A Phylogeny of the Ledrine Leafhoppers (Hemiptera: Cicadellidae) Based on Morphological Evidence

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Abstract

The leafhopper subfamily Ledrinae, as currently defined, contains the tribes Ledrini, Petalocephalini, Stenocotini, Thymbrini, and Xerophloeini. Recent studies, based on both molecular and morphological data, have called into question this classification, especially the inclusion of Stenocotini and Thymbrini within the subfamily and also the possible synonymy of Ledrini and Petalocephalini. We present our most recent hypotheses regarding the monophyly of the subfamily and each of its included tribes based on morphological data.

Introduction

The leafhopper subfamily Ledrinae, *sensu* Oman et al. 1990, comprises five tribes (Ledrini, Petalocephalini, Stenocotini, Thymbrini, and Xerophloeini), approximately 70 genera, and more than 450 species. There is, however, no consensus among workers that this tribal classification accurately reflects phylogeny (Metcalf 1962, Kramer 1966, Evans 1969, Linnavuori 1972, Hamilton 1983, Dietrich 2000, Fletcher 2002). In a recent molecular analysis that included a few ledrine species, Dietrich *et al.* (2001) found the tribes of Ledrinae to be polyphyletic within Cicadellidae, and both Dietrich (2000) and Szwedo (2002) have suggested that only Ledrini and Petalocephalini belong, and are synonymous.

With the exception the grass-feeding Xerophloeini, Ledrinae are arboreal. Some members of the group are among the largest of all leafhoppers, and several genera have pronota with ear- or winglike projections. As defined by Oman et al. (1990), the subfamily occurs worldwide, but is best represented in the Afrotropical, Australian, Indomalayan, and Neotropical regions.

Objectives

Our objectives are to: (1) test the monophyly of Ledrinae and its component tribes and selected genera using morphological data analyzed under rigorous phylogenetic criteria, (2) create robust definitions for the subfamily and its tribes that will form a basis for a comprehensive revision of the subfamily, and (3) provide a phylogenetic framework for understanding biological and geographical relationships among these leafhoppers.

Materials and Methods

Through requests to major collections worldwide, we sought representatives of all five tribes currently placed within Ledrinae and all genera of the tribes Ledrini and Petalocephalini. Our analysis included 48 cicadellid taxa representing 24 genera (one not yet described) from Ledrini and Petalocephalini, as well as one genus each from the tribes Stenocotini, Thymbrini, Xerophloeini, and Koebeliini, which Kramer (1966) moved from Ledrinae to its own subfamily. Two species of *Gypona* (Gyponinae) were designated as outgroup representatives. In total, 62 morphological characters (28 binary and 34 multi-state) of the head, thorax, and abdomen were scored, but potentially important features related to wing venation, leg chaetotaxy, and male/female genitalia remain to be compiled.

We analyzed the data using the parsimony criterion of PAUP* (Swofford, 2000) under the tree bisect and reconnect (TBR) branch-swapping routine. All characters were treated as unordered and assigned equal weight. A heuristic search was performed with 100 random addition replicates, saving 5 trees at each step of tree construction. As a final check, an additional analysis of 500 random addition replicates was performed to insure that the probable lowest cost trees had been obtained.

The number of changes for each internode of our final topology was calculated under ACCTRAN optimization using the “Describe Trees” function in PAUP*. Synapomorphies for internodes were determined by study of the lists of changes and apomorphies generated from this function. Bremer supports were calculated in TreeRot (Sorenson 1999) to assess node robustness.

