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Phylogeny and systematics of the leafhopper subfamily Ledrinae (Hemiptera: Cicadellidae)

JOSHUA R. JONES[1] & LEWIS L. DEITZ[2]
[1]Corresponding author: Department of Entomology, Texas A&M University, College Station, TX, 77843–2475, U.S.A.
E-mail: doc.jones3000@tamu.edu
[2]Department of Entomology, North Carolina State University, Raleigh, NC, 27695-7613, U.S.A.

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Joshua R. Jones & Lewis L. Deitz
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Table of contents

Abstract

Ledrinae represent a relatively small subfamily within the very large and diverse leafhopper family Cicadellidae. Prior to this study, the subfamily contained approximately 450 species in 5 tribes and 73 genera distributed worldwide, but primarily in Australia, Africa, and the Indomalayan region. Several authors have suggested Ledrinae are not monophyletic, and recent studies based on molecular and morphological data have called the existing classification into question. The goals of this study were to collect and analyze morphological data under rigorous phylogenetic criteria in order to test the monophyly of Ledrinae, provide robust definitions for the subfamily and its tribes, and provide a phylogenetic framework for understanding relationships among these leafhoppers. New phylogenetic hypotheses are presented here regarding the monophyly of Ledrinae and its included tribes. A total of 235 morphological characters were coded for 60 species from 31 genera in the tribes Ledrini and Petalocephalini, 5 species from the tribes Stenocotini, Thymbrini, and Xerophloeini, and 10 species selected as outgroups from various other cicadellid subfamilies. Data were analyzed in PAUP*, resulting in a single completely resolved topology with many well-supported nodes. Ledrinae, as previously defined, were found to be polyphyletic with respect to Stenocotini, Thymbrini, and various ledrine genera, which were placed with the outgroup taxa. Stenocotini and Thymbrini were placed with Tartessinae, agreeing with results of other recent studies. *Rubria*, *Hespenedra*, and the *Afrorubria* genus group formed independent lineages within Ledrinae. The tribe Xerophloeini was placed as a basal lineage within Ledrinae closely associated with the *Afrorubria* group. Ledrini and Petalocephalini, as previously defined, did not form monophyletic lineages, but were randomly interspersed (paraphyletic) with respect to one another. Stenocotini and Thymbrini are here removed to the subfamily Tartessinae, and Petalocephalini is made a synonym of Ledrini. The new tribes Afrorubrini, Hespenedrini, and Rubrini are described within Ledrinae by the first author, and several new informal genus groups are named. Within Ledrini, *Epiclinata* Metcalf is made a synonym of *Tituria* Stål, *Epiclinata planata* (Fabricius) and *Epiclinata flavomarginata* Kuoh & Cai are moved to *Tituria*, *Tituria obtusa* Walker is moved to *Thlasia* Germar, and two additional species are included in *Latycephala* McKamey as new combinations. Taxa placed outside of Ledrinae in this analysis are removed to other subfamilies or considered unplaced within Cicadellidae. This newly revised classification strengthens hypotheses that the Ledrinae are a very old group within Cicadellidae. As here defined, the subfamily includes five tribes with a total of 38 genera and approximately 300 species.

Key words: Afrorubrini, Auchenorrhyncha, distribution, Hespenedrini, Homoptera, identification, key, Ledrini, morphology, new tribe, phylogeny, Rubrini, Stenocotini, Thymbrini, Xerophloeini, revision

Introduction

Background

Ledrinae represent a relatively small subfamily within the very large and diverse leafhopper family Cicadellidae. The most recent accounting of the entire subfamily, by Oman *et al.* (1990), included 70 genera in five tribes—Ledrini, Petalocephalini, Stenocotini, Thymbrini, and Xerophloeini—with many genera unplaced, and represented approximately 450 described species. Ledrines occur on every continent except Antarctica, with the largest radiations occurring in Australia, Africa, and most extensively, Southeast Asia.

Taxonomically speaking, Ledrinae are an old group, with the first named species, *Cicada aurita*, described by Linnaeus in *Systema Naturae* (1758). Fairmaire (1855) later treated the group as a family, calling it *Ledrides*. Among currently recognized family groups in the Cicadellidae, only Eurymelinae Amyot and Serville, 1843 and Cicadellidae Latreille, 1825 (Dietrich and Deitz 1993), are older (though several names have been synonymized or suppressed—see Opinion 647 of the International Commission on Zoological Nomenclature, 1963). Most ledrine genera and species were described before 1933 by Fabricius (1794), Germar (1836, 1839), Spinola (1850, 1852), Walker (1851, 1857), Stål (1853, 1855, 1864, 1865), Signoret (1880), Kirkaldy (1901, 1903, 1906, 1907), Melichar (1924), Distant (1907, 1908), and Kato (1931, 1932). Other important workers have included Jacobi (1914, 1944), Evans (1936a, 1936b, 1937, 1939, 1954, 1959, 1966, 1969), Nast (1952), Kramer (1966), Linnavuori (1972), and most recently, Kuoh [=Ge] (1992) and Cai (Cai 1992, 1994b, 1997, 1998; Cai and He 1997, 2000; Cai and Huang 1998).

Ledrinae have been portrayed as living chiefly on trees and shrubs, with the grass-feeding Xerophloeini being exceptional (Dietrich 2000), and none appear to be major vectors of plant diseases (Nielson 1968). Interest in ledrines has often centered on their unique morphology and its possible implications for the evolutionary history of leafhoppers (Evans 1951, 1958; Ross, 1957). In general, ledrines have been characterized as large (the world's largest leafhopper, *Ledromorpha planirostris* Donovan from Australia, has been placed in the Ledrinae), green or brown, having flattened crowns and tibiae, reduced leg macrosetae, and a metathoracic femur macrosetal formula of 2+1. Other characteristics commonly associated with ledrines include the ocelli being located on or near the crown, the forewing venation being highly reticulate, and, like the only ledrine found in Europe, *Ledra aurita* Linnaeus, having large conspicuous projections off the pronotum. Presence of such projections has resulted in a number of treehoppers (Membracidae) being misplaced into Ledrinae, and vice versa (Goding 1903; Cryan *et al.* 2004).

Formal definitions for Ledrinae have been inexact or vague, and some characterizations of the subfamily have been based on *L. aurita*, undoubtedly one of the more derived members. The general features outlined above thus describe many members of the subfamily, but not all. Accordingly, many species that share these general characteristics, but which originate from other Auchenorrhyncha lineages, seem to have been included in Ledrinae in error.

Although their taxonomic position among the Cicadellidae is uncertain, Ledrinae appear to represent an old lineage. Fossil evidence (discussed in detail in "Biogeographic considerations and fossil evidence" below) seems to indicate that ledrine ancestors existed in the Lower Cretaceous (Shcherbakov 1992). Linnavuori (1972) suggested that most of the African ledrine genera originated during the Tertiary and that a few were of pre-Tertiary origin. Recent molecular analyses (Dietrich 2005) place some ledrine taxa basally within Cicadellidae + Membracidae, but with weak support.

Many ledrine taxa exhibit features thought to be ancestral among Cicadellidae, and some authors (Evans 1951, 1958; Ross, 1957) have used ledrine examples in making important inferences about cicadellid evolution. This is of some concern, when treating the subfamily as a single unit, as a number of recent molecular and morphological studies have strongly suggested that the subfamily as previously defined is polyphyletic. In a phylogenetic study of subfamily and tribal relationships within Cicadellidae based on 28S rDNA sequences (Dietrich *et al.* 2001), the tribe Xerophloeini was placed as sister to Aphrodinae and nested well within Cicadellidae, while Thymbrini and Stenocotini were placed in a clade together with Tartessinae in an unresolved and weakly supported position near the base of Cicadellidae. More recently, Xerophloeini were placed separately from but near to Ledrini + (Thymbrini + (Tartessinae + Stenocotini)), based on a combined Bayesian analysis of 28S rDNA and morphological characters (Dietrich *et al.* 2005).

The findings of Dietrich and coworkers have served to underscore the wide discrepancies in interpretations of the taxonomic limits of Ledrinae. Presently there is no consensus among workers that the tribal classifications proposed by either Metcalf (1962) or Oman *et al.* (1990) accurately reflect phylogeny (Kramer 1966, Evans 1969, Linnavuori 1972, Hamilton 1983, Dietrich 2000, Fletcher 2002). Dietrich (2000, 2005) and Szwedo (2002) have both suggested that only Ledrini and Petalocephalini belong, and with Hamilton (1983) have treated the latter tribe as a junior synonym of the former.

Evans (1966), Kramer (1966), and Linnavuori (1972) revised the New World, Australian, and African Ledrinae, respectively, and both Kramer and Linnavuori declined to recognize tribes. All three workers recommended the need for a world revision of Ledrinae, with Kramer stating that such a study was essential in order to formulate appropriate tribal arrangements. Evans and Linnavuori also expressed a need for a revision of the taxa of the Oriental region, with Linnavuori mentioning specifically the species in the genus *Tituria* Stål. *Tituria* is among the four largest genera in the tribes Ledrini and Petalocephalini, together with *Ledra* Fabricius, *Ledropsis* White, and *Petalocephala* Stål, and from the present study it appears that all four, in fact, need closer individual attention and revision.

Despite these suggestions and the considerable attention Ledrinae have received, no family-level world revision has yet been performed. Likewise, the subfamily has not been subject to any sort of comprehensive phylogenetic analysis.

This paper presents an extensive, genus-level, morphological phylogenetic treatment of the entire subfamily, while focusing on available genera for two of its largest tribes, Ledrini and Petalocephalini. The objectives were 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. As a result of these analyses, new taxonomic arrangements are proposed, new tribes are described (by the first author), and several new informal genus groups are named. A complete species-level monographic revision of the subfamily was not attempted at this time because of the limited availability of both type and non-type material, and the difficulty in treating the large number (>550) of available names at one time.

Literature review

The type genus of Ledrinae, *Ledra*, was described by Fabricius (1803). Fairmaire (1855) later placed *Ledra* in the new family *Ledrides*, but the name and status of the group fluctuated wildly after, being called variously Ledridae, Ledrina, Ledrini, Ledrida, and Ledrinae, and occupying the levels of tribe, subfamily, and family. After 1903 the group essentially settled to the rank of subfamily, though various authors continued to raise it to family status. Metcalf provided a complete bibliographic history up to 1955 in his General Catalogue of the Homoptera (1962). Opinion 647 of the International Commission on Zoological Nomenclature (1963) resolved a number of tediously complex nomenclatural issues related to family-group names for various taxa of leafhoppers, including Ledridae [it placed Ledridae Kirshbaum 1867 (type genus *Ledra* Fabricius 1803) on the Official List of Family-Group Names in Zoology, and placed Tettigonides Amyot and Serville (type genus *Tetigonia* Geoffroy 1762, an unavailable generic name) on the Official Index of Rejected and Invalid Family-Group Names in Zoology, thereby removing any possibility that the latter could be applied to a family group taxon (China 1961; International Commission on Zoological Nomenclature 1963)]. Simultaneously, Metcalf's Catalogue (1962) raised most existing subfamilies of Cicadellidae to the family rank, including Ledrinae, but Oman *et al.* (1990) did not follow this classification in their follow-up bibliography. Subsequent authors have continued to treat the group at both levels, with the majority now recognizing it as a subfamily of Cicadellidae, sensu Oman *et al.*, as is done here.

Early workers on the Ledrinae include Germar (1836), Spinola (1850, 1852), Stål (1853, 1855, 1864, 1865), Walker (1862), Signoret (1880), Kirkaldy (1901, 1903, 1906, 1907), Distant (1907, 1908), Melichar (1925), and Kato (1931). Particularly important early works were those that included illustrations, namely of Distant (1908), which included many beautiful drawings and descriptions of three new genera, Kato (1931), which described four genera new to Taiwan and Japan with high quality illustrations of each, and Kato (1933), which provided some of the first photographs of Ledrinae.

During the middle part of the last century, much of the work on Ledrinae was performed by Evans (1936a, 1936b, 1937, 1939, 1941, 1947, 1954, 1955, 1959, 1966, 1969), who described 15 new genera and created the new tribes Koebeliini, Ledrini, and Thymbrini, while making many important hypotheses about ledrine relationships (see "Past taxonomic treatments", below). Other works published during this period included those of Oman (1949), who described the tribe Xerophloeini and included *Xerophloea* Germar and *Epiclines* Amyot and Serville (= *Proranus* Spinola, though he did not describe the latter or give explicit similarities between the genera), Nast (1952), who discussed the limits of the genus *Petalocephala* (noting its urgent need for revision) and described a new genus, Ross (1957), who proposed a new classification for the Cicadellidae that included Ledrinae (see "Past taxonomic treatments", below), Nielson (1962), who revised *Xerophloea*, and Metcalf (1962), who erected the novel tribe Petalocephalini in the General Catalogue, but provided no formal description of the tribe or its members (the name appears to be a *nomum nudum*, and its status will be discussed in greater detail in the section on the tribe Ledrini).

Among the more important recent works on the subfamily as a whole have been the regional revisions by Kramer (1966), Evans (1966), and Linnavuori (1972), and a later publication by Evans (1969) that included species from New Guinea. Although the present analysis challenges several of their conclusions about taxonomic relationships and placements, each of these authors moved knowledge of the Ledrinae forward in a significant way.

Kramer (1966) considered the genera *Bascarrhinus* Fowler, *Platyhynna* Berg, *Clinonana* Osborn, *Proranus*, *Xerophloea*, *Ohausia* Schmidt, and his new genera *Hespenedra* Kramer and *Xedreota* Kramer, to constitute the Ledrinae of the New World, but made no formal tribal assignments. He (correctly) observed similarities between *Proranus* and *Xerophloea*, including the genitalia, metathoracic tibial "spines", facial sclerites, and forewing venation and punctation. He also stated that *Bascarrhinus* and *Platyhynna* were closer to "true *Ledra* Fabricius than any of the other New World genera on the basis of the habitus, forewing venation, and the reduced number of spines on the flattened metathoracic tibia." He moved *Clinonana* from Gyponinae (=Scarinae) to Ledrinae on the basis of similar metathoracic femur chaetotaxy (2+1), despite similarities in forewing venation and genitalia with *Prairiana* Ball (Gyponinae), stating, "it is perhaps best to consider *Clinonana* as a connecting link between the Ledrinae and Gyponinae with its subfamily placement a matter of choice."

Evans' 1966 revision of the Australian leafhoppers examined the three tribes found on the Australian continent: Ledrini, Stenocotini and Thymbrini. Describing new genera and species, he suggested that *Rubria* Stål was sufficiently unique to be placed in a separate tribe within Ledrinae, but he hesitated to do so, citing the need for a world revision of Ledrinae that includes members from the African and Oriental regions. He reemphasized his previously stated view (1947) that Ledrinae were derived from "ulopid stock" but presented a new hypothesis that Ledrini and Stenocotini had experienced parallel development, rather than that one had derived from the other, as he had previously suggested (Evans 1947—he had inferred that *Ledra* and Stenocotini were linked by the ledrine genus *Ledromorpha*—see "Past taxonomic treatments" below). He suggested that the Ledrini might have entered Australia from the north prior to the period of Tertiary isolation.

Linnavuori (1972) provided perhaps the best recent formalized definition for the subfamily Ledrinae (p. 204), but recognized no tribes in his revision of the African species, presumably because of his perceived need for a worldwide revision (p. 248). Like Evans, he considered Ledrinae to have derived from the ulopine stem because of its several similarities to the subfamily Ulopinae. He considered most of the African genera to belong to the *Petalocephala* group, but distinguished *Titiella* Bergroth, *Sichaea* Stål, and *Afrorubria* Linnavuori as having an isolated position belonging to the "original Cape fauna," with *Afrorubria* being most like *Petalocephala* and probably derived from it. He contrasted *Rubria* and *Afrorubria*, discussed the distinctive features of *Sichaea* and *Titiella*, and commented on the heterogeneity of three species groups within *Tituria* and the need for a revision of the genus in light of the Oriental species. He suggested that *Sichaea* might deserve to be placed into a separate tribe of its own within Ledrinae, but that a worldwide revision should precede such placement.

Evans (1969) described four new genera and many new species and provided an insightful discussion into the position of the ocelli in nymphs versus adults of Koebeliini, Ledrini, Stenocotini and Thymbrini, again asserting their collective origin from an ulopine stem. He rejected Kramer's removal of *Koebelia* Baker from Ledrini on account of ocelli position, and moved *Clinonana* back into Gyponinae based on tegminal venation and genitalia structure, and the shape and structure of the face, and abundance of spines on male sternite IX. He also pointed out that Ulopinae include members with [sexually] polymorphic wing expression, whereas Ledrinae do not.

Despite the various inclusions and rejections of genera within Ledrinae by these authors, Oman *et al.* in their bibliography and checklist of the Cicadellidae (1990), included *Clinonana*, *Ohausia* and three other unplaced genera, while excluding Koebeliini. In Ledrini and Petalocephalini they included 43 genera.

In the period since the key revisionary works of Kramer, Evans, and Linnavuori, several authors have published on the Ledrinae, particularly on species from the Indomalayan region. Kuoh (Kuoh 1991; Ge 1992) and Cai (1992, 1993, 1994a, 1994b), together (Cai and Kuoh 1991, 1993, 1994; Cai and Ge 1992; Kuoh and Cai 1993, 1994) and with other collaborators (Cai and Meng 1991; Cai and Mo 1992; Cai and Li 1995; Cai and Yang 1997; Cai and He 1997, 2000, 2002; Liang et al. 1997; Cai and Huang 1998; Cai and Shen 1998; Cai et al. 1998, 2001; Cai and Jiang 2000; Cen and Cai 2000), have described nine new genera and dozens of new species from China and Taiwan. Other important workers include Kwon and Lee (1978), who reviewed the Ledrinae of Korea, Ren and Zhang (2001), who surveyed the geographical distribution of Ledrinae in China, and Shih *et al.* (2001) who provided a checklist of genera and species from Taiwan.

Recent workers focusing on ledrine fauna in other parts of the world have included Cwikla (1987), who provided a formal phylogenetic analysis of the four species of the New World *Bascarrhinus*, using eleven morphological characters, and Szwedo (2002), who described the new xerophloeine genus, *Pariacaca* Szwedo, while providing valuable commentary on the history of tribal relationships in the Ledrinae. Szwedo considered the tribe Xerophloeini to include *Xerophloea*, *Proranus*, *Hespenedra* Kramer, *Xedreota*, "possibly *Clinonana*," and his new genus *Pariacaca*, but made no mention of *Piezauchenia* Spinola. He removed *Ohausia* from Ledrinae, concluding its subfamilial placement to be uncertain. He made, however, no formal inference as to the position of Xerophloeini within Ledrinae, and gave no discrete characters for the tribe.

The most recent papers that have addressed Ledrinae relationships have used molecular phylogenetic techniques; these will be addressed along with other important taxonomic works in the following section.

Past taxonomic and phylogenetic treatments

Historically, the subfamily Ledrinae has contained the tribes Koebeliini Evans 1947, Ledrini Evans 1947, Petalocephalini Metcalf 1962, Stenocotini Kirkaldy 1907, Thymbrini Evans 1936, and Xerophloeini Oman 1949. Oman (1949), and later Evans (1966), removed Koebeliini from Ledrinae by virtue of its ocelli being located on the face as opposed to the vertex or edge of the crown, and it is now understood to be a distinct lineage (Oman 1949; Kramer 1966; Evans 1969; Nielson 1985) properly belonging within Deltocephalinae (Dietrich 2000; Dietrich and Dmitriev 2003).

A number of treatments have addressed the position of various ledrine taxa within the Cicadellidae. Ross (1957) placed Ledrinae (Ledrini + Koebeliini + Stenocotini + Thymbrini) in his division Macropsides (with Hylicinae and Eurymelinae) based on metathoracic tibia chaetotaxy and the median metanotal suture. He placed Xerophloeini alone in their own division, Xerophloeides, based on the flatness of the crown, exposed proepisterna, dorsal ocelli, and other features. Evans (1958) argued that such phylogenetic arrangements placed too much emphasis on single characters not indicative of broad relationships across Cicadellidae, such as head shape, ocelli position, and leg chaetotaxy, while ignoring more important characters, such as wing venation and genitalia. He further argued that relationships were best explained when all characters were examined together and the broadest consensus was found. In offering his view of cicadellid relationships, he referenced his 1947 publication, “A Natural Classification of the Leafhoppers, Part 3.” In this comprehensive work on the Cicadellidae, he included *Xerophloea* within the tribe Ledrini (together with Koebeliini, Stenocotini and Thymbrini in the subfamily Ledrinae), based on characters of the face, pronotum, legs, wings, and genitalia, but gave no universally unifying features for the tribe, instead making use of “overlapping characters” to establish interrelationships. He pointed out the general occurrence of spatulate heads with dorsal ocelli, and flattened metathoracic tibia with reduced spinulation (all features mentioned by Ross 1957), but downplayed the role of the position of the ocelli in adults in determining subfamilial placement for genera (because of their varying position in nymphs). He discussed in detail the connection between *Ledra* and the Australian species *L. planirostris*, suggesting the latter could be placed in either Ledrini or Stenocotini on the basis of the ledrine-like spatulate head, dorsal ocelli, flattened tibia, and reticulate wing venation, and the stenocotine-like face and the first cubitus of the tegmen having several branches. He also noted similarities between the heads of *Stenocotis depressa* and *Koebelia californica*.

Metcalf (1962) made no formal taxonomic descriptions in the Catalogue, but did make a number of important decisions regarding the placement of taxa within Ledrinae. He created a new tribe, Petalocephalini, and listed all of the genera of Ledrini within it except *Ledra*, which he left alone in Ledrini, and treated Thymbrini as a subgroup of the Nearctic Koebeliini. Subsequent authors moved many genera back into Ledrini, and a few have listed genera under the tribe Petalocephalini sensu Metcalf, but no one has provided a key to the tribes of Ledrinae or a formal description for Petalocephalini.

Hamilton (1983), like Ross, proposed a novel classification for the Cicadellidae, basing it on the position of the ocelli, structure of the tentorium, shape of the mesonota and mesosterna, wing venation, macrosetae at the apices of the metathoracic femora, metathoracic tibial chaetotaxy, and metathoracic tibial pectens. He treated Petalocephalini as a junior synonym of Ledrini, and included only Ledrini and Xerophloeini within Ledrinae. Using an informal optimization of characters, he concluded that Ledrinae were a primitive lineage within Cicadellidae based on the dorsal position of the ocelli, that it was sister to a clade comprising Ulopinae, Aetalionidae, and Membracidae based on the T-shaped mesosternal sutures. While it made many new character observations and raised provocative possibilities for re-assessing relationships, his classification has not been widely accepted.

Dietrich *et al.* (2001) were the first to employ molecular data to attempt to decipher relationships among cicadellid subfamilies and tribes, using nucleotide sequences from the 28S ribosomal DNA. Included in their analyses were the ledrine genera *Proranus*, *Thymbris* Kirkaldy, *Stenocotis* Stål, and *Xerophloea*. In each of their two published trees, *Proranus* and *Xerophloea* were placed as sister taxa to Aphrodinae, and *Thymbris* and *Stenocotis* were placed in a clade with *Tartessus* Stål (Tartessinae). Basal branching relationships were unclear, with the two ledrine-containing clades being placed as sister to one another in one analysis, but relatively far apart in subsequent analyses that differed in the degree to which regions of ambiguous homology were included in the nucleotide alignment. The tree based on the more conservative dataset suggested that the Tartessinae + (Thymbrini + Stenocotini) clade might have a basal position within Cicadellidae, although its exact position was unresolved and branch support was low.

In a presentation at the 2005 Auchenorrhyncha Congress, Dietrich *et al.* (2005) shared the results of a follow-up study of cicadellid relationships based on Bayesian likelihood phylogenetic analysis of both 28S rDNA sequence data and morphological characters. This analysis included *Ledra*, *Putoniessa* Kirkaldy, *Stenocotis*, *Proranus*, and *Xerophloea*. Again, *Proranus* and *Xerophloea* were placed as sister taxa to one another, but they did not group with Aphrodinae. *Ledra* was placed together in a clade with *Putoniessa*, *Stenocotis*, and the tartessine genus *Neotartessus* F. Evans. While the tartessine and xerophloeine clades were placed near to each other and basal to the rest of Cicadellidae + Membracidae, basal nodes for both clades had low posterior probabilities.

Despite their limited sampling of ledrine taxa and molecular data and their slightly varying results, these analyses provide important clues to relationships among the tribes of Ledrinae, as well as to their deeper relationships to the rest of Cicadellidae.

Except for the works of Cwikla (1987) and Dietrich *et al.* (2001, 2005), the subfamily Ledrinae has received no formal phylogenetic treatment, and relationships among its constituent taxa have not been explicitly tested using modern phylogenetic methods. The results in those papers demonstrate that explicitly phylogenetic evaluations of characters and relationships add new perspectives and have the potential to provide improved estimates of natural relationships.

Materials and methods

Ingroup taxon sampling

An endeavor was made to obtain material representing every genus in the subfamily Ledrinae as recognized by Oman *et al.* (1990). This was a greater challenge than expected, as many of these genera are monobasic, known only from the type specimens of the described species, were not made available by collections, or the type specimens are simply unknown (and are possibly lost or destroyed). In some cases where type specimens were unknown, other representative material was available for examination. As much as possible, positively identified non-type material was requested for examination in order to avoid damage to type specimens. Specimens were acquired through requests to numerous institutions and personal visits to BMNH, INHS, MNHN, NMNS, NMWC, TARI, UDCC, and USNM (see Collection Coden List below).

The focus in this work was on the genera within the larger tribes Ledrini and Petalocephalini. However, many of the genera in all ledrine tribes were examined. A unique alphanumeric code was created for each of the specimens examined (i.e., JRJ_Led1_000) and a label with such codes affixed to the specimen pin. A list of the examined ingroup specimens from which characters were coded, with their unique identification numbers, is given ("Material Examined") under each genus heading within the sections for tribes included in Ledrinae, and under each genus heading within the "Taxa removed from Ledrinae" section.

Many more specimens were acquired through loans and were briefly examined than the smaller subset that was intensively studied for this analysis. A complete list of these specimens with their label information and corresponding codes can be obtained from the first author.

Outgroup taxon sampling

Additionally, a number of taxa belonging to other subfamilies of Cicadellidae (obtained from the INHS, NCSU, and USNM collections—see list of codens below) were examined and included as outgroups. Identification numbers and label and collection information for those taxa and for specimens of unidentified genera also included in the phylogenetic analysis but not in the taxonomic descriptions are given here:

Genus 1: 1 male, 1 female, Borneo, BPBM, JRJ_Led1_296–297.

Genus 2: 4 males, South Africa, SANC, JRJ_Led1_275–278.

Genus 3: 5 males, South Africa, SANC, JRJ_Led1_339, 345–348.

Genus 4: 4 males, South Africa, SANC, JRJ_Led1_313–316.

Aphrodes bicincta (von Schrank): 4 males, 7 females, U. S. A., NCSU, JRJ_Led1_225, 228–230, 233, 235–237, 239–241. Pl. 18B.

Bathysmatophorus shabliovskii Kusnezov: 4 males, 2 females, Russia, USNM, JRJ_Led1_426–428.

Coloborrhis corticina Germar: 3 males, 6 females, Kenya, Nigeria, South Africa, USNM, JRJ_Led1_375–377, 387–393. Pl. 14B.

Gypona decorata Fowler: 1 male, 2 females, Guiana, NCSU, JRJ_Led1_243–245.

Gypona testacea Metcalf: 3 males, 3 females, Guiana, NCSU, JRJ_Led1_246–251.

Iassus scutellaris (Fieber): 5 males, 5 females, Germany, NCSU, JRJ_Led_254–263. Pl. 18H.

Krisna sp: 1 male, 1 female, China, NCSU, JRJ_Led1_455–456.

Lystridea uhleri (Baker): 3 males, 3 females, U. S. A., USNM, JRJ_Led1_408–413.

Collection Coden List

The following codens are used herein to indicate collections where specimens are located (from Arnett *et al.*, 1993):

AMNH	American Museum of Natural History, New York, New York, U.S.A.
AMSA	Australian Museum, Sydney, New South Wales, Australia.
ASCU	Orange Agricultural Institute, Agricultural Scientific Collections Unit, Orange, New South Wales, Australia
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
BMNH	The Natural History Museum, London, United Kingdom.
CASC	California Academy of Sciences, San Francisco, California, U.S.A.
CNCI	Canadian National Collection of Insects, Ontario, Canada.
HNHM	Hungarian Natural History Museum, Budapest, Hungary.
INHS	Illinois Natural History Survey, Champaign, Illinois, U.S.A.
FSCA	Florida State Collection of Arthropods, Gainesville, Florida, U.S.A.
MNHN	Museum National d'Histoire Naturelle, Paris, France.
MZLU	Museum of Zoology, Lund University, Stockholm, Sweden.
NCSU	North Carolina State University Insect Collection, Raleigh, North Carolina, U.S.A.
NMNS	National Museum of Natural Science, Tai Chung, Taiwan, Republic of China.
NMWC	National Museum of Wales, Cardiff, Wales.
OSUC	The Ohio State Insect Collection, Columbus, Ohio, U.S.A.
SANC	South African National Collection of Insects, Pretoria, South Africa.
TARI	Taiwan Agricultural Research Institute Insect Collection, Wu Feng, Taiwan, Republic of China.
UDCC	University of Delaware Insect Collection, Newark, Delaware, U.S.A.
USNM	United States National Museum of Natural History, Washington, D.C., U.S.A.
ZMPA	Museum of the Institute of Zoology, Polish Academy of Science, Warsaw, Poland.

Morphological characters

Terminology used in this study is based on Dietrich (2005), Deitz (1975), Davis (1975), and the works of the numerous authors who have described Ledrinae (see above), and some terms were borrowed from A Glossary of Entomology (Torre–Bueno 1937). Table 1 (see Appendix) gives a complete list of characters and their states used in the present analysis. Table 2 (data matrix) gives the scored states for each character of each taxon in the analysis.

Among leafhoppers, many Ledrinae are morphologically distinctive. They are often large, occasionally colorful, and sometimes have ornate projections or texture on the head, pronota, and wings, reminiscent of their distant relatives the treehoppers (Membracidae). At first glance, members of a few of the genera might be easily mistaken for treehoppers. Presumably, most members of the subfamily exhibit some sort of crypsis, mimicking bark, slender stem nodules, stems, the surfaces of leaves, or parts of grasses or other plants. One undescribed genus in the analysis had stiffened subglobular forewings with the hind wings completely lost, and appeared rather beetle-like in dorsal view.

Characters of Ledrinae for this analysis were obtained in part from the literature, but much of the current project involved examining specimens in detail in order to discover new characters. At the outset of such examination, it was unknown which characters were phylogenetically informative and which were less informative. Character states were initially interpreted with homology inferred from position and greatest similarity. Early analyses thus contained many character states with inconsistent fit to resulting topologies, and on these trees, certain key taxa were highly labile in their placement under varying analysis conditions. This testing stage was important for establishing homology and defining states, and for approximately determining natural groupings. Some characters were easier than others to interpret and consistent enough to provide signal that established consistently recovered nodes in the various topologies. Taxa were re-examined following each set of analyses, in order to better understand characters and "double-check" their codings.

Each successive iteration allowed for adjustments to character interpretation and coding, and the results given here represent a final iteration of character analysis, in which the definition of characters and the delimitation of their states is generally concordant with other, less ambiguous, characters in the matrix (*sensu* Mickevich and Lipscomb 1991).

In the Ledrinae, external features on the dorsum and venter are plentiful, and some are fairly well conserved. On the crown, such features include the position of the ocelli relative to the eyes, the presence or absence of a swelling lateral to the ocellus and its degree of sclerotization, the shape of the crown margin, the shape of the area of the crown immediately behind the eyes and anterior to the posterior margin, the degree of expression of a carina posterior to this area, the shape of the posterior margins of the crown, and the expression of the longitudinal medial carina. Textures were especially difficult to characterize because they vary within taxa and are not always discretely expressed; nonetheless, a few consistent texture characters were ultimately included. In *Afrorubria* and associated genera, the crowns have a longitudinally costate texture (Pl. 7B_1; textures defined in Harris 1979, and Torre-Bueno 1937), which is diagnostic for this group. Other ledrines are variously punctate, acinose (with blueberry-like bumps—Pl. 7A_1) or colliculate (where the bumps begin to merge together). In the Ledrini especially, some of these bumps are pigmented, enlarged, sclerotized to form nodules, and/or associated with the presence of short stiff setae. In general, taxa in the Ledrini (see section for this tribe below) have crowns, pronota, and forewings that are irregular, textured, with nodules and depressions, setose, and have variously well-developed carinae. Some of these same features were observed in other tribes but were expressed inconsistently.

The pronotum exhibits several well-conserved features. Its shape in lateral view is variably differentiated (Pl. 6). Ledrini pronota are generally flat anteriorly and raised or humped (declivous) posteriorly (Pl. 6B_1), with the crown and forewings in separate, approximately parallel or subparallel, planes. The *Petalocephala* genus group and other ledrine tribes have only slightly humped or essentially flat pronota in lateral view (Pl. 6F), with the anterior portion of the body appearing slightly flexed forward and downward at a point just posterad of the mesoscutum (Pl. 6F_1). *Hespenedra* shares this feature. The species of *Rubria*, while having a slightly humped pronotum, have their head and pronotum flexed downward anterad of the posterior margin of the pronotum (Pl. 6D_1). Some clades show variation in the shape, position, and height of various longitudinal ridges or carinae, with some taxa having carinae near the anterior margin, some near the posterior margin, and some near both. A narrowly subtrapezoidal posterior margin of the pronotum (Pl. 2H–I) defines one clade of Australian Ledrini. The presence of a lateral carina and the expression of the pronotum laterally as rounded or triangular flaps is a feature of members of the *Petalocephala* genus group, although at least one member outside this grouping (*Eleazara*—not included in this analysis; Pl. 1G) also has this development. *Rubria* lacks the pronotal lateral carina, and has a boxlike shape to the side of the pronotum, which is also expressed in some members of the Indomalayan and Australian Ledrini.

The forewing cells of Ledrinae are coriaceous to opaque proximally and become opaque to translucent apically (nearly transparent in some Xerophloeini). The forewing venation of Ledrinae is normal or reticulate, with normal venation appearing to be the ancestral state and more derived ledrines having increasingly reticulate wing venation. Ledrinae lack an appendix on the forewing, except in the Xerophloeini (Pl. 11D_1), not including *Xedreota*.

Hind wing variation has not been previously investigated in the Ledrinae, and was only surveyed for a few characters in this study, and other characters may remain to be discovered. Ledrinae have the R and M veins not confluent, and the apical cells are often short (a character not coded in this analysis). In the group of southern African genera including *Afrorubria*, the hind wings are often vestigial or completely lost (Pl. 11C_1). *Afrorubria* has the hind wings developed, but *Sichaea* shows shriveled appendages still present (Pl. 11C_1). Three undescribed South African genera grouping with *Afrorubria* and *Sichaea* completely lack hind wings.

The face of ledrines, particularly the shape of the frontoclypeus and lora/genae, is expressed in a few consistent states. Ledrinae have a narrow frontoclypeus, which in the Xerophloeini (Pl. 10E, F_1) is somewhat broader apically and more swollen generally. Thus, in the Xerophloeini, the frontoclypeus is also easily visible in lateral view (Pl. 8E_1), more so than in other ledrines. Antennal ledges distinct from the crown margin were not observed in Ledrinae, except in *Xedreota* (Pl. 10E_2). One genus from South Africa with many similarities to the Neotropical *Xedreota* has a secondary marginal carina on the crown that appears to be a fused antennal ledge. The antennal pits are mostly shallow in Ledrinae, with the inner margins weakly- to well-developed into a bar running obliquely or parallel to the frontoclypeus, except in the Xerophloeini. The lora and genae are flatter in the *Afrorubria*-like genera (Pl. 9A, 11C), and the suture between them and the frontoclypeus is not deeply depressed, but in other Ledrinae, the lora/genae are tumid and angulate, with the sutural depression deep and distinct (Pl. 10D). In some Ledrini, the frontoclypeus is strongly flexed ventrad anteriorly (Pl. 9B, 10D_2). The base of the frontoclypeus is generally flat but often with a shallow longitudinal medial depression (Pl. 9C, E, 10D), and occasionally with longitudinal carinae (Pl. 9C_2–3, 10D). Perpendicular ridges indicating the inner muscle attachments of the cibarium (Pl. 9E_1) are often present, though sometimes vague.

The shape of the proepisternum is a potentially diagnostic feature for groupings within Ledrinae. In some (*Afrorubria* and *Rubria*), the proepisternum is small and tab-like and emerges visibly from underneath a narrow gena (Pl. 9A_1). In other ledrines, the proepisternum is enlarged and quadrate with marginal carinae, and appears as a plate not underlapping the genae (Pl. 9B_3, C_4). In the Australian Ledrini, this plate extends onto and merges with the lateral margin of the pronotum in a collar-like fashion (Pl. 9D_3, E_4).

Ledrinae are known for their characteristically flattened tibiae, especially their metathoracic tibiae, but this characteristic is actually only expressed in a few genera. In most genera the tibiae are quadrate in cross-section. In just a few genera are the metathoracic tibiae somewhat flattened (*Ezrana*, *Funkikonia*, *Ledropsis*) to foliate (*Ledra*—Pl. 12H). The macrosetae of the metathoracic tibia row II have some cucullae in nearly all ledrines, and in some ledrines, all the macrosetae are cucullate. Basal lineages within Ledrinae, i.e., Xerophloeini and the *Afrorubria*-like genera, have more robust and more numerous macrosetae in row II, but generally less than 8 (Pl. 12D–G). The macrosetae of row II of the most derived ledrines are reduced to only one to three macrosetae, arranged distally on the tibia (Pl. 12H).

Ledrini and *Hespenedra* have a triangular patch of flattened and brushlike or scalelike setae at the apex of row II of the mesotibia (Pl. 12A–C). In *Ledra* and a few other genera, the setae are truncated, scalelike, and in rows (Pl. 12C). In others, these setae have a yellow or golden color in dried specimens (Pl. 12A, B). Other setal rows on the tibiae are often reduced.

All Ledrinae appear to have a metathoracic femur macrosetal formula of 2 + 0 or 2 + 1 (rarely 2+1+1 in anomalous specimens), and when there are three macrosetae present, they are grouped together at the apex (Pl. 13, C–H). Non-ledrines appear to have other macrosetal arrangement formulae (Pl. 13, A–B).

Many members of the *Petalocephala* genus group, as well as a few genera outside this group, have the medial proepisternal plates strongly depressed between the forelegs (Pl. 11A, B_2). In the *Petalocephala* genus group, the anterior margin of the coxal bases posterior to the depression can be angulate (Pl. 11B_3). In this same group, many members have a fingerlike process extending laterally from meso- and metathoracic coxal bases (Pl. 11A_1).

Many characters were coded from the male and female genitalia. These features are quite variable both within and among ledrine genera. Scored variation for males included the shape of the anal tube, and the shape, position, and presence, absence, and form of various auxiliary processes of the styli, aedeagus, and pygofer (Pl. 14–16). In females, the shape of sternite VII, the shape, sclerotization, textures, and presence or absence of various groups of setae on the pygofer, and the shape, setal expression, and textures of the valvulae were useful (Pl. 17–19).

Most ledrine males have the apices of the styli acuminate and flexed downward (Pl. 14I_1, 15G_1, 16C_2). Some are recurved further, with the apical points secondarily directed anterad (Pl. 16E_3). Styli are generally long and slender and thicker medially where they meet the connective. The connective is often membranous and its shape is highly variable (and therefore not coded in the analysis), and can be small and platelike or long and narrow, with a laterally flattened medial portion (an exceptionally sclerotized connective can be seen in Pl. 16A, B). The aedeagus is generally slender in basal groups (often with various lobes—Pl.

16I_1), and broad in *Hespenedra* and some Ledrini (Pl. 16E, K). Some Australian Ledrini have segmented paraphyses (Pl. 14K_1, 16C_1, D_1; see Young 1977 for explanation of paraphyses) inserted toward the base of the aedeagus. The pygofer is variable in length, and in all Ledrinae the subgenital plates are dorsoventrally flattened at their bases and often laterally compressed apically (Pl. 14A_3, 16M_2), with rounded apices.

Female ledrines have variably slender and sclerotized valvulae. In the Ledrini, the valvulae have approximately parallel dorsal and ventral margins and are intermediately slender (Pl. 19A_1, B_1), as opposed to being very slender in some basal Ledrinae groups and outgroups, such as in *Xerophloea* (Pl. 19L_1) and *Stenoledra* Evans, a ulopine: (Pl. 19F_1). The valvulae II are also generally very sclerotized (Pl. 18E–F, I–L, 19A–C, I–J). In *Hespenedra* and some taxa in the *Petalocephala* genus group, valvulae II have a curved ventral margin and a medially peaked dorsal margin, and are of intermediate breadth (Pl. 18G_1, 19J). Valvulae I in all Ledrinae bear a fingerprint-like texture apically (Davis [1975] referred to this kind of texture as “strigate”), but *Afrorubria* and *Sichaea* (and also *Stenoledra*—Pl. 17H_1) also exhibit a longitudinal medial band of chevron-shaped grooves (Pl. 17D_1, G_2). Valvulae II bear numerous tiny dorsal teeth in a few taxa (*Rubria* and *Afrorubria*—Pl. 19D_1), but these auxiliary teeth are mostly absent in other ledrines. A sclerotized dorsal tooth is medially situated (Pl. 18J_1) in most members of the Ledrini. A more distal second dorsal tooth (Pl. 18J_2, K_1) is present in nearly all ledrines, and its position relative to the first tooth is a phylogenetically useful feature. The apex of valvulae II has a subtriangular to subpentagonal shape in lateral view (Pl. 19I_2; see also Pl. 18F, I–J) in most Ledrini, giving the apex the resemblance of a somewhat irregular arrowhead. The dorsal margin of the apex often retains a rhomboid to subrectangular shape, summarized herein as “quadrate” (see graphic overlain on Pl. 19I_2). Demarcating the anteriodorsal margin of this quadrate shape is the subapical notch (Pl. 18I_1, J_3). In a few outgroup and basal taxa, the apex of valvulae II is split and not heavily sclerotized (Pl. 18B_1, 19G). A lateral perpendicular keel is situated medially along valvulae II in some taxa (Pl. 18F_1, 19C_1).

A note should be made here about genitalic variation, especially of males, and its relation to the generic concepts presented herein. In this analysis, much work was done to explore the phylogenetic significance of observed features; however, developing cohesive and consistent definitions for the genera that incorporated the observed genitalic variation proved challenging, due primarily to a limited taxon sampling at the species level and the apparent high plasticity in expression of features across certain genera as they were defined prior to this study (particularly within the Ledrini, as it is newly redescribed in this paper). This was especially true in regards to secondary structures, which appeared to exhibit at least some regular patterns in their expression. The degree to which these structures were actually conserved at the subgeneric and supergeneric levels, however, was not clear, and discerning synapomorphy from symplesiomorphy is therefore not yet possible. Future taxonomic and phylogenetic work on the Ledrinae should include as many species as possible to explore intra- and intergeneric variation in the male genitalia and continue testing the monophyly of the genera.

All in all, the Ledrinae are character-rich, with a wealth of information to analyze and code. Additional characters and states might be obtained for future studies from the character complexes mentioned herein, or from others such as internal musculature and anatomy, immature stages or behavior, or from a more comprehensive survey that includes taxa not available for the current study.

Imaging, dissections, and distributions

Specimens were examined using a Leitz Wetzlar (Germany) dissecting microscope and a Cuda I–150 dual beam fiber optic light source at magnifications from 8 to 100x. As many ledrines are quite large, some characters could be viewed without the aid of magnification (i.e., relative ovipositor length).

Dissections of male and female genitalia were performed following protocols described in Deitz (1975). Following analysis of the genitalia, dissected material was stored in glycerin in a microvial attached to the base of the pin of the individual specimen with which it was originally associated.

Light micrographs were captured using two systems. The first was by the program QCapture using a Media Cybernetics Evolution MP Color digital camera (made by QImaging) mounted on an Olympus SZX12 microscope. Opelco and Fostec fiber optic lamps provided light. Images were first processed in Auto–Montage (Syncroscopy), blending as few as 8 and as many as 150 frames, then imported into Photoshop CS (Adobe) and processed for quality. The second system involved a Nikon Coolpix 4500 digital camera mounted on the Leitz microscope using a specialized ring adapter. Single photographs were captured and imported into Photoshop.

Digital manipulations varied for each photograph, but generally included the histogram stretch, saturation control, and color improvement (prior to black and white conversion). In some cases an unsharp mask was applied to increase visibility of certain features.

Scanning electron microscopy (SEM) of fine structure was done on a JEOL® JSM–5900LV. This microscope is capable of low vacuum imaging of uncoated material and allows the researcher to view safely museum specimens without negative effects to them. Digital output images were prepared in Photoshop.

Distributional data and plant host information were compiled from Metcalf (1962), McKamey (2000), and from label data on individual specimens. All distributional and plant host data on labels from positively identified specimens were recorded, including those from specimens not used in the phylogenetic analyses. Distributional data extracted from the literature was assumed to be based on accurately identified specimens, but could only be confirmed in cases where the actual specimens discussed in the literature were also made available for this study. Data were included for examined specimens of species in genera recognized to belong within Ledrinae in the present analyses (see individual taxon descriptions and Table 4b in Appendix). Plant host data were recorded in the following format: species binomial or trinomial (family).

Distributional data given in the "Range" section for each taxon are written serially as descending hierarchical political units, thusly: "political unit 1 (first political subunit 1: first political subunit 2, second political subunit 2; second political subunit 1)". Names recorded on labels but not in current political use are given in brackets immediately following the regional name in current use.

Phylogenetic analysis

In all, 235 morphological characters were given numerical scorings for phylogenetic analyses, and one distribution character was coded for post-analysis optimization. Binary and multistate characters were developed and scored in MacClade 4.06 OS X (Maddison and Maddison 2001). From MacClade, the resulting matrices were exported as NEXUS files and then imported into PAUP* 4.0b10 (Swofford 2002). Data were analyzed heuristically under the parsimony criterion using the tree bisect and reconnect (TBR) branch-swapping routine. All characters were treated as unordered and assigned equal weight, and multistate characters were treated as 'uncertain'. A heuristic search was performed with 500 random addition replicates, saving 2 trees at each step of tree construction.

Many characters and states were coded to be conditional (e.g., 15 was only able to be scored positively if 14 was state 1—see Table 1) rather than as single, multistate characters. This was done for several reasons. First, it reduced character states to their simplest expression. This enabled consistency to be maintained with coding done for other more complex character sets and states that occurred together but were difficult to score when considered simultaneously, and that, if undivided, would result in long, complicated, and unwieldy lists (e.g., characters 1–6). Second, it uncoupled characters from other potentially, but not confidently, related characters (e.g., characters 234-235). This agnostic approach may be disparaged for serving to artificially group together those taxa with shared absences, i.e., symplesiomorphies (a phenetic effect), by scoring absences twice (e.g., the protuberance might be scored as absent in 14, and therefore also score as *not* acute in 15). However, this approach appeared to be counterbalanced by the fact that it also doubly scored taxa bearing the character states in question (e.g., the protuberance could be scored as present in character 14 *and* acute in character 15). For all its weaknesses, this approach was preferred as a way to make the least number of assumptions (and thereby make more confident inferences) about the interrelatedness of characters and states.

This method seems to have the potential to provide more topological resolution but also yield more noise, evidenced by lower Bremer support values. However, this effect may be offset by inflation in the overall number of characters in the analysis, which may provide opportunities for (but not insure) a greater number of positive (synapomorphic) character correlations. In the analyses performed here, the result was a fully resolved tree with reasonably high Bremer support values for many clades (Figs. 1, 2).

The number of changes for each internode of the final topology was calculated under ACCTRAN optimization using the "Describe Trees" function in PAUP*. Synapomorphies for internodes were determined by studying the lists of changes and apomorphies generated from this function, and by using the "trace character" function of MacClade (Maddison and Maddison 2001). Bremer supports were calculated in TreeRot (Sorenson 1999) to assess reliability of node support in phylogeny estimates.

During examination of available ledrine specimens prior to the phylogenetic analysis, several taxa currently placed in Ledrinae were considered too highly divergent to belong to the subfamily. Potential non-ledrine taxa with which these genera might group (Aphrodinae, Iassinae, Scarinae, Tartessinae, Ulopinae) were selected and included in the analysis as outgroups. It was also hoped that one or more of these taxa might be identified as sister group to a core of species constituting monophyletic Ledrinae.

All analyses were rooted to *Bathysmatophorus shabliovskii* Kusnezov, or to *B. shabliovskii* and *Lystridea uhleri* (Baker) (both Cicadellinae: Errhomenini), putatively ancient leafhoppers, as outgroups (as recommended by C. H. Dietrich, personal communication).

Results and discussion

Phylogenetic results and discussion

Figure 1 shows the results of the initial phylogenetic parsimony analysis that included all of the taxa and characters surveyed. This tree is completely resolved and shows convincing character support for many nodes (putative Ledrinae is marked with a black star). The total length of the parsimony tree was 1719 steps.

Outgroup placements

As anticipated, several genera previously recognized to belong to Ledrinae were placed among the outgroup taxa in this analysis. These included *Bascarrhinus*, *Betsileonas* Kirkaldy, *Clinonana*, *Ledromorpha*, *Platyhynna*, and *Stenoledra*. Additionally, representatives of two tribes included by Oman *et al.* (1990) in Ledrinae, Stenocotini and Thymbrini, were also placed separately from all remaining Ledrinae.

Several of the outgroup placements were unexpected. *Iassus* Fabricius, a primarily Old World genus, was placed at the base of the tree. The other iassine in the analysis, *Krisna* Kirkaldy, which has Old and New World members, was placed separately. These divergent placements may be an artifact of character sampling, as few synapomorphic features of iassines were scored in the analysis. Bremer support for the placement of *Krisna* was low (1—see Fig. 1). *Krisna* grouped with two New World ledrine genera, *Bascarrhinus* and *Platyhynna*, which share the convergent hind wing R and M veins found in Iassinae, but differs from these taxa in many features, namely the shape of the frontoclypeus, the well produced mesoanterior margin of the antennal pit, the facial pit situated anterad of the frontoclypeus, the deep longitudinal median groove on the crown, and the inverted male genital capsule. *Bascarrhinus* and *Platyhynna* were well supported as sister taxa (Bremer value 11) and have been recognized elsewhere to belong together (Kramer 1966, Cwikla 1987). Despite their differences with *Krisna*, *Bascarrhinus* and *Platyhynna* shared more similarities with that genus than with any other taxon included in the initial analysis, and may belong within the New World Iassinae. If so, they may, however, merit higher level (tribe?) status because of their many unique synapomorphies. It is also possible they belong to another lineage not sampled in this analysis, or that they represent a lineage so unique and independent that they merit their own subfamily. Additional studies that include a more comprehensive sample of non-ledrine taxa will be required to accurately assign synapomorphy or convergence for many of these features and appropriately place these taxa within Cicadellidae.

Except for its small size, *Stenoledra*, in dorsal view (Pl. 5K), strongly resembles some ledrines (see for example, *Petalocephala bohemani* Stål, Pl. 3A), and Evans (1954) originally placed it in the Ledrinae for this reason (he thought it especially resembled *Rubria*, with its ocelli being closer to the eyes than to one another).

In the current analysis it grouped with *Coloborrhis* Germar, a member of Ulopini (subfamily Ulopinae). *Stenoledra* and *Coloborrhis* share many features that are synapomorphies for Ulopinae, including the carinate mesanepisternum (Pl. 8D_2) and the absence of macrosetae on the metathoracic femur and metathoracic tibia. In addition, these genera share a unique, broadly U-shaped sulcus on the mesoscutum (Pl. 7H_2), and the males have hinged or segmented subgenital plates (Pl. 14B_1, F_2). The placement of these two genera together with the New World Iassinae in these analyses is likely due to the similarity of, among other characters, the bulbous scutellum, the foliaceously expanded tibia on all legs, and a post-antennal lateral nodule (Pl. 8D_1), all which are probably symplesiomorphic or evolved in parallel in this case.

Evans (1969) described *Cololedra* from New Guinea, and placed it in Ledrinae on the basis of the dorsal position of the ocelli and the flattened shape of the metathoracic tibia. In this analysis it grouped with *Coloborrhis* and *Stenoledra* (Fig. 1). *Cololedra* differs from most Ledrinae in having well-developed platelike antennal ledges, also found in *Coloborrhis*, and in its lack of an anteriorly produced, ventrally concave crown. Though *Cololedra* and *Coloborrhis* share similarities of facial structure, *Cololedra* lacks a carinate mesanepisternum, retains macrosetae on its metathoracic legs, and, therefore, is probably not an ulopine, although it may belong to a closely related lineage. The R and M veins of the hind wing are convergent in *Cololedra*, suggesting that it may belong in Iassinae. In some regards, though, namely the longitudinal flexure of the body, longitudinal medial ridge on the pronotum, position of the ocelli, and other features (see section for *Cololedra* under “Taxa placed incertae sedis within Cicadellidae” below) *Cololedra* also resembles some basal membracids, but because the abdomen of the type (and only known) specimen is missing, and with it a number of important genitalic characters, its phylogenetic placement here must be viewed with caution.

The placement of Stenocotini and Thymbrini outside of other Ledrinae (Fig. 1, black squares) is not unexpected. Dietrich *et al.* (2001, 2005) presented molecular evidence that placed these tribes separate from, but proximate to, Ledrini, within Cicadellidae. Their placement in this analysis with Tartessinae is concordant with Dietrich *et al.*’s (2001, 2005) findings. This analysis also supports Tartessinae as sister group to Thymbrini + Stenocotini (Fig. 1). Given this result, it is suggested to move Stenocotini and Thymbrini from Ledrinae to Tartessinae (see “Taxa placed in subfamily Tartessinae Distant” under “Taxa removed from Ledrinae”, below). The placement of the Tartessinae + (Thymbrini + Stenocotini) clade with *Cololedra*, *Krisna*, and *Bascarrhinus* + *Platyhynna* (Bremer support 1) is also likely the result of inadequate outgroup character sampling.

Betsileonas, which has affinities with the deltocephaline tribe Penthimiini (not sampled, penthimiine characters not included) in the shape of the female ovipositor (Pl. 18C; personal communication, J. N. Zahniser), and with other Deltocephalinae in the setal arrangements of the metathoracic femur and tibia, forewing venation, integumentary texture, and other features (Dietrich and Rakitov, 2002), was placed in this analysis with *Clinonana* and *Gypona* Germar (Fig. 1). *Betsileonas* has a face structure similar to *Gypona* and *Clinonana* (pit anterior to frontoclypeus on face, absence of pigmentation), and these and other characters (ocelli position on head, transverse shallow wrinkles on the pronotum, broad appendix on the forewing, absence of intercalary setae on metathoracic tibia) support its position in the tree. *Betsileonas* also has a convergent R and M vein on the hind wing, a iassine feature. Although the placement of this group remains uncertain, it is clear from the current analysis that it does not belong in Ledrinae.

Clinonana was originally described in the Gyponinae (= Scarinae), but Kramer (1966) removed it to the Ledrinae because of its “general habitus” and the macrosetal formula of the metathoracic femur (see “Literature Review” above). It was placed in this analysis with *Gypona* with moderately high support (Fig. 1, Bremer = 4); as a result of this and its many morphological similarities with *Gypona*, *Clinonana* is returned to Scarinae (see discussion under “Genus *Clinonana* reinstated to Scarinae: Scarini” under “Taxa here removed from Ledrinae” below).

Two subfamilies that have previously been shown to be possible sister groups to Ledrinae have been the Iassinae and Aphrodinae (Dietrich 2005). In the first analysis (Fig. 1), neither *Iassus* nor *Krisna* was placed close to the main body of genera that appear to constitute Ledrinae. No morphological evidence was found to suggest that iassines and ledrines are sister taxa. *Aphrodes* (subfamily Aphrodinae) was placed much closer to

Ledrinae, although in the tree (Fig. 1) it grouped in a clade with *Betsileonas* and Scarinae as the closest relative to most Ledrinae. This sister group placement was only weakly supported (Bremer support 1). A second analysis (not shown), designed to limit the effects of conflicting signal by removing many of the divergent cicadellid taxa but retaining *Iassus* and *Aphrodes*, gave what may prove to be a more accurate placement, with *Aphrodes* placed as the immediate sister group to putative Ledrinae.

Ingroup placements

Figure 2 shows relationships among the genera herein recognized to belong within Ledrinae, and includes *Aphrodes* as an outgroup while excluding *Iassus*. This tree was generated using all of the coded phylogenetic characters and had a cost of 1185 steps. Support for a monophyletic Ledrinae (marked with a black star) that includes Xerophloeini and *Afrorubria* was fairly high (Bremer = 5). Characters uniting putative Ledrinae were the metathoracic tibia being intermediately flat to foliaceous in shape (character 123—see Table 2, Pl. 12D-H) and having fewer than 7 macrosetae in row II (character 124), at least some of the setal bases of the metathoracic tibial macrosetae being cucullate (character 125), metathoracic tarsomere I being short (later becoming long in the topology—character 129), the dorsal texture of valvulae I being strigate (character 214), and valvulae III being cupped (character 231). Support for several nodes within the Ledrinae was very high (> 5), and these well-supported nodes are distributed throughout the tree. Discussion of the taxa and characters in this analysis that constitute the basis for this new concept of Ledrinae follows.

Xerophloeines share many characteristics with Ledrinae, including the metathoracic femur macrosetae (formula 2 + 0) being grouped at the apex, the crown being flat and punctate, the face being foliaceous, and the macrosetae on the metathoracic tibia being somewhat reduced. But Xerophloeini are also quite different from most Ledrinae in the shape and punctation of the frontoclypeus, the lora and genae being essentially flat, the proepisternum being long and narrow, valvulae II of the ovipositor being very slender and only somewhat sclerotized, and the forewing having a broad appendix. They also have an exclusively New World distribution. It was anticipated that phylogenetic analysis might show them to not belong within Ledrinae. However, in these analyses (Figs. 1 and 2) they are given a basal placement within the subfamily in a clade with *Afrorubria* and several other South African genera (the "*Afrorubria* group", discussed in further detail below). One genus, *Proranus*, which was included by Oman *et al.* (1990) in Petalocephalini, was here placed with strong support as sister to *Xerophloea* in the Xerophloeini (several authors have previously proposed this relationship—see "Literature review" above and discussion under tribe Xerophloeini below).

Afrorubria is endemic to South Africa and differs from other ledrines in having an indistinct frontoclypeus, a somewhat convex face (most ledrines have a concave face), and the metathoracic femur macrosetae being long and striated (Pl. 13F). It also has valvulae II only somewhat sclerotized and very slender (Pl. 18A) and regular wing venation. The macrosetae of the metathoracic tibia are somewhat robust, more so than other ledrines, and with fewer cucullae, and none of the tibia are foliaceous (Pl. 12F). The crown has a parabolic silhouette dorsally (Pl. 4C), the pronotum is flat, and the overall texture of dorsum of the body is very smooth. Linnavuori (1972: 241) suggested the relationship between *Afrorubria* and Ledrinae is through *Petalocephala*, which also exhibits some of these reduced features. *Petalocephala* has the crown parabolic (Pl. 3A-C), the pronotum flat, and the tibiae not foliaceous, but has reticulate forewing venation and exhibits other differences, especially in the genitalia (which more closely resemble *Ledra* and other more robust ledrines). This analysis did not place *Afrorubria* and *Petalocephala* as sister groups to one another.

South African material sent from the SANC included specimens representing species that have not yet been described. Several of these are thought to represent new genera ("Genus 2," "Genus 3," and "Genus 4") and will be described in a later publication. Two of these, Genus 2 and Genus 3, which clearly belonged with *Afrorubria*, are very interesting in that they also exhibit characteristics of Xerophloeini, and their discovery was especially helpful in defining groundplan features in the subfamily. Genus 3, while having regular wing venation, crown texture, leg structure, and male genital structure similar to *Afrorubria*, also has an inflated frontoclypeus with punctuations characteristic of xerophloeines. The antennal pit and the shape of the crown adjacent to the frontoclypeus are very much like *Xerophloea* and *Proranus*.

Genus 4 has some similarities with *Xedreota*, a phylogenetically problematic xerophloeine genus. *Xedreota*, while having the punctate and convex frontoclypeus and slightly humped pronotum of *Xerophloea* and *Proranus*, lacks the appendix on the forewing, the deep and numerous punctuations of the dorsum, the long and narrow but exposed and punctate proepisternum, apical setae on the male pygofer, and its styli are sclerotized and not flat. Nevertheless, *Xedreota* was placed with *Xerophloea* in the analyses (Bremer support 3, Fig. 2). Genus 4 was placed within the clade containing the other *Afrorubria*-like taxa. Genus 4 and *Xedreota* share the angulate base of the frontoclypeus (Pl. 10E_1), the convex and punctate frontoclypeus, the dark pigmentation of the face, and slightly carinate antennal ledges.

The placement of the *Afrorubria* group and the Xerophloeini as sister groups appeared to be, at least in part, a result of the combined signal between Genera 3 and 4 of the *Afrorubria* group and *Xedreota*. This grouping had limited support (Bremer support = 1, Fig. 1; Bremer support = 0, Fig. 2), but was recovered in every analysis performed, including the analysis that included *Iassus* and *Aphrodes* but excluded other outgroups and divergent cicadellid taxa (not shown). In that analysis, the *Afrorubria* group and Xerophloeini were again placed together, but within an unresolved polytomy within a larger clade containing the remaining genera of Ledrinae. In all analyses, the *Afrorubria* group was supported as monophyletic (Bremer support = 6, Fig. 1; Bremer support = 3, Fig. 2), while *Xerophloea* + *Proranus* were consistently placed together (Bremer support = 10, Fig. 2) with *Xedreota* (Bremer support = 3, Fig. 2) forming the Xerophloeini (see Fig. 3, node 4).

While these results are not conclusive, they provide evidence for novel relationships, especially near the base of the Ledrinae tree. More will be said shortly on the age of the subfamily and its origins, but these new relationships considered together with the present known geographic distributions of these and the other tribes within Ledrinae suggest an old origin for the group.

As the clades containing the *Afrorubria* and Xerophloeini groups were reasonably well supported, and their association with Ledrinae also seems to be supported, they are here both treated as members of Ledrinae, and the *Afrorubria* group is given tribal rank (Afrorubrini Jones, new tribe). More discussion on their constituent genera and classification can be found under the Afrorubrini and Xerophloeini tribe headings below. Members of Afrorubrini are united by having a broad, sclerotized cone-shaped anal tube that is incomplete ventrally (Pl. 15E_1, F_1), as well as by other characters.

The genus *Rubria* was placed (Fig. 2) as sister to the remaining Ledrinae. It is distinct from other ledrines in that many of its features appear to be plesiomorphic or reduced—the lateral carina on the pronotum is absent, the scutellum is flat, wing venation is regular, the apical extension of the frontoclypeus is reduced, and the face is vaguely convex, somewhat like the afrorubrines and *Hespenedra*. Other plesiomorphic traits that unite the species of *Rubria* to one another are the lateral shape of the pronotum being boxlike, the prothoracic tibia being intermediately flat, and the face being completely covered by microtexture. Features that seem to be synapomorphies include the basal arms of valvulae I being connected by a sclerotized bridge, and the apex of the metathoracic femur (beyond the articulation with the tibia) where the macrosetae are attached being produced and narrow (Pl. 13E). Bremer support for the clade including the three species of *Rubria* was 10, support for the node immediately basad of this clade was 1 (in Fig. 1 it was 5), and support for the node subtending all Ledrinae as herein defined was 5 (8 in Fig. 1). Because *Rubria* exhibits these synapomorphies and was placed outside of the other ledrine genera with high support (including other Ledrinae from Australia), it is here placed in a separate tribe (Rubrini Jones, new tribe).

