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## A Revised Classification of the Phylinae (Insecta: Heteroptera: Miridae): Arguments for the Placement of Genera

RANDALL T. SCHUH<sup>1</sup> AND KATRINA L. MENARD<sup>2</sup>

### ABSTRACT

As a companion to the tribal-level phylogenetic analysis of Phylinae by Menard, Schuh, and Woolley (2013), a comprehensive generic classification of the subfamily is presented. Names used in the work of Menard et al. (2013) at the tribal/subtribal levels are documented in accordance with the International Code of Zoological Nomenclature (1999). The new tribal-level names Coatonocapsina, Decomiini, Exocarpocorini, Keltoniina, and Tuxedoina are introduced; the long unused or seldom-used tribal-level names Cremnorrhini Reuter, 1883, Exaeretina Puton, 1975, Nasocorini Reuter, 1883, Oncotylina Douglas and Scott, 1865, and Semiini Knight, 1923, are used and rediagnosed; Phylini Douglas and Scott, 1865, is given a more narrow conception than in previous classifications and the subtribe Phylina is recognized; Pilophorini Douglas and Scott, 1865, is conceived more broadly to include *Lasio-labops* Poppius and *Dilatops* Weirauch; Auricillocorini Schuh, 1984, is treated as a junior synonym of Hallodapini Van Duzee; and Pronotocrepini Knight, 1929, is treated as a junior synonym of Cremnorrhina, Reuter, 1883. Comments are made on some of the genera included in the analyses of Menard et al. (2013) and arguments are presented for the placement of all remaining genera of Phylinae, some of which are placed as incertae sedis—particularly within Phylina—because of insufficient evidence to place them with confidence in any currently recognized tribe/subtribe. *Lapazphylus* Carvalho and Costa, 1992, is treated as

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a junior synonym of *Nicholia* Knight, 1929; *Schuhistes* Menard, 2010, is treated as a junior synonym of *Parasciodema* Poppius, 1914; *Linacoris* Carvalho, 1983, is transferred from the Orthotylinae to Phylinae, Hallodapini; and the status of *Parapsallus* Wagner, 1952, is revised.

## INTRODUCTION

Menard et al. (2013) presented a phylogenetic analysis comprising representatives of 103 genera and 164 terminal taxa of Miridae: Phylinae from most major zoogeographic regions, with analyses including morphology and DNA sequence data from nuclear-ribosomal and mitochondrial genes. That work provided sufficient documentation to propose a revised tribal/subtribal classification, and as such was the first study to offer empirical support for dismantling of the long recognized—but clearly paraphyletic—Phylini. Nonetheless, the work of Menard et al. (2013) left many genera unplaced because the taxonomic sample was far from exhaustive. In this paper we (1) provide arguments for the placement of the genera not included in the taxon sample of Menard et al. (2013), (2) further discuss the monophyly of the tribes and subtribes recognized by them, (3) validate new tribal/subtribal names and document the reintroduction of long-unused names, (4) correct some long-standing errors of taxonomic placement, and (5) introduce new synonymy at the tribal and generic levels. Many of our arguments are based on published phylogenetic analyses involving genera in addition to those sampled by Menard et al. (2013), but at a more restricted level, as these are the best available sources of information from which to deduce relationships. We have also relied on extensive comments from colleagues to inform our decision making. Ultimately, many of our placements will benefit from the acquisition of sequence data for taxa in addition to those sampled by Menard et al. (2013), because it seems clear that we have not been able to observe sufficient morphological variation in the Phylinae to allow for the well-justified placement of many genera at the current time.

The present work is a companion to Menard et al. (2013) and provides the formal justification of new names used by them. The following tribal-level groupings are listed in the order presented on the summary cladogram taken from Menard et al. (2013) (fig. 1).

Phylinae Douglas and Scott, 1865

    Hallodapini Van Duzee, 1916

    Nasocorini Reuter, 1883

    Exaeretini Puton, 1875

    Cremnorrhini Reuter, 1883

        Cremnorrhina Reuter, 1883

        Coatonocapsina, new subtribe

    Phylini Douglas and Scott, 1865

        Keltoniina, new subtribe

        Phylina Douglas and Scott, 1865

        Oncotylinea Douglas and Scott, 1865

    Semiini Knight, 1923

        Exocarpocorina, new subtribe

Semiina Knight, 1923

Pilophorini Douglas and Scott, 1876

Leucophoropterini Schuh, 1974

Tuxedoina, new subtribe

Leucophoropterina Schuh, 1974

Higher-category synonyms are simply listed; a more detailed history of the usage of these names can be found by consulting Carvalho (1952, 1958) and Schuh (2002–2013). The list of valid generic names and other nomenclatural information under each tribe/subtribe is taken from the “On-line Systematic Catalog of Plant Bugs” (Schuh, 2002–2013). The index will facilitate locating genera in the revised classification.

Family-group names proposed by Douglas and Scott (1865), Reuter (1883 and elsewhere), and others for taxa now placed in the Phylinae were often based on autapomorphic characters. In most cases the taxa remained monotypic and eventually fell into disuse with the appearance of the Carvalho catalog (1952, 1958) in which most of them were not recognized as valid. Wagner (e.g., 1974, 1975) was one of the few modern authors to use several of the names that had long ago fallen into obscurity. Nonetheless, the diagnoses of Wagner (1974, 1975) for names such as Ectagelini and Exaeretini were once again based on autapomorphies and applied only to the Palearctic fauna. We have attempted to use older names whenever possible, if they are applicable in a broader context of morphology and geography. Genera previously placed in monotypic tribal groupings for which we can make no credible determination of close relatives, for the most part, we have placed as incertae sedis in larger tribes/subtribes to which they seem to be most closely related, with the default association being with Phylina, the traditional tribal dumping ground within the Phylinae.

The greatest numbers of genera to be assigned in the absence of DNA sequence data are from the Palearctic, with a lesser number from the limited fauna found in the Neotropics. The most modern classification of the Palearctic fauna is presented in *Catalogue of the Heteroptera of the Palearctic Region* (Kerzhner and Josifov, 1999), but it is simply a reflection of schemes in the primary literature and therefore by itself offers no information on relationships within the omnibus tribe Phylini. Although Wagner (1974, 1975) offered a more detailed hierarchic scheme than other authors, most aspects of that scheme were not incorporated into the work of Kerzhner and Josifov (1999). The diagnoses of all the suprageneric groupings recognized by Wagner (1974, 1975) are of limited utility in terms of identification or prediction. Furthermore, all of Wagner’s generic diagnoses lack comparative information. So, whereas the compendious nature and profuse illustration make the work of Wagner on the Miridae fauna of the Mediterranean Region an almost singular resource, the lack of comparative statements about relationships has led us to make many more interpretations than might otherwise have been the case concerning the Palearctic fauna.

Poverty of information about relationships is particularly acute for the true Neotropical fauna, and therefore many genera from the region are placed as incertae sedis with the Phylina. Whereas the long history of study suggests that the Palearctic Phylinae have diversified primarily in two lineages (Oncotylina, Phylina), no such assumptions can be made concerning the Neotropics.

The following formatting conventions are used for the presentation of generic names:

Valid genera are presented in ***boldface italics***.

Genera included in the analysis of Menard et al. (2013) are preceded by an asterisk (\*).

Genera transferred to tribes other than those in which they were placed in the classification of Schuh (2002–2013) are presented in *lightface italics*.

We have followed the concept of priority in the application of family-group names, in accordance with the International Code of Zoological Nomenclature (ICZN, 1999). We note, however, that Hallodapini—among other names—was proposed to replace an older name based on a junior synonym. In accordance with Article 40.2 of the Code “If...a family-group name was replaced before 1961 because of the synonymy of the type genus, the substitute name is to be maintained if it is in prevailing usage.” Therefore, some older names continue to remain as junior synonyms.

Comments are provided on some generic placements, but not for all. Our arguments for placement of taxa concentrate especially on those taxa that were not present in the sample of Menard et al. (2013). Generic synonyms are listed only where necessary to clarify nomenclatural history and argumentation; complete synonymies can be found by consulting Schuh (2002–2013), as can references to species mentioned in the text without bibliographic documentation. New tribal and generic synonymies are clearly indicated as such.

Diagnoses are provided for the tribes and subtribes. They attempt to summarize those characteristics that we have used to place genera within groups. We include some of the attributes listed as synapomorphic in the analyses of Menard et al. (2013), but note that many of those are highly homoplastic and often do not allow for the unique recognition of groups. For example, the pronotal collar, which in the scheme of Carvalho (1952) was diagnostic for the Hallodapini, has now been shown to occur in more than one monophyletic lineage of Phylinae (Hallodapini, Cremnorrhina, Semiina). Furthermore, some groupings derived from the work of Menard et al. (2013) have no apparent morphological synapomorphies, homoplastic or otherwise, forcing the conclusion that most of the grouping information comes from the sequence data. We offer explanatory comments in the Discussion sections for each tribe and subtribe to allow the reader to better understand the history and rationale for the group.

For each genus we give an indication of its distribution and the number of currently included species. Distributional information is organized around the concept of biogeographic regions, an approach that usually simplifies the presentation, but also can benefit from some explanation. In many cases we have provided a modifier such as “Southwest Nearctic,” “Palearctic: Central Asia,” or “Ethiopian: Southern Africa.” We also note that the fauna of Africa is doubtless a composite, so that assigning taxa described by Linnavuori (1975) from the Sudan to either the Palearctic or Ethiopian regions is not a clear-cut decision. The same reasoning applies to South America, which we refer to as belonging to the Neotropics, with the realization that the fauna of Chile and parts of Argentina have their primary biogeographic associations with New Zealand and Australia.

## CLASSIFICATION

Phylinae Douglas and Scott, 1865

Type genus: *Phylus* Hahn, 1831Tribe HALLODAPINI, Van Duzee, 1916 (type genus: *Hallodapus* Fieber, 1858)

Eroticoridae Douglas and Scott, 1865

Cremnocephalaria Reuter, 1909

Systellonotaria Reuter, 1912

Aeolorini Wagner, 1970

Aurillocorini Schuh, 1984, **new synonymy**

DIAGNOSIS: This grouping is united by the presence of a flattened pronotal collar in most included taxa. This character is present in other groups of Miridae (e.g., Orthotylinae: Nichomachini) and a few other Phylinae genera (*Coquillettia* Uhler, *Orectoderus* Uhler, *Teleorhinus* Uhler), but the shape of the collar, along with the predominantly slender, twisting shape of the endosoma and the projecting frons and clypeus are usually diagnostic for many members of this tribe.

DISCUSSION: The composition of this taxon has been relatively stable since the classification of Carvalho (1952, 1958), and as emended by Wagner (1974) and Schuh (1974, 1984). According to Menard et al. (2013), the recognition of the Aurillocorini by Schuh (1984) rendered Hallodapini paraphyletic on the basis of autapomorphic characters. Furthermore, the long-standing recognition of the flattened pronotal collar as a diagnostic feature of Hallodapini argues additionally for the inclusion of the South African genus *Eminoculus* Schuh. Schuh (1974: 160) noted “*Eminoculus* is the only known member of the Phylini with a well-developed flat pronotal collar. This structure suggests a relationship to the Hallodapini, but other characters, including the form of the male genitalia and the structure of the pulvilli, do not support such a relationship.” The analysis of Menard et al. (2013) indicates that *Eminoculus* is the sister group of the remaining Hallodapini, and we therefore place it within the tribe. We have treated Aurillocorini as a junior synonym of Hallodapini, in accordance with the results of Menard et al. (2013), even though this group as diagnosed by Schuh (1984) possesses distinctive features of the scent-gland auricle that suggest it is monophyletic. Neither do we recognize as subtribes other previously named groupings because the taxon sample analyzed by Menard et al. (2013) for the Hallodapini is too limited to argue for the placement of all recognized genera in monophyletic groupings, and the remaining taxa placed in Hallodapina would certainly form a paraphyletic group. Although Wagner (e.g., 1974) recognized the Aeolorini and Cremnocephalini, his diagnoses and taxon sample were restricted to the Mediterranean fauna. The position of many genera, possibly most particularly morphologically novel groups such as *Clapmarius* Distant, is unclear and will require an analysis based on a more robust taxon sample. The Nearctic genera *Coquillettia*, *Orectoderus*, and *Teleorhinus* were placed in the Hallodapini by Carvalho (1952, 1958), but are now placed in the Cremnorrhini.

Novel in this classification is the placement of *Ifephyllus* Linnavuori and *Linacoris* Carvalho in the Hallodapini, because both taxa lack the flattened pronotal collar otherwise almost univer-



sally present in the group. Additional details are discussed under the treatments of each of these genera. Also novel is the placement in Hallodapini of an apparently undescribed taxon from Bolivia in the work of Menard et al. (2013) on the basis of sequence data, because the Hallodapini—excepting *Cyrtopeltocoris* Reuter—have been considered exclusively Old World (but see discussion under *Tibiopilus* Carvalho and Costa and *Mendozaphylus* Carvalho and Carpintero).

***Acrorrhinium*** Noualhier, 1895 (Ethiopian, Indo-Pacific; 33 spp.)

***Aeolocoris*** Reuter, 1903 (Ethiopian, North Africa; 6 spp.)

\****Alloeomimus*** Reuter, 1910 (Paleotropical; 6 spp.)

***Artchawakomius*** Yasunaga, 2012 (Oriental; 2 spp.)

***Aspidacanthus*** Reuter, 1901 (Ethiopian/Southern Palearctic; 5 spp.)

***Auricillocoris*** Schuh, 1984 (Oriental; 3 spp.)

***Azizus*** Distant, 1910 (Indo-Pacific; 2 spp.)

***Bibundiella*** Poppius, 1914 (Ethiopian; 4 spp.)

***Boopidella*** Reuter, 1907 (Ethiopian: Pemba Island; 1 sp.)

***Carinogulus*** Schuh, 1974 (Ethiopian: South Africa; 4 spp.)

***Chaetocapsus*** Poppius, 1914 (Ethiopian: West Africa; 1 sp.)

***Clapmarius*** Distant, 1904 (Oriental; 4 spp.)

\****Cleotomiris*** Schuh, 1984 (Oriental; 6 spp.)

\****Cleotomiroides*** Schuh, 1984 (Oriental; 3 spp.)

\****Cremnocephalus*** Fieber, 1860 (Western Palearctic; 5 spp.)

Schuh et al. (2009) included *Cremnocephalus albolineatus* Reuter in their analysis of cimicomorphan relationships based on morphology and DNA sequence data. The taxon was placed in the Orthotyliinae. Menard et al. (2013) resequenced this taxon using specimens from the same collecting event, and found that *Cremnocephalus* is unequivocally a member of the Hallodapini. The placement of *Cremnocephalus* in the Orthotyliinae was the apparent result of confusion or contamination during the DNA sequencing done for the work of Schuh et al. (2009).

\****Cyrtopeltocoris*** Reuter, 1876 (Nearctic; 11 spp.)

Our data, including DNA sequences, corroborate the theory that *Cyrtopeltocoris* is a member of the true Hallodapini. Along with *Phoradendrepulus* Polhemus and Polhemus, the two appear to represent a monophyletic group and the only lineage in the tribe that occurs in the Nearctic.

***Diocoris*** Kirkaldy, 1902 (Ethiopian; 6 spp.)

\****Eminoculus*** Schuh, 1974 (Ethiopian: Namaqualand; 7 spp.)

This taxon was placed in the Phylini by Schuh (1974) and Schuh and Wu (2009). Our analyses suggest unequivocally that *Eminoculus* belongs to the Hallodapini, a placement that is indicated by the presence of the pronotal collar, an attribute observed by Schuh (1974) on the basis of the two species known at that time. The work of Schuh and Wu (2009) included one species, *Eminoculus atrisetosus* Schuh and Wu, that does not have a flattened collar, but that on the basis of other morphological attributes and host associations groups with the six other known *Eminoculus* spp.

*Formicopsella* Poppius, 1914 (Ethiopian; 3 spp.)

*Gampsodema* Odhiambo, 1960 (Ethiopian: East Africa; 1 sp.)

*Glaphyrocoris* Reuter, 1903 (Southern Palearctic/Ethiopian; 23 spp.)

*Hadrodapus* Linnavuori, 1996 (Ethiopian: West Africa; 1 sp.)

*Hallodapomimus* Herczek, 2000 (Baltic amber; 3 spp.)

\**Hallodapus* Fieber, 1858 (Paleotropical/Southern Palearctic; 47 spp.)

*Ifephyllus* Linnavuori, 1993a, **revised tribal placement** (Ethiopian: West Africa; 3 spp.)

This West African taxon was placed in the Pilophorini by Linnavuori (1993a) at the time of its original description. He noted that the claws lacked pulvilli, the posterior wall in the female was evaginated, and the secondary gonopore was well delimited. Kerzhner and Schuh (1995) moved *Ifephyllus* to the Phylini because of their interpretation of the structure of the male genitalia; we now place *Ifephyllus* in the Hallodapini in light of the following observations: Our examination of many specimens of *Ifephyllus apis* Linnavuori indicates that the parempodia are broadly expanded but are not obviously convergent apically as illustrated by Linnavuori (1993a), nor are they recurved as is the case in most taxa we place in the Pilophorini. We can confirm, as noted by Linnavuori (1993a), that the claws lack pulvilli and that the posterior wall in the female is evaginated. Whether the secondary gonopore is well delimited in the sense meant by Linnavuori is less clear, but it is certainly not of the type seen in most remaining members of the Phylinae. *Ifephyllus* shares the above features with *Linacoris*, in addition to the fact that neither taxon possesses flattened lanceolate setae. We place *Ifephyllus* in the Hallodapini because of its apparent relationships with *Linacoris* based on morphology and the placement of *Linacoris* in the Hallodapini in the analysis of Menard et al. (2013).

*Kapoetius* Schmitz, 1969 (Palearctic: Sudan; 1 sp.)

*Laemocoris* Reuter, 1879 (Ethiopian/Southern Palearctic; 17 spp.)

*Lapazphylus* Carvalho and Costa, 1992: see *Nicholia* Knight under Semiini, Semiina

*Leaina* Linnavuori, 1974 (Ethiopian: West Africa; 1 sp.)

This taxon from the Ivory Coast was correctly placed in the Hallodapini by Linnavuori (1974), but mistakenly put in the Phylini by Schuh (1995) and Schuh (2002–2013). We here correct that misplacement.

*Leptomimus* Herczek and Popov, 2010 (Baltic amber; 1 sp.)

*Lestonisca* Carvalho, 1988 (Ethiopian: West Africa; 1 sp.)

\**Linacoris* Carvalho, 1983, **revised subfamily placement** (Oriental; 1 sp.)

This taxon was placed in Orthotylinae by Carvalho (1983) on the basis of parempodial structure. Reexamination of the male and female genitalia indicates that it is a member of the Phylinae. It would appear that *Linacoris* is the sister group of *Ifephyllus* on the basis of parempodial structure, male genitalic structure, and the absence of any scalelike setae on the body. Although *Linacoris* lacks the flattened pronotal collar found in nearly all other members of the Hallodapini, we place it in the Hallodapini, following the results of Menard et al. (2013) (see also discussion under *Ifephyllus*). Additional species of this taxon from the Oriental Region remain to be described (M. Wall, personal commun.).

*Lissocapsus* Bergroth, 1903 (Ethiopian: Madagascar; 1 sp.)

*Malgacheocoris* Carvalho, 1952 (Ethiopian: Madagascar; 1 sp.)



