, Hecullus); or males and females macropterous (Tenucephalus, Bonanus); if macropterous, appendix restricted to anal margin, with three antepalpal cells, without reflexed costal veins.

Legs

Protrochanter often with stout apical seta. Profemur anteroventral row with AM1 seta only; intercalary row with one row of five or more fine setae; anteroventral row setae long or reduced or absent (some Tenucephalus). Protibia dorsal surface rounded, convex. Metafemur apical setae 2 + 2 + 1 or 2 + 2 + 0.

Male genitalia

Valve articulated with pygofer and subgenital plates. Pygofer with basolateral membranous cleft. Subgenital plate macrosetae scattered, irregularly arranged, or uniseriate laterally. Style broadly bilobed, median anterior lobe pronounced. Paraphyses absent or present (some Tenucephalus). Connective Y-shaped, rarely with anterior arms closely appressed (Tenucephalus); articulated with aedeagus, rarely fused to aedeagus (Tenucephalus). Aedeagus with one gonopore; often with sclerotized or setose phragma attaching dorsal part of sclerite X (absent in Acrolithus).

Female genitalia

Pygofer with macrosetae reduced or absent or with numerous macrosetae. Ovipositor not protruding far beyond pygofer apex or sometimes protruding (Bonanus, Tenucephalus). Ramus of first valvula relatively straight, not strongly arched. First valvula dorsal sculpturing pattern maculose to granulose; not reaching dorsal margin. First valvula ventroapical sculpturing distinctly delimited, subtriangular. Second valvula broad, often
with a slight dorsal hump near midlength; without dorsal median tooth; without dorsoapical teeth.

**Diagnosis**

Most Faltalini are distinguished from other tribes, including the morphologically similar tribe Hecalini, by the following combination of characters: dorsoventrally flattened leafhoppers; crown more or less produced; ocelli distant from eye; lateral frontal sutures meeting ocelli or closer to eye than ocelli; lateral margin of pronotum nearly as long as basal width of eye; male sometimes with sclerotized phragma between aedeagus and segment X; first valvula nearly straight, not humpbacked; first valvula dorsal sculpturing pattern maculose to granulose, submarginal; first valvula with distinctly delimited subtriangular ventroapical sculptured area; second valvula without dorsoapical teeth.

**Remarks**

Faltalini contains 11 genera and 31 described species. It ranges from the southwestern U.S.A. to Chile and Argentina. On the basis of the three exemplars included in the phylogenetic analyses presented here (Heculus, Kramerana and Tenecephalus), this tribe is strongly supported as monophyletic and was recovered sister to a clade including Deltocephalini, Paralimmini and Tertartostylini, although this hypothesis requires further support. Faltalini also bears a close resemblance to Hecalini and Dorycephalini in the following characters: head often produced or parabolic in shape; first valvula dorsal sculpturing pattern submarginal; first valvula relatively straight; first valvula with distinctly delimited apicoventral sculptured area; second valvula without dorsal teeth. Faltalini differs from those tribes in the following characters: ocelli usually somewhat distant from eye (close to eye in Hecalini and Dorycephalini); first valvula dorsal sculpturing pattern maculose to granulose (finely granulose in Hecalini and Dorycephalini); first valvula not humpbacked (humpbacked in Hecalini and Dorycephalini); ventral margin of second valvula straight (concave in Hecalini and Dorycephalini). *Tenecephalus* and *Bonamus* form a morphologically distinct group within the tribe, possessing the following characters: body long and slender; both genders macropterous; ovipositor extending well beyond pygofer apex. These somewhat morphologically distinct genera make the tribe as a whole more difficult to characterize morphologically, but some characters, especially of the female genitalia, support a relationship to other Faltalini and 28S rDNA data very strongly support this relationship. Specimens of *Egenus* and *Hecalcorica* have not been examined, but are tentatively placed here based on their original descriptions. Known hosts are grasses.

*Included genera:*

- *Acrolithus* Freytag & Ma (transferred from Athysanini)
- *Aequcephalus* DeLong & Thambimuttu 1973 (transferred from Athysanini)
- *Bonamus* Oman (transferred from Hecalini)

*Clorindaia* Linnnavuori (transferred from Athysanini)

*Egenus* Oman (transferred from Athysanini)

*Faltula* Oman (transferred from Athysanini)

*Hecalcorica* Nielson (transferred from Hecalini)

*Heculus* Oman (transferred from Athysanini)

*Kramerana* DeLong & Thambimuttu (transferred from Athysanini)

*Tenacephalus* DeLong (transferred from Athysanini)

*Virgulana* DeLong & Thambimuttu (transferred from Athysanini)


**Supporting Information**

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/j.1365-3113.2010.00522.x

**Table S1.** List of taxa included in the study with voucher numbers and GenBank accession numbers.

**Table S2.** A list of morphological characters used in the analysis.

**Table S3.** Morphological data matrix.

**Table S4.** Ninety-five per cent confidence intervals of Bremer support values.

Please note: Neither the Editors nor Wiley-Blackwell are responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

**Acknowledgements**

We thank Roman Rakitov for his generous assistance in the molecular laboratory and advice on many aspects of this project, Dmitry Dmitriev for advice on morphological characters and Daniela Takiya for assistance in the laboratory. We are indebted to Jason Cryan, Norman Johnson, Luciana Musetti, Roman Rakitov, Michael Stillier, Mike Irwin, Terry Erwin, Adam Wallner, Vinton Thompson, Daniela Takiya, Murray Fletcher, Mick Webb, Charles Bartlett, Andy Deans, Mike Sharkey, Norm Penny and the California Academy of Sciences for the donation or loan of specimens used in this study. We extend our gratitude to Man-Miao Yang, Jing-Fu Tsai, P. Huang, J.-Y. Lio and Hsien-Tzung Shih for hosting a visit to Taiwan, to Michael Stiller for hosting a visit to South Africa and to Gustavo Moya-Raygoza for hosting a visit to Mexico. We are grateful to M. Webb, S. McKamey and D. Takiya for thorough reviews and thoughtful suggestions that greatly improved the manuscript. JNZ thanks the Department of Entomology and the School of Integrative Biology at University of Illinois, Urbana-Champaign for thorough reviews and thoughtful suggestions that greatly improved the manuscript.
of Illinois at Urbana-Champaign for supporting his doctoral studies. This research was supported in part by grants from the National Science Foundation (DEB 9978026, 0529679, 084162) and the University of Illinois Research Board.

References


Sorenson, M.D. (1999) *TreeRat, version 2*, Boston University, Boston, Massachusetts.


Accepted 20 November 2009
First published online 23 March 2010