Kramer (1966) treated eight New World genera as belonging to Ledrinae in his revision. Three (*Proranus*, *Xedreota*, *Xerophloea*) are here recognized to belong to Xerophloeini. Four others (*Bascarrhinus*, *Clinonana*, *Ohausia* Schmidt, *Platyhynna*) are here removed from Ledrinae (see “Taxa removed from Ledrinae” below). The last, *Hespenedra*, was placed in this analysis within Ledrinae but separate from other groups (Fig. 2). Despite its placement between Afrorubrini and the higher ledrines, *Hespenedra* shares many affinities with the complex of genera that includes *Petalocephala* and *Neotituria* Kato (with which it was not placed in the final analysis, but was in earlier ones not here presented). Like them, it has a parabolic crown shape, the marginal carina of the crown is mostly complete but thickened and textured near the eyes, the crown transverse camber is weakly curved, the pronotum is flat, the forewings are reticulate with many cross veins, and the body is longitudinally flexed after the scutellum, which is a synapomorphy for the group of *Petalocephala*-like genera (node 16, Fig. 3). *Hespenedra* differs in having a somewhat convex face like Afrorubrini and Rubrini. It resembles Rubrini in having the apical process of the metathoracic femur on which the macrosetae are mounted narrow and extended (Pl. 13C). *Hespenedra* is united with the genera of Ledrinae which comprise the clade to which is it sister in the tree (Fig. 2) by the pronotum having an uneven texture (= "torose"), the proepisternum being easily visible and not underlapping the genae (Pl. 9C_4), the forewing venation being reticulate, the male plates being dorsoventrally flattened basally and then laterally flattened apically, the setae of the male pygofer being short, valvulae II possessing a second dorsal tooth positioned closer to the apex than to the first tooth (Pl. 18G_2), and perhaps most diagnostic, the triangular patch of scalelike setae on the apex of row II on the metatibia (Pl. 12A_1) being present. Bremer support for the node immediately subtending *Hespenedra* is 5 (Fig. 2) and for the one more distad 9. Szwedo (2002) considered the genus to belong within Xerophloeini, but evidence here does not support such a placement. *Hespenedra* appears to occupy a unique position within Ledrinae, neither very close nor very far from Xerophloeini, but endemic to the New World. Because of its well supported but phylogenetically and geographically isolated position, it is here placed in a separate tribe (Hespenedrini Jones, new tribe). *Hespenedra* can be easily identified by the thick patch of short, white, stubby setae on the plantar surface (platellae?) of metathoracic tarsomere I (Pl. 13K).

The remaining genera of Ledrinae can be grouped into a single large tribe, the Ledrini (node 12, Fig. 3). They are united by the apex of the frontoclypeus being narrow and more well defined (and sometimes secondarily reduced—Pl. 9D_2, 10D_2), the anterior tentorial pits being positioned adjacent to the frontoclypeus as sutures or wrinkles that are sometimes open, the scutellum having slightly carinate raised lateral margins that are sometimes developed and swollen (Pl. 7G_1), metathoracic tarsomere I having lateral setae emerging from scalloped bases (Pl. 13L), the female pygofer being longer than the valvulae in un-dissected specimens, and valvulae II being completely sclerotized, with a subapical dorsal notch (Pl. 18J_3) and the dorsal margin of the apex quadrate (Pl. 19I_2).

Within this group, nodal support for genera and intergeneric relationships were generally low (Fig. 2), but a few clades were well supported. The clade containing *Epiclinata* (herein a new junior synonym of *Titurìa*—see discussion for that genus below), *Neotituria*, *Petalocephala*, *Thlasia*, and *Tituria*, was supported by a Bremer value of 4 (Fig. 2). Features uniting this group include the pronotum being flat, the body being longitudinally flexed (seen in lateral view—Pl. 6F_1) after the scutellum, and the pygofer being somewhat loosely associated with the blades and valvulae of the ovipositor (viewed in un-dissected specimens). Many species in this group are green or yellow, have a smooth and shiny appearance, and have lateral flap-like extensions off the pronotum. While this group is clearly monophyletic, relationships among the genera are uncertain, and in earlier analyses (with alternative interpretations of a few character states, not shown) they polarized differently (*Petalocephala* was placed as basal to the rest of the taxa in the clade, who all possess lateral extensions, instead of in a derived position, where it ultimately optimized). The phylogenetic limits of this group are also not clear. In these analyses (Figs. 1–3), *Dusuna* Distant (which had high support—Bremer 8—for its monophyly) was placed as sister to the other taxa within the clade. Synapomorphies for this relationship include the anterior margin of the pronotum being essentially straight (*Dusuna*'s is slightly more curved in the middle), the fore edge of the forewing possessing a secondary carina in many genera (Pl. 11E_1), and the inner margin of the antennal pit forming a ridge, more or less developed, and parallel to the frontoclypeus (Pl. 10D_3, 11B_1). *Dusuna* also possesses lateral flap-like extensions off the pronotum (Pl. 1E–F). *Dusuna*'s pronotum, however, is somewhat humped, and it has affinities with other genera also having the pronotum intermediately humped (smaller size; the coronal area immediately behind the eye being narrow and not carinate posteriorly), namely *Parapetalocephala* Kato, *Hangklipia* Linnavuori (moderately high Bremer support—5), and *Titiella* (high Bremer support—6). Because the phylogenetic limit of the genera associated with *Petalocephala* remains unclear, and because designating the *Petalocephala*-like taxa as an independent tribe would leave several proximate genera (*Hangklipia*, *Titiella*, and *Parapetalocephala*) in a paraphyletic basal grade, it seems best to treat these genera as an informal genus group within Ledrini, rather than as a distinct tribe. They are here designated as the *Petalocephala* genus group comprising *Neotituria*, *Petalocephala*, *Thlasia*, and *Tituria*, and possibly *Dusuna* and others. Members of the group have the crown punctate, anterior margin of the pronotum straight or slightly curving anterad medially, the body flexed in lateral view, lateral extensions sometimes present on the pronotum, the metathoracic tibia intermediately foliaceous with macrosetae of row II having some cucullate bases, and the inner margins of the antennal pit as an elbowed ridge with the longer part parallel to the frontoclypeus.

The position of the few other genera sharing some similarities with *Dusuna* (*Hangklipia*, *Parapetalocephala*, *Titiella*) is uncertain, but they appear to show some affinities to both Ledrini and the distantly related *Afrorubria*. The face of *Titiella* (Pl. 10C) is similar to that of *Afrorubria* (Pl. 9A)—it is strongly convex, and the margin between the frontoclypeus and the genae is somewhat weakly expressed (Pl. 10C_1). *Titiella punctigera* (Stål) and *Afrorubria mitellata* Naudé (not included in these analyses) are alike in this regard. These apparent symplesiomorphies presumably contributed to the signal pulling *Hangklipia* and *Titiella* to the base of the Ledrini clade. Further, non-phylogenetic, similarities among *Afrorubria*, *Hangklipia* and *Titiella* concern their apparently sympatric distributions—they are each endemic to South Africa (Linnavuori identified them as belonging to the same "Cape fauna" and possibly being "Pre-Tertiary relicts"—1972: 205), and their host plants (see "Host plants" under descriptions for these genera) include various low woody shrubs (although not necessarily the same ones) growing in mountainous habitats ("mountain fynbos slopes" on many pin labels). Nevertheless, *Titiella*, and more so *Hangklipia*, have many characteristics that place them squarely within Ledrini, for example, the larger quadrate proepisternum (*Afrorubria*'s is small and tab-like).

Hangklipia and *Titiella* have low support here (Bremer = 1, Fig. 2) as sister taxa, but always grouped together in the various analyses and seemed inseparable. While the face of *Titiella* is convex and that of *Hangklipia* is concave, their legs are very similar, they are very close in overall size (smaller than many other Ledrini), and they share numerous other characteristics.

Parapetalocephala, of Indomalayan distribution, is slightly longer and more slender (Pl. 2K) than *Dusuna* (Pl. 1E, F), *Hangklipia* (Pl. 2A) or *Titiella* (Pl. 3K). The specimen available for this analysis, *Parapetalocephala testacea* Cai and Kuoh (not the type species), has the wing cells depressed much like those of *Dusuna*, but lacks lateral extensions on the pronotum and other features of the latter. The crowns of *Parapetalocephala*, *Hangklipia* and *Titiella* all strongly resemble one another in shape. *Dusuna*'s crown is very short, pentagonal, smooth, and untextured dorsally except for some punctuations (Pl. 1E–F, 7E), and is more like those in the *Petalocephala* genus group.

Support for the clade of Ledrini containing its remaining genera was very high (Bremer = 7, Fig. 2), and its members were united by several synapomorphies (see Fig. 3, node 22, and Table 3, "List of apomorphies," in Appendix), including the presence of a swelling laterad of each ocellus, the inner antennal margin being a bar more or less expressed and oblique to the frontoclypeus (Pl. 9B_2, 10_3), and the pygofer usually having pigmented spots (Pl. 17B_2). These genera have a broad Old World distribution and are found in Australia, Africa, the Indomalayan region, and Europe. Many of the examined genera of this group were placed as para- or polyphyletic, indicating that existing taxonomic definitions for them are weak (Fig. 2) or that those species have been inaccurately placed. The genus *Confucius*, to which *Beniledra* (African) and an undescribed genus from Borneo ("Genus 1") were closely associated, was placed at the base of this clade as a paraphyletic assemblage. Some component of the genus *Confucius* is undoubtedly a natural grouping, and Linnavuori (1972: 207) has suggested characters that differentiate *Confucius* from the closely associated genus *Ledropsis* (see discussions for *Confucius* and *Ledropsis* below). But the present constitution of *Confucius* seems to comprise an assemblage of closely related species at various stages of divergence from which the remaining lineages of Ledrini have split.

The clade placed distally to *Beniledra*, *Confucius* and Genus 1 had strong support (Bremer = 7, Fig. 2) and many synapomorphies. Some of these include the pronotum being steeply declivous in lateral view (Pl. 6B_1, 8B, C), the face having numerous coarse setae, the fore edge of the forewing having numerous setae, the pro- and mesothoracic tibia being at least somewhat foliaceous with their faces tuberculate, metathoracic tarsomere I being long (Pl. 13J; Genus 1 also has this feature), the style having a secondary process (Pl. 15G_1, 16C_2), and other features.

Within this group, the clade containing three species of the genus *Ledra* had moderate to low node support (but *Ledra* was polyphyletic with respect to *Ledra tuberculifrons* Walker), as did the clades containing *Platyledra*, (*Ledropsella* + *Jukaruka)*, and (*Ezrana primitiva* + *Ledropsis froggatti* + *Porcorhinus mastersi*) (see "Remarks" under the taxonomic section for each of these genera below). *Ledropsis* was grossly polyphyletic. The grouping of (*Platyledra* + (*Jukaruka* + *Ledropsella*)) + (*E. primitiva* + (*L. froggatti* + *P. mastersi*)) was very well supported as monophyletic (Bremer = 8) and comprised species found only in Australia. Synapomorphies for this clade included the median longitudinal carina on the crown being well developed to lamellate (Pl. 7D, 8B_1), the posterior margin of the pronotum being medially peaked posterad (Pl. 7D_4), the pronotum bearing a medial crest (Pl. 8B_3), sublateral longitudinal ridges on the scutellum being absent, the proepisternum being collarlike (Pl. 9E_4), the metathoracic femur macrosetal formula being 2 + 0 (Pl. 13G) and not 2 + 1, and metathoracic tarsomere I bearing many short setae (Pl. 13J).

The clade containing *Platyledra*, *Ledropsella* and *Jukaruka* was united by the scutellum being produced and spikelike (Pl. 7D_5), the median longitudinal carina on the crown bearing an additional median process (Pl. 8B_2), and the swelling laterad to the ocellus being sclerotized and dark (Pl. 7A_2—a characteristic also developed in *Ledra*, Pl. 7F_3). Together these taxa form the *Jukaruka* genus group.

(*E. primitiva* + (*L. froggatti* + *P. mastersi*)) was supported by the posterior margin of the pronotum being subtrapezoidal in shape (Pl. 2H–I, 3G), the median perpendicular keel on the face of each side of valvulae II extending from the first dorsal tooth (Pl. 18F_1; this feature appears to be weakly expressed also in *P. acuminata*; see Pl. 19C_1), and setae on the crown being absent. More is said about the taxonomic implications of this grouping on the included taxa under the descriptions for *Ezrana*, *Ledropsis*, and *Porcorhinus* below.

Ledra, *Ledropsis discolor,* one unidentified *Ledropsis* species, and the female species identified as *Funkikonia* were placed together, but with minimal Bremer support value (Fig. 2). *Funkikonia tuberculata* (Kato), which was placed with the other *Funkikonia* species in prior analyses (not shown), was placed separately in this final analysis. While it is clear that all these species are closely related, exact relationships among them seem murky. At this point, few conclusions can be drawn from their phylogenetic placements except that they are distinct from the Australian fauna, and more derived than *Confucius*. They are referred herein as the *Ledropsis*-like species or the *Ledropsis* species group (a paraphyletic group of genera and species).

A tree summarizing hypothesized relationships among genera of Ledrinae is given in Fig. 3. The analysis which generated this tree included only one species from each genus, except in cases where polyphyly was exhibited in the other trees, such as with *Ledropsis*, or where multiple species were needed to provide the full range of sampled characters, for example with genitalic characters (*Dusuna* and *Confucius*). Analysis in PAUP* yielded 5 similar trees, and one whose topology was most similar to that in Fig. 2 was chosen on which to generate a list of apomorphies. Nodes on this tree are numbered and correspond to the apomorphy list (Table 3 in the Appendix). A new classification for the Ledrinae is given below, and includes five tribes (three new), 38 genera, and approximately 300 species.

Biogeographic considerations and fossil evidence

The present analysis provides evidence for sister group relationships among small taxonomic groups that are widely separated geographically (Fig. 4). Putative sister groups Xerophloeini (~25 described species in four genera) and Afrorubrini (~12 described and undescribed species in two genera), for example, are separated by thousands of miles of ocean. The tribe Hespenedrini (one known species), found only in Chile, appears to share a close relationship with the *Petalocephala* group in Ledrini, whose distribution is exclusively Old World. Furthermore, Rubrini (~5 described species), found only in Australia, is placed as sister group to Hespenedrini + Ledrini. Optimization of the distributions of all the sampled taxa on the final topology (not shown) is inconclusive—both Old and New World regions optimize equally to the basal nodes within the subfamily.

In the case of the Ledrinae, an evaluation of the character distributions of the basal-most taxa in the analysis indicates that the most plesiomorphic ledrines have a simpler body plan, a more convex face, a smaller and less well-developed proepisternum, shorter metathoracic legs that are squared in cross section, more macrosetae in row II of the metathoracic tibia, regular wing venation, and a smaller overall size—*Rubria*, *Afrorubria*, *Hespenedra*, and *Xerophloea* are all approximately 4–8 mm in length. These features likely were present in the ancestral lineage or lineages from which the tribes of Ledrinae derived. Many of these characteristics are shared by *Aphrodes*, which was included in this analysis as an outgroup and with which these taxa were most closely placed.

Assuming the monophyly of Ledrinae, it seems very likely that the ancestral ledrine lineage evolved as a distinct entity prior to the breakup of Gondwana. If Ledrinae diverged from other Cicadellidae prior to the splitting of Australia from Africa and South America (which would indicate an ancient origin for Ledrinae within Cicadellidae), it would place the origin of Ledrinae as early as the late Jurassic or early Cretaceous, close in age to the earliest described fossils of Cicadellidae (Hamilton 1990, 1992; Shcherbakov 1992). This hypothesis is supported by recent fossil evidence. Shcherbakov (1992) transferred several fossil species from the Upper and Lower Cretaceous, originally placed by Hamilton in the tribe Paracarsonini (Jascopidae), to Ledrinae. The hypothesis for an old lineage of Ledrinae is also supported by recent molecular analyses of Cicadellidae (Dietrich *et al.* 2005), in which Xerophloeini and Ledrini were placed near the base of the tree.

The phylogenetic position of the Paracarsonini fossils to extant taxa of Ledrinae was not explicitly tested here using phylogenetic methods. However, a post-analysis examination of illustrations in the literature (Hamilton 1990) provides useful clues to their probable position within the phylogeny. Hamilton's (1990) drawings of the two included genera, *Paracarsonus* and *Platyjassites*, are more or less clear (though many key features are obscured or missing) and include ventral views of the head and body and fore- and hind wing venation. From these views, it appears that *Paracarsonus* shares many distinctive features with extant Xerophloeini, several of which were first observed by Shcherbakov (1992). These include the frontoclypeus being convex, punctate, and broad throughout its length, the lora being reduced, the crown margin being carinate, the antennal pits being reduced or absent, the crown being foliaceous but short, and the forewing possessing an appendix (which appears somewhat reduced from extant Xerophloeini excluding *Xedreota*). Other xerophloeine features that appear to be visible (but not conclusively) in the drawings include the vertex being essentially flat (weakly cambered transversely), the forewings being sharply angled at the first claval vein, and the proepisternum being small and tab-like and underlapping the genae. The metathoracic femur macrosetae and metathoracic tibiae are mostly obscured or missing. Shcherbakov (1992), from examinations of photographs of the type specimen, suggested that Hamilton's (1990) assertions and drawings to the effect that *Paracarsonus* possesses very short metathoracic tibia, long metathoracic basitarsomeres, and small claws [not xerophloeine characteristics], were misinterpretations of the fossil, views shared by the authors of this paper. All of the positively identifiable features indeed seem to indicate that *Paracarsonus* belongs within Xerophloeini. Its weakly expressed appendix may indicate a phylogenetic position between *Xedreota* and other extant xerophloeine genera.

Hamilton's (1990) illustrations of *Platyjassites* indicate that it also belongs within Ledrinae. The wide and flattened face, reduced frontoclypeus, narrow genae, squared anterior margin of the forewings in cross section with a punctate texture, and quadrate pro- and mesothoracic tibia lacking large marginal macrosetae are all features shared with many species in the subfamily. No lateral view of the specimen is shown, but in ventral view it appears to have a flattened crown. Shcherbakov (1992) observed that both *Platyjassite*s (and *Paracarsonus*) have several wing features (not coded in the present analysis) shared with Ledrinae (specifically *Destinia* Nast [only available from the original descriptions and illustrations and not coded in this analysis], and *Hespenedra*). These include the R-fork being situated proximally, the M_{3+4} + CuA_1 anastomosis in the forewings being short, R_1 being short, the 1st apical cell being angulate at r-m, the 2nd apical cell being short, the 3rd and 4th apical cells being narrow, and the appendix being wide in the hind wing.

Platyjassites seems to belong within the *Petalocephala* genus group. The frontoclypeus is somewhat convex and appears flattened, and has well-defined lateral margins, similar to *Dusuna* or *Tituria obtusa* Walker (see Pl. 10D). However, in Hamilton's illustrations, the specimens appear to lack lateral pronotal extensions and well-defined inner margins of an antennal pit present in those taxa, and the antennae are situated adjacent to the lateral sutures of the frontoclypeus, rather than further away as in *T. obtusa* and many petalocephalines. In overall shape, ventrally they resemble some *Petalocephala*, as observed by Hamilton (1990). Their proepisterna, similar to those of *T. obtusa* (Walker) and other members of the *Petalocephala* genus group, appear to be situated near to the genae and far from the eyes, and are less well-developed than other members of Ledrini. The shape of the crown margin and the posterior margin of the head behind the eyes being perpendicular to the body axis are strongly reminiscent of *Thlasia* or *Tituria*. Curiously, though, the crown margin wraps slightly around the anterior margin of the eyes (observed by Hamilton 1990) more so than in any extant Ledrinae species observed in this analysis. The apex of the metathoracic femora and most of the meso- and metatibia are missing in the fossil specimens, making evaluation of diagnostic characters there impossible. Because those and other key diagnostic features are missing (textures on the crown and pronotum, shape of the pronotum laterally, overall shape of body in lateral aspect, features on the meso- and metathoracic legs, features of the male and female genitalia), an exact determination of proper placement within Ledrini may not be possible, although inclusion of the available information in a future phylogenetic analysis is desirable and may be informative.

In light of the considerable evidence just given and in Shcherbakov (1992) for the inclusion of *Paracarsonus* and *Platyjassites* within Ledrinae, a few important implications for the age of the family and its ancestral distribution follow. First, the old age of the fossils and their apparent position within the ledrine phylogeny presented here strongly suggest that Ledrinae are in fact an ancient lineage among Cicadellidae, appearing at least as early as the Lower Cretaceous (Aptian). By comparison, the oldest known membracoid fossils considered ancestral to the extant Cicadellidae (Shcherbakov 1992) are from the Upper Jurassic, and early provisionally-placed Cicadellidae are from the Lower Cretaceous (Berriasian, Valanginian). In contrast, the oldest known fossil of Membracidae comes from the much younger Dominican amber of the Eocene-Miocene (Shcherbakov 1992). Second, it demonstrates that species of Xerophloeini and Ledrini, whose present day members have mutually exclusive distributions in the New and Old Worlds, respectively, were once found together in ancient north-eastern Brazil. If the relationships among the basal ledrine clades presented in this study are real (though well-resolved, Bremer supports were low—Fig. 2), the origins of these lineages are likely separated by millions of years of evolution, during which time sister lineages whose extant members are distributed only in Africa (Afrorubria), Chile (Hespenedrini), and Australia (Rubria) also split off. The presence of fossil petalocephaline Ledrini in New World deposits strongly suggests that lineage-splitting (tribe forming) events corresponding to their appearances in the phylogeny and subsequent dispersal occurred much earlier than the breakup of Gondwana, and positively before South America split from Africa. Tribe formation, followed by the vicariance of ancient supercontinental fragmentation (Eastern Gondwana [South America + Africa] separating first from Western Gondwana [Antarctica + India + Australia], and these masses subsequently dividing—Scotese 2002) and subsequent speciation and extinction appear to be better explanations for the current distribution of the tribes of Ledrinae than ancient supercontinental fragmentation followed by tribe formation and then long-distance dispersal events to the remote corners of the world.

Other authors have also commented on the age of the subfamily Ledrinae and its lineages. Linnavuori (1972:205) stated that Ledrinae appeared to have already diverged from the 'ulopine stem' during the late Mesozoic, and that most of the African genera evolved during the Tertiary. *Sichaea* [Afrorubrini] and *Titiella* [basal Ledrini], he suggested, might be 'pre-Tertiary relicts'. Evans (1966) spoke briefly about ledrine phylogeography in Australia, suggesting that the Australian ledrine genera entered the continent from the north prior to the period of Tertiary isolation.

Regarding Evans' statement, it is not clear whether he considered any of the Australian genera to be more ancestral than the others. His statement probably is correct, but may not apply to all ledrines in Australia. The analysis in this paper demonstrates that the Australian ledrine fauna comprises two distinct lineages, one being the more ancient Rubrini, and the other being the more derived *Jukaruka* genus group (Ledrini). The amount of apparent genetic distance between these two lineages suggests that they may, in fact, have entered the continent separately, at different times. It seems likely that the older Rubrini (or rubrine ancestors) entered much earlier, probably prior to the Tertiary isolation. The *Jukaruka* genus group, on the other hand, probably did not evolve until after the Tertiary isolation, and so would have entered Australia more recently, likely via an Indomalaysian route. The clade comprising the *Ledropsis*-like species and the *Jukaruka* genus group appears to have evolved from *Confucius*-like ancestors (Figs. 1–3), but its extant members are absent in Africa. Extant *Confucius* species, however, are found primarily in Africa, with specimens examined for this study also being recorded from India, Sri Lanka, and Hong Kong (not *Confucius*?). The *Ledropsis*-like species + *Jukaruka* genus group clade may have originated from *Confucius*-like ancestors after they had dispersed to Asia (via India?), and then later radiated to their current distributions throughout Europe, Asia, and Australia.

Further morphological and molecular phylogenetic analyses of Ledrinae and other putatively basal Cicadellidae, as well as more explicit biogeographic testing, should shed more light on their age estimates and ancestral geographic distributions.

Family Cicadellidae Latreille

Subfamily Ledrinae Fairmaire

Type genus Ledra Fabricius, 1803.

Primary Synonymy. Ledrides Fairmaire, 1855: 140 [treated as family]. Ledridae Kirshbaum, [1867] 1868: 14 [treated as subfamily]; International Commission on Zoological Nomenclature Opinion 647 (1963). Ledrides Sahlberg 1871: 67 [treated as tribe]. Ledrinaria Distant 1907:185 [treated as division].

Description. Medium or large leafhoppers. Dorsum often coarsely pitted or knobbed. Head spatulate, anterior margin often lamellate. Crown often uneven with shallow ridges or knobs, median longitudinal carina more or less complete, marginal carina more or less complete. Ocelli located on disk of crown, generally closer to each other than to eyes. Face usually concave, especially near anterior and lateral margins. Frontoclypeus narrow, long (anterior portion reduced in some taxa), more or less distinct, not extending onto upper margin of head, maxillary sutures present or absent, genae narrow. Antennae very short, first two segments small and unadorned with auxiliary setae. Proepisternum entirely exposed and variously expressed. Pronotum generally with carinate dorsolateral margins (absent in Rubrini) that are sometimes developed laterally into triangular, subtriangular, or ovoid flap-like extensions; dorsal surface with or without dorsal longitudinal rows of tubercles or carinae, these sometimes developed into crests, earlike flanges, or horns. Forewings coriaceous, punctate, sometimes flexed downward at second claval vein, claval area sometimes pigmented, veins slightly raised, claval veins not confluent, venation regular or reticulate in apical two-thirds of wing. Hind wings with R and M veins free and not confluent distally. Legs densely setose, pro- and mesothoracic legs without macrosetae. Metathoracic legs relatively short, metathoracic femur macrosetae formula 2 + 0 or 2 + 1, occasionally 2 + 1 + 1, with macrosetae grouped at apex of femur. Metathoracic tibia row II with some or all macrosetae cucullate, almost always less than 9 in number, with hairlike intercalary setae.

Male genitalia: Macrosetae lacking. Valve small, fused with pygofer. Genital plates generally narrow, more or less parallel-sided, usually as long or longer than pygofer. Styles often long and narrow, but sometimes short, often with apex flexed ventrad or recurved anterad, sometimes with additional processes. Connective band- or platelike, but generally not strongly sclerotized, often membranous and indistinct. Aedeagus variable in shape, with or without subapical and apical processes and auxiliary lobes. Segment X (anal tube) often with ventral lobe.

Female genitalia: Macrosetae lacking. Sternite VII posterior margin generally emarginated medially. Valvulae I bases acutely angled at articulation, generally not connected to one another by a sclerotized bridge. Valvulae II long and moderately to very slender, sometimes broader medially and curved ventrally, sclerotized or not, with two more or less sclerotized dorsal teeth, supernumerary teeth present in some species, subapical notch generally present.

Range. Worldwide, with principal extant radiations in the Afrotropical, Australian, and Indomalayan regions.

Ecology. Generally associated with trees and woody plants, but some Ledrinae are found in grasses. Nielson (1968) lists no Ledrinae as vectors of plant diseases.

Remarks. The subfamily Ledrinae is here designated to include the tribes Afrorubrini Jones (new tribe), Hespenedrini Jones (new tribe), Ledrini, Rubrini Jones (new tribe), and Xerophloeini.

Key to the tribes of Ledrinae

1a. Mesothoracic tibia row II with triangular patch of scalelike setae apically (Pl. 12A–C); forewing with at least some extra cross veins; Old World species (except Hespenedrini: *Hespenedra*)........ 2

1b. Mesothoracic tibia row II without triangular patch of scalelike setae apically; forewing without extra crossveins; Old and New World species........ 3

2a. Face concave, or if convex, then plantar surface of metathoracic tarsomere I with short or long setae, but none of them fingerlike or white; Old World species .... Ledrini

2b. Face flattened but not concave, metathoracic tarsomere I ventral surface with uniform covering of short fingerlike white setae (Pl. 13K); New World species .... Hespenedrini Jones (new tribe)

3a. Crown with longitudinally costate texture (Pl. 7B_1); anal tube of males broad, conelike (Pl. 15E–F); species from southern Africa .... Afrorubrini Jones (new tribe)

3b. Crown with acinose/colliculate texture (Pl. 7A_1); Australian or New World species 4

4a. Frontoclypeus strongly convex and visible in lateral view (Pl. 8E_1), punctate, crown short and lamellate only near eyes, forewing with broad appendix (except *Xedreota*); New World species .... Xerophloeini

4b. Frontoclypeus not strongly convex or punctate, crown long and lamellate, more or less convex, forewing appendix absent or vestigial; Australian species .... Rubrini Jones (new tribe)

Tribe Afrorubrini Jones, new tribe

Type genus Afrorubria Linnavuori 1972

Description. Head spatulate, more or less lamellate toward anterolateral margins. Crown flat or weakly transversely flexed at medial carina, outline parabolic or triangular and narrowing in front of eyes, with longitudinal costate texture converging toward midline anteriorly; medial longitudinal carina present and more or less developed; margin with two complete parallel carinae, furrowed in between. Ocelli present, vestigial, or absent. Face flattish or somewhat convex; maxillary sutures present but sometimes nearly indistinct; frontoclypeus weakly or strongly convex, lateral margins indistinct or distinct; lora and genae flattish; antennal ledge absent or very weakly developed, and, if present, indistinguishable from secondary marginal carina of crown. Posterior margin of head strongly curved or subtrapezoidal, anterior margin reaching nearly to but not past transect connecting anterior margin of eyes. Pronotum flat, with a short fine lateral carina, sometimes weakly expressed. Mesoscutum and scutellum flat, with transverse minute wrinkles or costate texture. Forewing venation regular, with short apical cells, punctate, punctuations more or less expressed. Proepisternum visible but small and tab-like. Pro- and mesothoracic leg chaetotaxy reduced. Metathoracic femur macrosetal formula 2 + 0. Metathoracic tibia rows I and II with stout macrosetae, rows III and IV with fine setae and/or macrosetae. Metathoracic tarsomere I short, with short ventral ridge, and a more or less dense covering of short setae distally.

Male genitalia: Genital capsule medium to small in size; anal tube wide, somewhat sclerotized, triangular or cone-shaped in dorsal view, ventral lobe lacking, circular or tubelike in distal view, sclerotization incomplete ventrally.

Female genitalia: Valvulae II long and slender, somewhat sclerotized, with a small dorsal tooth situated one third of the total length from the apex.

Range. Afrotropical region.

Ecology. *Afrorubria* occurs on trees, woody shrubs, and leafy forbs. "Genus 4," placed with Afrorubrini in this analysis, is found on leafy forbs and grasses.

Remarks. Linnavuori (1972: 248) suggested that *Sichaea* might merit its own tribe within Ledrinae, but mentioned the need to examine species from other parts of the world to make this determination.

Two additional undescribed genera that appear to belong in this tribe were discovered in material sent from the SANC, and were included in this analysis ("Genus 2," "Genus 3" in phylogenetic analysis). Both were collected by sweeping/vacuuming in grasses and forbs.

The following discribed genera are here placed in Afrorubrini: *Afrorubria* and *Sichaea*.

Key to the genera of Afrorubrini

1a. Ocelli present; posterior margin of crown curving anterad medially; body yellow or green or both in dried specimens, color often arranged in longitudinal stripes on the crown and pronotum (Pl. 4C) .... *Afrorubria*

1b. Ocelli absent or very reduced and difficult to see; posterior margin of crown subtrapezoidal; body yellowish brown in dried specimens (Pl. 4D) .... *Sichaea*

Genus *Afrorubria* Linnavuori

(Pl. 4C, 7B, 8A, 9A, 12F, 13F, I, 15E, F, 17D, 18A)

Afrorubria Linnavuori 1972: 205, 240.
Type species. *Acocephalus vitticollis* Stål 1855.
Synonymy. None.

Description. Adapted from Linnavuori (1972): "Narrow, medium sized leafhoppers, often with fulvous markings on crown and pronotum. Apical cells elytra in male +/– infuscate, 1st apical cell usually with a small dark spot. Body elongate and rather depressed. Head parabolic, broader than pronotum, anterior margin sharp, formed of a shallow score, bordered by a ridge both above and below, only extreme apex of head rounded, sides of head usually +/– foliaceous. Face flat or slightly convex, bluntly angular in outline below eyes; anteclypeus a little broadening apicad; frontoclypeus parallel-sided in lower part, triangularly tapering dorsad in upper one, lateral frontal sutures in upper part, postfrontal suture and epistomal suture indistinct; lora of normal size; genae strongly notched near eyes, antennal depressions shallow; microsculpturing of face faint, formed of irregular rugosities. Crown parabolic, with a faint median carina, disk flattish, with dense irregular longitudinal rugosities; ocelli far from each other; eyes elongate. Anterior tentorium branches (fig. 24 b) reduced. Pronotum flattish, lateral margins parallel, longish and carinate, anterior margin distinctly curvate, posterior margin medially insinuated; anterior margin of disk with longitudinal rugosities, other parts densely transversely wrinkled. Scutellum with a distinct transverse furrow, base rugose, apex transversely wrinkled. Elytra (fig. 24 c) usually longer than abdomen, narrow, semitransparent, only indistinctly punctate, venation regular, no extra cross veins, outer subapical cell absent, central and inner subapical cells closed. Pro- and mesothoracic tibia gracile, apex with two spines on lower surface. Metathoracic femur with two macrosetae. Metathoracic tibia gracile, outer surface with two longitudinal rows of spines, inner surface with short stiff hairs, apex with two transverse rows of spines on ventral surface. 1st joint of metathoracic tarsi with a transverse row of several well developed spines on ventral surface of apex."

Species. [5]: *curta* Linnavuori; *flavida* (Evans); *mitellata* (Naudé); *ramosa* Linnavuori; *vitticollis* (Stål).

Range. Democratic Republic of the Congo [Zaire] (Parc National Upemba: Buye–Bala, Kabwe s. Muye); South Africa (Caffraria; Cape Province: Ceres, Gansbaai, Kougaberg (Bavianskloof), Mossel Bay; Derdepoort; East London: Gonubie; East Cape Province: Katberg; East Transvaal: Babanonga, Zululand: Eshowei; Natal: Umdloti; North Transvaal: Letaba Valley, Moketski; Orange Free State: Harrismith; Pilansburg; Pondoland: Port St. John; Pretoria; Sir Lowry's Pass; Stellenbosch Jonkershoek; St. Lucia Estuary; Transvaal: Rustenburg; Umkomaas; West Cape Province: Du Toitskloof Pass, Hottentotsholland Nature Reserve, Nature's Valley).

Host plants. *Chrysophyllum* sp. (Sapotaceae); *Clerodendrum glabrum* (Verbenaceae); *Cliffortia atrata* (Rosaceae); *Cliffortia Serpyllifolia* (Rosaceae); *Lippia javanica* (Verbenaceae); *Rhus leptodictya* (Anacardiaceae); *Stoebe* sp. (Asteraceae); *Ursinia caledonica* (Asteraceae).

Material examined. *A. vitticollis*: 1 male, 2 females, South Africa, AMNH, Led1_001–003, 2 females, 2 (abdomen missing), South Africa, SANC, JRJ_Led1_466, 472–473, 478; *A. mitellata*: 3 males, 5 females, South Africa, SANC, JRJ_Led1_469–471, 481–484.

Remarks. Of the genera of Afrorubrini, *Afrorubria* is the most like *Petalocephala* in body shape and general appearance. Linnavuori (1972: 241) believed *Afrorubria* was a derivative of *Petalocephala* stock, and that its reduced puncturing, regular wing venation, reduced setal covering on the legs, and more developed leg spinulation were derived states. It appears that the exact opposite is true—*Petalocephala* and other Ledrinae are derived from leafhoppers more closely resembling Afrorubrini. The features of *Afrorubria* that Linnavuori mentioned as derived seem to instead demonstrate *Afrorubria*'s greater proximity to ancestral lineages (possibly Aphrodinae).

Host plant information was recorded by A. L. Capener and M. Stiller (SANC), who collected much of the available material. From the numerous plant species on which the genus has been discovered, it appears that *Afrorubria* is somewhat of a generalist. The plants listed include trees, woody shrubs, and low-growing leafy forbs in five different families.

Genus *Sichaea* Stål

(Pl. 4D, 6E, 11C, 17G)

Sichaea Stål, 1866: 106.
Type species. Acocephalus missellus Stål, *1855: 98.*
Synonymy. None.

Description. Adapted from Linnavuori (1972): "Small brown species. Body small and broad, anteriorly flattened. Head broader than pronotum, broadly spatulate, anterior margin lamellate. Face broad; anteclypeus tapering apicad, strongly swollen, shiny; frontoclypeus narrow and rather parallel-sided, moderately convex, irregularly rugose; genae strongly notched below eyes, episternum visible; lora narrow; ocellocular broad, antennae inserting much beyond eyes, antennal pits shallow, without any dorsal ledge. Crown slightly concave, anterior margin sharp and slightly upturned, disk irregularly punctate and longitudinally costate, ocelli absent or vestigial, coronal suture indistinct. Anterior tentorium branches reduced, membranous. Pronotum short and broad, lateral margins short, subparallel, carinate, anterior margin curvate, basal margin shallowly insinuated, disk densely and rather coarsely punctate and rugose. Scutellum with base shagreened and medially punctate, apex somewhat swollen and transversely rugose. Forewings coriaceous, strongly convex, densely and coarsely punctate, appendix absent, apical cells short, 3 closed apical cells. Legs short. Pro- and mesothoracic tibia only slightly flattened, gracile, not spinose, outer surface with a very indistinct longitudinal surface sulcus. Metathoracic femora rather short and flattened, apical macrosetae formula 2 + 0. Metathoracic tibia only slightly flattened, angular in section, rows I and II each with a line of stout macrosetae, rows III and IV with delicate macrosetae and short fine setae, apical margin of undersurface with a row macrosetae, tarsi setose. Male genitalia: Genital segment without macrosetae. Pygophore short and broad, sclerified; side lobes very short, triangular, without appendages. Anal tube broadly conical, short but extending beyond pygophore, sclerified. Valve rounded. Genital plates sharply triangular. Stylus elongate, apophysis short, digitate, preapical angle blunt, basal part narrowish. Connective small. Penis symmetrical, socle small, stem tubular, recurved dorsad, provided with apical processes, gonopore apical."

Species. [2]: *missella* (Stål); *coriaria* Stål.

Range. South Africa (Caffraria; Durban, Natal; Terra Capensis; Umtentweni).

Host plants. Unknown.

Material examined. *Sichaea* sp.: 4 females, 1 (abdomen missing), South Africa, AMNH, JRJ_Led1_274, 474–477.

Remarks. Linnavuori (1972) seemed somewhat hesitant to place *Sichaea* with *Afrorubria*, stating that it "resembles to some extent *Afrorubria* in the general habitus and in the male genitalia," but then suggesting that it "possibly merits a tribe of its own" [within the Ledrinae], because of its small size. As shown in the phylogenetic analysis, the two genera clearly belong together. Minor differences, such as the presence or absence of ocelli, are insignificant: in some examined specimens of *Sichaea* the ocelli were retained (in one specimen of the closely related undescribed "Genus 3," they were completely absent). In all species of Afrorubrini they are small. Linnavuori's concern about *Sichaea*'s small size is resolved by the undescribed specimens, which were as small (Genus 2) and smaller (Genus 3). Linnavuori's suggestion that the genus merited it own tribe applies to all the genera in this distinct group.

Tribe Hespenedrini Jones, new tribe

Type genus Hespenedra Kramer 1966

Description. Moderately large leafhoppers. Dorsum texture acinose-colliculate, rugose, punctate. Head spatulate, more or less lamellate toward anterolateral margins; crown parabolic, longer in females than in males, flat; longitudinal medial carina complete; marginal carina complete or incomplete, sometimes converging into crown texture laterally; ocelli closer to each other than to eyes, equidistant from hind and anterior margins in male, distance to anterior margin in female greater; surface with depressions and pits, more so in females; several deep pits arranged in a row, or two rows in the female, running from ocellus to point where longitudinal carina meets crown apex; anterior margin of pronotum slightly overlapping posterior margin of crown, straight, except laterally near the eyes, where it angles posterolaterally; pronotum essentially flat, with some depressions; mesoscutum and scutellum flat; forewings punctate, setose, sharply angled at second claval vein; claval area punctate, flat, and in same plane with mesoscutum and scutellum; remaining portion of wings angled downward; claval suture strongly depressed; veins raised, reticulate; face flattened, somewhat convex; frontoclypeus narrow, long, with apical extension; base with cibarial muscle attachment ridges visible laterally; row of pits running adjacent to the frontoclypeus from antennal bases to point where longitudinal medial carina on frontoclypeus meets crown apex, corresponding to pits on dorsal surface of crown; lora somewhat tumid, slightly angulate, genae narrow; proepisternum large, quadrate, situated proximate to lateral edge of pronotum; lateral carina of pronotum distinct; femora round, short, somewhat robust, with setae reduced; mesothoracic femur row II apex with triangular patch of scalelike yellowish setae; metathoracic tibia with two short macrosetae mounted on a narrow, prominent base; apical macrosetal formula 2 + 1; pro- and mesotibia intermediately flattened; metathoracic tibia quadrate in cross section, outer surface flat with carinate edges, setal rows reduced, row II with approximately six macrosetae, all bases cucullate; metathoracic tarsomere I intermediately long, plantar surface bearing numerous short stout white setae. Male genitalia: aedeagus short, somewhat broad throughout length; intermediately wide in distal view, with a ventroapical groove; connective long and narrow, medial section thin in dorsal view, flat in lateral view; subgenital plates shorter than pygofer, dorsoventrally flattened basally, laterally compressed distally; anal tube broad in dorsal view. Female genitalia: broadest medially, with two sclerotized dorsal teeth and numerous other less sclerotized dorsal teeth.

Range. Neotropical.

Ecology. Unknown.

Remarks. Besides Xerophloeini, Hespenedrini represent the only extant ledrine tribe distributed in the New World. Szwedo (2002) postulated that *Hespenedra* belonged in Xerophloeini, but in this analysis it is shown to be clearly distinct within Ledrinae and much closer to Ledrini.

This tribe is monotypic, and includes *Hespenedra*.

Genus *Hespenedra* Kramer

(Pl. 4H–I, 9C, 12A, G, 13C, K, 18G)

Hespenedra Kramer, 1966: 492, figs. 62–69.
Type species. Thlasia chilensis Spinola 1852: 277, by original designation.
Synonymy. None.

Description. Adapted from Kramer (1966): "Moderately large (8.75–11 mm.) robust leafhoppers; head gross and well-produced beyond eyes, coronal suture and lateral margins carinate, ocelli on crown anterior to eyes, closer to midline than to lateral margins; in lateral view with crown flat, face oblique and nearly flat, area from eye to apex foliaceous, clypeus and clypellus clearly visible; clypellus base bearing paired sublateral carinae converging medially into a single longitudinal carina on apical extension in males, medially depressed longitudinally; in facial view the clypellus, lora, and clypeus slightly tumid, genae broad, lateral frontal sutures terminating at antennal bases, with a variably developed carina on midline from between antennae to apex of head, antennae moderately short, anterior and mesad of eyes, distant from lateral margins of head; pronotum short, widest posteriorly, anterior margin straight, posterior margin shallowly indented, carinate laterally, longitudinally depressed medially, females with a slight longitudinal carina in the depression extending anteriorly to the anterior margin; scutellum large, broader than long; forewings moderately long and broad, punctate-rugulose, with extra crossveinlets apically, appendix absent, claval area strongly pigmented with creamy white pigmentation in males; legs not particularly stout, macrosetae on metathoracic tibiae greatly reduced in number but clearly visible, not hidden by hairs; formula of macrosetae at apex of metathoracic femur 2–1–0. Male genitalia: genital capsule partly withdrawn into abdomen concealing base of valve, anal tube not large, connective modified Y-shape, style long with one apical lobe, aedeagus short and stout with paired ventral processes. Female genitalia: seventh sternum longer than preceding segment and with ovipositors not extending much beyond pygofer."

Species. [1]: *chilensis* (Spinola).

Range. Chile (Arauco Province: Contulme, Palo Botado; Concepcion Province: Hualpen; Isla Chiloe: Dalcahue; Llanquihue Province: Lago Chapo; Valdivia Province: Chesque).

Host plants. Unknown.

Material examined. *H. chilensis*: 3 males, 1 female, Chile, USNM, JRJ_Led1_060–062, 064, 1 male, 1 female, Chile, AMNH, JRJ_Led1_063, 065.

Remarks. *Hespenedra* shares many similarities with the *Petalocephala* genus group, particularly the shape of the face, the carination of the frontoclypeus, the shape of the body in lateral and dorsal views, and the straight anterior margin of the pronotum. Males of *Hespenedra* have the clavus punctate and pigmented very much like some species in *Thlasia* and a number of unidentified species of Ledrini from China. Females have longer crowns than males, similar to many ledrine genera. These similarities are not well understood, and may be merely convergent features, or retained plesiomorphies.

Despite these similarities, *Hespenedra* exhibits many character states that are unique among Ledrinae. For example, the plantar surface of metathoracic tarsomere I bears an elongate ovoid pad of short stout white setae not seen in any other group in this study. Because *Hespenedra* is currently monotypic, however, it is unclear whether or not this character is simply diagnostic for *H. chilensis*, or if it is also phylogenetically significant for the genus or tribe. Also, the connective is longer and more sclerotized than that of most other ledrines, and the aedeagus and styles are shorter and more robust. These differences taken in context of the topology presented herein seem to indicate its ancestral and removed position within the Ledrinae. The long and narrow median stem of the connective is somewhat like some members of the *Petalocephala* genus group, and the central area of the proximal end that is not sclerotized and appears hollowed, is similar to that of *Proranus* (Xerophloeini), *Afrorubria* (Afrorubrini), and *Beniledra* (Ledrini). The aedeagus is also short in *Thlasia* and *Hangklipia*, and the styles of *Hespenedra* are apically flexed downward like most Ledrini.

The narrowed and elongate base on which the apical macrosetae of the metathoracic femur are mounted (Pl. 13C) strongly resembles that in *Rubria* (Rubrini—Pl. 13E), which may be *Hespenedra*'s closest extant relative. (Figs. 1–3)

The statement in Kramer's description that the connective is a "modified Y-shape" may falsely imply a relationship with other leafhopper subfamilies defined by having the connective Y-shaped.

Tribe Ledrini

Type genus Ledra Fabricius 1803

Primary Synonymy. Petalocephalini Metcalf 1962, unavailable name, NEW SYNONYM.

Description. Dorsum coarsely pitted or knobbed. Head spatulate and lamellate or foliaceous anterolaterally. Crown uneven with shallow ridges or knobs. Face generally concave. Episternum of pronotum entirely exposed, large, quadrate and situated ventrally, or collar-like and wrapping around laterally onto pronotum. Forewings punctate, venation reticulate in apical two-thirds. Mesothoracic tibia row II apex with long triangular patch of scalelike setae sometimes arranged in row perpendicular to axis of leg. Male genitalia: Pygofer with or without basidistal processes, with or without inner dorsomedial subapical processes; plates as long as or longer than pygofer, originating from pygofer dorsoventrally depressed, then often flexing along their axes to become laterally compressed and slightly cuplike apically; segment X (anal tube) usually with ventral lobe; aedeagus highly variable, with or without subapical and apical processes; paraphyses sometimes present. Female genitalia: Valvulae II long and moderately slender, usually well-sclerotized, usually with a primary subapical dorsal tooth situated closer to apex than to midpoint, often with a secondary subapical dorsal tooth situated between primary tooth and apex, and a subapical dorsal notch occurring immediately posterad of second tooth; supranumerary teeth generally absent; median perpendicular keel sometimes present.

Range. Afrotropical, Australian, Indomalayan, and Palearctic regions.

Ecology. Generally associated with trees and woody shrubs, both conifers and angiosperms.

Remarks. Metcalf (1962), in his General Catalogue of the Homoptera, created the new tribe Petalocephalini to include all of the genera formerly in the tribe Ledrini, except *Ledra*. However, he provided no formal description for this new tribe. Articles 13.1 and 13.1.1 of the International Code of Zoological Nomenclature (1999) explain that "every new name published after 1930 must…be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon…" The exclusionary clause that would validate new names lacking such a description if a subsequent author treated them as valid (Art. 13.2.1) only applies to names first published after 1930 and before 1961.

Though at least one author has placed a new genus in Petalocephalini (Cai 1994b), no one has made a formal description of the tribe or used it in a key. Kramer (1966) and Linnavuori (1972) refrained from recognizing any tribes in their revisions of the New World and African Ledrinae. Evans (1969) recognized Ledrini but not Petalocephalini, and Hamilton (1983) Dietrich (2000, 2005), and Szwedo (2002) treated Petalocephalini as a junior synonym of Ledrini.

Various authors (Ren and Zhang 2001; Shih *et al.* 2001) have removed some of the genera of Petalocephalini to Ledrini, and Oman *et al.* (1990) included ledrine genera in both tribes. When the genera of

Petalocephalini and Ledrini are coded according to their respective placements (not shown) sensu Oman *et al.*, they appear as grossly polyphyletic.

As Petalocephalini appears to be an invalid name, it is therefore recognized here as unavailable. That it is paraphyletic with respect to Ledrini and has been treated by a junior synonym of Ledrini by several authors are additional reasons to officially remove it from usage.

The following described genera are here considered to belong in Ledrini: *Arenoledra*, *Beniledra*, *Chatura*, *Complanledra*, *Confucius*, *Destinia*, *Destinoides*, *Dusuna*, *Eleazara*, *Ezrana*, *Funkikonia*, *Hangklipia*, *Jukaruka*, *Kuohledra*, *Laticorona*, *Ledra*, *Ledropsella*, *Ledropsis*, *Midoria*, *Neotituria*, *Paraconfucius*, *Parapetalocephala*, *Petalocephala*, *Petalocephaloides*, *Platyjassites*, *Latycephala*, *Platyledra*, *Porcorhinus*, *Thlasia*, *Titiella*, and *Tituria*.

Cwikla (1987) suggested that the Chilean species *Ledra episcopalis* Walker (not available for examination)—considered by Kramer (1966) to be of uncertain placement within Ledrinae—superficially resembled *Bascarrhinus*. It is herein considered unplaced within Ledrinae until it can be examined.

Several ledrine genera that were not available for examination in this study have been weakly characterized, and their formal descriptions do not provide sufficient diagnostic features to satisfactorily distinguish them from other genera, as noted in their sections. For this reason they are not included in the key to the Ledrini genera below. The extinct genus *Platyjassites* is also not included.

Key to selected genera of Ledrini

(not including *Arenoledra* Kuoh, *Complanledra* Cai, *Destinia* Nast, *Destinoides* Cai & He, *Laticorona* Cai, *Midoria* Kato, *Paraconfucius* Cai, *Petalocephaloides* Kato, *Platyjassites* Hamilton or *Latycephala* McKamey)

1a. Anterior portion of body, in lateral view, appearing flexed ventrad from point posterad of scutellum, (Pl. 6F_1), with dorsum of head, pronotum and scutellum essentially in the same plane; pronotum not especially declivous or humped (exception: *Dusuna*), with extensions often produced laterally from dorsolateral margins (Pl. 1E-F, 2J, 3H-J, 4A-B; exception: *Petalocephala*, Pl. 3A-C); lateral area of crown immediately mesoposterad of eye and anterior to coronal hind margin deep; coronal hind margin posterad of eye not carinate (Pl. 7E_3); lateral margins of crown immediately in front of eyes usually parallel to convergent, but not divergent (as in Pl. 10A_1; *Petalocephala* genus group) 2

1b. Anterior portion of body not flexed ventrad in lateral view, or only slightly so, with dorsum of head, pronotum and scutellum not appearing to be in same plane; pronotum often declivous or humped (Pl. 6B_1), without lateral extensions (exception: *Eleazara*); lateral area of crown immediately mesoposterad of eye and anterior to coronal hind margin varying from narrow to moderately deep; coronal hind margin posterad of eye carinate or not; lateral margin of crown immediately in front of eyes usually parallel to divergent, but not convergent (Pl. 7D_1) 6

2a. Pronotum without lateral extensions (Pl. 3A–C) .... *Petalocephala*

2b. Pronotum with lateral extensions (Pl. 1E–F, 2J, 3H–J, 4A–B, 7E).......... 3

3a. Pronotal lateral extensions broad, with margins subtriangular and/or rounded (Pl. 1E–F, 3H–J, 7E) 4

3b. Pronotal lateral extensions broad, with margins triangular and acute (Pl. 2J, 4A–B) 5

4a. Pronotum in lateral view distinctly declivous (Pl. 7E), forewing cells strongly depressed, forewing veins raised (Pl. 1E-F) .... *Dusuna*

4b. Pronotum in lateral view intermediately declivous to essentially flat, forewing cells not depressed, forewing veins not especially raised (Pl. 3H-J) .... *Thlasia*

5a. Lateral extensions of pronotum broad and well developed (Pl. 4A–B).......... *Tituria*

5b. Lateral extensions of pronotum narrow and not well developed (Pl. 2J) ....*Neotituria*

6a. Coronal setae (or their vestigial bases) absent.......... 7

6b. Coronal setae (or their vestigial bases) present 10

7a. Large leafhoppers (15-20 mm), crown large, very foliaceous, pentagonal, forewing venation highly reticulate, body orangish brown (Pl. 1A).......... *Beniledra*

7b. Medium to small leafhoppers (~5-8 mm), crown not especially large, and only somewhat foliaceous, if at all, not pentagonal; forewings with regular venation, but if reticulate, then with only a few cross veins present 8

8a. Face expanded, convex, only anterolateral margins flattened, lateral margins between lora/genae and frontoclypeus not especially depressed (Pl. 10C_1) .... *Titiella*

8b. Face not expanded, concave, flattened, with lateral margins between lora/genae depressed and well defined 9

9a. Pronotum with a weakly expressed median longitudinal carina present anteriorly (Pl. 2K).......... *Parapetalocephala*

9b. Pronotum without a median longitudinal carina, but occasionally with a weakly expressed median longitudinal groove present anteriorly or completely (Pl. 2A) .... *Hangklipia*

10a. Metathoracic tarsomere I not especially columnar or robust compared with other tarsomeres, in ventral view shorter to coequal in length with remaining tarsomeres combined (Pl. 11B_4, 12B); anterolateral portions of face without setae; pronotum not strongly declivous in lateral view (Pl. 6D-F) ....*Confucius*

10b.Metathoracic tarsomere I columnar, more robust compared to other tarsomeres, in ventral view slightly (Pl. 12H) to considerably (Pl. 13J) longer than remaining tarsomeres combined; anterolateral portions of face with setae; pronotum strongly or intermediately declivous posterad and flattening anterad in lateral view (Pl. 6B_1, 8B-C).... 11

11a. Pronotum with two submedian ridges, two sublateral longitudinal ridges, or both; submedian rows sometimes very weakly developed; outer ridges sometimes high and lamellate, or developed into paired crests or "ears" 12

11b. Pronotum without paired submedian rows (but sometimes with single median ridge or crest) sublateral rows/ processes present or absent 14

12a. Pronotum produced laterally (Pl. 1G) ....*Eleazara*

12b. Pronotum not produced laterally 13

13a. Metathoracic tibia not foliaceously dilated ....*Chatura*

13b. Metathoracic tibia foliaceously dilated (Pl. 12H) .... *Ledra*

14a. Proepisternum large, quadrate, not collar-like, not extending laterally onto sides of pronotum (Pl. 9B_3); species from Indomalayan region 15

14b. Proepisternum large and collar-like, wrapping around sided of pronotum anteriorly (Pl. 9D_3, E_4); species from Australia 16

15a. Forewing with a large, more or less developed, sclerotized tubercle at first split of M vein (Pl. 1I, 6B_2) .... *Funkikonia/Kuohledra*

15b. Forewing without large sclerotized tubercle at first split of M vein (Pl. 2F–G).. *Ledropsis*

16a. Posterior margin of pronotum distinctly and narrowly subtrapezoidal in shape (Pl. 1H, 2H–I, 3G)......................... 17

16b. Posterior margin of pronotum not distinctly and narrowly subtrapezoidal in shape (Pl. 7D; *Jukaruka* genus group).. 18

17a. Pronotum with pair of large, well developed sublateral horns or processes; body color yellowish in dried specimens (Pl. 3G).. *Porcorhinus*

17b. Pronotum without sublateral processes; body color brown in dried specimens (Pl. 1H, 2H–I) ....*Ezrana* (and *Ledropsis froggatti*)

18a. Crown distinctly acuminate apically (Pl. 3D–F, 10I); pronotum slightly compressed dorsoventrally in lateral view .. .. *Platyledra*

18b. Crown not acuminate apically, pronotum not especially compressed in lateral view 19

19a. Frontoclypeus expanded, filling area of face and almond-shaped, with deeply invaginated lateral margins (Pl. 9E) .. .. *Ledropsella*

19b. Frontoclypeus not expanded and filling area of face, and lateral margins not deeply invaginated (Pl. 9D) . *Jukaruka*

Genus *Arenoledra* Kuoh

Arenoledra Kuoh, 1992:254, 307.
Type species. *A. nigrimaculata* Kuoh, 1992: 255, 307, fig. 13, by original designation.
Synonymy. None.

Description. Kuoh (Ge 1992): "The vertex of the head as long as breadth between eyes or shorter, nail shape, the body above densely covered [with] granules as rough as sandpaper, the veins of tegmina radialized towards the apex, especially in the process of pygofer which differs from *Petalocephala* and the shape of the aedeagus and styli differs from both of them [*Petalocephala* and *Latycephala*]."

Species. [4]: *nigrifrons* Kuoh; *nigrimaculata* Kuoh; *ochracea* Kuoh; *tubularis* Cai & Sun.

Range. China (Lushui, Yunnan, Weixi).

Host plants. Unknown.

Material examined. None.

Remarks. The type specimen of *Arenoledra nigrimaculata*, which was not made available for this study, appears to be located in either the Institute of Zoology, Chinese Academy of Sciences (Academica Sinica), Beijing, or in Anhui Agricultural College, Anhui, China (Ge 1992). Based on Kuoh's description of the genus and drawings of *A. nigrimaculata*, the exact phylogenetic placement of this genus is uncertain, but it appears to be very similar to *Midoria* and *Latycephala*. All three genera may be proximate to *Hangklipia* or *Parapetalocephala* (Kuoh stated that *Arenoledra* was between *Petalocephala* and *Platycephala* [=*Latycephala* McKamey]). A 2004 collecting expedition in Taiwan in which the first author participated (organized by C. H. Dietrich, INHS, and host M. M. Yang, Chung Hsing University, Taichung) yielded a few specimens resembling *Arenoledra*, and a number of specimens borrowed from the TARI and NMNS collections vaguely resemble Kuoh's illustrations, but it will be necessary to examine his type material in order to make a positive identification. These specimens ultimately were not included in the phylogenetic analysis.

Genus *Beniledra* Linnavuori

(Pl. 1A, 7G, 10H, 12B, 14A, 17E)

Beniledra Linnavuori, 1972: 213.
Type species. *B. peculiaris* Linnavuori, 1972: 214, fig. 5b, 8a–b, by original designation.
Synonymy. None.

Description. Linnavuori (1972): "Large brown leafhoppers. Body elongate, tapering caudad. Crown foliaceous, pentagonal, with lateral margins strongly diverging apicad in front of eyes, disk conspicuously elevated medially, flat laterally, irregularly microsculptured with longitudinal furrows and obsolete punctures, ocelli closer to each other than to eyes. Face strongly concave in upper part, lower portions flat, anteclypeus parallel-sided. Pronotum long, lateral margins long, parallel and carinate, anterior margin straight, basal margin strongly insinuated medially, disk densely punctate, swollen basally and medially, sloping apicad and laterad, lateral and apical margins flat. Elytra long, vertical, broadening apicad, apex truncate, apical margin shallowly concave, cells coriaceous and densely punctate, clavus and apical two-thirds of corium with numerous extra cross veins. Legs as in *Petalocephala*. Male genitalia: Pygophore dorsally incised to base, side lobes triangular, without appendages. Anal tubes tapering apicad, dorsal surface with a deep inverted V-shaped median notch. Genital plates sharply triangular. Stylus elongate, apophysis with a hook-shaped apex. Connective a small plate. Penis with long tubulous stem, gonopore subapical on the dorsal surface. Posterior margin of 7th sternite [of female] undulate."

Species. [1]: *peculiaris* Linnavuori.

Range. Angola (Singombe); Cameroon (Region du N'ten); Central African Republic [Republic of Central Africa] (Boukoko, La Maboke); Congo (Dimonika, Kivu); Democratic Republic of the Congo [Zaire] (Beni forest, Buma).

Host plants. *Nanniophytum africanum* (Euphorbiaceae).

Material examined. *B. peculiaris*: 1 male, 1 female, Congo, AMNH, JRJ_Led1_015, 20; 3 males, 3 females, Cameroon, Central African Republic, Congo, MNHN, Led1_016–021.

Remarks. *Beniledra* is monobasic. The type specimen is unknown, but nearly a dozen unidentified specimens were found in the MNHN, and two of the paratypes from Linnavuori's personal collection were made available by the AMNH.

Beniledra has many affinities to *Confucius*, including the metathoracic tarsomere being short and the tibia not being especially foliaceous. The large size, long broadly triangular wings that meet to form a peak over the hind part of the abdomen, highly reticulate venation, and the large, flat, pentagonally-shaped crown make *Beniledra* readily distinguishable from all other Ledrini.

Genus *Chatura* Distant
(Pl. 1B)

Chatura Distant, 1908: 176.
Type species. *C. nigella* Distant 1908:176, fig. 116, by original designation.
Synonymy. None.

Description. Distant (1908): "Vertex about as long as breadth between eyes and almost as long as pronotum and scutellum united, not angulated in front of eyes, the lateral margins continuous from eyes to apex; face broad between the eyes, angularly narrowed anteriorly; pronotum short, considerably shorter than vertex, with four central ridges, the lateral margins sinuate, anterior and posterior margins nearly straight, the latter only slightly concavely sinuate; scutellum discally foveate; legs moderately short, posterior tibia not foliaceously dilated, outwardly somewhat strongly spinose; forewings short, more or less granulose, apices broadly rounded."

Species. [1]: *nigella* Distant.

Range. Sri Lanka [Ceylon] (Maskeliya).

Host plants. Unknown.

Material examined. None (see remarks below).

Remarks. *Chatura*, which is monobasic, resembles *Ledra* in general appearance, and is known only from the type specimens. It was photographed early in this study (Pl. 1B—along with the *Eleazara*, which is also resembles) but was not available for later examination. Distant's distinguishing features for *Chatura* are the metathoracic tibiae being "not foliaceously dilated", as opposed to *Ledra*'s, which generally are, the crown being non-angulate in front of the eyes, and the pronotum being [relatively] short. The latter two characters are probably sex-specific (Distant described a single female) and may not apply to males. It is not known if all described members of *Ledra* have foliaceous metathoracic tibiae; at least some of those that do not could probably appropriately be moved to this genus.

Genus *Complanledra* Cai

Complanledra Cai, 1998: 213.
Type species. *C. complana* Cai 1998: 214, fig. 3, by original designation.
Synonymy. None.

Description. Cai and Huang (1998): "Medium-sized leafhopper, body flat, light brunneus. Head spatulate and ventrally concave, median length of crown shorter than interocular width in male, the lateral margins straight in front of eyes and then oblique to apex, which is obtusely angulate. Eyes and ocelli prominent, ocelli situated in the line of anterior margin of eyes, nearer to each other than to eyes. Pronotum as long as crown, anterolaterally foveately depressed and declivous, with a shallow medial slit on apical part, lateral margins straight and parallel to each other, posterior margin concavely sinuous. Scutellum moderately large, slightly shorter than pronotum in length. Forewings long and narrow, semihyaline, costal margin and inner margin parallel, veins raised in relief and reticulate, base of vein A_1 crestiformly prominent. Legs moderately long and slender, with a white fringe of hairlike spines, metathoracic tibia somewhat foliaceously dilated, apical half of outer margin with several dentate-like spines. Male abdominal sternum VIII longer than sternum VII, posterior margin concave. Pygofer large and broad, with smaller process on apical half of ventral margin. Plates pod-shaped, long and narrow. Connective depressed, plate-shaped. Styli long and narrow, with distal parts inflected. Aedeagus tubulose, bent, with apical part swollen."

Species. [1]: *complana* Cai & Huang.

Range. China (Yunnan).

Host plants. Unknown.

Material examined. None.

Remarks. *Complanledra* is monobasic. Cai and Huang stated that it is closely allied to *Funkikonia*, but distinguished by having a "flat body, the crown as long as the pronotum in the male, the lateral margins of pronotum straight and parallel [to] each other, the metathoracic tibia somewhat foliaceously dilated and the bent apex of the styli without processes." They also indicated that the type specimens of *Complanledra* and two newly described species of *Funkikonia* were located at the Institute of Zoology, Chinese Academy of Sciences (Academica Sinica), Beijing, and the NMNS. However, no specimen matching the description of *Complanledra* was observed in material received from NMNS, and material at the Chinese Academy of Sciences was not made available for this project (no response was received to letters or emails).

Genus *Confucius* Distant

(Pl. 1C–D, 18E)

Confucius Distant, 1907: 191.
Type species. *C. granulatus* Distant 1907: 191, by original designation.
Synonymy. None.

Description. Linnavuori (1972): "Narrow medium-sized leafhoppers. Colouring brownish, sometimes with a greenish tinge. Body parallel-sided, convex. Upper surface densely punctate and +/– granulose. Head strongly produced, in ♂ much shorter than in ♀, spatulate, anterior margin broadly foliaceous. Face concave, lower part short, nearly semicircular in outline; anteclypeus parallel-sided; frontoclypeus narrow and flat, parallel-sided in lower part, sharply triangularly tapering upwardly in front of antennal pits; lora elongate, genae flattish, antennal pits shallow. Crown convex, strongly sloping laterad, slightly upcurved apically, with a faint median carina, ocelli closer to each other than the eyes. Pronotum with lateral margins long, subacute, insinuated, diverging caudad, anterior margin curved, hind margin distinctly insinuated medially, humeral angles blunt, disk in basal part convex, sloping apicad. Elytra narrow, coriaceous, densely punctate, apical and subapical area with extra cross veins. Fore and middle tibiae moderately flattened, apical margin of hind femora with 3 spines, hind tibiae with one longitudinal row of distinct spines, those of the second row delicate, apex with two transverse rows of distinct spines, also apex of 1st joint of hind tarsi with a transverse spine row. Male genitalia as in *Petalocephala*. Side lobes of pygophore with falcate appendages. Stylus elongate, apophysis only slightly hooked apically. Penis flattened, provided with longitudinal lamellae and sometimes with apical processes, gonopore on the ventral surface. Hind margin of 7th sternite (♀) medially insinuated."