- Mimocoris* J. Scott, 1872 (Southern Palearctic; 2 spp.)  
*Myombea* China and Carvalho, 1951 (Ethiopian; 1 sp.)  
*Myrmicomimus* Reuter, 1881 (Southern Palearctic; 1 sp.)  
*Neolaemocoris* Wagner, 1975 (Palearctic: North Africa; 1 sp.)  
*Omphalonotus* Reuter, 1876 (Southern Palearctic; 3 spp.)  
*Pangania* Poppius, 1914 (Ethiopian; 3 spp.)  
*Paralaemocoris* Linnavuori, 1964 (Southern Palearctic; 4 spp.)  
*Phoradendrepulus* Polhemus and Polhemus, 1985 (Southwest Nearctic; 1 sp.)  
See discussion under *Cyrtopeltocoris*.  
*Podullahas* Schuh, 1984 (Oriental: Borneo; 2 spp.)  
*Pongocoris* Linnavuori, 1975 (Ethiopian: East Africa; 1 sp.)  
*Ribautocapsus* Wagner, 1962 (Palearctic: Spain, France; 1 sp.)  
*Ruwaba* Linnavuori, 1975 (Southern Palearctic; 2 spp.)  
*Skukuza* Schuh, 1974 (Ethiopian: East and South Africa; 3 spp.)  
*Sohenus* Distant, 1910 (Oriental: India, Sri Lanka; 2 spp.)  
*Syngonus* Bergroth, 1926 (Ethiopian: West Africa; 2 spp.)  
*Systellonotidea* Poppius, 1914 (Ethiopian: West Africa; 2 spp.)  
*Systellonotopsis* Poppius, 1914 (Ethiopian: East and South Africa; 2 spp.)  
*Systellonotus* Fieber, 1858 (Palearctic; 21 spp.)  
*Trichophorella* Reuter, 1905 (Ethiopian; 9 spp.)  
*Trichophthalmocapsus* Poppius, 1914 (Ethiopian; 8 spp.)  
*Vitsikamiris* Polhemus, 1994 (Ethiopian: Madagascar; 1 sp.)  
*Wygomiris* Schuh, 1984 (Oriental; 7 spp.)  
*Zaratus* Distant, 1909 (Oriental: India, Thailand; 2 sp.)

DECOMIINI, **new tribe** (type genus: *Decomia* Poppius, 1915)

DIAGNOSIS: Taxa we include in this group are relatively small, have transparent areas on the hemelytron, may have distinctive large pulvilli (*Decomia*), and have distinctive oval or parallel-sided bodies. The vestiture of the dorsum comprises a single type of short, appressed, neatly organized setae.

DISCUSSION: The type genus *Decomia* Poppius was originally described from Taiwan (Poppius, 1915). Subsequently China (1927) placed a single species (as *Torma* China) from West Africa in a distinct genus; later Knight (1935) described a single species (as *Torma*) from Samoa; Schuh (1984) treated all of these taxa as belonging to *Decomia* and described a large number of new *Decomia* species ranging from Malaya and the Philippines to the Solomon Islands. Schuh (1984) placed *Decomia* and several other genera from Southeast Asia in an omnibus Phylini. We here offer arguments for transfer of those genera to the distinct tribal-level grouping Decomiini, based largely on the DNA sequencing and analyses of Menard et al. (2013).

\**Aurantiocoris* Schuh and Schwartz, 2004 (Western Nearctic; 2 spp.)

Although the placement of this taxon might be uncertain on the basis of morphology

alone, the analysis of Menard et al. (2013) consistently placed *Aurantiocoris* within the Decomiini as here delimited.

\****Decomia*** Poppius, 1915 (Paleotropical; 37 spp.)

See also comments under Decomiini.

\****Decomioides*** Schuh, 1984 (Oriental; 10 spp.)

This taxon was placed in the omnibus Phylini by Schuh (1984), and compared to *Decomia*. We here place it in the Decomiini on the basis of DNA sequence data and its similarity of appearance to *Decomia*. Both *Decomia* and *Decomioides* have features distinctive to themselves, such as the enlarged pulvilli and distinctive endosoma and left paramere in the former, and the distinctive “rod” in the endosoma in the latter. Nonetheless, they share a similar habitus, with the head concave behind and obscuring the anterior margin of the pronotum, the elongate ovoid body form, and the presence of a single type of setae in the vestiture of the body. The distribution of *Decomioides* was described by Schuh (1984) as more restricted than that of *Decomia*, ranging from Hong Kong through the Philippine Islands to the Solomon Islands, but it has recently been recorded from Thailand by Yasunaga (2010).

\****Malaysiamiris*** Schuh, 1984 (Oriental; 11 spp.)

This taxon was placed in the omnibus Phylini by Schuh (1984), and compared to other taxa that we here place in the Decomiini. Although the male genitalia are distinctive to the genus, the head is concave behind and the vestiture is formed of a single type of setae and are reminiscent of the situation seen in *Decomia*; the analysis of Menard et al. (2013) also places the genus in the Decomiini. The distribution of *Malaysiamiris* is similar to that of *Decomioides*, but a single species is known from New Caledonia; the known distribution was recently further expanded by the description of a species from Thailand by Yasunaga (2010).

***Malaysiamiroides*** Schuh, 1984 (Oriental: Borneo; 4 spp.)

This taxon was placed in the omnibus Phylini by Schuh (1984), and compared to other taxa that we here place in the Decomiini. Although the male genitalia are distinctive to the genus, the head is concave behind and the vestiture is formed of a single type of setae and is reminiscent of that seen in *Decomia*. For these reasons we are placing *Malaysiamiris* in the Decomiina. The known distribution is currently restricted to northern Borneo.

***Rubrocuneocoris*** Schuh, 1984 (Oriental/Pacific; 12 spp.)

Described on the basis of three species from the Southeast Asia, this taxon now contains 12 species ranging from the Korean peninsula, Japan, and Nepal to the islands of the tropical Western Pacific. Schuh (1984) commented that *Rubrocuneocoris* most closely resembles *Decomioides*; he also noted the similarity of corial and cuneal markings in *Rubrocuneocoris* and *Decomia*, and the enlarged hind femora, an attribute shared by *Decomia*, *Decomioides*, and *Rubrocuneocoris*. It is because of these morphological similarities, and the distribution in the Indo-west Pacific, that we place *Rubrocuneocoris* in the Decomiini.

Tribe NASOCORINI Reuter, 1883 (type genus: *Nasocoris* Reuter, 1879)

Boopidocoraria Reuter, 1883

Chlamydatini Kirkaldy, 1902

Oligobiellini Kirkaldy, 1906

Atomomophoraria Wagner, 1974

DIAGNOSIS: Menard et al. (2013) did not find any morphological synapomorphies for the Nasocorini among the characters coded in their analysis; however, most members of this tribe have a flat vertex, rather short and wide hind femora, row of spicules on the dorsal margin of the hind femur, gonopore sclerite, sericeous or serrated scalelike setae, sometimes dark, erect setae, and/or cushionlike pulvilli covering the entire ventral surface of the claw.

DISCUSSION: The family-group name Nasocoraria was proposed by Reuter (1883) with a single included genus. The analyses of Menard et al. (2013) and our present attempts to place all genera of Phylinae in a unified classification suggest that both names are applicable to a monophyletic group containing *Nasocoris*, as well as *Campylomma*, *Chlamydatus*, *Megalopsallus*, *Spanagonicus*, and other genera. As discussed below under *Nasocoris*, morphology and host associations suggest a close relationship between the Nearctic *Megalopsallus* and Palearctic *Nasocoris*. We therefore apply a much broader conception of Nasocorini than that proposed by Reuter (1883) and treat Chlamydatini—among other names—as junior synonyms. Furthermore, we include many more genera than were present in the analyses of Menard et al. (2013).

Several of the genera we place in Nasocorini share novel characters that have been recognized by prior authors. For example, a row of spicules on the dorsal distal margin of the hind femur occurs in *Atractotomus*, *Campylomma*, *Kasumiphylus*, *Pinomiris*, *Rhinacloa*, and *Salicarus* and has been treated by Schuh and Schwartz (1985) and Schwartz and Stonedahl (2004) as suggesting a relationship among these genera. Some genera have flattened scalelike setae covering part or all of the body, a setal type that is seldom seen elsewhere in the Phylinae except Pilophorini, where the setae are laceolate. Many genera have a slender, delicate endosoma apparently formed of a single strap and with a single apical projection. *Campylomma* and some other genera, on the other hand, have two apical blades with the endosoma apparently formed of two distinct straps, but nonetheless share features in common with those taxa with a single endosomal strap. In those members with enlarged pulvilli, the pulvillus is broad, fleshy, cushionlike, and adnate to the entire ventral surface of the claw (see further comments under included genera). Although some of the above-mentioned morphological features suggest a possible subdivision of the Nasocorini into monophyletic subgroups, such as Chlamydatina and Nasocorina sensu stricto, we refrain from formal recognition of such groups at this time because of the confusing nature of variation among these characters and the limited sample of taxa for which sequence data are available.

***Adenostomocoris*** Schuh and Schwartz, 2004 (Southwest Nearctic; 2 spp.)

We are placing this taxon in the Nasocorini because of its small size and the delicate endosoma strongly bent at the middle, with a single, short apical projection and a well-developed gonopore sclerite. The pulvilli are adnate to and cover nearly the entire ventral surface of the claw, a characteristic also seen in species of *Megalopsallus*, among other taxa placed in the Nasocorini by Menard et al. (2013).

***Agrametra*** Buchanan-White, 1878 (St. Helena Island; 1 sp.)

This is one of several nominal genera described from the mid-Atlantic island of St. Helena that appear to represent a small radiation of endemic taxa with a highly split generic taxonomy, in

a fauna otherwise composed of mostly widespread species. The work of Schmitz (1976) provided detailed illustrations indicating that the endosoma is tubular proximal to the secondary gonopore and that the apex is elongate and filamentous in *Agrametra*, *Helenocoris*, *Hirtopsallus*, *Naresthus*, *Neisopsallus*, and *Oligobiella*; the male genitalia of *Lopsallus* are unknown and the apex of the endosoma of *Insulopus* is short, although the basal portion might otherwise be considered similar to that found in *Agrametra* and the other genera previously mentioned. We have placed all of these genera in the Nasocorini on the basis of their small size and relatively simple endosomal structure. Furthermore, these genera would seem to be related to *Chlamydatatus* based on the broad pulvillus almost reaching apex of the claw, many details of endosomal structure, the long, thin, S-shaped vestibulum, body proportions, and head structure.

\***Arctostaphylocoris** Schuh and Schwartz, 2004 (Western Nearctic; 2 spp.)

We place this taxon the Nasocorini on the basis of its small size, dark coloration, simple endosoma with a subapical secondary gonopore, and the presence of weakly scalelike setae on the dorsum. Schuh and Schwartz (2004) treated the genus as related to *Chlamydatatus* and *Salicarus*.

**Atomophora** Reuter, 1879 (Palearctic; 13 spp.)

This taxon was placed in its own subtribe by Wagner (1974), an approach rejected by Linnavuori (1990), who related it to *Camptotylidea* and *Taeniophorus*, all three of which he said were related to the *Phylus* group. We argue that the small size and simple male genitalia suggest a relationship with the other genera we place in the Nasocorini.

**Atomoscelis** Reuter, 1875 (Palearctic; 8 spp.)

We place this taxon in the Nasocorini because of the generally small size and the simple endosoma. *Atomoscelis* spp. feed almost exclusively on species of Chenopodiaceae, as do members of the genera *Megalopsallus* and *Solenoxyphus*.

**Atractotomoidea** Yasunaga, 1999 (Japan, Nepal, Thailand; 5 spp.)

Yasunaga (1999) compared this taxon to *Atractotomus*, a comparison we believe is valid based on the serrate gonopore sclerite, long, sometimes swollen, antennal segment II equal in length to basal width of pronotum, and body proportions. A relationship with *Phoenicocoris* is suggested by the shape of endosoma. Yasunaga (2010) stressed the asymmetry of the dorsal labiate plate as an apomorphy of the genus, but judging from the published photos, the structure discussed by him is just an expanded S-shaped vestibulum similar to that of *Larinocerus* and *Hambletoniola*.

\***Atractotomus** Fieber, 1858 (Holarctic; 46 spp.)

See discussions in Stonedahl (1990).

\***Badezorus** Distant, 1910 (Palearctic; 6 spp.)

*Badezorus* spp. are very similar to species of *Atomoscelis* and some other taxa we place in the Nasocorini in terms of size, coloration, and structure of the head; indeed, some species now placed in *Badezorus* were previously placed in *Atomoscelis*. These considerations and the sequence data of Menard et al. (2013) have determined our placement of *Badezorus*. Nonetheless, antennal coloration in *Badezorus* is also similar to that found in some taxa we place in the Exaeretina, although many members of that grouping are larger in size than all *Badezorus* spp.

**Beckocoris** Knight, 1968 (Western Nearctic; 5 spp.)

See discussion under *Lattinophylus*.

**Bergmiris** Carvalho, 1984 (Neotropical: Argentina; 2 spp.)

We tentatively place this taxon in the Nasocorini because of its relatively small size, dark coloration, and relatively simple endosoma. Although not all members of the tribe possess these characteristics, they are common to many. *Bergmiris* shares with *Larinocerus*, *Hambletoniola*, most *Atractotomus* spp., *Caiganga*, and *Tapuruyunus* an enlarged second antennal segment. Under our conception, Nasocorini is a group of worldwide distribution and the occurrence of *Bergmiris* in Argentina complements that distribution (see also discussion under *Caiganga* and *Tapuruyunus*).

**Boopidocoris** Reuter, 1879 (Palearctic; 3 spp.)

Although Reuter (1883) erected a new monotypic tribe for *Boopidocoris*, few subsequent authors have recognized that higher taxon. In his revision of the genus, Linnavuori (1995) related *Boopidocoris* to *Solenoxyphus*, by implication, on the structure of the endosoma, with a characteristic shape of the apex and a series of teeth near the secondary gonopore; they also share a similar color pattern. We place *Boopidocoris* in the Nasocorini based on the simple endosoma with a single apical spine and its apparent relationship to *Solenoxyphus*.

**Caiganga** Carvalho and Becker, 1957 (Neotropical: southern Brazil; 1 sp.)

This taxon was described on the basis of a single male from Santa Catarina, Brazil, which the authors did not dissect. It has received no further mention in the literature since its description. Based on the dark coloration, the enlarged second antennal segment, and the distribution, we suggest that *Caiganga* may be synonymous with *Bergmiris* Carvalho, 1984, but that the antennae in the holotype of the former are deflated. We therefore place *Caiganga* in the Nasocorini for the same reasons given for *Bergmiris*.

**Camptolyidea** Wagner, 1957 (Palearctic; 30 spp.)

This taxon was recently revised by Konstantinov (1999) who agreed with Linnavuori (1990) in treating it as related to *Atomophora* and *Taeniophorus*. We place it in the Nasocorini because of the pulvilli that are attached over much of the ventral surface of the claw and the simple endosoma.

\***Campylomma** Reuter, 1878 (Old World, including Australia; 134 spp.)

See Schuh (1984).

**Chinacapsus** Wagner, 1961 (Palearctic: Madeira Island; 12 spp.)

Wagner (1961, 1975) placed *Chinacapsus* from Madeira, *Lindbergopsallus* from the Canary Islands, and the more widespread *Paramixia* Reuter in what he called the *Cephalocapsus* group on the basis of parempodial structure. Schuh (1974) showed that *Paramixia* belonged to the Pilophorini, a position that is corroborated by the work of Schuh and Menard (2011) and Menard et al. (2013). Schuh and Schwartz (1988) demonstrated that *Sthenaridea* was the senior synonym of *Paramixia* and *Cephalocapsus*. Thus, even though the association of *Chinacapsus* with *Cephalocapsus* was in error, the association of *Chinacapsus* and *Lindbergopsallus* seems valid on the basis of parempodial structure, but this condition is not unique to these taxa because structurally similar apically converging parempodia are also found in several other



groups, including *Aurillocoris* Schuh and its near relatives (Hallodapini), *Moissonia* (Exaeretini), and the *Melaleucooides* group of genera (Exocarpocorina). Although endosomal structure is relatively consistent within both *Chinacapsus* and *Lindbergopsallus*, there are distinct differences between them. The habitus, ratios, and vestiture of *Chinacapsus* fit well within the *Chlamydatus* group of genera; the male genitalia are also most similar to those of *Phoenicocoris*, *Salicarus*, *Chlamydatus*, and related genera. The same may be true for *Lindbergopsallus*, however the latter has an atypical, apically twin-bladed endosoma. Schwartz and Stonedahl (2004) documented similarly fleshy parempodia in *Phoenicocoris dissimilis* Reuter. On the basis of these observations we place *Chinacapsus* in the Nasocorini. See also comments under *Dominiquella*, *Liviopsallus*, and *Nubaia*, which we place in the Phylini: Phylina.

\****Chlamydatus*** Curtis, 1833 (Holarctic; 32 spp.)

See Schuh and Schwartz (2005).

***Chlamyopsallus*** Schwartz, 2005 (Western Nearctic; 1 sp.)

We are placing this taxon in the Nasocorini because of its small size and the delicate endosoma with two short apical projections. The pulvilli are adnate to and cover nearly the entire ventral surface of the claw, a characteristic also seen in species of *Megalopsallus*, among other taxa placed in the Nasocorini. This taxon has numerous long, erect, dark setae on the dorsum, an attribute unlike other species we place in the tribe.

***Hambletoniola*** Carvalho, 1954 (Western Nearctic; 1 sp.)

The distinctive antennal structure and male and female genitalic morphology of this taxon suggest that it is the sister group of *Larinocerus* Froeschner (Henry and Schuh, 1979). Because the analysis of Menard et al. (2013) placed *Larinocerus* in the Nasocorini, we also include *Hambletoniola*.

***Helencoris*** Schmitz, 1976 (St. Helena Island; 1 sp.)

See discussion under *Agrametra*.

***Hirtopsallus*** Schmitz, 1976 (St. Helena Island; 1 sp.)

See discussion under *Agrametra*.

***Insulopus*** Schmitz, 1976 (St. Helena Island; 1 sp.)

See discussion under *Agrametra*.

***Karocris*** V. Putshkov, 1975 (Palearctic: Central Asia; 1 sp.)

The taxon is undoubtedly closely related to *Phoenicocoris*, and we therefore place it in the Nasocorini. The two taxa differ in details of vestiture and coloration of legs, among other attributes; *Karocris* feeds on *Seriphidium* (Asteraceae), rather than conifers as in *Phoenicocoris*.

***Kasumiphylus*** Schwartz and Stonedahl, 2004 (Palearctic: Japan; 1 sp.)

This taxon was described as part of the revision of *Phoenicocoris* by Schwartz and Stonedahl (2004). The small size, scalelike setae, and endosomal structure argue for its placement in the Nasocorini, as is also the case for *Phoenicocoris*.

***Knightomiroides*** Stonedahl and Schwartz, 1996 (Western Nearctic; 1 sp.)

We place this taxon in the Nasocorini on the basis of its small size, large pulvilli adnate to the entire ventral surface of the claw, scalelike setae, and endosomal structure similar to that seen in *Phoenicocoris*.



***Lamprosthenarus*** Poppius, 1914 (Ethiopian; 1 sp.)

Schuh (1974) presented data for specimens that he placed in this nominal genus. He compared the male genitalia (Schuh, 1974: figs. 255–257) with those of *Coatonocapsus*, although we now believe a more accurate comparison is with *Campylomma*, a group that Schuh (1974) did not treat, and we therefore place *Lamprosthenarus* in the Nasocorini. Although the endosoma bears similarities with *Campylomma*, the rather heavily punctured dorsum is rare in the Phylinae, and the shining black coloration of the body in *Lamprosthenarus* is unlike what is seen in most *Campylomma* species.

\****Larinocerus*** Froeschner, 1965 (Western Nearctic; 2 spp.)

Although the male and female genitalia of *Larinocerus* and *Hambletoniola* are much larger and more heavily sclerotized than those in the other genera placed in this tribe, the results of Menard et al. (2013) consistently place *Larinocerus* with genera such as *Atractotomus*, *Megalopsallus*, and *Rhinacloa*. *Larinocerus* and *Hambletoniola* have scalelike setae on the antennae (see scanning micrographs in Henry and Schuh, 1979), rather than on the body as seen in many other members of this tribal grouping.