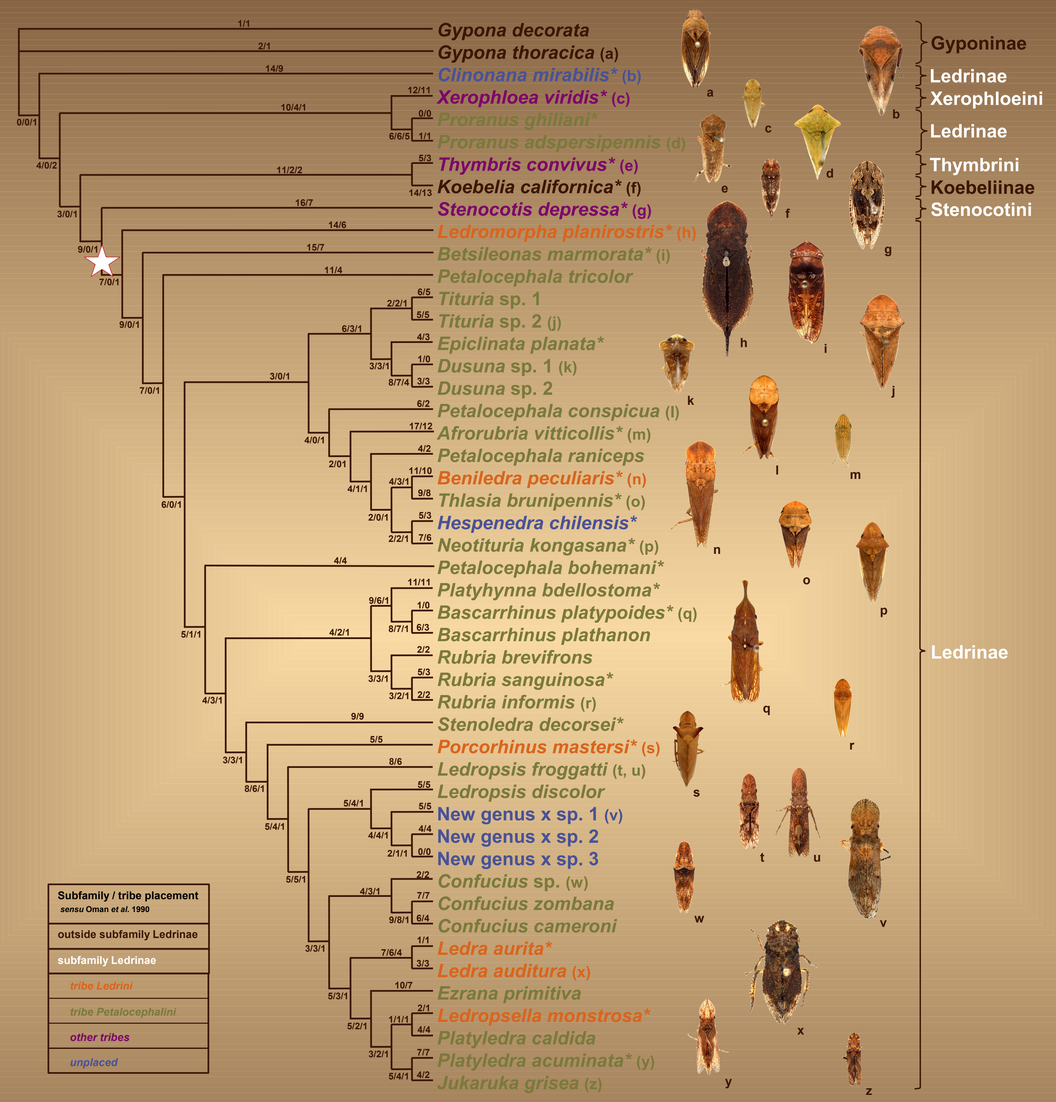

Fig. 1. Single most parsimonious topology for Ledrinae based on 62 morphological characters. Numbers at internodes (4/2/1) represent, respectively, number of character state changes between nodes; number of those changes which are unambiguously placed; and Bremer support value for succeeding node. Asterisks (*) mark type species for the genera. Numbers after species names correspond to photographs at the right. Except in a few cases, Bremer supports are minimal for all nodes. The star ★ marks the boundary of Ledrinae according to our analysis. Thymbrini, Stenocotini, and Xerophloeini are all placed outside of Ledrinae, along with *Clinonana* and *Proranus*. Ledrini is broadly polyphyletic with respect to Petalocephalini, but Ledrini + Petalocephalini (minus *Clinonana* and *Proranus* and including unplaced *Hespenedra* and New genus x) is resolved as monophyletic.