Species. [9]: *bituberculatus* Distant; *cameroni* Distant; *dispar* Nast; *granulatus* Distant; *maculatus* Cai; *nigristigmatus* Kuoh and Cai; *ocellatus* Distant; *poleman* Linnavuori; *zombanus* (Distant).

Range. Central African Republic [Republic of Central Africa]; China (Hainan Island; Hong Kong Island); Democratic Republic of the Congo [Zaire]; "East Africa"; Guinea (Nimba); India (Sikkim); Liberia (Suokoko); Malawi; South Africa; Sri Lanka; Tanzania; Uganda (Kampala); Zimbabwe [Rhodesia].

Host plants. Unknown.

Material examined. *C. cameroni*: 1 male, Uganda, AMNH, Led1_040; *C. dispar*: 1 female, India, BMNH, JRJ_Led1_041; *C. zombanus*: 1 male, Guinea, AMNH, JRJ_Led1_042, 1 male, Liberia, USNM, JRJ_Led1_043.

Remarks. *Confucius* is very similar to *Ledropsis*, but differs in not having very flattened tibia (the tibia are quadrate) and the metathoracic tarsomere I not being long and setose (as explained by Linnavuori 1972: 207) as in more derived ledrines. Its placement in the analysis basal to the *Ledropsis*-like species

(Indomalayan) and the *Jukaruka* (Australian) genus group indicates that *Confucius* represents an ancestral lineage from which the latter two clades are derived. The genus as presently constituted appears to be paraphyletic.

Many of the described species of *Confucius* are found in Africa, and Africa may be the point of origin for the genus.

Genus *Destinia* Nast

Destinia Nast, 1952: 35.
Type species. *D. maja* Nast, 1952: 36, pl. V, figs. 7–9, pl. VI, figs. 10–15; by original designation.
Synonymy. None.

Description. Nast (1952): "Head shorter than breadth between the eyes; general shape of it not parabolic; its margin before the eyes with a distinct angle, thus the anterior part of the margin, when prolonged backwards, runs far outside the eyes. Ocelli nearer to each other than to the eyes. Pronotum broad, in the middle longer than head; its anterior border straight, slightly diverging backwards; posterior border deeply sinuate. Scutellum as long as pronotum (*D. maja* sp. n.) or somewhat longer (*D. producta* sp. n.). Forewings 3 times longer than broad, apex rounded; venation simpler than in *Petalocephala* Stål, in the apical part there is no reticulation; only the space between costal margin and radius as well as the basal part of the clavus are punctured. Hind wings vitreous. Metathoracic tibia not flattened, with 5 spines. Pygofer provided with a horizontal process on its upper hind angle; parameres thick, bent downwards."

Species. [2]: *maja* Nast; *producta* Nast.

Range. Indonesia (Sumatra: Soekaranda).

Host plants. Unknown.

Material examined. None.

Remarks. Specimens of *Destinia*, including the type specimen for *D. maja*, were unavailable for this study. Nast stated that his types were in the Polish Museum of Zoology, but requests to collections managers at the ZMPA were unreturned.

Nast (1952) stated that *Destinia* differs from *Petalocephala* "in form of the head and in venation of the forewings," and in his description of *Destinia*, he stated that the head is angulate instead of parabolic, that it is shorter than the distance between the eyes, and that the wings have "simpler" venation. Vertex length and shape and degree of wing reticulation alone, however, are of dubious diagnostic utility in the Ledrini, as the former appear to be sexually determined in many species, a difference Nast himself (1952: 33) earlier points out, and species-level variation of venation in forewings of *Petalocephala* is uncertain.

Nast (1952) described and illustrated the male of the type species of *Petalocephala*, *P. bohemani* (Stål). In his illustrations, the head is slightly longer than the pronotum and is parabolic, in the latter feature appearing much like the female (females examined in this study had the head parabolic and approximately 1.5 times longer than the pronotum—Pl. 3A). Other ledrine genera having heads shorter than the pronotum (*Parapetalocephala* Kato, 1931) and not parabolic (*Midoria* Kato, 1931; *Funkikonia* Kato 1931) were described previously, and some have been described since (*Arenoledra* Kuoh, *Latycephala* McKamey). It may be that these genera are all unique from *Petalocephala* and *Destinia*, but several of them have not been well-characterized.

Regarding wing venation, the range of expression of reticulation in forewings of *Petalocephala* species is not presently clear—*P. bohemani* appears to have very reticulate wing venation, but it is not certain this is the case for all species in the genus. In Nast's illustrations of *Destinia* forewings, venation is mostly regular, but there are several extra cross veins apically.

Comparisons of the genitalia of the *Destinia* species to *P. bohemani* show many similarities and a similar basic overall structure (aedeagus intermediate in width at base with apical and subapical processes, styles broad with apices pointed ventrad, plates dorsoventrally flattened basally and laterally compressed apically). But some features may be unique to *Destinia* in their particular combination, in addition to the head shape and wing venation characters; they include the scutellum + post-scutellum being as long as or nearly as long as the pronotum, the presence of the ventrodistal lobe on the anal tube, the shape of the styles, which appears to be short and relatively thick distally posterad of the point of attachment with the connective, the basidistal processes of the pygofer being absent, and a pair of dorsoapical lobes of the pygofer being present (it is not clear from Nast's drawings if these are the same structures as the inner, subapical, dorsomedial processes seen in other genera).

Examination of the type specimens of *Destinia* and comparison to many *Petalocephala* species would contribute greatly to confirming the validity of *Destinia* as an independent genus and determining the phylogenetic position of its species within Ledrini.

Genus *Destinoides* Cai and He

Destinoides Cai and He, 2000: 57.
Type species. *Destinoides fasciata* Cai and He 2000: 57, by original designation.
Synonymy. None.

Description. From Cai and He 2000: "This genus most closely resembles *Destinoides* [sic= "*Destinia*"] Nast, but can be readily distinguished by the forewings with reticulate venation, the hind margin of male abdominal sternum VII emarginate, the pygofers with plate-like processes, and by the slender aedeagus with processes on apex."

Species. [2]: *fasciata* Cai and He; *latifrons* (Walker).

Range. China (Hainan, Xizang, Yunnan); India (Sikkim); Sri Lanka [Ceylon]; Vietnam.

Host plants. Unknown.

Material examined. None.

Remarks. This taxon suffers from the same ambiguity as *Destinia* (see 'Remarks' for *Destinia*), which is that none of its characteristic features are clear synapomorphies, but rather exist in some form or another in several other genera of Ledrini. It is not clear either whether the symplesiomorphic features mentioned by Cai and He represent even a unique combination. In the illustrations given by Cai and He (2000), the aedeagus is exceptionally (but not uniquely) slender, but not one of the other features mentioned in the description of the genus sets it apart, suggesting that this genus is synonymous with an existing taxon, perhaps *Petalocephala*. The weakness of the characterizations of existing genera, however, including *Petalocephala*, precludes making an accurate placement.

Genus *Dusuna* Distant

(Pl. 1E–F, 7E, 11E)

Dusuna Distant, 1907: 188.
Type species. *D. mouhoti* Distant 1907: 188, by original designation.
Synonymy. None.

Description. From Cai and Yang (1997): "Medium-sized leafhoppers. Body broad and flat coarsely punctate. Coloration brownish. Crown small and short, triangular, about half as long as breadth between eyes. Ocelli placed behind the line of anterior margin of eyes, nearer to each other than to eyes. Face bent into two planes, along the line between antennae, frontoclypeus broad and large, antennal depressions rather deep. Pronotum transverse, gradually rising from anterior to posterior margin, much longer than crown, the lateral areas obtuse-angularly produced, anterior margin behind head excised, posterior margin sinuate. Scutellum shorter than pronotum, disk concave, the middle part of basal margin, basal angles and anterior half moundly prominent. Tegmina relatively short, anterior margin sinuate, apical margin roundly truncate, veins prominent and marginally punctate, on posterior half the disk divided into foveate cellular areas, clavus uneven, clava1 veins crestiformly prominent and the middle part of them coalescent. Legs moderately long and slender, hind tibiae not foliaceously dilated, spined on margin, apical half of outer margin with several dentate spines. Posterior margin of 7th sternite of female sinuate, that of 8th sternite of male nearly rectilinear. Apical half of pygofer with a process, convex, wooden dipper-shaped. Subgenital plate broad and short. Connective a thin piece, nearly cruciate. Style long and narrow, apical part bent as a long hook. Aedeagus curvate, shaft tubulose, ampliate subterminal with a pair of processes, phallotreme on the tip.”

Species. [5]: *bimaculata* Cai & Kuoh; *brunnea* Cai & Yang; *dohertyi* Distant; *mouhoti* Distant; *nigrofasciata* Cai & Kuoh.

Range. China (Hainan; Yunnan: Lancang: Menglang); Malaysia; Thailand.

Host plants. Unknown.

Material examined. *Dusuna* sp. 1: 1 female, China, NMNS, JRJ_Led1_044; *Dusuna* sp. 2: 1 male, China, NCSU, JRJ_Led1_045.

Remarks. *Dusuna*, with *Hangklipia*, *Parapetalocephala*, and *Titella*, has the pronotum intermediately declivous and is small in size (relative to other ledrines). In some phylogenetic analyses (not shown), this complex of species formed a monophyletic group, although the final trees did not show this. Like *Thlasia* in the *Petalocephala* genus group, *Dusuna*’s lateral carinae are produced but not triangular, and *Dusuna* shows some affinities to both *Thlasia* and *Tituria* in overall body shape, in ventral flexion of the crown, in reduction of the distal portion (apical extension) of the frontoclypeus, and in the shape of the inner margin of the antennal pit. Its present placement adjacent to the *Petalocephala* genus group appears to be supported by these synapomorphies.

In the two specimens examined, the cells of the forewings were conspicuously depressed (a trait only seen elsewhere in *Parapetalocephala testacea* Cai & Kuoh). A number of undescribed species from the Philippines and Malaysia (in the USNM and MNHN collections) that lack depressed wing cells may belong to or be closely associated with *Dusuna*.

Genus *Eleazara* Distant

(Pl. 1G)

Eleazara Distant, 1908: 182.
Type species. *E. aedificatura* Distant 1908: 182, fig. 120, by original designation.
Synonymy. None.

Description. Distant (1908): “Head broad, short, angulate, straight in front of eyes and then oblique to apex, which is angulate; ocelli on posterior vertical area; head beneath foliaceous, recurved anteriorly, face elongate, broadest between eyes, much narrowed anteriorly, less so posteriorly; pronotum longer than vertex, the lateral areas laminately subangularly dilated, anterior margin nearly straight, posterior margin concavely sinuate; scutellum with a central elevated crest-like process; legs of moderate length, posterior tibia slightly dilated, outwardly spinose; tegmina rugose and granulose, the veins, especially on apical area, elevated and prominent.”

Species. [3]: *aedificatura* Distant; *distanti* Schmidt; *yangi* Cai & He.

Range. China; India (Assam, Dikrang Valley); Indonesia (Sumatra).

Host plants. Unknown.

Material examined. None.

Remarks. The type specimen of *E. aedificatura* was photographed early on in this study (at BMNH) but was not later available for examination. From the photograph (Pl. 1G), and Distant’s drawing and description (1908: 182), this species appears to be closely related to *Ledra* and the *Ledropsis*-like species. Like *Ledra* (and *Chatura*), it has four longitudinal rows (of tubercles—outer rows; of carinae—inner rows) on the pronotum. In Distant's (1908) illustration, the long metathoracic tarsomere I can clearly be seen, further indicating its affinity to *Ledra* and the *Ledropsis*-like species. But like *Dusuna* and members of the *Petalocephala* genus group, *E. aedificatura* has lateral pronotal extensions, demonstrating the plasticity of this latter character across Ledrini. *E. aedificatura* is known only from the type specimen.

Genus *Ezrana* Distant
(Pl. 1H, 17A–B, 18F)

Ezrana Distant, 1908: 177.
Type species. *E. pygmaea*, Distant 1908: 17, fig. 117, by original designation
Synonymy. None.

Description. Distant (1908): "Male. Head shorter than breadth between eyes; ocelli very prominent, placed on disk behind middle and slightly nearer to each other than to eyes, lateral margins straight for a short distance in front of eyes, then narrowed to apex, which is obtusely acute; pronotum non-carinate, but centrally longitudinally sulcate, lateral margins a little concavely sinuate; posterior angles subprominent, posterior margin sinuate; other characters generally as in *Ledra*. Legs imperfectly seen, owing to corrosion, in typical specimen, but the posterior tibiae not foliaceously dilated."

Species. [2]: *primitiva* Evans; *pygmaea* Distant.

Range. Australia (Queensland); India (Bombay).

Host plants. Unknown.

Material examined. *E. primitiva*: 1 female, Australia, USNM, JRJ_Led1_051.

Remarks. A unique feature of the single specimen of *Ezrana* examined, *Ezrana primitiva* Evans, is a vertically oriented keel descending approximately halfway down the face of each side of valvulae II from the first dorsal tooth (Pl. 18F_1). This feature is shared by *Ledropsis froggatti* Distant and *Porcorhinus mastersi* Goding—both also Australian species that are morphologically distinctive in their own right—and seems from the phylogenetic analysis to be a synapomorphy uniting their respective genera, but this may be an artifact of taxon sampling. At the very least it seems to be symplesiomorphic for some part of the Australian fauna. From the phylogenetic analysis it seems that the species group including *E. primitiva, L. froggatti* and *P. mastersi* (Figs. 1–3) is part of a larger, distinct Australian clade recently separated from the Indomalayan fauna (see "Phylogenetic results and discussion" above). It would be interesting to see if the type species, *E. pygmaea* (location of type specimen unknown) has the keel on valvulae II.

The available specimen of *E. primitiva*, a female, appears to violate at least two defining features for *Ezrana* given by Distant (1908: 177), the "posterior tibia not foliaceously dilated" and the "pronotum non-carinate." *E. primitiva*, which is large and distinctive in these respects, probably belongs in its own genus.

L. froggatti (and *Ledropsis crocina* Distant, which was only briefly examined and not included in analysis) lacks a pronotal crest and foliaceous tibia, and in this regard accords with Distant's (1908) description for *Ezrana*. However, *L. froggatti* lacks prominent ocelli and a central longitudinal sulcus on the pronotum, and its head in both the male and female is longer than the breadth between the eyes, violating these characters for *Ezrana*.

It is unclear at this point whether *L. froggatti* (and *L. crocina*) should be placed within *Ezrana* or accorded its own genus. Decisions involving the classification of *L. froggatti*, *Ezrana*, *E. primitiva*, and the other Australian species can best be made by a species-level revision of the Australian fauna, and by comparing types of each of these species with newly collected material that includes males and females.

Genus *Funkikonia* Kato
(Pl. 1I, 6B, 9B)

Funkikonia Kato, 1931: 438.
Type species. *Ledra tuberculata* Kato, 1929:545, fig. 2, a–c, by original designation.
Synonymy. None.

Description. Adapted from Kato (1931): Vertex of head about as long as breadth between eyes and almost as long as pronotum, the lateral margins obliquely straight for a little in front of eyes and then obliquely subangularly pointed to apex, strongly centrally longitudinally ridged, with a more obscure short oblique ridge on each side; eyes and ocelli very prominent, the latter placed on disk behind middle and distinctly nearer to each other than to eyes. Pronotum convex, without central longitudinal carina, each side deeply sinuated; tegmina subhyaline, veins prominent; posterior tibiae non-dilated. Aedeagus without subapical processes.

Species. [3]: *taiwana* Cai & Huang; *tuberculata* (Kato); *zheana* Cai & Huang.

Range. China (Zhejiang: Longwangshan), Taiwan (Funkiko; Sungkang; Tsui Feng).

Host plants. *Acer palmatum* (Japanese maple).

Material examined. *F. tuberculata*: 1 male, Taiwan, TARI, JRJ_Led1_449, 1 (abdomen missing), Taiwan, TARI, JRJ_Led1_101; *Funkikonia* sp. 1: 1 female, Taiwan, NCSU, JRJ_Led1_099; *Funkikonia* sp. 2: 1 female, China, USNM, JRJ_Led1_100.

Remarks. Kato (1931) stated that the type specimen of *F. tuberculata* was in his personal collection. The current location of his collection, however, is unknown. It may now be in any one of a number of Oriental institutions, or may have been lost altogether.

Two male ledrines from the TARI collection (JRJ_Led1_101, 449) were identified by the first author as *F. tuberculata* and used in the phylogenetic analyses. Females of *Funkikonia*, however, are undescribed. Kato's (1931) characters for crown shape describe a male, but probably do not apply to females, if the species are sexually dimorphic, as in other similar species. Unidentified ledrine females examined from the TARI and NMNS collections, though differing from *F. tuberculata* in size and texture, nevertheless first appeared to belong to this genus, and were identified as such for use in the phylogenetic analyses (*Funkikonia* sp. 1, *Funkikonia* sp. 2). The analyses, however, instead placed them separately from *F. tuberculata* as sister to *Ledropsis* (in part) + *Ledra* (in part) (Figs. 1–3). The unidentified females, then, may not belong to *Funkikonia*; or, the separate placement may be an artefact of inadequate taxon sampling or differential character sampling of males and females. The females identified as *Funkikonia* are larger and have more produced crowns than *F. tuberculata*, and are more tuberculate in overall dorsal texture. It is possible that the female examined from Taiwan (JRJLed1_099) may belong to one of two described species (both males) of *Funkikonia* from Taiwan.

Members of this genus strongly resemble *Ledropsis* in overall body shape and the abruptly declivous pronotum, and are closely related to it, as shown in the analyses. Kato's 1931 redescription of *Funkikonia* does not actually explain how the two genera differ. The key diagnostic character for *F. tuberculata*—the large sclerotized tubercle on the forewings—is present, though generally far less produced and sclerotized, in many other ledrine species, including *Petalocephala* and *Tituria*, and may be a plesiomorphic and/or highly plastic character. It is given by Cai and He (1997) as a diagnostic character for *Kuohledra* Cai and He, which may therefore be a synonym of *Funkikonia* (see discussion under *Kuohledra*). In *F. tuberculata* and the unidentified *Funkikonia* female specimens, the tubercle has a texture that is sandpaper-like, granular, punctate, or a combination of these. This suite of accompanying textures for the tubercle may be synapomorphic for *Funkikonia*.

Kato's original description of *Funkikonia* (1929) provides only general states of color and texture but little that is useful for making these distinctions.

Genus *Hangklipia* Linnavuori
(Pl. 2A, 16E–F)

Hangklipia Linnavuori, 1972: 235.
Type species. *Camptelasmus signatus* Linnavuori 1961: 457, by original designation.
Synonymy. None.

Description. Linnavuori (1972): “Resembling *Petalocephala* but smaller, length <10 mm. Elytra (fig. 21 e) with regular venation, only apical area of corium with a few extra cross veins, subapical area with two long parallel-sided cells. Male genitalia as in *Thlasia*.”

Species. [2]: *signata* (Linnavuori); *gibber* (Naudé).

Range. South Africa (God’s Window; Kougaberg; Kraaifontein; Strand; West Cape Province).

Host plants. *Cliffortia serpyllifolia* (Rosacea); *Passerina montana* (Thymelaceae).

Material examined. *H. gibber*: 1 male, 1 female, South Africa, SANC, JRJ_Led1_058–059; *H. signata*: 2 males, South Africa, SANC, Led1_052, 057, 1 (abdomen missing), South Africa, SANC, JRJ_Led1_53, 1 male, South Africa, MZLU, JRJ_Led1_056.

Remarks. This genus is very similar to *Titiella* but lacks the expanded and convex face. Its concave face and well-defined (although small) frontoclypeus is much more like that of more derived ledrines. It shares some morphological similarities with *Dusuna*, *Parapetalocephala*, and *Titiella*. The aedeagus of the males (Pl. 16E–F) is roughly somewhat similar in shape to those in *Thlasia* (Pl. 16K), as stated by Linnavuori, to which it seems to be only distantly related within Ledrini.

Genus *Jukaruka* Distant
(Pl. 2B, 7A, D, 8B, 9D, 13G–H, J, 14K)

Jukaruka Distant, 1907: 190.
Type species. J. typica Distant, 1907: 190, by monotypy.
Synonymy. None.

Description. Distant (1907): “Vertex of head about as long as space between eyes, centrally carinate; ocelli situate at about middle of vertex; head beneath foliaceous, face elongate, narrowed anteriorly, its disk centrally sulcate; pronotum longer than broad, centrally longitudinally laminately ridged; legs slender, posterior tibiae not foliaceously dilated, posterior coxae with a short spine; tegmina obliquely vertical, the veins on apical area coarse and reticulate. Allied to *Ledra* from which it differs by the single laminate ridge to the pronotum, the position of the ocelli, the non-dilated posterior tibiae, and the more slender and elongate form; by the last character it is allied to *Confucius* Dist.”

Species. [2]: *grisea* Evans; *typica* Distant.

Range. Australia (Queensland: Blumberg [Birdwood]).

Host plants. Unknown.

Material examined. *J. grisea*: 3 males, Australia, ASCU, JRJ_Led1_066–068.

Remarks. Males of *Jukaruka* and *Ledropsella* are very similar. Specimens of *Jukaruka* can be distinguished by their lower median longitudinal pronotal crests (Pl. 8B_3) and larger, more open faces, with the crown margin further from the frontoclypeus anterolaterally (Pl. 9D) and the frontoclypeus less convex. *Jukaruka* may be slightly larger also—the *J. grisea* specimens were all 9.5-10 mm in length, while a new undescribed male of *Ledropsella* (see remarks for *Ledropsella* below) was at most 9 mm in length (its wing apices were torn off). The only known female of *Ledropsella* is even smaller, 6 mm in length

Females of *Jukaruka* are unknown. No females of *Jukaruka* were described by Evans (1966, 1969), and all the specimens provided by the ASCU for this study were males of the species *J. grisea*. It will be very interesting to see if females of *Jukaruka* resemble those of *Ledropsella* in having shorter subovoid wings (Pl. 2E) when female specimens are finally collected and described.

Genus *Kuohledra* Cai and He

Kuohledra Cai and He, 1997: 8, 14.
Type species. *K. kuohi* Cai and He, 1997: 8, 14, fig. 1, A–N, by original designation.
Synonymy. None.

Description. Cai and He (1997): "Medium or large leafhoppers. Body elongate, parallel-sided, coarsely granulate and punctate. Colouring brownish. The anterior margin of head foliaceous. Vertex obtusely angulate and obliquely angulate in front of eyes, surface nearly smooth and deflected on each side. Eyes very prominent. Ocelli placed on the transect of anterior margins of eyes, nearer to each other than to eyes, with a crescent impression on each outside. Face concave, frontoclypeus long and narrow, antennal ledges and pits distinct. Pronotum transverse, gradually arising from anterior to posterior margins, strongly deflected on each side, disk in basal part convex, anterior margin slightly curved, lateral margin diverging caudad, posterior margin distinctly insinuated medially. Scutellum small, the basal angles and anterior half moundly prominent, disk concave. Tegmina subhyaline with a knob on middle, reticious and prominent veins with scattered granules, the base of 1st claval vein crestiformly prominent. Metathoracic tibiae usually not foliaceously dilated. Posterior margin of 7th or 8th tergite medially insinuated. Pygofer with a shoehorn-shaped process. Subgenital plate pod-shaped. Style long and narrow, usually with a process near tip. Aedeagus long and curvate, shaft tubulose, subterminal ampliate with a pair of well developed processes, phallotreme on the dorsal surface."

Species. [3]: *kuohi* Cai & He; *zhaoi* Cai & He; z*hengi* Cai & He.

Range. China.

Host plants. Unknown.

Material examined. None.

Remarks. The type specimen of *Kuohledra kuohi*, deposited in the Institute of Zoology, Chinese Academy of Sciences (Academica Sinica), Beijing, was unavailable for examination. Cai and He (1997: 14) explained that *Kuohledra* differs from *Funkikonia* in the former having a "nearly smooth crown and strongly elevated pronotum". These character state differences seem reasonably simple to interpret initially; however, when specimens of *Ledropsis* are also considered, clear differentiation becomes difficult. Many specimens of *Ledropsis* often have a nearly smooth crown and strongly elevated pronotum.

Because Kato (1931) did not specifically provide diagnostic features to differentiate *Funkikonia* from *Ledropsis*, differentiating *Kuohledra* from *Funkikonia* on the basis of two features that are common in *Ledropsis* means possibly misidentifying a specimen of *Ledropsis* as *Kuohledra*, and vice versa.

Both *Kuohledra* and *Funkikonia* possess a large tubercle in the center of the forewing. Cai and He listed the "knob" (tubercle) in the center of the wing as a diagnostic character for *Kuohledra*, but Kato did not for *Funkikonia*. Kato did, however, give it for *F. tuberculata*, its type species. The possession of this tubercle, and distinct textures associated with it (see 'Remarks' under description for *Funkikonia* above), may serve as better diagnostic features to separate out *Kuohledra* and *Funkikonia* from *Ledropsis*; further examination of specimens is necessary to be sure.

Comparison of the male genitalia from the specimen presumed to *F. tuberculata* (JRJLed_449) with Cai and He's drawings for *Kuohledra* showed there to be a strong general resemblance, but a few differences. In Cai and He's drawings of *K. kuohi*, the inner, subapical, dorsomedial processes of the pygofer are less sclerotized and not hooklike, the apex of aedeagus is narrower, and it has a pair of well developed subapical processes. In the specimen of *F. tuberculata*, the inner subapical processes of the pygofer are more sclerotized and hooklike, the apex of the aedeagus is slighter wider in lateral aspect before narrowing, and the subapical processes are lacking.

The present phylogenetic analysis shows that even within a genus, the expression of textures on the dorsum and subapical processes on the pygofer can be rather labile. Across Ledrinae, and even in non-ledrines, the expression of subapical processes of the aedeagus can also be quite labile, although their presence or absence seems to be more conserved within a genus. While a possibility of plasticity of expression of the aedeagal subapical processes exists across the species in these two genera, utilizing the presence or absence of the processes as a diagnostic feature differentiating *Kuohledra* and *Funkikonia* seems reasonable, based on the few specimens and illustrations seen. But again, further examination of specimens is necessary to be sure.

Examination and comparison of the type specimens of *K. kuohi* and *F. tuberculata*, along with the other described species of *Kuohledra* and positively identified similar species of *Ledropsis*, will best answer this question, but obtaining these types and material for examination may not be possible. Until then, *Kuohledra* and *Funkikonia* may be treated separately and distinguishable by these genitalic features. Without examination of male genitalia, they will not key out separately.

Genus *Laticorona* Cai

Laticorona Cai, 1994b: 205, 208.
Type species. L. aequata Cai, 1994b: 205, 208, fig. 1, A–L, by original designation.
Synonymy. None.

Description. Cai (1994b): “The new genus…closely resembles to [sic] *Petalocephala* Stål, but differs in every element of the male genitalia, especially in the pygofer with apex bifurcated, the aedeagus with a pair [of] long processes, and the style with a long spin on apex, also by the pattern of the crown.”

Species. [2]: *aequata* Cai; *longa* Cai.

Range. China (Fujian: Sangang; Sichuan: Emei Mts; Zhejiang: Longquan: Fengyang Mt.).

Host plants. Unknown.

Material examined. None.

Remarks. Cai stated that the type specimen of *L. aequata* is located at the Anhui Agricultural College (now Anhui Agricultural University). It was unavailable for this study.

The aedeagal processes shown in Cai’s (1994b) illustrations are very unusual in that they arise from near the base of the shaft, close to the connective. They are flat, slender, and acuminate, and twist on their axis at midlength. It is not yet clear how much variation in aedeagal structure occurs within *Petalocephala*; among the specimens directly examined in this analysis, the subapical processes were short and flat (Pl. 16H_2), but illustrations of other described *Petalocephala* species shows a range of variation in subapical process expression. Those of the closely related genus *Neotituria* are situated medially and only somewhat flattened. Auxiliary processes were also observed rising from the base of the aedeagus in *J. grisea* and *Platyledra caldida* Evans, but those were interpreted to be different structures, the paraphyses; they are thick and medially articulated.

The phylogenetic independence of *Laticorona* from *Petalocephala* is uncertain. The shape of its head (narrowing in front of eyes), pronotum (shallowly curving between the eyes), and especially its face (unproduced inner margins of antennal pit, long and narrow frontoclypeus without distinct lateral muscle ridges, unproduced lora/genae) are like those of the genera in the *Petalocephala* genus group. At present, differentiation of *Laticorona* from *Petalocephala* appears to only be possible by dissection and examination of male genitalia.

Genus *Latycephala* McKamey

Latycephala McKamey, 2005: 506 (replacement name for *Platycephala* Kuoh).
Type species. *Platycephala tortilla* Kuoh, 1992: 251, 306, fig. 9, by original designation.
Synonymy. Platycephala Kuoh, 1992: 250 (type species *Platycephala tortilla* Kuoh, 1992:0251), preoccupied (by *Platycephala* Fallén, 1820).

Description. Ge (1992): "This genus most closely resembles *Petalocephala* Stål, but can be readily distinguished by the vertex of the head much shorter than breadth between eyes, the lateral margins of vertex arched, the anterior margin upturned and ventrally longitudinally carinate raised, by the basal area of face without a strong central ridge, the anteclypeus rectangle, especially in the pygofer, which has a process, the aedeagus with long laminate processes in pairs and in the styli with some denticles near apex."

Range. China (Sichuan; Yunnan).

Species. [6]: *decussata* (Kuoh); *graminea* (Kuoh); *laminata* (Kuoh); *sanguineomarginata* (Kuoh); *tortilla* (Kuoh); *viridula* (Kuoh).

Host plants. Unknown.

Material examined. None.

Remarks. The type specimen of *P. tortilla* may be located in either The Institute of Zoology, Academica Sinica, Beijing, or in "Anhui Agricultural College", Anhui, China.

Kuoh (Ge 1992) stated that this genus is "near to" *Arenoledra* and *Petalocephala*. From Kuoh's drawings, the key features distinguishing *Latycephala* seem to be the crown being shorter than the distance betwen the eyes, the presence of denticles on the styli, and the highly developed paired processes of the adeagus. This genus seems to be very similar to *Arenoledra* Kuoh and *Midoria* Kato.

McKamey (2005), when he provided the replacement name *Latycephala*, appears to have omitted two species included by Ge (1992) in *Platycephala* as new combinations. Their corrected new combinations follow.

Latycephala sanguineomarginata (Kuoh [Ge in Chen, 1992]), NEW COMBINATION.

Synonymy. Petalocephala sanguineomarginata Kuoh 1985: 273, 278, new species; *Platycephala sanguineomarginata* (Ge, 1992: 254, 307), new combination.

Latycephala viridula (Kuoh [Ge in Chen, 1992]), NEW COMBINATION.

Synonymy. Petalocephala viridula Kuoh 1985: 274, 278, new species; *Platycephala viridula* (Ge, 1992: 254, 307), new combination.

Genus *Ledra* Fabricius

(Pl. 2C–D, 7F, 12C, H, 14C, 16G, 18J)

Ledra Fabricius, 1803: 24.
Type species. *Cicada aurita* Linnaeus 1758: 435, by subsequent designation of Latreille, 1810: 434.
Synonymy. Ledraria Rafinesque 1815: 121.

Description. Distant (1908): "Head with vertex laminate, transverse, obtusely angulate anteriorly and obliquely angulate in front of eyes; pronotum hexagonal, more or less longitudinally ridged, sometimes with laminate processes, anterior margin nearly straight, wider than the posterior margin which is deeply sinuate; scutellum somewhat small; tegmina coriaceous or semicoriaceous, the veins prominent; head beneath foliaceous before the face; posterior tibiae laminately widened, outwardly remotely dentate and ciliate. The foliaceously or laminately widened posterior tibiae and the laterally angulate vertex in front of eyes are distinctive characters of this genus."

Species. [48]: *arcuatifrons* Walker; *auditura* Walker; *aurita* (Linnaeus); *bilobata* Schumacher; *buschi* Schmidt; *cingalensis* Distant; *concolor* Walker; *conicifrons* Walker; *conifera* Walker; *cordata* Cai & Meng; *depravata* Jacobi; *dilatata* Walker; *dilatifrons* Walker; *dorsalis* Walker; *episcopalis* Walker; *fumata* Ge 1992; *gibba* Walker; *hyalina* Kuoh & Cai; *imitatrix* Jacobi; *intermedia* Distant; *kosempoensis* Schumacher; *laevis* Walker; *lamella* Kuoh & Cai; *lineata* Walker; *longifrons* Walker; *muda* Distant; *mutica* Fabricius; *nigra* Ge 1992; *nigrolineata* Kuoh & Cai; *obtusifrons* Walker; *orientalis* Ôuchi; *pallida* Kuoh & Cai; *planifrons* Walker; *punctata* Walker; *quadricarina* Walker; *ranifrons* Walker; *reclinata* Distant; *rubiginosa* Ge 1992; *rubricans* Ge 1992; *rugosa* Walker; *serrulata* Fabricius; *solita* (Walker); *sternalis* Jacobi; *sublata* Distant; *truncatifrons* Walker; *tuberculifrons* Walker; *viridipennis* Latreille.

Range. Bhutan; China (Nauking; Shanghai; Sichuan: Mt. Omei; S. Kwangtung; South Manchuria; Sozhou; Tibet); Europe (widespread); Guinea (Seredou); India (Amatti; Assam; Bangalore; Chabus; Coimbatore; Goa; Kerala; Maharashta; Mysore; Punjab; S. Coorg); Indonesia: Borneo (Pontianak), Java (Tjiangsana: Mt. Djampang), Sumatra (Brastagi); Japan (Fujiyama; Mt. Tanzawa; Nagoya; Nikko; Shimabara; Takayama; Tokyo; Unzen); Malaysia (Perak); Philippines (Luzon: Butuan, Los Banos, Mt. Makiling, Nueva Viscaya; Mindanao: Cotobato, Surigao); South Korea (Gangwon; Jeonlanam; Keumsan; L'Ile de Quelpart [Jeju-do]); Russia (Maritime Territory); Sri Lanka; Taiwan (Hassenzan; Hualien; Kao Hsiung; Ilan: Fu Shan; Nantou; Taitung); Thailand (Bangkok; Chalbadan; Lampoon; Khorat; Sahanpur); Union of Myanmar [Myanmar] (Myitkyina).

Host plants. *Quercus* spp. (Fagaceae); Pinaceae.

Material examined. *L. aurita*: 1 male, 1 female, Germany, NCSU, JRJ_Led1_076, 078, 1 male, 1 female, France, USNM, JRJ_Led1_075, 077; *L. auditura*: 1 male, Japan, NCSU, JRJ_Led1_071, 2 females, Japan, Russia, AMNH, JRJ_Led1_069–070; *L. mutica*: 1 male, India, BMNH, JRJ_Led1_074, 2 females, India, USNM, JRJ_Led1_079–080; *L. tuberculifrons*: 1 female, Indonesia (Java), MZLU, JRJ_Led1_073.

Remarks. *Ledra* is the oldest described and second largest genus in Ledrini (43 described species), and possibly the most widespread in distribution. It contains *L. aurita*, the only ledrine species found in Europe, where it is reportedly common. While one genus, *Funkikonia*, has been split from *Ledra*, as presently constituted its monophyly is not certain—*L. tuberculifrons*, for example, was placed separately from other *Ledra* in the present analysis. It is also certain that at least some of its described species are synonyms. Judging from the abundance of unidentified material made available by various collections for this study, additional species remain to be discovered and described. The genus merits revision.

As shown in the analysis above, the core group of species that constitute a monophyletic *Ledra* appears to be among the most derived groups within Ledrinae, and judging by its large number of species and wide distribution, it is also one of the most successful genera. This is of interest, because it would have begun to radiate later than other ledrine genera. Like many Ledrinae, *Ledra* is arboreal, and its close association with oaks and pines, common in the northern temperate regions of the Eurasian continent (and probably more so after the end of the most recent ice ages) may have facilitated its radiation there. The complete absence in Europe of Ledrinae besides *L. aurita* may be due to ice age glaciation events that wiped out other ancestral ledrine lineages less suited to colder temperatures.

The most conspicuous members of *Ledra* have ear-like projections off the pronotum, but not all do—most have either the outer (sublateral) or inner rows (submedial), or both, present on the pronotum (as do *Chatura* and *Eleazara*). These rows may be highly developed into “ears,” or reduced to thin carinae or even a line of tubercles. All members of the genus appear to have dark brown coloration and a dorsal surface with some or many bumps, swellings, and projections reminiscent of bark, and all seem to have foliaceous tibia. This camouflage may also have aided *Ledra* in its successful radiation.

Genus *Ledropsella* Evans
(Pl. 2E, 9E)

Ledropsella Evans, 1966: 101.
Type species. Platyledra monstrosa Evans, 1939: 45, fig. 17G, by original designation.
Synonymy. None.

Description. Evans (1966): "The face of the head is longer than wide and the labium reaches as far as the mesothoracic coxae. The ante-clypeus is pear shaped and the lora anteriorly concave and posteriorly convex. The front-clypeus, which is oval in shape, is margined by deep channel-like longitudinal depressions. The antennal pits are basin-like depressions and antennal ledges are obsolete. The crown of the head, which is equal in length to the pronotum, is spatulate. There is a median longitudinal carina which is raised into a small crest in alignment with the ocelli, which are on oblique prominences."

The pronotum, anteriorly, is in alignment with the crown and has 3 longitudinal ridges in line with those on the crown. It is raised posteriorly and has a median longitudinal crest. The propleura form overhanging flaps which partly enfold the face of the head. The scutellum is anteriorly flat and raised posteriorly. The tegmina, which are broadest beyond the apex of the claval suture, have reticulate venation. The tibiae of all 3 pairs of legs are externally flattened, and the metathoracic tibiae are margined by a row of minute, even spines. The ovipositor does not extend beyond the folded tegmina."

Species. [1]: *monstrosa* (Evans).

Range. Australia (Western Australia: King George's Sound, Midland).

Host plants. Unknown.

Material examined. *L. monstrosa*: (type specimen) 1 female, Australia, ASCU, JRJ_Led1_087; *Ledropsella* sp. 1 male, labeled as *Jukaruka grisea*, Australia, ASCU, JRJ_Led1_088.

Remarks. *Ledropsella* is monobasic, previously known only from the type specimen (a female), which was made available for this study. It was in very poor condition, being completely covered in fungus. Despite this netlike covering, nearly all of the important features could be seen, including the shape of the crown and pronotum.

In describing *Ledropsella*, Evans (1966: 101) stated that it differs from *Platyledra* "particularly in the shape of the pronotum." He did not say, however, how it differs from *Jukaruka*, with which it is more similar (and with which it came out as sister group in the present analysis). From comparison of the type specimen of *L. monstrosa* with specimens made available for this study of *J. grisea*, *Ledropsella* appears to be distinguishable by several features. First, the median longitudinal carina on its pronotum is raised at its most dorsal point to a small but high crest, higher than that of *J. grisea*. Second, its face is smaller, with the margins of the crown drawn in close to the frontoclypeus (Pl. 9E). In *L. monstrosa*, the proximity of the crown margin to the convex and almond-shaped frontoclypeus (Pl. 9E_2) results in the lateral margins forming deep invaginations or "channels". These diagnostic features can be extracted from Evans' (1966) description. Also, in *L. monstrosa* the outer margin of the crown is carinate, and the inner margin is subcarinate, giving the impression that in cross section the margin is thickened and quadrate (Pl. 9E_3), while the margin of *Jukaruka* is thinner and not quadrate (Pl. 9D_1). This difference is of uncertain phylogenetic importance.

A single specimen (JRJ_Led1_088) among four males from the ASCU labeled as *J. grisea* keyed to *Ledropsella* (Fletcher 2006)* by virtue of its pronotal crest. Further examination showed that it also exhibited the facial features of *Ledropsella*, and appears to be a new species for the genus, the first male observed. It differed from the type specimen of *L. monstrosa* in size (it was approximately 9 mm long, while *L. monstrosa* was 6 mm), coloration (*L. monstrosa* is darker overall, with a pattern of lightly colored nodules and spots on the faces between setal rows 2 and 3 of the foliate tibia) and wing shape (*L. monstrosa*'s wings are shorter and subovoid—see Pl. 2E), in which it was more like the *J. grisea* specimens. From comparison of these two specimens, the differences in size and color appear to be phylogenetically insignificant at the intrageneric level. It also appears that wing shape is a sexually dimorphic character in the genus. The terminalia of this new male was not dissected for this study and will be described in a future publication.

Considering the fact that ledrine males tend to be shorter and more compact than females where sexual dimorphism exists, males of *L. monstrosa* must be among the smallest in size of the highly derived, reticulate-winged brown ledrines. To this end it will be very informative to capture in a single sample conspecific males and females.

*Photographs of *Ledropsella* in the "Identification Key and Checklists for the Leafhoppers and Treehoppers of Australia and neighbouring areas (Hemiptera: Cicadellidae, Membracidae)" (Fletcher 2006) appear to be of an undescribed male (elongate crown and parallel-sided wings), and possibly a species different than the type specimen—perhaps the same as the new male specimen discussed here.

Genus *Ledropsis* White

(Pl. 2F–G, H–I, 8C, 15G–H, 18I)

Ledropsis White, 1844: 425.
Type species. *L. cancroma* White, 1844: 425, by monotypy.
Synonymy. Scaphocephalus Matsumura, 1905: 52 (type species *Petalocephala discolor* Uhler, 1896: 290).

Description. Adapted from Evans (1966): The face of the head is concave and the labium, which is short and proximally, together with the prothoracic coxae, sunk below the level of the mesosternum, projects at right angles to the head. The maxillary plates overlap the anteclypeus antero-laterally and the slightly swollen lora slope inwardly. The antennae are situated on the posterior margins of deep lateral depression. The crown is convex with an obscure central ridge and is widest across the eyes. The eyes protrude beyond the margin of the head and the ocelli are closer to each other than to the eyes on each side. The pronotum is collar-like and raised posteriorly. The venation of the tegmen is distally reticulate. The tegmina of male insects are parallel-sided; those of females are wider at the apex than at the base. The tibiae are flattened and parallel-sided; metathoracic tibiae somewhat foliaceous. Metathoracic tarsomere I long, setose.

Species. [19]: *angularis* Distant; *cancroma* White; *crocina* Distant; *discolor* (Uhler); *froggatti* Distant; *koreana* (Matsumura); *lutescens* Distant; *maculata* Distant; *naso* Walker; *obligens* (Walker); *producta* (Melichar); *punctulata* (Melichar); *quinquepunctata* Bierman; *rubromaculata* Laidlaw; *singalensis* Distant; *takasagona* Kato; *testacea* Distant; *umbrata* Cai & Kuoh; *wakabae* Kato.

Range. Australia (New South Wales; Queensland: Burleigh, Landsborough); China (Fukien Province; Guizhou Province: Wongmo Co.; Hong Kong; Manchuria [Manchukuo]); East Malaysia (Sabah [British North Borneo]); India [Hindustan] (Bengal; Bihar; Chennai [Madras]; Kodagu [Coorg]; Orissa; Sikkim); Indonesia (Java; Sumatra); Japan (Honshu; Kamakora; Kyushu; Mt. Hukumi; Shikoku); Korea; Philippines (Palawan); Republic of Singapore [Singapore Island]; Sri Lanka [Ceylon]; Taiwan.

Host plants. Unknown.

Material examined. *L. discolor*: 1 male, Japan, USNM, JRJ_Led1_94, 1 male, Japan, ASCU, JRJ_Led1_93, 2 females, Japan, NCSU, JRJ_Led1_089–090; *L. froggatti*: 3 males, 3 females, Australia, USNM, JRJ_Led1_091–092, 095–098; *Ledropsis* sp. 1: labeled as *Confucius* sp., 2 males, Philippines, USNM, JRJ_Led1_038–039.

Remarks. *Ledropsis* is among the larger genera of Ledrinae, with 18 described species. Like *Petalocephala* and *Confucius*, many of its species exhibit simplified morphologies—i.e, lacking projections or conspicuous textures on the crown, pronotum, and wings—whereas other members have such armature. Kato (1931) and Cai and He (1997) have described genera very similar to *Ledropsis* (see earlier discussions of *Funkikonia* and *Kuohledra*) that possess a few slight differences.

It is probable that *Ledropsis* is polyphyletic and that some of its species belong in other genera. For example, the type species of *Ledropsis*, *L. cancroma* (not available for examination), is probably part of the Indomalayan fauna, while *L. froggatti* clearly belongs with the separate Australian fauna. Two other *Ledropsis* species in the analysis, *L. discolor* and one unidentified species of *Ledropsis* (incorrectly labeled as *Confucius* sp.) were placed with *Funkikonia* and *Ledra* in the present analysis, both part of the Indomalayan fauna. *Ledropsis* appears to be primarily Indomalayan.

The species *L. froggatti* seems to be part of a group with *E. primitiva* and *Porcorhinus* (Figs. 1–3), and should be removed from *Ledropsis* at some point. Its exact placement within the Australian fauna remains uncertain (see remarks for *Ezrana* above). *L. crocina* (only briefly examined—see remarks for *Ezrana* above) shares many similarities with *L. froggatti* and should probably also be removed. Though these removals considerably shrink the range of the genus (eliminating it from Australia), *Ledropsis* still has a wide distribution. It may be part of an older lineage from which the Australian clade is derived (nodes 27, 30, Fig. 3). A revision of the genus may answer this question, and is necessary to make any conclusions.

Distant (1908) believed *Confucius* was allied to *Ledropsis*, but differed in the crown not being longer than the breadth between the eyes. In the instance of *Ledropsis discolor*, this difference is void, as males have short angulate crowns, while females have long curved ones. Kato (1931: 436—footnote) first pointed out the similarity between Distant’s definition for *Confucius* (vertex not longer than breadth between eyes, sinuate lateral margins) and the male of *L. discolor*, but concluded that the genera were different because in the female of *L. discolor*, the vertex is “distinctly longer than the breadth between [the] eyes.” However, sexual dimorphism seems to exist in some species of *Confucius* as well. *C. cameroni* males (Pl. 1C) strongly resembles *L. discolor* (Pl. 2F) males in the truncated and angulate shape of the crown (and, incidentally, in the overall color patterning and texture). Linnavuori (1972: 207—see “Remarks” for *Confucius*) may have solved the confusion by observing important and useful differences in the metathoracic tibia and metathoracic tarsomere I; he regarded *Ledropsis* and *Confucius* as separate genera; however, he did not examine the type species of *Confucius*. Representatives of the type species for both genera were also unavailable for this study, making final delineation here difficult.

In light of the absence of type material, the data from non-type material, and the probability that types will not be found, it seems useful to accept Linnavuori’s features of metathoracic tibia shape and metathoracic tarsomere I length as diagnostic for differentiating *Ledropsis* and *Confucius*. Based on Linnavuori’s concept of *Confucius*, then, some its members may need to be moved to *Ledropsis*, and some species of *Ledropsis* may need to be moved to *Confucius* or to other genera. At this point, *Ledropsis* seems to be primarily an Indomalayan genus, and *Confucius* primarily an African one, with some members extending across southern Asia into India and Sri Lanka.

Genus *Midoria* Kato

Midoria Kato, 1931: 439.
Type species. M. capitata Kato, 1931: 439, fig. 1, by original designation.
Synonymy. None.

Description. Kato (1931): “Closely allied to *Daimachus* DIST, but differs as follows: —Vertex of head at base twice as broad as long, anteriorly obtusely pointed, the lateral margins truncate, base convexly sinuate, frons about as long as broad, somewhat prominent; ocelli placed middle of vertex, nearer to each other than to eyes and just on a line drawn through the anterior margin of eyes; pronotum convex, about twice as long as vertex, slightly broadened posteriorly; scutellum triangular, at base about as broad as long; posterior tibieae somewhat widened, outer edge neither expanded nor foliaceous, outwardly strongly spinose.”

Species. [3]: *annulata* Cai & Jiang; *capitata* Kato; *hei* Cai & Jiang.

Range. Taiwan (Koshun [Kankau])

Host plants. Oak (*Quercus* sp.).

Material examined. None.

Remarks. Kato’s remark that *Midoria* is closely allied to *Daimachus* (not available for examination) is probably misleading—*Daimachus* is currently placed in the Ulopinae (Oman *et al.* 1990). While ulopines and ledrines share many characters (reduced leg spinulation, crown sometimes produced or flattened, texture of the dorsum sometimes punctate), they are clearly distinct from one another. Kato's characters (ocelli position, metathoracic tibia) and illustration for *Midoria* suggest it is a ledrine, perhaps proximate to *Hangklipia* or *Parapetalocephala*.

The location of the type specimen for *M. capitata* is unknown.

Genus *Neotituria* Kato

(Pl. 2J, 14D, 18K)

Neotituria Kato, 1932: 220.
Type species. Ledropsis kongasana Matsumura 1915: 173, by original designation.
Synonymy. None.

Description. Kato (1931): "Closely allied to *Tituria* Stål, but differs from it by the posterior lateral angles obtusely angulated."

Species. [1]: *kongosana* (Matsumura).

Range. China (Chi Kiang: Hangchow, Mokansan; Guizhou; Kwangtung; Szechwan: Yachow; Tianjin); Japan; Korea (Posaksa Keumsan); Russia (Maritime Territory); Taiwan (Hualien: Tayuling; Kaohsiung; Nantou: Meifeng, Sungkang; Tsuifeng).

Host plants. Leguminaceae.

Material examined. *N. kongasana*: 1 male, China, CAS, JRJ_Led1_105, 1 female, Russia, AMNH, JRJ_Led1_106, 1 female, China, NCSU, JRJ_Led1_110, 2 males, 2 females, Taiwan, TARI, JRJ_Led1_107–109, 111.

Remarks. *Neotituria* is monobasic; however, many species recently described in *Tituria* (Cai and Li 1995; Ge, 1992: 247–249, 305–306) probably belong to it. *Neotituria* appears to be an exclusively Oriental lineage distinct from *Tituria* in general body form, and should be redescribed when more species can be properly associated with *kongasana*. Among the numerous *Neotituria*-like specimens made available for this study from various collections (many identified as *N. kongasana*), many subtle variations were seen in body size and color (some have beautiful, two-toned, green and brown wings). Examinations of male genitalia seems critical for making proper identification, and probably many new species remain to be described.

Genus *Paraconfucius* Cai

Paraconfucius Cai, 1992: 266.
Type species. P. pallidus Cai 1992: 266, 268, figs. 1–9, by original designation.
Synonymy. None.

Description. Cai (1992): "This genus is closely allied to *Confucius* Distant, from which it may be separated by the following characters 1) crown broad and short, median length less than one-half transocular width of head; 2) pronotum no[t] strongly foveate on each side behind anterior margin; 3) metathoracic tibiae slightly laminately widened; 4) style with a process near apex; 5) aedeagus slender, pipe-like, no larger apical process."

Species. [1]: *pallidus* Cai.

Range. China (Anhui: Yungusi of Mt. Huangshan).

Host plants. Unknown.

Material examined. None.

Remarks. *Paraconfucius* is monobasic. The type specimen of *P. pallidus* is deposited at Anhui Agricultural University, and was unavailable for this study. From Cai's description of the genus and drawings of *P. pallidus*, *Paraconfucius* appears to be more closely related to *Ledropsis* than *Confucius*, and may even be a synonym of *Ledropsis*. Examination of the type specimen of *P. pallidus* is necessary to be certain.

Genus *Parapetalocephala* Kato
(Pl. 2K, 18L)

Parapetalocephala Kato, 1931: 435.
Type species. P. montana Kato 1931: 435, fig. 2, by original designation.
Synonymy. None.

Description. Kato (1931): "Head shorter than breadth between eyes, centrally longitudinally convexly ridged, ocelli prominent, placed on disk and slightly nearer to each other than to eyes, subconically narrowed anteriorly, with the lateral margins in a line with the outer margin of the eyes, in front of each ocellus slightly hollowed; pronotum convex, with a very short longitudinal carination anteriorly, each side of which largely hollowed; scutellum distinctly shorter than pronotum, middle largely hollowed; tegmina narrow, veins prominent; frons and gena much prominent."

Species. [3]: *dimorpha* Kwon & Lee; *montana* Kato; *testacea* Cai & Kuoh.

Range. Taiwan (Chiayi Hsien: Alishan; Mt. Niitaka; Nantou Hsien: Tungpu; Taichung: Anmanshan; Tainan); Korea

Host plants. Unknown.

Material examined. *P. testacea*: 1 male, 1 female, Taiwan, TARI, JRJ_Led1_272–273; *Parapetalocephala* sp.: 1 female, Taiwan, TARI, JRJ_Led1_467.

Remarks. Two specimens of *Parapetalocephala testacea* were identified from material obtained from TARI, and were used in this analysis. A third unidentified specimen of *Parapetalocephala* from TARI was also briefly examined. The cells of the forewing appear to vary in their degree of depression between the two species examined, with *P. testacea* having more deeply depressed cells.

Genus *Petalocephala* Stål
(Pl. 3A–C, 10G, 11A, 13D, L, 16H, 19A–B)

Petalocephala Stål, 1854: 251.
Type species. P. bohemani Stål, 1854: 251, by original designation.
Synonymy. Pachyledra Schumacher 1912: 248 (type species *P. kamerunensis* Schumacher 1912: 249).

Description. Stål 1854 (as quoted by Distant 1908): "Body very oblong or a little elongate, depressed; head clypeated, foliaceously produced anteriorly; vertex somewhat flattened; face beneath eyes strongly and abruptly, thence gradually, narrowed, margins very slightly defined; front small, narrow, flattish; eyes small; ocelli situate towards base of vertex, farther removed from the eyes than from each other; pronotum transversely sexangular, not or only slightly anteriorly narrowed, the lateral margins acute, anterior lateral much longer than posterior lateral, anterior margin slightly rounded; scutellum triangular subequilateral; tegmina subcoriaceous, pellucid, densely punctate, tectiform, anteriorly conjointly convex, clavus very broad before the middle, corium obliquely rounded at apex, veins somewhat irregularly anastamosed towards apex; legs somewhat short, anterior coxa free, posterior tibiae remotely dentate."

Species. [89]: *adelungi* (Melichar); *alata* Evans; *arcuata* Cai & Kuoh; *armata* Evans; *bainbriggei* Distant; *aluchestanica* Dlabola; *bazarakana* Dlabola; *bicolor* Distant; *bipunctata* Melichar; *bohemani* Stål; *castanea* Kato; *cephalotes* Distant; *chlorocephala* (Walker); *chlorophana* Kuoh; *confusa* Distant; *conica* (Walker); *conspersa* Kuoh; *conspicua* Distant; *convexifrons* Schumacher; *cultellifera* (Walker); *declivis* Walker; *duodiana* Kuoh; *engelhardti* Kusnezov; *enigmoides* Evans; *eurglobata* Cai & He; *fasciifrons*

Melichar; *formosana* (Matsumura); *fuscomarginata* Cai & Kuoh; *fusiformis* (Walker); *glauca* (Melichar); *gonzalezi* Lindberg; *grandiosa* Dlabola; *granulosa* Distant; *hearsayi* Distant; *horishana* (Matsumura); *hornei* Distant; *insignis* Distant; *ixion* Linnavuori; *kamerunensis* (Schumacher); *kempi* Singh-Pruthi; *koshunensis* Schumacher; *latifrons* (Walker); *limbata* Evans; *manchurica* Kato; *nigrella* Evans; *nigrilinea* (Walker); *obtusa* Kuoh; *ochracea* Cai & Kuoh; *perakensis* Distant; *perductalis* (Kirby); *philippina* Stål; *pilka* Evans; *planata* Evans; *porrigens* Walker; *potanini* Melichar; *pullata* Evans; *pulsata* Evans; *punctatissima* Stål; *quadrimaculata* (Matsumura); *raniceps* Jacobi; *remota* (Melichar); *rubromarginata* Kato; *rubromarginella* Kuoh; *rufa* Cen & Cai; *rufomarginata* Kuoh; *sanguineomarginata* Kuoh; *scutellaris* Linnavuori; *signata* Distant; *skoba* Evans; *spicata* Evans; *stellata* Evans; *subacta* Walker; *subaquila* Distant; *tabulata* Distant; *taihorensis* Schumacher; *taikosana* Kato; *tenuifrons* (Walker); *trispicula* Evans; *turgida* Linnavuori; *umbrosa* Distant; *unicolor* Cen & Cai; *uniformis* Distant; *viridis* Cai & He; *viridula* Kuoh; *vittata* (Matsumura); *wahlbergi* Stål; *walkeri* (Melichar).

Range. Angola; Benin (Parakou); Bhutan; Cameroon; Central African Republic (Banqui; Kapou; Kivu; La Maboke); China (Hainan: Ta Hian; Guizhou: Pingtang Co.; Hong Kong; Kiangsi; Kwangtung); Congo (Dimonika; Elisabethville; Faradje; Flandria; Gorge de la Pelenge; Gwanga; Lulua: Kapanga; Ubangl: Bosobolo); Côte d'Ivoire [Ivory Coast] (Blekoun); Ghana; Guinea; India (Cherangode; Coimbatore; Kerala; Kodaikanal; Nedungadu; S. Malabar); Indonesia (Borneo: Kuching; Java: Batavia, Soekaboemi, Wijnkoopsbay; Sumatra: Mt. Simasopa, Prapat); Japan (Loochoo Island); Kenya; Liberia (Bomboma; Mt. Coffee; Suakoko); Mozambique (Delagoa Bay [Maputo Bay]); New Guinea (Wisselmeren); Nigeria; Philippines (Luzon: Butuan, Limay, Mt. Banahao, Mt. Makiling; Mindanao: Surigao; Negros: Dumaguete); Rwanda (Nduga); Singapore; Sudan; Taiwan (Heng Chun; Nantou Hsien: Howang, Jenai Chungyang, Meifeng, Mt. Po Jing Cha, Puli, Sungkang, Tungpu, Wushe; Pingtung Hsien: Kenting; Suisha; Taichung: Anmashan, Chingshan; Taitung: Yenping); Thailand (Chiang); Togo; Uganda (Ruwenzore); Vietnam (Hoa Binh); Yemen; Zimbabwe [Rhodesia].

Host plants. *Acoranthera schimperi* v. *deflersi* (Apocynaceae), *Indigofera oblongifolia* (Fabaceae), *Theobroma cacao* (Malvaceae).

Material examined. *P. bohemani*: 1 female, Indonesia (Java), BMNH, JRJ_Led1_116, 1 female, New Guinea, ASCU, JRJ_Led1_121, 1 female, New Guinea, BPBM, JRJ_Led1_291; *P. conspicua*: 1 male, Singapore, USNM, JRJ_Led1_187, 1 male, (location not given), MNHN, JRJ_Led1_132, 4 male, China, India, NCSU, JRJ_Led1_134–136, 138; *P. raniceps*: 1 female, Congo, OSUC, JRJ_Led1_130, 1 male, 1 female, Central African Republic, MNHN, JRJ_Led1_126, 131, 1 (abdomen missing), Nigeria, AMNH, JRJ_Led1_128, 3 males, 2 females, Côte d'Ivoire [Ivory Coast], Liberia, USNM, JRJ_Led1_123–125, 127, 129.

Remarks. *Petalocephala* is the largest genus (87 described species) in Ledrini and has a distribution almost as great as that of *Ledra* (except it is not found in Europe). Many of its species are indistinguishable except by dissection and examination of the male genitalia. It is probable that several of its described species are redundant. At present, the taxonomic limits of *Petalocephala* are not yet well understood (see discussion for *Destinia* Nast above).

In general body shape and with its quadrate (in cross section) non-foliaceous tibia, *Petalocephala* strongly resembles *Hespenedra* and *Rubria*. It is possible that its torpedo-like shape and reduced features represent an ancestral ground plan in Ledrinae, and that *Petalocephala* therefore represents a basal ledrine lineage. In some early phylogenetic analyses utilizing fewer characters and taxa (not shown), *Petalocephala* was, in fact, placed at the base of the Ledrini clade, closer to *Hespenedra* and *Rubria*. However, in the final analyses with all of the taxa and characters (Figs. 1–3), it was placed in a position as one of the most derived taxa within the *Petalocephala* genus group. Other features of *Petalocephala* actually display similarities with more derived taxa—in characters of the male genitalia, for example, some *Petalocephala* species are very similar to *Ledra*. Based on all the evidence assembled here, it seems more likely that the reduced features and shape of *Petalocephala*, *Hespenedra* and *Rubria* represent an ecologically generalized condition on which many ledrine (and non-Ledrinae) taxa have converged.

Petalocephala, which lacks lateral extensions on the pronotum, was placed as sister group to *Neotituria*, which retains the pronotal extensions, in the phylogenetic analyses (Figs. 1–3). It seems logical to hypothesize that lateral extensions from the pronotum are a derived condition in the *Petalocephala* genus group; however, this was not demonstrated in the analyses.

Genus *Petalocephaloides* Kato

Petalocephaloides Kato, 1931: 436.
Type species. P. laticapitata Kato, 1931: 436, fig. 7, by original designation.
Synonymy. None.

Description. Kato (1931): "Head large, vertex about as long as breadth between eyes, including eyes broader than pronotum, ocelli not prominent, placed on disk almost middle and slightly nearer to each other than to eyes, lateral margins gradually narrowed to apex, centrally longitudinally sulcate; pronotum about as long as vertex, more or less convex, central longitudinal carina wanting; scutellum centrally foveate; tegmina coriaceous, veins prominent, sparingly granulate."

Species. [1]: *laticapitata* Kato.

Range. Taiwan (Mt. Taihei; Mt. Taiko)

Host plants. Unknown.

Material examined. None.

Remarks. Kato's description of *P. laticapitata* is of a female. He made no examination of genitalia and no reference to leg or tarsal characters that might distinguish *P. laticapitata* from other closely related ledrine genera. It is possible that this species is a junior synonym of one in another genus, perhaps for which only a male has been described. The location of the type specimen of *P. laticapitata*, part of Kato's (1931) personal collection, is unknown.

Genus *Platyledra* Evans
(Pl. 3D–F, 10I, 16C–D, 19C)

Platyledra Evans, 1936: 39.
Type species. P. hirsuta Evans, 1936: 40, figs. 5a, 5b, by original designation.
Synonymy. None.

Description. Evans (1936): "The head is spatulate, narrowing apically to a point; dorsally it is convex, ventrally concave. The lateral sutures of the frons are deep, the lora depressed, and the clypeus small and pear-shaped. The maxillary plates are narrow. The ocelli are on the dorsal surface, well in front of the eyes, and are closer to the eyes on each side than to each other. There is a well-defined dorsal median longitudinal keel that extends on to the pronotum, and the head, which has in addition irregular small ridges on its dorsal surface, is wider medianly [sic] than across the eyes. The pronotum is collar-like and more or less rectangular, the tegmina are coriaceous, the veins raised in relief, and the venation reticulate. The metathoracic tibiae are flattened and spineless, each of the outer edges bearing a fringe of short hairs only. The ovipositor, which extends well beyond the apex of the folded tegmina, is concave ventrally and tectiform dorsally."

Species. [3]: *acuminata* (Distant); *caldida* Evans; *hirsuta* Evans.

Range. Australia (Queensland: Caloundra; South Australia: Ooldea; Victoria: Toolangi)

Host plants. Tomatoes (Solanaceae).

Material examined. *P. acuminata*: 1 female, Australia, ASCU, JRJ_Led1_142; *P. caldida*: 1 male, Australia, USNM, JRJ_Led_143; *P. hirsuta*: 1 female, Australia, BMNH, JRJ_Led1_144.

Remarks. Members of *Platyledra* are defined by their acuminate crowns and dorsoventrally depressed pronota bearing a single medial longitudinal crest. They form a monophyletic group (the *Jukaruka* genus group) with *Jukaruka* and *Ledropsella*.

Genus *Porcorhinus* Goding
(Pl. 3G)

Porcorhinus Goding, 1903: 38.
Type species. P. mastersi Goding, 1903: 38, pl. I, figs. 12, 15, 16, by original designation.
Synonymy. Gudwana Distant, 1917: 189 (type species *Gudwana typica* Distant 1917: 189).