***Lattinophylus*** Schuh, 2008 (Western Nearctic; 1 sp.)

This taxon was described by Schuh (2008) in conjunction with revisions of the genera *Beckocoris* Knight and *Nevadocoris* Knight. All three genera have restricted and broadly overlapping distributions that surround the Great Basin of western North America. They also feed primarily on genera of Asteraceae, with *Beckocoris* and *Nevadocoris* specializing on members of the toxic genus *Tetradymia* and *Lattinophylus* on *Artemisia*. All three genera have a relatively simple endosoma with a small or reduced secondary gonopore, moderately large to large pulvilli covering nearly the entire ventral surface of the claw, and numerous scalelike setae of the type seen in *Atractotomus*, *Phoenicocoris*, and *Rhinacloa*. The analyses of Menard et al. (2013) grouped taxa with scalelike setae in the Nasocorini, and for that reason we place these three genera in that higher taxon. Among North American genera placed in the Nasocorini, *Lattinophylus* is distinctive because of the strong brachyptery in the females.

***Lindbergopsallus*** Wagner, 1962, (Palearctic: Canary Islands; 5 spp.)

See discussion under *Chinacapsus*.

***Lopsallus*** Schmitz, 1976 (St. Helena Island; 1 sp.)

See discussion under *Agrametra*.

***Maurodactylus*** Reuter, 1878 (Palearctic; 6 spp.)

We place this taxon in the Nasocorini based on similarity of body form to genera such as *Megalopsallus* and *Nasocoris* and the simple structure of the endosoma, similar to that seen in the *Chlamydatus-Phoenicocoris-Salicarus* group of genera.

\****Megalopsallus*** Knight, 1927 (Nearctic; 29 spp.)

Schuh (2000) revised this genus and subsumed within it *Merinocapsus* Knight, the latter action corroborated by the analyses of Menard et al. (2013). The somewhat heterogeneous habitus and male genitalic structure of this group might offer reasons to question its monophyly. Nonetheless, the four species included in the analysis of Menard et al. (2013) form

a monophyletic group and corroborate the conclusions of Schuh (2000b) concerning the composition of group. Most *Megalopsallus* spp. feed on halophytes. See also comments under *Nasocoris*.

***Monosynamma*** J. Scott, 1864 (Holarctic; 3 spp.)

We place this taxon in the Nasocorini because of similarity of external morphology and male genitalic structure with that seen in *Chlamydatus* and related genera. According to F. Konstantinov (personal commun.) Wagner's (1975) placement of the taxon would allow for a similar conclusion.

***Naresthus*** Schmitz, 1976 (St. Helena Island; 1 sp.)

See discussion under *Agrametra*.

***Nasocoris*** Reuter, 1879 (Palearctic; 16 spp.)

This taxon is morphologically similar to *Megalopsallus*, including the structurally simple endosoma. All but two of the known species are documented as breeding on *Ephedra* spp. (Ephedraceae), a habit seen elsewhere in the Phylinae only in several *Megalopsallus* spp. from North America and two of the numerous *Camptotylidea* spp. from the Palearctic. We therefore place *Nasocoris* in the same group with *Megalopsallus* and use the oldest applicable family-group name, Nasocorini. *Nasocoris* might be related to *Solenoxyphus* and *Boopidocoris* based on details of endosomal structure.

***Neisopsallus*** Schmitz, 1976 (St. Helena Island; 2 spp.)

See discussion under *Agrametra*.

***Neophylus*** Carvalho and Costa, 1992 (Nearctic: Mexico; 1 sp.)

This taxon was placed in the Phylini by Carvalho and Costa (1992). We tentatively place it in the Nasocorini based on the simple structure of the male genitalia, the small size, and the dark coloration. The general appearance is similar to that of *Tuxedo*, but all known species of that genus have two, small, sclerotized apical appendages on the endosoma, do not have a dense vestiture on the dorsum, and show moderate to strong sexual dimorphism. For these reasons we reject, for the time being, placement of *Neophylus* in the Leucophoropterini: Tuxedoina. Examination of specimens and verification of additional morphological details will help to corroborate or reject our placement.

***Nevadocoris*** Knight, 1968 (Western Nearctic; 5 spp.)

See discussion under *Lattinophylus*.

***Nigrimiris*** Carvalho and Schaffner, 1973 (Neotropical: Southern Brazil; 1 sp.)

We place *Nigrimiris* in the Nasocorini on the basis of the small size and simple form of the endosoma. The dark coloration is also concordant with many members of the group.

***Nigrocapillocoris*** Wagner, 1973 (Palearctic: France, Corsica; 1 sp.)

This taxon was originally treated as a subgenus of *Sthenarus*. Wagner and Weber (1978) gave it generic status. The preponderance of evidence suggests membership in the Nasocorini.

***Oligobiella*** Reuter, 1885 (St. Helena Island; 1 sp.)

See discussion under *Agrametra*.

***Orthopidea*** Reuter, 1899 (Palearctic: Mediterranean; 2 spp.)

Wagner (1975) placed *Orthopidea* in his *Plagiognathus* group. Nonetheless, the taxon shares many features of the *Chlamydatus* group of genera, e.g., the structure of the head and pretarsus. The male genitalia are similar to those of *Salicarus*, although the endosoma bears only a single blade apically. For these reasons we place *Orthopidea* in the Nasocorini.

***Phaxia*** Kerzhner, 1984 (Palearctic: Mongolia; 1 sp.)

*Phaxia* is based on the single species, *P. festiva* Kerzhner, obviously named for its pleasing appearance and distinctive coloration. It is recorded as feeding on *Atraphaxis pungens* (Polygonaceae) (Kerzhner, 1984). Males of this small, sexually dimorphic species are about 3.5 mm in length. The dorsum is highly polished with a single type of pubescence. The pronotum is campanulate and similar in shape to that of *Tytthus* spp.; indeed Kerzhner (1984) compared *Phaxia* with *Tytthus*, *Ephippicoris*, and *Plesiodema*. On the basis of small size and the form of the endosoma we suggest that this taxon may rather be related to members of the Nasocorini, and we provisionally place it in that tribe.

***Phoenicocoris*** Reuter, 1875 (Holarctic; ~15 spp.)

In North America most of the species now placed in this taxon were placed in *Lepidosallus* Knight (= *Atractotomus* Fieber) by H.H. Knight. The disposition of species from the Palearctic has a more complicated history. The revision of *Phoenicocoris*, an exclusively conifer-feeding assemblage, by Schwartz and Stonedahl (2004) produced a morphologically and biologically homogeneous group that shares features in common with *Atractotomus*, including a partial row of spicules on the dorsodistal surface of the hind femur as well as similarities in the structure of the endosoma and the presence of broad scalelike setae in all known species. We therefore place *Phoenicocoris* in the Nasocorini.

***Pinomiris*** Stonedahl and Schwartz, 1996 (Western Nearctic; 2 spp.)

We place this taxon in the Nasocorini on the basis of its small size, large pulvilli adnate to the entire ventral surface of the claw, flattened scalelike setae, and endosomal structure similar to that seen in *Phoenicocoris*.

***Pruneocoris*** Schuh and Schwartz, 2004 (Western Nearctic; 1 sp.)

We are placing this taxon in the Nasocorini because of its small size and delicate endosoma with a single, short, apical projection. The pulvilli are adnate to and cover nearly the entire ventral surface of the claw and there are flattened scalelike setae that are reminiscent of those seen in most species of *Atractotomus* and other taxa we place in the Nasocorini.

**\**Psallomimus*** Wagner, 1951 (Ethiopian/southern Palearctic; 6 spp.)

This taxon was placed in the Nasocorini in the total-evidence analyses of Menard et al. (2013) and possesses a coiled endosoma, a feature seen in some other members of the group.

**\**Rhinacloa*** Reuter, 1876 (Neotropical and Mexico; 39 spp.)

See Schuh and Schwartz (1985).

***Salicarus*** Kerzhner, 1962 (Palearctic; 10 spp.)

The small size, possession of scalelike setae, and simple structure of the endosoma argue for

placement of this taxon in the Nasocorini (see discussion in Schwartz and Stonedahl, 2004).

***Solenoxyphus*** Reuter, 1875 (Palearctic; 16 spp.)

We place this taxon in the Nasocorini because of the relatively simple structure of the endosoma and other similarities of morphology and appearance that the genus shares with species of *Megalopsallus*. The habit of feeding on Chenopodiaceae is an attribute also shared with most species of *Megalopsallus*.

\****Spanagonicus*** Berg, 1883 (New World; 2 spp.)

This taxon is unusual in the tribe because of the sexual dimorphism in the antennae and the contrasting pale fascia on the dorsum. Nonetheless, the analysis of Menard et al. (2013) placed *Spanagonicus* in the Nasocorini, a placement that would seem to be corroborated by the small size and small, simple endosoma.

***Squamophylus*** Carvalho and Costa, 1992 (Nearctic: Mexico; 1 sp.)

This taxon has all of the diagnostic features of *Atractotomus*, including squamate setae, a sigmoid endosoma and a terminal secondary gonopore as illustrated by Carvalho and Costa (1992). We therefore place it in the Nasocorini.

***Sthendaropsis*** Poppius, 1912 (Palearctic; 11 spp.)

These small compact bugs have the head concave behind and bear scalelike setae of the type found in many *Atractotomus* spp. For these reasons we place the taxon in the Nasocorini. The tube-shaped endosoma with the secondary gonopore at the extreme apex is structurally similar to that of *Spanagonicus*.

***Taeniophorus*** Linnavuori, 1952 (Palearctic; 1 sp.)

See discussion under *Atomophora* and *Camptotylidea*.

***Tannerocoris*** Knight, 1970 (Western Nearctic; 1 sp.)

We place this taxon in the Nasocorini based on the presence of elongate scalelike setae on the pronotum, the large pulvilli adnate to the entire ventral surface of the claw, and the simple C-shaped endosoma. The pulvilli and the coloration pattern are reminiscent of *Beckocoris* spp.

***Tapuruyunus*** Carvalho, 1946 (Neotropical: Brazil; 1 sp.)

This taxon shares with the more recently described *Bergmiris* and *Caiganga* attributes that suggest that these taxa may be synonymous. These include the dark coloration, relatively small size, inflated antennae, and in the case of *Bergmiris* spp. and *Tapuruyunus*, a simple endosoma with a long, free, sclerotized terminal spine (see also discussions under *Bergmiris* and *Caiganga*).

***Thymopsallus*** Linnavuori, 1975 (Palearctic: Ethiopia; 2 spp.)

We place this taxon in the Nasocorini based on characters in the original description and subsequent redescriptions of the genus by Linnavuori (1975, 1991). Linnavuori (1975) considered the genus to be most closely related to *Platypsallus* Sahlberg (= *Chlamydatus*). Furthermore, the pronounced clypeus, the brachypterous condition seen both in males and females, the “pear-shaped” and somewhat dorsally depressed habitus, and the long arcuate endosoma with apical processes are characteristics shared with many taxa we place in the Nasocorini.

***Tijucaphylus*** Carvalho and Costa, 1992 (Neotropical: Brazil; 1 sp.)

This small, compact-bodied, monotypic taxon from southern Brazil has the head concave behind; the endosoma forms single coil, has a single, short, apical spine, and the secondary gonopore is subtended by a row of sawlike teeth. Based on the small size and form of the endosoma we place *Tijucaphylus* in the Nasocorini.

***Tunisiella*** Carapezza, 1997 (Palearctic: North Africa; 1 sp.)

We place this taxon from North Africa in the Nasocorini on the basis of its small size and the relatively simple structure of the endosoma.

***Voruchia*** Reuter, 1879 (Palearctic: Turkey; 1 sp.)

Although this taxon has not received substantive mention in the literature since its original description it appears to be closely related to *Solenoxyphus* (F. Konstantinov, personal commun.) and we therefore place it in the Nasocorini.

Tribe EXAERETINI Puton, 1875 (type genus: *Exaeretus* Fieber, 1864)

*Camptotylaria* Reuter, 1891

*Tuponiina*, Wagner, 1952

DIAGNOSIS: On the basis of morphological characters included in the analysis of Menard et al. (2013) this taxon is defined by a relatively long labium that extends past the hind coxae. However, our examination of a broader sample of taxa and consideration of prior diagnoses indicates that the structure of the pretarsus, with elongate claws and minute or completely absent pulvilli, seems to offer the strongest set of diagnostic morphological features for the group. Additional observations on the included taxa suggest that members also possess a relatively distinct large and twisted secondary gonopore, twisted, S-shaped endosoma composed of two straps united by a membrane and often with serrations, and most members having dark or sericeous setae on the hemelytron. Some members have an elevated posterior lobe on the left paramere. Wagner (e.g., 1975) treated some groups as lacking pulvilli entirely (e.g., *Anonychiella*, *Aphaenophyes*) whereas they actually have minute pulvilli.

DISCUSSION: The analyses of Menard et al. (2013) recognized a monophyletic group, including *Moissonia* and *Tuponia*. Based on the work of Wagner (1975) and Konstantinov (2008b) we conclude that the senior name for this group is *Exaeretina* Puton, 1875 (see also comments below under *Camptotylus*). We provide below arguments for assigning additional genera to this grouping over and above those included in the analyses of Menard et al. (2013).

***Anonychiella*** Reuter, 1912 (Palearctic; 9 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws with minute pulvilli; we have followed his approach.

***Aphaenophyes*** Reuter, 1899 (Palearctic; 4 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws without pulvilli; we have followed his approach.

***Atractotomimus*** Kiritschenko, 1952 (Palearctic; 3 spp.)

Our examination of *Atractotomimus limonii* Putshkov indicates that the general appearance and antennal structure are similar to those seen in males of *Campylomma* spp.,



but differ from that taxon in not showing sexual dimorphism. The endosoma, however, has two short terminal processes, not the elongate blades seen in most *Campylomma* spp., and the hind femur lacks the row of spinules seen in *Campylomma* and some other genera we place in the Nasocorini. The structure of endosoma and characteristically elongate claw with minute pulvillus apparently relate *Atractotomimus* to *Tuponia*. We therefore tentatively place the genus within Exaeretina in accordance with Wagner's concept.

***Auchenocrepis*** Fieber, 1858 (Palearctic; 6 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws without pulvilli; we have followed his approach.

***Brendaphylus*** Yasunaga, 2013 (Oriental; 1 sp.)

Based on the similarity of structure of the endosoma with that of *Gonoporomiris*, the sharing with *Moissonia* spp. of a somewhat elevated posterior lobe of the left paramere, and the weakly lamellate parempodia, we place *Brendaphylus* in the Exaeretini.

***Camptotylus*** Fieber, 1860 (Palearctic; 8 spp.)

We place *Camptotylus* (a senior synonym of *Exaeretus* Fieber, 1864, on which the family-group name is based) with *Tuponia* because of the complete lack of a pulvillus (also in *Moissonia*) and the association with *Tamarix*, a similarity pointed out by Konstantinov (2008). The structure of the male genitalia supports this placement: all species of *Camptotylus* have a relatively large laminate subapical outgrowth on the phallosome, a feature also observed in *Yotvata*, *Eurycranella*, *Voruchiella*, as well as in many *Tuponia*, *Compsonannus*, and *Camptozorus* spp.

***Camptozorus*** Kerzhner, 1996 (Palearctic: Central Asia; 3 spp.)

This taxon currently comprises three species. Kerzhner (1996) related it to *Badezorus* and *Camptotylus*, genera that we do not place in the same tribe. We provisionally place *Camptozorus* in the Exaeretini because of the elongate claws that lack pulvilli.

***Chrysochnodes*** Reuter, 1901 (Palearctic: Mediterranean; 3 spp.)

The taxonomic history of this taxon was reviewed by Carapezza (1994), who pointed out that one of the included species, *C. rufus* Wagner, actually belonged to *Icodema*, to which he transferred it. Furthermore, he noted the "serrate ridge" on the dorsal margin of the endosoma, a structural feature similar to that seen in *Moissonia* and *Megalodactylus*. We therefore place *Chrysochnodes* in the Exaeretini, even though it has larger pulvilli than most taxa we place in the tribe.

***Compsonannus*** Reuter, 1902 (Palearctic; 10 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws without pulvilli; we have followed his approach.

***Eumecotarsus*** Kerzhner, 1962 (Palearctic; 4 spp.)

Kerzhner (1962) and Seidenstücker (1980) presented information on the structure of the male genitalia of this taxon, which is apparently related to the *Tuponia* group of genera. The endosoma is generally C-shaped and very short, as in *Dasycapsus*, with two lateral straps delimited by finely serrate membrane; the secondary gonopore is not evident. The claws are *Tuponia*-like in structure, with minute pulvilli.



***Eurycranella*** Reuter, 1904 (Palearctic; 3 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws with minute pulvilli; we have followed his approach.

***Frotaphylus*** Carvalho, 1984 (Neotropical: Brazil; 1 sp.)

We place this taxon in the Exaeretina on the basis of its apparent similarity to *Gonoporomiris*, including the very short endosoma and the elevated posterior process of the left paramere, the latter attribute also seen in taxa such as *Moissonia*, which we place in this subtribe.

***Gonoporomiris*** Henry and Schuh, 2002 (Neotropical: Florida, Caribbean; 2 spp.)

Henry and Schuh (2002) placed this taxon in the Phylini, without further comment on its relationships. These small, seldom-collected bugs have a short endosoma that is largely occupied by an outsized secondary gonopore. We are tentatively placing *Gonoporomiris* in the Exaeretina because of the shape of the posterior process of the left paramere, which is elevated in a way most frequently seen in *Moissonia*. The endosoma in *Moissonia* is short, robust, and C-shaped, a situation not unlike that seen in *Gonoporomiris*, although the gonopore is never so greatly enlarged in the former genus.

***Hyalopsallus*** Carvalho and Schaffner, 1973 (Neotropical: Caribbean, Brazil; 1 sp.)

On the basis of body form, the hyaline hemelytra, and the form of the male genitalia *Hyalopsallus* appears to be related to *Moissonia*.

***Hadrophyes*** Puton, 1874 (Palearctic; 4 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws without pulvilli; we have followed his approach.

***Megalodactylus*** Fieber, 1858 (Palearctic; 2 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws without pulvilli; we have followed his approach. The shape of, and a series of rectangular teeth on, the endosoma further relate the genus to *Moissonia*.

\****Moissonia*** Reuter, 1894 (Circumtropical; ~40 spp.)

The taxonomic history of this genus involves lengthy synonymy. It is not entirely clear to us that all species currently placed in the genus belong there, but we nonetheless argue that for the moment the broader concept of this group as applied by Linnavuori (1993a) is superior to recognizing several segregate genera, which may or may not be monophyletic, as done by Schuh (1984).

***Opuna*** Kirkaldy, 1902 (Oriental-Pacific; 7 spp.)

Schuh (1984) placed species in addition to the Hawaiian type species in this genus, admitting that the taxa that he grouped together might not form a monophyletic group. Allowing for that possibility, we nonetheless place *Opuna* in the Exaeretini because of the moderately fleshy parempodia, the elevated posterior process of the left paramere, and endosomal structure similar to that found in *Moissonia* spp.

***Pastocoris*** Reuter, 1879 (Palearctic; 2 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws with minute pulvilli; we have followed his approach.

***Psallopsis*** Reuter, 1901 (Palearctic; 15 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws with

minute pulvilli; we have followed his approach.

***Randallopsallus*** Yasunaga, 2013 (Oriental: Thailand; 1 sp.)

Yasunaga (2013) mentioned the similarity in appearance of this taxon with species of *Psallus*, but noted that this was superficial. We place *Randallopsallus* in the Exaeretini because of the elevated posterior process of the left paramere as seen in species of *Moissonia*, *Gonoporumiris*, and other taxa we place in the Exaeretini. The lamellate parempodia of *Randallopsallus* also conform to the type seen in *Moissonia* spp.

\****Tuponia*** Reuter, 1875 (Palearctic; 87 spp.)

***Voruchiella*** Poppius, 1912 (Palearctic; 8 spp.)

This taxon was allied with *Tuponia* by Wagner (1975) based on the elongate claws with minute pulvilli; we have followed his approach.

***Yotvata*** Linnavuori, 1964 (Palearctic; 14 spp.)

Although we have found no comparisons of *Yotvata* and *Camptotylus* in the literature, we propose that the structure of the endosoma, with a medial secondary gonopore, a long apex, and the left paramere with a dorsomedial process suggest a close relationship between these two nominal genera. The elongate and narrow claws with minute pulvilli are also in accordance with this placement. *Camptotylus* feeds on Tamaricaceae whereas available host data suggest that *Yotvata* breeds on a variety of plant taxa.