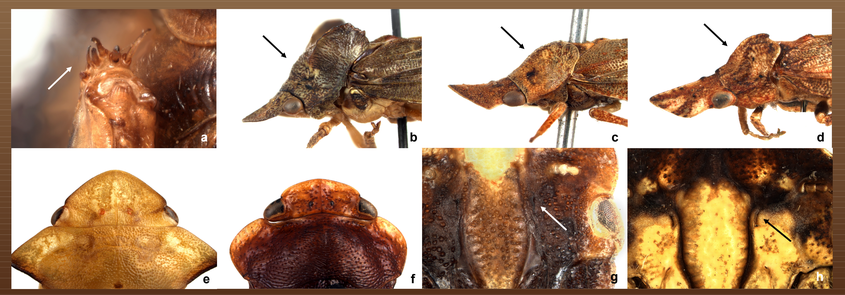

Fig. 2. Characters for Ledrinae. (a) hind femur macrosetae: *Betsileonas marmorata*; (b-d) pronotum steeply declivous in lateral view: *Ledra aurita*, *Confucius cameroni*, *Jukaruka grisea*; (e-f) orientation of eyes on head: *Epiclinata planata* and *Dusuna* sp. 2.; (g-h) pinched anterior tentorial pits: *J. grisea* and *L. aurita*.

Results and Discussion

We obtained a single most parsimonious tree with 459 steps (Fig. 1). All nodes are well resolved and most genera represented by more than one exemplar are preserved as monophyletic. Bremer supports for most nodes, however, are quite low. Among our most significant findings:

- Ledrinae appears to be paraphyletic with respect to tribes Stenocotini, Thymbrini, and Xerophloeini (Fig. 1g, e, and c), which are all placed outside of Ledrini and Petalocephalini (Fig. 1: green and orange-colored species names) in our topology, along with Koebeliinae (Fig. 1f);
- Two ledrine genera, *Clinonana* and *Proranus* (Fig. 1b and d), are also placed outside of Ledrini and Petalocephalini, and next to *Gypona* and *Xerophloea* (Fig. 1a and c) respectively;
- Ledrini and Petalocephalini are randomly interspersed and polyphyletic with respect to one another, but together appear to form a monophyletic group (minus *Clinonana* and *Proranus*);
- Stenocotini is placed as closest sister taxon to Ledrini + Petalocephalini.

The phylogenetic boundary of Ledrini + Petalocephalini (and thus Ledrinae) remains an open question, as both *Ledromorpha* and *Betsileonas* (Fig. 1h and i), monobasic genera, are placed outside of all other species of Ledrini and Petalocephalini. These genera are highly autapomorphic, and all character changes arising along the internodes outside of either of these taxa are “ambiguous”, indicating they could optimize elsewhere in the topology. Despite these uncertainties, it is clear that Stenocotini, Thymbrini, and Xerophloeini do not belong within Ledrinae, and so we place a white star outside of *Ledromorpha* representing the boundary of Ledrinae (Fig. 1).

Summary and Significance

Our results (Fig. 1) support the views of Dietrich *et al.* (2001) concerning the polyphyly of Ledrinae, and Dietrich (2000) and Szwedo (2002) relative to the synonymy of Ledrini and Petalocephalini. They also concur with Dietrich *et al.* and Szwedo regarding the sister group relationship between *Proranus* and Xerophloeini. In our analysis *Clinonana* is shown to belong outside of Ledrinae, and Stenocotini is placed as closest sister taxon to Ledrinae + Petalocephalini.

As the most extensive phylogenetic analysis of the Ledrinae to date, this study is an important first step in establishing the monophyly and taxonomic limits of the subfamily and its subordinate tribes. With the addition of further characters and taxa (especially more genera from China and southeast Asia), we hope to establish a robust, reliable classification that will set to rest the current uncertainties, facilitate identification, and provide a sound basis for understanding biological and geographical patterns among these leafhoppers.

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