Description. Goding (1903): "Head large, porrect, quadrangular, superior surface nearly horizontal, lightly convex and furnished with a strong median horizontal longitudinal carina; ocelli below a line passing through centre of the prominent eyes, nearer to each other than to the eyes. Prothorax, for some distance from the base, convex, nearly horizontal, conforming to the base of the porrect head, after which it is broadened, vertical, and produced above each lateral angle in a large, triquetrous, conical, ear-shaped horn, which extends upward, outward and forward, the apex turned a little backward; the dorsum is very broad between these horns, and destitute of a median longitudinal carina; destitute of a posterior process, the posterior edge deeply and broadly sulcate forward. Scutellum as long as broad, the apex pointed, base rounded. Tegmina long, broad, reticulate, with numerous venules; clavus very broad at base, gradually acuminate to apex, with two veins. Wings very large, nearly equal in size to the tegmina, with the four apical cells, the first and third very long, the second shortest. Legs very long, femora slender, cylindrical and curved; tibiae slender, quadrilateral, the posterior pair with a row of denticles along the posterior edge; tarsi normal."

Species. [1]: *mastersi* Goding.

Range. Australia (New South Wales: Springwood, Sydney; Queensland: Mt. Tambourine)

Host plants. Unknown.

Material examined. *P. mastersi*: 1 female, 1 (abdomen missing), Australia, ASCU, JRJ_Led1_145, 468.

Remarks. *Porcorhinus* is monobasic. It is at once recognizable by its prominent pronotal horns, as well as its smooth texture and deep yellow color (in dried specimens).

Porcorhinus appears to belong to a group of species within the Australian Ledrini that also includes *E. primitiva* and *L. froggatti* (which may deserve its own genus), united by the perpendicular keel (Pl. 18F_1) on valvulae II of the females, the subtrapezoidal shape of the posterior margin of the pronotum (Pl. 1H, 2H–I, 3G), and the absence of coronal setae.

Genus *Thlasia* Germar
(Pl. 3H–I, 10D, 14H–I, 16K)

Thlasia Germar, 1836: 71.
Type species. T. brunnipennis Germar 1836: 72, by original designation.
Synonymy. None.

Description. Linnavuori (1972): "Resembling *Tituria* but body smaller. Pronotum much less strongly protruding laterad, humeral angles only roundedly prominent, posterior margin distinctly insinuated. Side lobes rounded, ventral margin with a long appendage. Apophysis of stylus hook-shaped apically. Penis short, lamellate, without appendages, gonopore subapical on the ventral surface."

Species. [10]: *borealis* Jacobi; *brunnipennis* Germar; *cingulata* Jacobi; *corona* Linnavuori; *emmrichi* Zhang and Yang; *funebris* Jacobi; *jacobii* Zhang and Yang; *longicornis* Zhang and Yang; *obtusa* (Walker); *symmetrica* Jacobi.

Range. Cameroon (Nkolbisson; Yaounde); Central African Republic (Bangui; Boukoko; La Maboke); Congo (Stanleyville); China (Fujian [Fukien], Kuatun); Côte d'Ivoire [Ivory Coast] (Lamto); Gambia; Guinea (Friguiagbe; Nimba); Liberia (Suakoko); Nigeria (Gangare); Senegal (Casamance); South Africa (Cape of Good Hope; Cape Province: Assegaaibos, Grahamstown; Pirie Forest; Rustenburg); Tanzania (Kasulo Province: Buhoro Bunganda); Uganda (Kampala).

Host plants. Unknown.

Material examined. *T. brunipennis*: 1 male, South Africa, AMNH, JRJ_Led1_174, 3 females, South Africa, SANC, Led1_172–173, 175; *T. corona*, South Africa, BMNH, 2 males, JRJ_Led1_170–171; *Tituria obtusa*: 1 female, Liberia, USNM, JRJ_Led1_179, 1 male, 1 female, Gambia, Tanzania, MZLU, JRJ_Led1_180, 183, 2 males, 3 females, Central African Republic, Guinea, Côte d'Ivoire [Ivory Coast], Senegal, MNHN, JRJ_Led1_176–178, 181–182.

Remarks. *Thlasia* is similar to *Tituria*, but differs in having the pronotal extensions broad but not distinctly acute, and the forewings flexed downward at the second claval vein in one or both sexes. In the species observed (all African) the claval area is pigmented with a variably pink and cream-colored glossy texture. These features do not appear to be unique to *Thlasia*, however. *Proranus*, *Hespenedra*, and some species of *Petalocephala* all have wings strongly flexed at the second claval vein, and *Hespenedra* and several unidentified species of Ledrini (*Petalocephala*?) from Africa and China exhibit claval pigmentation.

Species recently described from China (Zhang et al. 2004), based on the wing venation, shape of the pronotum and male genitalia, appear to constitute a heterogeneous group. Some exhibit slight similarities to the African species in shape of the aedeagus or pronotum, but probably none of them belong within *Thlasia* as it is currently defined (*sensu* Linnavuori 1972). They may belong within any number of genera (possibly among the Oriental genera that have been weakly characterized), and appear to be more closely related to *Hangklipia* or *Parapetalocephala*.

Linnavuori (1972: 224) observed *T. obtusa* (Walker) to differ from other *Tituria*, placing it in its own monobasic species group within *Tituria*. In this analysis, *T. obtusa* was placed with *Thlasia corona* Linnavuori. While its aedeagus is more similar to those of *Tituria* and some *Petalocephala* species, the other phylogenetic data suggest it properly belongs with the *Thlasia* species, and it is here placed within *Thlasia* with the new combination given below. Range information above thus includes label data for *T. obtusa*.

Thlasia obtusa (Walker, 1851), NEW COMBINATION.

Synonymy: *Epiclines obtusa* Walker, 1851: 832 [not *Tituria obtusa* Kato, 1931].

Genus *Titiella* Bergroth

(Pl. 3K, 10C, 19I)

Titiella Bergroth, 1920: 29 (replacement name for *Titia* Stål).
Type species. Acocephalus punctiger Stål, 1855: 98, by original designation.
Synonymy. Titia Stål, 1866: 105 (type species *Acocephalus punctiger* Stål, 1855: 98), preoccupied.

Description. Linnavuori (1972): "Rather small, robust, yellowish species. Head a little broader than pronotum. Face in profile flattish both in upper and lower parts but remarkably convex in the middle; anteclypeus broadening apicad; frontoclypeus narrow, nearly parallel-sided in lower portion, triangularly tapering upwardly above the level of antennal pits, convex in the middle, sloping both dorsad and ventrad, postclypeus finely punctate, frons shiny and nearly impunctate; genae strongly notched below eyes, episternum therefore entirely exposed; area between eyes and frontoclypeus somewhat convex with a depression at antennal pits; antennae short. Crown triangularly produced, margins subacute but not foliaceous; disk strongly convex medially, concavely sloping laterad, irregularly punctate and rugose; ocelli a little behind the middle of the crown on either side of coronal suture. Pronotum with lateral margins slightly insinuated, disk remarkably convex basally, sloping apicad, rather coarsely and densely punctate, each puncture bearing a short seta. Scutellum small, punctate. Elytra coriaceous, rather finely and densely punctate, two closed subapical cells, only the 5th apical cell with a few extra cross veins. Structure of legs as in *Petalocephala*. Posterior margin of 7th sternite [of female] concave."

Species. [2]: *punctigera* (Stål); *humerosa* (Naudé).

Range. South Africa (Cape of Good Hope; Cape Province: Hankey, Keurboom River, Kougaberg, Stellenbosch; East Cape Province: Katberg; West Cape Province: Du Toitskloof Pass, Elim; Transvaal: God's Window)

Host plants. *Chondropetalum microcarpum*, *Ischyrolepis* sp. (Restionaceae).

Material examined. *T. humerosa*: 1 female, South Africa, BMNH, JRJ_Led1_201; *T. punctiger*: 1 female, South Africa, BMNH, JRJ_Led1_197; *Titiella* spp.: 3 females, South Africa, BMNH, JRJ_Led1_198–200, 7 females, South Africa, SANC, JRJ_Led1_196, 202–208.

Remarks. Linnavuori (1972) placed *Titiella* in Ledrinae after examining the facial sclerites, and considered it to be part of the "original Cape fauna". Among Ledrini, *Titiella* is unique in having a convex face. The facial shape and structure are roughly reminiscent of that of Afrorubria, in which the face is somewhat flat to convex, but not concave as in other ledrines. Specimens of *Afrorubria mitellata* Naudé and *Afrorubria* sp. from the SANC (not included in this analysis: Led1_320–344, 469–471) have the face somewhat convex and the margin between the frontoclypeus and the lora and genae weakly defined. These similarities with *Titiella*, however, appear to be due to convergence. Although *Titiella* seems similar to *Afrorubria* in the ways described, it was placed with *Hangklipia* in the present analyses, which Linnavuori stated was closer to *Thlasia* and *Petalocephala* based on the male genitalia. *Titiella* and *Hangklipia* are similar in size and overall shape, and they share several other features (see list of apomorphies in Table 3 of Appendix). It is possible, though, that their placement as sister taxa is an artifact of character sampling, namely due to a lack of characters of the male genitalia—males are undescribed for *Titiella* and were not found among material borrowed and examined for this study. Examination of males of Titiella could shed new light on the relationship between *Titiella* and *Hangklipia*.

Genus *Tituria* Stål

(Pl. 4A–B, 6F, 11B, 15D, 16A, B, L, M, 17I, 19J)

Tituria Stål, 1865: 158 [as subgenus *Petalocephala (Tituria)*, elevated to genus by Stål (1866)].
Type species. Petalocephala (Tituria) nigromarginata Stål, 1865: 158, by subsequent designation of Metcalf (1962b).
Synonymy. Epiclines Amyot and Serville, 1843: 577 (type species: *Membracis planata* Fabricius, 1794: 11, by monotypy), NEW SYNONYM. *Epiclinata* Metcalf 1952: 228, replacement name for *Epiclines* Amyot and Serville 1843: 577, preoccupied [by *Epiclines* Chevrolat, 1838] (type species: *Membracis planata* Fabricius, 1794: 11), NEW SYNONYM.

Description. Linnavuori (1972): "Resembling *Petalocephala* but body shorter and much robuster [sic]. Crown shorter, +/– triangular or pentagonal in outline. Pronotum very broad, lateral margins strongly diverging caudad, the triangular wing-shaped humeral lobes extending laterad much beyond elytra, body therefore strongly constricted at base of elytra. Anterior margins of pronotum nearly straight."

Species. [39]: *acutangulata* Distant; *angulata* (Matsumura); *antica* (Walker); *assamensis* Distant; *borneensis* Distant; *chersonesia* Distant; *chinensis* Distant; *clypeata* Cai; *colorata* Jacobi; *costalis* Jacobi; *crinita* Cai; *cuneata* Distant; *flavimacula* Cai & Shen; *flavomarginata* (Kuoh & Cai); *forficula* Linnavuori; *fusca* Cai & Li; *fuscipennis* Kato; *hebes* (Walker); *hyalina* Cai & Kuoh; *innotata* Cai & Li; *javanensis* Distant; *laboulbenii* (Signoret); *laticoronata* Cai; *lokandu* Linnavuori; *maculata* Kuoh; *nigricarinata* Kuoh; *nigrina* Cai & Kuoh; *nigrivena* Cai; *nigromarginata* (Stål); *obliqua* (Walker); *obtusa* Kato; *plagiata* Kuoh; *planata* (Fabricius); *pyramidata* Cai; *recta* Cai & Mo; *sativa* Cai & Shen; *timorensis* Distant; *virescens* Kuoh; *viridula* Linnavuori.

Range. Central African Republic (Boukoko; La Maboke); China (Guizhou: Guiyang City, Sinan Co.; Hainan: Liamui; Henan: Mt. Funiu; Shandong: Kungyushan, Taishan); Congo (Mayombe; Tshuapa: Ikela); India (Anamalai Hills; Calcutta); Gabon (Bas–Ogooué); Indonesia (Java: Mt. Djampang, Soekaboemi; Sumatra: Benkoelen); Japan (Okinawa); Laos; Malaysia (Borneo: Lebang hara; Island of Penang; Tebong); Singapore; South Africa (Durban; Natal: Umkomaas); Taiwan (Chipon; Eboshiyama; Ilan; Hualien Fuynan; Kaohsiung; Kueishan; Kuraru; Nantou Hsien: Howang, Jenai Yuaanfeng, Fenghuangku, Meifeng, Shanlinchi; Yuchih Lienhuachi; Pingtung Hsien: Chilushui, Kenting, Nanjenshan, Ouluanpi, Pishshieechao, Shantimen, Tsaopu; Roshan; Taipei: Yangmingshan; Taitung: Chihpen, Peinan Lichia, Taien Tupan, Yenping); Thailand (Chiang; Krabi; Mewah Valley; Metah Valley); Vietnam (Chapa: Tonkin; Hoa Binh).

Host plants. Unknown. The very flat, diamond-shaped nymphs have been seen by the first author on dark green leaves of woody shrubs.

Material examined. *T. antica*: 2 males, 2 females, South Africa, SANC, Led1_184–187; *T. forficula*: 1 (abdomen missing), Congo, AMNH, JRJ_Led1_192, 3 females (including type specimen—195), Central African Republic, MNHN, JRJ_Led1_193–195; *Tituria* sp.: 2 males, 2 females, China, Japan, Taiwan, NCSU, JRJ_Led1_188–190, 192.

Remarks. Metcalf, in his Catalogue (1962b), recognized the monobasic genus *Epiclinata* with type species *Membracis planata* Fabricius, 1794. He had earlier (1952) given the name *Epiclinata* as a replacement name for the genus *Epiclines* Amyot & Serville, which was preoccupied by *Epiclines* Chevrolat, 1838. It appears, however, that neither Metcalf, nor any author before him, has properly fixed the type species of *Epiclines* Amyot & Serville according to the rules of the Code of Zoological Nomenclature, as explained below.

In 1843 Amyot & Serville gave *Ledra planata* (Fabricius) [*Membracis planata* Fabricius, 1794] as the sole representative (and thus type species by implicit monotypy) for their new genus *Epiclines*. However, in their description, they gave as an identifying character “prothorax incliné presque verticalement.” This feature matches the later described New World genus *Proranus* Spinola, 1850 (see Pl. 4J, 6C) but not the Old World species *M. planata* (Pl. 4B, 6F), a fact pointed out by subsequent authors (Stål 1865, 1866; Distant 1907, 1908). Amyot and Serville likely relied solely on Fabricius’ original description to identify their specimen, as no illustrations of *M. planata* appear to have been in existence at that time (Metcalf 1962b).

It is clear that Amyot & Serville misidentified a specimen, possibly of *Proranus*, as *M. planata*, but the exact species they had in hand when they made their identification is not known. In such cases of misidentification, previous versions of the Code required authors to submit a case in question to a committee of the Commission of Zoological Nomenclature for their judgment in assigning a type species. Neither Metcalf, nor any of several other authors who recognized *M. planata* as the type species of *Epiclines* (see Metcalf 1962b), applied to the Commission for such resolution.

The most recent version of the Code (Fourth Edition, 1999) provides for authors to subsequently fix the type species of a genus in the case of misidentification. Article 70.3 allows for two options: selecting the species indicated by the name chosen by the original author(s) (70.3.1), or selecting the taxonomic species actually described (70.3.2) The latter option assumes that an author knows which species was actually described by the original authors. In this case, the species is not known; thus, that path is not available. The former article becomes the only option. *M. planata* is here fixed as the type of *Epiclines* Amyot & Serville (and thus *Epiclinata* Metcalf). This accords with Metcalf’s earlier designation, which was performed without authority, and maintains stability with existing names (i.e., *Proranus*, *Epiclinata*).

In the phylogenetic analyses performed in this paper, *M. planata* has been demonstrated to belong in a clade with species of *Tituria*, and it is herein transferred to *Tituria*. *Epiclines* becomes the senior synonym for this genus, but as a junior homonym, is not available. *Tituria* is the next oldest name, and take priority. *Epiclinata* becomes a junior synonym of *Tituria*. *Epiclinata flavomarginata* Kuoh & Cai, 1992 is also here moved to *Tituria*.

Tituria is the third largest genus of Ledrini, and like *Petalocephala* and *Ledra*, has a broad distribution. Many of its recently described Asian species appear to belong in *Neotituria* (see remarks for *Neotituria*), but the phylogenetic limits of both genera have not yet been adequately established. *Tituria antica* (Walker), placed by Linnavuori (1972: 225) in its own monobasic species group within *Tituria*, strongly resembles members of *Thlasia* in aedeagal structure and was placed near to, but not with, *Thlasia* in the phylogenetic analysis (Figs. 1–3). *Tituria* needs to be revised, and with it *Thlasia* and *Neotituria*. A taxon-based (non-regional) species–level treatment of all members of the *Petalocephala* genus group is warranted.

Among the borrowed material of *Tituria* were some very large specimens, with one unidentified female from Gabon (MNHN collection) measuring 24 millimeters in length and being quite robust. Some unidentified females of *Ledra* from Sumatra measured 23.5 mm in length, but were not quite as robust. These are among the largest species of Ledrinae and Cicadellidae.

Tituria flavomarginata (Kuoh & Cai, 1992), NEW COMBINATION.

Synonymy: *Epiclinata flavomarginata* Kuoh & Cai, 1992: 136, new species.

Tribe Rubrini Jones, new tribe

Type genus Rubria Stål, 1865

Description. Medium to moderately sized leafhoppers. Crown texture acinose, without depressions or irregularities; crowns of males shorter, roughly pentagonal, in females longer, sometimes much longer than in males, more parabolic, sometimes much longer than in males, setae absent, longitudinal medial carina complete, marginal carina present or absent, short depressed groove immediately laterad of ocelli in some species, crown transversely cambered; head lamellate, face microtextured, dark pigmentation absent, overall concave but medially somewhat convex, anterolateral margins not especially foliate; frontoclypeus with depressed lateral margins; epistomal suture incomplete; lora/genae somewhat tumid; anterior tentorial pit a thin slit slightly open, adjacent to frontoclypeus. Pronotum devoid of depressions, transversely wrinkled, lateral carina absent, lateral margins angled, giving sides of pronotum a boxlike shape; head and pronotum moderately flexed ventrally at posterior margin of pronotum; proepisternum small, tab-like, underlapping genae; scutellum flat; forewing venation regular, veins not raised, setae on fore edge of forewing absent; pro- and mesothoracic tibia intermediately quadrate, mesotibia row II apical triangular patch of scalelike setae absent; metathoracic femur macrosetae formula 2 + 0, macrosetae mounted on a narrow, prominent base. Male genitalia: aedeagus slender throughout; apex of style flexed ventrally but not subsequently curving anterad; subgenital plates dorsoventrally depressed; pygofer with inner, subapical, dorsomedial processes. Female genitalia: ovipositor shorter than pygofer; basal arms of valvulae I connected by sclerotized bridge, texture strigate; valvulae II strongly sclerotized, first and second dorsal teeth absent; ten or fewer non-sclerotized dorsal teeth present.

Range. Australian region.

Ecology. Unknown, but presumably Rubrini are all arboreal. K. Menard (personal communication) reported collecting specimens on *Melaleuca* in New South Wales.

Remarks. Evans (1966: 96) conjectured that *Rubria* might appropriately be split from Ledrini into its own tribe, but he refrained from doing so until a study of Ledrinae from the African, Australian, and Oriental regions could be performed together. The present study confirms Evans' observation of *Rubria*'s distinctness within Ledrinae. Evans also stated that Ledrinae are essentially tropical, but that many of the Australian ledrines were endemic. All Australian ledrines, in fact, are endemic to the region, with the Rubrini being found primarily in Australia and Tasmania. A single species described from New Guinea (Evans 1969), was unavailable for this study, but from the description is of dubious placement. Evans (1966) stated that *Rubria* occurred in the Australian and Oriental regions; except for the New Guinea specimen, no material has been recorded outside of Australia or Tasmania.

Evans' hypothesis that the Ledrinae entered Australia from the North prior to the Tertiary isolation probably only applies to the Rubrini (see "Biogeographic considerations and fossil evidence" under Results and Discussion section above).

This tribe is monotypic, and includes *Rubria*.

Genus *Rubria* Stål

(Pl. 4E–G, 6D, 7C, 10A, 13E, 16J, 19D)

Rubria Stål, 1865: 158.
Type species. *Petalocephala (Rubria) sanguinosa* Stål, 1865: 158, by original designation.
Synonymy. Ledracephala Evans, 1947: 252 (type species: *Ledra brevifrons* Walker, 1851: 825).

Description. Evans (1966): "The anteclypeus narrows anteriorly and extends beyond the margin of the maxillary plates. The post clypeus widens progressively posteriorly as far as the antennae, which lie posterior to the eyes. The antennal depressions are basin-like and antennal ledges are lacking. An obscure epistomal suture is retained, and the frons, which is ill-defined, is either concave or raised medially. The crown of the head, which is longer in the male than in the female [error—vice versa], is spatulate and transversely convex, or widely tectiform, with a median longitudinal ridge. It may be as long or more than twice the length of the pronotum. The ocelli are nearer to each other than to the eyes. The pronotum is laterally wide and on a single plane (not humped posteriorly). The tegmina are steeply tectiform and have normal venation, sometimes with accessory costal veinlets. The metathoracic tibiae have 2 widely spaced spines mounted on prominent spurs and a row of evenly spaced long spines."

Species. [7]: *brevifrons* (Walker); *informis* (Kirkaldy); *ingens* (Kirkaldy); *rugosa* Evans; *sanguinosa* (Stål); *sidnica* (Stål); *smalei* Evans.

Range. Australia (New South Wales: Conan, Ebor, Mt. Kosciusko, New England, Sydney, Wilson's Valley; North Australia [=Northern Territory?]; Queensland: Birkdale, Brisbane, Cairns, Tambourine, Tibrogargen; South Australia: Peebinga; Victoria: Bendigo, Mount Donna Buang); New Guinea (Kassam); Tasmania (Lake St. Clair; New Norfolk).

Host plants. Some species collected in Malaise traps in *Nothofagus* (Nothofagaceae) and *Eucalyptus* (Myrtaceae) forests. *R. informis* reportedly collected (K. Menard, personal communication) on *Melaleuca* (Myrtaceae) in New South Wales.

Material examined. *R. brevifrons*: 1 male, 2 females, Australia, ASCU, JRJ_Led1_157–158, 163; *R. informis*: 1 male, Australia, USNM, JRJ_Led1_160, 1 male, 1 female, Australia, BMNH, JRJ_Led1_159, 1 male, 1 female, Australia, AMNH, JRJ_Led1_164; *R. sanguinosa*: 1 female, Australia, BMNH, 1 female, Australia, MNHN, 1 female, Australia, USNM, JRJ_Led1_166, 3 females, Australia, BPBM, JRJ_Led1_293–295, 1 male, 3 females, Australia, ASCU, JRJ_Led1_165, 450, 479; *Rubria* sp.: 1 male, Australia, BPBM, JRJ_Led1_292.

Remarks. Stål (1865) created *Rubria* as a subgenus of *Petalocephala* Stål, and Evans (1966) elevated it to generic rank.

Rubria is very similar to *Petalocephala* in shape and texture, but differs in having a slightly more convex face, smaller, more tab-like proepisterna, in the lateral carinae of the pronotum being absent, in the metathoracic femur apical macrosetae being mounted on a prominent narrowed base, and in the forewings having regular venation. It is among the oldest lineages in Ledrinae and appears to be the sister group to Hespenedrini + Ledrini.

Tribe Xerophloeini

Type genus Xerophloea Fabricius 1803

Primary Synonymy. None.

Description. Medium to large leafhoppers. Crown flattened and spatulate, anterior margin foliaceous; ocelli on crown, closer to each other than to eyes, texture coarsely rugose or deeply punctate; face convex; frontoclypeus expanded and convex, visible in lateral view, with numerous punctuations; antennal pits weakly defined or absent, inner margins sometimes a thin carina adjacent to frontoclypeus; antennal ledges absent or present, if present, then as a thin anterior carina projecting forward only slightly and merging with the marginal carina of the crown; pronotum broad and usually distinctly elevated, often with distinct ridges, texture coarsely rugose or deeply punctate; forewing venation simple with cells well defined, appendix absent or present, but if present, generally broad and reaching completely around apex of wing; proepisternum exposed, large, long and narrow, or small and tab-like; metathoracic femur apical macrosetal formula 2+1; metathoracic tibia rows I and II with large macrosetae. Male genitalia: pygofer with or without apical setal patch; aedeagus often with laterally compressed and more-or-less triangular dorsomedial lobe, long and slender apically, often curving dorsad. Female genitalia: valvulae II long and very slender, moderately sclerotized.

Range. Nearctic and Neotropical regions.

Ecology. Generally associated with grasses, although the first author has collected *Proranus* in mixed forbs on steep, tree-covered hillsides, above streams in south-central Guatemala. Lawson (1931) noted that members of *Xerophloea* are occasionally abundant in an area, and Oman (1949) suggested that during those times, *Xerophloea* might constitute a forage pest. Some species of *Xerophloea* may be vectors of plant disease (Nielson 1962).

Remarks. *Xerophloea* Germar was placed in its own subfamily by Oman (1943), and Evans (1947) was the first to include it in Ledrinae. Later (1949), Oman elevated it to tribal level within Ledrinae. Szwedo (2002) considered this tribe to include a number of genera, namely *Proranus*, *Xerophloea*, *Pariacaca*, *Hespenedra*, *Xedreota*, and possibly *Clinonana*, but he gave no characters uniting the group. In this analysis, *Hespenedra* and *Clinonana* are shown to not belong within Xerophloeini, while *Proranus*, *Xerophloea*, and *Xedreota* do. *Pariacaca*, though not examined, appears from Szwedo's drawings and description to also belong in Xerophloeini. *Piezauchenia* Spinola 1850, included in Xerophloeini by Linnavuori (1959), was not available for examination, and its placement is here considered *incertae sedis* within Cicadellidae. The extinct genus *Paracarsonus*, treated above in "Biogeographic considerations and fossil evidence" under Results and Discussion section, is also herein recognized to belong to Xerophloeini.

Though distinct in many ways, Xerophloeini share many features with other Ledrinae and especially some herein newly recognized members of Afrorubrini. *Xedreota* and "Genus 4" have distinct similarities (see discussion for *Xedreota*), as do *Xerophloea* and one undescribed afrorubrine genus ("Genus 3" in phylogenetic analysis). In general, Afrorubrini and Xerophloeini share valvulae II being long and slender and intermediately sclerotized, with two dorsal teeth and other supernumerary teeth. *Proranus*, *Xedreota*, *Xerophloea*, Genus 2, Genus 3, and Genus 4 all share punctuations on the frontoclypeus, and the frontoclypeus being expanded and convex with the anterior foliaceous portion of the crown short.

The following genera are herein included in Xerophloeini: *Paracarsonus*, *Pariacaca*, *Proranus*, *Xedreota*, and *Xerophloea*. The extinct genus *Paracarsonus* is not treated here.

Key to the genera of Xerophloeini

1a. Pronotum flat or only slightly humped in lateral view 2
1b. Pronotum strongly arched forward or humped in lateral view 3
2a. Forewing with broad appendix, overall color green .... *Xerophloea*

2b. Forewing without broad appendix, overall color brown .... *Xedreota*
3a. Dorsum of crown nearly horizontal .... *Pariacaca*
3b. Dorsum of crown strongly declivous .... *Proranus*

Genus *Pariacaca* Szwedo

Pariacaca Szwedo, 2002: 155.
Type species: *P. icanoensis* Szwedo, 2002: 155, 158, figs. 1–18.
Synonymy: None.

Description: Szwedo (2002): “Diagnosis: In general appearance similar to the genera *Xerophloea* Germar, 1839 and *Proranus* Spinola, 1850, but distinctly smaller than *Proranus* Spin. Head, in lateral view, declivent toward apex, face not horizontal (in *Xerophloea*, if declivent—then less). Vertex convex, with distinct mediolateral carinae and anteriad [sic] transverse carina (transverse carina absent in *Xerophloea*), median carina not complete, present only anteriad [sic] of connection with transverse carina. Interocular width of vertex more than twice its mid-length (at most twice its mid length in *Xerophloea*). Anteclypeus protruding below the lower margin of genae. Pronotum distinctly inflated and declivent cephalad, with distinct median carina. Four stout setae on the plantar surface of metathoracic basitarsomere (three in *Xerophloea*). Lobe of pygofer angulately wide in median portion (rounded in *Xerophloea*), with three rows of stout thick setae and with a dozen or so, longer and more slender setae in lower portion.

“Description: Robust leafhoppers with head, pronotum, mesonotum and basal portion of tegmina with numerous circular pits, frequently with a short seta arising from center of each pit (figs. 1, 5, & 18). Head slightly narrower than pronotum, vertex with anterior margin rounded, in lateral view declivent toward apex, with distinct mediolateral carinae. Disc of vertex convex, with deep posteromedian concavity between lateral carinae and transverse anterior carina. Eyes well developed, ocelli on disc of vertex (fig. 1). Face in lateral view not horizontal, with frontoclypeus slightly swollen. Anteclypeus slightly swollen in upper portion, with lateral margins slightly diverging, then distinctly converging, lower portion of anteclypeus distinctly exceeding the line of lower angles of genae (fig. 2). Pronotum large, slightly wider than head, distinctly inflated almost from anterior margin (fig. 1). Tegmen with appendix extending around tegmen apex, venation distinct (fig. 5). Wings with venation pattern as in *Xerophloea*, with four apical cells (fig. 6). Male genitalia with pygofer lobes wide, with stout setae and fine chatae (fig. 12). Male genital plates elongate with fine chetae. Styles widened apicad, with obtusely angulate apex and small anteapical projection. Aedeagus laterally compressed, extreme base produced for attachment with connective, sub-basally broadened, tapered anteriorly to nearly tube-like apical part, slightly curved dorsad, gonopore apical (figs. 14–17).”

Range: Argentina (Chaco de Santiago del Estero: Rio Salado).

Species. [1]: *icanoensis* Szwedo.

Host plants. Unknown

Material examined. None.

Remarks. From Szwedo’s drawings, this genus is strongly allied to *Xerophloea*. The strongly expressed punctation, appendix on the forewings, metathoracic femur macrosetae formula, metathoracic tibia macrosetal rows, metathoracic tarsomere I shape, tuft of short stiff setae at the apex of the pygofer, narrow parallel-sided pygofer plates, and median dorsal lobe on the aedeagus support this relationship.

Genus *Proranus* Spinola
(Pl. 4J–K, 6C, 15B, I, 16I, 17F)

Proranus Spinola 1850: 122.
Type species. *P. ghilianii* Spinola 1850: 124, by original designation.
Synonymy: None.

Description: Kramer's (1966) description: "Moderate sized (9–12.5 mm.) robust, strongly convex leafhoppers whose outlines often approach a diamond shape; head always clearly produced beyond eyes with anterior margin acute to rounded, ocelli small on crown mesad of anterior edges of eyes, in lateral view with head strongly declivent toward apex, face horizontal, clypeus and clypellus clearly visible, suture between them concave, in facial view clypellus with margins usually bowed and narrowest apically, clypeus narrow with lateral sutures terminating slightly beyond antennal bases located just below margin of head away from eyes, both clypellus and clypeus convex, genae and lora comparatively narrow; pronotum always broadest posteriorly at humeral angles, in lateral view convex, declivent cephalad with lateral margin carinate; scutellum of moderate breadth and length; forewings long, broad, and punctate, punctures most numerous in opaque clavi, each puncture usually with a minute scale-like seta at center, often with extra veinlets distally, appendix well developed, and running from claval apex around distal margin to area of outer apical cell, forewings at rest excluding clavi held vertically; legs moderately stout with spines of metathoracic tibia less numerous than in usual leafhopper type; spinulation of metathoracic femur 2–1–0. Male genitalia: genital capsule partly withdrawn into abdomen with valve hidden by preceding abdominal sternum; pygofer shorter than plates, always with a cluster of stout setae on distal portion, mainly membranous dorsally; anal tube gross with first segment entirely sclerotized and large; plates elongate oval with hairs on dorsal portion; valve distinct; connective stout and elongate, styles flat, moderately long, with one apical lobe, lobe with a single small tooth on inner edge near apex; aedeagus stout, transverse, shaft narrowed, extreme base produced for attachment with connective, base produced dorsally as a wide, high, slightly anteriorly curved portion. Female genitalia: pregenital sternum long, longer than preceding two abdominal sterna, divided on median line to base and appearing as two lobes; ovipositors about as long as pygofer."

Species. [4]: *adspersipennis* Stål; *ambitus* Kramer; *ghilianii* Spinola; *infractus* Kramer.

Range: Bolivia; Brazil ("Para"); Colombia; Guatemala; Panama; Paraguay; Peru; Venezuela.

Host plants. Unknown.

Material examined. *P. adspersipennis*: 1 male, 2 females, Bolivia, Brazil, USNM, Led1_148–149, 156, 1 male, Panama, NCSU, JRJ_Led1_150; *P. ghilianii*: 1 male, Brazil, OSUC, JRJ_Led1_146, 1 male, 1 female, Columbia, Panama, JRJ_Led1_153–154, 1 female, Venezuela, USNM, JRJ_Led1_152, 1 male, 1 female, Paraguay, Peru, AMNH, JRJ_Led1_151, 155.

Remarks. See comments under "Remarks" for the genus *Tituria* in the tribe Ledrini, above. Oman (1949) appears to have been the first to place *Proranus* (=*Epiclines*) in Xerophloeini.

Members of this genus are very robust and treehopper-like, and specimens are sometimes found with unsorted Membracidae in collections.

Genus *Xedreota* Kramer

(Pl. 4L, 10E, 12D, 17J, 19K)

Xedreota Kramer, 1966: 495, figs. 70–73.
Type species. *Xerophloea tuberculata* Osborn, 1938: 16, pl. 4, fig. 23, by original designation.
Synonymy: None.

Description: Kramer: "Moderately large (8–9.5 mm.) robust leafhoppers; head produced beyond eyes but not strongly so, anterior margin carinate, ocelli on crown anterior to eyes, closer to midline than to lateral margins; in lateral view face oblique with clypeus and clypellus clearly visible; in facial view with clypeus and clypellus rather flat, genae broad, lateral frontal sutures terminating below apex of head mesad of and beyond antennal bases, antennae of moderate length and development, located in the upper inner edge of a broad depression between eye and clypeus; pronotum about as wide as head, anterior margin rounded, posterior margin oblique laterally and indented mesally, carinate laterally; scutellum about as broad as long; forewings long, moderately broad, variably punctate, without extra crossveinlets apically, appendix absent; legs moderately stout with spines of metathoracic tibia less numerous than in usual leafhopper type;

spinulation of metathoracic femur 2–1–1–1. Male genitalia, male unknown; female genitalia, seventh sternum longer than preceding segment and with ovipositors not extending much beyond pygofer.”

Species. [1]: *tuberculata* (Osborn).

Range: Brazil; Guyana.

Host plants. Unknown.

Material examined. *X. tuberculata*: 1 male, 3 females, Guiana, MNHN, JRJ_Led1_369–371, 373, 3 females, Guiana, USNM, JRJ_Led1_368, 372–373.

Remarks. See comments under “Remarks” for the genus *Tituria* in the tribe Ledrini, above. Oman (1949) appears to have been the first to place *Proranus* (=*Epiclines*) in Xerophloeini.

Members of this genus are very robust and treehopper-like, and specimens are sometimes found with unsorted Membracidae in collections.

Genus *Xerophloea* Germar

(Pl. 5A, 8E, 10F, 11D, 12E, 15C, 19L)

Xerophloea Germar 1839: 190.

Type species. *X. grisea* Germar, 1839: 190 (= *Cercopis viridis* Fabricius, 1794: 50), by monotypy.

Synonymy: *Mesodicus* Fieber 1866: 501 (type species *M. foveolatus* Fieber, 1866: 501). *Parapholis* Uhler, 1877: 461 (type species *P. peltata* Uhler, 1877: 461).

Description: Kramer (1966): “Small to moderate sized (4.5–8.9 mm.) robust, convex, leafhoppers; head slightly narrower than pronotum, variably produced beyond eyes with anterior margin acute to rounded, ocelli small on crown mesad of anterior edges of eyes, in lateral view crown highly variable, horizontal, upturned, or somewhat declivent toward apex, face oblique, clypeus and clypellus clearly visible, suture between them flat or slightly concave, in facial view clypellus tapering toward apex, clypeus narrow with lateral sutures terminating slightly beyond antennal bases located below margin of head away from eyes, both clypellus and clypeus usually slightly convex, genae and lora comparatively narrow; pronotum always broadest posteriorly at humeral angles, in lateral view highly variable from almost flat to strongly convex, usually somewhat declivent cephalad, lateral margin carinate; scutellum of moderate breadth and length; head, pronotum, and scutellum variably pitted; forewings long, moderately broad, and punctate, punctation variable but usually heaviest in opaque clavus and basally along costal margin, each puncture usually with minute scale-like seta at center, almost never with extra veinlets distally, appendix well developed and running from claval apex around distal margin to area of outer apical cell, forewings at rest tectiform; legs moderately stout with spines of metathoracic tibia less numerous than in usual leafhopper type; spinulation of metathoracic femur 2–1–0, but often appearing as 3–0–0. Male genitalia: genital capsule partly withdrawn into abdomen with valves concealed by preceding abdominal sternum, pygofer shorter than plates, always with a cluster of stout setae on distal portion, mainly membranous dorsally; anal tube large; plates elongate oval and often lightly hirsute; valve distinct; connective stout and elongate; styles flat, moderately long, with one apical lobe, lobe with a single small tooth on inner edge near apex; aedeagus stout, transverse, narrowing toward apex, extreme base produced for attachment with connective, base produced dorsally as a wide, high, slightly anteriorly curved portion. Female genitalia: pregenital sternum long, longer than preceding two abdominal sterna, divided on median line to base and appearing as two lobes; ovipositors about as long as pygofer.”

Species. [12]: *breviceps* Osborn; *cephalica* Oman; *difformis* Oman; *elegans* Oman; *elongata* Oman; *gigas* Oman; *magna* Oman; *majesta* Lawson; *major* Baker; *peltata* (Uhler); *robusta* Lawson; *viridis* (Fabricius).

Range: Nearctic and Neotropical.

Host plants. Poaceae.

Material examined. *X. viridis*: 2 males, 5 females, Jamaica, Puerto Rico, U.S.A., NCSU, Led1_214–219, 485.

Remarks. *Xerophloea* is widely distributed in the New World, with a few species being described from South America (Argentina, Brazil, and Guyana), and the type species being recorded from as far north as British Columbia and Massachusetts, across the Caribbean, and south to Tierra del Fuego. A record for *Xerophloea foveolata* (Fieber 1866) from Southern Europe (Metcalf 1962) is probably an error, as Szwedo (2002) has pointed out.

The last revision of *Xerophloea* was performed by Nielson (1962).

Taxa removed fom Ledrinae

The following taxa are here removed from Ledrinae: *Bascarrhinus*; *Betsileonas*; *Camptelasmus* Spinola; *Caxia* Melichar; *Clinonana*; *Cololedra*; *Eogypona* Kirkaldy; *Hemipeltis* Spinola; *Ledrocorrhis* Evans, *Ledromorpha*, *Ohausia*; *Piezauchenia*; *Platyhynna*; *Stenoledra*, *Turitia* Schumacher, Stenocotini, and Thymbrini.

Taxa placed incertae sedis within Cicadellidae

Bascarrhinus Fowler, 1898: 214. Type species: *B. platypoides* Fowler, 1898: 214, pl. 13, fig. 11, by monotypy. *Bascarrhinus* is very similar to *Platyhynna* in facial structure, genitalia, wing venation, and leg structure and shape. These two genera also have the R and M veins of the hind wing convergent, and may belong with the New World Iassinae. They were placed with *Krisna* Kirkaldy in this analysis (Fig. 1) with weak support (Bremer = 1), but not with *Iassus*. In many ways these genera were unlike any Iassinae examined (see “Phylogenetic results and discussion”). *Bascarrhinus* and *Platyhynna* are so unique that they together may deserve tribal or possibly subfamily status. Kramer’s assertion (1966: 477) that they “are closer to true *Ledra*…than any of the other New World genera on the basis of the habitus, forewing venation, and the reduced number of spines on the flattened metathoracic tibia” ignores obvious differences between these genera and *Ledra* (and all Ledrinae) in facial structure (wide and truncated frontoclypeus with a large pit anteriorly; prominent swollen inner antennal bars, and numerous other features) and genitalia (inverted genital capsule and several other features). *Bascarrhinus* is known from Costa Rica, Ecuador, and Panama. Material examined: *B. plathanon*: 1 male, 2 females, Costa Rica, Panama, USNM, JRJ_Led1_012–014; *B. platypoides*: 3 females, Panama, USNM, JRJ_Led1_009–011. Pl. 5B.

Betsileonas Kirkaldy, 1903: 13. [replacement name for *Thaumastus* Stål, 1864, and not *Thaumastus* Martens, 1860] Type species: *Ledra marmorata* Blanchard, 1840: 194, by original designation. *Betsileonas* is monobasic. The type specimen for *L. marmorata* is lost, but material was located in the MNHN for examination and was included in this analysis. The dorsal integumentary texture, forewing venation, postero-apical position of the forewing appendix, setal arrangements on the metathoracic femur and tibia, and shape of valvulae II are similar to some Penthimiinae, but its convergent R and M veins are a characteristic of Iassinae. Evans (1947) placed this genus in tribe Penthimiini in the subfamily Jassinae, but later (1954) included it under tribe Ledrini in the Ledrinae. This species, known from Madagascar, is very large (19 mm) and colorful. All museum specimens were in very poor condition and probably very old (a label on a single specimen gave the collection date as 1871). It appears to not have been recently collected, and may now be extinct. Material examined: *B. marmorata*: 2 females, 2 (abdomen missing), Madagascar, MNHN, JRJ_Led1_022–025. Pl. 5C, 13A, 18C.

Camptelasmus Spinola, 1850: 110. Type species: *C. caffer* Spinola, 1850: 111, by monotypy. Linnavuori (1972: 246) stated that the type specimen of *C. caffer* is lost, specimens are small, the ocelli are absent, and the taxonomic position is “obscure”. Until this holotype can be found, the phylogenetic position of *Camptelasmus* will probably remain unknown, and the genus is here removed from Ledrinae.

Caxia Melichar, 1924: 201. Type species: *C. projecta* Melichar, 1925: 359, by original designation. Melichar described the small genus (6 mm) *Caxia* from New Guinea but provided no illustrations. It is not certain if the type specimen of *C. projecta,* deposited in the “Mus. in Budapest” (HNHM?), still exists (inquiries made to the HNHM were not answered). *Caxia*’s phylogenetic position is unknown and it is here removed from Ledrinae.

Cololedra Evans, 1969: 744. Type species. *C. declivata* Evans, 1969: 744, fig. 2G-I, by original designation. The type specimen of *C. declivata* (from BPBM) was examined and included in this analysis (see “Phylogenetic results and discussion”) and was shown to not belong within Ledrinae. Its prominent antennal ledges and the shape of the head and face are reminiscent of *Coloborrhis* Germar, but *Cololedra* lacks a carinate and developed mesanepisternum, and does not appear to be a ulopine. In the strong flexure, deep wrinkling, and longitudinal ridge of the pronotum, the position of the ocelli on the front of the head, the extremely long hairlike setae covering its entire body, and the tibia having flat faces, it resembles some membracids (i.e., *Microcentrus*) and aetalionids. It differs primarily in the episternum being divided by a suture and in having rows of robust setae on the metathoracic tibia. The abdomen of the type specimen is missing, further making assessment of relationships difficult. Its placement is uncertain, and *Cololedra* is here removed from Ledrinae. The type specimen of *Cololedra* was collected in New Guinea. Material examined: *C. declivata*: 1 (abdomen missing—type specimen), New Guinea, BPBM, JRJ_Led1_270. Pl. 5D, 6A.

Eogypona Kirkaldy, 1901: 38. Type species: *E. kirbyi* Kirkaldy, 1901: 39, by original designation. The location of the type specimen for *E. kirbyi* is unknown. Nast (1952) stated that *Destinia* is “somewhat similar to *Eogypona*…and differs from it in the shape of the forewings and in more reduced venation as well as in other characters.” *Eogypona* may belong in Ledrinae—Kirkaldy’s (1901) description is inconclusive—but in the absence of the type specimen and illustrations for examination, it seems best to remove it for now. The type species was described from Ceylon (= Sri Lanka).

Hemipeltis Spinola, 1850: 132. Type species: *H. chilensis* Spinola, 1852: 302, by subsequent designation. While some characters in Spinola’s description (given in Kramer 1966—short antennae; division of genae from face only visible in ventral view of the head; genae flat; face shorter and narrower than cephalic projection in ventral view; pronotum weakly tilted forward, rugulose) and *H. trigonus (*forewing reticulate; metathoracic tibia somewhat compressed) are ledrine-like, a few characters seem to contrast with Ledrinae (ocelli absent; the forewing having an outer membrane [= appendix?]). The face not being visible in lateral view rules out these species being xerophloeines. Kramer (1966) stated that “hopefully, at some time in the future, additional specimens from Central Chile representing the two species of *Hemipeltis* will be collected; only then can the problem of placement be clarified.” M. Nielson recently revealed (personal communication) that the type specimens of *Hemipeltis* and *Piezauchenia* (see below) are kept at the University of Turin, Italy. Unfortunately they were not available for this study. Examination of either new specimens or the types is needed in order to determine the position of both *Hemipeltis* and *Piezauchenia*. Based on the present information which suggests it does not belong, *Hemipeltis* is here removed from Ledrinae.”

Ohausia Schmidt, 1911: 299. Type species: *O. nigra* Schmidt, 1911: 301, by original designation. Linnavuori (1972), citing characters of the metathoracic legs—“very long and slender tibia, with complete spinulation (rows PD and AD with a dozen or so setae, row PV with numerous thin setae), as well as characters of the head and hind wing venation”—concluded that the subfamilial placement of *Ohausia* was uncertain. Based on Kramer's (1966) illustrations of the head and forewings it differs greatly from Ledrinae, and is here removed from the subfamily.

Piezauchenia Spinola, 1850: 58. Type species: *P. aphrophoroides* Spinola, 1852: 288, by monotypy. Linnavuori (1959:12) provisionally moved this genus to Xerophloeini from its position in Selenocephalini (Deltocephalinae) because Spinola’s description did not identify it as a deltocephaline. The type specimen of *P. aphrophoroides* was recently discovered to reside at the University of Turin, Italy (see section for *Hemipeltis* above) but was unavailable for this study. The position of *Piezauchenia* is unclear as of now, and it is here removed from Xerophloeini and Ledrinae.

Platyhynna Berg, 1884: 26. Type species: *Epiclines bdellostoma* Berg, 1879: 235, by monotypy. This Neotropical genus, which bears a rough resemblance to some Ledrini, such as *Ledropsis*, is closely related to

Bascarrhinus (see discussion above). Material examined: *P. bdellostoma*: 1 male (paratype), Brazil, USNM, JRJ_Led1_141; *Platyhynna* spp.: 2 males, Bolivia, FSCA, JRJ_Led1_139–140. Pl. 5E, 9F, 14J.

Turitia Schumacher, 1912: 248. Type species: *T. uniformis* Schumacher, 1912. According to Linnavuori (1972), the type specimen of *T. uniformis* is unknown; it is probably lost. Schumacher's description lacks figures, and it is unclear from the text description that *Turitia* is a ledrine, and it is therefore removed from Ledrinae.

Taxa placed in subfamily Tartessinae Distant

Subfamily Tartessinae here includes the tribes Stenocotini and Thymbrini (new placements) and Tartessini, here designated to contain all of the genera and species treated in Tartessinae by F. Evans in her 1981 revision (Evans, F. 1981). Dietrich *et al.*'s (2001, 2005) molecular and morphological analyses of the Membracoidea and Cicadellidae, respectively, found evidence placing these tribes together in a monophyletic group. The present analysis indicates that Tartessinae is sister group to Stenocotini + Thymbrini. The specimens of Tartessini available for this study strongly resemble *Thymbris* in general body shape and structure of the head. Other characters that unite these taxa include the ocelli being located on the crown margin and the presence of transverse wrinkles on the face and pronotum, long and dense apical setae on the male subgenital plates, even dorsal sclerotization of the female pygofer, numerous dorsal teeth on valvulae II, and mottled pigmentation on valvulae III. Tartessini differs from Stenocotini and Thymbrini in having robust tibial chaetotaxy, a well-developed appendix on the forewing, and very delicate non-sclerotized valvulae. Evidence in this study for a sister group relationship between Stenocotini and Thymbrini included the metathoracic apical macrosetae formula being 2+1, the depression between the frontoclypeus and lora/genae being weakly expressed, the setae on the pygofer being abundant, and the basal arm of valvulae I being sclerotized and connected by a bridge of sclerotized tissue. A presumed connection between *Ledra* and *Ledromorpha* Stål (here moved into Stenocotini) is attributed to convergence.

Although only a few genera of each of the tribes of Tartessinae were included in this phylogenetic analysis, most of the genera of Stenocotini and Thymbrini were examined, though not all with the same level of detail. Taxa that were examined are indicated below with an asterisk (*****).

Tartessini are distributed in the Australian and Indomalayan regions, and comprise approximately 130 species in 37 genera. Thymbrini are found in Australia and New Zealand. Stenocotini are endemic to Australia.

Tribe Stenocotini Kirkaldy 1906. Type genus *Stenocotis* Fabricius 1803. Extensive work on the Stenocotini was done by Evans (1937, 1938, 1941, 1947, 1951, 1954, 1966). These genera are found exclusively in Australia.

The following genera belong in Stenocotini:

****Anacotis*** Evans, 1937: 161. Type species: *A. hackeri* Evans, 1937: 162, figs. 16, 17.

****Kyphocotis*** Kirkaldy, 1906: 370. Type species: *K. tessellata* Kirkaldy, 1906: 371, pl. XXV, figs. 1, 2.

Kyphoctella Evans, 1966: 111. Type species: *K. distorta* Evans, 1966: 111, fig. 18: I, J.

****Ledracotis*** Evans, 1937: 162. Type species: *L. gunnensis* Evans 1937: 162, figs. 18, 19.

****Ledromorpha*** Stål, 1864: 68. Type species: *Fulgora planirostris* Donovan, 1805: 1.

Endemic to Australia, *Ledromorpha* has many features that resemble the genus *Ledra* (not found in Australia), such as large size, brown color, reticulate forewings, and lamellate tibia, but these appear to be the result of ecological convergence. Among Stenocotini, *Ledromorpha*'s closest relative seems to be *Stenocotis* Stål. Its large, spatulate crown, broad wingspan, and long ovipositor make it the largest known leafhopper species in the world. No males of *Ledromorpha* have ever been found, and the species appears to be parthenogenetic. It is found on and under bark of *Eucalyptus*. Material examined: *L. planirostris*: 1 female, Australia, MNHN, JRJ_Led1_083, 2 females, Australia, USNM, JRJ_Led1_085–086, 2 females, Australia, ASCU, JRJ_Led1_084, 480. Pl. 5G.

***Smicrocotis** Kirkaldy, 1906: 370. Type species: *S. obscura* Kirkaldy 1906: 370.

***Stenocotis** Stål, 1854: 254. Type species: *S. depressa* Walker 1851: 817. Material examined: *S. depressa*: 1 female, Australia, CAS, JRJ_Led1_223, 1 male, 1 female, Australia, NCSU, JRJ_Led1_222, 224, 2 males, 1 female, Australia, ASCU, JRJ_Led1_220–221. Pl. 5F, 10B, 14E, 19E.

Tribe Tartessini Distant, 1908. Type genus *Tartessus* Stål, 1865. This tribe is known from Australia, Indonesia (Moluccas), New Caledonia, New Guinea and adjacent islands, and the Indomalayan region.

Tartessini includes 37 genera and was revised (as subfamily Tartessinae) by Faith Evans (1981), who gave a complete treatment of most of the species and all of the tartessine genera.

Specimens in the present analysis were examined from the following genera:

***Brunotartessus** F. Evans, 1981: 130, figs. 9 A–E. Type species: *Bythoscopus fulvus* Walker, 1851: 866. Material examined: B. fulvus (labeled as *Tartessus australicus*): 1 male, 1 female, Australia, USNM, Led1_424–425. Pl. 5L, 14G, 17K.

***Tartessus** Stål, 1865: 156. Type species: *Bythoscopus malayus* Stål, 1859: 290. Material examined: T. swezeyi: 1 male, 1 female, Guam, NCSU, JRJ_Led1_252–253. Pl. 17C, 19G.

Tribe Thymbrini Evans, 1936. Type genus *Thymbris* Fabricius, 1803. Thymbrini are distributed in Australia and New Zealand.

The following genera belong in Thymbrini:

***Alseis** Kirkaldy, 1907: 37. Type species: A. osborni Kirkaldy 1907: 38.

***Epipsychidion** Kirkaldy, 1906: 345. Type species: E. epipyropsis Kirkaldy, 1906: 346, pl. XXIII, figs. 4–6.

***Hackeriana** Evans, 1936: 67. Type species: *H. huonensis* Evans, 1936: 68, pl. XIX, figs. 6a, b.

***Ledraprora** Evans, 1936: 40. Type species: *L. insularis* Evans, 1936: pl. XIV, figs. 7a–d.

***Ledrella** Evans, 1936: 40. Type species: *L. brunnea* Evans, 1936: 40, pl. XIV, figs. 9a–c.

***Macroceps** Signoret, 1879: 53. Type species: *M. fasciatus* Signoret, 1880: 364, pl. 10, fig. 89. Material examined: *M. fasciatus*: 2 females, Australia, AMNH, JRJ_Led1_264–264, 2 males, 2 females, Australia, BMNH, JRJ_Led_266–268; *M. tamarensis*: 1 female, Tasmania, USNM, JRJ_Led1_265, 1 female, Tasmania, BMNH, JRJ_Led_269. Pl. 5H.

Microledrella Evans, 1969: 745. Type species: *M. minuta* Evans 1969: 745, fig. 4: A, B.

Mitelloides Evans, 1939: 46. Type species: *M. moanensis* Evans 1939: 46, figs. 9, 10.

***Novothymbris** Evans, 1941: 162. Type species: *Diedrocephala zealandica* Myers, 1923: 409, fig. 3.

***Putoniessa** Kirkaldy, 1907: 50. Type species: *P. dignissima* Kirkaldy, 1907: 50.

Putoniessiella Evans, 1969: 746. Type species: *P. sagitta* Evans 1969: 747, fig. 4: E–G.

***Rhotidoides** Evans, 1936: 59. Type species: *R. norfolkensis* Evans, 1936: 60, pl. XVIII, figs. 5a–e.

***Rhotidus** Walker, 1862: 318. Type species: *R. cuneatus* Walker, 1862: 319, pl. XV, fig. 5. Synonymy: *Rhothidus* Stål, 1865: 157 (type species: *Ledra navicula* Walker, 1851: 826).

Stenalsella Evans, 1966:111. Type species: *S. testacea* Evans, 1966: 117, fig. 19: B1, B2.

Thymbrella Evans, 1969: 747. Type species: *T. tamminensis* Evans 1969: 747, fig 4: H–J.

***Thymbris** Kirkaldy, 1907: 49. Type species: *T. inachis* Kirkaldy, 1907: 49, pl. II, figs. 19, 20. Material examined: *T. convivus*: 1 male, 1 female, Australia, USNM, JRJ_Led1_210, 212, 2 males, 2 females, Australia, ASCU, JRJ_Led1_209, 211, 213. Pl. 5I, 19H.

Genus *Clinonana* reinstated to Scarinae: Gyponini

Clinonana Osborn, 1938: 13. Type species: *C. magna* Osborn, 1938: 13, pl. I, fig. 2. *Clinonana* was originally described in Gyponinae Stål, 1870 (= Scarinae Amyot and Serville, 1843), but Kramer (1966) considered it to belong to Ledrinae based on the formula of the macrosetal formula of the metathoracic femur (2+1) and its “general habitus.” While other similarities exist between this genus and many ledrines—including the position of the ocelli on the crown, the punctate texture of the dorsum, the large size, green color, and most notably, the laterally produced carinate extensions off the pronotum (reminiscent of *Tituria* and *Neotituria*)—these characteristics can all be attributed to plesiomorphy, ecological convergence, or both. A close examination of the metathoracic femur of *C. mirabilis* reveals numerous smaller auxiliary setae subapical to the apical macrosetae of which Kramer makes no mention (Pl. 13B), which are completely uncharacteristic of ledrines (except *Xedreota*), and other characters such as the shape of the face and presence of the complete appendix on the forewing are all characteristic of Scarinae. The phylogenetic analyses herein (see "Phylogenetic results and discussion" section under Results and Discussion, above) placed *Clinonana* with *Gypona* Germar. Material examined: *C. mirabilis*: 1 male, 3 females, 1 (abdomen missing), Guiana, NCSU, JRJ_Led1_031–032, 034–035, 037, 2 males, 2 females, Guiana, MNHN, JRJ_Led1_029–030, 033, 036. Pl. 5J, 13B, 15A, 18D.

Genera *Ledrocorrhis* and *Stenoledra* removed to Ulopinae: Ulopini

Ledracorrhis Evans, 1959: 497. Type species: *L. rugosa* Evans, 1959: 498, fig. 6, A, B. Evans described *Ledracorrhis* from Madagascar. Although he stated (1959: 496) that the type specimen of *L. rugosa* was given by The Scientific Institute of Madagascar (l'Institut scientifique de Madagascar) to the "Muséum de Paris," workers at MNHN have been unable to locate it (T. Bourgoin, personal communication), and it appears to be lost. Based on Evans' description and illustrations, *Ledracorrhis* does not appear to belong in Ledrinae but rather in Ulopinae. Evans compared *Ledracorrhis* to *Coloborrhis* Germar and gave the following characters (translated here from the original French): 'coarse punctation; head spatulate to projecting on the vertex; pronotum sloping anteriorly and toward the widely separated posterior projections; venation of the tegmen reticulate; the Y-shaped vein present in the clavus; the mesanepisternum a lobe on the same plane with the forewings and with the same sculpturing as the tibia; the tibia flattened; epicranial sutures present; and the spurs [Evans uses "éperons", which translates as 'spurs' and might indicate the apical macrosetae] and projecting spines [row II macrosetae?] on the metathoracic tibia absent.' He also states that it is larger in size than *Coloborrhis*.

Stenoledra Evans, 1954: 93. Type species: *S. decorsei* Evans, 1954: 93, figs. 10–11. *Stenoledra*, described from Madagascar, in dorsal view strongly resembles some petalocephalines such as *Petalocephala bohemani*, but is much smaller (length 6 mm). Laterally, its carinate mesanepisternum can be seen, and its broad U-shaped suture on the mesoscutum is identical to that of *Coloborrhis*. Apical macrosetae on the metathoracic femur and lateral macrosetae on the metathoracic tibia are absent. Its valvulae are long and slender (Pl. 19F_1). Material examined: *S. decorsei*: 1 female, Madagascar, MNHN, JRJ_Led1_169, 1 male, 1 female, Madagascar, ASCU, JRJ_Led1_168–169. Pl. 5K, 7H, 8D, 14F, 17H, 19F.

Summary and conclusions

Many authors have suggested that the subfamily Ledrinae is polyphyletic. Dietrich *et al.* (2001) proposed that Thymbrini and Stenocotini descend from a recent common ancestor of Tartessinae. The work reported here supports these hypotheses. A number of taxa previously recognized to belong to Ledrinae are here moved to other subfamilies (26 genera) or placed incertae sedis within Cicadellidae (11 genera).

This research (Figs. 1–3) supports the views of Dietrich (2000) and Szwedo (2002) that Petalocephalini is synonym of Ledrini. It also concurs with Dietrich *et al.* (2001), Szwedo (2002), and Oman (1949) regarding the placement of *Proranus* in Xerophloeini, and some evidence is given supporting Dietrich *et al.*'s (2001) hypothesis that Xerophloeini are derived from an aphrodine lineage. Evans' (1966) suggestion that *Rubria* merits tribal status within Ledrinae is here supported, and this genus is herein given tribal rank. The phylogenetic limits of Ledrini have also been given herein as far as can be discerned from the present analyses and data.

In this paper, phylogenetic evidence is presented for relationships among the five tribes of Ledrinae and their possible source lineages, and among the genera of Ledrini. The tribes here recognized to belong within Ledrinae (see Table 4) are: Afrorubrini (2 genera), Hespenedrini (1 genus), Ledrini (30 extant genera, 1 fossil genus), Rubrini (1 genus), and Xerophloeini (4 extant genera, 1 fossil genus). Although not comprehensive, this work is intended to revise and stabilize the classification of the subfamily and provide a solid foundation for further analyses of its constituent tribes and genera. Much work remains, particularly in regards to the abundance of Ledrini genera and species native to China and the Indomalayan region, and the four largest genera of Ledrini—*Ledra*, *Ledropsis*, *Petalocephala*, and *Tituria*—which appear to exhibit some para- or polyphyly in this study. Appropriate follow-up work should address the species composition of each of these and their sister genera, revise their placements, and possibly describe further genera and species within the tribe. It is important to point out that the emphasis in this study on creating a working genus-level phylogeny does not provide the same level of resolution as a comprehensive species-level revision, and future revisions at the species level will likely bring more phylogenetic information to light and clarify the hypotheses proposed herein.

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), it is hoped that a robust, reliable classification may be established 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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References

Amyot, C. J. B., and Serville, A. (1843) *Histoire naturelle des insectes. Hémiptères.* [Deuxième partie. Homoptères. Homoptera Latr. pp. 455–676]. Librairie Encyclopédique de Roret, Paris, France, lxxvi + 676 pp.

Arnett, R. H., Jr., Samuelson, G. A. and Nishida, G. M. (1993) *Insect and Spider Collections of the World.* 2nd edition. Flora and Fauna Handbook 11. Sandhill Crane Press, Gainesville, Florida, vi + 310 pp.

Berg, C. (1879a) Hemiptera Argentina (continuacion). *Anales de la Sociedad Científica Argentina,* 8, 241–272.

Berg, C. (1879b) *Hemiptera, Homoptera Latr. Hemiptera Argentina enumeravit speciesque novas descripsit Carolus Berg.* Bonarie, ex typographiae P. E. Coni, Hamburgo, 1879, viii + 316 pp.

Cai, P. (1992) A new genus and species of Ledridae (Homoptera: Cicadelloidea). *Entomotaxonomia*, 14, 265–268.

Cai, P. (1993) Five new species of the genus *Tituria* from China (Homoptera: Cicadelloidea: Ledridae). *Acta Zoologica* Sinica, 39, 41–47.

Cai, P. (1994a) A new species of the genus *Confucius* from China (Homoptera: Cicadelloidea: Ledridae). *Journal of Anhui Agricultural University*, 21, 78–80.

Cai, P. (1994b) A new genus and two new species of Ledridae from China (Homoptera: Cicadelloidea). *Acta Entomologica Sinica*, 37, 205–208.

Cai, P. and Ge, Z. (1992) Three new species of the genus *Petalocephala* from China (Homoptera: Cicadelloidea: Ledridae). *Zoological Research*, 13, 117–121.

Cai, P. and He, J. (1997) A new and a newly recorded genera of Ledridae from China, with descriptions of four new species. *Wuyi Science Journal*, 13, 8–14.

Cai, P. and Huang, K. (1998) Two new species of the genus *Funkikonia* Kato and a new allied genus (Homoptera: Cicadellidae: Ledrinae). *Journal of Anhui Agricultural University*, 25, 211–216.

Cai, P. and Jiang, J. (2000) Two new species of the genus *Midoria* Kato from China (Homoptera: Cicadellidae: Ledrinae). *Acta Entomologica Sinica*, 43, 413–416.

Cai, P. and Kuoh, C. (1991) Four new species of Ledridae from Guizhou, China (Homoptera: Cicadelloidea). *Journal of Anhui Agricultural College*, 18, 101–106.

Cai, P. and Kuoh, C.-L. (1993) A newly recorded genus and two new species of Ledridae from China (Homoptera: Cicadelloidea). *Acta Zootaxonomica Sinica*, 18, 447–450.

Cai, P. and Kuoh, C.-L. (1994) A new species of the genus *Parapetalocephala* (Homoptera: Cicadelloidea: Ledridae). *Acta Entomologica Sinica*, 37, 97–98.

Cai, P. and Li, Z. Z. (1995) Two new species of the genus *Tituria* from China (Homoptera: Ledridae). *Acta Zootaxonomica Sinica*, 20, 86–89.

Cai, P. and Meng, X. (1991) A new species of the genus *Ledra* from China (Homoptera: Cicadelloidea: Ledridae). *Journal of Anhui Agricultural College*, 18, 169–171.

Cai, P. and Mo, T. (1992) Notes on a new species of *Tituria* and *T. cuneata, T. nigrivena* (Homoptera: Cicadelloidea: Ledridae). *Journal of Anhui Agricultural College*, 19, 133–137.

Cai, P. and Shen, X. (1998) New species of family Cicadellidae from Mt. Funiu in Henan Province. *In*: Shen, X. and Shi, Z. (Eds.), *Insects of the Funiu Mountains Region (1).* China Agricultural Scientech Press, Beijing, pp. 37–52.

Cai, P., Sun, J., Jiang, J., Britton, K. O., and Orr, D. (2001) A list of Chinese Cicadellidae (Homoptera) on Kudzu, with description of new species and new records. *Scientia Silvae Sinicae*, 37, 92–100.