Tribe CREMNORRHINI Reuter, 1883 (type genus: *Cremnorrhinus* Reuter, 1880)

DIAGNOSIS: The analyses of Menard et al. (2013) united several genera within this tribe, including multiple undescribed genera from South Africa and Australia, predominantly based on molecular information; unifying morphological characters are yet to be identified based on their generalized codings for the entire Phylinae. It is likely that a more refined morphological analysis of the taxa in this tribe, and the description of the undescribed taxa, will reveal diagnostic characters.

DISCUSSION: This tribal-level grouping was proposed by Reuter (1883) to include only the genus *Cremnorrhinus*. As presented here the concept of this higher-category name is much broader, including the Cremnorrhina clade as well as the Coatonocapsina as recovered by Menard et al. (2013). See also comments below under Cremnorrhina.

Subtribe Cremnorrhina Reuter, 1883 (type genus: *Cremnorrhinus* Reuter, 1880)

Harpoceridae Douglas and Scott, 1865

Pronotocrepini Knight, 1929, **new synonym**

DIAGNOSIS: Members of this subtribe have an elongate postocular region (Menard et al., 2013). Additional characters shared by this group, but which are not uncontradicted synapomorphies, include a relatively pronounced frons and clypeus, creating a conical shape to the head in dorsal view, enlarged usually free pulvilli, and strong sexual dimorphism.

DISCUSSION: Wagner (1974) was apparently the first author subsequent to Reuter (1883) to recognize this group; he included the genera *Cremnorrhinus*, *Macrotylus*, and *Utopnia*. The structure of the head and male genitalia of *Cremnorrhinus* show similarities with those of *Macrotylus*, as suggested by Wagner (1974) and as confirmed by F. Konstantinov (personal commun.). We therefore apply this name to the grouping that includes the Pronotocrepini of Wyniger (2010),

because of the close relationship between *Macrotylus* and *Pronotocepris* as demonstrated by the analysis of Menard et al. (2013). We have chosen not to further divide the subtribe at the present time because we do not have sufficient data for all included taxa to argue for the recognition of additional monophyletic groups. We predict ultimate recognition of a monophyletic group under the name Pronotoceprina with inclusion of at least those taxa included by Wyniger (2010).

Although the name Harpoceridae was proposed earlier than Cremnorrhina, for the moment we do not treat it as the senior synonym because of the doubtful placement of its type genus *Harpocera*.

\****Amblytylus*** Fieber, 1858 (Palearctic; 10 spp.)

This taxon is placed in the Cremnorrhina based on the analyses of the Menard et al. (2013). The endosoma is relatively short and stout with two apical spines (Matocq and Pluot-Sigwalt, 2012); the pulvilli are large, extending over most of the length of the claw, in accordance with other members of the Cremnorrhina. According to Matocq and Pluot-Sigwalt (2012), *Amblytylus* is most closely related to *Megalocoleus*, but we argue that the more relevant comparison is with *Lopus*, based on the projecting head, the enlarged pulvilli, the structure of the endosoma with two short apical spines, and the habit of feeding strictly on Poaceae. Furthermore, the literature indicates that the delimitation of the two genera, one from another, has been a subject of ongoing confusion. The presumption of a relationship between *Amblytylus* and *Lopus* is evident in the work of Wagner (1975).

***Brachyceratocoris*** Knight, 1968 (Southwest Nearctic; 1 sp.)

We place this taxon in the Cremnorrhina because of the prominent frons and clypeus and large free pulvilli. In addition to the characters listed above, the numerous erect setae on the dorsum and the structure of the endosoma suggest a relationship to *Macrotylus*.

***Calidroides*** Schwartz, 2005 (Southwest Nearctic; 2 spp.)

This taxon is closely related to *Strophopoda* Van Duzee based on the structure of the head, endosoma, and the large, free pulvilli (Schwartz, 2005). See also arguments under *Strophopoda*.

\****Coquillettia*** Uhler, 1890 (Western Nearctic; 35 spp.)

This taxon was placed in the Hallodapini by Carvalho (1952, 1958) on the basis of the flattened pronotal collar, and ostensibly grouped with the other North American genera *Orectoderus* and *Teleorhinus*; Wyniger (2012) placed *Coquillettia*, and the two closely related new genera *Leutiola* Wyniger and *Ticua* Wyniger, in the Phylini. The analyses of Menard et al. (2013) indicated that *Coquillettia* belongs to a more broadly conceived Cremnorrhina, which can be diagnosed on the basis of the projecting head and the enlarged, and in this case free, pulvilli. The endosoma is heavily sclerotized and forms a single fused strap of tubular form, although not as heavy as that seen in those taxa placed in the Pronotoceprini by Wyniger (2010).

***Cremnorrhinus*** Reuter, 1880 (Palearctic: Eastern Mediterranean; 1 sp.)

See discussion under Cremnorrhina.

***Dacota*** Uhler, 1872 (Holarctic; 3 spp.)

This taxon has traditionally been placed in the Phylini, because it lacked the distinguishing attributes of other tribes. We here move *Dacota* to the Cremnorrhina on the basis of the

endosomal structure similar to that seen in *Ethelastia* and *Orectoderus*, the projecting head, the enlarged flaplike pulvilli that are adnate over most of the length of the claw, unlike the situation seen in many members of the subtribe, and the strong sexual dimorphism.

\****Denticulophallus*** Schuh, 1974 (Ethiopian: South Africa; 1 sp.)

The taxon was placed in the Phylini at the time of its description. The analyses of Menard et al. (2013) indicated that *Denticulophallus* groups with other genera we place in the Cremnorrhina, an association that is corroborated by the projecting head and the enlarged free pulvilli.

***Ethelastia*** Reuter, 1876 (Palearctic: Central Asia; 2 spp.)

See Konstantinov (2008c) and discussion in Wyniger (2010).

***Euderon*** Puton, 1888 (Palearctic: North Africa; 1 sp.)

The description and illustrations of Wagner (1970) indicate the prognathous nature of the head, with the clypeus protruding, as well as claws with long free pulvilli. We therefore tentatively place this taxon in the Cremnorrhini, Cremnorrhina, in spite of the autapomorphic condition seen in the distally inflated second antennal segment and the elevated posterior margin of the pronotum. Apparently the only known specimen of this species is the holotype (Wagner, 1970).

***Excentricoris*** Carvalho, 1955 (Palearctic; 4 spp.)

We place this taxon in the Cremnorrhina on the basis of the large, free pulvilli, weakly basally toothed claws, and strongly projecting frons and clypeus. The swollen antennae are simply autapomorphic, in a taxon that might otherwise be placed in *Macrotylus*.

***Guentherocoris*** Schuh and Schwartz, 2004 (Southwest Nearctic; 1 sp.)

*Guentherocoris atritibialis* (Knight) was originally placed in *Psallus* because of the woolly vestiture. Schuh and Schwartz (2004) described a new genus to accommodate the taxon because it did not possess the diagnostic features of any described genus. We are placing *Guentherocoris* in the Cremnorrhina because it has a clypeus easily visible from above (although the head is not protuberant) and large free pulvilli.

***Harpocera*** Curtis, 1838 (Palearctic; 7 spp.)

The second antennal segment in the males of *Harpocera* has a terminal modification, presumably used for grasping the female during copulation. The pulvilli are relatively large and attached to the expanded base of the claw, a condition similar to that seen in many of the genera we place in the Cremnorrhina, and the head is weakly prognathous with the clypeus visible from above. *Harpocera* has distinctly carinate anterior angles of the pronotum, a feature observed in many genera placed in the Pronotocrepini by Wyniger (2010). All known species are strongly sexually dimorphic, in addition to the antennal modifications. The left paramere has an elevated posterior lobe similar to what is seen in *Moissonia*, but we believe arguments for placement of *Harpocera* in the Cremnorrhina are stronger than for association with *Moissonia*. All but one species have hosts listed as *Quercus*. The autapomorphic condition of the antennae has led to the placement of this genus in its own higher taxon (see subtribal synonymy and discussion).

***Leutiola*** Wyniger, 2012 (Western Nearctic; 3 spp.)

See comments under *Coquillettia*.

**Lopidodenus** V. Putshkov, 1974 (Palearctic: Central Asia; 3 spp.)

Members of this taxon are pale in color, moderately sexually dimorphic, moderately prognathous, and have an elongate slender endosoma with a single apical spine and the secondary gonopore well removed from the apex. *Lopidodenus* is apparently closely related to *Lopus* based on size, body proportions, somewhat protruding clypeus, vestiture type, coloration, and especially the large free pulvillus that reaches almost to the apex of the claw. We therefore place *Lopidodenus* in the Cremnorrhina.

**Lopus** Hahn, 1833 (Western Palearctic; 3 spp.)

We place this taxon in the Cremnorrhina because of similarity of structure of the head and the endosoma with that of *Amblytylus* spp., the pretarsus with long free pulvilli, and the placement of *Amblytylus* in the analyses of Menard et al. (2013). Both groups feed exclusively on grasses. See also arguments under *Amblytylus*.

\***Macrotylus** Fieber, 1858 (Holarctic, South Africa; 69 spp.)

This is the largest single genus we place in the Cremnorrhina. Its currently recognized distribution includes the Holarctic as well as two species from South Africa. The enlarged free pulvilli attached near the base of the basally toothed claw and the elongate head, with protruding clypeus, are characters used to diagnose the genus, but are certainly not exclusive to it. A review of this group, particularly with investigation of genitalic structure in the North American taxa, is overdue.

**Orectoderus** Uhler, 1876 (Western Nearctic; 5 spp.)

See Wyniger, 2010.

**Pachyxyphus** Fieber, 1858 (Western Palearctic; 5 spp.)

We tentatively place this taxon in the Cremnorrhina because of the relatively large pulvilli that are free from the claw except at the base, the prognathous head and prominent clypeus, and the heavy black setae on the dorsum. The endosoma has a membranous lobe with a series of rectangular teeth (Wagner, 1975; Ribes and Ribes, 2000) and overall shape similar to that of *Moissonia*. All known members feed on the Cistaceae.

**Paralopus** Wagner, 1957 (Palearctic: Eastern Mediterranean, Iran; 2 spp.)

Linnavuori (1994), in his revision of this taxon, related it to *Lopus*, primarily on the basis of pretarsal structure. We follow his theory and place *Paralopus* in the Cremnorrhina.

\***Pronotocrepis** Knight, 1929 (Western Nearctic; 1 sp.)

See Wyniger, 2010.

**Shendina** Linnavuori, 1975 (Nearctic: Northern Sudan; 1 sp.)

We place this taxon in the Cremnorrhina because of the basally toothed claw and the elongate free pulvillus as described by Linnavuori (1975, 1993a). The globose shape of the head also conforms to what is frequently seen in members of the Cremnorrhina, although the clypeus is less strongly protruding than in many taxa. The structure of the endosoma also appears to conform to other members of the Cremnorrhina.

**Strophopoda** Van Duzee, 1916 (Western Nearctic; 1 sp.)

We place this taxon in the Cremnorrhina because of the heavily sclerotized endosoma, the prominent frons and clypeus, and large free pulvilli (see Schwartz, 2005). Although much smaller in size than the taxa included in Pronotocrepini by Wyniger (2010), *Strophopoda* has



many similarities in overall morphology with other taxa we place in the Cremnorrhina.

\**Teleorhinus* Uhler, 1890 (Western Nearctic; 3 spp.)

See Wyniger, 2010.

*Ticua* Wyniger, 2012 (Western Nearctic; 3 spp.)

See comments under *Coquillettia*.

*Utopnia* Reuter, 1881 (Palearctic: Eastern Mediterranean; 1 sp.)

We place this taxon in the Cremnorrhina because of the similarity of pretarsal structure with that of *Macrotylus*, and the association of these genera by Wagner (1974).

*Zinjolopus* Linnavuori, 1975 (Palearctic: Sudan; 2 spp.)

Linnavuori (1975) related *Zinjolopus* to *Paralopus*, both of which accordingly should be related to *Lopus*. We therefore place this taxon in the Cremnorrhina.

Coatonocapsina, **new subtribe** (type genus: *Coatonocapsus* Schuh, 1974)

DIAGNOSIS: This grouping is heterogeneous in coloration, overall appearance, and to some degree, structure of the genitalia. The majority of the taxa are over 3.5 mm in length, have weak to strong sexual dimorphism, and have a bifurcate apex of the endosoma.

DISCUSSION: The total-evidence analyses of Menard et al. (2013) brought together a group of primarily South African taxa. Some of these taxa for which sequence data are available remain undescribed and represent ostensible new genera.

\**Austropsallus* Schuh, 1974 (Ethiopian: South Africa; 6 spp.)

*Austropsallus* is one of the largest genera of this grouping, with at least six species described from South Africa (Schuh 1974). All species have an endosoma with a bifurcate apex, moderate sexual dimorphism, and are fairly large in size, characteristics consistent with many of the other genera in this group.

*Capecapsus* Schuh, 1974 (Ethiopian: South Africa; 1 sp.)

*Capecapsus* was hypothesized by Schuh (1974) to be most closely related to *Coatonocapsus* Schuh based on shared sexual dimorphism and the structure of the male genitalia. This monotypic genus has a coiled endosoma, as do members of *Coatonocapsus*, but does not have the bifurcate endosomal apex of *Austropsallus* spp. and some *Coatonocapsus* spp.

\**Coatonocapsus* Schuh, 1974 (Ethiopian: South Africa; 4 spp.)

This genus is closely related to the genera *Austropsallus* and *Capecapsus* according to Schuh (1974), based on the form of the male genitalia. The endosoma of the *Coatonocapsus* shares the coiled characteristic of *Capecapsus* (Schuh 1974). This taxon also shows the sexual dimorphism of *Parasciodema* Poppius.

\**Heterocapillus* Wagner, 1960 (Palearctic; 11 spp.)

Our examination of the literature suggests that *Heterocapillus*, a group that is currently bound together primarily by the inflated second antennal segment, is in need of revision (see Stonedahl, 1990; Konstantinov, 2008d); our concept of the genus in the work of Menard et al. (2013) is based on what we believe to be *H. genistae* (Lindberg, 1948), which is not the type species. This taxon was placed in the Coatonocapsina in the POY analysis of Menard et al. (2013), although its position across all methods of analysis was not stable.



\**Parasciodema* Poppius, 1914 (Ethiopian: Southern Africa; 3 spp.)

*Schuhistes* Menard 2010, **new synonymy**

Schuh (1974) placed *Parasciodema* in the Phylini, as had Carvalho (1958). His arguments were based largely on characters that it lacked. We note that *Parasciodema* shares several features in common with *Schuhistes* Menard, including the enlarged pulvilli that are adnate to the claw, the short transverse head, the simple setae on the dorsum, and the similarity of structure of the endosoma. We also note that all known specimens of *Parasciodema* are male, and that most of them were collected at lights, according to Schuh (1974). This suggests that the females are brachypterous, as is the case in *Schuhistes* spp.; the distributions of the two genera are also broadly overlapping. Based on these factors and nearly identical genitalia of *S. lekkersingia* and *P. abicoxa*, we have concluded that *Schuhistes* is a junior synonym of *Parasciodema* **new synonymy**. This action creates the new combinations *Parasciodema lekkersingia* (Menard) and *Parasciodema lyciae* (Menard).

We note that whereas *Parasciodema* might be construed to be related to *Karoocapsus* Schuh on the basis of coloration and sexual dimorphism, *Parasciodema* spp. for which data are available appear to be phytophagous and host specific on *Lycium* (Solanaceae); although sexually dimorphic, they are at most vaguely mimetic with the females having relatively weakly reduced wings. *Karoocapsus*, on the other hand, is usually collected in small numbers with no obvious pattern of host association, and most species show pronounced sexual dimorphism, with the females being strongly myrmecomorphic and micropterous whereas the males have elongate, fully developed wings.

Tribe PHYLINI Douglas and Scott, 1865, *sensu stricto* (type genus: *Phylus* Hahn, 1831)

DIAGNOSIS: The Phylini continues to be an amalgam of genera lacking easily characterized unifying morphological characters. The group shows great diversity in the Northern Hemisphere; most of the taxa from the Southern Hemisphere that we place in the Phylini are placed *incertae sedis* because we lack evidence to place them elsewhere. Nonetheless, the evidence seems to suggest that the tribe is predominantly Northern Hemisphere in distribution.

DISCUSSION: This taxon was treated as an omnibus grouping without unique defining characters by Carvalho (1952, 1958), an approach that has been followed by subsequent authors such as Schuh (1974, 1984, 1995) and Kerzhner and Josifov (1999), even though a large number of names are available for the recognition of segregate groupings (e.g., Wagner, 1974, 1975). Based on the analyses of Menard et al. (2013), and additional argumentation, we offer the first attempt to place many genera in better justified groupings than is the case with the conspicuously paraphyletic Phylini *sensu* Carvalho. We recognize three subtribes, none of which show strong congruence with the genus groups recognized by Wagner (1975), who was the only modern author prior to this work to attempt to subdivide the Phylini. See also comments under *Oncotylina* and *Phylina*.

Keltoniina, **new subtribe** (type genus: *Keltonia* Knight, 1966)

DIAGNOSIS: Morphological characters uniting this lineage include eyes that are parallel to the anterior margin of the pronotum and that take up less than half the total height of the head in lateral view in both sexes, a scent gland that is relatively small, and the pygophore in the male taking up greater than one-half the total length of the abdomen, according to Menard et

al. (2013). The genera currently included in this subtribe also share long, prominent setae on the hemelytron intermixed with some sericeous setae, creating a black-and-white patterning, an attribute that is particularly obvious in *Keltonia* and *Pseudatomoscelis*.

DISCUSSION: This grouping was recognized in all analyses of Menard et al. (2013) based on *Keltonia* and *Reuteroscopus*. Their analyses helped clarify the relationships of *Reuteroscopus*, many members of which have autoapomorphic ornamental structures on the endosoma of a type seldom seen elsewhere in the Phylinae (but see also *Waupsallus* below).

\**Keltonia* Knight, 1966 (Nearctic, including Mexico; 13 spp.)

See discussion under *Pseudatomoscelis* and revision of Henry (1991).

*Pseudatomoscelis* Poppius, 1911 (Caribbean, Mexico; 4 spp.)

This taxon was grouped by Henry (1991) with *Keltonia* Knight. His analysis is the most thorough available, and we therefore place *Pseudatomoscelis* in the Keltoniina, a grouping supported on the basis of color, setal, and endosomal characters.

\**Reuteroscopus* Kirkaldy, 1905 (New World; 54 spp.)

See discussion under Keltoniina.

*Waupsallus* Linnavuori, 1975 (Ethiopian; 5 spp.)

Although it differs in several unique ways, particularly the bizarre branched form of the right paramere, we place *Waupsallus* in the Keltoniina because of the similarity of structure of the apical portion of the endosoma to what is seen elsewhere only in *Reuteroscopus*.

Subtribe Phylina, Douglas and Scott, 1865 (type genus: *Phylus* Hahn, 1831)

Psallidae Douglas and Scott, 1865

Xenocorini Kirkaldy, 1906

Ectagelini Wagner, 1969

DIAGNOSIS: Morphological characters uniting this grouping include the labium reaching past the hind coxae and the calli not visible on the pronotum (Menard et al., 2013). The morphology of the male genitalia in *Phylus* and *Psallus*, the two genera that were part of the molecular sample of Menard et al. (2013) offers no obvious set of similarities that clearly unites these two genera from the Palearctic, although the molecular data always group them together.

DISCUSSION: As the nominal subtribe, this taxon contains *Phylus* Hahn and its relatives. Thus, the reader will find in the following list a large number of cross-references pointing to the revised placement of genera because of the omnibus nature of Phylini as conceived by prior authors. Unfortunately, the taxon sample of sequence data treated by Menard et al. (2013) for the Phylina was limited to species of *Phylus* and *Psallus* Fieber, so that the remaining taxa in the subtribe are placed on the basis of morphological similarity alone, or they represent taxa that we treat as incertae sedis, where data are insufficient to place them with confidence in any other tribe at the present time.

*Acrotelus* Reuter, 1885: see Phylini, Oncotyline

*Adelphophylus* Wagner, 1959 (Palearctic: Balkans; 2 spp.)

We place this taxon in the Phylina because of its presumed relationship to *Phylus*. Wagner (1975) placed the genus in his *Phylus* group.

*Adenostomocoris* Schuh and Schwartz, 2004: see Nasocorini

*Agrametra* Buchanan-White, 1878: see Nasocorini

***Agraptocoris*** Reuter, 1903 (Palearctic: Mongolia, Tibet; 2 spp.)

We leave this taxon in the Phylini: Phylina for lack of information that would allow us to comment further on its subtribal placement. Illustrations of the male genitalia of *Agraptocoris oncotyloides* Vinokurov were published by Vinokurov and Kanyukova (1995).

*Alloeotarsus* Reuter, 1885: see Phylini, Oncotyline

***Alnopsallus*** Duwal, Yasunaga, and Lee, 2010 (Himalayan: Nepal; 2 spp.)

We maintain the placement of this taxon in the Phylina because the structure of the male genitalia and the overall appearance suggest a relationship to the Holarctic fauna.

***Alvarengamiris*** Carvalho, 1991, **incertae sedis** (Neotropical: Amazonia; 3 spp.)

This taxon is recorded as feeding on a single species of palm. The natural history and the general appearance of these bugs, excepting the absence of novel antennal structure, are similar to that of *Anomalocornis*; the structure of the endosoma is somewhat different. These attributes, in association with geographical proximity would suggest these taxa are closely related. It is our surmise that they might find their closest relatives in the genus group containing *Platyscytus* and what we believe to be its near relatives, and possibly also *Parafulvius*. Nonetheless, we assign *Alvarengamiris* incertae sedis within Phylina for lack of information allowing for a more compelling tribal placement (see also discussion under *Parafulvius*).

***Amazonophilus*** Carvalho and Costa, 1993, **incertae sedis** (Neotropical: Amazonia; 1 sp.)

See discussion under *Platyscytus*.

*Amblytylus* Fieber, 1858: see Cremnorrhini, Cremnorrhina

*Americodema* T. Henry, 1999: see Phylini, Oncotyline

*Ampimpacoris* Weirauch and Schuh, 2011: see Semiini, Exocarporina

***Anapsallus*** Odhiambo, 1960, **incertae sedis** (Ethiopian: East and West Africa; 2 spp.)

This taxon was originally placed in the Hallodapini by Odhiambo (1960) but later transferred to the Phylini by Schuh (1974). Linnavuori (1993a) illustrated the male genitalia, showing that the endosoma is long and filamentous, the head is distinctly prognathous, and the second antennal segment is swollen. Aside from the swollen antennae, these characteristics are similar to the condition seen in *Plagiognathidea*, and we suggest further comparison of these two genera should be undertaken. Schuh (1974) suggested that *Plagiognathidea* might be related to *Platyscytus* from the New World tropics on the basis of the filamentous endosoma. We leave *Anapsallus* (and *Plagiognathidea*) in the Phylina for lack of any evidence for its placement in another tribal-level grouping.

*Ancoraphylus* Weirauch, 2007: see Semiini, Exocarporina

*Angelopsallus* Schuh, 2006: see Phylini, Oncotyline

***Anomalocornis*** Carvalho and Wygodzinsky, 1945, **incertae sedis** (Neotropical: Amazonia; 7 spp.)

The diagnosis for this taxon includes the second antennal segment in the male being folded basally and doubled back on itself, whereas it is of typical structure in the female (Couturier and Costa, 2002). Seven species are currently included in the genus; those for which host information is available are documented as feeding on palms (Costa and Couturier, 2012). We have placed *Anomalocornis* as incertae sedis within Phylina for lack of informa-

tion to allow for a more informed placement of the taxon within the classification of the Phylinae. Carvalho (1984) described the new genus *Arlemiris* with a single included species. Based on the structure of the male genitalia as illustrated by Carvalho, we judge *Arlemiris* to be closely related to *Anomalocornis*, or possibly synonymous with it.

*Anonychiella* Reuter, 1912: see Exaeretini

*Antepia* Seidenstücker, 1962: see Phylini, Oncotyliina

*Aphaenophyes* Reuter, 1899: see Exaeretini

*Araucanophylus* Carvalho, 1984: see Semiini, Exocarporina

*Arctostaphylocoris* Schuh and Schwartz, 2004: see Nasocorini

*Arizonapsallus* Schuh, 2006: see Phylini, Oncotyliina

***Arlemiris*** Carvalho, 1984, **incertae sedis** (Neotropical: Amazonia; 1 sp.)

See discussion under *Anomalocornis*, Phylina.

*Asciodema* Reuter, 1878: see Phylini, Oncotyliina

*Atomophora* Reuter, 1879: see Nasocorini

*Atomoscelis* Reuter, 1875: see Nasocorini

*Atractotomimus* Kiritshenko, 1952: see Exaeretini

*Atractotomoidea* Yasunaga, 1999: see Nasocorini

*Atractotomus* Fieber, 1858: see Nasocorini

*Auchenocrepis* Fieber, 1858: see Exaeretini

*Aurantiocoris* Schuh and Schwartz, 2004: see Decomiini

*Austropsallus* Schuh, 1974: see Cremnorrhini, Coatnocapsini

*Badezorus* Distant, 1910: see Nasocorini

*Basileobius* Eyles and Schuh, 2003: see Semiini, Exocarporina

*Beckocoris* Knight, 1968: see Nasocorini

*Bergmiris* Carvalho, 1984: see Nasocorini

***Bicurvicoris*** Carvalho and Schaffner, 1973, **incertae sedis** (Neotropical: Southern Mexico; 1 sp.)

We place this taxon as *incertae sedis* in the Phylina until such time as specimens can be examined to provide a more in-depth assessment of its placement in the overall classification.

*Bisulcopsallus* Schuh, 2006: see Phylini, Oncotyliina

*Boopidocoris* Reuter, 1879: see Nasocorini

***Botocudomiris*** Carvalho, 1979, **incertae sedis** (Neotropical: Brazil; 1 sp.)

This taxon derives its name from the apparently ventrally elongate clypeus. In the absence of any persuasive evidence for its tribal placement, we leave *Botocudomiris* *incertae sedis* in the Phylina.

*Brachyarthrurum* Fieber, 1858: see Phylini, Oncotyliina

*Brachyceratocoris* Knight, 1968: see Cremnorrhini, Cremnorrhina

***Brachycranella*** Reuter, 1905, **incertae sedis** (Ethiopian: Namibia; 1 sp.)

This genus was described on the basis of a single female. The green spots on the hemelytra are easily seen in the dorsal and ventral photographs of the holotype of the type species deposited in the Swedish Museum of Natural History, as are the long black tibial spines with black bases. Examination of additional specimens and male genitalia will help to refine the placement of this taxon.

*Caiganga* Carvalho and Becker, 1957: see Nasocorini  
*Calidroides* Schwartz, 2005: see Cremnorrhini, Cremnorrhina  
*Camptotylidea* Wagner, 1957: see Nasocorini  
*Camptotylus* Fieber, 1860: see Exaeretini  
*Camptozorus* Kerzhner, 1996: see Exaeretini  
*Campylomma* Reuter, 1878: see Nasocorini  
*Capecapsus* Schuh, 1974: see Cremnorrhini, Coatonocapsina  
*Cariniocoris* T. Henry, 1989: see Phylini, Oncotyline  
*Ceratopsallus* Schuh, 2006: see Phylini, Oncotyline  
*Cercocarpopsallus* Schuh, 2006: see Phylini, Oncotyline  
*Chiloephyllus* Carvalho, 1984: see Semiini, Exocarpocorina  
*Chinacapsus* Wagner, 1961: see Nasocorini  
*Chlamydatius* Curtis, 1833: see Nasocorini  
*Chlamyopsallus* Schwartz, 2005: see Nasocorini  
*Chlorillus* Kerzhner, 1962: see Phylini, Oncotyline  
*Chrysochnoodes* Reuter, 1901: see Exaeretini  
*Coatonocapsus* Schuh, 1974: see Cremnorrhini, Coatonocapsina  
*Compsidolon* Reuter, 1899: Phylini, Oncotyline  
*Compsonannus* Reuter, 1902: see Exaeretini

***Conostethus*** Fieber, 1858, **incertae sedis** (Holarctic; 9 spp.)

Matocq (1991) presented the most up-to-date review of the Palearctic members of this genus, with illustrations of the male genitalia and habitus that conform to the structure also seen in *Conostethus americanus* Knight, the single New World species. Available data suggest that *Conostethus americanus* is a grass feeder (see Wheeler, 2001). Data for the Palearctic are ambiguous, although general habitat information suggests grass feeding, as for example, their being collected on coastal dunes (Matocq, 1991). The grass-feeding habits might suggest a relationship with *Amblytylus* and *Lopus*, but the head structure is unlike that of members of the Cremnorrhina; the long, slender claws with tiny pulvilli are similar in structure to those of taxa we place in the Exaeretini. For the moment we place *Conostethus* as incertae sedis in the Phylina for lack of any clear-cut information to place it in any other tribal grouping.

*Coquillettia* Uhler, 1890: see Cremnorrhini, Cremnorrhina

***Crassicornus*** Carvalho, 1945, **incertae sedis** (Neotropical; 8 spp.)

See comments under *Platyscytus*.

*Crassomiris* Weirauch, 2006b: see Phylini, Oncotyline

*Cremnorrhinus* Reuter, 1880: see Cremnorrhini, Cremnorrhina

*Criocoris* Fieber, 1858: see Semiini, Semiina

*Cyrtodiridius* Eyles and Schuh, 2003: see Semiini, Exocarpocorina

*Dacota* Uhler, 1872: see Cremnorrhini, Cremnorrhina

*Damioscea* Reuter, 1883: see Phylini, Oncotyline

***Darectagela*** Linnavuori, 1975, **incertae sedis** (Palearctic: Somalia; 1 sp.)

We tentatively place this taxon in the Phylina pending examination of specimens.



***Darfuromma*** Linnavuori, 1975, **incertae sedis** (Ethiopian: Sudan, Nigeria; 1 sp.)

We place this taxon as *incertae sedis* in the Phylina pending a more critical analysis, including the examination of specimens. The illustrations and comments of Linnavuori (1975) indicate that the structure of the endosoma in *Darfuromma* is novel, being “unusually short and straight, broadening apicad, gonopore far from apex in the basal part” (see also discussion under *Nubaia*).

*Dasycapsus* Poppius, 1912: see Phylini, Oncotyline

*Decomia* Poppius, 1915: see Decomiini

*Decomioides* Schuh, 1984: see Decomiini

*Denticulophallus* Schuh, 1974: see Cremnorrhini, Cremnorrhina

***Dignaia*** Linnavuori, 1975, **incertae sedis** (Palearctic: Sudan; 1 sp.)

We place this taxon as *incertae sedis* in the Phylina pending a more critical analysis, including the examination of specimens and the male genitalia. The illustrations of Linnavuori (1975) do not include the endosoma, making placement of the taxon more problematic.

*Dilatops* Weirauch, 2006: see Pilophorini

***Dominiquella*** Linnavuori, 1983, **incertae sedis** (Ethiopian: Senegal; 1 sp.)

Linnavuori (1983) placed this taxon in what he referred to as the *Paramixia* (= *Sthenaridea*) group (see also comments under *Chinacapsus*, Nasocorini), an artificial assemblage of taxa because of the inclusion of *Sthenaridea*, a member of the Pilophorini. This placement may indicate a relationship between *Dominiquella* and *Chinacapsus*, among other genera. The data of Menard et al. (2013) are insufficient to determine whether taxa such as *Chinacapsus* and *Dominiquella*, which share weakly fleshy recurved parempodia with *Moissonia* (included as *Ellenia* by Linnavuori, 1983), are actually closely related. We therefore place *Dominiquella* as *incertae sedis* within the Phylina.

***Ectagela*** Schmidt, K., 1939, **incertae sedis** (Palearctic/Ethiopian; 20 spp.)

Wagner (1969) erected the new tribe Ectagelini for the reception of this speciose taxon that ranges from northern Africa to Iran, because the novel structure of the male genitalia did not associate it with any recognized groupings. Most subsequent authors have not adopted this aspect of Wagner’s classification. There is little doubt that the structure of the endosoma in *Ectagela* is distinctive, as illustrated for many species by Linnavuori (1975, 1993a), but this does not help to place the taxon in the classification of the Phylinae more broadly. No authors have commented on what the nearest relatives of *Ectagela* might be, and we therefore treat it as *incertae sedis* within the Phylina until additional information becomes available.

***Ellacapsus*** Yasunaga, 2013, **incertae sedis** (Oriental: Thailand; 1 sp.)

We follow Yasunaga (2013) in placing this taxon in the Phylina, because data are insufficient to make a more informed disposition within phylinae classification. The flat, scalelike setae might suggest placement in the Nasocorini, but that seems to be negated by the structure of the endosoma, which is more like that seen in the Keltoniina. The enlarged and flattened second antennal segment seems of little use in placing the taxon.

*Eminoculus* Schuh, 1974: see Hallodapini

*Ephippiocoris* Poppius, 1912: see Leucophoropterini, Tuxedoina



***Eremophylus*** Yasunaga, 2001, **incertae sedis** (Palearctic: Japan; 1 sp.)

In his description of this taxon Yasunaga (2001) indicated that there were no known close relatives. We therefore place *Eremophylus* as incertae sedis within the Phylini, Phylina.

*Euderon* Puton, 1888: see Cremnorrhini, Cremnorrhina

*Eumecotarsus* Kerzhner, 1962: see Exaeretini

*Europiella* Reuter, 1909: see Phylini, Oncotyline

*Eurycolpus* Reuter, 1875: see Phylini, Oncotyline

*Eurycranella* Reuter, 1904: see Exaeretini

*Excentricoris* Carvalho, 1955: see Cremnorrhini, Cremnorrhina

*Exocarpocoris* Weirauch, 2007: see Semiini, Exocarpocorina

***Farsiana*** Linnavuori, 1998, **incertae sedis** (Palearctic: Iran; 1 sp.)

As part of his description Linnavuori (1998) illustrated the novel endosoma of this monotypic taxon from Iran. We place *Farsiana* as incertae sedis within Phylina until such time as additional information becomes available to refine its placement in the overall classification of the Phylinae.

*Frotaphylus* Carvalho, 1984: see Exaeretini

*Galbinocoris* Weirauch, 2006: see Phylini, Oncotyline

***Gedioris*** Wagner, 1964 (Palearctic: North Africa, Arabian Peninsula; 3 spp.)

The endosoma in this taxon bears a prominent apical spine. We tentatively place *Gedioris* in the Phylina in the absence of information to make a more refined tribal-level association.

***Ghazalocoris*** Linnavuori, 1975, **incertae sedis** (Ethiopian: Sub-Saharan; 1 sp.)

We place this taxon as incertae sedis in the Phylina pending a more critical analysis, including the examination of specimens and details of the male genitalia.

*Glaucopterum* Wagner, 1963: see Nasocorini

*Gonoporomiris* Henry and Schuh, 2002: see Exaeretini

*Gonzalezinus* Carvalho, 1981: see Semiini, Exocarpocorina

***Gressittocapsus*** Schuh, 1984, **incertae sedis** (Oriental: New Guinea; 1 sp.)

Schuh (1984) placed this taxon in the Phylini. He noted that it was distinctive within the Phylinae because of its rugulose dorsum and the unusual structure of the male genitalia.

We have placed *Gressittocapsus* as incertae sedis because there is no clear way to relate it to any other described genera.

*Guentherocoris* Schuh and Schwartz, 2004: see Cremnorrhini, Cremnorrhina

*Hadrophyes* Puton, 1874: see Exaeretini

*Halormus* Eyles and Schuh, 2003: see Semiini, Exocarpocorina

*Hamatophylus* Weirauch, 2006: see Phylini, Oncotyline

*Hambletoniola* Carvalho, 1954: see Nasocorini

*Harpagophylus* Schuh and Weirauch, 2010: see Semiini, Exocarpocorina

*Harpocera* Curtis, 1838: see Cremnorrhini, Cremnorrhina

*Helenocoris* Schmitz, 1976: see Nasocorini

*Heterocapillus* Wagner, 1960: see Cremnorrhini, Coatocapsina

*Hirtopsallus* Schmitz, 1976: see Nasocorini

*Hoplomachidea* Reuter, 1909: see Semiini, Semiina

*Hoplomachus* Fieber, 1858: see Phylini, Oncotyliina

*Hyalopsallus* Carvalho and Schaffner, 1973: see Exaeretini

**Icodema** Reuter, 1875 (Western Palearctic; 1 sp.)

We have placed this genus in the Phylina based on some similarities in the structure of the endosoma to *Psallus* spp. This placement suggests that *Icodema* is not closely related to *Americodema* Henry, *Occidentodema* Henry, and *Lineatopsallus* as the contrasting black stripes on the antennae and femora might suggest (see also discussion in Henry, 1991, 1999).

*Ifephyllus* Linnavuori, 1993a: see Hallodapini

**Indatractus** Linnavuori, 1975, **incertae sedis** (Palearctic: Eritrea, Saudi Arabia; 2 spp.)

Linnavuori (1975) related this taxon to *Atractotomus* based on the shape of the head and presumably by the fact that the second antennal segment is swollen. We place *Indatractus* as incertae sedis within Phylina pending additional information to refine its placement in the overall classification of the Phylinae.

*Insulaphyllus* Weirauch, 2006a: see Phylini, Oncotyliina

*Insulopus* Schmitz, 1976: see Nasocorini

**Izyaius** Schwartz, 2006, **incertae sedis** (Eastern Nearctic; 1 sp.)

This taxon was erected by Schwartz (2006) to accommodate *I. sericeus* (Heidemann), a species previously placed in *Plesiodema*. Schwartz (2006) illustrated and described the male genitalia for *Izyaius*, indicating that the structure was such that no existing genus could accommodate this taxon; he also provided scanning electron micrographs, illustrated female genitalic structure, and provided host information. Further study will be needed to provide a more nuanced placement of *Izyaius*, and we therefore treat it as incertae sedis within Phylina.

*Jiwarli* Soto and Weirauch, 2009: see Semiini, Exocarpocorina

*Josifovius* Konstantinov, 2008: see Phylini, Oncotyliina

**Juniperia** Linnavuori, 1965, **incertae sedis** (Palearctic: Turkey; 1 sp.)

We place this taxon as incertae sedis within the Phylina for lack of the necessary information to place it more accurately in one of the other tribes that we recognize.

*Karocris* V. Putshkov, 1975: see Nasocorini

*Karoocapsus* Schuh, 1974: see Semiini, Semiina

*Kasumiphylus* Schwartz and Stonedahl, 2004: see Nasocorini

*Keltonia* Knight, 1966: see Phylini, Keltoniina

*Kmentophyllus* Duwal, Yasunaga, and Lee, 2010: see Phylini, Oncotyliina

**Knightsensis** Schaffner, 1978, **incertae sedis** (Nearctic: Southern Mexico; 1 sp.)

This taxon has the appearance of some genera we place in the Nasocorini. The endosoma is slender and tubular and more like we place in the Semiina. We recommend additional study to determine the proper position of *Knightsensis*.

*Knightomiroides* Stonedahl and Schwartz, 1996: see Nasocorini

*Knightophylina* Schaffner, 1978: see Phylini, Oncotyliina

*Knightopiella* Schuh, 2004: see Phylini, Oncotyliina

*Knightopsallus* Schuh, 2006: see Phylini, Oncotyliina

***Lalyocoris*** Linnavuori, 1993a, **incertae sedis** (Ethiopian: East Africa; 1 sp.)

*Lalyocoris minutissimus* (Linnavuori, 1975) was placed in *Pilophorus* Hahn at the time of its original description. Schuh (1989) treated the taxon as incertae sedis within *Pilophorus*. Linnavuori (1993a) moved the species to the new genus *Lalyocoris* and placed it in the Phylini because it had setiform parempodia, had a distinct secondary gonopore (based on his observations), and did not have an evaginated posterior wall in the female. Because of ambiguity in interpretation of the character complement of the minute specimens belonging to this taxon, we place it as incertae sedis in the Phylina, with the recognition that this is only a placement of convenience, not one indicating relationship.