Cai, P. and Yang, J. (1997) A new species of the genus *Dusuna* with a redescription of its generic characters (Homoptera: Cicadelloidea, Ledridae). *Entomological Journal of East China*, 6, 1–3.

Cen, Y.-W. and Cai, P. (2000) Two new species of the genus *Petalocephala* Stål (Homoptera: Cicadellidae: Ledrinae) from China. *Entomotaxonomia*, 22, 247–250.

China, W. E. (1961) *Cicadella* Latreille, 1817: proposed validation under the plenary powers (Insecta, Hemiptera). Z. N. (S.) 457. *Bulletin of Zoological Nomenclature*, 18, 161–167.

Cryan, J. R., Robertson, J. A. and Deitz, L. L. (2003) *The New World Treehopper Tribe Microcentrini (Hemiptera: Membracidae: Stegaspidinae): Monographic Revision and Phylogenetic Position.* Thomas Say Monographs, Entomological Society of America, Lanham, Maryland, iii + 103 pp.

Cwikla, P. S. (1987) Review of the ledrine genus *Bascarrhinus* (Homptera: Cicadellidae) with description of a new species. *Annals of the Entomological Society of America*, 80, 429–434.

Dallas, W. S. (1867) Insecta. [Translation of the keys in Stål 1866a, Fieber 1866a, and Signoret 1866a]. *Zoological Record*, 3, 558–561, 567, 569, 571–573.

Davis, R. B. (1975) Classification of selected higher categories of auchenorrhynchous Homoptera (Cicadellidae and Aetalionidae). *United States Department of Agriculture Technical Bulletin, Agricultural Research Service,* 194, 1–52.

Deitz, L. L. (1975) Classification of the higher categories of the New World treehoppers (Homoptera: Membracidae). *North Carolina Agricultural Experimental Station Bulletin*, 225, i–ii, 1–177.

Dietrich, C. H. (2000) *Guide to the subfamilies of leafhoppers (Cicadellidae),* Center for Biodiversity, Illinois Natural History Survey. Available from: http://www.inhs.uiuc.edu/~dietrich/subfam/guide.html (12 Mar. 2009).

Dietrich, C. H. (2005) Keys to the families of Cicadomorpha and subfamilies and tribes of Cicadellidae (Hemiptera: Auchenorrhyncha). *Florida Entomologist*, 88, 502–517.

Dietrich, C. H. and Deitz, L. L. (1993) Superfamily Membracoidea (Homoptera: Auchenorrhyncha). II. Cladistic analysis and conclusions. *Systematic Entomology*, 18, 297–311.

Dietrich, C. H. and Dmitriev, D. A. (2003) Reassessment of the leafhopper tribes Koebeliini Baker and Grypotini Haupt (Hemiptera: Cicadellidae). *Annals of the Entomological Society of America*, 96, 766–775.

Dietrich, C. H., Dmitriev, D. A., Rakitov, R. A., Takiya, D. M. and Zahniser, J. N. (2005) Phylogeny of Cicadellidae (Cicadomorpha: Membracoidea) based on combined morphological and 28S rDNA sequence data. Abstract of 12th International Auchenorrhyncha Congress and 6th International Workshop on Leafhoppers and Planthoppers of Economic Significance. University of California, Berkeley, August 7–12, 2005. Berkeley.–P. S–13–S–15.

Dietrich, C. H. and Rakitov, R. A. (2002) *Some remarkable new deltocephaline leafhoppers (Hemiptera: Cicadellidae: Deltocephlinae) from the Amazonian rainforest canopy.* Journal of the New York Entomological Society, 110, 1–48.

Dietrich, C. H., Rakitov, R. A., Holmes, J. L., and Black, W. C., IV. (2001) Phylogeny of the major lineages of Membracoidea (Insecta: Hemiptera Cicadomorpha) based on 28S rDNA sequences. *Molecular Phylogenetics and Evolution*, 18, 293–305.

Distant, W. L. (1907) Contributions to a knowledge of the Ledrinae. *Annales de la Société Entomologique de Belgique*, 51, 185–197.

Distant, W. L. (1908) *Homoptera. Rhynchota vol. 4. The Fauna of British India including Ceylon and Burma*. Taylor and Francis, London, xv + 501 pp.

Esaki, T. and Ito, S. (1954) *A tentative catalogue of the Jassoidea of Japan and her adjacent territories.* Japan Society for the Promotion of Science, Ueno Park, Tokyo, 315 pp.

Evans, J. W. (1936a) Australian leafhoppers (Jassoidea, Homoptera). Part 4 (Ledrinae, Ulopidae, and Euscelidae, Paradorydiini). *Papers and Proceedings of the Royal Society of Tasmania*, 1936, 37–50.

Evans, J. W. (1936b) Australian leafhoppers, (Jassoidea, Homoptera). Part 5. Euscelidae, (in part). *Papers and Proceedings of the Royal Society of Tasmania*, 1936, 51–71.

Evans, J. W. (1937) Australian leafhoppers. Part 7. Stenocotidae. *Memoirs of the Queensland Museum*, 11, 157–164.

Evans, J. W. (1938) A contribution to the study of the Jassoidea (Homoptera). *Papers and Proceedings of the Royal Society of Tasmania*, 1938, 19–55.

Evans, J. W. (1939) Some new Australian leafhoppers (Homoptera, Jassoidea). *Transactions of the Royal Society of South Australia*, 63, 44–50.

Evans, J. W. (1941) New leafhoppers (Homoptera, Jassoidea) from Western Australia. *Journal of the Royal Society of Western Australia*, 27, 143–163.

Evans, J. W. (1947) A natural classification of the leaf-hoppers (Jassoidea, Homoptera). Part 3: Jassidae. *Transactions of the Royal Entomological Society of London*, 98, 105–271.

Evans, J. W. (1951) Some notes on the classification of the leafhoppers (Jassoidea, Homoptera) with special reference to the Nearctic fauna. *Commentationes Biologicae Societas Scientiarum Fennica*, 12, 1–11.

Evans, J. W. (1954) Les Cicadellidae de Madagascar (Homopteres). *Memoires de l'Institut Scientifique de Madagascar*, Série E, 4, 87–137.

Evans, J. W. (1955) Cicadellidae (Hemiptera Homoptera). *Exploration du Parc National de l'Upemba Mission G.F. De Witte*, 37, 1–44.

Evans, J. W. (1958) Character selection in systematics with special reference to the classification of the leafhoppers (Insecta, Homoptera, Cicadelloidea). *Systematic Zoology*, 7, 126–131.

Evans, J. W. (1959) Quelques nouveux cicadellides (Homopteres) de Madagascar. Observations sur la signification évolutive de la spéciation dans le genre *Coloborrhis* Germar. *Memoires de l'Institut Scientifique de Madagascar*, Série E, 11, 496–498.

Evans, J. W. (1966) The leafhoppers and froghoppers of Australia and New Zealand (Homoptera: Cicadelloidea and Cercopoidea). *Australian Museum Memoir*, 12, 1–347.

Evans, J. W. (1969) Characteristics and components of Ledridae and some new genera and new species from Australia and New Guinea. *Pacific Insects*, 11, 735–754.

Evans, F. (1981) The Tartessinae of Australia, New Guinea and some adjacent islands (Homoptera: Cicadellidae). *Pacific Insects*, 23, 112–188.

Fabricius, J. C. (1794) Ryngota. Entomologia Systematica Emendata et Aucta. Secundum classes, ordines, genera, species adiectis synonimis, locis, observationibus, descriptionibus, Hafniae, Proft, 4, 1–472.

Fabricius, J. C. (1803) Systema Rhyngotorum secundum ordines, genera, species, adiectis synonymis, locis, observationibus, descriptionibus, C. Reichard, Brunsvigae, 1803, x, 1–314.

Fairmaire, L. M. H. (1855) 2e Division.–Homopterès . Musée Scolaire Dayrolle. Histoire Naturelle de la France. IIe partie–Hémiptères. (Punaises, cigales, pucerons, cochenilles, etc.), É. Deyrolle, Paris, 1855, 1–206.

Fieber, F. X. (1866) Neue Gattungen und Arten in Homoptern (Cicadina Bur.). Verhandlungen de Kaiserlich–Königlichen Zoologisch–botanischen Gesellschaft in Wien, 16, 497–516.

Fletcher, M. J. (2006) *Identification Key and Checklists for the Leafhoppers and Treehoppers of Australia and neighbouring areas* (Hemiptera: Cicadellidae, Membracidae)* *NZ component in collaboration with Marie–Claude Larivière, Landcare Research, Auckland, New Zealand. New South Wales Agriculture, Orange Agricultural Institute. Available from: http://www.agric.nsw.gov.au/Hort/ascu/leafhop/cica0.htm (12 Mar. 2009).

Fletcher, M.J. (2002) *Tribe Petalocephalini*. New South Wales Agriculture, Orange Agricultural Institute. Available from: http://www.agric.nsw.gov.au/Hort/ascu/leafhop/petalo.htm (12 Mar. 2009).

Ge, Z. [Kuoh, C.-L.] (1992) Homoptera: Cicadelloidea. *In*: Chen, S. (Ed), *The series of the scientific expedition to the Hengduan Mountains, Qinghai–Xizang Plateau. Insects of the Hengduan Mountains Region. Vol. 1.* Science Press, Beijing, ii + 1538 pp.

Germar, E. F. (1836) Description de deux nouvelles Cigales. *Revue Entomologique*. Gustave Silbermann, Strassburg and Paris, 4, 71–73.

Germar, E. F. (1839) Drei neue Gattungen der Cicadinen, aufgestellt vom Herausgeber. *Entomologische Zeitschrift*, 1, 187–192.

Goding, F. W. (1903) A monograph of the Australian Membracidae. *Proceedings of the Linnean Society of New South Wales*, 28, 2–41.

Hamilton, K. G. A. (1983) Classification, morphology and phylogeny of the family Cicadellidae (Rhynchota: Homoptera). *In*: Knight, W. J., Pant, N. C. Robertson, T. S. and Wilson, M. R. (Eds), *Proceedings of the 1st International Workshop on Biotaxonomy, Classification and Biology of Leafhoppers and Planthoppers (Auchenorrhyncha) of Economic Importance, London, 4–7 October 1982*. [Cover title: 1st International Workshop on Leafhoppers and Planthoppers of Economic Importance.]. Commonwealth Institute of Entomology, London, ii + 500 pp.

Hamilton, K. G. A. (1990) Insects from the Santana Formation, Lower Cretaceous, of Brazil. Chap. 6. Homoptera. *Bulletin of the American Museum of Natural History*, 195: 82–122.

Hamilton, K. G. A. (1992) Lower Cretaceous Homoptera from the Koonwarra fossil bed in Australia, with a new superfamily and synopsis of Mesozoic Homoptera. *Annals of the Entomological Society of America*, 85: 423–430.

Harris, R. A. (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology*, 28, 1–31.

International Commission on Zoological Nomenclature. (1963) Opinion 647. *Cicadella* Latreille, 1817 (Insecta, Hemiptera); validation under the plenary powers. *Bulletin of Zoological Nomenclature*, 20, 35–38.

International Commission on Zoological Nomenclature. (1999) *International Code of Zoological Nomenclature. 4th edition*. International Trust for Zoological Nomenclature, c/o The Natural History Museum, London, xxix + 306 pp.

Jacobi, A. (1914) Bemerkungen über Jassinae (Homoptera, Cicadoidea). *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin*, 1914, 379–383.

Jacobi, A. (1944) Die Zikadenfauna der Provinz Fukien in Südchina and ihre tiergeographischen Beziehungen. *Mitteilungen der Münchener Entomologischen Gesellschaft*, 34, 5–66.

Kato, M. (1929) Descriptions of some new Formosan Homoptera. *Transactions of the Formosa Natural History Society*, 19, 540–551.

Kato, M. (1931) Japanese Ledridae. *Dobutsugaku Zasshi*, 43, 431–440.

Kato, M. (1932) Notes on some Homoptera from south Manchuria, collected by Mr. Yukimichi. *Kontyû*, 5, 216–229.

Kato, M. (1933) Homoptera. *Three-colour Illustrated Insects of Japan (Kosei–kaku, Tokyo)*, 4, 1–9.

Kirkaldy, G. W. (1900) Bibliographical and nomenclatorial notes on the Rhyncota. No. 1. *The Entomologist*, 33, 238–243.

Kirkaldy, G. W. (1901) Further notes on some Sinhalese Rhynchota. *The Entomologist*, 33, 293–295.

Kirkaldy, G. W. (1903) Einige neue und wenig bekannte Rhynchoten. *Wiener Entomologische Zeitung*, 22, 13.

Kirkaldy, G. W. (1906) Leafhoppers and their natural enemies. Part IX, Leafhoppers, Hemiptera. *Bulletin of the Hawaiian Sugar Planters Association Division of Entomology*, 1, 271–479.

Kirkaldy, G. W. (1907) Leafhoppers–Supplement. (Hemiptera). *Bulletin of the Hawaiian Sugar Planters Association Division of Entomology*, 3, 1–186.

Kirschbaum, C. L. (1868) Die Cicadinen der gegend von Wiesbaden und Frankfurt A.M. nebst eineranzahl neuer oder Schwer zu unterscheidender Arten aus anderen Gegenden Europa's Tabellarisch Beschrieben. *Jahrbücher des Vereins für Naturkunde im Herzogthum Nassau*, 21–22, 1–202.

Kramer, J. P. (1966) A revision of the New World leafhoppers of the subfamily Ledrinae (Homoptera: Cicadellidae). *Transactions of the American Entomological Society*, 92, 469–502.

Kuoh, C. (1981) Homoptera: Cicadelloidea. *In*: *Insects of Xizang 1*. Science Press, Beijing, pp. 195–219.

Kuoh, C.-L. (1985) Six new species of the genus *Petalocephala* (Homoptera: Ledridae). *Entomotaxonomia*, 6, 271–278.

Kuoh, C.-L and Cai, P. (1992) A new species of the genus *Epiclinata* from China (Homoptera: Cicadelloidea: Ledridae). *Acta Zoologica Sinica*, 38, 136–138.

Kuoh, C.-L. and Cai, P. (1993) A new species of the genus *Confucius* (Homoptera: Cicadelloidea, Ledridae). *Acta Entomologica Sinica*, 36, 479–481.

Kuoh, C.-L. and Cai, P. (1994) Four new species of the genus *Ledra* (Homoptera: Ledridae). *Acta Zootaxonomica Sinica*, 19, 195–201.

Kwon, Y. J. and Lee, C. E. (1978) A review of the Ledridae of Korea (Homoptera: Cicadellidae). *Nature and Life (Kyungpook Journal of Biological Sciences)*, 8, 65–72.

Lawson, P. B. (1931) The genus *Xerophloea* in North America (Homoptera, Cicadellidae). *Pan-Pacific Entomology*, 7, 159–169.

Liang, A., Cai, P., Kuoh, C. and He, J. (1997) Homoptera: Cicadellidae. In: Yang, X. (Ed.), *Insects of the Three Gorge Reservoir Area of Yangtze River.* Chongqing Press, Chongqing, pp. 324–348.

Linnaeus, C. (1758) II. Hemiptera. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, L. Salvii, Stockholm, 1, 434–457.

Linnavuori, R. (1959) Revision of the Neotropical Deltocephalinae and some related subfamilies (Homoptera). *Suomalaisen Elain–ja Kasvitieteellisen Seuran Vanamon Elaintieteellisia Julkaisuja*, 20, 1–370.

Linnavuori, R. (1972) Revisional studies on African leafhoppers (Homoptera Cicadelloidea). *Revue de Zoologie et de Botanique Africaines*, 86, 196–252.

Maddison, D. R. and Maddison W. P. (2002) *MacClade 4: Analysis of Phylogeny and Character Evolution.* Version 4.06. Sinauer Associates, Sunderland, Massachusetts.

McKamey, S. H. (2000) *Checklist of Leafhopper Species 1758–1955 (Hemiptera: Membracoidae: Cicadellidae and Myserslopiidae) with Synonymy and Distribution [Catalogue of the Homoptera, Fascicle 6, Abridged]*, USDA Agricultural Research Service, Systematic Entomology Laboratory, National Museum of Natural History. Available from: http://www.sel.barc.usda.gov/selhome/leafhoppers/PDF/checklist.pdf [pdf version]; http://www.sel.barc.usda.gov/selhome/leafhoppers/HTML/html_main.html [html version] (12 Mar. 2009).

McKamey, S. H. (2005) Further new genus-group names in the Cicadellidae (Hemiptera). *Proceedings of the Entomological Society of Washington*, 108, 502–510.

Melichar, L. (1924) Monographie der Cicadellinen I. *Annales Historico-Naturales Musei Nationalis Hungarici*, 21, 195–243.

Melichar, L. (1925) Monographie der Cicadellinen II. *Annales Historico-Naturales Musei Nationalis Hungarici*, 22, 329–410.

Metcalf, Z. P. (1952) New names in the Homoptera. *Journal of the Washington Academy of Science*, 42, 226–231.

Metcalf, Z. P. (1962a) *General Catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Part 3, Gyponidae.* United States Department of Agriculture, Agricultural Research Service, Washington, D. C., 229 pp.

Metcalf, Z. P. (1962b) *General Catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Part 4, Ledridae*. United States Department of Agriculture, Agricultural Research Service, Washington, D. C., 147 pp.

Metcalf, Z. P. (1962c) *General Catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Part 5, Ulopidae.* United States Department of Agriculture, Agricultural Research Service, Washington, D. C., 95 pp.

Metcalf, Z. P. (1963) *General Catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Part 8, Aphrodidae.*United States Department of Agriculture, Agricultural Research Service, Washington, D. C., 268 pp.

Metcalf, Z. P. (1964a) *General Catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Part 11, Coelidiidae.* United States Department of Agriculture, Agricultural Research Service, Washington, D. C., 182 pp.

Metcalf, Z. P. (1964b) *General Catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Bibliography of the Cicadelloidea (Homoptera: Auchenorhyncha).* United States Department of Agriculture, Agricultural Research Service, Washington, D. C., 349 pp.

Metcalf, Z. P. (1965) *General Catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Part 1, Tettigellidae.* United States Department of Agriculture, Agricultural Research Service, Washington, D. C., 730 pp.

Metcalf, Z. P. (1966) *General Catalogue of the Homoptera. Fascicle VI, Cicadelloidea. Part 15, Iassidae.* United States Department of Agriculture, Agricultural Research Service, Washington, D. C., 229 pp.

Mickevich, M. and Lipscomb, D. L. (1991) Parsimony and the choice between alternative transformations for the same data set. *Cladistics*, 7, 111–139.

Nast, J. (1952) Notes on some Ledrinae (Homoptera: Jassidae). *Annales Musei Zoologici Polonici*, 15, 33–42.

Nielson, M. W. (1962) A revision of the genus *Xerophloea* (Homoptera: Cicadellidae). *Annals of the Entomological Society of America*, 55, 234–244.

Nielson, M. W. (1968) The leafhopper vectors of phytopathogenic viruses (Homoptera: Cicadellidae): taxonomy biology, and virus transmission. *United States Department of Agriculture Technical Bulletin*, 1382, i–ii, 1–368.

Nielson, M. W. (1985) Leafhopper systematics. *In*: Nault, L. R. and Rodriguez, J. G. (Eds), *The Leafhoppers and Planthoppers*. Wiley & Sons, New York, 500 pp.

Oman, P. W. (1936) South American leafhoppers of the genus *Xerophloea* Germar (Homoptera). *Revue d'Entomologie*, 6, 394–401.

Oman, P. W. (1949) The Nearctic leafhoppers (Homoptera: Cicadellidae). A generic classification and check list. *Memoirs of the Entomological Society of Washington*, 3, 1–253.

Oman, P. W., Knight, W. J., and Nielson, M. W. (1990) *Leafhoppers (Cicadellidae): a Bibliography, Generic Check-list and Index to the World Literature 1956–1985*. CAB International Institute of Entomology, Wallingford, Oxon, United Kingdom, iii + 368 pp.

Rafinesque, C. S. (1815) *Analyse de la nature ou tableau de l'univers et des corps organisés.* Aux dépens de l'auteur, Palerme. 224 pp.

Ren, L. and Zhang, Y. (2001) The geographical distribution of Ledrinae (Homoptera) in China. *Journal of Gunagxi Agriculture and Biological Science*, 20, 102–107.

Ross, H. H. (1957) Evolutionary developments in the leafhoppers, the insect family Cicadellidae. *Systematic Zoology*, 6, 69, 87–97.

Sahlberg, J.R. (1871) Öfversigt af Finlands och den Skandinaviska hälfons Cicadariae. I. *Notiser ur Sällskapets pro Fauna et Flora Fennica Förhandlingar*, 9, 1–506.

Scotese, C.R. (2002) PALEOMAP website. Available from: http://www.scotese.com/earth.htm (12 Mar. 2009).

Shcherbakov, D. E. (1992) The earliest leafhoppers (Hemiptera: Karajassidae n. fam.) from the Jurassic of Karatau. *Neus Jahrbuch für Geologie und Paläontologie Monatshefte*, 1992, 39–51.

Shih, H. T., Ho, C. C., Yang, J. T. and Chen, S. P. (2001) Checklist of Ledridae (Homoptera: Cicadelloidea) from Taiwan. *Journal of Agricultural Research of China*, 50, 66–76.

Signoret, V. A. (1880) Essai sur les Jassides Stål, Fieb. et plus particulièrement sur les Acocéphalides Puton. *Annales de la Société entomologique de France*, 10, 347–366.

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

Spinola, M. (1850) Di alcuni generi d'insetti artroidignati nuovamente proposti dal socio attuale Signor Marchese Massimiliano Spinola nella sua tavola sinottica di questo ordine che precede la presente memoria. *Modena Memorie di Matematica e Fisica della Società Italiana delle Scienze, residente in Modena*, 25, 61–138.

Spinola, M. (1852) Orden VII. Hemipteros. *Gay's Historia Fisica y Politica de Chile* [C. Gay, Paris, France or Santiago, Chile], 7, 238–305.

Stål, C. (1853) Nya genera bland Hemiptera. *Öfversigt af Kongliga Svenska Vetenskaps–Akadamiens Förhandlingar*, 10, 231–255.

Stål, C. (1855) Hemiptera från Kaferlandet. *Öfversigt af Kongliga Svenska Vetenskaps–Akadamiens Förhandlingar*, 12, 89–100.

Stål, C. (1864) Hemiptera nonnulla nova vel minus cognita. *Annales de la Société entomologique de France*, 4, 47–68.

Stål, C. (1865) Homoptera nova vel minus cognita. *Öfversigt af Kongliga Svenska Vetenskaps–Akademiens Förhandlingar*, 22, 145–165.

Stål, C. (1866) Membracida and Centrotida. *Hemiptera Africana*, 4, 1–276.

Stål, C. (1869) Hemiptera Fabriciana. Fabricianska Hemipterarter, efter de i Köpenhamn och Kiel förvarade typeexemplaren granskade och beskrifne. 2. *Kongliga Vetenskaps Academiens Handlingar*, 8, 1–130.

Swofford, D. L. (2002) *PAUP* Phylogenetic Analysis Using Parsimony (*and other methods). Version 4.0b10.* Sinauer Associates, Sunderland, Massachusetts.

Szwedo, J. (2002) Studies on Xerophloeini leafhoppers with description of *Pariacaca icanoensis* gen. and sp. nov. from Argentina (Hemiptera: Cicadomorpha: Cicadellidae: Ledrinae). *Genus*, 13, 153–163.

Torre-Bueno, J. R. de la. (1937) *A glossary of entomology.* Brooklyn Entomological Society, Brooklyn, New York, i–ix, 1–336 pp.

Walker, F. (1851) *List of the specimens of homopterous insects in the collection of the British Museum*. Order of Trustees, London, 3, 637–907.

Walker, F. (1857) Catalogue of the homopterous insects collected at Singapore and Malacca by Mr. A. R. Wallace, with descriptions of new species. *Journal of the Proceedings of the Linnean Society*, 1, 82–100.

Walker, F. (1862) Characters of undescribed species of Homoptera in the collection of F.P. Pascoe, F.L.S. *Journal of Entomology*, 1, 303–319.

Wu, C. F. (1935) *Order XV. Homoptera. Catalogus Insectorium Sinensium. (Catalogue of Chinese Insects).* China Fan Memorial Institute of Biology, Peiping, 634 pp.

Young, D. A. (1977) Taxonomic study of the Cicadellinae (Homoptera: Cicadellidae). Part 2. New World Cicadellini and the genus *Cicadella*. *North Carolina Agricultural Experimental Station Bulletin*, 239, 1–1135.

Zhang, Y., Yang, L., Webb, M. D., and Sun, Q. (2004) Type specimens of Jacobi's 'Fukien' leafhoppers and description of new species from China (Insecta: Auchenorrhyncha: Cicadellidae, Penthimiinae). *Entomologische Abhandlungen*, 62, 83–92.

Appendix

List of tables

List of figures and plates

TABLE 1. Morphological characters and states used in phylogenetic analysis of Ledrinae.

HEAD

Crown

1 Crown texture {punctate}: 0, not punctate; 1, punctate (Pl. 7A_1)

2 Crown texture {acinose/colliculate}: 0, not acinose or colliculate; 1, acinose or colliculate (Pl. 7A_1)

3 Crown texture {rugose}: 0, not rugose; 1, rugose near eyes only; 2, rugose in multiple areas

4 Crown texture {longitudinally costate}: 0, not longitudinally costate; 1, longitudinally costate (Pl. 7B_1)

5 Crown texture {torose}: 0, not torose; 1, torose, with large swellings, depressions, or irregular deformations of shape (Pl. 7D_2)

6 Crown texture {nodulate}: 0, not nodulate; 1, nodulate (Pl. 7F_2)

7 Crown setae: 0, absent; 1, present

8 Crown setae {form}: 0, short and very thin; 1, short and thick with apex somewhat flattened and wider than base, mildly scalelike or clubbed; 2, long and thick

9 Median longitudinal groove: 0, absent; 1, thin, shallow, at posterior margin only; 2, deep groove (*Bascarrhinus*, *Platyhynna*)

10 Median longitudinal fold: 0, absent; 1, broad or narrow, raised above adjacent areas (Pl. 1B)

11 Median longitudinal carina: 0, absent; 1, present (complete or incomplete)

12 Median longitudinal carina {expression}: 0, present only anteriorly; 1, present only posteriorly; 2, complete and low; 3, complete and high, lamellate (Pl. 8B_1); 4, present only anteriorly at apex of long crown extension (*Bascarrhinus*)

13 Median longitudinal carina (posteromedial fin}: 0, absent; 1, present (Pl. 8B_2)

14 Swelling or protuberance laterad of ocelli: 0, absent; 1, present (Pl. 7A_2)

15 Swelling or protuberance laterad of ocelli {expression}: 0, not acute anterad and darkly sclerotized apically; 1, acute and darkly sclerotized apically (Pl. 7F_3)

16 Short shallow groove immediately laterad of ocelli: 0, absent; 1, visible below surface (*Afrorubria* and *Sichaea*); 2, a crease on surface (Pl. 7C_1)

17 Ocelli {position}: 0, absent; 1, on margin; 2, on crown disk

18 Ocelli {position on crown disk}: 0, greater than one eye length from transect connecting foremargin of eyes; 1, within one eye length of transect connecting foremargin of eyes; 2, between eyes or on transect connecting foremargin of eyes

19 Ocelli {size}: 0, small; 1, intermediate in size; 2, large

20 Ocelli marginal ring {expression}: 0, thin to medium red or yellow color; 1, thick and opaque (*Bascarrhinus*) ; 2, blends with coronal texture and difficult to distinguish from crown, with ocelli sometimes also raised on a shallow stalk or protuberance (Pl. 8C_1)

21 Crown anterad of transect connecting foremargin of eyes vs. crown immediately at transect connecting foremargin of eyes: 0, narrows; 1, widens or is parallel or subparallel before tapering

22 Crown shape in males: 0, not acute, subacute, ovate or pentagonal; 1, acute or subacute and pentagonal or subpentagonal; 2, acute and ovate (Pl. 3E)

23 Crown shape in females: 0, not acute, subacute, ovate or pentagonal; 1, acute or subacute and pentagonal or subpentagonal; 2, acute and ovate (Pl. 3D, F)

24 Crown {anterior prolongation}: 0, not prolonged anteriorly; 1, prolonged anteriorly (*Bascarrhinus*)

25 Eye orientation {relative to midline}: 0, oblique (near 45°) to longitudinal midline; 1, subparallel or intermediately angled to longitudinal midline; 2, parallel or nearly parallel to longitudinal midline

26 Crown area posterolateral to eyes and anterior to hind margin of crown: 0, narrow with carina only (Pl. 8A_3); 1, broad without carina (Pl. 3B-C, H-J, 4A-B); 2, slightly broadened (intermediate) with carina (Pl. 7C_2); 3, narrow without carina (Pl. 7E_3)

27 Crown hind margin {shape}: 0, laterally not extending posterad of medial section of pronotum foremargin (overall shape is mildly curving or approximately straight: Pl. 3H, 4A-B); 1, laterally extending posterad of medial section of pronotum (overall margin shape is curving or trapezoidal)

28 Crown anterior marginal carina: 0, incomplete or absent; 1, complete; 2, mostly complete, tuberculate toward eyes; 3, complete near eye and in front but thickened at corner

29 Crown anterior marginal secondary carina: 0, absent; 1, present (Pl. 8A_2)

30 Crown {lamellateness}: 0, not or only weakly lamellate; 1, lamellate near antennae or at lateral margins for a short distance only; 2, strongly lamellate for a short or long distance

31 Crown transverse camber: 0, sharply angled (Pl. 10I_1); 1, curved; 2, depressed between midline and eyes (Pl. 10H_1); 3, variously curved or angled, but weakly (Pl. 10G_1)

32 Head inclination relative to body axis: 0, normal, approximately parallel to substrate (Pl. 6B); 1, steep and nearly perpendicular to substrate (Pl. 6C_1); 2, steep but subvertical (Pl. 6A_1)

Face

33 Crown margin: 0, not thicker with squared edge; 1, thicker with squared edge (Pl. 9E_3)

34 Antennal pocket inner margin: 0, not developed; 1, weakly developed; 2, strongly developed (Pl. 10D_3); 3, a thin carina only (Pl. 10E_2, F_2)

35 Antennal pocket inner margin {form}: 0, a bar or swelling, oblique and often constricted or weakly developed where it meets frontoclypeus (Pl. 9B_2); 1, a transverse bar, broad and contiguous with frontoclypeus (Pl. 9F); 2, a bar or swelling, parallel to frontoclypeus and often constricted or weakly developed where it meets frontoclypeus (Pl. 10D_3); 3, a bar or swelling, oblique and not constricted where it meets frontoclypeus (Pl. 10B_4)

36 Antennal pocket anterolateral margin: 0, not developed; 1, carinate, forming a distinct antennal ledge (Pl. 10B_4, E2)

37 Antennal ledge: 0, a thin carina only (Pl. 10E_2); 1, a flat well-produced plate contiguous with anterior margin of crown; 2, appearing wrinkled or pinched (Pl. 10B_1); 3, flat and somewhat produced, contiguous with lateral margin of crown (Pl. 9F)

38 Frontoclypeus marginal sutures {extension}: 0, not transversing antennal bar or ridge mesoanterad of antennae; 1, transversing antennal bar or ridge mesoanterad of antennae (Pl. 10B_3)

39 Frontoclypeus marginal sutures {divergence}: 0, not widely divergent; 1, widely divergent (Pl. 10B_2)

40 Antennal posterolateral nodule: 0, absent; 1, present (Pl. 8D_1, 9F_4)

41 Frontoclypeus base {width}: 0, very wide (Pl. 9F_1); 1, narrow, apparently narrow and approximately parallel (Pl. 9B); 2, intermediately wide (Pl. 10F)

42 Frontoclypeus base {shape}: 0, swollen high above lora/genae; 1, margin flush with lora/genae and not depressed; 2, somewhat swollen but below lora/genae, and lora/genae tumid or carinate or both; 3, somewhat swollen but not high above lora/genae, and lora/genae not tumid or carinate

43 Frontoclypeus base {medial shape}: 0, swollen medially; 1, depressed medially (Pl. 9C, E); 2, flat, or only slightly swollen medially (Pl. 9A, B, 10A, C); 3, torose or angulate medially (Pl. 10E_1)

44 Frontoclypeus {length}: 0, long, or with long apical extension, apical extension possibly vestigial or reduced Pl. 9B_1); 1, short or apparently short, apical extension absent or apparently absent (Pl. 9F)

45 Frontoclypeus apical extension {shape}: 0, well-defined by lateral sutures or depressions, broad throughout (Pl. 10F_1); 1, well-defined by lateral sutures or depressions and narrowing to a swollen ridge, not narrowing much, or vaguely fading Pl. 10A, D); 2, not well-defined by lateral sutures or depressions and vaguely fading or expanding apicad and laterad (Pl. 9A)

46 Frontoclypeus medial transverse flexure: 0, slight; 1, great (Pl. 9B_1, 10D); 2, absent

47 Frontoclypeus {shape}: 0, not almond-shaped and expanded to just before apex of face; 1, almond-shaped and expanded to just before apex of face (Pl. 9E_2)

48 Medial groove or pit anterad of frontoclypeus: 0, absent; 1, present (Pl. 9F_2)

49 Frontoclypeus carinae: 0, absent; 1, a single medioapical carina (Pl. 9C_2); 2, bicarinate basally (Pl. 9C_3)

50 Frontoclypeus base lateral perpendicular ridges (cibarial muscle attachments): 0, absent; 1, present (Pl. 9E_1)

51 Frontoclypeus {texture}: 0, not punctate with setae arising from punctations; 1, punctate, often with setae arising from punctations (Pl. 10E, F)

52 Face transverse wrinkles: 0, absent; 1, costate apically; 2, invaginations or folds at point of flexure

53 Face microsetae or microtexture: 0, absent; 1, present around antennae; 2, present all over or in multiple places

54 Genal rugosities: 0, absent; 1, present (Pl. 10B_5)

55 Facial setae {development}: 0, absent or almost absent; 1, moderately distibuted; 2, numerous throughout (Pl. 10I)

56 Facial setae {thickness}: 0, very fine, short; 1, very fine, long; 2, coarse, short; 3, coarse, long (Pl. 10I)

57 Setae under crown lip: 0, variously scattered, dense or not; 1, distinct row around edge; 2, a thick patch of stiff setae on underneath edge of corner of margin of crown just anterior to eyes and antennae

58 Dark facial pigmentation (black, dark brown, or dark red): 0, absent; 1, present

59 Anterior tentorial pit: 0, absent; 1, a large deep hole (Pl. 9F_3); 2, a wrinkle; 3, a depression; 4, a small hole or slit; 5,a small hole behind antennae

60 Antennal segment I {size and shape}: 0, small, inner margin (closest to face— often difficult to see) cup-shaped; 1, large, round, cup-shaped, with cup open on all sides and overlapping segment II; 2, large, oblong, cup-shaped, open along inner margin only (closest to face); 3, small, cup-shaped, open on all sides, not overlapping segment II

THORAX

Pronotum

61 Pronotum {shape} in lateral view: 0, flat or approximately flat (Pl. 6F); 1, slightly humped, medially or posteriorly (intermediate) (Pl. 6D); 2, flat anteriorly and abruptly declivous posteriorly (Pl. 6B_1); 3, strongly humped from anterior to posterior margin (Pl. 6A, C)

62 Side of pronotum: 0, not boxlike, without dorsomedial and ventrolateral sharp bend and carinate or not; 1, boxlike, with dorsomedial and ventrolateral sharp bend and carinate or not (Pl. 8A_4, D)

63 Pronotum lateral carina: 0, absent; 1, dorsal or medial; 2, ventral

64 Pronotum lateral extensions: 0, absent; 1, present

65 Pronotum lateral extensions {shape in dorsal view}: 0, rounded (Pl. 7E) ; 1, broadly triangular with acute margin (Pl. 4A, B); 2, weakly developed, somewhat triangular (Pl. 4J, 5J)

66 Pronotum foremargin: 0, curved, medial section between eyes; 1, curved, medial section anterad to eyes; 2, curved, medial section posterad to eyes; 3, straight; 4, trapezoidal

67 Hind margin of pronotum: 0, curved or emarginate; 1, trapezoidal (Pl. 2H, I, 3G); 2, straight (Pl. 5D)

68 Hind margin of pronotum: 0, without median peak; 1, with median peak; 2, curved with median point directed posterad

69 Transverse parallel or subparallel pronotal wrinkles: 0, absent; 1, shallow (Pl. 4E-G); 2, deep (Pl. 5F, H)

70 Pronotal tubercules: 0, absent; 1, present

71 Torosities/irregularities: 0, absent or slightly humped only; 1, present as large swellings, protrusions, invaginations, and/or irregular deformations of shape (Pl. 7D_2)

72 Paired sublateral anterior longitudinal ridges (in line with projections next to ocelli on crown): 0, absent; 1, present (Pl. 7D_3)

73 Pronotal median or submedian posterior longitudinal row(s): 0, absent; 1, a single row of tubercules, or a single carina or lamina; 2, a double row of tubercules, carinae, or laminae

74 Pronotal median or submedian posterior longitudinal row(s) {form}: 0, a single row of tubercules; 1, a single carina or ridge (Pl. 4J, 7E); 2, a single elevated crest (Pl. 8B_3); 3, two rows of tubercules (Pl. 2D); 4, two carinae or elevated crests (Pl. 2C)

75 Pronotal sublateral rows: 0, absent; 1, present as two sublateral rows of tubercules or carinae; 2, present as ears or horns (*Ledra*, *Porcorhinus*)

Mesoscutum

76 Visible part of mesoscutum {dimensions}: 0, with width less than three times length; 1, with width three times length or more (Pl. 7H_1)

77 Mesoscutal sulcus deeply invaginated posteriorly and broadly U-shaped: 0, absent; 1, present (*Stenoledra*: Pl. 7H_2, *Coloborrhis*)

78 Mesoscutum {development}: 0, undeveloped; 1, with lateral rounded swellings or thin low ridges (Pl. 7G_1)

79 Mesoscutum medial swelling: 0, absent; 1, present

Scutellum

80 Scutellum {development}: 0, flat; 1, with a medial swelling of any kind

81 Scutellum (form): 0, slighty swollen, a bulb, or a spike; 1, swelling longitudinally but not transversely

82 Scutellum {spike or swelling}: 0, with a strongly developed spike (Pl. 7D_5); 1, with a rounded swelling, roughly quadrate basally (Pl. 6A_2)

83 Scutellum longitudinal depression: 0, absent; 1, present (Pl. 7G_2)

Proepisternum

84 Proepisternum: 0, not visible; 1, underlapping genae (Pl. 9A_1); 2, not underlapping genae (Pl. 9B-E)

85 Proepisternum {size and form}: 0, small,tablike (Pl. 9A_2); 1, large, quadrate (Pl. 9B_3, C_4); 2, long, narrow; 3, collarlike, extending laterally onto sides of pronotum

Metaepisternum

86 Metaepisternum: 0, not large, quadrate, even with forewing and pronotum over middle leg, with forewing texture; 1, large, quadrate, even with forewing and pronotum over middle leg, with forewing texture (*Stenoledra*: Pl. 8D_2, *Coloborrhis*)

Forewings

87 Wings of females: 0, macropterous; 1, brachypterous

88 First anal vein: 0, slightly raised at base, not sharp or carinate; 1, raised at base, high and carinate; 2, slightly raised at base, sharp or carinate

89 Wing veins: 0, not raised above wing surface; 1, raised above wing surface

90 Wing cells: 0, not deeply depressed below wing veins; 1, deeply depressed below wing veins (Pl. 1E, F, 2K)

91 Nodule or sclerotized thickening at first split of M vein: 0, absent; 1, present

92 Nodule or sclerotized thickening at first split of M vein expression; 0, not very large; 1, very large (Pl. 6B_2)

93 Nodules on veins: 0, absent; 1, present

94 Nodules in cells: 0, absent; 1, present

95 Wing camber: 0, gradual (most species); 1, intermediate; 2, sharply angled at first claval vein

96 Claval suture {depression}: 0, flat, not depressed; 1, weakly depressed; 2, strongly depressed

97 First claval vein pigmentation: 0, not pigmented; 1, pigmented

98 Clavus {pigmentation}: 0, not pigmented; 1, with lighter pigment inside first claval vein

99 Claval veins: 0, free; 1, confluent

100 Forewing venation: 0, normal; 1, predominantly reticulate in distal two thirds; 2, entirely reticulate

101 Forewing {reticulation}: 0, with a few crossveins or intercalary veins; 1, many crossveins present; 2, strongly reticulate, venation obscured

102 Appendix: 0, absent; 1, fused with edge of forewing, very thin, short, or expanded edge at junction with claval suture only; 2, broad or narrow, obvious (Pl. 11D_1)

103 Fovea on wing: 0, absent; 1, few in number; 2, numerous (Pl. 7G, H)

104 Setae on wings: 0, absent; 1, present

105 Setae: 0, predominantly on basal half or in claval area of wing; 1, throughout wing or on wing veins

106 Setae {distribution}: 0, present on wing veins; 1, present along margins of wing veins

107 Setae on inner margin of leading edge of forewing: 0, absent; 1, present

108 Setae on leading edge of forewing: 0, absent; 1, sparse or moderate in number; 2, abundant

109 Leading edge of forewing: 0, flat; 1, divided by secondary longitudinal carina (Pl. 11E_1)

110 Overall wing coloration: 0, not pigmented, and/or opaque, lacking all coloration; 1, pigmented and or opaque, with some coloration

Hind wing

111 Hind wing: 0, fully developed; 1, shrunken, vestigial, or absent (Pl. 11C_1)

112 R&M veins: 0, not confluent ; 1, confluent

Legs

113 Triangular sclerites immediately anteromedial of mesothoracic coxal plates: 0, shallow or not depressed posteriorly; 1, depressed posteriorly (Pl. 11B_2)

114 Anterior edge of mesothoracic coxal plates (hind edge of triangular depression): 0, not abrupt, without abrupt edge medially; 1, abrupt, with abrupt edge medially (Pl. 11B_3)

115 Prothoracic tibia: 0, more or less round or oval in cross section, with thin or wide groove on outer face, groove often with carinate edge; 1, quadrate or flattened in cross section, with wide groove on outer face, groove often with carinate edges; 2, foliaceous

116 Mesocoxal horn: 0, absent, small, or vestigial; 1, present, large, long, curved, obvious (15A_1)

117 Mesothoracic tibia: 0, more or less round or oval in cross section, with thin or wide groove on outer face, groove often with carinate edge; 1, quadrate or flattened in corss section, with wide groove on outer face, groove often with carinate edges; 2, foliaceous

118 Triangular patch of brushlike or scalelike setae at apex of row II of mesotibia: 0, absent; 1, present

119 Triangular patch of brushlike or scalelike setae at apex of row II of mesotibia {arrangement}: 0, not arranged in parallel rows perpendicular to axis of tibia (Pl. 12A, B); 1, arranged in parallel rows perpendicular to axis of tibia (Pl. 12C)

120 Metathoracic femur macrosetae formula: 0, 0+0; 1, 2+0 (Pl. 13E); 2, 2+1 or 2+1+1 (Pl. 13D); 3, other (Pl. 13A)

121 Metathoracic femur macrosetae form: 0, present, long, deeply striated (Pl. 13F); 1, present, short, not deeply striated (Pl. 13G)

122 Patella-like extension of femur over femur-tibia joint (serves as base for macrosetae): 0, absent; 1, present, intermediate in length and width (Pl. 13H); 2, present, long or narrow or both (Pl. 13E)

123 Metathoracic tibia: 0, quadrate or flattened with fluted edges (groove broad) and setal row II with cucullate bases (Pl. 12E-G); 1, foliaceous, with setal row II consisting of setae with cucullate bases and intercalated hairlike setae (Pl. 12H); 2, heavily spined or with or more rows of long robust setae (Pl. 12D)

124 Number of macrosetae in AD row of hind tibia: 0, absent; 1, 7 or fewer; 2, 8 or more

125 Metathoracic tibia row II cucullae: 0, absent, no setal bases cucullate; 1, present, some macrosetal bases cucullate; 2, present, bases of all large setae cucullate

126 Metathoracic tibia row II hairlike setae (intercalaries): 0, absent or sparse; 1, numerous and obvious (Pl. 12H)

127 Foliaceous tibia faces {tubercules}: 0, not tuberculate; 1, tuberculate

128 Foliaceous tibia faces {short stiff setae}: 0, without setae; 1, with numerous setae

129 Metathoracic tarsomere I: 0, short; 1, intermediate in length (Pl. 13K, L); 2, long (Pl. 13J)

130 Ridge on metathoracic tarsomere I: 0, absent or short; 1, long

131 Short ridge on metathoracic tarsomere I: 0, low, weakly developed, or absent; 1, high, well developed (Pl. 13I)

132 Long ridge on metathoracic tarsomere I: 0, low, weakly developed; 1, high, well developed

133 Groove on metathoracic tarsomere I: 0, absent; 1, present

134 Scalloped setal bases on inside of metathoracic tarsomere I: 0, absent; 1, present (Pl. 13L)

135 Metathoracic tarsomere I ventral microsetae or microtexture: 0, absent; 1, distributed in proximal half only; 2, distributed all over or medially only

136 Metathoracic tarsomere I dorsolateral long setae: 0, absent; 1, distributed on distal half only; 2, distributed all over tarsomere; 3, distributed laterally or dorsally or both, but not on plantar surface

137 Metathoracic tarsomere I short coarse setae: 0, absent; 1, normal; 2, thick, white, and fingerlike (Pl. 13K)

138 Metathoracic tarsomere I ventral short coarse setae: 0, distributed all over; 1, distributed in longitudinal groove

139 Metathoracic tarsomere I lateral fingerlike setae: 0, absent; 1, present

ABDOMEN

140 Body {shape}: 0, not flexed longitudinally at abdomen immediately posterior to scutellum in lateral view; 1, flexed longitudinally at abdomen immediately posterior to scutellum in lateral view (Pl. 6F)

Male genitalia

141 Genital capsule: 0, not inverted; 1, inverted (Pl. 14J_1)

Aedeagus

142 Base of aedeagus in lateral aspect {thickness}: 0, intermediately thick (Pl. 16G); 1, thick; 2, slender (Pl. 16I)

143 Apex of aedeagus in lateral aspect {thickness}: 0, intermediately thick; 1, thick (Pl. 16E); 2, slender (Pl. 14A)

144 Apex of aedeagus in dorsal or ventral aspect {width}: 0, intermediately wide; 1, wide; 2, slender (Pl. 16F)

145 Apical or subapical bulb (dorsal aspect): 0, absent; 1, present (Pl. 16H_1)

146 Apical or first subapical process: 0, absent; 1, present (Pl. 16L_1)

147 Subapical or second subapical process: 0, absent; 1, present (Pl. 16L_2)

148 Subapical process {shape}: 0, long, slender; 1, very short (small points only); 2, long or short and flat (Pl. 16H_2)

149 Subapical process {direction at base}: 0, directed apicad; 1, directed basad; 2, directed laterad

150 Subapical process (apical barb}: 0, without apical barb; 1, with apical barb

151 Gonopore {shape}: 0, simple, round, small, not appearing as a split or groove; 1, appearing as a split or groove

152 Ventral split or groove (ventro-lateral aspect): 0, absent; 1, present (Pl. 16F_3)

153 Dorsal hook: 0, absent; 1, present (Pl. 16J_1)

154 Paired sclerotized medial points on dorsal margin: 0, absent; 1, present (Pl. 16E_2, F_1)

155 Transverse medial carina on dorsal margin {anterad of paired sclerotized medial points}: 0, absent; 1, present (Pl. 16E_1, F_2)

156 Basal lobe: 0, absent; 1, present dorsally (Pl. 16I_1); 2, present ventrally as a medial fin; 3, present ventrally as a fingerlike lobe; 4, present as a swelling

Paraphyses

157 Paraphyses: 0, absent; 1, present (Pl. 14K_1, 20C_1, D_1)

158 Articulation of paraphyses: 0, absent; 1, present (Pl. 16D_1)

Connective

159 Connective {shape}: 0, not short and wide, not U-shaped; 1, short and wide, U-shaped (*Gypona*, *Clinonana*)

Styli

160 Styles {orientation relative to rest of genital capsule}: 0, in line with long axis of pygofer and body; 1, pointed ventrally (*Platyhynna*: Pl. 14J, *Bascarrhinus*)

161 Styles {apical sclerotization}: 0, not scelotized apically; 1, sclerotized apically

162 Shape of apex: 0, not acuminate (Pl. 15I_1); 1, acuminate (= first apical point)

163 Shape of apex: 0, not clubbed, toggle or T-shaped, or foot shaped and large, (apically expanded); 1, clubbed, toggle or T-shaped, or foot shaped and large, (apically expanded)

164 Primary apical flexure: 0, not bent, curved, or angled ventrad; 1, bent, curved, or angled ventrad (Pl. 14I_1, 16C_2); 2, bent, curved, or angled dorsad

165 Secondary apical flexure: 0, not recurving anteriorly; 1, recurving anteriorly (Pl. 16E_3)

166 Second apical point: 0, absent; 1, present, dorsal; 2, present, ventral (Pl. 15G_1, 16C_2)

167 Second apical point {direction}: 0, directed apicad; 1, directed ventrad (like first apical point), near first apical point; 2, directed dorsad

168 Medial ventral lobe: 0, absent; 1, present

169 Ventral subapical patch of setae: 0, absent; 1, present (Pl. 15H_1)

Pygofer subgenital plates

170 Plates {shape}: 0, compressed laterally; 1, depressed dorsoventrally; 2, depressed dorsoventrally basad and compressed laterally distad (Pl. 16M_2)

171 Plates {shape}: 0, slender or acuminate; 1, broad or triangular

172 Plates {length relative to pygofer}: 0, about same length as pygofer; 1, much longer than pygofer (Pl. 14A_3); 2, much shorter than pygofer (Pl. 14J)

173 Plates {thickness}: 0, thin, not inflated; 1, thick, inflated (Pl. 16C_3)

174 Plates {segmentation}: 0, one-segmented; 1, two-segmented (Pl. 14B_1, F_2)

175 Plate apex {shape}: 0, round; 1, acute only; 2, acute and with one or two additional lobes (Pl. 14B, F_1)

176 Long apical bristles: 0, absent; 1, present (Pl. 14E_1, G_1)

177 Plates {pigmentation}: 0, without pigmented spots; 1, with pigmented spots

Pygofer

178 Pygofer {elongation}: 0, not elongate; 1, elongate, narrow (Pl. 14J)

179 Inner, subapical, dorsomedial processes: 0, absent; 1, present

180 Inner, subapical, dorsomedial processes {shape}: 0, not hook shaped; 1, hook shaped (Pl. 14C_1)

181 Basidistal processes: 0, absent; 1, present (Pl. 14H_1)

182 Tuft of long, subapical setae: 0, absent; 1, present (Pl. 15C_1)

183 Tuft of apical setae: 0, absent; 1, present (Pl. 15B_1)

184 Pygofer apex: 0, not long and fingerlike or triangular; 1, long and fingerlike or triangular (Pl. 14C)

Anal tube

185 Base of anal tube (segment X): 0, not like a ring; 1, like a ring or tube, but incomplete ventrally (Afrorubrini: Pl. 15F_1)

186 Anal tube in dorsal view: 0, not big and conelike; 1, big and conelike (Afrorubrini: Pl. 15E_1)

187 Anal tube ventrodistal lobe: 0, absent; 1, present (Pl. 14A_1)

Female genitalia

Sternite VII

188 Sternite VII lateral margins: 0, even with margin of tergite VII; 1, anterad to margin of tergite VII; 2, extending posterad to margin of tergite VII

189 Sternite VII {shape}: 0, not medially emarginated; 1, medially emarginated

190 Sternite VII {shape}: 0, not sublaterally emarginated; 1, sublaterally emarginated:

191 Sternite VII medial margin {shape}: 0, reaches far past lateral edges (may be tab-like); 1, does not reach far past lateral edges

Sternite VIII

192 Spiracle on venter of abdominal segment VIII adjacent to ovipositor: 0, absent, not visible; 1, small but visible; 2, large, conspicuous

Pygofer

193 Pygofer {length}: 0, not longer than valvulae III; 1, longer than valvulae III

194 Pygofer {ventral shape}: 0, curved; 1, somewhat flattened ventrally or with weakly expressed depression along margin adjacent to valvulae III ; 2, flat ventrally, depressed along margin adjacent to valvulae III

195 Pygofer {contour of apex of in lateral view}: 0, round, robust; 1, free, thin, wavy or with medial depressions

196 Pygofer apex: 0, closed, in tight contact with ovipositor blades; 1, open, in loose contact of free from ovipositor blades

197 Pigmented spots: 0, absent; 1, present

198 Mottled pigmentation: 0, absent; 1, present (Pl. 17B_2)

199 Dorsal dark coloration: 0, absent; 1, present (Pl. 17C_1)

200 Tubercules, or tuberculate texture: 0, absent; 1, present (Pl. 17B_1)

201 Pygofer setae {abundance}: 0, absent; 1, somewhat abundant; 2, abundant

202 Pygofer setae {length}: 0, short; 1, medium; 2, long

203 Pygofer setae {thickness}: 0, none; 1, thin; 2, thick

204 Pygofer macrosetae: 0, absent; 1, present

Ovipositor

205 Apex of ovipositor (Valvulae I + III) {relative to apex of forewings}: 0, not extending beyond wings, or equal in length to wings; 1, extending beyond wings

Valvulae I

206 Base shape {basal arm and distal arm connection}: 0, irregular, indistinct; 1, curved, rounded; 2, angled (Pl. 17A_1)

207 Base angle {shape}: 0, obtuse 1, acute or square (Pl. 17A_1)

208 Valvulae I basad vesicles: 0, absent; 1, present

209 Basal arm {development}: 0, not especially sclerotized or developed; 1, sclerotized or developed

210 Basal arm {sclerotization}: 0, with a carina or bridge connecting arm bases; 1, with heavily sclerotized basal and dorsal margins on each arm; 2, with a medial large knob, tubercule or other thickening on each arm; 3, with a mass of medial non- or partially-sclerotized material between arm bases

211 Valvulae I shape: 0, with a single curve; 1, recurved apically (Pl. 18L_2, of recurved valvulae II)

212 Valvulae I dorsal texture: 0, absent; 1, parallel longitudinal strigae (Pl. 17G_1); 2, filelike; 3, reticulate or scalelike; 4, fingerprintlike strigae (Pl. 17E_1, I_1)

213 Valvulae I texture medial chevrons: 0, absent; 1, present (Pl. 17G_2, H_1)

214 Valvulae I apex texture: 0, perpendicular strigae; 1, reticulate, scalelike, or filelike; 2, fingerprintlike strigae

215 Valvulae I fingerprint texture: 0, strongly expressed with deep grooves; 1, weakly expressed or with very fine grooves

216 Valvulae I texture distribution: 0, dorsal and/or medial to apex; 1, in a distinct narrow rectangular band along dorsal margin to apex only (Pl. 17J_1)

Valvulae II

217 Valvulae II {sclerotization}: 0, not sclerotized; 1, somewhat sclerotized; 2, completely or strongly sclerotized

218 Valvulae II {shape in lateral aspect}: 0, long and moderately slender (Pl. 18I, J, K, 19B, C, I); 1, broadest medially, boat shaped, with a dorsal peak (Pl. 18D_1); 2, long and very slender (Pl. 18A, H, L, 19D, F, K, L); 3, broadest basally or medially, not boat-shaped

219 Apex {shape}: 0, not pentagonal or subrectangular (quadrate) beyond apical notch; 1, pentagonal or subrectangular (quadrate) beyond apical notch (Pl. 19I_2)

220 Apex {shape}: 0, sharply acute (Pl. 18A, C); 1, not sharply acute

221 Subapical dorsal notch: 0, absent; 1, present (Pl. 18I_1, J_3)

222 First dorsal tooth : 0, absent; 1, distinct, sclerotized (Pl. 18J_1)

223 Second dorsal tooth: 0, absent; 1, distinct, sclerotized (Pl. 18J_2)

224 First dorsal tooth {position}: 0, near midpoint (within basal half); 1, more apical (within apical half: Pl. 18J_2)

225 Second dorsal tooth {position}: 0, closer to apex than to first tooth (Pl. 18J_2, 19I_1); 1, closer to first tooth than to apex (Pl. 19B); 2, halfway in between first and second tooth

226 Auxilliary dorsal teeth {instead of or in addition to first and second dorsal teeth}: 0, absent; 1, eleven or more in number (Pl. 18C_1); 2, ten or fewer in number (Pl. 19D_1)

227 Blade dorsal split: 0, absent or subapical only; 1, extending apicad of mid length (Pl. 18B); 2, extending from second tooth to apex, intermediate (Pl. 19G, K_1)

228 Ventral split: 0, narrow or closed for most or all of length; 1, clearly to widely open in distal half

229 Median perpendicular keel on sides of blade: 0, absent; 1, present (Pl. 18F_1)

230 Blade surface lateral parallel wrinkles perpendicular to blade axis: 0, absent; 1, distinct, deep

Valvulae III

231 Valvula shape: 0, essentially flattened or thickened or both; 1, cuplike or thin or both

232 Pigmented spots: 0, absent; 1, present

233 Mottled pigmentation: 0, absent; 1, present

234 Valvulae III setae: 0, absent; 1, present, not numerous; 2, present, numerous

235 Valvulae III setae {length}: 0, short; 1, long

OTHER CHARACTERS

236 Geographic region: 0, Palearctic; 1, Indomalayan; 2, Australian; 3, Nearctic; 4, Neotropical; 5, Afrotropical

TABLE 2. Ledrinae character matrix

										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Afrorubria vitticollis	0	0	1	1	0	0	0	?	0	0	1	2	0	0	?	1	2	1	0	0	1	0	0	0	1	0	1	1	1	0
Bascarrhinus plathanon	1	1	2	0	0	0	1	1	2	1	1	4	0	0	?	0	2	1	2	1	1	0	0	1	2	2	1	3	0	2
Bascarrhinus platypoides	1	1	2	0	0	0	1	1	2	1	1	4	0	0	?	0	2	1	2	1	1	0	0	1	2	2	1	3	0	2
Beniledra peculiaris	0	1	0	0	1	0	0	?	0	0	1	1	0	1	0	0	2	2	1&2	0	1	1	1	0	1	1	0	2	0	2
Betsileonas marmorata	0	1	2	1	1	0	0	?	1	0	0&1	2	0	0	?	0	2	2	1	0	1	0	0	0	0	0	1	1	1	2
Clinonana mirabilis	0	1	2	0	0	0	0	?	0	0	0	?	0	0	?	0	2	2	2	0	0	0	0	0	0	0	1	0	0	1
Cololedra declivata	0	1	0	0	1	0	1	2	0	0	0	?	0	0	?	0	1	?	1	0	0	0	0	0	1	0	1	0	0	0
Confucius cameroni	0	1	0	0	1	1	1	1	0	1	1	1	0	1	0	0	2	1	0	2	1	1	?	0	2	1	0	1	1	2
Confucius dispar	0	1	0	0	1	0	1	1	1	1	1	1	0	1	0	0	2	1	1	0	1	?	0	0	2	1	0	1	1	2
Confucius zombanus	0	1	0	0	1	1	1	1	0	0	1	1	0	?	?	0	2	2	1	0	1	0	?	0	2	1	0	1	0	2
Dusuna sp. 1	1	0	0	0	1	0	0	?	0	1	0	?	0	0	?	0	2	2	1	0	1	?	0	0	0	1	0	1	0	2
Dusuna sp. 2	1	0	0	0	1	0	0	?	0	1	1	0	0	0	?	0	2	2	1	0	1	0	?	0	0	3	0	1	0	2
Epiclinata planata	1	1	1	0	0	0	0	?	1	0	1	0	0	0	?	0	2	2	1	0	1	1	0	0	0	1	0	1	1	2
Ezrana primitiva	1	1	2	0	1	0	1	1	0	1	1	3	0	1	0	0	2	1	1	2	1	?	1	0	2	2	1	1	0	2
Funkikonia sp. 1	1	1	1	0	1	1	1	1	0	0	1	0	0	1	0	0	2	1	0	2	1	?	2	0	2	1	0	1	1	2
Funkikonia sp. 2	1	1	1	0	1	1	1	0	0	0	1	1	0	1	0	2	2	2	0	2	1	?	2	0	2	1	0	1	0	2
Funkikonia tuberculata	0	1	1	0	1	1	1	0	1	1	0	?	0	1	0	0	2	1	0	2	1	1	?	0	2	1	0	1	1	2
Hangklipia gibber	0	1	0	0	1	0	0	?	0	1	1	2	0	1	0	0	2	1	0	0	1	0	0	0	1	3	1	0&1	0	0&2
Hangklipia signata	1	1	2	0	1	0	0	?	0	?	1	2	0	1	0	0	2	1	0	0	1	0	?	0	1	3	1	1	1	2
Hespenedra chilensis	1	1	2	0	1	0	0	?	0	0	1	2	0	0	?	0	2	1	0	0	1	0	0	0	1	2	1	2	0	0&2
Jukaruka grisea	1	1	1	0	1	1	1	1	0	1	1	3	1	1	1	0	2	1	0	2	1	1	?	0	2	2	1	1	0	2
Ledropsella monstrosa	1	1	1	0	1	1	1	1	0	1	1	3	1	1	1	0	2	1	1	2	1	?	1	0	2	2	1	1	0	2
Ledropsella sp.	1	1	1	0	1	1	1	1	0	1	1	3	1	1	1	0	2	1	0	2	1	1	1	0	2	2	1	1	0	2
Ledra auditura	1	1	2	0	1	1	1	1	1	1	1	0	0	1	1	0	2	2	1	2	1	1	1	0	2	1	0	1	1	2
Ledra aurita	1	1	1	0	1	1	1	1	1	1	0	?	0	1	1	0	2	2	1	2	1	1	1	0	1	1	0	1	1	2
Ledra mutica	0	1	1	0	1	1	1	1	1	1	0	?	0	1	1	0	2	2	1	2	1	1	1	0	2	2	0	1	0	2
Ledra tuberculifrons	1	1	1	0	1	1	1	1	1	1	1	1	0	1	0	0	2	1	0	2	1	?	1	0	1	1	0	1	1	2
Ledramorpha planirostris	0	1	1	0	1	0	0	?	0	0	0	2	0	0	?	0	2	0	0	0	1	0	0	0	0	3	1	1	0	2
Ledropsis discolor	0	1	0	0	1	1	1	1	1	0	1	?	0	1	0	2	2	2	0	2	1	1	0	0	1	2	0	1	0	2
Ledropsis froggatti	1	1	0	0	1	0	1	1	0	1	1	2	0	1	0	2	2	1	0	0&2	1	1	0	0	1	2	1	2	0	2
Ledropsis sp. 1	0	1	2	0	1	1	1	1	0	0	0	?	0	1	1	0	2	2	1	2	1	0	?	0	2	3	?	1	0	2
Neotituria kongasana	1	1	2	0	0	0	0	?	1	0	1	2	0	0	?	0	2	2	0	0	1	0	0	0	1	2	1	2	0	2
Parapetalocephala testacea	1	1	1	0	1	0	0	?	0	1	0	?	0	0	?	1	2	2	0	0	1	1	0	0	1	3	1	1	1	2
Petalocephala bohemani	1	1	1	0	0	0	0	?	1	0	1	1	0	0	?	0	2	2	1	0	1	?	0	0	1	2	0	2	0	2
Petalocephala conspicua	1	1	1	0	0	0	0	?	1	0	1	2	0	0	?	0	2	2	1	0	1	0	0	0	1	1	0	2	1	2
Petalocephala raniceps	1	1	1	0	0	0	0	?	1	0	1	2	0	0	?	0	2	2	1	0	1	0	0	0	1	1	0	2	0	2
Platyhynna bdellostoma	1	1	2	0	1	0	1	1	2	0	0	?	0	0	?	0	2	1	1	0	1	1	?	0	1	2	1	3	0	2
Platyhynna sp. 1	1	1	2	0	1	0	1	1	2	?	0	1	0	0	?	0	2	?	?	0	1	1	?	0	1	2	1	3	0	2
Platyledra acuminata	0	1	2	0	1	1	1	1	0	1	1	3	0	1	1	0	2	1	0	2	1	?	2	0	2	2	1	1	0	2
Platyledra caldida	0	1	0	0	1	1	1	1	1	1	1	3	0	1	1	0	2	1	1	2	1	2	?	0	2	2	1	1	0	2
Platyledra hirsuta	0	1	2	0	1	1	1	1	0	1	1	3	1	1	1	0	2	1	0	2	1	?	2	0	2	2	1	1	0	2
Porcorhinus mastersi	0	1	2	0	1	0	1	?	0	1	1	3	0	1	0	0	2	1	0	2	1	?	1	0	1	2	1	2	0	2
Proranus adspersipennis	0	1	2	0	0	0	1	1	1	0	0	?	0	0	?	0	2	2	1	0	1	0	0	0	0	0	1	1	0	1
Proranus ghilianii	1	1	2	0	0	0	1	1	1	0	0	?	0	0	?	0	2	2	1	0	1	0	0	0	0	0	1	1	0	1
Rubria brevifrons	0	1	1	0	0	0	0	?	0	0	1	2	0	0	?	2	2	1	0	0	1	1	0	0	1	2	1	2	0	2
Rubria informis	1	1	1	0	0	0	0	?	1	0	1	2	0	0	?	0	2	1	0	0	1	1	0	0	1	2	1	0	1	2
Rubria sanguinosa	1	1	0	0	0	0	0	?	0	0	1	2	0	0	?	2	2	1	0	0	1	?	0	0	1	0	1	0	0	2
Sichaea sp. 1	0	0	0	1	0	0	0	?	0	0	1	2	0	0	?	1	0&2	?	?	?	1	?	0	0	1	0	1	1	1	0
Stenoledra decorsei	1	0	1	0	0	0	0	?	0	0	0	?	0	0	?	0	2	1	0	0	1	0	0	0	2	2	1	1	0	2
Thlasia brunipennis	1	1	0	0	0	0	0	?	0	0	1	2	0	0	?	0	2	2	1	0	1	1	0	0	1	1	0	2	0	2
Thlasia corona	1	1	0	0	0	1	0	?	0	0	1	2	0	0	?	0	2	2	1	0	1	1	?	0	1	1	0	2	1	2
Titiella humerosa	1	1	2	0	1	0	0	?	0	1	0	?	0	1	0	0	2	1	0	0	1	?	0	0	1	3	1	1	1	0
Titiella punctiger	1	1	2	0	1	0	0	?	0	1	0	?	0	1	0	0	2	1	0	0	0	?	0	0	1	3	1	1	1	0
Tituria antica	1	1	1	0	0	1	0	?	1	0	1	0	0	0	?	0	2	2	1	0	1	1	0	0	0	1	0	1	1	2
Tituria forficula	1	1	2	0	1	0	0	?	0	0	1	2	0	0	?	0	2	2	1	0	1	0	0	0	0	1	0	2	1	2
Tituria obtusa	1	1	0	0	0	1	0	?	0	0	1	2	0	0	?	0	2	2	1	0	1	1	1	0	1	1	0	2	0	2
genus 1	0	1	1	0	1	1	1	1	0	1	1	2	0	1	0	2	0&2	1	1	2	1	1	1	0	2	1	0	1	0	2
genus 2	0	0	0	1	0	0	0	?	0	0	0	?	0	0	?	0	2	1	?	?	0	0	?	0	1	0	1	1	1	0
genus 3	1	0	1	1	0	0	0	?	0	0	1	2	0	0	?	0	2	1	0	0	1	0	?	0	1	0	1	1	1	1
genus 4	0	0	0	1	0	0	0	?	0	0	1	2	0	0	?	0	0	?	?	?	0	0	0	0	1	0	1	1	1	0
Stenocotis depressa	0	1	2	0	1	0	1	1	0	0	0	?	0	0	?	0	1	?	0	0	1	?	0	0	1	3	1	1	1	0
Macroceps fasciatus	0	0	0	0	0	0	0	?	0	0	0	?	0	0	?	0	1	?	0	0	0	0	0	0	1	0	1	0	0	0
Thymbris convivus	0	0	0	0	0	0	0	?	0	0	0	?	0	0	?	0	1	?	0	0	0	0	0	0	1	0	1	0	0	0
Xedreota tuberculata	1	1	2	0	1	0	1	0	0	0	1	2	0	0	?	0	2	1	1	0	1	1	1	0	0	0	1	1	1	0
Xerophloea viridis	1	1	2	0	1	0	1	1	0	0	1	2	0	0	?	0	2	1	1	0	1	1	1	0	0	1	1	1	0	1
Aphrodes bicinctus	0	1	2	0	0	0	0	?	0	0	1	2	0	0	?	0	2	1	0	0	0	0	0	0	1	0	1	2	0	0
Bathysmatophorus shabliovskii	0	0	3	0	1	0	0	?	0	0	1	1	0	0	?	0	2	1	0	0	0	0	0	0	1	2	1	0	0	0
Coloborrhis corticina	1	1	0	0	1	0	1	1	0	0	1	1	0	0	?	0	1	?	1	0	0	0	0	0	1	0	1	0	0	0
Gypona decorata	0	0	3	0	0	0	0	?	0	0	0	?	0	0	?	0	2	2	1	0	0	0	0	0	1	2	1	3	0	1
Gypona thoracica	0	0	3	0	0	0	0	?	0	0	0	?	0	0	?	0	2	2	1	0	1	1	1	0	1	2	1	3	1	1
Iassus scutellaris	0	0	0	0	0	0	0	?	1	0	0	?	0	0	?	0	1	?	1	0	0	0	0	0	0	0	1	0	0	0
Krisna sp. 1	0	0	3	0	0	0	0	?	1	0	0	?	0	0	?	0	1	?	1	0	0	0	0	0	0	0	1	0	0	0
Lystridea uhleri	0	0	3	0	0	0	1	0	0	0	1	1	0	0	?	0	2	2	0	0	0	0	0	0	1	2	1	0	0	0
Tartessus australicus	0	0	3	1	0	0	0	?	0	0	0	?	0	0	?	0	1	?	0	0	0	0	0	0	0	0	1	0	0	0
Tartessus swezeyi	0	0	3	0	0	0	0	?	0	0	0	?	0	0	?	0	1	?	0	0	0	0	0	0	1	0	1	0	0	0