*Lamprosthenarus* Poppius, 1914: see Nasocorini

*Larinocerus* Froeschner, 1965: see Nasocorini

***Lasiolabopella*** Schuh, 1974, **incertae sedis** (Ethiopian: South Africa; 1 sp.)

Schuh and Wu (2009) used this taxon as an outgroup in their phylogenetic analysis of *Eminoculus*. The rationale for that decision was apparently based on the presumed similarity of structure of the endosoma in the two genera and the weakly stylate eyes. The analysis of Menard et al. (2013) indicates that *Eminoculus* is allied to the Hallodapini, an association supported by the presence of a pronotal collar in all but one species. The pronotal collar is absent in *Lasiolabopella* as are most other attributes of *Eminoculus*. Until additional analytical studies are undertaken, we place *Lasiolabopella* as incertae sedis in the Phylina.

*Lasiolabops* Poppius, 1914: see Pilophorini

*Lattinophylus* Schuh, 2008: see Nasocorini

*Leaina* Linnavuori, 1974: see Halladapini

***Lepidargyrus*** Muminov, 1962 (Palearctic; 14 spp.)

Superficially this taxon is easily confused with species of *Oligotylus* Van Duzee, some *Plagiognathus* spp., and *Psallus* sensu stricto, on the basis of the large size, woolly pubescence, and frequently dark coloration in all three genera. Indeed, many species of the genus were placed in *Psallus* (*Apocreminus*) by Wagner (1975) and other authors, on the basis of their superficial appearance to true *Psallus* spp. We place *Lepidargyrus* in the Phylina on the basis of the relatively simple endosoma, with a single apical projection as is usually seen in *Psallus* spp. One species, *L. ancorifer* (Fieber) is introduced into North America.

***Lepidocapsus*** Poppius, 1914, **incertae sedis** (Ethiopian; 2 spp.)

This taxon was originally based on a species from East Africa. Schuh (1974) subsequently described a species from the Western Cape region of South Africa; both have a terete second antennal segment. Absent SEM examination, the scalelike setae appear lanceolate and similar to those seen in the Pilophorina. Nonetheless, the structure of the pretarsus and the male genitalia are unlike anything seen in Pilophorina. We place *Lepidocapsus* as incertae sedis in the Phylina until such time as further studies of this taxon are undertaken.

*Leptidolon* Reuter, 1904: see Semiini, Exocarporina

***Leptoxanthus*** Reuter, 1905, **incertae sedis** (Ethiopian: Namibia; 1 sp.)

The type female, the only known specimen of this taxon is deposited in the Swedish Museum of Natural History, according to the website of that institution. Because the place-

ment of the taxon cannot be determined from examination of the Web-based photographs or the original description, we place *Leptoxanthus* as *incertae sedis* until additional studies of this taxon, including male specimens, are conducted.

*Leucodellus* Reuter, 1906: see Phylini, Oncotylinea

*Leucophylus* Duwal, Yasunaga, and Lee, 2010: see Phylini, Oncotylinea

*Leutiola* Wyniger, 2012: see Cremnorrhini, Cremnorrhina

*Lindbergopsallus* Wagner, 1962: see Nasocorini

*Lineatopsallus* T. Henry, 1991: see Phylini, Oncotylinea

*Litoxenus* Reuter, 1885: see Phylini, Oncotylinea

***Liviopsallus*** Carapezza, 1982 (Palearctic: Sicily; 1 sp.)

This taxon was related to the *Cephalocapsus* group of Wagner by Carapezza (1982) because of the apparent similarity of pretarsal structure, including fleshy parempodia. Nonetheless, the endosoma is of a type similar to that seen in *Psallus* sensu stricto. We believe the relationships of *Liviopsallus* could benefit from further enquiry (see also comments under *Chinacapsus*, Nasocorini).

*Lopidodenus* V. Putshkov, 1974: see Cremnorrhini, Cremnorrhina

*Lopsallus* Schmitz, 1976: see Nasocorini

*Lopus* Hahn, 1833: see Cremnorrhini, Cremnorrhina

*Macrotylus* Fieber, 1858: see Cremnorrhini, Cremnorrhina

*Maculamiris* Weirauch, 2006a: see Phylini, Oncotylinea

*Malacotes* Reuter, 1878: see Phylini, Oncotylinea

*Malaysiamiris* Schuh, 1984: see Decomiini

*Malaysiamiroides* Schuh, 1984: see Decomiini

*Marrubiocoris* Wagner, 1970: see Phylini, Oncotylinea

*Maurodactylus* Reuter, 1878: see Nasocorini

*Mecenopa* Eyles and Schuh, 2003: see Semiini, Exocarpocorina

*Megalocoleus* Reuter, 1890: see Phylini, Oncotylinea

*Megalodactylus* Fieber, 1858: see Exaeretini

*Megalopsallus* Knight, 1927: see Nasocorini

*Melaleucoides* Schuh and Weirauch, 2010: see Semiini, Exocarpocorina

***Mendozaphylus*** Carvalho and Carpintero, 1991, *incertae sedis* (Neotropical: Argentina; 1 sp.)

This taxon was placed in the Hallodapini by its authors. They compared it solely with *Tuxenella* Carvalho (Orthotylineae), with the admission that this was a comparison based only on similarity of appearance and not an indicator of relationship. This placement was rejected by Kerzhner and Schuh (1995) and Schuh (1995), who placed *Mendozaphylus* in the Phylini because they did not believe any true Hallodapini were known from South America and because *Mendozaphylus* did not have male genitalia of the distinctive form seen in many Hallodapini. *Mendozaphylus mendocinus* Carvalho and Carpintero, as illustrated by its authors, does have a pronotal collar, but one that is not typical of the type found in the Hallodapini. The rather simple endosoma illustrated by Carvalho and Carpintero (1991) suggests that *Mendozaphylus* might equally be related to the Leucophorop-

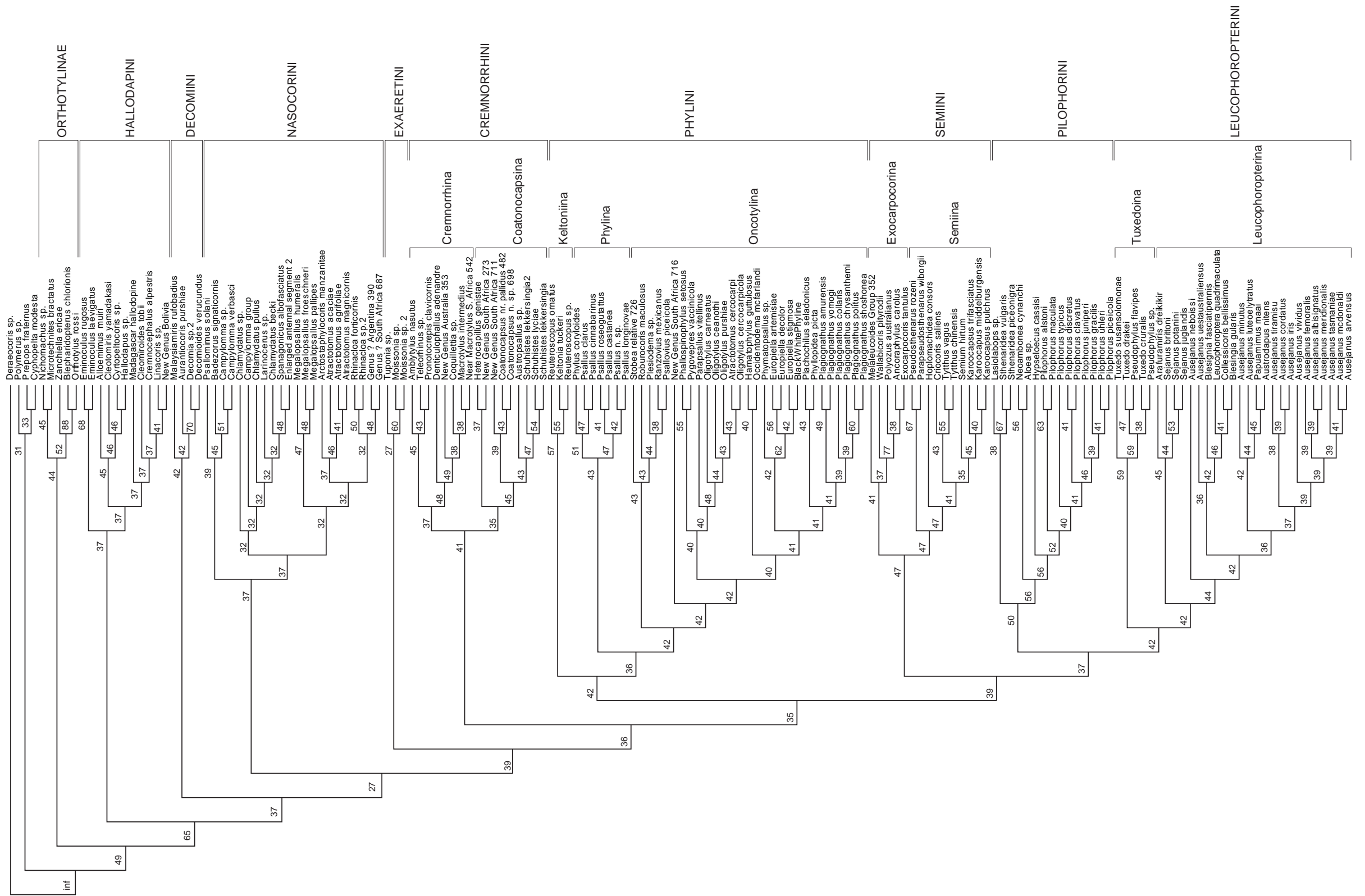


FIG. 1. Cladogram of relationships of Phylinae from Menard et al. (2013), which forms the framework for the classification presented in this paper.

terini as opposed to the Hallodapini. Because this paper is not designed to conduct additional specimen examinations, we retain *Mendozaphylus* incertae sedis within Phylina until such type as additional information regarding its placement becomes available.

***Millerimiris*** Carvalho, 1951, **incertae sedis** (Ethiopian: Central Africa; 1 sp.)

Schuh (1974) moved this genus to the Phylini from the Orthotylini, where Carvalho had placed it at the time of its description. Linnavuori (1975) independently also placed *Millerimiris* in the Phylini. The taxon is unique with the Phylinae in possessing a heavily punctate dorsum. There is insufficient information available at present to make a credible tribal assignment.

***Mixtecimiris*** Carvalho and Schaffner, 1973, **incertae sedis** (Nearctic: Central Mexico; 1 sp.)

*Mixtecimiris* was originally placed in the Orthotylini because of the fleshy recurved parempodia. The male genitalia are nonetheless of the Phylinae type. Existing knowledge does not allow a more precise tribal placement of *Mixtecimiris*, so we leave the taxon in the Phylina as incertae sedis.

*Moiseevichia* Schuh, 2006: see Phylini, Oncotylini

*Moissonia* Reuter, 1894: see Exaeretini

*Monocris* V. Putshkov, 1974: see Semiini, Semiina

*Monospatha* Eyles and Schuh, 2003: see Semiini, Exocarporina

*Monosynamma* J. Scott, 1864: see Nasocorini

*Myrmicopsella* Poppius, 1914: see Semiini, Semiina

*Nanopsallus* Wagner, 1952: see Phylini, Oncotylini

*Naresthus* Schmitz, 1976: see Nasocorini

*Nasocoris* Reuter, 1879: see Nasocorini

***Natalophylus*** Schuh, 1974, **incertae sedis** (Ethiopian: South Africa; 1 sp.)

This taxon was described on the basis of its superficial similarity to *Phylus*. Further study may help to clarify the position of this taxon, but for the moment we place it incertae sedis within Phylina.

*Neisopsallus* Schmitz, 1976: see Nasocorini

*Neophylus* Carvalho and Costa, 1992: see Nasocorini

*Neopsallus* Schuh and Schwartz, 2004: see Phylini, Oncotylini

*Nevadocoris* Knight, 1968: see Nasocorini

*Nicholia* Knight, 1929: see Semiini, Semiina

*Nigrimiris* Carvalho and Schaffner, 1973: see Nasocorini

*Nigrocapillocoris* Wagner, 1973: see Nasocorini

***Nubaia*** Linnavuori, 1975, **incertae sedis** (Palearctic: Sudan; 1 sp.)

This taxon was originally described on the basis of a single female specimen. Linnavuori (1975) related *Nubaia* to *Lindbergopsallus* and *Dominiquella* and later to *Darfuromma* (Linnavuori, 1993a), presumably because of the weakly fleshy parempodia. Linnavuori's (1993a) illustrations of the short stout endosoma in *Nubaia* and *Darfuromma* would seem to indicate a close relationship between these two taxa, although the endosoma in *Lindbergopsallus* is quite different in structure and we have placed that taxon in the Nasocorini in view of its apparent close relationship to *Chinacapsus*. See also comments under *Chinacapsus*.

*Occidentodema* T. Henry, 1999: see Phylini, Oncotylini



*Oligobiella* Reuter, 1885: see Nasocorini  
*Oligotylus* Van Duzee, 1916: see Phylini, Oncotyline  
*Omocoris* Lindberg, 1930: see Phylini, Oncotyline  
*Oncotylidea* Wagner, 1965: see Phylini, Oncotyline  
*Oncotylus* Fieber, 1858: see Phylini, Oncotyline  
*Opisthotaenia* Reuter, 1901: see Phylini, Oncotyline  
*Opuna* Kirkaldy, 1902: see Exaeretini  
*Oreocapsus* Linnavuori, 1975: see Phylini, Oncotyline

***Orthonotus*** Stephens, 1829 (Palearctic; 22 spp.)

Wagner (1975) placed *Orthonotus* in the *Phylus* group of genera. Although the very strong sexual dimorphism in some species might suggest distinctness from the morphologically monotonous *Phylus*, there is a strong resemblance between macropterous forms in the two genera. We therefore maintain *Orthonotus* in the Phylina.

*Orthopidea* Reuter, 1899: see Nasocorini  
*Pachyxyphus* Fieber, 1858: see Cremnorrhini, Cremnorrhina  
*Parachlorillus* Wagner, 1963: see Phylini, Oncotyline

***Parafulvius*** Carvalho, 1954, **incertae sedis** (Neotropical: Amazonia; 4 spp.)

At the time of its original description, Carvalho (1954) placed this taxon in the Cylapinae: Fulviini; he compared its general appearance with that of *Amblytylus* (Phylini). Schuh (1974) subsequently moved *Parafulvius* to the Phylini. More recently Costa and Couturier (2000) documented a new species of *Parafulvius* as feeding on the inflorescences of palms in the Amazon. As did Carvalho (1954) and Schuh (1974), those authors compared the taxon with *Amblytylus*. It is our conclusion that comparison of *Parafulvius* with *Alvarengamiris* may be more productive. Both groups are known to feed on palm inflorescences, both have somewhat flattened bodies, anteriorly projecting heads, an elongate labium reaching well onto the abdomen, and elongate claws without obvious pulvilli (Costa and Couturier, 2002, for *Alvarengamiris*; Costa and Couturier, 2000, for *Parafulvius*; personal obs.). The available illustrations of the male genitalia are more difficult to compare but do not preclude the recognition of similarities in the structure of the endosoma and the left paramere. See also discussion under *Alvarengamiris*.

*Paralopus* Wagner, 1957: see Cremnorrhini, Cremnorrhina  
*Parapseudosthenarus* Schuh, 1974: see Semiini, Semiina  
*Parasciodema* Poppius, 1914: see Semiini, Coatonocapsina  
***Paravoruchia*** Wagner, 1959 (Palearctic: Greece; 1 sp.)

The structure of the endosoma in this taxon is consistent with its placement in the *Phylus* group.

*Paredrocoris* Reuter, 1878: see Phylini, Oncotyline  
*Pastocoris* Reuter, 1879: see Exaeretini  
*Phaeochiton* Kerzhner, 1964: see Phylini, Oncotyline  
*Phallospinophylus* Weirauch, 2006b: see Phylini, Oncotyline  
*Phaxia* Kerzhner, 1984: see Nasocorini  
*Phoenicocoris* Reuter, 1875: see Nasocorini  
*Phyllophidea* Knight, 1919: see Phylini, Oncotyline  
**\**Phylus*** Hahn, 1831 (Palearctic; 8 spp.)

*Phymatopsallus* Knight, 1964: see Phylini, Oncotyline

*Piceophylus* Schwartz and Schuh, 1999: see Phylini, Oncotyline

*Pimeleocoris* Eyles and Schuh, 2003: see Semiini, Exocarporina

*Pinomiris* Stonedahl and Schwartz, 1996: see Nasocorini

*Pinophylus* Schwartz and Schuh, 1999: see Phylini, Oncotyline

*Placochilus* Fieber, 1858: see Phylini, Oncotyline

***Plagiognathidea*** Poppius, 1914, **incertae sedis** (Ethiopian; 5 spp.)

See comments under *Anapsallus*, Phylini, Phylina.

*Plagiognathus* Fieber, 1858: see Phylini, Oncotyline

***Platyscytisca*** Costa and Henry, 1999, **incertae sedis** (Neotropical: Brazil; 2 spp.)

See discussion under *Platyscytus*.

***Platyscytus*** Reuter, 1907, **incertae sedis** (Neotropical; 21 spp.)

This taxon has the superficial appearance of members of the *Zanchius* complex of genera (Orthotylineae), with a delicate, pale body often ornamented with some bright-colored spots. The endosoma of species currently placed in *Platyscytus* is often very long and coiled, a condition seen elsewhere only in *Bisulcopsallus* (Phylini: Oncotyline). Nonetheless, *Platyscytus* does not possess attributes used by Schuh (2006a) to assign genera, including *Bisulcopsallus*, to the *Phymatopsallus* group of genera. On the basis of general appearance, the exerted dorsoventrally elongate head, protuberant eyes, and distribution in the Neotropics, we suggest that *Platyscytus* is most closely related to *Amazonophilus*, *Crassicornus*, and *Platyscytisca*. Although this assertion in part contradicts the conclusions of Costa and Henry (1999) with regard to *Platyscytisca*, we agree that these taxa are in need of revision. We have retained all three genera as incertae sedis within Phylini, because of a lack of information to make a better-informed tribal placement.

*Plesiodema* Reuter, 1875: see Phylini, Oncotyline

*Pleuroxonotus* Reuter, 1903: see Phylini, Oncotyline

*Polyozus* Eyles and Schuh, 2003: see Semiini, Exocarporina

***Porophoroptera*** Carvalho and Gross, 1982, **incertae sedis** (Australian; 1 sp.)

Available information on this taxon leaves its relationship to other genera of Phylinae unclear, especially in regard to the endosoma which is nearly rectangular in shape and dissimilar to any other known genera of Phylinae. For this reason we place it as incertae sedis in the Phylina, as was done by Menard and Schuh (2011).

*Pronototropis* Reuter, 1879: see Phylini, Oncotyline

*Pruneocoris* Schuh and Schwartz, 2004: see Nasocorini

*Psallodema* V. Putshkov, 1970: see Phylini, Oncotyline

*Psallomimus* Wagner, 1951: see Nasocorini

*Psallomorpha* Duwal, Yasunaga, and Lee, 2010: see Phylini, Oncotyline

*Psallopsis* Reuter, 1901: see Exaeretini

*Psallovius* Henry, T., 1999: see Phylini, Oncotyline

**\**Psallus*** Fieber, 1858 (Holarctic; 151 spp.)

Most classifications of *Psallus* have included a number of subgenera. There is little reason to believe that these species groupings are tied together by characters other than the form

of the vestiture. Until a more detailed analysis of *Psallus* sensu lato is published we refrain from introducing additional taxonomic decisions, but assert that we have little confidence in the monophyly of a broadly conceived *Psallus*, especially if that concept fails to consider the validity of *Sthenarus*.

*Pseudatomoscelis* Poppius, 1911: see Cremnorrhini, Keltoniina

*Pseudophylus* Yasunaga, 1999: see Leucophoropterini, Tuxedoina

*Pseudosthenarus* Poppius, 1914: see Semiini, Semiina

*Pygovepres* Weirauch, 2006b: see Phylini, Oncotyline

*Quercophylus* Weirauch, 2006b: see Phylini, Oncotyline

*Quernocoris* Weirauch, 2006a: see Phylini, Oncotyline

*Rakula* Odhiambo, 1967: see Semiini, Semiina

*Ranzovius* Distant, 1893: see Phylini, Oncotyline

*Reuteroscopus* Kirkaldy, 1905: see Phylini, Keltoniina

*Rhinacloa* Reuter, 1876: see Nasocorini

*Rhinocapsus* Uhler, 1890: see Phylini, Oncotyline

*Roburocoris* Weirauch, 2009: see Phylini, Oncotyline

***Roudairea*** Puton and Reuter, 1886, **incertae sedis** (Palearctic: North Africa to Iran; 4 spp.)

The novel external and genitalic morphological characteristics of this taxon leave in question its placement within the tribes/subtribes recognized in this study. We therefore place it *incertae sedis* within the Phylina.

*Rubellomiris* Weirauch, 2006b: see Phylini, Oncotyline

*Rubeospineus* Weirauch, 2006b: see Phylini, Oncotyline

*Rubrocuneocoris* Schuh, 1984: see Decomiini

*Sacculifer* Kerzhner, 1959: see Leucophoropterini, Tuxedoina

*Salicarus* Kerzhner, 1962: see Nasocorini

*Salicopsallus* Schuh, 2006: see Phylini, Oncotyline

***Sasajiphylus*** Yasunaga, 2001, **incertae sedis** (Palearctic: Japan; 1 sp.)

Like Yasunaga (2001), we have insufficient information at the present time to make a definitive assessment of the relationships of this taxon. We therefore place it in the Phylina.

*Schaffneropsallus* Schuh, 2006: see Phylini, Oncotyline

*Schuhistes* Menard, 2010: see Cremnorrhini, Coatonocapsina

*Semium* Reuter, 1876: see Semiini, Semiina

*Shendina* Linnavuori, 1975: see Cremnorrhini, Cremnorrhina

*Solenoxyphus* Reuter, 1875: see Nasocorini

***Somalocoris*** Linnavuori, 1975, **incertae sedis** (Palearctic: Somalia; 1 sp.)

This monotypic taxon from Somalia is placed *incertae sedis* in the Phylina because at the present time no characters serve to relate it to any other tribal-level grouping.

*Spanagonicus* Berg, 1883: see Nasocorini

*Squamophylus* Carvalho and Costa, 1992: see Nasocorini

*Stenoparia* Fieber, 1870: see Phylini, Oncotyline

*Sthenaropsidea* Henry and Schuh, 2002: see Phylini, Oncotyline

*Sthenaropsis* Poppius, 1912: see Nasocorini

***Sthenarus*** Fieber, 1858 (Palearctic; 2 spp., 2 extralimital)

We associate this nominal genus with *Psallus* because of the great structural similarity of the endosoma with that of *Psallus* sensu stricto spp. We note that two of the species currently residing in *Sthenarus*, from Texas and Australia, are placed there simply because the classical taxon served as a dumping ground and are in need of reexamination to determine their genus of proper placement.

***Stibaromma*** Odhiambo, 1961, **incertae sedis** (Ethiopian: Central Africa; 1 sp.)

This taxon was compared with *Cephalocapsus* Poppius and *Schroederiella* Poppius by Odhiambo (1961) on the basis of the fleshy parempodia. Both of those genera are junior synonyms of *Sthenaridea* (Pilophorini). The endosoma of *Stibaromma* as illustrated by Odhiambo (1961) cannot belong to *Sthenaridea* because it possesses a sclerotized secondary gonopore. Odhiambo (1961) also compared *Stibaromma* with *Criocoris* and *Psallus*, comparisons we consider meaningless in the context of our present knowledge of the Phylinae. Linnavuori (1993a) placed *Stibaromma* adjacent to *Millerimiris*, *Waupsallus*, and *Moissonia*, presumably on the basis of parempodial structure, but otherwise there would seem to be no relationship. Because of the ambiguous nature of these comparisons we leave *Stibaromma* as incertae sedis within Phylina.

*Stictopsallus* Schuh, 2006: see Phylini, Oncotyline

*Stirophylylus* Eckerlein and Wagner, 1965: see Phylini, Oncotyline

*Stoebea* Schuh, 1974: see Phylini, Oncotyline

*Strophopoda* Van Duzee, 1916: see Pronotocrepini, Cremnorrhina

*Taeniophorus* Linnavuori, 1952: see Nasocorini

*Tannerocoris* Knight, 1970: see Nasocorini

*Tapirula* Carapezza, 1997: see Leucophoropterini, Tuxedoina

*Tapuruyunus* Carvalho, 1946: see Nasocorini

*Thermocoris* Puton, 1875: see Phylini, Oncotyline

*Thoth* Linnavuori, 1993a: see Semiini, Semiina

*Thryptomenomiris* Schuh and Weirauch, 2010: see Semiini, Exocarpocorina

*Thymopsallus* Linnavuori, 1975: see Nasocorini

***Tibiopilus*** Carvalho and Costa, 1993, **incertae sedis** (Neotropical: Amazonia; 1 sp.)

This taxon was placed in the Hallodapini by Carvalho and Costa, presumably because they interpreted the anterior pronotal margin as being in the form of a depressed collar. Kerzhner and Schuh (1995) did not accept this placement, in part because no other credible representatives of the Hallodapini were known from the Neotropics. We therefore treat the taxon as incertae sedis within Phylini in the absence of further information and analysis concerning its tribal-level placement.

*Ticua* Wyniger, 2012: see Cremnorrhini, Cremnorrhina

*Tijucaphylus* Carvalho and Costa, 1992: see Nasocorini

*Tinicephalus* Fieber, 1858: see Phylini, Oncotyline

*Tragiscocoris* Fieber, 1861: see Phylini, Oncotyline

***Trevessa*** China, 1924, **incertae sedis** (Indian Ocean: Rodriguez Island; 1 sp.)

This taxon was described on the basis of two female specimens. It has received no subse-

quent study and no males have become available. We therefore place the taxon in the Phylina as *incertae sedis*.

*Tunisiella* Carapezza, 1997: see Nasocorini

*Tuponia* Reuter, 1875: see Exaeretini

*Tuxedo* Schuh, 2001: see Leucophoropterini, Tuxedoina

*Tytthus* Fieber, 1864: see Semiini, Semiina

*Utopnia* Reuter, 1881: see Cremnorrhini, Cremnorrhina

*Vanduzeephylus* Schuh and Schwartz, 2004: see Phylini, Oncotyline

*Vesperocoris* Weirauch, 2006a: see Phylini, Oncotyline

***Villaverdea*** Carvalho, 1990, ***incertae sedis*** (Neotropical: Coastal Peru; 1 sp.)

This taxon possesses no obviously distinctive features, a situation that leaves its placement obscure. It is possible that *Villaverdea* bears a relationship to *Reuteroscopus*, but establishing that connection will require work that is beyond the scope of this paper.

*Viscacoris* Weirauch, 2009: see Phylini, Oncotyline

*Voruchia* Reuter, 1879: see Nasocorini

*Voruchiella* Poppius, 1912: see Exaeretini

*Wallabicoris* Schuh and Pedraza, 2010: see Semiini, Exocarpocorina

*Waupsallus* Linnavuori, 1975: see Phylini, Keltoniina

***Widdringtoniola*** Schuh, 1974, ***incertae sedis*** (Ethiopian: South Africa; 1 sp.)

The taxon was described by Schuh (1974) as occurring on *Widdringtonia*, a native South African member of the Cupressaceae. The single known small species has no distinctive features that allow it to be easily allied with any of the tribes/subtribe we recognize. We therefore place it *incertae sedis* in the Phylina.

*Xiphoidellus* Weirauch and Schuh, 2011: see Semiini, Exocarpocorina

*Xiphoides* Eyles and Schuh, 2003: see Semiini, Exocarpocorina

*Yotvata* Linnavuori, 1964: see Exaeretini

***Zakanocoris*** V. Putshkov, 1970 (Palearctic: South Russian, Iran; 1 sp.)

This taxon was recorded as feeding on *Acer* (Aceraceae) from Stavropol, Russia, by Putschkov and later from Iran by Linnavuori (2010). The structure of the male genitalia is of the *Psallus* *sensu stricto* type (F. Konstantinov, personal commun.) and we therefore maintain the placement of this taxon in the Phylini, Phylina.

***Zanchiophylus*** Duwal, Yasunaga, and Lee, 2010, ***incertae sedis*** (Palearctic: Nepal; 1 sp.)

This taxon received its name because of the pale green coloration and the superficial resemblance to *Zanchius* Distant (Orthotylinae). We find no characteristics that straightforwardly relate *Zanchiophylus* to any particular tribe and therefore place it *incertae sedis* in the Phylina.

*Zinjolopus* Linnavuori, 1975: see Cremnorrhini, Cremnorrhina

*Zophocnemis* Kerzhner, 1962: see Phylini, Oncotyline

Subtribe Oncotyline Douglas and Scott, 1865 (type genus: *Oncotylus* Fieber, 1858)

Plagiognathina, Reuter, 1875

DIAGNOSIS: The study of Menard et al. (2013) united the Oncotyline primarily on molecular characters, but this diverse lineage unfortunately was not united by any morphological



synapomorphies. A more intensive morphological study of this grouping will likely reveal diagnostic characters, particularly within the male genitalia.

**DISCUSSION:** We are using the name *Oncotylinina*, first proposed at the family level by Douglas and Scott (1865). This name has seen little use in the modern literature, except in an informal sense by Wagner (e.g., 1975) as the *Oncotylus* group. On the basis of priority we are treating *Oncotylinina* as the senior synonym of the also little-used name *Plagiognathina* (Reuter, 1875). This is the largest assemblage of phylinae genera with a distribution restricted almost exclusively to the Holarctic. It is also a group for which Menard et al. (2013) were able to adduce a substantial sample of sequence data.

We have placed all Nearctic genera with small reddish species described by Weirauch (e.g., 2006a, 2006b, 2009) in the *Oncotylinina* because four of these—*Hamatophylus*, *Phallospinophylus*, *Pygovepres*, and *Roburocoris*—were placed in the group in the combined analysis of Menard et al. (2013). These taxa all have largely overlapping distributions, primarily in the southwestern United States and adjacent Mexico. In spite of the variation in endosomal structure, the general appearance and the sequence data suggest that they are all fairly closely related.

***Acrotelus*** Reuter, 1885 (Palearctic; 8 spp.)

We place this taxon in the *Oncotylinina* because of its similarity of appearance to *Oncotylus*. The secondary gonopore is located near the apex of the relatively simple endosoma, a structural situation similar to that seen in *Dasycapsus*. Most species appear to have a single type of pubescence on the dorsum. See also comments under *Litoxenus*.

***Allootarsus*** Reuter, 1885 (Palearctic; Iberian Peninsula; 1 sp.)

We place this taxon in the *Oncotylinina* based on the structural similarity of the endosoma with that of *Plagiognathus* spp. (Wagner, 1975: fig. 737; Ribes, 1978: figs. 36–40)

***Americodema*** T. Henry, 1999 (Nearctic; 2 spp.)

We have placed this taxon, in conjunction with *Cariniocoris* Henry and *Occidentodema* Henry, in the *Oncotylinina* on the basis of a keel on the pygophore, the similarity of structure of the endosoma with that of *Plagiognathus*, and the fact that sequence data for the related genus *Occidentodema* place it in the *Oncotylinina*.

***Angelopsallus*** Schuh, 2006 (Western Nearctic: Baja California; 1 sp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and therefore included in the *Oncotylinina* (see *Phymatopsallus*).

***Antepia*** Seidenstücker, 1962 (Palearctic: Turkey; 1 sp.)

Seidenstücker (1960) placed *Antepia* in the *Oncotylinina*. Although we are uncertain as to his conception of the subtribe, we tentatively maintain that placement for the genus. The structure of the endosoma is similar to that found in *Solenoxyphus* and *Boopidocoris* (see *Nasocorini*), although larger and without teeth. The minute subapical tooth on the claw may suggest relation to *Eurycolpus*, which we also place in the *Oncotylinina*. This taxon is said to live on *Liliaceae*, a host association that may merit further investigation because of the rarity of this association in the *Phylinae* and most other *Miridae*.



**Arizonapsallus** Schuh, 2006 (Southwest Nearctic; 1 sp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and is therefore included in the Oncotyline (see *Phymatopsallus*).

**Asciodema** Reuter, 1878 (Palearctic; introduced to Nearctic; 1 sp.)

This taxon is now monotypic, all previously recognized species having been synonymized with the type. The general appearance is similar to that of *Amblytylus* and some *Plagiognathus* spp. The male genitalia of *A. obsoleta* (Fieber) are similar to those of many *Compsidolon* species, e.g., *C. pumilum* (Jakovlev), *C. parviceps* (Wagner); we therefore place *Asciodema* in the Oncotyline.

**Bisulcopsallus** Schuh, 2006 (Southwest Nearctic; 7 spp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and is therefore included in the Oncotyline (see *Phymatopsallus*).

**Brachyarthrum** Fieber, 1858 (Palearctic; 1 sp.)

This widely distributed taxon has been carried by inertia in the literature without serious study or incorporation into revisionary works; the only illustrations of the male genitalia are from Kerzhner (1988: fig. 52: 20, 21). It has rather short, distinctly lamellate and parallel parempodia of the type seen in *Phoenicocoris dissimilis*, minute claws strongly bent at the middle with minute pulvilli, and a very long, slender endosoma, somewhat reminiscent of halodapines or *Sthenaridea*, but with a bifurcate apex and an apically placed secondary gonopore. The general habitus of *Brachyarthrum* is that of most any *Plagiognathus* sp. and we therefore provisionally place *Brachyarthrum* in the Oncotyline. The hosts are recorded as *Populus* spp., *Chosenia arbutifolia*, and several other members of the Salicaceae.

**Cariniocoris** T. Henry, 1989 (Nearctic; 3 spp.)

See discussion under *Americodema*.

**Ceratopsallus** Schuh, 2006 (Western Nearctic; 10 spp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and is therefore included in the Oncotyline (see *Phymatopsallus*).

**Cercocarpopsallus** Schuh, 2006 (Western Nearctic; 2 spp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and is therefore included in the Oncotyline (see *Phymatopsallus*).

**Chlorillus** Kerzhner, 1962 (Palearctic: Eastern Mediterranean, South Russia; 2 spp.)

The taxon was originally described as a subgenus of *Plagiognathus*. The taxon has many male genitalic features typical of *Phaeochiton* and *Europiella*, including the degree of twisting, closely spaced sclerotized ridges on the lateral strap, two apical blades, location and shape of the secondary gonopore, and the C-shaped sclerotized band. The elongate head, color pattern, vestiture of dorsum, and relatively large, apically free pulvilli are also in accordance with the placement of *Chlorillus* within Oncotyline.

**Compsidolon** Reuter, 1899 (Palearctic; 57 spp.)

This genus has a long and varied history concerning its circumscription and division into subgenera. *Compsidolon* sensu lato is currently not monophyletic and the same seems to be true for three of the four subgenera recognized by Wagner. Additional data are clearly needed

to determine the monophyly of the recognized subgenera and to circumscribe a monophyletic group. It would be helpful to have sequence data for a sample of species to test the validity of the placement of *Compsidolon* within the Oncotylinea as well as the monophyly of the group.

***Crassomiris*** Weirauch, 2006b (Western Nearctic; 2 spp.)

See Discussion under Oncotylinea.

***Damioscea*** Reuter, 1883 (Palearctic: Southern Russia; 1 sp.)

This taxon was related to *Megalocoleus* by Linnavuori (1993b) and we therefore place it in the Oncotylinea (see also comments under *Megalocoleus*).

***Dasycapsus*** Poppius, 1912 (Palearctic: North Africa; 3 spp.)

See comments under *Megalocoleus*.

**\**Europiella*** Reuter, 1909 (Holarctic; 31 spp.)

See Schuh (2004b).

***Eurycolpus*** Reuter, 1875 (Palearctic; 5 spp.)

This taxon was related to *Oncotylus* by Konstantinov (2008a) and we therefore place it in the Oncotylinea.

***Galbinocoris*** Weirauch, 2006a (Southwest Nearctic; 1 sp.)

See Discussion under Oncotylinea.

***Glaucopterum*** Wagner, 1963 (Palearctic; 23 spp.)

Although this genus is not monophyletic, the type species as well as the majority of remaining species are related to *Plagiognathus-Europiella-Phaeochiton* spp. They share several common traits in the structure of endosoma, e.g., characteristic curvature, several closely spaced ridges on the lateral strap, one strap terminating before the secondary gonopore, the apex deeply divided into two branches, and the secondary gonopore located on a membrane. All other characters also seem to be in agreement with the placement of *Glaucopterum* within Oncotylinea. Also see comments on *Phaeochiton*.

**\**Hamatophylus*** Weirauch, 2006a (Nearctic, including Mexico; 1 sp.)

***Hoplomachus*** Fieber, 1858 (Holarctic; 4 spp.)

This taxon, with one species in the Nearctic and three in the Palearctic, has erect bristlelike setae on the dorsum, a prognathous head, and claws with moderately elongate, free pulvilli, attributes that might suggest placement in the Cremnorrhina. Nonetheless, the male genitalia and pretarsus in *Hoplomachus* are very similar to what is seen in *Tinicephalus* and the habitus is similar to some *Plagiognathus* spp. The preponderance of the evidence argues for placement in the Oncotylinea.

***Insulaphylus*** Weirauch, 2006a (Nearctic: Channel Islands; 2 spp.)

See Discussion under Oncotylinea.

***Josifovius*** Konstantinov, 2008 (Nearctic: North Africa; 1 sp.)

We place this taxon in the Oncotylinea based on comparisons made by Konstantinov (2008a). Nonetheless, the endosoma in *Josifovius* and *Dasycapsus* shows similarities with the *Pseudosthenarus* group of genera (see Schuh and Salas, 2011); the African distribution of all these taxa, even if amphiequatorial, might also suggest a possible relationship.

***Kmentophylus*** Duwal, Yasunaga, and Lee, 2010 (Palearctic: Nepal; 1 sp.)

This taxon was related to *Plagiognathus* in its original description. We concur with this

assessment, though suggest that it may show a closer relationship with *Europiella* based on the structure of the endosoma. We therefore place *Kmentophylus* in the Oncotylinea.

***Knighthylinia*** Schaffner, 1978 (Nearctic: Mexico; 1 sp.)

We place this taxon in the Oncotylinea based on its similarity of appearance with some other New World members of the group and the structure of the endosoma.

***Knightopiella*** Schuh, 2004 (Western Nearctic; 1 sp.)

The taxon was originally placed in *Europiella* by Knight (1968). It was placed in *Megalopsallus* in error by Kerzhner and Schuh (1995) and later Schuh (2004b) erected a new genus for the single included species because of the distinctive nature of the male genitalia. No character or combination of characters indicates a clear tribal/subtribal placement; our placement is therefore based largely on geographic association. We note that whereas Schuh (2004b) compared this taxon with *Megalopsallus* and *Europiella*, it is actually most easily confused with species of *Nevadocoris* on the basis of the pale coloration and sericeous vestiture, a comparison that Schuh (2008) failed to make.

***Knightsallus*** Schuh, 2006 (Southwest Nearctic; 1 sp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and is therefore included in the Oncotylinea (see *Phymatopsallus*).

***Leucodellus*** Reuter, 1906 (Nearctic: Central Asia and China; 6 spp.)

This taxon was revised by Li and Liu (2007), who removed prior confusion concerning the generic diagnosis. We place *Leucophylus* in the Oncotylinea based on the similarity of structure of the endosoma with genera such as *Plagiognathus*.