...continued below

TABLE 2. (continued)

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Afrorubria vitticollis	3	0	0	0	?	0	?	0	0	0	1	3	2	0	2	2	0	0	0	1	0	0	0	1	0	0	0	0	0	0
Bascarrhinus plathanon	2	0	0	2	1	1	1	1	0	0	0	3	2	1	?	?	0	1	0	1	0	2	1	0	1	1&3	0	1	1	0
Bascarrhinus platypoides	2	0	0	2	1	1	1	1	0	0	0	3	2	1	?	?	0	1	0	1	0	2	1	1	1	1&3	2	1	1	0
Beniledra peculiaris	2	0	0	2	0	0	?	0	0	0	1	2	1	0	1	0	0	0	1&2	1	0	0	1	1	1	2	1	0	2	0
Betsileonas marmorata	2	0	0	0	?	0	?	1	0	0	0	3	2	0	1	1	0	1	0	1	0	0	1	0	2	1	1	0	0	2
Clinonana mirabilis	3	0	0	3	2	0	?	0	0	0	0	1	2	1	?	1	0	1	0	1	0	0	0	1	1	1	1	0	3	1
Cololedra declivata	?	2	0	0	?	1	3	1	0	0	0	3	2	1	?	?	0	0	0	1	0	0	1	0	2	3	1	1	5	0
Confucius cameroni	2	0	0	2	0	0	?	0	0	0	1	2	2	0	1	0	0	0	0	1	1	0	1	1	1	0	0	1	2	0
Confucius dispar	1	0	0	2	0	0	?	0	0	0	1	2	2	0	1	0	0	0	0	1	0	0	1	1	1	0	0	1	2	0
Confucius zombanus	2	0	0	2	0	0	?	0	0	0	1	2	2	0	1	0	0	0	2	1	0	0	1	0	1	2	0	1	2	0
Dusuna sp. 1	1&2	0	0	1	2	0	?	0	0	0	1	2	2	0	1	1	0	0	0	1	0	0	1	0	1	0	1	0	2	0
Dusuna sp. 2	1&2	0	0	1	2	0	?	0	0	0	1	2	2	0	1	1	0	0	0	1	0	0	1	0	1	0	1	1	2	0
Epiclinata planata	3	0	0	2	2	0	?	0	0	0	1	2	2	0	1	1	0	0	0	1	0	0	1	1	1	0	1	0	2	0
Ezrana primitiva	1	0	0	2	0	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	1	1	2	3	1	1	2	0
Funkikonia sp. 1	1	0	0	2	0	0	?	0	0	0	1	2	1	0	1	0	0	0	0	0	0	0	2	1	1	3	1	0	2	0
Funkikonia sp. 2	1	0	0	2	0	0	?	0	0	0	1	2	2	0	1	0	0	0	0	1	0	0	2	1	2	3	1	1	2	0
Funkikonia tuberculata	1	0	0	2	0	0	?	0	0	0	1	2	2	0	1	0	0	0	0	1	0	0	2	1	1	1	1	1	2	0
Hangklipia gibber	1&2	0	0	0	?	0	?	0	0	0	1	2&3	1&2	0	1	0&1	0	0	0	1	0	0	1	0	1	0	1	0	2	0
Hangklipia signata	2&3	0	0	0	?	0	?	0	0	0	1	2	1&2	0	1	1	0	0	0	1	0	0	1	0	1	0	1	0	2	0
Hespenedra chilensis	3	0	0	0	?	0	?	0	0	0	1	2	1	0	2	0	0	0	1&2	1	0	0	1	1	1	0	1	0	2&5	0
Jukaruka grisea	0	0	0	1	0	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	1	0	2	3	1	1	2	0
Ledropsella monstrosa	0	0	1	1	0	0	?	0	0	0	1	2	1	0	1	2	1	0	0	1	0	0	2	0	2	3	1	1	2	0
Ledropsella sp.	0	0	1	1	0	0	?	0	0	0	1	2	1	0	1	2	1	0	0	1	0	0	1	1	2	3	1	1	2	0
Ledra auditura	1	0	0	2	0	0	?	0	0	0	1	2	1	0	1	0&1	0	0	0	1	0	0	2	0	2	3	1	1	1	0
Ledra aurita	0&2	0	0	2	0	0	?	0	0	0	1	2	1	0	1	1	0	0	0	1	0	0	2	1	2	3	1	1	1	0
Ledra mutica	0	0	0	2	0	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	2	0	2	1&3	1	0	2	0
Ledra tuberculifrons	1&2	0	0	2	0	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	2	1	2	3	1	1	1&2	0
Ledramorpha planirostris	1	0	0	2	3	1	2	1	1	0	1	1	2	0	1	0	0	0	0	0	0	2	1	1	2	2&3	1	1	2	0
Ledropsis discolor	1	0	0	2	0	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	2	0	2	1&2	1	1	2	0
Ledropsis froggatti	1	0	0&1	1	0	0	?	0	0	0	1	2	1&2	0	1	0	0	0	0	0&1	0	0	2	0	2	1&2	1	0	2	0
Ledropsis sp. 1	1&2	0	0	2	0	0	?	0	0	0	1	2	1	0	1	0	0	0	2	1	0	0	2	0	2	3	1	0	2	0
Neotituria kongasana	3	0	0	1	2	0	?	0	0	0	1	2	1	0	1	0	0	0	1&2	0	0	0	1	1	1	0	1	0	2	0
Parapetalocephala testacea	2	0	0	0	?	0	?	0	0	0	1	2	2	0	1	1	0	0	0	1	0	0	1	1	1	0	1	0	2	0
Petalocephala bohemani	1	0	0	1	2	0	?	0	0	0	1	2	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	2	0
Petalocephala conspicua	3	0	0	1	2	0	?	0	0	0	1	2	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	2	0
Petalocephala raniceps	3	0	0	1	2	0	?	0	0	0	1	2	1	0	1	0	0	0	1&2	0	0	0	1	1	1	0	1	0	2	0
Platyhynna bdellostoma	1	0	0	2	1	1	1	0	0	1	0	3	2	1	?	?	0	1	0	1	0	2	2	1	2	1	2	0	1	0
Platyhynna sp. 1	3	0	?	2	1	1	1	0	0	1	0	3	2	1	?	?	?	1	0	?	0	2	2	?	1	1&3	1	1	1	0
Platyledra acuminata	0	0	0	0	?	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	2	0	2	3	1	1	2	0
Platyledra caldida	0	0	0	0	?	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	2	0	2	3	1	1	2	0
Platyledra hirsuta	0	0	0	0	?	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	2	0	2	3	1	1	2	0
Porcorhinus mastersi	0	0	0	1	0	0	?	0	0	0	1	2	2	0	1	0	0	0	0	1	0	0	1	1	1	1	1	0	2	0
Proranus adspersipennis	3	1	0	3	2	0	?	0	0	0	2	0	0	0	0	1	0	0	0	1	1	0	1	0	1	2	1	0	5	3
Proranus ghilianii	3	1	0	3	2	0	?	0	0	0	2	0	0	0	0	1	0	0	0	1	1	0	2	0	1	2	1	0	5	3
Rubria brevifrons	1	0	0	0	?	0	?	0	0	0	1	2	2	0	2	0	0	0	1	1	0	0	2	1	0	0	0	0	4	0
Rubria informis	1&2	0	0	0	?	0	?	0	0	0	1	2	2	0	2	0&1	0	0	0	1	0	0	2	1	1	0	1	0	2&4	0
Rubria sanguinosa	1	0	0	0	?	0	?	0	0	0	1	2	2	0	2	0	0	0	0	1	0	0	2	1	2	0	1	0	2&4	0
Sichaea sp. 1	3	0	0	0	?	0	?	0	0	0	1	3	2	0	2	2	0	0	0	0	0	0	0	1	0	?	0	0	0&2	0
Stenoledra decorsei	1	0	0	0	?	0	?	0	0	1	2	2	2	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	5	0
Thlasia brunipennis	3	0	0	1	2	0	?	0	0	0	1	2	1&2	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	2	0
Thlasia corona	3	0	0	2	2	0	?	0	0	0	1	2	1&2	0	1	0	0	0	0&2	1	0	0	1	0	1	1	1	1	2	0
Titiella humerosa	2	0	0	0	?	0	?	0	0	0	1	2	2	0	2	2	0	0	0	1	0	0	1	1	1	0	1	0	2	0
Titiella punctiger	2	0	0	0	?	0	?	0	0	0	1	2	2	0	2	2	0	0	0	1	0	0	1	1	1	0	0	0	2	0
Tituria antica	3	0	0	1	2	0	?	0	0	0	1	2	2	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	2	0
Tituria forficula	1&2	0	0	2	2	0	?	0	0	0	1	2	1	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0	2	0
Tituria obtusa	2&3	0	0	2	2	0	?	0	0	0	1	2	1	0	1	0	0	0	0&2	1	0	0	1	0	1	0	1	0	2	0
genus 1	3	0	0	0	?	0	?	0	0	0	1	2	2	0	1	0	0	0	0	1	0	0	1	1	1	2	1	1	2	0
genus 2	?	0	0	0	?	0	?	0	0	0	1	2	2	0	2	2	0	0	0	1	0	0	0	1	0	?	0	0	2&5	0
genus 3	3	0	0	0	?	0	?	0	0	0	2	0	0	0	0	2	0	0	0	1	1	0	0	1	1	0	1	1	2&5	0
genus 4	3	0	0	0	?	1	0	1	0	0	1	0	3	0	0	2	0	0	0	0	1	0	1	1	1	0	1	1	5	0
Stenocotis depressa	?	0	0	2	3	1	2	1	1	0	1	1	2	0	1	2	0	0	0	0	0	2	1	1	1	0	1	1	2	0
Macroceps fasciatus	?	0	0	0	?	1	0	1	0	0	2	1&2	2	1	?	?	0	0	0	0	0	1	1	1	1	0	1	1	5	0
Thymbris convivus	?	0	0	0	?	1	0	1	0	0	2	1&2	2	1	?	?	0	0	0	0	0	1	1	1	1	0	1	0	5	0
Xedreota tuberculata	3	0	0	0	?	1	0	1	0	0	2	3	3	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	5	0
Xerophloea viridis	3	0	0	3	2	0	?	0	0	0	2	0	0	0	0	0	0	0	0	1	1	0	1	1	1	2	1	0	2	3
Aphrodes bicinctus	?	0	0	0	?	0	?	1	0	0	0	1	2	0	0	?	0	0	0	1	0	0	1	1	0	?	0	1	5	0
Bathysmatophorus shabliovskii	?	0	0	0	?	0	?	1	0	0	0	0	0	1	?	?	0	0	0	1	0	0	0	0	1	3	1	1	5	0
Coloborrhis corticina	?	2	0	0	?	1	3	1	0	1	0	2	2	1	?	?	0	0	0	1	0	0	1	0	2	3	1	1	5	0
Gypona decorata	?	0	0	0	?	0	?	0	0	0	0	1	2	1	?	?	0	1	0	1	0	0	0	1	0	?	0	0	0	1
Gypona thoracica	?	0	0	3	2	1	0	0	0	0	0	1	2	1	?	?	0	1	0	1	0	0	0	1	1	0	0	0	0	1
Iassus scutellaris	?	0	0	0	?	0	?	0	0	0	0	0	0	1	?	?	0	0	0	1	0	0	1	1	1	0	0	0	0	0
Krisna sp. 1	?	0	0	0	?	1	0	1	0	0	0	3	2	1	?	?	0	0	0	1	0	1	1	1	1	1	0	0	5	3
Lystridea uhleri	?	0	0	0	?	1	0	1	0	0	0	0	0	1	?	?	0	0	0	1	0	0	0	1	1	0	0	1	5	0
Tartessus australicus	?	0	0	0	?	1	0	1	0	0	0	3	2	1	?	?	0	0	0	1	0	1	1	1	1	0	0	1	5	0
Tartessus swezeyi	?	0	0	0	?	1	0	1	0	0	0	3	2	1	?	?	0	0	0	0	0	1	1	0	1	0&1	1	1	5	0

...continued below

TABLE 2. (continued)

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Afrorubria vitticollis	0	1	1&2	0	?	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	?	?	0	1	0	0	0	0	0	0
Bascarrhinus plathanon	1	1	1	0	?	4	0	0	2	0	0	0	1	1	0	0	0	0	0	0	?	?	0	1	0	0	0	?	0	0
Bascarrhinus platypoides	1	1	0	0	?	4	0	0	2	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	?	0	0
Beniledra peculiaris	0&1	0	1	0	?	4	1	2	0	0	1	0	0&1	1	0	0	0	1	0	1	1	?	1	2	1	0	0	2	1	0
Betsileonas marmorata	1	1	2	0	?	2	0	1	1	0	1	0	0	?	0	0	0	0	0	1	1	?	0	1	0	0	0	?	?	0
Clinonana mirabilis	1	0	1	1	2	0	0	0	1&2	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	0	0	0
Cololedra declivata	3	0	1	0	?	0	2	0	2	0	1	0	1	1	0	0	0	0	0	1	0	1	0	0	?	0	0	?	1	0
Confucius cameroni	1	0	1	0	?	4	0	0	0	1	1	0	0	?	0	0	0	1	0	1	1	?	0	2	1	0	0	0	1	0
Confucius dispar	1	0	1	0	?	0	0	0	0	0	1	0	0	?	0	0	0	1	0	1	1	?	?	2	1	0	0	2	1	0
Confucius zombanus	1	0	1	0	?	0	0	0	0	1	1	0	0	?	0	0	0	1	0	1	1	?	1	2	1	0	0	0	1	0
Dusuna sp. 1	1	0	1	1	0	3	1	0	1	0	1	0	0	?	0	0	0	1	1	1	0	?	0	2	1	0	0	2	0	1
Dusuna sp. 2	1	0	1	1	0	3	1	0	1	0	1	0	1	1	0	0	0	1	1	1	0	?	0	2	1	0	0	2	0	1
Epiclinata planata	0	0	1	1	1	3	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	?	0	2	1	0	0	?	0	0
Ezrana primitiva	2	1	0	0	?	0	1	2	0	1	1	1	1	2	1	0	0	1	1	1	0	?	1	2	3	0	0	1	1	1
Funkikonia sp. 1	2	1	0	0	?	4	0	1	0	1	1	0	0	?	0	0	0	1	0	1	0	?	0	2	1	0	0	1	1	0
Funkikonia sp. 2	2	1	1	0	?	0	0	1	0	1	1	0	0	?	0	0	0	1	0	1	0	?	0	2	1	0	0	1	1	0
Funkikonia tuberculata	2	1	1	0	?	4	0	0	0	1	1	0	0	?	0	0	0	1	0	1	0	?	1	2	1	0	0	1	1	0
Hangklipia gibber	1	0	1	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	?	?	0	2	1	0	0	0	0	0
Hangklipia signata	1	0	1	0	?	0	0	0	0	0	1	0	0	?	0	0	0	1	0	1	0	?	1	2	1	0	?	0	0	0
Hespenedra chilensis	0	0	1	0	?	0	0	0&1	0	0	1	0	0	?	0	0	0	0	0	1	?	?	0	2	1	0	0	0	1	0
Jukaruka grisea	2	1	1&2	0	?	4	0	2	0	1	1	1	1	2	0	0	0	0	0	1	0	0	0	2	3	0	0	2	1	0
Ledropsella monstrosa	2	1	1	0	?	4	0	0	0	1	1	1	1	2	0	0	0	0	0	1	0	0	0	2	?	0	0	0	1	0
Ledropsella sp.	2	1	1	0	?	4	0	2	0	1	1	1	1	2	0	0	0	0	0	1	0	0	0	2	3	0	0	2	1	0
Ledra auditura	2	0	1	0	?	0	0&1	1	0	1	1	1	2	3	2	0	0	1	0	1	0	?	0	2	1	0	0	0	1	0
Ledra aurita	2	0	1	0	?	0	0	1	0	1	1	1	0&2	3	2	0	0	1	0	1	0	?	0	2	1	0	0	0	1	0
Ledra mutica	2	1	1&2	0	?	0	0	0	0	1	1	1	2	4	1	0	0	1	0	0	0	?	1	2	1	0	0	2	1	0
Ledra tuberculifrons	2	1	0	0	?	0	0	0	0	1	1	1	2	0	1	0	0	1	0	1	0	0	0	2	1	0	0	2	1	1
Ledramorpha planirostris	1	0	1	0	?	1	1	0	2	0	1	0	0	?	0	0	0	0	0	0	0	?	0	1	0	0	0	?	1	0
Ledropsis discolor	2	0	1	0	?	0	0	0	0	1	1	0	0	?	0	0	0	1	0	1	0	?	0	2	1	0	0	1	1	0
Ledropsis froggatti	1	1	0	0	?	4	1	0	0	0	1	0	0	?	0	0	0	0	0	1	?	?	1	2	3	0	0	0	1	0
Ledropsis sp. 1	2	1	0	0	?	0	0	1	0	1	1	0	0	?	0	0	0	1	0	1	0	?	1	2	1	?	0	2	0	0
Neotituria kongasana	0	0	1	1	1	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	?	?	0	2	1	0	0	0	1	0
Parapetalocephala testacea	1	0	1	0	?	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	1	?	0	2	1	0	0	2	1	1
Petalocephala bohemani	0	1	0	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	?	0	2	1	0	0	0	0	0
Petalocephala conspicua	0	0	1	0	?	0	0	0	0	0	1	0	0	?	0	0	0	0	0	0	?	?	0	2	1	0	0	0	1	0
Petalocephala raniceps	0	0	1	0	?	0	0	0	0	0	1	0	0	?	0	0	0	0	0	0	?	?	0	2	1	0	0	0	0	0
Platyhynna bdellostoma	2	0	1	0	?	4	0	0	2	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	?	0	0	0
Platyhynna sp. 1	2	0	1	0	?	4	?	?	2	0	1	?	1	1	0	?	0	0	0	0	0	1	0	?	?	0	0	?	0	0
Platyledra acuminata	1	1	0	0	?	4	0	2	0	0	1	1	1	2	0	0	0	0	0	1	0	0	0	2	3	0	0	2	1	0
Platyledra caldida	2	1	0	0	?	4	0	2	0	1	1	1	1	2	0	0	0	0	0	1	0	0	0	2	3	0	0	2	1	0
Platyledra hirsuta	2	1	0	0	?	4	0	2	0	0	1	1	1	2	0	0	0	0	0	1	0	0	0	2	3	0	0	2	1	0
Porcorhinus mastersi	2	1	0	0	?	0	1	0	0	0	1	0	0	?	2	0	0	0	0	1	?	?	0	2	3	0	0	?	0	0
Proranus adspersipennis	3	0	1	1	2	0	0	0	0	0	0	0	0	?	0	1	0	0	0	0	?	?	0	2	2	0	0	0	0	0
Proranus ghilianii	3	0	1	1	2	0	0	1	2	0	0	0	1	1	0	1	0	0	0	0	?	?	0	2	2	0	0	0	0	0
Rubria brevifrons	1	1	0	0	?	0	0	1	2	0	0	0	0	?	0	0	0	0	0	0	?	?	0	1	0	0	0	0	?	0
Rubria informis	1	1	0	0	?	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	?	?	0	1	0	0	0	0	0	0
Rubria sanguinosa	0	1	0	0	?	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0	?	0	1	0	0	0	?	0	0
Sichaea sp. 1	0	1	1&2	0	?	0	0	0	1	0	1	0	0	?	0	0	0	0	0	0	?	?	0	1	0	0	0	0	0	0
Stenoledra decorsei	0	1	2	0	?	4	0	0	0	0	0	0	0	?	0	1	1	0	0	0	?	?	0	1	0	1	0	0	?	0
Thlasia brunipennis	0	0	1	1	0	3	0	0	0	0	1	0	0	?	0	0	0	0	0	0	?	?	1	2	1	0	0	0	0	0
Thlasia corona	0	0	1	1	0	3	0	0	0	1	1	0	0	?	0	0	0	0	0	1	1	?	1	2	1	0	0	2	0	0
Titiella humerosa	2	0	1	0	?	0	0	0	0	0	1	0	0	?	0	0	0	0	0	1	1	?	0	2	1	0	0	2	1	0
Titiella punctiger	2	0	1	0	?	0	0	0	0	0	1	0	0	?	0	0	0	1	0	1	1	?	0	2	1	0	0	0	1	0
Tituria antica	0	0	1	1	1	3	0	0	0	1	0	0	0	?	0	0	0	0	0	0	0	?	0	2	1	0	0	?	0	0
Tituria forficula	0	0	1	1	1	3	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	?	0	2	1	0	0	?	0	0
Tituria obtusa	0	0	1	1	0	3	0	0	0	0	1	0	0	?	0	0	0	1	0	1	1	?	1	2	1	0	0	2	0	0
genus 1	0	1	1	0	?	4	0	0	0	0	1	0	0	?	0	0	0	1	0	1	?	?	0	2	1	0	0	0	1	1
genus 2	0	1	1&2	0	?	0	0	0	1	0	0	0	0	?	0	0	0	0	0	1	?	?	0	1	0	0	?	?	0	0
genus 3	1	1	1&2	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	?	?	0	1	0	0	?	?	0	0
genus 4	0	1	1	0	?	0	0	0	1	0	0	0	0	?	0	0	0	0	0	0	?	?	0	1	0	0	0	?	0	0
Stenocotis depressa	1	0	1	0	?	1	0	0	2	0	1	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	0	1	0
Macroceps fasciatus	3	0	1	0	?	1	0	0	2	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	?	0	0
Thymbris convivus	3	0	1	0	?	1	0	0	2	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	?	1	0
Xedreota tuberculata	1	0	1	0	?	0	0	0	0	0	1	0	0	?	0	0	0	0	0	1	?	?	0	1	0	0	0	2	0	0
Xerophloea viridis	1	0	1	0	?	0	0	1	0	0	1	0	1	1	0	1	0	0	0	1	0	?	0	2	2	0	0	2	0	0
Aphrodes bicinctus	0	0	1	0	?	4	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	?	0	0	?	0	0	0	0	0
Bathysmatophorus shabliovskii	0	0	1	0	?	0	0	0&1	1	0	1	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	1	0	0	0
Coloborrhis corticina	3	1	0	0	?	4	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	1	0	1	0	1	0	0	1	0
Gypona decorata	1	0	1	0	?	0	0	0	1	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	?	0	0
Gypona thoracica	1	0	1	0	?	0	0	0	1	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	0	0	0
Iassus scutellaris	1	0	1	0	?	0	0	0	2	0	1	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	0	?	0
Krisna sp. 1	1	0	1	0	?	0	0	0	2	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	1	0	0	0	1	0
Lystridea uhleri	0	0	1	0	?	0	0	0	1	0	1	0	0	?	0	0	0	0	0	1	1	?	0	1	0	0	1	0	1	0
Tartessus australicus	0	0	1	0	?	0	0	0	2	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	0	0	0
Tartessus swezeyi	1	0	1	0	?	1	0	0	2	0	0	0	0	?	0	0	0	0	0	1	0	?	0	1	0	0	0	0	0	0

...continued below

TABLE 2. (continued)

	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Afrorubria vitticollis	0	0	0	0	1	1	0	0	0	0	?	1	0	0	?	?	0	0	0	1	0	0	0	0	0	0	0	0	?	1
Bascarrhinus plathanon	0	0	0	0	0	1	0	0	0	1	1	1	2	1	1	1	1	2	0	1	0	1	1	0	2	0	2	0	?	1
Bascarrhinus platypoides	0	0	0	0	0	0	0	0	0	1	1	1	2	1	1	1	1	2	0	1	0	1	0	0	2	0	2	0	?	1
Beniledra peculiaris	0	0	0	0	1	1	0	0	0	1	1	1	2	1	1	0	1	1	0	1	0	0	1	0	1	1	1	1	0	1&2
Betsileonas marmorata	0	0	0	0	0	1	0	1	0	2	1	2	1	0	?	?	1	0	0	1	0	1	0	0	1	0	1	0	?	3
Clinonana mirabilis	0	0	0	0	0	0	0	0	0	0	0	2	2	1	0	1	1	1	0	1	0	0	0	0	1	0	1	0	?	3
Cololedra declivata	0	0	0	0	0	2	0	0	0	1	0	2	2	1	1	?	1	1	0	1	0	1	0	0	2	0	1	0	?	2
Confucius cameroni	1	0	1	1	1	1	1	1	0	1	0	1	2	1	1	1	1	1	0	1	0	0	1	1	1	0	1	1	1	2
Confucius dispar	0	0	1	1	1	1	0	0	0	1	0	1	2	1	1	1	1	1	0	1	0	0	1	1	1	1	1	1	0	2
Confucius zombanus	1	0	1	1	1	1	0	0	0	1	1	1	2	1	1	?	1	1	0	1	0	0	1	0	0	0	0	1	1	2
Dusuna sp. 1	0	0	0	0	2	1	0	0	1	0	0	1	2	1	1	1	1	1	1	1	0	0	1	0	0	1	0	1	0	2
Dusuna sp. 2	0	0	0	0	2	1	0	0	1	0	0	1	2	1	1	1	1	1	1	1	0	0	1	0	0	1	0	1	0	1
Epiclinata planata	0	0	0	0	0	1	0	0	0	1	1	1	2	1	1	1	1	0	1	1	0	0	1	1	0	1	0	1	0	1
Ezrana primitiva	1	1	0	0	0	2	0	0	0	1	1	1	2	1	1	0&1	1	2	0	1	0	0	0	0	2	?	2	1	0	1
Funkikonia sp. 1	1	1	1	1	0	2	0	0	0	1	1	1	2	1	1	0&1	1	2	0	1	0	0	1	0	2	0	2	1	1	2
Funkikonia sp. 2	1	1	1	1	0	2	1	0	0	1	1	1	1	1	1	?	1	2	1	1	0	0	0	0	2	0	2	1	1	2
Funkikonia tuberculata	1	1	1	1	0	2	0	0	0	1	1	1	1	1	1	0&1	1	2	0	1	0	0	0	0	2	0	2	1	1	2
Hangklipia gibber	0	0	1	1	1	2	0	0&1	0	0	0	1	2	1	1	0&1	1	1	0	1	0	0	1	0	1	0	1	1	0	2
Hangklipia signata	0	0	1	0	2	2	1	1	0	0	0	1	2	1	1	1	1	1	0	1	0	0	1	0	1	0	1	1	0	2
Hespenedra chilensis	0	0	0	0	2	1&2	0&1	0&1	0	1	1	1	2	1	1	?	1	1	0	1	0	0	1	0	0	0	0	1	0	2
Jukaruka grisea	1	0	1	1	0	1	0	0	0	1	1	1	2	1	1	0&1	1	2	0	1	0	0	0	0	2	0	2	1	0	1
Ledropsella monstrosa	1	1	0	0	1	2	0	0	0	1	1	0	2	1	1	?	1	1	0	1	0	0	?	0	2	?	2	?	?	1
Ledropsella sp.	1	0	1	1	0	1	0	0	0	1	1	0	2	1	1	0&1	1	2	0	1	0	0	0	0	2	0	2	1	0	1
Ledra auditura	0	0	1	1	0	2	0	0	0	1	1	1	2	1	1	?	1	2	0	1	0	0	1	0	2	0	2	1	1	2
Ledra aurita	0	0	1	1	0	2	0	0	0	1	1	1	2	1	1	1	1	2	0	1	0	0	1	0	2	1	2	1	1	1
Ledra mutica	0	0	1	1	0	1&2	0	0	0	1	1	1	1	1	1	0	1	2	0	1	0	0	1	0	2	0	2	1	1	2
Ledra tuberculifrons	1	1	1	1	0	1	0	0&1	0	1	1	1	1	1	1	0&1	1	1	1	1	0	0	0	0	2	0	2	1	1	2
Ledramorpha planirostris	0	0	0	0	2	2	0	0	1	2	2	1	0	1	1	?	1	1	0	1	0	0	0	0	2	1	2	0	?	2
Ledropsis discolor	0	0	1	1	1	2	0	0	0	1	1	1	2	1	1	0&1	1	2	0	1	0	0	1	0	2	0	2	1	1	2
Ledropsis froggatti	0	0	0	0	0	2	0	0	0	1	1	1	2	1	1	?	1	2	0	1	0	0	0	0	2	0	2	1	0	1
Ledropsis sp. 1	0	0	1	1	0	2	0	0	0	1	1	0	2	1	1	0&1	1	1	1	1	0	0	0	0	2	1	2	1	1	2
Neotituria kongasana	1	0	0	0	0	2	0	0	0	1	1	1	1	1	1	?	1	1	1	1	0	0	1	1	0	1	0	1	0	2
Parapetalocephala testacea	0	0	0	0	2	2	1	0	0	1	0	1	2	1	1	0&1	1	1	0	1	0	0	1	1	0	1	0	1	0	2
Petalocephala bohemani	1	0	0	0	1	1	0	1	0	1	1	1	2	1	1	?	1	1	1	1	0	0	1	0	0	1	0	1	0	2
Petalocephala conspicua	1	0	0	0	1	1	0	0	0	1	1	1	2	1	1	1	1	1	1	1	0	0	1	0	0	1	0	1	0	1
Petalocephala raniceps	0	0	0	0	1	1	0	0	0	1	1	1	2	1	1	?	1	1	1	1	0	0	1	0	0	1	0	1	0	2
Platyhynna bdellostoma	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	0	0	0	1	?	?	2	0	2	0	?	1
Platyhynna sp. 1	0	?	0	0	0	2	0	0	0	1	1	1	2	1	?	1	1	1	?	0	0	1	?	?	2	?	2	0	?	1
Platyledra acuminata	1	0	1	1	0	2	0	0	0	1	1	1	1	1	1	0	1	2	0	1	0	0	0	0	2	0	2	1	0	1
Platyledra caldida	1	0	1	1	0	2	0	0	0	1	1	1	1	1	1	0&1	1	2	0	1	0	0	?	?	2	?	2	1	0	1
Platyledra hirsuta	1	1	1	1	0	1	0	0	0	1	1	1	1	1	1	0	1	2	0	1	0	0	0	0	2	0	2	1	0	1
Porcorhinus mastersi	0	0	0	0	0	1	1	0	0	1	1	1	2	1	1	1	1	2	0	1	0	0	0	0	2	0	2	?	?	1
Proranus adspersipennis	0	0	0	0	2	1	0	1	0	0	?	2	2	1	1	?	1	1	0	1	0	0	0	0	0	1	0	0	?	2
Proranus ghilianii	0	0	0	0	2	1	0	1	0	0	?	2	2	1	1	?	1	1	0	1	0	0	0	0	0	1	0	0	?	2
Rubria brevifrons	0	0	0	0	0	1	0	0	0	0	?	1	1	0	?	?	1	0	0	1	0	0	1	0	1	0	1	0	?	1
Rubria informis	0	0	0	0	0	2	0&1	0&1	0	0	?	1	2	1	1	1	1	0	0	1	0	0	1	0	1	0	1	0	0	1
Rubria sanguinosa	0	0	0	0	0	2	0	0	0	0	?	1	1	0	?	?	1	0	0	1	0	0	1	0	1	0	1	0	?	1
Sichaea sp. 1	0	0	0	0	1	1	0	0	0	0	?	0	0	0	?	?	1	0	0	1	1	?	0	0	0	0	0	0	?	1
Stenoledra decorsei	0	0	0	0	0	1	0	0	0	1	0	1	2	1	1	?	1	0	0	1	0	0	0	0	2	1	2	0	?	0
Thlasia brunipennis	1	0	0	0	2	1	0	0	0	1	1	1	2	1	1	?	1	1	0	1	0	0	1	0	0	1	0	1	0	2
Thlasia corona	1	0	0	0	2	1	1	1	0	1	1	1	2	1	1	0&1	1	1	1	1	0	0	1	0	0	1	0	1	0	2
Titiella humerosa	0	0	0	0	2	2	1	0	0	0	?	1	2	1	1	1	1	1	0	1	0	0	1	0	0	0	0	1	0	2
Titiella punctiger	0	0	0	0	1	2	0	0	0	0	?	0	2	1	1	?	1	0	0	1	0	0	1	0	0	0	0	1	1	2
Tituria antica	0	0	0	0	0	1	0	0	0	1	1	1	2	1	1	?	1	1	1	1	0	0	1	1	0	1	0	1	0	2
Tituria forficula	1	0	0	0	0	1	0	0	0	1	1	1	2	1	1	?	1	1	1	1	0	0	1	1	0	1	0	1	0	2
Tituria obtusa	1	0	0	0	2	1	1	1	0	1	1	1	2	1	1	?	1	1	0	1	0	0	1	0	0	1	0	1	0	2
genus 1	0	0	0	0	1	2	0	0	0	1	0	1	2	1	1	0&1	1	1	1	1	0	0	1	0	0	1	1	1	1	2
genus 2	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	?	1	0	0	1	1	?	0	0	0	0	0	0	?	1
genus 3	0	0	0	0	1	0	0	0	0	0	?	0	2	1	1	?	1	0	0	1	1	?	?	?	0	0	0	0	?	1
genus 4	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	?	1	1	0	1	1	?	0	0	0	0	0	0	?	1
Stenocotis depressa	0	0	0	0	2	2	0	0	1	1	1	1	0	1	1	0	1	1	1	1	0	0	1	0	2	0	1	0	0	2
Macroceps fasciatus	0	0	0	0	0	2	0	0	0	0	?	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	?	2
Thymbris convivus	0	0	0	0	0	2	0	0	0	0	?	1	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	?	2
Xedreota tuberculata	0	0	0	0	0	1	0	0	0	0	?	1	2	1	1	?	1	1	0	1	0	0	1	0	0	1	0	0	?	1
Xerophloea viridis	0	0	0	0	1	1	0	1	0	0	?	2	2	1	1	1	1	1	0	1	0	0	0	0	0	1	0	0	?	2
Aphrodes bicinctus	0	0	0	0	0	1	0	0	0	0	?	1	0	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	?	3
Bathysmatophorus shabliovskii	0	0	0	0	0	0	1	0	0	0	0	2	0	1	1	0&1	1	0	0	1	0	0	0	0	1	0	1	0	?	3
Coloborrhis corticina	0	0	0	0	0	1	0	0	0	1	1	1	2	1	1	1	1	0	0	1	0	0	0	0	2	1	2	0	?	0
Gypona decorata	0	0	0	0	0	0	0	0	0	0	?	2	1	1	0	0&1	1	1	0	1	0	0	0	0	0	0	0	0	?	3
Gypona thoracica	0	0	0	0	0	0	0	0	0	0	?	2	0	1	0	?	1	1	0	1	0	0	0	0	0	0	0	0	?	3
Iassus scutellaris	0	0	0	0	0	1	0	0	0	0	0	2	2	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	?	2
Krisna sp. 1	0	?	0	0	0	1	0	0	0	1	0	2	2	0	?	0	1	1	0	1	0	0	0	0	1	0	1	?	?	2
Lystridea uhleri	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	?	0	0	0	1	0	0	0	0	1	0	1	0	?	3
Tartessus australicus	0	0	0	0	0	2	0	0	0	0	?	2	0	1	1	?	1	0	0	1	0	0	0	0	0	0	0	0	?	3
Tartessus swezeyi	0	0	0	0	0	2	0	0	0	0	?	2	0	1	1	0&1	1	1	0	1	0	0	0	0	0	0	0	0	?	3

...continued below

TABLE 2. (continued)

	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150
Afrorubria vitticollis	0	1	0	1	1	0	0	0	1	0	1	?	0	0	2	3	0	?	0	1	0	2	2	2	0	0	1	0	1	0
Bascarrhinus plathanon	1	2	1	2	0	1	0	1	2	0	0	?	0	0	0	3	1	0	0	0	1	0	0	1	0	0	0	?	?	0
Bascarrhinus platypoides	1	2	1	1	0	1	0	1	2	0	0	?	0	0	0	2	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Beniledra peculiaris	1	2	0	1	2	1	0	0	1	0	0	?	0	1	0	2	0	?	0	0	0	0	2	2	0	1	0	?	?	0
Betsileonas marmorata	0	0	2	2	0	0	0	0	2	0	1	?	0	0	2	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Clinonana mirabilis	0	0	2	2	0	0	0	0	2	0	1	?	0	1	2	3	0	?	0	0	0	2	2	0	0	1	1	0	1	0
Cololedra declivata	0	0	0	2	0	1	0	1	2	0	0	?	0	0	2	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Confucius cameroni	1	1	0	1	1	1	0	0	1	0	0	?	0	1	1	3	0	?	0	0	0	1	1	2	0	0	0	?	?	0
Confucius dispar	1	1	0	1	1	1	0	0	1	0	0	?	0	1	1	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Confucius zombanus	1	1	0	1	1	1	0	0	1	0	0	?	0	1	1	2	0	?	0	0	0	0	2	2	0	0	0	?	?	0
Dusuna sp. 1	1	1	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Dusuna sp. 2	1	1	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	0	0	2	2	2	0	0	0	?	?	0
Epiclinata planata	1	1	0	1	2	0	0	0	1	0	0	?	0	1	1	3	0	?	0	1	0	0	1	0	0	1	0	?	?	0
Ezrana primitiva	1	2	1	1	2	1	0	1	2	0	?	?	1	0	2	3	1	0	0	0	?	?	?	?	?	?	?	?	?	?
Funkikonia sp. 1	1	0	1	1	2	1	1	1	2	0	?	?	?	1	0	2	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Funkikonia sp. 2	1	0	1	1	2	1	1	1	2	0	?	?	0	1	0	2	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Funkikonia tuberculata	1	0	1	1	2	1	1	1	2	0	?	?	0	1	0	2	0	?	0	0	0	0	1	0	1	0	1	1	2	0
Hangklipia gibber	1	1	0	1	1	1	0	0	1	0	1	?	1	1	1	1&3	0	?	0	0	0	0	1	0	0	0	0	?	?	0
Hangklipia signata	1	1	0	1	1	1	0	0	1	0	1	?	0	1	1	3	0	?	0	0	0	0	1	2	0	0	0	?	?	0
Hespenedra chilensis	1	2	0	1	2	1	0	0	1	0	?	?	0	0	0	3	2	0	0	1	0	0	0	0	0	0	1	0	0	0
Jukaruka grisea	1	2	1	1	2	1	1	1	2	0	?	?	0	1	0	3	1	0	0	0	0	0	0	0	0	0	0	?	?	0
Ledropsella monstrosa	1	2	1	1	2	1	1	1	2	0	?	?	0	1	0	0	1	0	0	0	?	?	?	?	?	?	?	?	?	?
Ledropsella sp.	1	2	1	1	2	1	1	1	2	0	?	?	0	1	0	0	1	0	?	0	?	?	?	?	?	?	?	?	?	?
Ledra auditura	1	1	1	1	2	1	1	1	2	0	0	?	1	1	0	2	0	?	0	0	0	0	0	0	0	0	1	0	0	0
Ledra aurita	1	1	1	1	2	1	1	1	2	0	0	?	1	1	0	2	0	?	0	0	0	0	0	0	0	0	1	0	0	0
Ledra mutica	1	1	1	1	2	1	1	1	2	0	0	?	0	1	0	2	0	?	0	0	0	0	0	0	0	0	1	0	0	0
Ledra tuberculifrons	1	1	1	1	2	1	1	1	2	0	?	?	0	1	0	2	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Ledramorpha planirostris	1	1	1	2	1	1	0	1	2	1	?	0	0	0	0	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Ledropsis discolor	1	1	1	1	2	1	1	1	2	0	0	?	1	1	0	2	0	?	0	0	0	0	0	0	0	0	1	0	2	0
Ledropsis froggatti	1	1	1	1	2	1	0	1	2	0	?	0	1	0	0	3	1	0	0	0	0	0	0	1	0	0	0	?	?	0
Ledropsis sp. 1	1	1	1	1	1	1	1	1	1	0	?	?	0	1	0	2	0	?	0	0	0	0	0	2	0	0	1	0	0	0
Neotituria kongasana	1	1	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	1	0	1	1	0	0	0	1	2	0	1
Parapetalocephala testacea	1	1	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Petalocephala bohemani	1	1	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	1	?	?	?	?	?	?	?	?	?	?
Petalocephala conspicua	1	2	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	1	0	0	0	2	1	0	1	2	0	0
Petalocephala raniceps	1	1	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	1	0	0	0	2	0	1	1	0	0	0
Platyhynna bdellostoma	1	1	1	1	0	1	0	1	1	0	0	?	0	0	0	0	1	0	0	0	1	2	2	0	0	0	0	?	?	0
Platyhynna sp. 1	?	0	1	2	?	?	?	?	?	?	?	?	0	0	?	?	1	0	?	0	1	2	2	0	0	0	0	?	?	0
Platyledra acuminata	1	2	1	1	2	1	1	1	2	0	?	0	1	0	0	3	1	0	0	0	?	?	?	?	?	?	?	?	?	?
Platyledra caldida	1	2	1	1	2	1	1	1	2	0	?	0	1	1	0	3	1	1	0	0	0	0	0	0	0	0	0	?	?	0
Platyledra hirsuta	1	2	1	1	2	1	1	1	2	0	?	0	0	0	0	3	1	1	0	0	?	?	?	?	?	?	?	?	?	?
Porcorhinus mastersi	1	2	1	2	2	1	0	1	2	0	?	?	1	1	0	3	1	0	0	0	?	?	?	?	?	?	?	?	?	?
Proranus adspersipennis	0	1	0	1	1	1	0	0	1	0	1	?	0	0	2	3	0	?	0	0	0	2	2	2	0	0	0	?	?	0
Proranus ghilianii	0	1	0	1	1	0	0	0	1	0	1	?	0	0	2	3	0	?	0	0	0	0	2	2	0	0	0	?	?	0
Rubria brevifrons	1	2	0	1	1	1	0	0	1	0	0	?	0	0	1	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Rubria informis	1	2	0	1	1	1	0	0	0	0	0	?	0	0	2	0	0	?	0	0	0	2	2	2	0	0	0	?	?	0
Rubria sanguinosa	1	2	0	1	1	0	0	0	1	0	0	?	0	0	1	3	0	?	0	0	0	2	2	2	0	0	0	?	?	0
Sichaea sp. 1	0	1	0	1	1	1	0	0	0	0	?	?	0	1	2	3	0	?	0	1	?	?	?	?	?	?	?	?	?	?
Stenoledra decorsei	?	0	1	0	0	1	0	1	0	0	0	?	0	0	0	0	0	?	0	0	0	1	0	2	0	0	0	?	?	0
Thlasia brunipennis	1	1	0	1	2	1	0	0	1	0	1	?	0	1	1	3	0	?	0	1	0	1	1	2	0	0	0	?	?	0
Thlasia corona	1	1	0	1	2	1	0	0	1	0	1	?	0	1	1	3	0	?	0	1	0	0	1	1	0	1	0	?	?	0
Titiella humerosa	1	1	0	1	1	1	0	0	1	0	0	?	0	1	1	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Titiella punctiger	1	1	0	1	1	1	0	0	1	0	0	?	0	1	1	3	0	?	0	0	?	?	?	?	?	?	?	?	?	?
Tituria antica	1	1	0	2	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	1	0	0	1	0	0	0	0	?	?	0
Tituria forficula	1	1	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	1	?	2	2	0	0	1	1	0	0	0
Tituria obtusa	1	1	0	1	2	1	0	0	1	0	0	?	0	1	1	3	0	?	0	1	0	2	2	0	0	0	1	0	0	0
genus 1	1	1	1	1	2	1	0	1	2	0	0	?	0	0	0	2	0	?	0	0	0	1	0	1	0	1	1	0	0	0
genus 2	0	1	0	1	1	1	0	0	1	0	1	?	0	0	2	0	0	?	0	1	0	2	2	2	0	0	1	0	0	0
genus 3	0	0	0	1	1	1	0	0	1	0	1	?	0	0	2	3	0	?	0	1	0	2	2	2	0	0	1	0	1	0
genus 4	0	1	0	1	1	1	0	0	1	0	1	?	0	0	2	3	0	?	0	1	0	0	2	2	0	1	1	0	1	0
Stenocotis depressa	1	1	0	1	2	1	0	0	2	1	?	1	1	0	0	3	0	?	0	0	0	1	0	0	0	0	0	?	?	0
Macroceps fasciatus	0	1	2	2	1	1	0	0	1	1	?	1	0	0	0	3	0	?	0	0	0	1	2	2	0	1	1	0	0	0
Thymbris convivus	0	1	2	2	1	1	0	0	1	1	?	1	0	0	0	3	0	?	0	0	0	0	0	2	0	0	0	?	?	0
Xedreota tuberculata	0	1	2	2	1	1	0	0	1	0	1	?	0	0	2	3	0	?	0	0	0	0	2	2	0	0	0	?	?	0
Xerophloea viridis	0	0	0	1	1	1	0	0	1	0	1	?	0	0	2	3	0	?	0	0	0	2	2	2	0	0	0	?	?	0
Aphrodes bicinctus	0	0	2	2	0	1	0	0	2	0	0	?	0	0	0	2	1	0	1	0	0	2	2	2	0	0	1	0	1	0
Bathysmatophorus shabliovskii	0	0	2	2	0	0	0	0	2	0	0	?	0	0	2	3	0	?	0	0	0	1	2	2	0	1	0	?	?	0
Coloborrhis corticina	?	0	1	0	0	1	0	1	0	0	?	?	0	0	0	1	0	?	0	0	0	1	0	2	0	0	0	?	?	0
Gypona decorata	0	0	2	2	0	0	0	0	2	0	1	?	0	0	2	0	0	?	0	0	0	0	0	2	0	1	1	0	1	0
Gypona thoracica	0	0	2	2	0	0	0	0	2	0	1	?	0	0	2	0	0	?	0	0	0	2	2	2	0	1	1	0	1	0
Iassus scutellaris	0	0	2	2	0	1	0	0	2	0	0	?	0	1	2	3	0	?	0	0	0	1	2	2	0	0	0	?	?	0
Krisna sp. 1	1	0	1	2	0	0	0	0	2	0	0	?	0	0	2	0	1	?	1	0	0	1	2	2	0	0	0	?	?	?
Lystridea uhleri	0	0	2	2	0	0	0	0	2	0	0	?	0	0	2	3	0	?	0	0	0	0	2	2	0	0	0	?	?	0
Tartessus australicus	0	1	2	2	1	1	0	0	2	0	1	?	0	0	2	3	0	?	0	0	0	2	2	2	0	0	1	0	0	0
Tartessus swezeyi	0	1	2	2	1	1	0	0	2	0	1	?	0	0	2	3	0	?	0	0	0	1	2	2	0	1	0	?	?	0

...continued below

TABLE 2. (continued)

	151	152	153	154	155	156	157	158	159	160	161	162	163	164	165	166	167	168	169	170	171	172	173	174	175	176	177	178	179	180
Afrorubria vitticollis	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	?
Bascarrhinus plathanon	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	?	0	?	?	0	?	?	?	1	0	?
Bascarrhinus platypoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Beniledra peculiaris	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	?
Betsileonas marmorata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Clinonana mirabilis	0	0	0	0	0	0	1	0	1	0	1	1	1	1&2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?
Cololedra declivata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Confucius cameroni	0	1	0	0	0	3	0	0	0	0	1	1	0	1	1	0	0	0	0	2	1	1	0	0	0	0	0	0	1	0
Confucius dispar	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Confucius zombanus	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	?
Dusuna sp. 1	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?
Dusuna sp. 2	0	0	0	0	0	0	0	0	0	?	1	1	0	1	1	0	0	0	0	?	1	1	0	0	0	0	0	0	0	?
Epiclinata planata	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0
Ezrana primitiva	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Funkikonia sp. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Funkikonia sp. 2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Funkikonia tuberculata	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0
Hangklipia gibber	1	1	1	1	1	4	0	0	0	0	1	1	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	?
Hangklipia signata	1	1	0	1	1	4	0	0	0	0	1	1	0	1	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	?
Hespenedra chilensis	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	2	0	2	0	0	0	0	0	0	0	?
Jukaruka grisea	0	1	0	0	0	0	1	1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	?
Ledropsella monstrosa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ledropsella sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ledra auditura	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	1	2	0	0	0	0	0	0	1	0	1	1
Ledra aurita	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	2	0	0	0	0	0	0	0	0	1	1
Ledra mutica	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	2	0	0	0	0	0	0	0	0	1	1
Ledra tuberculifrons	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ledramorpha planirostris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ledropsis discolor	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	1
Ledropsis froggatti	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	?	?	0	1	1	0	0	0	0	0	0	0	0	0	?
Ledropsis sp. 1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	2	0	1	0	0	0	0	0	0	1	0
Neotituria kongasana	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	0	1	0	0	0	0	0	0	1	1
Parapetalocephala testacea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Petalocephala bohemani	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Petalocephala conspicua	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	2	0	1	0	0	0	0	0	0	0	?
Petalocephala raniceps	0	0	0	0	0	0	0	0	0	?	1	1	0	1	0	0	0	0	0	?	0	1	0	0	0	0	0	0	1	1
Platyhynna bdellostoma	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	?	0	2	1	0	1	0	0	1	0	?
Platyhynna sp. 1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	?	0	2	1	0	1	0	0	1	0	?
Platyledra acuminata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Platyledra caldida	1	1	0	0	0	0	1	1	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	?
Platyledra hirsuta	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Porcorhinus mastersi	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Proranus adspersipennis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	?
Proranus ghilianii	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	?
Rubria brevifrons	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Rubria informis	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Rubria sanguinosa	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	2	0	0	1	0	0	0	0	0	0	0	0	1	0
Sichaea sp. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Stenoledra decorsei	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	0	0	1	1	1	2	0	0	0	1	0
Thlasia brunipennis	0	1	0	0	0	4	0	0	0	0	1	1	0	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	?
Thlasia corona	1	0	0	0	0	4	0	0	0	0	1	1	0	1	1	0	0	0	0	2	0	1	0	0	0	0	0	0	0	?
Titiella humerosa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Titiella punctiger	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tituria antica	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	2	0	1	0	0	0	0	0	0	1	0
Tituria forficula	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	2	0	?	?	?	?	?	?	?	?	?	0	0	?
Tituria obtusa	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	2	0	1	0	0	0	0	0	0	0	?
genus 1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	2	1	1	0	0	0	0	1	0	0	?
genus 2	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?
genus 3	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	?
genus 4	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	?
Stenocotis depressa	0	0	0	0	0	2	0	0	0	0	1	1	0	1	0	1	0	0	0	2	0	1	0	0	0	1	0	0	0	?
Macroceps fasciatus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	?
Thymbris convivus	0	0	0	0	0	2	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	?
Xedreota tuberculata	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0	0	0	?
Xerophloea viridis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	?
Aphrodes bicinctus	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?
Bathysmatophorus shabliovskii	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	1
Coloborrhis corticina	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0	0	0	0	0	1	0	1	1	1	2	0	0	0	0	?
Gypona decorata	1	0	1	0	0	0	0	0	1	0	1	1	1	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	?
Gypona thoracica	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?
Iassus scutellaris	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	1	0
Krisna sp. 1	0	1	0	0	0	0	0	0	0	1	1	1	0	2	0	0	?	0	0	1	0	2	1	0	0	1	0	0	0	?
Lystridea uhleri	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	2	2	1	0	0	0	0	0	0	0	1	1	0	1	0
Tartessus australicus	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0
Tartessus swezeyi	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	?

...continued below

TABLE 2. (continued)

	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
	8	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**8**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**
Afrorubria vitticollis	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	?	0	0	?
Bascarrhinus plathanon	0	0	0	0	0	0	0	2	1	1	0	2	1	1	1	0	0	0	0	0	2	1	1	0	0	2	1	0	1	0&1
Bascarrhinus platypoides	?	?	?	?	?	?	?	2	1	1	0	2	1	1	1	1	0	0	0	0	2	1	1	0	0	?	?	0	1	0&1
Beniledra peculiaris	0	0	0	0	0	0	1	2	1	1	0	1	1	1	1	0	1	0	1	0	1	0	1	0	0	2	1	0	1	1
Betsileonas marmorata	?	?	?	?	?	?	?	?	0	1	0	1	1	1	1	1	0	0	0	0	1	2	1	0	0	2	1	0	1	1
Clinonana mirabilis	0	1	0	1	0	0	0	2	1	1	1	2	0	0	0	0	0	0	1	0	1	1&2	0	1	0	0	?	1	1	1&3
Cololedra declivata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Confucius cameroni	1	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Confucius dispar	?	?	?	?	?	?	?	?	1	1	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	2	1	0	0	0&1
Confucius zombanus	1	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dusuna sp. 1	?	?	?	?	0	0	0	?	1	1	0	1	1	0	0	0	0	0	0	0	2	0	1	0	0	2	1	0	0	1
Dusuna sp. 2	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Epiclinata planata	0	0	0	0	0	0	1	2	1	1	0	1	1	0	0	1	0	0	0	0	2	0	1	0	0	2	1	0	1	1
Ezrana primitiva	?	?	?	?	?	?	?	?	1	1	0	1	1	2	1	0	1	1	0	1	2	0	1	0	1	0	?	0	1	1
Funkikonia sp. 1	?	?	?	?	?	?	?	?	1	1	0	1	0	2	1	0	1	0	0	0	2	2	1	0	0	2	1	0	0	1
Funkikonia sp. 2	?	?	?	?	?	?	?	?	1	1	0	1	0	2	1	1	1	1	0	0	2	1&2	1	0	0	2	1	0	1	1
Funkikonia tuberculata	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hangklipia gibber	1	0	0	0	0	0	1	?	1	1	0	1	1	0	0	1	0	0	0	1	1	0	1	0	1	2	1	0	0	1
Hangklipia signata	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hespenedra chilensis	0	0	0	0	0	1	0	?	1	1	0	0	0	0	0	0	0	0	0	0	1	0	?	0	1	2	1	0	0	1
Jukaruka grisea	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ledropsella monstrosa	?	?	?	?	?	?	?	?	1	0	0	?	1	1	0	0	?	1	?	1	?	?	1	?	0	?	?	?	?	?
Ledropsella sp.	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ledra auditura	0	0	0	1	0	0	1	0	1	1	0	1	1	2	1	0	1	0	0	1	1	0	1	0	0	2	1	0	1	1&2
Ledra aurita	0	0	0	1	0	0	1	0	1	1	0	1	1	2	1	1	1	1	0	1	1	0	1	0	0	2	1	0	1	1&2
Ledra mutica	0	0	0	1	0	0	0	2	1	0	0	1	1	2	1	0	1	1	0	1	1	0	1	0	0	2	1	0	1	1
Ledra tuberculifrons	?	?	?	?	?	?	?	?	0	1	0	0	1	2	1	1	?	1	?	1	?	?	1	?	0	?	?	?	?	?
Ledramorpha planirostris	?	?	?	?	?	?	?	2	0	1	1	2	0	2	1	0	0	1	0	1	1	0	1	0	1	2	1	0	1	0&1
Ledropsis discolor	0	0	0	0	0	0	1	2	1	1	0	1	1	2	1	1	1	0	0	1	1	0	1	0	0	2	1	0	0	1
Ledropsis froggatti	0	0	0	0	0	0	0	0	1	0	0	1	1	2	1	1	0	1	0	1	1	0	1	0	0	2	1	0	0	1
Ledropsis sp. 1	0	0	0	0	0	0	1	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Neotituria kongasana	0	0	0	0	0	0	0	2	1	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	2	1	0	0	1
Parapetalocephala testacea	?	?	?	?	?	?	?	?	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	1	0	0	1
Petalocephala bohemani	?	?	?	?	?	?	?	2	1	0	0	0	1	1	1	1	0	0	0	0	1	0	1	0	0	2	1	0	0	1
Petalocephala conspicua	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?
Petalocephala raniceps	0	0	0	0	?	?	?	2	1	0	0	1	1	0	1	1	0	0	0	0	2	0	1	0	0	2	1	0	1	0&1
Platyhynna bdellostoma	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Platyhynna sp. 1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Platyledra acuminata	?	?	?	?	?	?	?	?	1	1	0	0	1	2	1	1	1	1	0	1	2	1	1	0	1	2	1	0	1	1
Platyledra caldida	0	0	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Platyledra hirsuta	?	?	?	?	?	?	?	?	1	0	0	0	1	2	1	0	1	1	0	1	2	0	0	0	1	2	1	0	1	1
Porcorhinus mastersi	?	?	?	?	?	?	?	?	1	1	0	0	1	1	0	0	0	0	0	1	0	?	0	0	1	2	1	0	1	1
Proranus adspersipennis	0	0	1	0	0	1	0	2	1	0	0	1	1	0	1	1	0	0	0	0	2	1	1	0	0	0	?	0	0	?
Proranus ghilianii	0	0	1	0	0	1	0	2	1	0	0	1	0	0	1	0	0	0	0	0	2	1	1	0	0	0	?	0	0	?
Rubria brevifrons	?	?	?	?	?	?	?	0	1	1	0	1	0	0	0	1	0	0	0	0	1	2	1	0	0	2	1	0	0	0
Rubria informis	0	0	0	1	0	0	0	2	1	1	0	1	0	0	0	0	0	0	0	0	1	0&2	1	0	0	2	1	0	0	0
Rubria sanguinosa	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0&2	1	0	0	2	1	0	0	0
Sichaea sp. 1	?	?	?	?	?	?	?	0	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0	?
Stenoledra decorsei	0	0	0	0	0	0	0	2	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	?	0	0	?
Thlasia brunipennis	1	0	0	0	0	0	1	2	1	1	0	0	1	0	0	1	0	0	0	0	2	0	0	0	1	2	1	0	0	1
Thlasia corona	1	0	0	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Titiella humerosa	?	?	?	?	?	?	?	?	1	0	0	0	1	0	0	1	0	0	0	1	2	0	0	0	0&1	2	0	0	0	1
Titiella punctiger	?	?	?	?	?	?	?	?	1	1	0	0	1	0	0	1	0	0	0	1	2	0	0	0	0&1	2	0	0	0	1
Tituria antica	0	0	0	1	0	0	1	2	1	1	0	1	1	0	0	1	0	0	0	1	2	0&1	1	0	1	2	1	0	0	1
Tituria forficula	0	0	0	1	0	0	1	2	1	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	1	2	1	0	1	0&1
Tituria obtusa	0	0	0	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	0	0	1	0	0	0	1	2	1	0	0	1
genus 1	1	0	0	0	0	0	0	?	1	0	0	0	0	1	0	0	1	1	1	1	2	0	1	0	0	2	1	0	0	2
genus 2	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
genus 3	0	0	0	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
genus 4	1	0	0	0	1	1	0	?	?	?	?	?	0	1	0	0	?	?	?	?	?	?	?	?	1	?	?	?	?	?
Stenocotis depressa	1	0	0	0	0	1	0	2	0	1	1	2	0	1	1	0	0	1	1	0	1	0&1	1	0	1	2	1	0	1	0&1
Macroceps fasciatus	0	0	0	1	0	0	0	?	0	1	0	1	0	0	0	0	0	1	1	0	2	1	1	0	0	2	1	0	1	0&1
Thymbris convivus	1	0	0	0	1	1	0	?	1	1	0	2	0	1	0	0	0	0	1	0	2	1&2	1	0	1	2	1	0	1	0&1
Xedreota tuberculata	0	0	0	0	0	0	0	?	1	0	1	1	0	1	0	0	0	0	1	0	2	0&1	1&2	0	0	1	?	1	1	0&1
Xerophloea viridis	0	0	1	0	0	0	0	?	1	0	0	1	0	0	0	0	0	0	0	0	?	?	0	0	0	2	1	0	0	?
Aphrodes bicinctus	0	1	0	0	1	1	0	?	1	0	0	1	0	0	0	0	0	1	0	0	?	?	1	0	1	2	1	0	0	0
Bathysmatophorus shabliovskii	1	0	0	0	0	1	0	2	1	1	0	1	0	0	1	0	1	1	0	0	1	2	1	0	1	1	?	1	1	1
Coloborrhis corticina	0	0	0	1	0	0	0	?	1	1	0	1	0	1	0	0	?	0	?	0	?	?	1	?	0	?	?	?	?	?
Gypona decorata	0	1	0	0	0	0	0	2	1	1	0	2	1	0	0	0	0	0	1	0	1	0	0	1	0	2	1	1	1	0&1
Gypona thoracica	1	1	0	1	0	0	0	1	1	1	0	2	0	0	0	0	0	0	1	0	1	0	?	1	0	2	1	1	0	0
Iassus scutellaris	0	0	0	0	0	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	1	1&2	0	0	0	2	1	0	0	0
Krisna sp. 1	1	0	0	0	0	0	0	2	1	0	0	2	1	0	0	?	0	0	1	0	0	?	?	1	?	2	1	0	1	0&1
Lystridea uhleri	0	0	0	0	0	1	0	1	1	1	0	1	0	0	1	0	0	1	0	0	1	2	1	0	1	0	?	1	1	3
Tartessus australicus	0	0	0	0	0	0	0	?	1	0	1	2	0	0	0	0	0	0	1	0	1	&1&	0	1	0	0	?	0	0	1
Tartessus swezeyi	0	0	0	1	0	0	0	?	1	1	0	2	0	0	0	0	0	0	1	0	1	1	0	1	0	0	?	0	0	?

...continued below

TABLE 2. (continued)

	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
Afrorubria vitticollis	0	1	1	0	?	0	1	2	0	0	0	1	0	1	?	2	0	0	0	0	1	0	0	1	1	5
Bascarrhinus plathanon	0	2	0	1	?	0	2	2	1	1	0	1	1	1	1	2	0	0	0	0	0	0	0	1	0	4
Bascarrhinus platypoides	0	2	0	1	?	0	2	2	1	1	0	1	1	1	1	2	2	0	0	0	0	0	0	0	?	4
Beniledra peculiaris	0	4	0	2	0	0	2	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	?	5
Betsileonas marmorata	?	4	0	2	0	0	2	3	0	0	0	0	0	?	?	1	1	0	0	0	0	0	0	0	?	5
Clinonana mirabilis	0	4	0	2	0	0	2	1	0	0	0	1	0	0	?	0	0	0	0	0	0	0	0	2	1	4
Cololedra declivata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
Confucius cameroni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5
Confucius dispar	0	4	0	2	0	0	2	2	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1
Confucius zombanus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5
Dusuna sp. 1	0	4	0	2	0	0	2	2	1	0	1	1	1	1	2	0	0	0	0	0	1	0	0	1	0	1
Dusuna sp. 2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Epiclinata planata	0	4	0	2	0	0	2	1	1	1	1	1	1	0	1	2	0	0	0	1	1	0	0	2	1	1
Ezrana primitiva	0	4	0	2	0	0	1	1	1	1	1	1	1	0	1	2	2	0	1	1	1	0	0	0	?	2
Funkikonia sp. 1	0	4	0	2	0	0	2	2	1	1	1	1	1	1	0	2	0	1	0	0	1	1	0	2	1	1
Funkikonia sp. 2	0	4	0	2	0	0	2	2	1	1	1	1	1	1	0	0	0	1	0	0	1	1	0	1	1	1
Funkikonia tuberculata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Hangklipia gibber	0	4	0	2	0	0	2	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	0	?	5
Hangklipia signata	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5
Hespenedra chilensis	0	4	0	2	0	0	0	1	0	0	0	1	1	1	0	1	2	0	0	0	1	0	0	1	0	4
Jukaruka grisea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
Ledropsella monstrosa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	2
Ledropsella sp.	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
Ledra auditura	0	4	0	2	0	0	2	2	1	0	1	1	1	1	0	0	0	1	0	0	1	1	0	2	1	1
Ledra aurita	0	4	0	2	0	0	2	2	1	1	1	1	1	1	0	0	0	1	0	0	1	1	0	2	1	0&1
Ledra mutica	0	4	0	2	0	0	2	2	1	1	1	1	1	1	2	0	0	1	0	0	1	1	0	2	1	1
Ledra tuberculifrons	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	2
Ledramorpha planirostris	?	4	0	2	1	0	0	2	0	1	0	0	0	?	?	1	0	0	0	1	0	0	1	2	1	2
Ledropsis discolor	0	4	0	2	0	0	2	2	1	0	1	1	1	1	0	0	0	1	0	0	1	1	0	1	1	1
Ledropsis froggatti	0	4	0	2	0	0	?	0	1	1	1	1	1	0	1	2	2	1	1	0	1	0	0	0	?	2
Ledropsis sp. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Neotituria kongasana	0	4	0	2	0	0	0	1	1	1	0	1	1	1	1	2	0	0	0	0	1	0	0	1	1	0&1
Parapetalocephala testacea	1	4	0	2	0	0	1	2	1	0	1	1	1	1	0	2	2	0	0	0	1	0	0	2	0	1
Petalocephala bohemani	0	4	0	2	0	0	2	2	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	2
Petalocephala conspicua	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Petalocephala raniceps	0	4	0	2	0	0	2	2	1	1	0	1	1	1	1	0	0	0	0	0	1	0	0	1	0	5
Platyhynna bdellostoma	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	4
Platyhynna sp. 1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	4
Platyledra acuminata	0	4	0	2	1	0	1	0	0	1	0	1	1	1	1	2	2	1	1	0	1	0	0	0	?	2
Platyledra caldida	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
Platyledra hirsuta	0	4	0	2	1	0	1	0	0	1	0	1	1	1	1	2	2	1	0	0	1	0	1	1	0	2
Porcorhinus mastersi	0	4	0	2	1	0	2	0	1	1	1	1	1	0	1	2	0	1	1	0	1	0	0	1	0	2
Proranus adspersipennis	1	1	0	2	0	0	1	2	1	0	0	0	0	?	?	1	0	0	0	0	1	0	0	2	1	4
Proranus ghilianii	1	1	0	2	0	0	1	2	1	0	0	0	0	?	?	1	0	0	0	0	1	0	0	1	0	4
Rubria brevifrons	1	4	0	2	1	0	0	2	1	0	0	0	0	?	?	2	2	0	0	0	1	0	0	1	0	2
Rubria informis	0	4	0	2	0	0	2	2	0	0	0	0	0	?	?	2	0	0	0	0	1	0	0	1	1	2
Rubria sanguinosa	0	4	0	2	0	0	2	2	1	1	0	0	0	?	?	2	0	0	0	0	1	0	0	2	0&1	2
Sichaea sp. 1	1	1	1	0	?	0	1	2	0	0	0	1	0	1	?	2	2	0	0	0	1	0	0	0	?	5
Stenoledra decorsei	0	0	1	2	0	0	1	2	0	1	0	1	0	1	?	1	2	0	0	0	1	0	0	2	0	5
Thlasia brunipennis	0	4	0	2	0	0	2	0	1	0	1	1	1	1	0	2	2	0	0	0	1	0	0	1	0	5
Thlasia corona	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5
Titiella humerosa	0	4	0	2	0	0	2	0	1	1	1	1	1	0	0	2	0	0	0	0	1	0	0	0	?	5
Titiella punctiger	0	4	0	2	0	0	1	0	1	0	1	1	1	0	0	2	1	0	0	0	1	0	0	0	?	5
Tituria antica	0	4	0	2	0	0	2	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	5
Tituria forficula	0	4	0	2	0	0	2	1	1	1	1	0	1	?	1	2	0	0	0	0	1	0	1	1	0	5
Tituria obtusa	0	4	0	2	0	0	1	0	1	0	1	1	1	1	0	2	2	0	0	0	1	0	0	1	0	5
genus 1	0	4	0	2	0	0	0	2	0	1	0	1	1	1	0	0	2	0	0	0	1	0	1	0	?	2
genus 2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5
genus 3	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5
genus 4	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	5
Stenocotis depressa	0	4	0	2	0&1	0	1	1	0	1	1	0	0	?	?	1	2	0	0	1	0	0	1	2	0	2
Macroceps fasciatus	0	4	0	2	1	1	?	1	0	1	0	1	0	0	?	1	0	0	0	0	0	0	1	1	1	2
Thymbris convivus	?	4	0	2	1	1	1	1	0	1	0	0	0	?	?	1	0	0	0	0	0	0	1	2	1	2
Xedreota tuberculata	?	4	0	2	1	1	1	2	0	1	0	1	0	1	?	1	2	0	0	0	1	0	0	1	1	4
Xerophloea viridis	?	?	?	?	?	?	1	2	0	1	0	0	0	?	?	1	0	0	0	0	1	0	0	1	0	3&4
Aphrodes bicinctus	?	?	?	?	?	?	1	0	0	0	0	1	0	0	?	1	1	0	0	0	0	0	0	1	0	0&3
Bathysmatophorus shabliovskii	0	3	0	1	?	0	1	0	0	0	0	0	0	?	?	1	1	1	0	0	1	0	1	2	1	0
Coloborrhis corticina	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	5
Gypona decorata	0	4	0	2	0	0	2	0	0	1	0	1	1	0	1	0	2	0	0	0	0	0	0	0	?	4
Gypona thoracica	0	4	0	2	0	0	2	0	0	1	0	1	1	0	1	2	2	0	0	0	0	0	0	0	?	4
Iassus scutellaris	0	2	0	2	?	0	1	2	0	0	0	0	0	?	?	2	2	0	0	0	1	0	0	0	?	0
Krisna sp. 1	0	2	0	1	0	0	0	2	1	1	1	1	1	1	1	2	2	0	0	0	0	0	0	1	0	1
Lystridea uhleri	0	0	0	1	?	0	1	2	1	0	0	0	0	?	?	2	0	0	0	0	1	0	1	2	1	3
Tartessus australicus	0	3	0	2	?	0	0	0	0	1	0	1	0	1	?	1	1	1	0	0	0	0	1	2	1	2
Tartessus swezeyi	0	1	0	2	0	0	0	0	0	0	0	0	0	?	?	1	1	1	0	1	1	0	1	2	1	1&2

TABLE 3. List of apomorphies for summary analysis of Ledrinae genera (Fig. 3). Characters are listed with states in parentheses. Unambiguous (non-homoplastic) changes are marked by an asterisk (*).

Bathysmatophorus shabliovskii	5(1)*, 54(0)*, 56(3)*, 57(1), 97(1)*, 102(2)*, 142(1), 146(1)*, 153(1)*, 175(1)*, 180(1)*, 181(1)*, 188(2), 197(1)*, 206(1), 210(1), 212(3), 227(1), 228(1)*
Lystridea uhleri	7(1)*, 18(2)*, 36(1)*, 81(1)*, 89(1)*, 107(0)*, 163(1)*, 166(2)*, 167(2)*, 168(1)*, 170(0)*, 176(1)*, 177(1)*, 210(3), 218(2), 219(1)*, 226(2)
Node 1	227(1)
Aphrodes bicinctus	2(1), 3(2), 12(2), 26(0), 28(2), 42(1)*, 43(2), 44(0), 53(1), 55(0)*, 66(4)*, 69(0), 71(0), 80(0)*, 84(0)*, 87(0), 96(1), 115(0), 117(0), 126(1), 135(0)*, 136(2)*, 137(1)*, 139(1)*, 142(2), 147(1)*, 164(2)*, 179(0), 182(1)*, 185(1), 190(0), 195(0), 206(2), 208(0), 209(0), 222(1), 231(0)*, 233(0), 234(1), 235(0)
Node 2	2(1), 3(2), 12(2), 43(2), 44(0), 53(1), 87(0), 195(0), 206(2), 208(0), 209(0), 233(0), 35(0)
Node 3	1(1), 21(1), 26(0), 57(1), 69(0), 96(1), 103(2), 115(0), 117(0), 120(1), 125(1), 126(1), 129(1), 179(0), 188(2), 190(0), 198(0), 205(0), 212(4), 214(2), 218(2), 224(1), 227(0), 234(1)
Node 4	5(1), 7(1)*, 19(1)*, 22(1), 23(1), 25(0)*, 28(1), 41(2), 43(0), 51(1), 61(1), 65(2), 88(2), 108(1)*, 116(1)*, 122(1), 131(1), 186(0), 201(2)*, 202(1), 211(1), 220(1)
Xedreota tuberculata	29(1), 36(1)*, 42(3)*, 43(3), 50(0)*, 52(1)*, 113(1)*, 153(1)*, 165(1)*, 169(1)*, 175(1)*, 191(1)*, 194(1)*, 199(1)*, 206(1)*, 208(1)*, 209(1)*, 215(1)*, 216(1)*, 222(1), 227(2), 235(1)
Node 5	8(1), 30(1)*, 34(3)*, 38(0), 56(2)*, 58(0)*, 60(3)*, 68(1)*, 73(1)*, 76(1)*, 84(2)*, 85(2)*, 95(1), 98(1)*, 102(2)*, 120(2)*, 123(0), 124(1), 156(1)*, 161(0)*, 162(0)*, 166(2)*, 183(1)*, 212(1)
Proranus ghilianii	5(0), 9(1)*, 11(0)*, 18(2)*, 22(0), 23(0), 32(1)*, 46(1)*, 53(2)*, 54(0)*, 61(3)*, 64(1)*, 69(2)*, 71(0), 80(0)*, 88(0), 95(2), 126(0)*, 186(1), 195(1)*, 206(0), 219(1)*, 220(0)
Xerophloea viridis	26(1)*, 59(2)*, 122(0), 142(2), 203(0)*
Node 6	28(1), 38(0), 41(2), 43(0), 51(1), 61(1), 123(0), 124(1), 131(1)
Genus 3	2(0), 3(1), 4(1), 29(1), 30(1)*, 46(2), 53(0), 62(1), 71(0), 95(1)*, 96(0), 102(0), 111(1), 140(1), 142(2), 147(1), 172(1), 175(1)*, 185(1)
Node 7	2(0), 4(1), 29(1), 46(2), 62(1), 71(0), 96(0), 102(0), 111(1), 140(1), 147(1), 172(1), 185(1)
Genus 4	1(0), 3(0), 17(0)*, 21(0), 36(1)*, 38(1)*, 41(1), 43(3), 50(0)*, 61(0), 69(1), 80(0), 103(0), 108(1)*, 122(1), 146(1)*, 168(1), 181(1), 194(1)*, 205(1)*
Node 8	1(0), 3(0), 21(0), 41(1), 61(0), 69(1), 103(0), 122(1)
Genus 2	11(0)*, 42(2), 43(2), 45(2), 51(0), 53(0), 55(0), 57(0), 58(0), 136(0)*, 142(2), 149(0)*, 164(1), 172(0)*
Node 9	43(2), 45(2), 51(0), 53(0), 55(0), 57(0), 58(0), 202(0), 211(1), 222(1), 227(2)
Afrorubria vitticollis	3(1)*, 16(1), 21(1), 42(3), 59(0), 80(0), 95(1), 96(1), 102(1)*, 104(0), 107(0)*, 111(0)*, 126(0)*, 142(2), 164(1), 168(1), 181(1), 188(1), 190(1), 195(1)*, 206(0), 211(0), 212(1), 213(1), 214(0), 226(2), 227(0), 235(1)
Sichaea sp.1	16(1), 21(1), 42(3), 50(0)*, 59(02), 71(1)*, 80(0), 95(1), 96(1), 104(0), 129(0)*, 134(1)*, 188(0), 190(1), 191(1)*, 203(0)*, 206(0), 212(1), 213(1), 214(0), 226(2), 234(0)*
Node 10	1(1), 8(1), 21(1), 30(2)*, 38(0), 41(1), 42(2)*, 45(2)*, 57(1), 58(0)*, 59(2)*, 96(2)*, 103(1), 113(1)*, 120(1), 121(1)*, 122(2), 123(0), 124(1), 125(1), 129(1), 135(1)*, 149(0), 164(1)*, 198(0), 202(0), 205(0), 212(4), 214(2), 218(2), 219(1), 224(1), 226(2), 227(0)
Rubria sanguinosa	3(0)*, 16(2)*, 26(0), 31(1)*, 53(2)*, 55(2)*, 62(1)*, 63(0)*, 71(0), 80(0)*, 104(0)*, 142(2), 163(1)*, 166(1)*, 167(2)*, 185(1), 190(0), 196(1)*, 217(2)*, 220(1)*

Node 11	5(1)*, 28(1), 69(0), 84(2)*, 85(1)*, 89(1), 95(2)*, 103(2), 108(1)*, 115(0), 117(0), 118(1)*, 120(2)*, 126(1), 152(1), 165(1)*, 170(2)*, 172(1), 179(0), 188(2), 192(0)*, 210(1), 222(1), 223(1)*, 227(2), 234(0)
Hespenedra chilensis	28(2), 43(1)*, 49(12)*, 100(1)*, 101(1)*, 125(2)*, 135(0)*, 137(2)*, 140(1)*, 143(0)*, 144(0)*, 147(1)*, 172(2), 205(1)*, 217(0)*, 218(1)*, 219(0), 226(1), 234(1)
Node 12	10(1), 14(1), 26(3), 29(1)*, 31(2), 45(1), 46(1), 61(1)*, 78(1)*, 122(1), 134(1)*, 186(0)*, 193(1), 221(1)
Hangklipia signata	54(0)*, 83(1)*, 89(0), 93(1)*, 97(1)*, 98(1)*, 115(1)*, 117(1)*, 131(1)*, 143(1)*, 151(1)*, 154(1)*, 155(1)*, 156(4)*, 181(1)*
Node 13	11(0), 22(1), 81(1)*, 152(0), 187(1)
Titiella punctiger	21(0)*, 30(0)*, 45(2), 46(2)*, 57(0)*, 61(2)*, 95(1)*, 102(0)*, 108(0)*, 119(1)*, 196(1)*, 200(1)*, 201(2)*, 203(0)*, 207(0)*, 218(0)*, 224(0)*, 227(1)*
Node 14	3(0), 14(0), 18(2)*, 88(2)*, 100(1)*, 116(1)*, 125(2)*
Parapetalocephala testacea	3(1), 16(1)*, 73(1)*, 90(1)*, 97(1)*, 114(1)*, 190(0)*, 193(0), 211(1)*, 234(2)*
Node 15	11(1), 19(1)*, 26(1)*, 27(0)*, 29(0)*, 34(1), 46(0), 96(1)*, 101(1), 217(2)*, 226(0), 227(0)
Node 16	64(1)*, 66(3)*, 81(0)*, 89(0)*, 109(1), 142(1), 148(2), 201(2)*, 234(1)
Node 17	2(0)*, 12(0), 22(0), 25(0)*, 46(1), 54(0)*, 67(1)*, 69(1)*, 79(1)*, 90(1)*, 99(1)*, 100(0)*, 101(0), 142(2), 171(1), 187(0), 192(1), 225(2)
Dusuna sp 1	11(0)*
Dusuna sp 2	26(3)*, 58(1)*, 73(1)*, 120(1)*
Node 18	5(0)*, 10(0)*, 28(2), 31(3)*, 61(0)*, 78(0)*, 80(0)*, 88(0)*, 91(1), 140(1)*, 143(1)*, 196(1)*, 218(0), 226(2)
Thlasia brunipennis	83(1)*, 109(0), 131(1)*, 152(1)*, 156(4)*, 172(0)*, 181(1)*, 203(0)*, 205(1)*, 227(2)*
Node 19	3(1)*, 9(1)*, 65(1)*, 71(0)*, 95(0)*, 114(1), 144(0)*, 151(1), 179(1)*, 218(1), 235(1)
Node 20	12(0)*, 25(0)*, 28(1), 29(1)*, 91(0), 142(0), 192(1)*
Epiclinata planata	34(2)*, 46(1)*, 108(0)*, 120(1)*, 126(0)*, 146(1)*, 151(0), 209(1)*, 220(1)*, 224(0)*, 225(1)*, 230(1)*, 234(2)*
Tituria antica	6(1)*, 70(1)*, 124(2)*, 184(1)*, 200(1)*, 205(1)*, 218(0), 226(0), 235(0)
Node 21	22(0), 26(2)*, 43(1)*, 50(0)*, 66(0)*, 147(1), 150(1), 164(0), 165(0), 180(1), 187(0), 195(1)*, 201(1)*
Neotituria kongasana	3(2)*, 19(0)*, 27(1)*, 49(12)*, 80(1)*, 89(1)*, 96(2)*, 103(1)*, 196(0)*, 217(0)*, 220(1)*, 221(0)*, 225(1)*
Petalocephala bohemani	12(1)*, 31(1)*, 62(1)*, 63(0)*, 64(0)*, 95(1)*, 98(1)*, 114(0), 190(0)*, 194(1)*, 218(2), 226(0)
Node 22	1(0)*, 12(1)*, 14(1), 23(1), 34(2), 35(0)*, 56(2), 83(1), 95(1)*, 115(1), 117(1)*, 136(2), 165(0)*, 194(1)*, 195(1)*, 197(1)*
Beniledra peculiaris	10(0)*, 28(2)*, 43(1)*, 49(12)*, 66(4)*, 67(1)*, 68(2)*, 106(0)*, 122(2)*, 135(0)*, 146(1)*, 192(1)*, 199(1)*, 209(1)*, 218(0)*, 219(0)*, 221(0)*, 225(1)*
Node 23	7(1)*, 18(1), 25(2)*, 31(1), 57(0), 58(1)*, 74(0), 93(1)*, 94(1)*, 125(1), 177(1), 181(1), 188(0), 200(1)*
Confucius dispar	9(1)*, 23(0), 29(1)*, 56(0), 101(0), 114(1)*, 136(3), 203(0)*, 234(1)
Node 24	6(1)*, 70(1), 88(0)*, 91(1), 115(0), 116(0), 119(1)*, 198(1), 201(2), 220(1), 227(2)
Confucius zombanus	10(0)*, 18(2), 22(0)*, 31(2), 49(2)*, 54(0)*, 117(0)*, 172(0)*
Node 25	3(1)*, 20(2)*, 57(1), 61(0), 62(1)*, 66(4), 81(0), 83(0), 96(2)*, 123(1)*, 125(2), 128(1)*, 129(2)*, 135(0)*, 143(0)*, 144(0), 147(1)*

Genus 1	12(2)*, 16(2)*, 31(3), 34(0)*, 70(0), 90(1)*, 91(0), 93(0)*, 94(0)*, 101(0), 109(1)*, 116(1), 134(0)*, 142(1)*, 144(1), 146(1)*, 171(1)*, 187(0)*, 190(0)*, 193(0)*, 195(0)*, 199(1)*, 210(2)*, 217(0)*, 219(0)*, 221(0)*, 233(1)*
Node 26	9(1), 19(0)*, 29(1), 53(2)*, 56(1), 61(2), 92(1)*, 95(0)*, 108(2)*, 113(0)*, 115(2)*, 117(2)*, 127(1)*, 149(2), 166(1)*, 170(1)*, 179(1), 81(0), 194(2), 209(1), 228(1)
Funkikonia tuberculata	8(0)*, 11(0)*, 83(1), 88(1)*, 103(1)*, 122(0)*, 143(1)*, 145(1)*, 148(1)*
Node 27	1(1)*, 43(1)*, 55(2)*, 56(3), 66(0), 72(1)*, 167(1)*, 172(0)*, 177(0)*, 180(1)
Node 28	25(1)*, 196(1)*, 201(1), 227(0), 232(1), 234(2)*
Ledra tuberculifrons	63(0)*, 73(2)*, 75(1)*, 88(2)*, 90(1)*, 96(1)*, 103(1)*, 108(1)*, 109(1)*, 189(0)*
Node 29	18(2)*, 62(0)*, 74(3), 91(0)*, 92(0)*, 113(1)*, 133(1)*, 192(1)*, 235(1)*
Ledra aurita	11(0)*, 15(1)*, 19(1)*, 31(02)*, 46(1)*, 59(1)*, 68(1)*, 75(2)*, 116(1)*, 120(1)*, 149(0), 163(1)*, 164(0)*, 168(1)*, 169(1)*, 170(2)*, 184(1)*
Ledropsis discolor	1(0)*, 3(0)*, 10(0)*, 16(2)*, 23(0)*, 26(2)*, 29(0), 54(0)*, 72(0)*, 88(1)*, 95(1)*, 188(2), 198(0)*, 209(0), 220(0)*, 234(1)*
Node 30	9(0), 12(3)*, 26(2)*, 27(1)*, 29(0), 34(1), 73(1), 74(2), 78(0), 85(3)*, 93(0), 94(0), 119(0)*, 120(1)*, 122(2)*, 136(3)*, 137(1)*, 147(0)*, 179(0), 187(0)*, 205(1), 217(1), 218(0)*, 225(1)*, 226(2)*
Node 31	3(2)*, 6(0)*, 53(1), 63(0)*, 67(1)*, 83(1), 127(0)*, 133(1)*, 134(0), 144(1), 151(1), 165(1), 169(1), 192(1), 224(0)*, 229(1)*
Ezrana primitiva	19(1)*, 34(2), 68(2)*, 75(1)*, 78(1), 79(1)*, 88(1)*, 90(1)*, 135(2)*, 206(0)*, 218(1)*, 228(0)*, 230(1)*
Node 32	25(1)*, 28(2)*, 43(2), 56(1)*, 58(0)*, 70(0)*, 72(0)*, 73(0), 91(0)*, 92(0)*, 197(0)*, 201(0), 217(2)
Ledropsis froggatti	3(0)*, 12(2)*, 16(2)*, 23(0)*, 53(2), 54(0)*, 61(1)*, 66(4), 122(1)*, 190(0)*, 196(1)*, 201(1), 205(0), 209(0)*
Porcorhinus mastersi	1(0)*, 31(0)*, 55(1)*, 75(2)*, 83(0), 89(0)*, 96(1)*, 97(1)*, 124(2)*, 134(1), 192(0), 194(1)*, 195(0)*, 198(0)*, 203(0)*, 215(1)*, 227(0)*, 234(1)*
Node 33	13(1)*, 15(1)*, 31(0)*, 54(0)*, 66(4), 106(0), 152(1), 157(1), 158(1), 190(0)*, 215(1), 219(0), 221(0), 233(1)
Ledropsella monstrosa	19(1)*, 33(1)*, 46(2)*, 47(1)*, 95(1)*, 102(0)*, 108(1)*, 136(0)*, 194(1)*, 195(0)*, 205(0)
Node 34	23(2), 68(2)*, 88(2)*, 93(1), 94(1), 96(1)*, 203(0), 234(1)
Jukaruka grisea	53(1)*, 92(0)*
Platyledra hirsuta	1(0)*, 3(2)*, 34(0)*, 63(0)*, 70(0)*, 103(1)*, 134(0)*, 138(1)*

TABLE 4a. Comparison of classifications of Ledrinae. Oman *et al*. (1990): 5 tribes, 73 genera (9 unplaced). Total genera per tribe are given in brackets.

Ledrini [6]	Petalocephalini [33]	Stenocotini [6]	Thymbrini [16]	Xerophloeini [3]	unplaced within Ledrinae [9]
Cololedra	*Afrorubria*	*Anancotis*	*Alseis*	*Pariacaca*	*Arenoledra*
Ledra	*Bascarrhinus*	*Kyphocotis*	*Epipsychidion*	*Piezauchenia*	*Caxia*
Ledracorrhis	*Beniledra*	*Kyphoctella*	*Hackeriana*	*Xerophloea*	*Clinonana*
Ledromorpha	*Betsileonas*	*Ledracotis*	*Ledroprora*		*Complanledra*
Ledropsella	*Camptelasmus*	*Smicrocotis*	*Ledrella*		*Hemipeltis*
Porcorhinus	*Chatura*	*Stenocotis*	*Macroceps*		*Hespenedra*
	Confucius		*Microledrella*		*Paraconfucius*
	Destinia		*Mitelloides*		*Latycephala*
	Dusuna		*Novothymbris*		*Sichaea*
	Eleazara		*Putoniessa*		
	Eogypona		*Putoniessiella*		
	Epiclinata		*Rhotidoides*		
	Ezrana		*Rhotidus*		
	Funkikonia		*Stenalsella*		
	Hangklipia		*Thymbrella*		
	Jukaruka		*Thymbris*		
	Kuohledra				
	Laticorona				
	Ledropsis				
	Midoria				
	Neotituria				
	Parapetalocephala				
	Petalocephala				
	Petalocephaloides				
	Platyhynna				
	Platyledra				
	Proranus				
	Rubria				
	Stenoledra				
	Thlasia				
	Titiella				
	Tituria				
	Turitia				

TABLE 4b. Comparison of classifications of Ledrinae. This paper: 5 tribes, 38 genera (all placed). Geographic distributions are given in parentheses (see Fig. 4), and total extant genera per tribe in brackets.

Afrorubrini (South Africa) [2]	Hespenedrini (Chile) [2]	Ledrini (Old World) [29]	Rubrini (Australia) [1]	Xerophloeini (New World) [4]	removed from Ledrinae (worldwide)
Afrorubria	*Hespenedra*	*Arenoledra*	*Rubria*	*Pariacaca*	Stenocotini
Sichaea		*Beniledra*		*Proranus*	(with *Ledromorpha*)
		Chatura		*Xedreota*	Thymbrini
		Complanledra		*Xerophloea*	
		Confucius			*Bascarrhinus*
		Destinia			*Betsileonas*
		Destinoides			
		Dusuna			*Camptelasmus*
		Eleazara			*Caxia*
		Ezrana			*Clinonana*
		Funkikonia			*Cololedra*
		Hangklipia			*Eogypona*
		Jukaruka			*Hemipeltis*
		Kuohledra			*Ledracorrhis*
		Laticorona			*Ohausia*
		Latycephala			*Piezauchenia*
		Ledra			*Platyhynna*
		Ledropsella			*Stenoledra*
		Ledropsis			*Turitia*
		Midoria			
		Neotituria			
		Paraconfucius			
		Parapetalocephala			
		Petalocephala			
		Petalocephaloides			
		Platyledra			
		Porcorhinus			
		Thlasia			
		Titiella			
		Tituria			

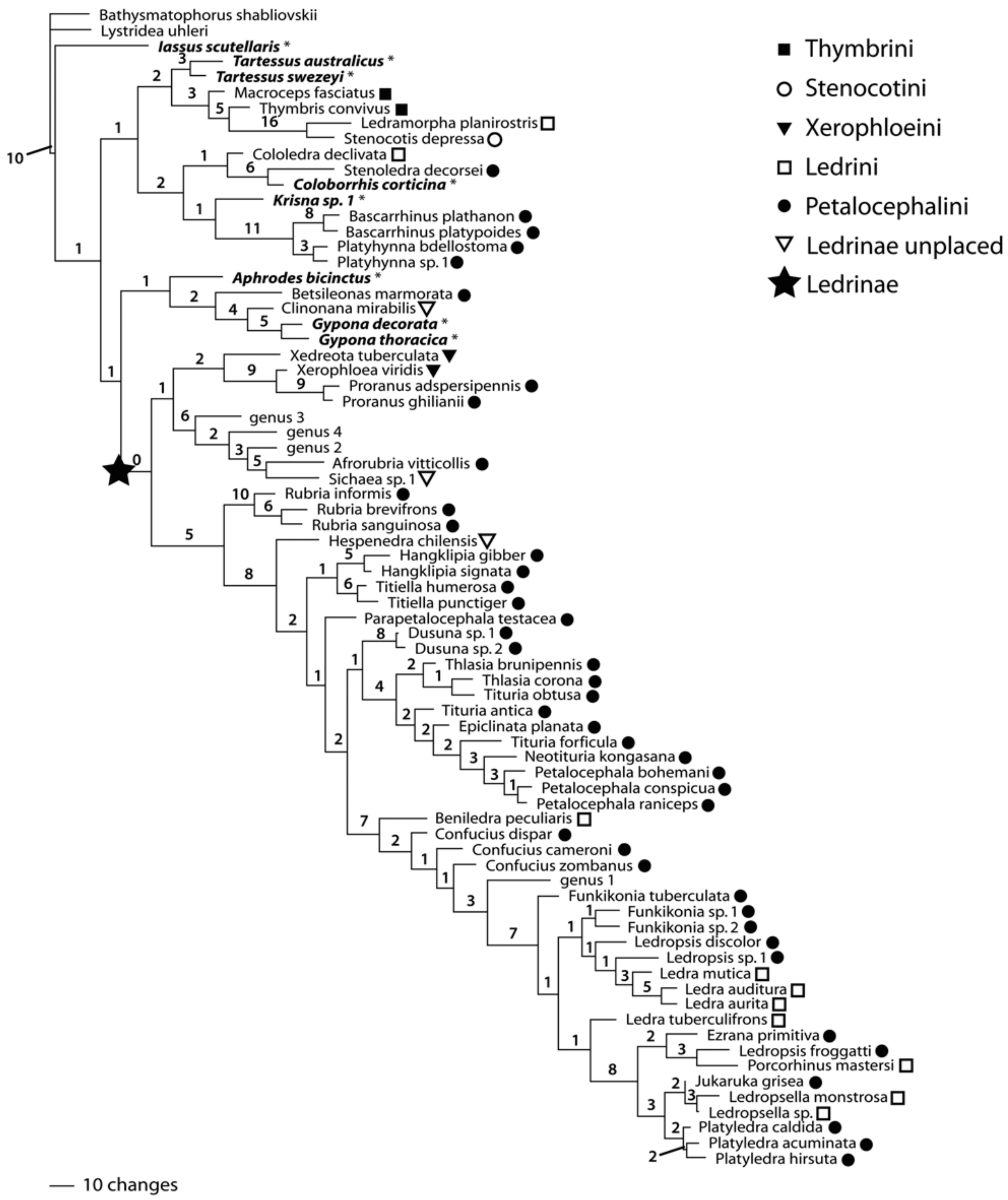

FIGURE 1. Phylogram of relationships generated from cladistic analysis of entire dataset: {= [Ledrinae *sensu* Oman *et al.* (1990) dataset] + [dataset of non-ledrine taxa included to provide resolution to ingroup taxa anticipated to ultimately place outside of Ledrinae (marked in italic bold with an asterisk*)]}. Analysis in PAUP* was rooted to *Bathysmatophorus shabliovskii*, and resulted in a single most parsimonious tree with a cost of 1719 steps. Bremer support values are given above the branch to which they correspond. Squares, circles and triangles indicate tribal placements of included genera in Oman *et al.* (1990). The boundary of Ledrinae, as it is here recognized, is marked with a black star.

FIGURE 2. Phylogram of relationships generated from cladistic analysis of pruned dataset, including only species herein recognized to belong to the subfamily Ledrinae. Analysis in PAUP* was again rooted to *B. shabliovskii*; *Aphrodes* was included as putative sister group to the Ledrinae. This second analysis resulted in a single most parsimonious tree with a cost of 1185 steps. Bremer support values are given above the branch to which they correspond; the black star marks the phylogenetic boundary of Ledrinae. Ingroup resolution is topologically identical to that in Fig. 1, but branch lengths and Bremer supports vary.

FIGURE 3. Phylogram of summarized relationships among Ledrinae genera generated from a reduced dataset including single exemplars of each available genus. If available, the type species was chosen (marked with an asterisk*). Additional exemplars were included in cases where polyphyly among species was demonstrated in previous analyses, and where a male and a female of different species in the genus were needed to provided all of the pertinent characters (i. e., genitalia). Analysis (in PAUP*, rooted to *B. shabliovskii*, with *Aphrodes* included as putative sister group to the Ledrinae) resulted in five equally parsimonious trees (cost 933). The selected topology differs slightly from Fig. 2 in the placement of *E. planata* as sister to *T. antica*, in *Titiella* and *Hangklipia* not being placed as sister taxa, and in *Jukaruka* being placed with *Platyledra* instead of *Ledropsella*. Numbers at internodes correspond to a list of apomorphies generated from this analysis (see Table 1). Higher taxa within Ledrinae recognized herein, including new tribes (with their distributions), and informal genus and species groups, are indicated by symbols. The inclusion of *Dusuna* within the *Petalocephala* genus group is at present uncertain, as indicated by the question marks above the open triangles.

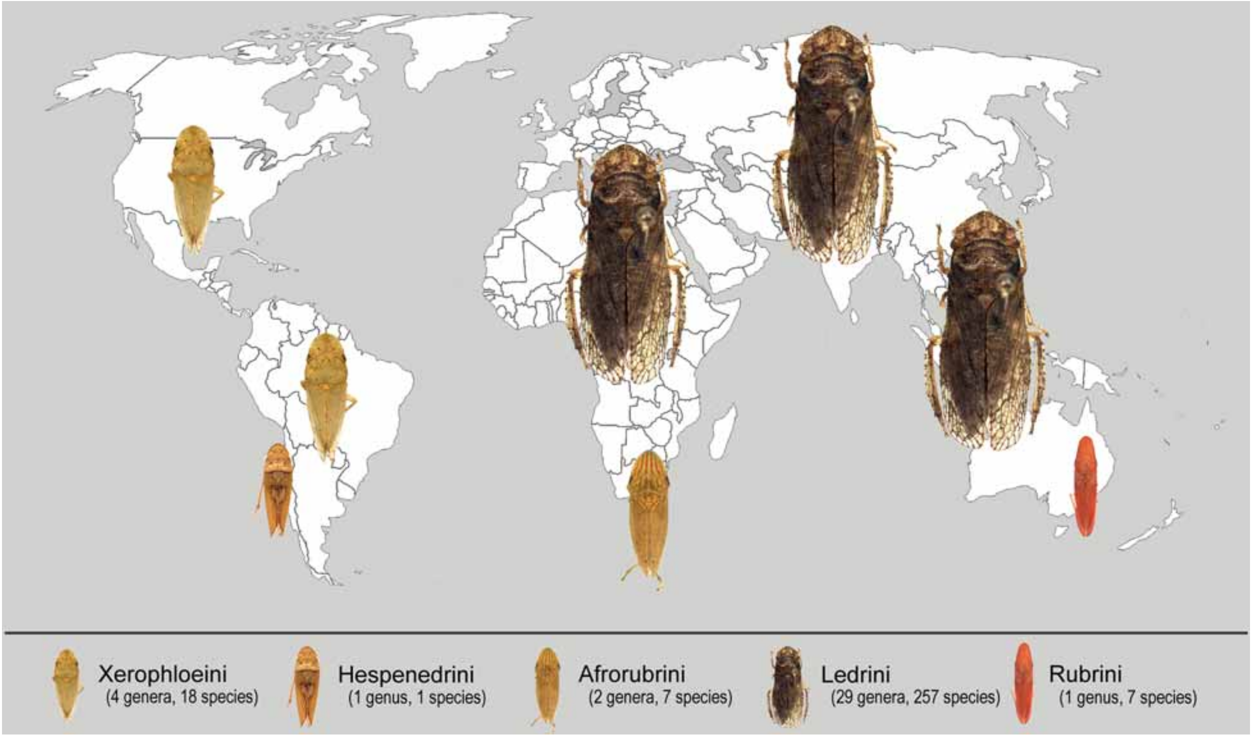

FIGURE 4. World map showing distributions of Ledrinae tribes recognized herein. Collective sizes of representative taxa on map correspond roughly with numbers of extant genera per respective tribe (see Table 4); Xerophloeini, for example, contain 4 extant genera, as illustrated by the two images of *Xerophloea* displayed over North and South America. Xerophloeini and Hespenedrini are exclusively New World tribes, while extant Ledrini, Afrorubrini and Rubrini are distributed exclusively in the Old World. A single fossil genus and species, each from Brazil (not indicated), has also been described in Xerophloeini and Ledrini, respectively.

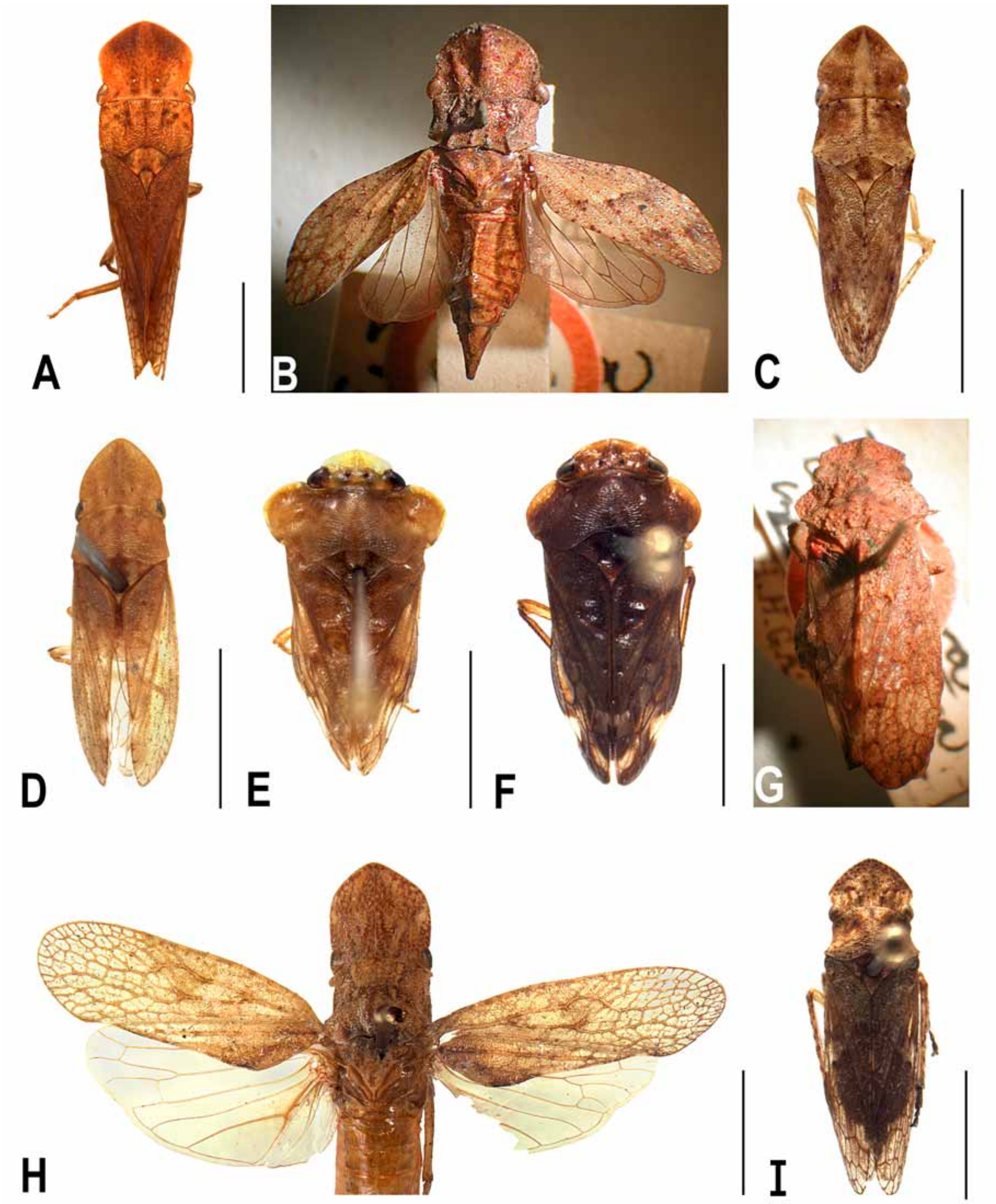

PLATE 1. A–I, Ledrini: dorsal aspect. A. *Beniledra peculiaris* Linnavuori, #JRJ_Led1_018, ♂. B. *Chatura nigella* Distant, BMNH, ♀. C. *Confucius cameroni* Distant, #JRJ_Led1_040, ♂. D. *Confucius dispar* Nast, #JRJ_Led1_041, ♀. E. *Dusuna* sp. 1, #JRJ_Led1_044, ♀. F. *Dusuna* sp. 2, #JRJ_Led1_045, ♂. G. *Eleazara aedificatura* Distant, BMNH, ♀. H. *Ezrana primitiva* Evans, #JRJ_Led1_051, ♀. I. *Funkikonia tuberculata* (Kato), #JRJ_Led1_449, ♂. Bars = 5 mm.

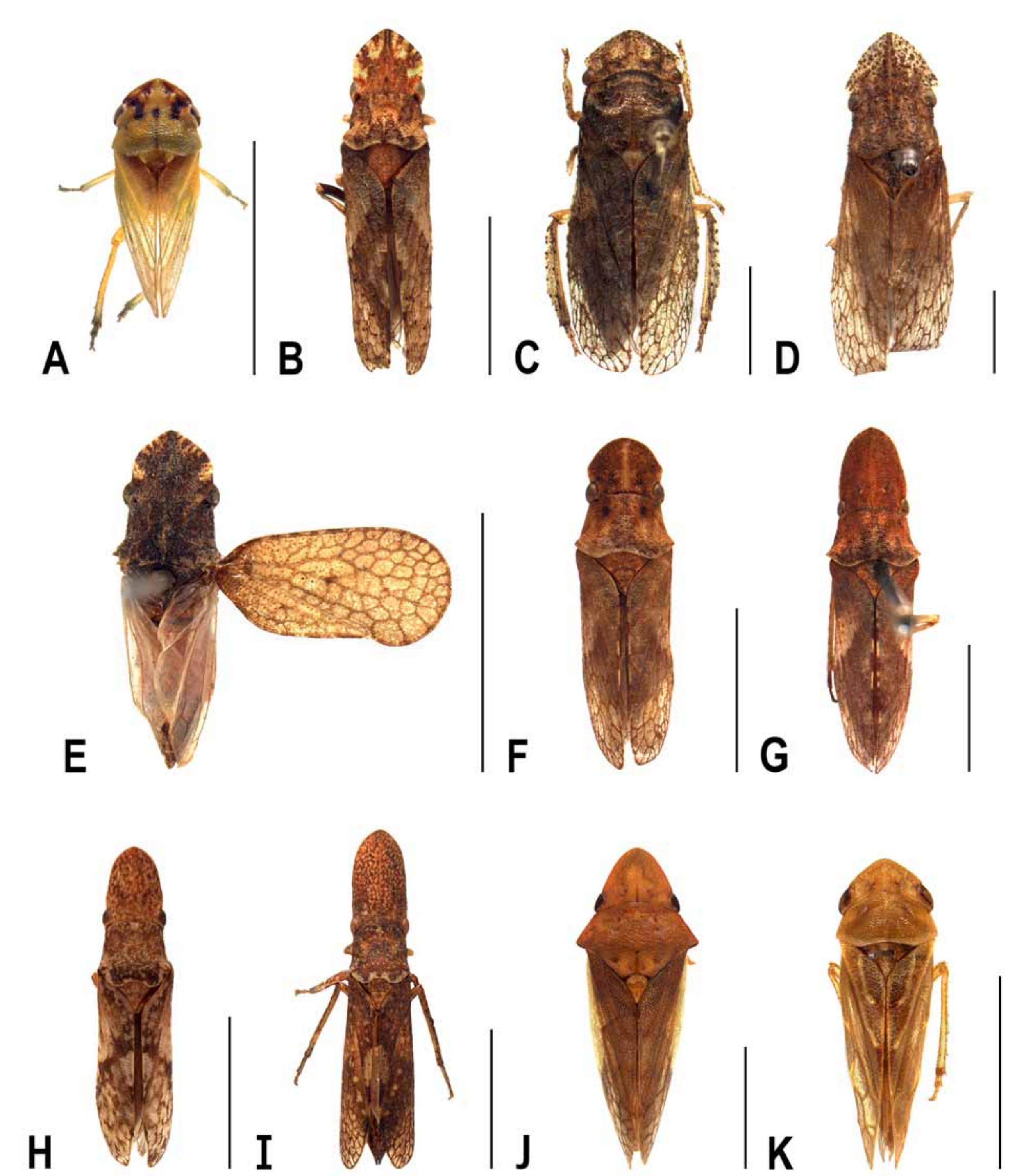

PLATE 2. A–K, Ledrini: dorsal aspect. A. *Hangklipia signata* (Linnavuori), #JRJ_Led1_057, ♂. B. *Jukaruka grisea* Evans, #JRJ_Led1_066, ♂. C. *Ledra aurita* (Linnaeus), #JRJ_Led1_077, ♀. D. *Ledra mutica* Fabricius, #JRJ_Led1_080, ♀. E. *Ledropsella monstrosa* (Evans), #JRJ_Led1_087, ♀. F. *Ledropsis discolor* (Uhler), JRJ_Led1_093, ♂. G. *Ledropsis discolor* (Uhler), #JRJ_Led1_089, ♀. H. *Ledropsis froggatti* Distant, #JRJ_Led1_096, ♂. I. *Ledropsis froggatti* Distant, #JRJ_Led1_098, ♀. J. *Neotituria kongasana* (Matsumura), #JRJ_Led1_111, ♀. K. *Parapetalocephala testacea* Cai & Kuoh, #JRJ_Led1_273, ♀. Bars = 5 mm.

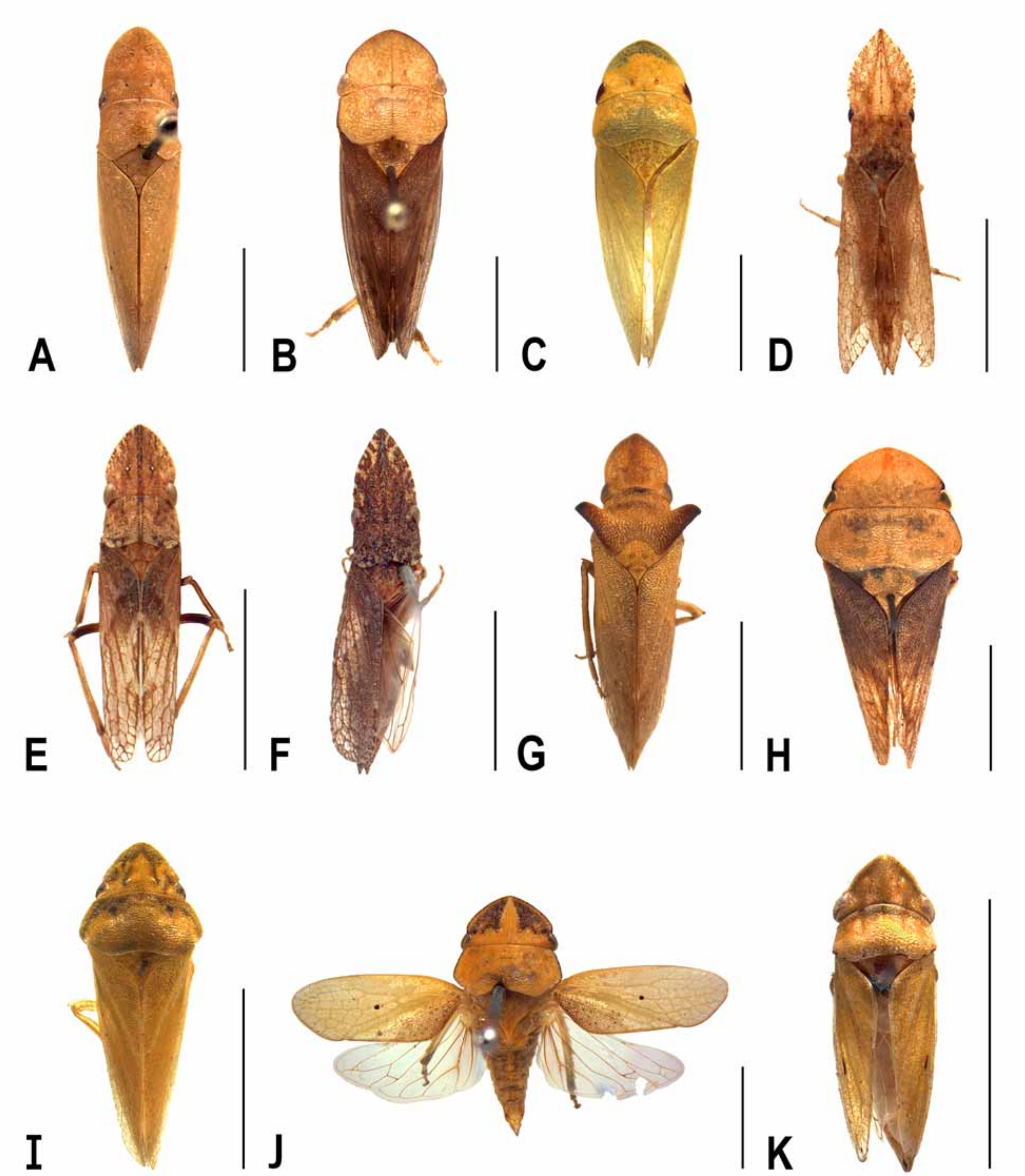

PLATE 3. A–K, Ledrini: dorsal aspect. A. *Petalocephala bohemani* Stål, #JRJ_Led1_121, ♀. B. *Petalocephala conspicua* Distant, #JRJ_Led1_132, ♂. C. *Petalocephala raniceps* Jacobi, #JRJ_Led1_128 ♂. D. *Platyledra acuminata* (Distant), #JRJ_Led1_142, ♀. E. *Platyledra caldida* Evans, #JRJ_Led1_143, ♂. F. *Platyledra hirsuta* Evans, #JRJ_Led1_144, ♀. G. *Porcorhinus mastersi* Goding, #JRJ_Led1_145, ♀. H. *Thlasia brunnipennis* Germar, #JRJ_Led1_174, ♂. I. *Thlasia brunnipennis* Germar, #JRJ_Led1_172, ♀. J. *Thlasia corona* Linnavuori, #JRJ_Led1_170, ♂. K. *Titiella punctigera* (Stål), #JRJ_Led1_197, ♀. Bars = 5 mm.

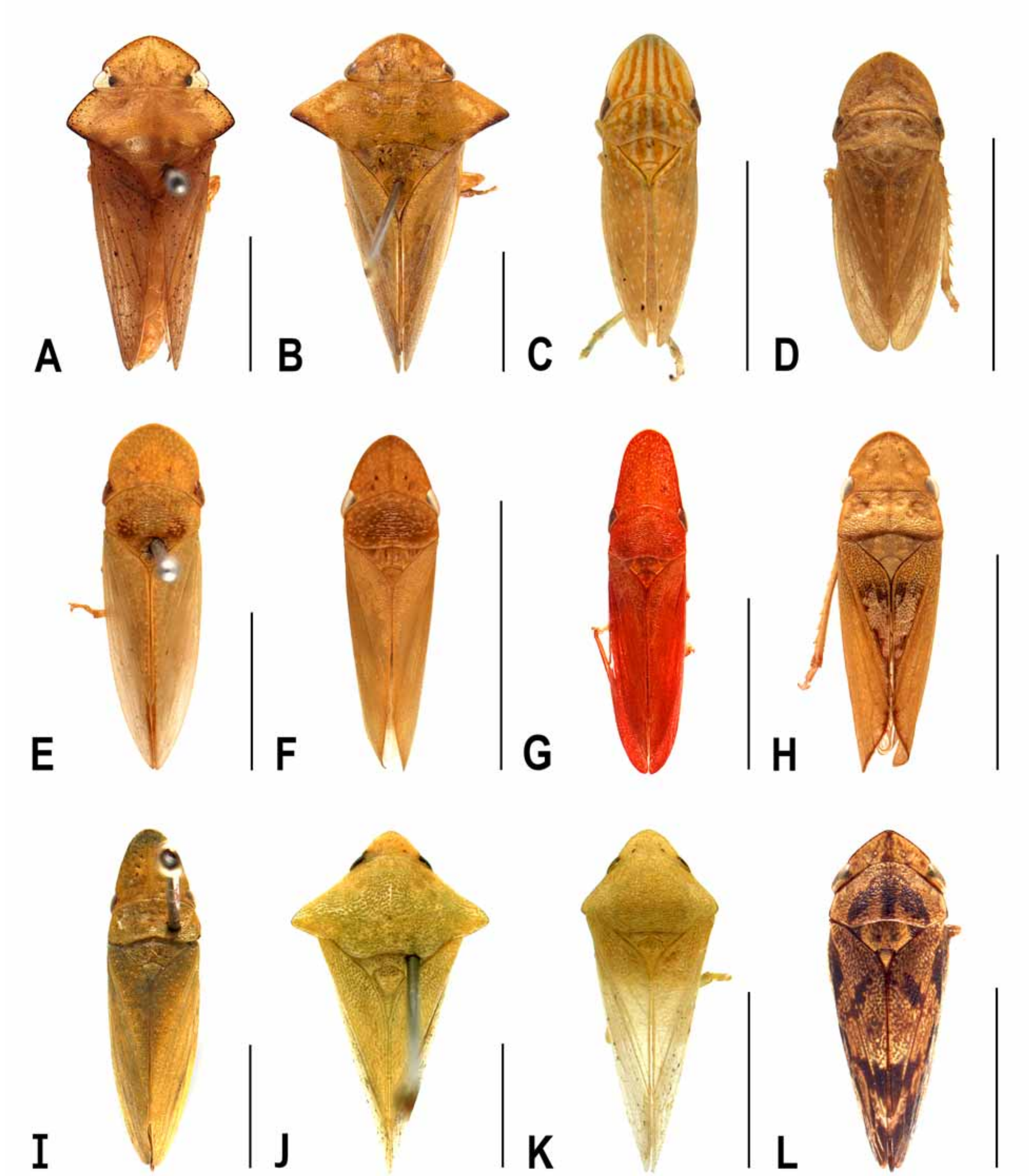

PLATE 4. A–B, Ledrini: dorsal aspect. A. *Tituria antica* (Walker), #JRJ_Led1_185, ♂. B. *Tituria planata* (Fabricius), #JRJ_Led1_049, ♀. C–D, Afrorubrini: dorsal aspect. C. *Afrorubria vitticollis* (Stål), #JRJ_Led1_003, ♀. D. *Sichaea* sp., #JRJ_Led1_274, ♂. E–G, Rubrini: dorsal aspect. E. *Rubria brevifrons* (Walker), # JRJ_Led1_158, ♀. F. *Rubria informis* (Kirkaldy), #JRJ_Led1_159, ♀. G. *Rubria sanguinosa* (Stål), #JRJ_Led1_162, ♀. H–I, Hespenedrini: dorsal aspect. *Hespenedra chilensis* (Spinola), #JRJ_Led1_064, ♂. I. *Hespenedra chilensis* (Spinola), #JRJ_Led1_065, ♀. J–L. Xerophloeini: dorsal aspect. J. *Proranus adspersipennis* Stål, #JRJ_Led1_149, ♀. K. *Proranus ghilianii* Spinola, #JRJ_Led1_152, ♀. L. *Xedreota tuberculata* (Osborn), #JRJ_Led1_370, ♀. Bars = 5 mm.

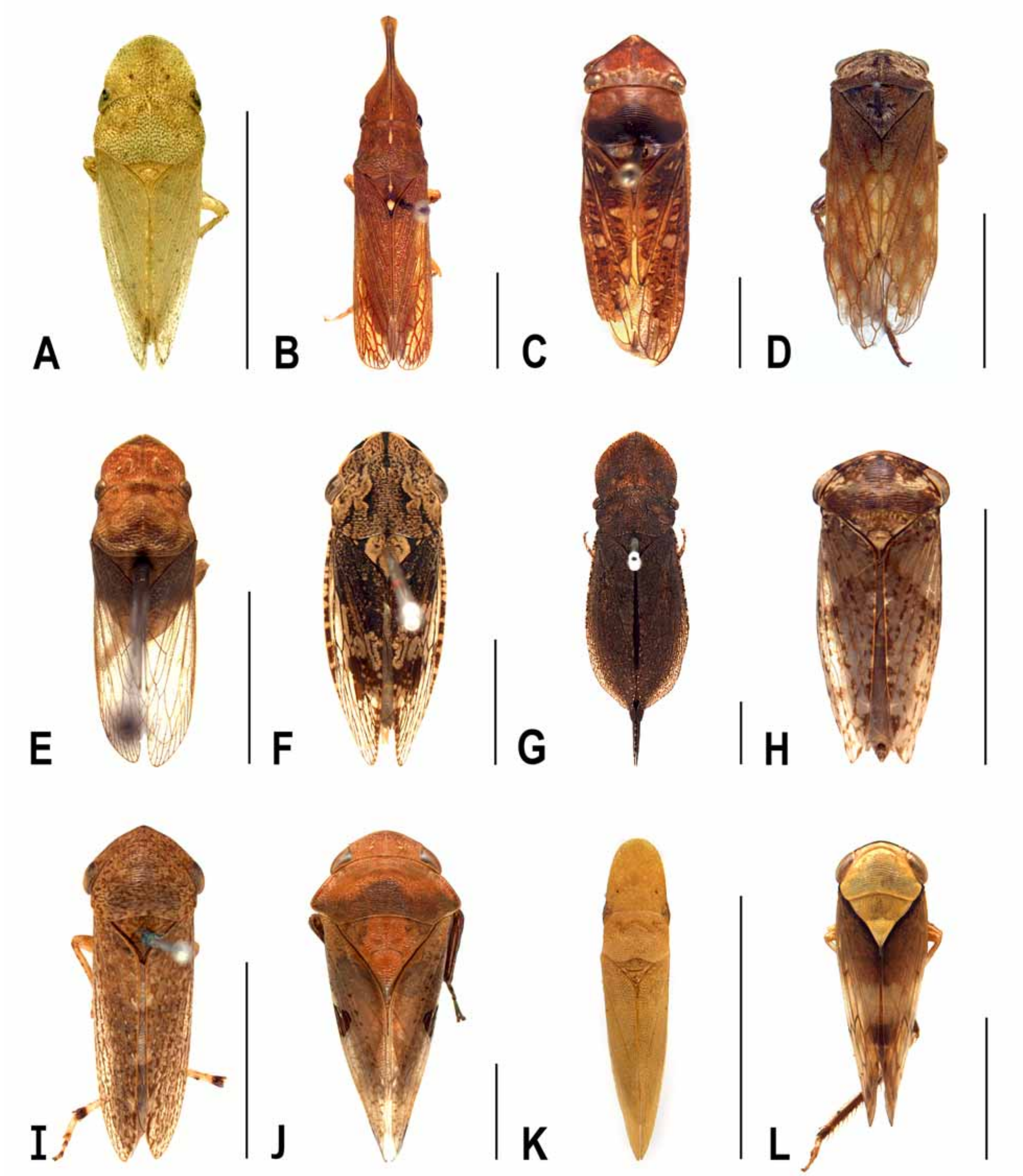

PLATE 5. Taxa in analysis, dorsal aspect. A. Xerophloeini: *Xerophloea viridis* (Fabricius), #JRJ_Led1_215, ♀. B–E, Unplaced taxa removed from Ledrinae. B. *Bascarrhinus platypoides* Fowler, #JRJ_Led1_010, ♀. C. *Betsileonas marmorata* (Blanchard), #JRJ_Led1_022, (abdomen missing). D. *Cololedra declivata* Evans, #JRJ_Led1_270, (abdomen missing). E. *Platyhynna bdellostoma* (Berg), #JRJ_Led1_274, ♂. F–G, Stenocotini. F. *Stenocotis depressa* (Walker), #JRJ_Led1_221, ♂. G. *Ledromorpha planirostris* (Donovan), #JRJ_Led1_084, ♀. H–I, Thymbrini. H. *Macroceps fasciatus* Signoret, #JRJ_Led1_265, ♀. I. *Thymbris convivus* (Stål), #JRJ_Led1_209, ♂. J. Scarini: *Clinonana mirabilis* (Spångberg), #JRJ_Led1_030, ♂. K. Ulopini: *Stenoledra decorsei* Evans, #JRJ_Led1_169, ♀. L. Tartessini: *Brunotartessus fulvus* (Walker), JRJ_Led1_424, ♀. L. Bars = 5 mm.

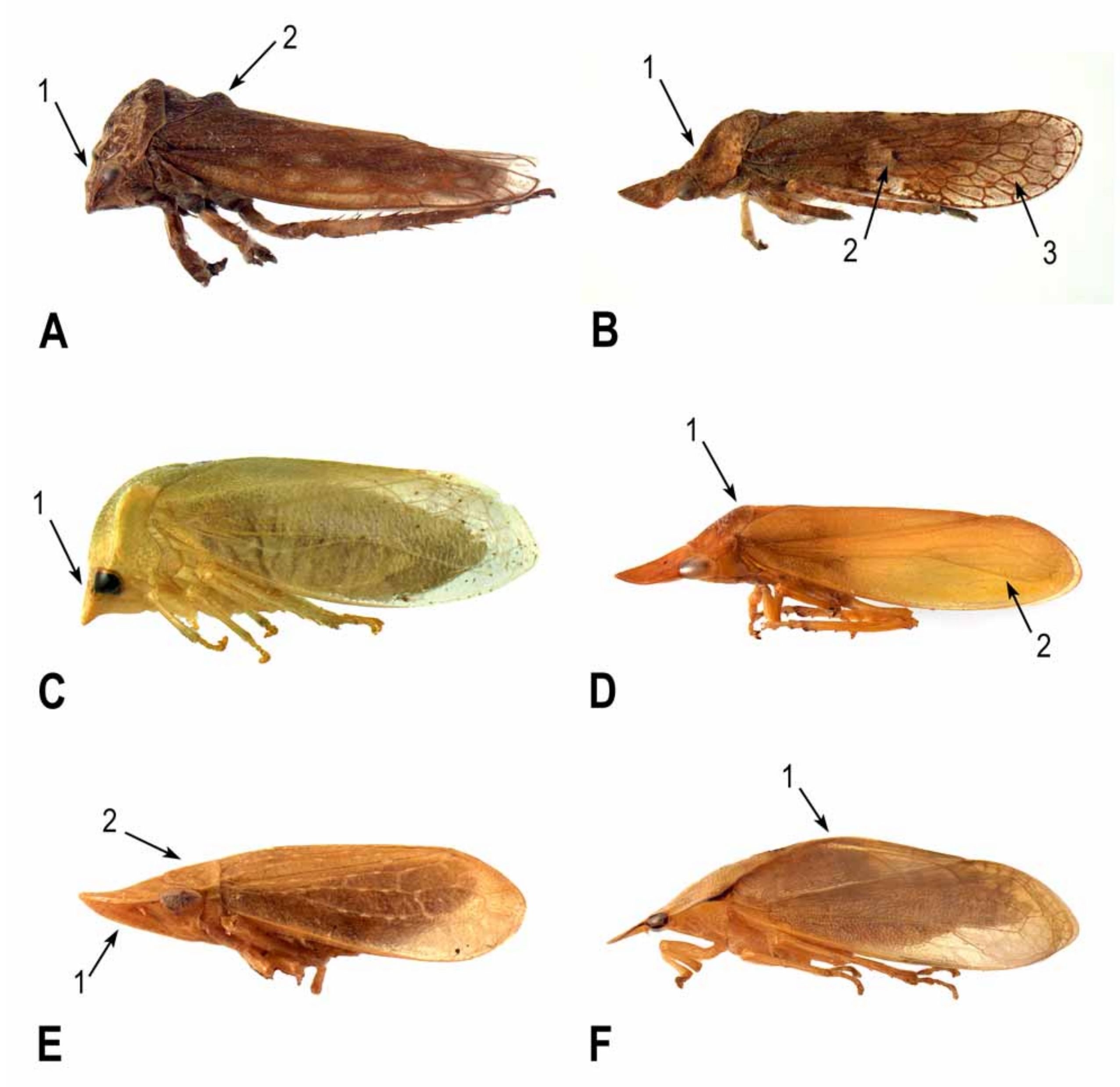

PLATE 6. Taxa in analysis: lateral aspect. A. *C. declivata*: (1) crown inclination steep but subvertical; (2) scutellum swollen. B. *F. tuberculata*: (1) pronotum flat anteriorly and steeply declivous posteriorly; (2) large sclerotized tubercle at first split of M vein; (3) venation reticulate. C. *P. adspersipennis*: (1) head inclined nearly perpendicular to substrate. D. *R. informis*: (1) head and pronotum flexed forward at posterior margin of pronotum (a feature not included in phylogenetic analysis); (2) venation regular. E. *Sichaea* sp.: (1) face flat and slightly convex; (2) pronotum flat. F. *T. planata*: (1) body appearing flexed forward at point posterad of scutellum.

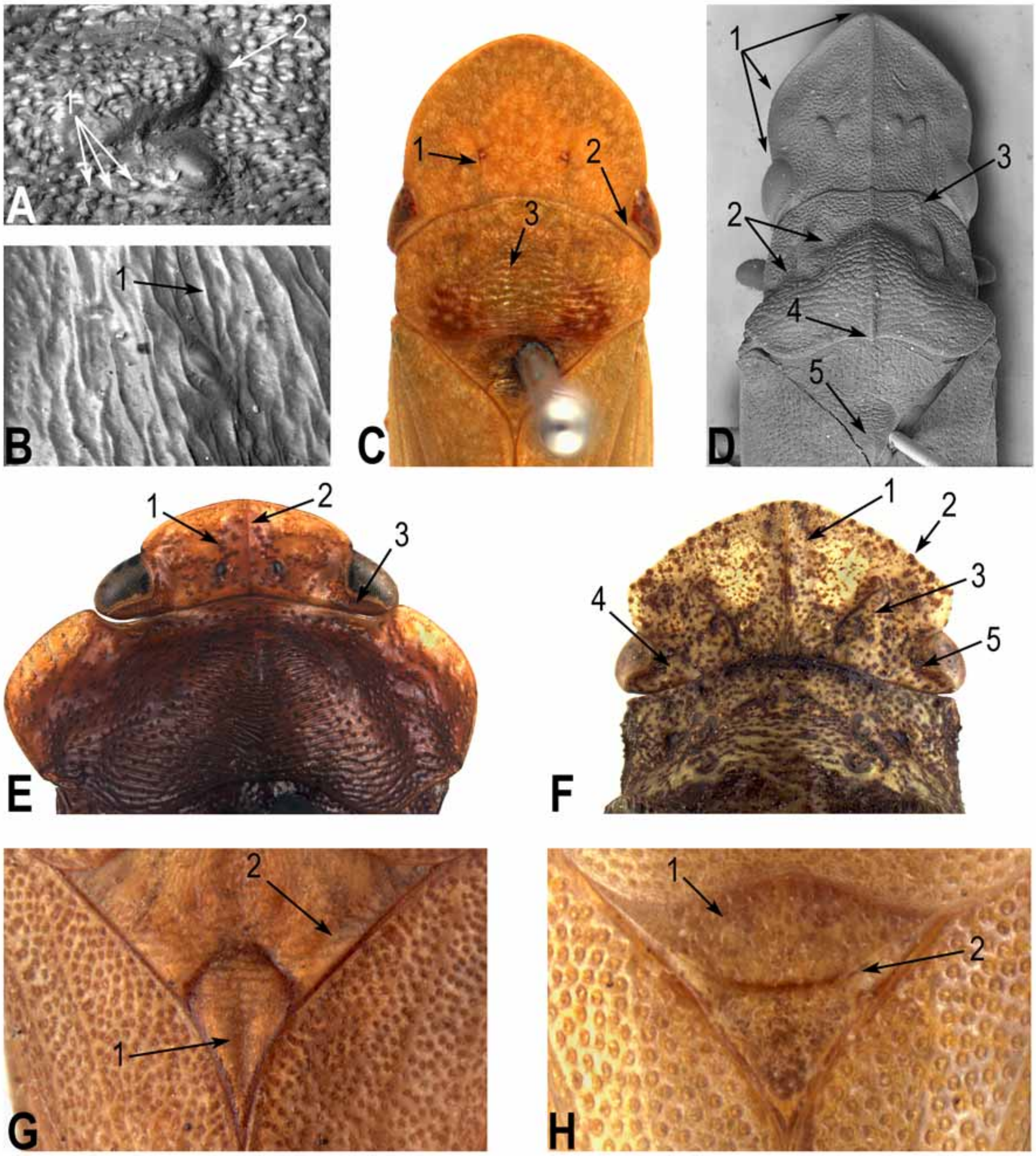

PLATE 7. Characters and states in analysis: crown, pronotum, mesoscutum, and scutellum. A. *J. grisea*, crown: (1) texture punctate and acinose; (2) process laterad of ocellus. B. *A. vitticollis*, crown: (1) longitudinally costate texture. C. *R. brevifrons*: (1) groove adjacent to ocelli; (2) area behind eyes intermediately broad, with carina; (3) transverse shallow wrinkles on pronotum. D. *J. grisea*: (1) crown pentagonal; (2) pronotum irregular with deep depressions; (3) anterior margin of pronotum with sublateral longitudinal ridges in line with processes laterad of ocelli; (4) posterior margin of pronotum with an inverse medial peak; (5) scutellum spikelike. E. *Dusuna* sp. 2: (1) crown texture punctate; (2) longitudinal marginal carina complete anteriorly only; (3) crown area behind eye thin without a carina. F. *L. aurita*: (1) crown with median longitudinal fold; (2) tuberculate; (3) with sclerotized ridge laterad of ocellus; (4) rugose near eyes; (5) with club-like setae. G. *B. peculiaris*: (1) mesoscutum with lateral ridges; (2) scutellum with median longitudinal depression. H. *S. decorsei*: (1) mesoscutum more than three times wider than long; (2) mesoscutal sulcus broadly U-shaped.

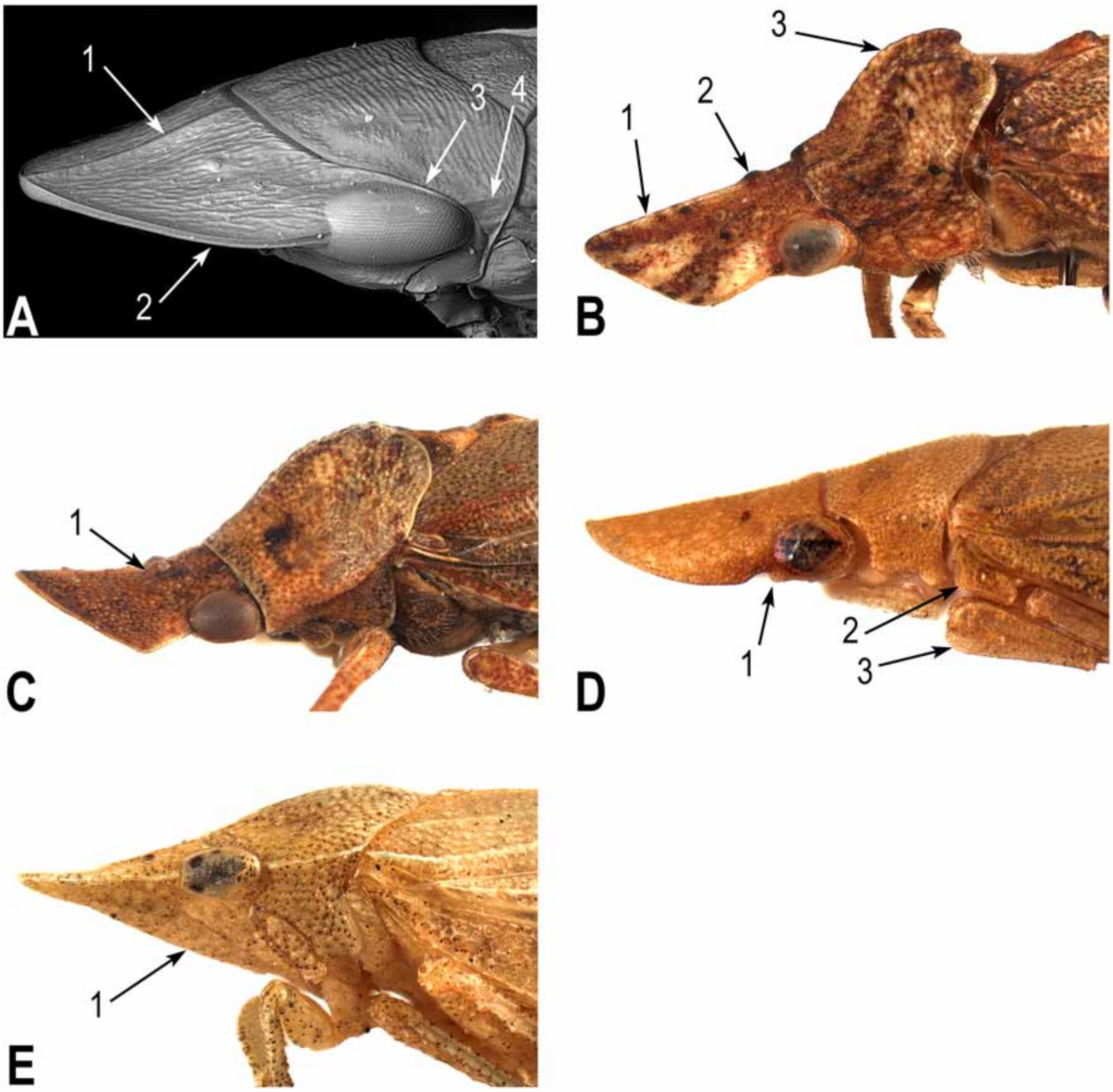

PLATE 8. Characters and states in analysis: crown and pronotum, lateral aspect. A. *A. vitticollis*: (1) crown with complete longitudinal medial carina; (2) primary and secondary marginal carinae; (3) area behind eyes narrow and carinate; (4) pronotum boxlike laterally. B. *J. grisea*: (1) median longitudinal carina high and lamellate; (2) posteromedial fin on longitudinal median carina; (3) pronotum median ridge a high crest. C. *L. discolor*: (1) ocelli raised on a protuberance. D. *S. decorsei*: (1) post antennal nodule; (2) metepisternum large, quadrate, even with forewing and pronotum above mesothoracic leg; (3) pro- and mesothoracic tibiae foliaceous and flat. E. *X. viridis*: (1) frontoclypeus visible in lateral aspect.

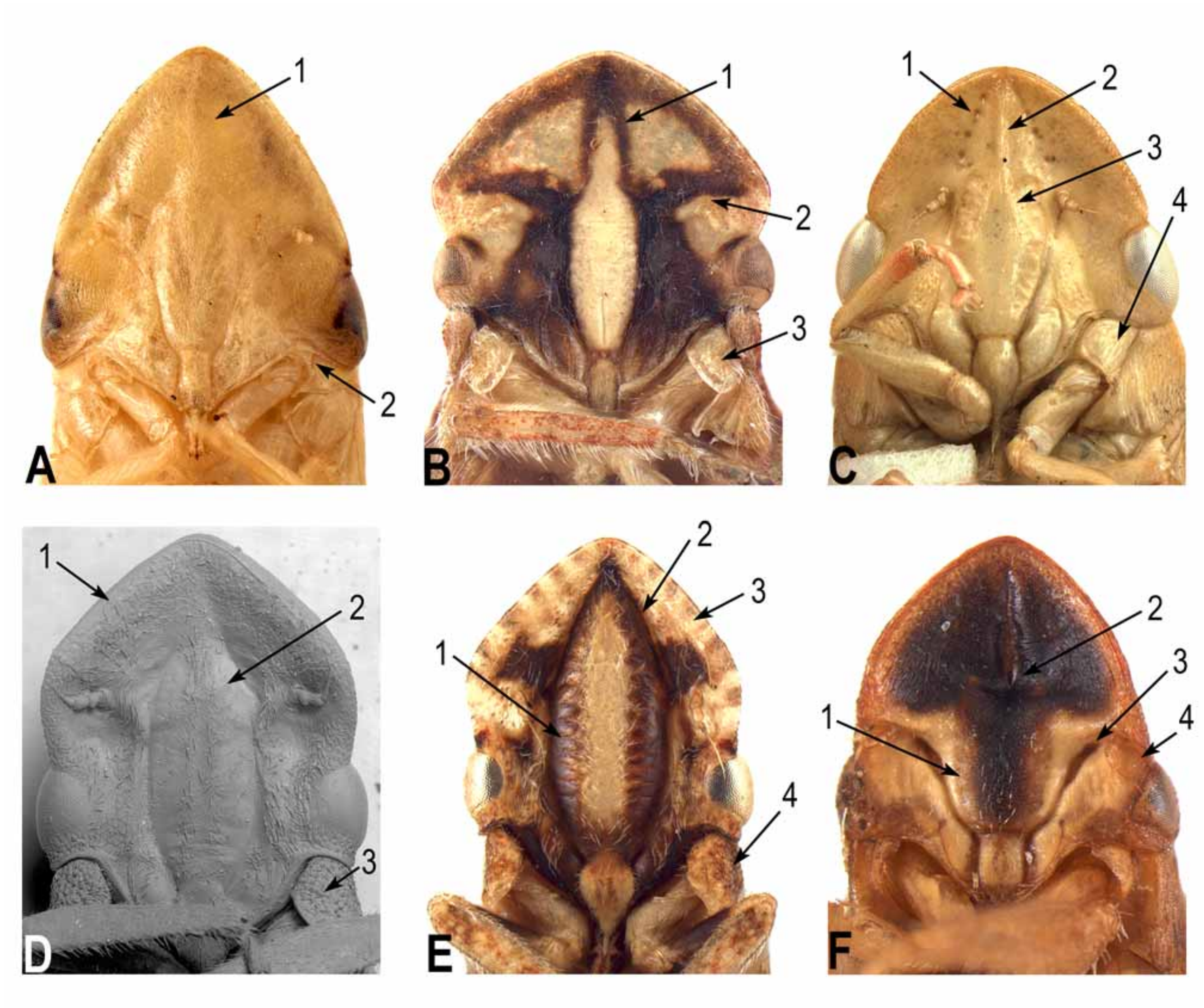

PLATE 9. Characters and states in analysis: face in ventral aspect. A. *A. vitticollis*: (1) frontoclypeus apical extension not well defined; (2) proepisternum small, tab-like, underlapping genae. B. *F. tuberculata*: (1) frontoclypeus apical extension well defined, narrow; (2) inner margin of antennal pit well developed, oblique; (3) proepisternum large, quadrate, not underlapping genae. C. *H. chilensis*: (1) row of pits; (2) frontoclypeus apical extension with median longitudinal carina; (3) frontoclypeus base bicarinate; (4) proepisternum large and quadrate. D. *J. grisea*: (1) margin of crown not squared in cross section; (2) frontoclypeus not expanded and almond-shaped, not filling face. (3) proepisternum large, collar-like, extending laterally onto pronotum. E. *Ledropsella* sp.: (1) frontoclypeus base with lateral perpendicular ridges; (2) Frontoclypeus almond-shaped, filling face; (3) margin of crown squared in cross section; (4) proepisternum large, collar-like, extending laterally onto pronotum. F. *Platyhynna* sp.: (1) frontoclypeus wide, short; (2) medial pit and groove anterior to frontoclypeus; (3) anterior tentorial pit large, open; (4) post antennal nodule.

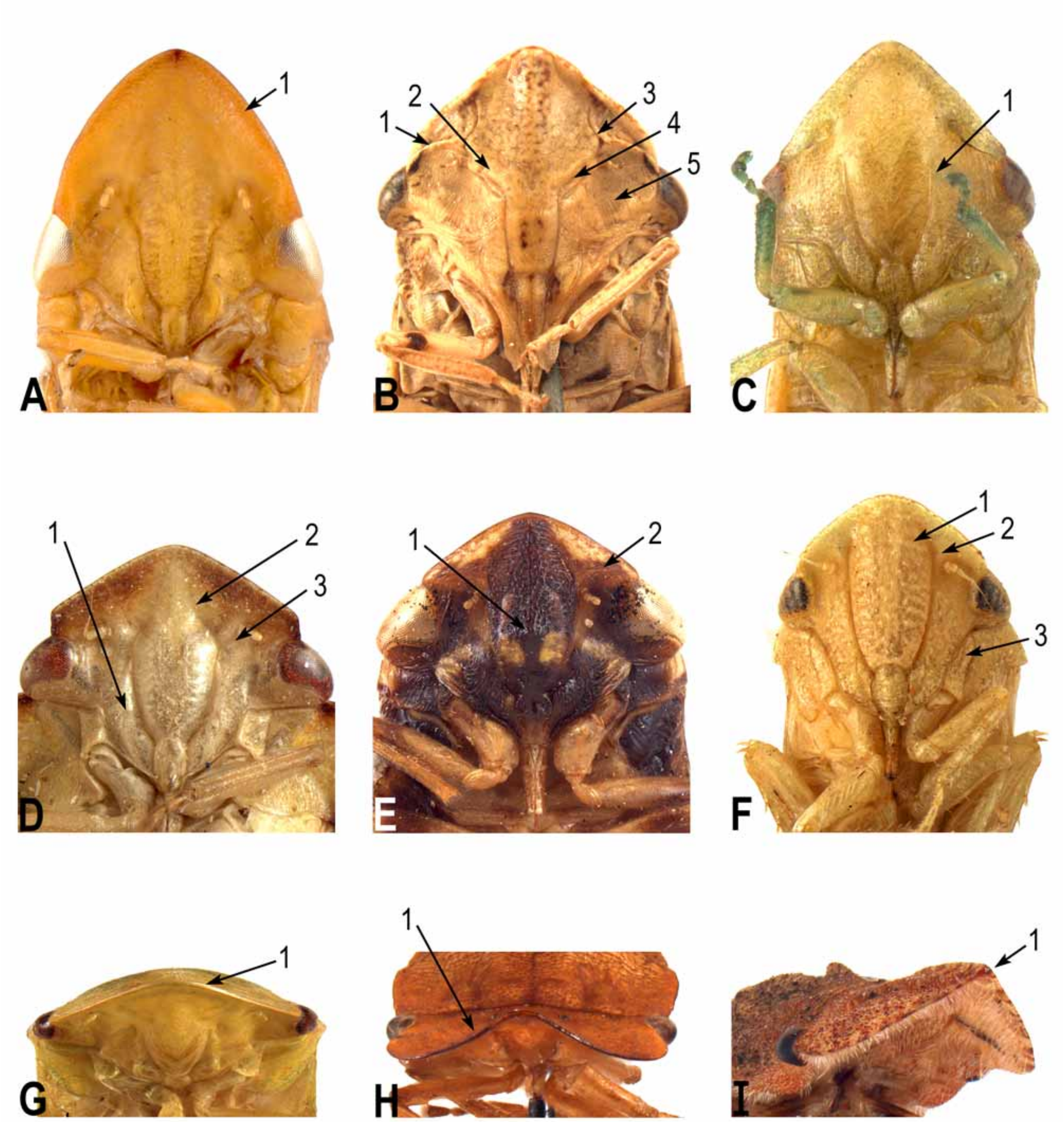

PLATE 10. A–F, Characters and states in analysis: face in ventral aspect, cont. A. *R. informis*: (1) crown margin not carinate. B. *S. depressa*: (1) antennal ledge appearing pinched or wrinkle-like; (2) frontoclypeus marginal sutures widely divergent and (3) crossing bar in front of antennae; (4) antennal pit inner margin a bar continuous with frontoclypeus, 45°; (5) genal rugosities. C. *Titiella humerosa* (Naudé): (1) suture between frontoclypeus and genae weakly developed. D. *Thlasia obtusa* (Walker): (1) lora/genae tumid and angulate; (2) apex of frontoclypeus flexed ventrad; (3) antennal pit inner margin somewhat well developed, approximately parallel to frontoclypeus. E. *X. tuberculata*: (1) frontoclypeus medially angulate, punctate; (2) antennal ledge a thin carina. F. *X. viridis*: (1) frontoclypeus broad throughout; (2) antennal pit inner margin a thin ridge; (3) proepisternum long and narrow. G–I, Characters and states in analysis: face in anterior aspect. G. *P. raniceps*: (1) crown transverse camber weakly curved. H. *B. peculiaris*: (1) crown transverse camber depressed adjacent to midline. I. *P. acuminata*: (1) crown transverse camber sharply angled.

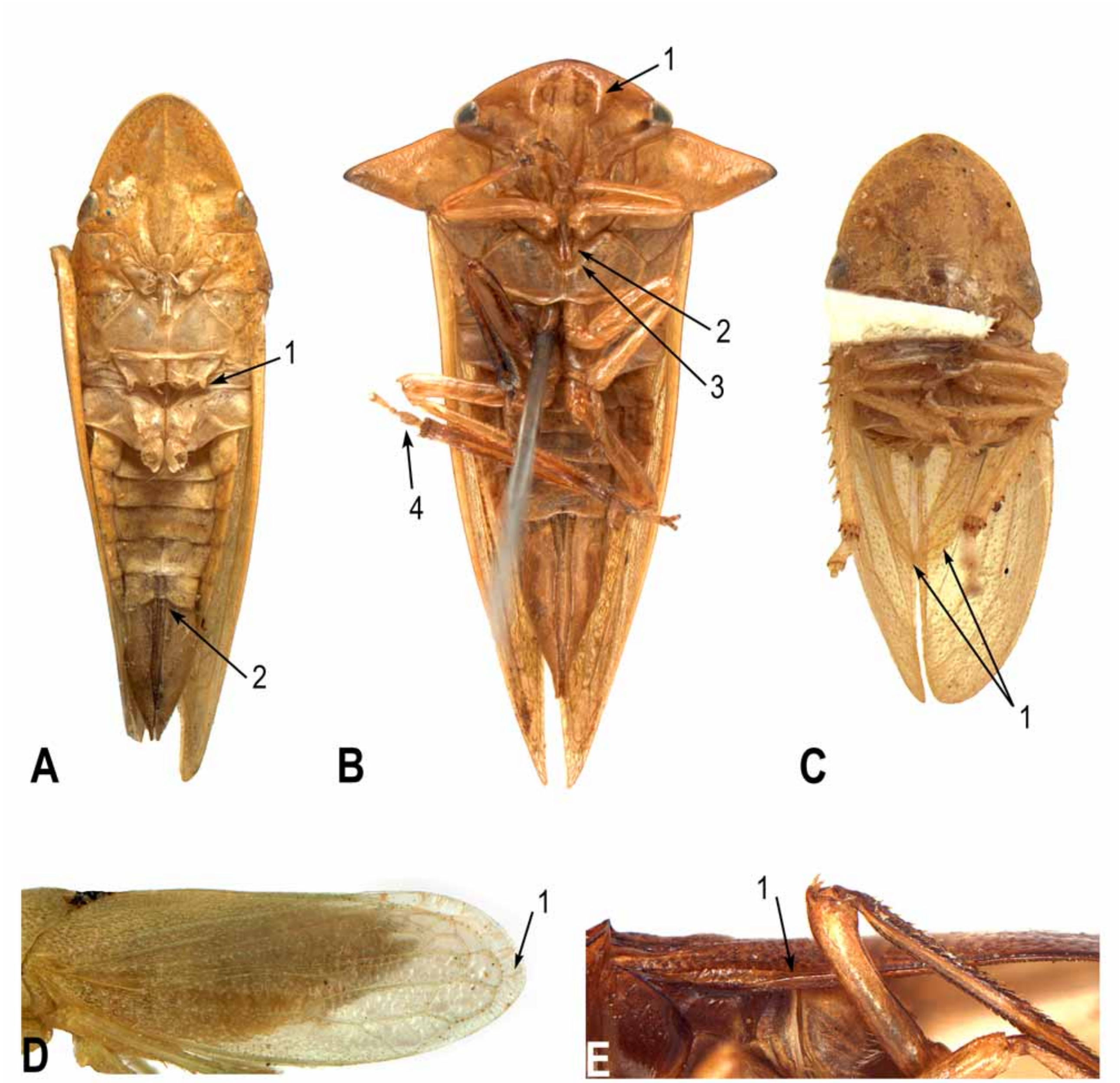

PLATE 11. Characters and states in analysis: sternites and wings, ventral and lateral aspects. A. *P. raniceps*: (1) mesocoxal horn; (2) sternite VII emarginate. B. *T. planata*: (1) antennal pit inner margins well developed, parallel to frontoclypeus; (2) median triangular depression between forelegs clearly depressed posteriorly; (3) fore edge of mesocoxa abrupt and angulate; (4) metathoracic tarsomere I intermediate in length. C. *Sichaea* sp.: (1) hind wings highly reduced. D. *X. viridis*: (1) appendix broad. E. *Dusuna* sp. 2: (1) leading edge of forewing divided by secondary longitudinal carina.

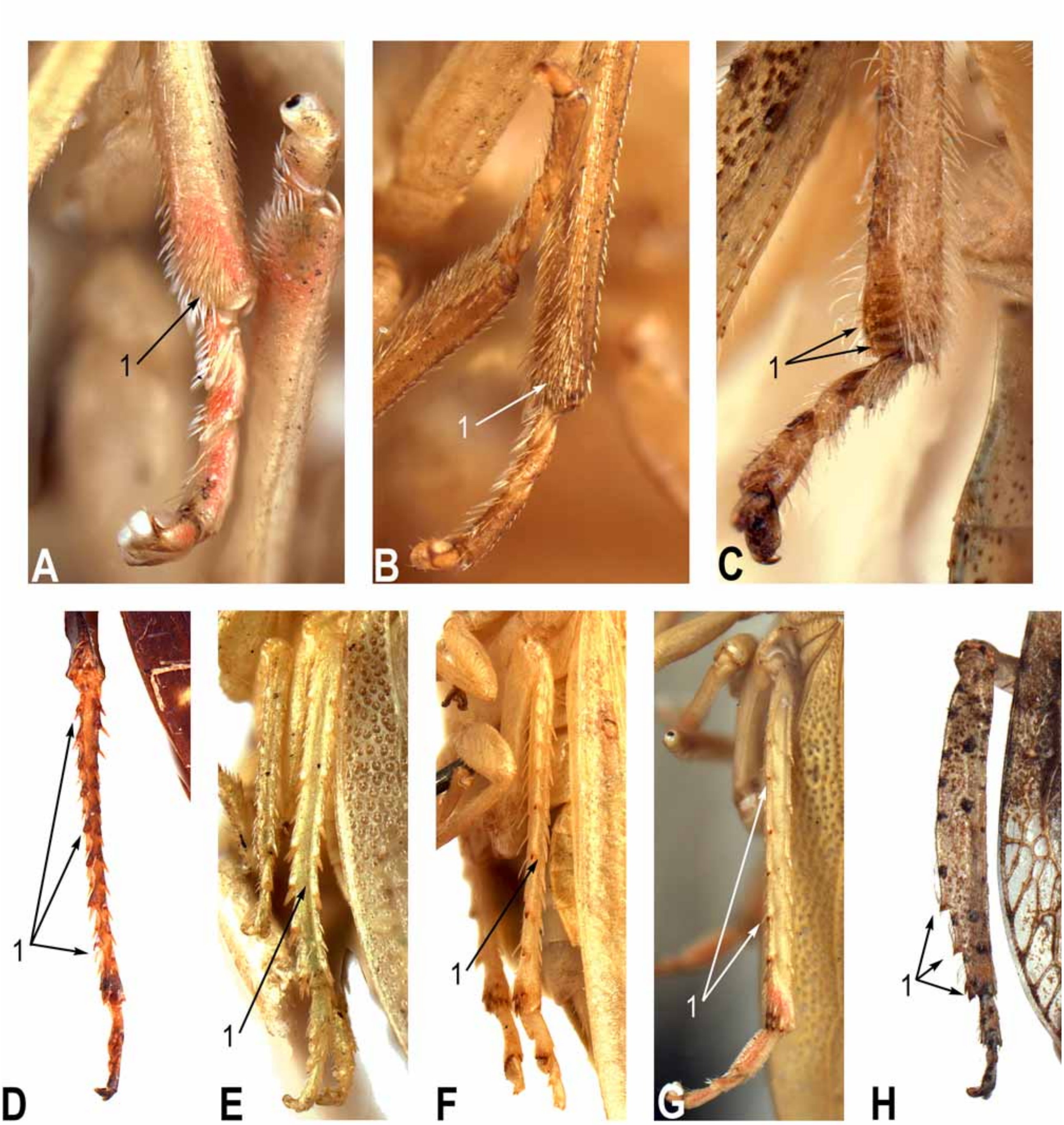

PLATE 12. Characters and states in analysis: meso- and metathoracic tibiae of Ledrinae. A–C, Mesotibial row 2 apical triangular setae patch. A. *H. chilensis*: setae brushlike, not in rows. B. *B. peculiaris*: setae brushlike, not in rows. C. *Ledra auditura* Walker: setae scalelike, in rows. D–H, Metathoracic tibia. D. *X. tuberculata*: (1) row II with more than nine primary setae on stout setal bases. E. *X. viridis*: (1) face between rows I and II a broad groove, tibia quadrate in cross-section. F. *A. vitticollis*: (1) face between rows I and II a broad groove, tibia quadrate in cross-section. G. *H. chilensis*: (1) setal bases in row II cucullate. H. *L. auditura*: (1) tibia foliaceous, with setal row II consisting of primary setae with cucullate bases and intercalated hairlike setae.

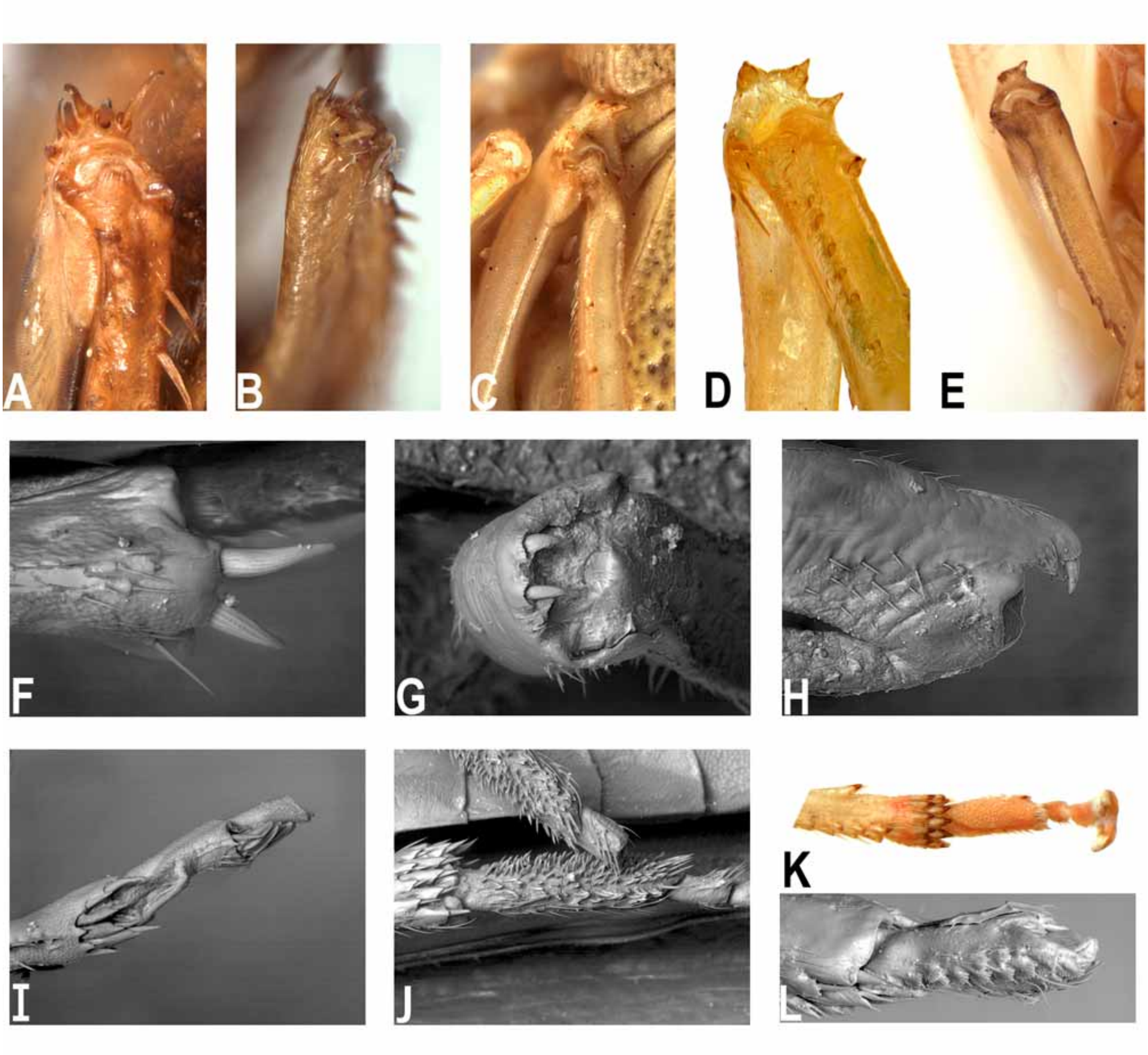

PLATE 13. Characters and states in analysis: metathoracic femur apical macrosetae, and metathoracic tarsomere I. A–H, Metathoracic femur apical macrosetae. A. *B. marmorata*: numerous macrosetae. B. *C. mirabilis*: macrosetae formula apparently 2 + 1 + 1. C. *H. chilensis*: macrosetae on a long and narrowing process, formula 2 + 1. D. *P. raniceps* Linnavuori: macrosetae formula 2 + 1. E. *R. informis*: macrosetae on a long and narrowing process, formula 2 + 0. F. *A. vitticollis*: apex of metathoracic femur in dorsal aspect showing macrosetae long and striated. G. *J. grisea*: macrosetae short and not striated. H. *J. grisea*: apex of metathoracic femur in lateral aspect showing macrosetae mounted on an intermediately long but not narrowing base. I–L, Metathoracic tarsomere I. I. *A. vitticollis*: tarsomere I intermediately long, with a short well developed ridge, and microtexture all over. J. *J. grisea*: tarsomere I long, with short, coarse ventral setae. K. *H. chilensis*: tarsomere I intermediately long, short coarse ventral setae short, thick, white, and fingerlike. L. *P. raniceps*: tarsomere I lateral setal bases scalloped.

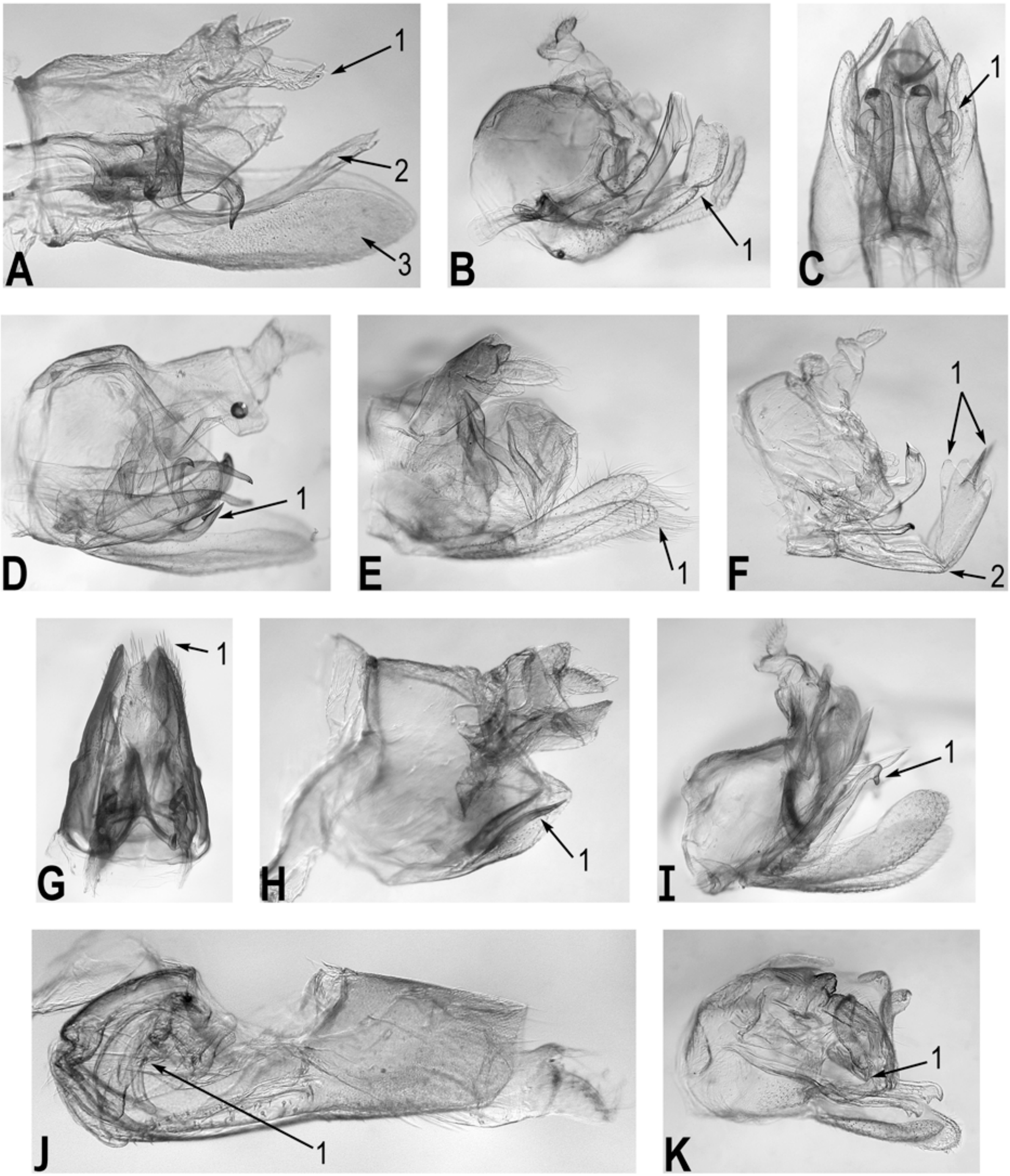

PLATE 14. Characters and states in analysis: male genital capsule and structures, lateral and ventral aspects. A. *B. peculiaris*, lateral aspect: (1) anal tube ventrodistal lobe; (2) aedeagus long and slender throughout; (3) plates long. B. *Coloborrhis corticina* Germar, lateral aspect: (1) plates articulated. C. *L. mutica*, ventral aspect: (1) pygofer inner subapical processes hook-shaped. D. *N. kongasana*, lateral aspect: (1) style with apical barb. E. *S. depressa*, lateral aspect: (1) plates with very long apical setae. F. *S. decorsei*, lateral aspect: (1) style apices trilobed, medial lobe acuminate; (2) plates articulated. G. *B. fulvus*, ventral aspect: (1) plates with very long apical setae. H. *T. brunnipennis*, lateral aspect: (1) pygofer basidistal processes. I. *T. corona*, lateral aspect: (1) style with a single apical point directed ventrad. J. *Platyhynna* sp., lateral aspect: genital capsule withdrawn into pygofer, aedeagus inverted. K. *J. grisea*, lateral aspect: (1) articulation of paraphyses.

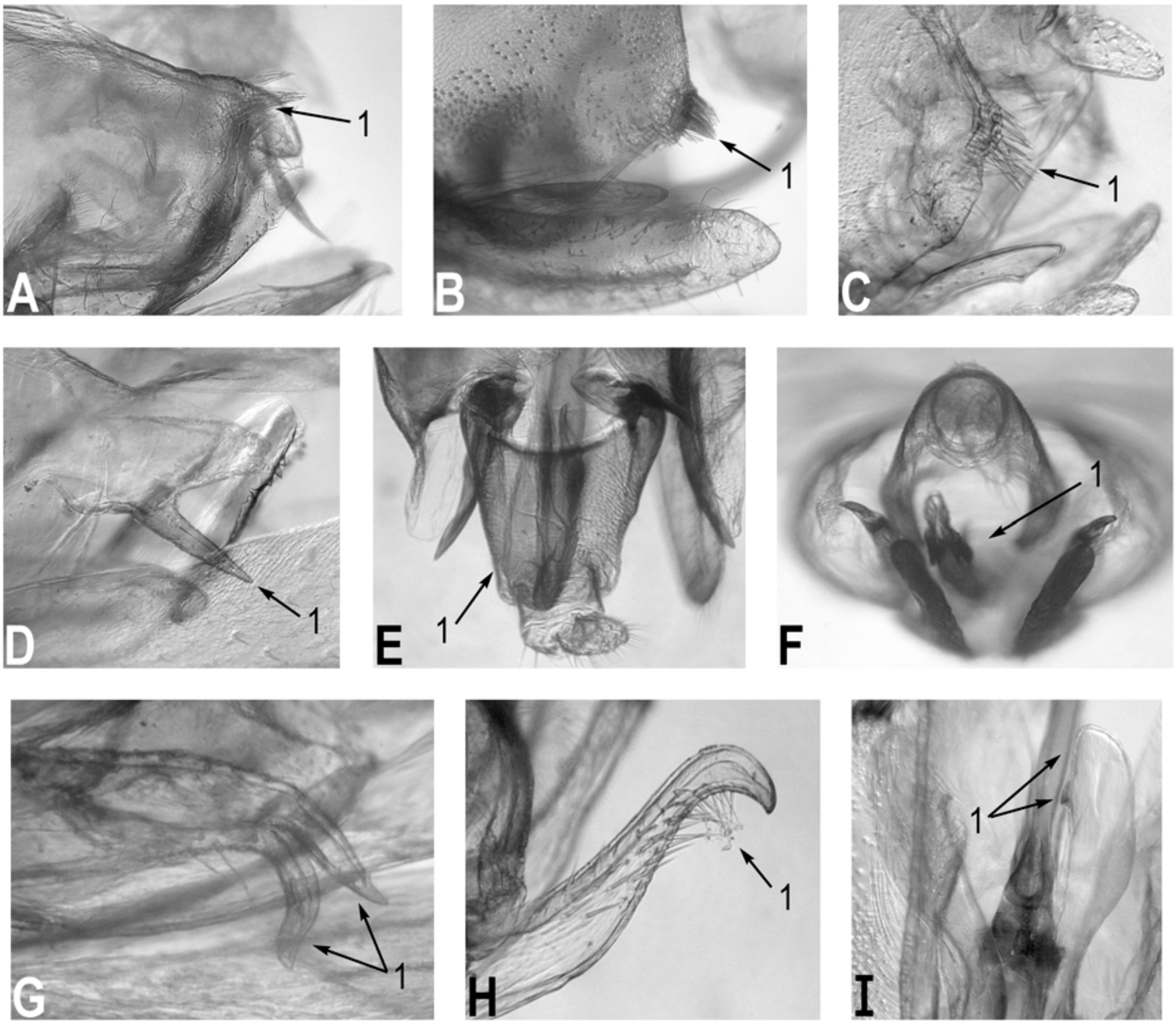

PLATE 15. Characters and states in analysis: male genitalia. A. *C. mirabilis*: (1) pygofer subapical setae patch, lateral aspect. B. *P. adspersipennis*: (1) pygofer apical setae patch, lateral aspect. C. *X. viridis*: (1) pygofer apical setae patch, lateral aspect. D. *T. antica*: (1) pygofer subapical process not hooklike, lateral aspect. E. *A. vitticollis*: (1) anal tube broad, conelike, and sclerotized, ventral aspect. F. *A. vitticollis*: (1) anal tube incomplete ventrally, distal aspect. G. *L. discolor*: (1) style apex with two points directed ventrad, lateral aspect. H. *L. froggatti*: (1) style subapical ventral setae patch, lateral aspect. I. *P. adspersipennis*: (1) style flat with apex rounded and subapical ventral point, ventral aspect.

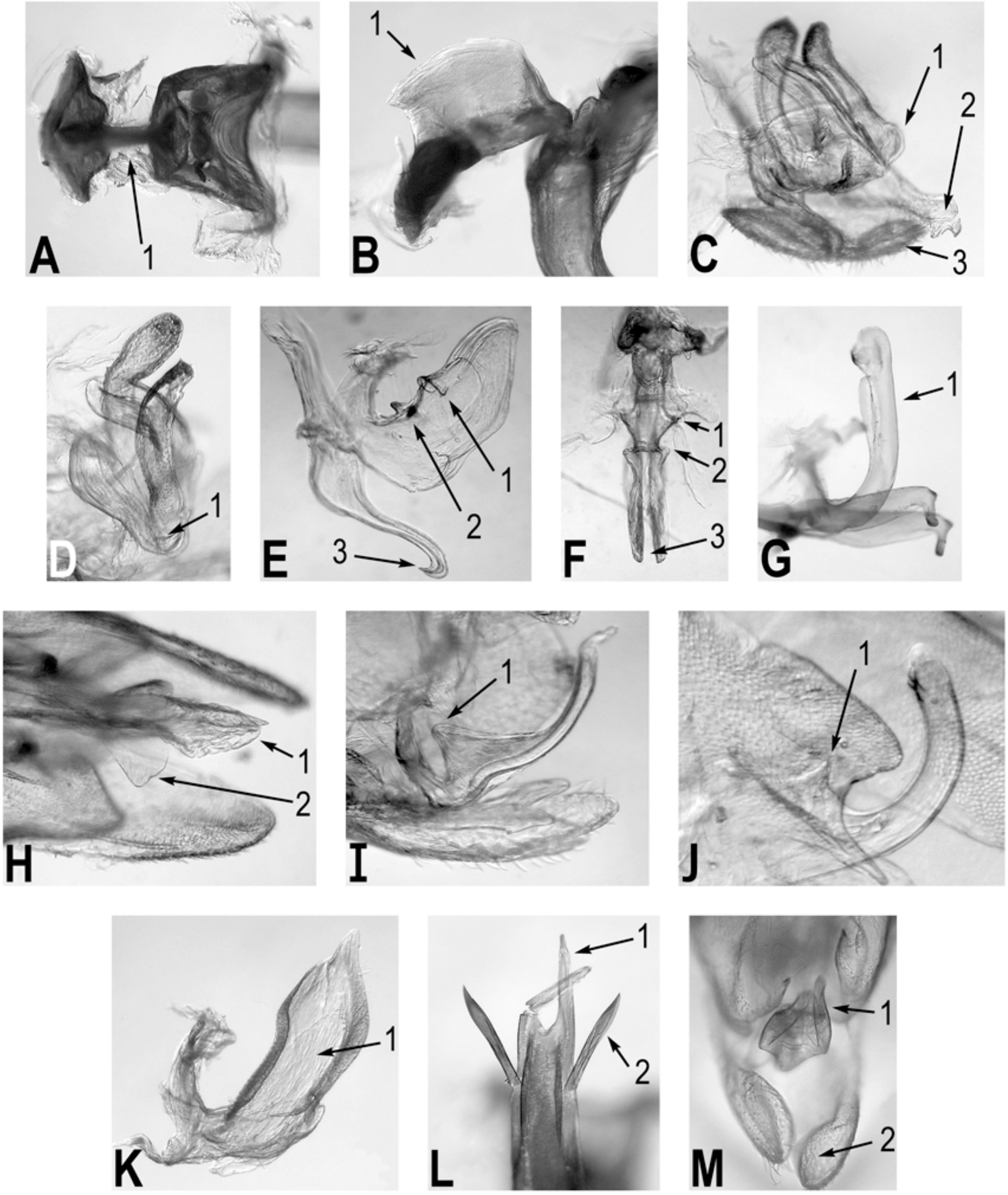

PLATE 16. Characters and states in analysis: male genitalia: connective, paraphyses and aedeagus. A. *Tituria forficula* Linnavuori, dorsal aspect: (1) connective slender medially. B. *T. forficula*, lateral aspect: (1) connective a high fin medially. C. *P. caldida* Evans, distal aspect: (1) paraphyses articulated; (2) style with 2 apical points directed ventrad; (3) plates compressed dorsoventrally. D. *P. caldida*, lateral aspect: (1) paraphyses articulated. E. *H. signata* Linnavuori, lateral aspect: (1) aedeagus with dorsal bridge and (2) paired dorsal points; (3) styli apices recurving anterad. F. *H. signata*, dorsal aspect: (1) aedeagus with paired dorsal points and (2) paired dorsal bridge; (3) gonopore a groove. G. *L. aurita*, lateral aspect: (1) aedeagus intermediately broad throughout. H. *P. conspicua*, dorsal aspect: (1) aedeagus apical bulb; (2) subapical processes short and flat. I. *P. ghilianii*, lateral aspect: (1) dorsomedial lobe of aedeagus. J. *R. informis*, lateral aspect: (1) dorsomedial lobe of aedeagus hooklike. K. *T. brunnipennis*, lateral aspect: (1) aedeagus broad throughout. L. *T. forficula*, ventral aspect: (1) aedeagus apical and subapical processes. M. *T. planata*, distal aspect: (1) aedeagus apex with apical processes; (2) plates laterally compressed apically.

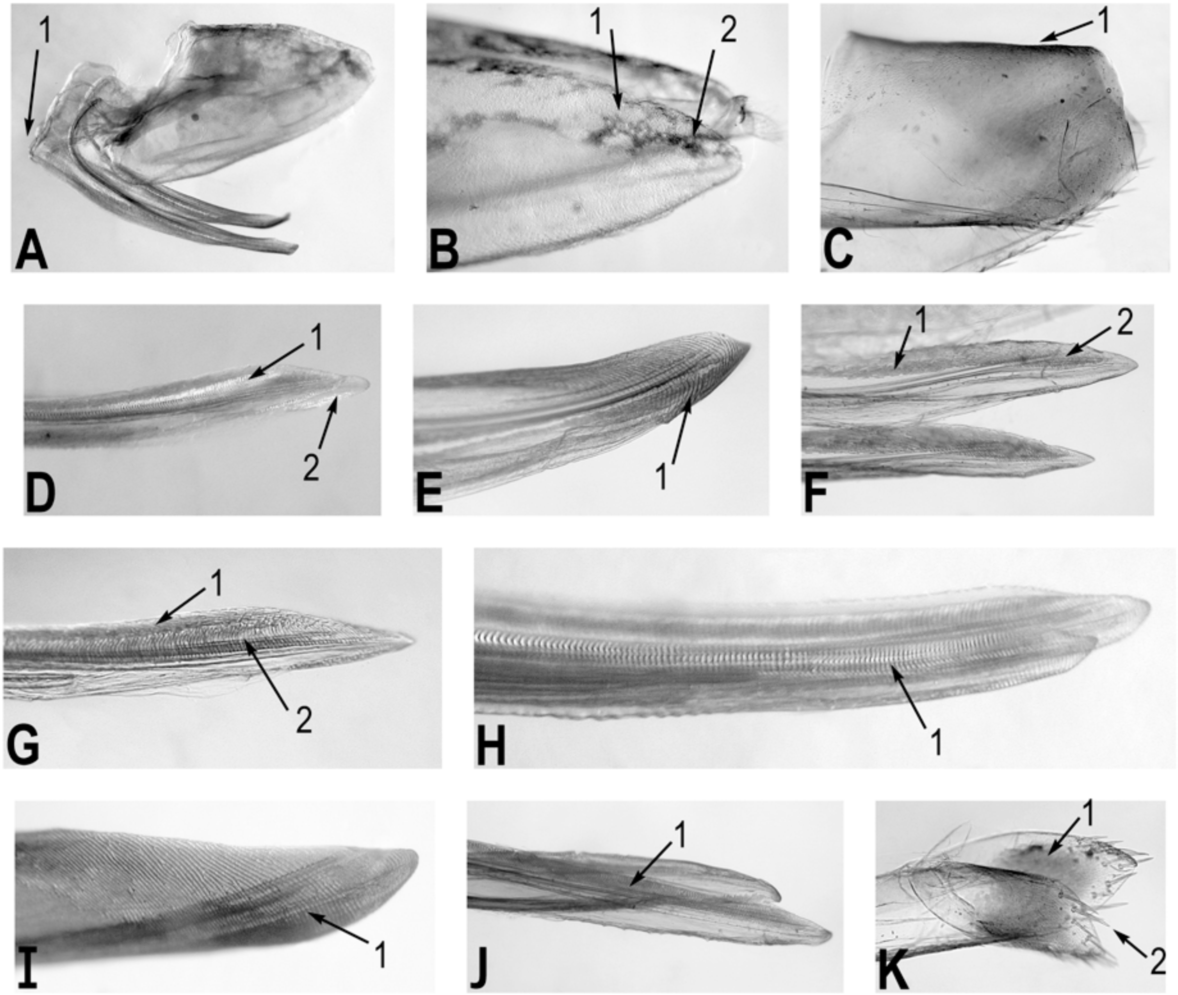

PLATE 17. Characters and states in analysis: female genitalia: pygofer, valvulae I and III, lateral aspect. A. *E. primitiva*: (1) valvulae I bases acutely angled. B. *E. primitiva*: (1) pygofer tuberculate with (2) mottled pigmentation. C. *Tartessus swezeyi* Metcalf: (1) pygofer sclerotized and appearing darkened dorsally. D. *A. vitticollis*: (1) valvulae I texture medial chevrons; (2) apical texture perpendicular strigae. E. *B. peculiaris*: (1) valvulae I texture strigate. F. *P. ghiliani*: (1) valvulae I dorsal texture parallel longitudinal strigae; (2) apex texture strigate. G. *Sichaea* sp.: (1) valvulae I dorsal texture parallel longitudinal strigae; (2) medial chevrons. H. *S. decorsei*: (1) valvulae I texture medial chevrons. I. *T. forficula*: (1) valvulae I apex texture strigate. J. *X. tuberculata*: (1) valvulae I texture in a narrow band along dorsal margin. K. *B. fulvus*: (1) valvulae III apices with mottled pigmentation and (2) numerous long setae.

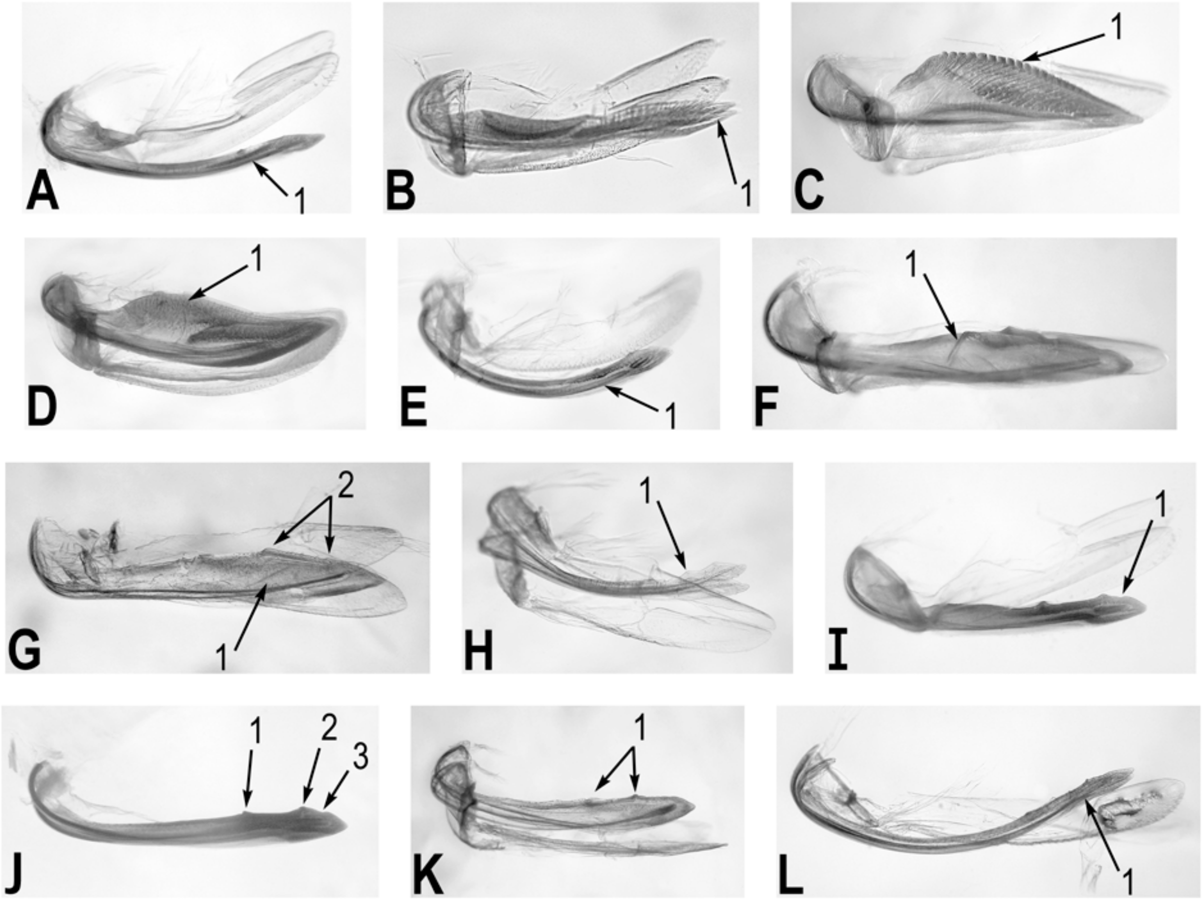

PLATE 18. Characters and states in analysis: female genitalia: valvulae II, lateral aspect. A. *A. vitticollis*: (1) valvulae somewhat sclerotized. B. *Aphrodes bicincta* (von Schrank): (1) valvulae apex split. C. *B. marmorata*: (1) numerous dorsal teeth (>11). D. *C. mirabilis*: (1) valvulae broadest medially, boat-shaped. E. *C. dispar*: (1) valvulae long and very slender. F. *E. primitiva* Evans: (1) median perpendicular keel. G. *H. chilensis*: (1) valvulae of intermediate breadth; (2) dorsal tooth II closer to apex than to dorsal tooth I. H. *Iassus scutellaris* (Fieber): (1) valvulae II blade split from tooth II to apex. I. *L. discolor*: (1) subapical dorsal notch. J. *L. aurita*: (1) dorsal tooth I closer to apex than midpoint; (2) dorsal tooth II closer to apex than to dorsal tooth I; (3) subapical dorsal notch. K. *N. kongasana*: (1) dorsal tooth II closer to dorsal tooth I than to apex. L. *P. testacea*: (1) valvulae II with a secondary curve (coded for valvulae I).

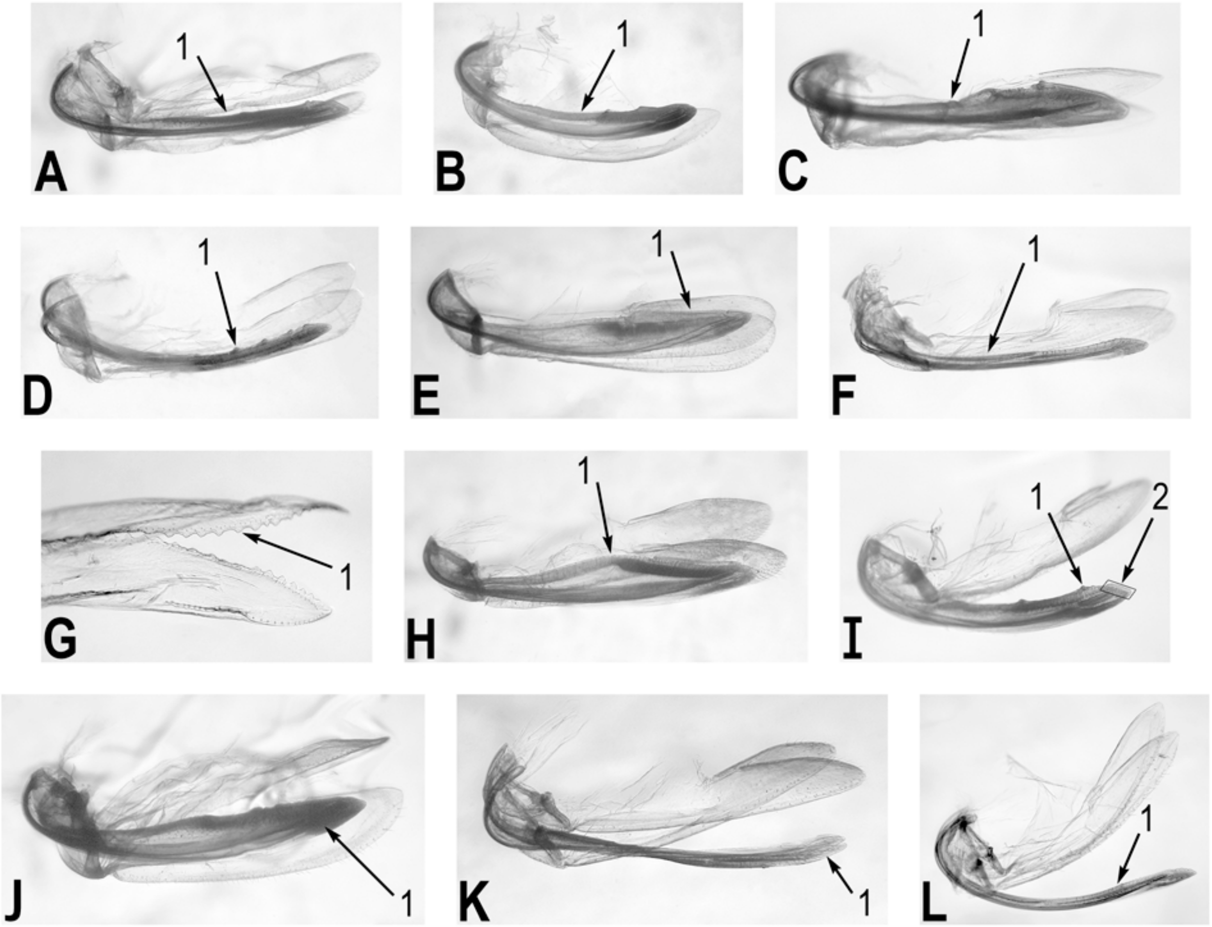

PLATE 19. Characters and states in analysis: female genitalia: valvulae II, lateral aspect, cont. A. *P. bohemani*: (1) valvulae long and intermediately slender. B. *P. raniceps*: (1) valvulae long and intermediately slender. C. *P. acuminata*: (1) medial perpendicular keel. D. *R. sanguinosa*: (1) dorsal teeth <10. E. *S. depressa*: (1) numerous dorsal teeth (>11). F. *S. decorsei*: (1) valvulae long and very slender. G. *T. swezeyi*: (1) numerous dorsal teeth (>11), blade not sclerotized. H. *T. convivus*: (1) valvulae broadest medially, boat-shaped. I. *T. humerosa*: (1) dorsal tooth II closer to apex than to dorsal tooth I; (2) valvulae apex shape subrectangular. J. *T. planata*: (1) blade strongly sclerotized. K. *X. tuberculata*: (1) valvulae blade split from dorsal tooth II to apex. L. *X. viridis*: (1) valvulae long and very slender.