***Lineatopsallus*** T. Henry, 1991 (Nearctic: Southwestern United States, Baja California; 2 spp.)

This genus was used by Henry (1991) as an outgroup for his revision of *Keltonia* and *Pseudatomoscelis*. The spotted dorsum in combination with the elongate phallus and the morphologically elaborate left paramere suggest that *Lineatopsallus* may actually be most closely related to the *Phymatopsallus* group of genera. We therefore place the taxon in the Oncotylinea.

***Litoxenus*** Reuter, 1885, (Eastern Palearctic; 1 sp.)

This taxon was last documented in the key by Kerzhner (1964) to the Heteroptera of the European USSR. The bugs are small, pale colored; the dorsum is covered with short, reclining black setae; the head is weakly exerted from the pronotum; the appendages are relatively short; and the basally broadened of claw is of the *Macrotylus* type and has a long free pulvillus. The endosoma as illustrated by Kerzhner (1964) is small, broadened basally, and with a single apical spine. Although the claw structure might suggest a relationship with the Cremonorrhina, we place *Litoxenus* in the Oncotylinea because the preponderance of the evidence, including the overall body proportions, head structure, coloration, and pretarsal structure, suggests a relationship with *Acrotelus*. The endosoma in both genera is in the form of a simple, short C-shaped tube terminating with an oval secondary gonopore, *Litoxenus* differing from *Acrotelus* by its possession of a single apical blade.

***Maculamiris*** Weirauch, 2006a (Nearctic; Channel Islands, Baja California; 2 spp.)

We place this taxon in the Oncotylinea because of its similarity of appearance with other small red Phylinae from the southwestern United States. See also discussion under Oncotylinea.

***Megalocoleus*** Reuter, 1890 (Western Palearctic; 17 spp.)

In his revision of *Megalocoleus*, Matocq (2004; see also Matocq and Pluot-Sigwalt, 2012) commented on its close relationship with *Amblytylus*, *Dasycapsus*, and *Tinicephalus*. Although the relationship of *Megalocoleus* with the last two taxa may be valid, we argue for the placement of *Amblytylus* in the Cremnorrhina, based on the analyses of Menard et al. (2013).

***Malacotes*** Reuter, 1878 (Western Palearctic; 5 spp.)

This taxon was last treated by Wagner (1975), who placed it in his *Plagiognathus* group. The structure of the endosoma with two apical blades and other attributes have led us to concur with Wagner's judgment.

***Marrubiocoris*** Wagner, 1970 (Palearctic: North Africa; 1 sp.)

This taxon was placed in the *Plagiognathus* group by Wagner (1975), a position that we maintain based on the structure of the endosoma.

***Moiseevichia*** Schuh, 2006 (Ethiopian: South Africa; 2 spp.)

See comments under *Stoebea* below.

***Nanopsallus*** Wagner, 1952 (Southwestern Palearctic; 1 sp.)

The male genitalia of *Nanopsallus* were illustrated by Wagner (1975). The single recognized species is known to feed on *Cirsium* (Asteraceae) in the eastern Mediterranean and Asia Minor. Although the general aspect of the taxon is very much like that of some *Megalopsallus* spp., male genitalic structure as well as characters of external morphology clearly relate the genus with *Compsidolon* sensu stricto, and the type species in particular. Also see comments under *Compsidolon*.

***Neopsallus*** Schuh and Schwartz, 2004 (Western Nearctic; 1 sp.)

We place this taxon in the Oncotyline because of several features it shares with genera such as *Oligotylus*, including the dense covering of woolly setae on the dorsum. The endosoma is unique among western North American taxa; the pulvilli are adnate to and cover nearly the entire ventral surface of the claw.

**\**Occidentodema*** T. Henry, 1999 (Western Nearctic; 3 spp.)

See discussion under *Americodema*.

**\**Oligotylus*** Van Duzee, 1916 (Western Nearctic; 15 spp.)

See Schuh (2000a).

***Omocoris*** Lindberg, 1930 (Palearctic; 3 spp.)

This taxon was recently revised by Konstaninov (2008a), who related it to *Oncotylus* and *Eurycolpus*. On that basis we place *Omocoris* in the Oncotyline. The alary sexual dimorphism in *Omocoris* is virtually unique within nonmimetic members of the Phylinae, the females being reminiscent of members of the Halticini, such as *Dimorphocoris* Reuter and *Compositocoris* Schwartz, Schuh, and Tatarnic. The green coloration, at least in *O. euryophthalmus* Carapezza, is also unusual in the Phylinae.

***Oncotylicidea*** Wagner, 1965 (Palearctic: Turkey; 1 sp.)

We place this taxon in the Oncotyline because of the similarity of structure of the endosoma with other members of the group such as *Plagiognathus*.

**Oncotylus** Fieber, 1858 (Holarctic; 20 spp.)

This taxon has been placed in the Phylini by all modern authors, with only Wagner (e.g., 1975) placing it in a distinct genus group. Because *Oncotylus* was not part of the sample of Menard et al. (2013) our arguments for its tribal/subtribal placement must be based on morphology alone. Nonetheless, *Oncotylus* shares attributes in common with many *Plagiognathus* species, including body form, frequently black-spotted tibiae, a single type of pubescence on the dorsum (always dark in *Oncotylus*; sometimes mixed with sericeous setae in *Plagiognathus* spp.), and feeding on annual plant species, although many *Plagiognathus* spp. are known to breed on perennials and woody plants. The single species of *Oncotylus* recorded from the western Nearctic, *Oncotylus guttulatus* Uhler, is in need of additional study to determine whether it is congeneric with the type, *O. punctipes* Reuter, from the Palearctic.

**Opisthotaenia** Reuter, 1901 (Palearctic; 3 spp.)

We place this taxon in the Oncotyline because of the similarity of appearance with species of *Phyllopiidea* from the Nearctic, including similarity of structure of the endosoma, and its resemblance to *Hoplomachus* and *Thermocoris* (Seidenstücker, 1968) in the Palearctic. *Phyllopiidea* spp. breed on *Artemisia* spp. (Asteraceae) whereas *Opisthotaenia* spp. breed on the Boraginaceae.

**Oreocapsus** Linnavuori, 1975 (Palearctic: North Africa, Yemen; 7 spp.)

Members of this taxon have an elongate endosoma with two short apical spines of a type frequently seen in the Oncotyline. We therefore place *Oreocapsus* in that subtribe.

**Parachlorillus** Wagner, 1963 (Palearctic: Mediterranean; 2 spp.)

We place this taxon in the Oncotyline based on its apparent relationship with *Chlorillus* and its possession of attributes relating it to the *Plagiognathus* group of genera.

**\*Parapsallus** Wagner, 1952, **revised status** (Palearctic; 1 sp.)**\*Parapsallus vitellinus** (Scholtz, 1847), **revised combination**

This taxon has been placed in *Plagiognathus* by some authors (e.g., Schuh, 2001) because of the similarity of structure of the endosoma with two elongate, flattened apical blades, but the analyses of Menard et al. (2013) placed it in a distinct lineage within the Oncotyline.

**Paredrocoris** Reuter, 1878 (Palearctic: Southern Russia, Iran; 5 spp.)

Members of this taxon occur primarily in southern Russia. Those with known hosts feed on *Euphorbia* spp. The general appearance is that of some western North American *Plagiognathus* spp. and the structure of the male genitalia would appear to be concordant with that view. We therefore place *Paredrocoris* in the Oncotyline.

**Phaeochiton** Kerzhner, 1964 (Palearctic; 3 spp.)

We place this taxon in the Oncotyline because of the similarity of structure of the endosoma with that found in *Plagiognathus* and *Europiella*.

**\*Phallospinophylus** Weirauch, 2006 (Western Nearctic; 1 sp.)**\*Phyllopiidea** Knight, 1919 (Western Nearctic; 2 spp.)**\*Phymatopsallus** Knight (Western Nearctic, incl. northern Mexico; 5 spp.)

Of those genera that Schuh (2006a) treated as part of the *Phymatopsallus* group, Menard et al. (2013) were able to include sequence data for this taxon, which placed it in the Oncotyline.



***Piceophylus*** Schwartz and Schuh, 1999 (Eastern Nearctic; 1 sp.)

We place this taxon in the Oncotylinea based on the conifer-feeding habits and the similar type of sexual dimorphism seen in the *Pinophylus*. The structure of the endosoma does not offer an indication of a close relationship with other genera.

***Pinophylus*** Schwartz and Schuh, 1999 (Nearctic; 3 spp.)

In their original description Schwartz and Schuh (1999) related this taxon to their new genus *Coniferocoris*, which Schwartz (2006) later treated as a junior synonym of *Plesiodema* Reuter. We treat *Pinophylus* as belonging to the Oncotylinea on the basis of the similarity in male genitalic structure with that of *Plesiodema* and the overall arguments presented by Schwartz and Schuh (1999). See also arguments under *Plesiodema* (Oncotylinea).

***Placochilus*** Fieber, 1858 (Palearctic; 2 spp.)

The male genitalic structure in this taxon with the characteristic shape of the apical endosomal blades is typical of many genera placed in the Oncotylinea. Other characters including vestiture and structure of the head and pretarsus argue for placement of *Placochilus* in the Oncotylinea.

**\**Plagiognathus*** Fieber, 1858 (Holarctic; 121 spp.)

See Schuh (2001) for a detailed presentation on this taxon.

***Plesiodema*** Reuter, 1875 (Holarctic; 7 spp.)

The analyses of Menard et al. (2013) placed *Plesiodema* in the Oncotylinea in a clade with *Psallovirus*. Even though the morphology of the endosoma as documented by Schwartz (2006) and Schwartz and Schuh (1999) implies a close relationship with *Pseudophylus* and *Tuxedo* (Leucophopterini: Tuxedoina), the combined analysis—including DNA sequence data—suggests that the structural similarity of the endosoma is the result of convergence. All *Plesiodema* spp. are restricted to the Holarctic and feed on conifers; the Tuxedoina also have a Holarctic distribution, but none of its members are known to feed on conifers.

***Pleuroxonotus*** Reuter, 1903 (Palearctic: Mediterranean to Central Asia; 4 spp.)

Most authors (e.g., Linnavuori, 1971, 1988, Konstantinov, 2008a) have considered *Pleuroxonotus* and *Pronototropis* to be closely related; on the basis of morphology they can be placed in the Oncotylinea. Linnavuori (1971) suggested that both might be related to *Amblytylus* because of the carinate lateral pronotal margin, an idea that does not receive support from the results of Menard et al. (2013).

***Pronototropis*** Reuter, 1879 (Palearctic: Southern Russia; 1 sp.)

See comments under *Pleuroxonotus*.

***Psallodema*** V. Putshkov, 1970 (Palearctic: Central Asia; 4 spp.)

We place this taxon in the Oncotylinea because of its similarity to many species now placed in *Compsidolon*. The endosoma is robust, C-shaped, with a large subapical secondary gonopore and peculiar flattened apical blade.

***Psallomorpha*** Duwal, Yasunaga, and Lee, 2010 (Palearctic: Nepal; 6 spp.)

This taxon has the general appearance of many *Psallus* spp. (Duwal et al., 2010), but the endosoma is elongate, slender, with an elongate apex in the form of a single spine, and the



secondary gonopore is well removed from the apex. Based on the apparent relationship with at least some *Compsidolon* species (F. Konstantinov, personal commun.), we place *Psallomorpha* in the Oncotylinea.

\***Psallovius** T. Henry (Nearctic; 5 spp.)

\***Pygovepres** Weirauch, 2006b (Western Nearctic; 1 sp.)

**Quercophylus** Weirauch, 2006b (Western Nearctic: California; 1 sp.)

See Discussion under Oncotylinea.

**Quernocoris** Weirauch, 2006a (Western Nearctic: California; 1 sp.)

See Discussion under Oncotylinea.

\***Ranzovius** Distant, 1893 (New World; 10 spp.)

This taxon is novel in the Miridae for its habit of living exclusively in spider webs, but based on the analyses of Menard et al. (2013) its relationships are with noncommensal taxa.

**Rhinocapsus** Uhler, 1890 (Eastern Nearctic; 2 spp.)

Examination of the male genitalia in this Ericaceae-feeding group suggests that it is closely related, if not synonymous, with *Plagiognathus* (M. Schwartz, personal commun.).

\***Roburocoris** Weirauch, 2009 (Nearctic: Southwest and Mexico; 4 spp.)

**Rubellomiris** Weirauch, 2006b (Nearctic: California; 3 spp.)

See Discussion under Oncotylinea.

**Rubeospineus** Weirauch, 2006b (Nearctic: Oregon, California, Baja California; 3 spp.)

See Discussion under Oncotylinea.

**Sacculifer** Kerzhner, 1959 (Palearctic: Central Asia, China; 2 spp.)

We place this taxon in the Oncotylinea on the basis of the general appearance of *Sacculifer* spp. with *Plesiodesma*. The endosoma in *Sacculifer* appears to be unique which may draw into question our placement of the taxon.

**Salicopsallus** Schuh, 2006 (Western Nearctic; 2 spp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and we therefore include it in the Oncotylinea.

**Schaffneropsallus** Schuh, 2006 (Nearctic: Southern Mexico; 1 sp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and we therefore include it in the Oncotylinea.

**Sthenaropsidea** Henry and Schuh, 2002 (Eastern Nearctic; 1 sp.)

We are placing this taxon in the Oncotylinea because of the simple vestiture on the dorsum, the small pulvilli, and the similarity of endosomal structure with other members of the subtribe, such as *Americodema*.

**Stenoparia** Fieber, 1870, (Palearctic: Mediterranean to Iran; 1 sp.)

Seidenstücker (1962) compared *Stenoparia* with *Conostethus* and *Pronototropis*. Later, Wagner (1975) mentioned the similarity of endosomal structure in *Stenoparia* and *Conostethus*. *Stenoparia* appears to be most similar to *Pronototropis* in the head structure, body proportions, vestiture, coloration, shape of the claw, degree of pulvillar development, and form of the endosoma (F. Konstantinov, personal commun.). We therefore place *Stenoparia* in the Oncotylinea.

***Stictopsallus*** Schuh, 2006 (Western Nearctic; 1 sp.)

This taxon was placed in the *Phymatopsallus* group of genera by Schuh (2006a) and we therefore include it in the Oncotylinea.

***Stirophyllus*** Eckerlein and Wagner, 1965 (Palearctic: Spain, North Africa; 4 spp.)

Linnavuori (1971) provided a lengthy discussion of this taxon, comparing it with *Taeniophorus* (Nasocorini) and *Amblytylus* (Cremnorrhini: Cremnorrhina). *Stirophyllus* appears to be similar to the latter genus, although differing in the small pulvilli and peculiar serrate subapical lamella of the endosoma. Both genera feed exclusively on grasses. We suggest that the placement of *Stirophyllus* bears further investigation and treat its placement in the Oncotylinea as provisional.

**\**Stoebea*** Schuh, 1974 (Ethiopian: South Africa; 3 spp.)

Schuh (1974) did not illustrate or comment on the structure of the right paramere in the three new species that he included in this genus, saying only that it was typical of the Phylini. Further examination indicates that in fact the right paramere is greatly elongate and covers most of the phallotheca in repose, a situation similar to that seen in the more recently described *Moiseevichia* Schuh from South Africa. These two genera share not only the form of the right paramere, but also the type of brachyptery in the females, the presence of sericeous setae, the pattern of coloration and spotting on the dorsum, and the feeding by all known species on members of the Asteraceae, although in *Moiseevichia* they are not restricted to a single genus as current data suggest is the case for *Stoebea* spp. *Stoebea* differs from *Moiseevichia* in having a single apical spine on the endosoma (Schuh, 1974 : figs. 280, 283, 285), whereas *Moiseevichia* spp. have two apical spines (Schuh, 2006b: fig. 14; Schuh, 2009: fig. 5). We place *Stoebea* and *Moiseevichia* in the Oncotylinea on the basis of the total-evidence analysis of Menard et al. (2013).

***Tapirula*** Carapezza, 1997 (Palearctic: Tunisia; 1 sp.)

Based on the habitus and endosomal illustrations provided by Carapezza (1997) we believe this taxon may be closely related to *Sacculifer*. We therefore place it in the Oncotylinea, because we have placed *Sacculifer* there.

***Thermocoris*** Puton, 1875 (Palearctic: Asia Minor, North Africa; 3 spp.)

We place this Palearctic taxon in the Oncotylinea because of its similarity to *Oncotylus* and other taxa we place in the subtribe.

***Tinicephalus*** Fieber, 1858 (Palearctic; 14 spp.)

See comments under *Megalocoleus*.

***Tragiscocoris*** Fieber, 1861 (Palearctic: Mediterranean; 2 spp.)

We place this taxon in the Oncotylinea because of the similarity of endosomal structure to that seen in *Asciodema*, including the general shape and the flattened, broadly rounded apical blade of the endosoma.

***Vanduzeephyllus*** Schuh and Schwartz, 2004 (Western Nearctic; 1 sp.)

The endosoma of this taxon is similar in structure to that of some *Plagiognathus* spp.; the body form is also reminiscent of *Plagiognathus*. We therefore include this nominal genus in the Oncotylinea.

***Vesperocoris*** Weirauch, 2006a (Western Nearctic: California; 1 sp.)

See Discussion under Oncotylinea.

***Viscacoris*** Weirauch, 2009 (Southwest Nearctic, Mexico; 4 spp.)

We place this Nearctic taxon in the Oncotylinea because of its similarity of structure and appearance with other Nearctic taxa such as *Pygovepres* and *Roburocoris*, which were placed in the classification based on sequence data and morphology. See also Discussion under Oncotylinea.

***Zophocnemis*** Kerzhner, 1962 (Palearctic: Central Asia; 1 sp.)

This taxon has been associated with *Plagiognathus* by most authors (e.g., Kerzhner, 1964). The structure of the male genitalia is reminiscent of *Plagiognathus*, but sufficiently different that Schuh (2001) chose to treat *Zophocnemis* as a distinct genus.

Tribe SEMIINI Knight, 1923 (type genus: *Semium* Knight, 1976)

DIAGNOSIS: Characters uniting this tribe in Menard et al. (2013) include eyes that are parallel to the anterior margin of the pronotum, the relatively small scent gland, and the highly sclerotized ventral sack in females. Additionally, male genitalic characters observed to be consistent with this group are the possession of either a relatively simple, elongate, tubular endosoma with or without a well-developed secondary gonopore, or the endosoma may be relatively broad, flat, and T-shaped with a medial, well-developed, secondary gonopore and lateral straps.

DISCUSSION: This higher taxon was originally proposed to contain only the genus *Semium* Reuter; it was placed in the Orthotylineae by Knight (1923) at the time of its description, as was the type genus by Carvalho (1952, 1958). Our conception of the tribe is much broader than that of Knight (1923), includes two subtribes, and for the first time associates the morphologically unusual *Semium* with a discrete assemblage of other phylinae genera rather than placing it in the omnibus Phylini as done by Schuh (1974, 1995).

Exocarpocorina, **new subtribe** (type genus: *Exocarpocoris* Weirauch, 2007)

DIAGNOSIS: Members of this subtribe share the unique asymmetrical sclerites of the female vestibulum, the morphological elaborations of the posterior wall of the female genitalia, and the horizontally expanded central portion of the left paramere.

DISCUSSION: The analyses of Menard et al. (2013) assigned five Australian genera to this higher taxon. Three of those—*Ancoraphylus*, *Exocarpocoris*, and *Polyozus*—were treated by Weirauch (2007) as closely related on the basis of the distinctive morphology of the male and female genitalia. *Wallabicoris*, has very different male genitalic morphology, but shares similarities of the female genitalic morphology (Weirauch and Schuh, 2011) and DNA sequence data (Menard et al., 2013). The fifth genus sequenced by Menard et al. (2013) belongs to the *Mela-leuroides* group (Schuh and Weirauch, 2010), an assemblage with endosomal morphology with many similarities to what is seen in *Exocarpocoris* and its relatives. The analysis of Weirauch and Schuh (2011) used morphology only for a taxon set differing from that of Menard et al. (2013). We have concluded that the latter analysis is a more accurate representation of relationships because of the large amount of sequence data it contains, and we therefore treat *Xiphoides* and *Xiphoidellus* as more closely related to *Wallabicoris* + *Araucanophylus* than to taxa from South Africa as proposed by Weirauch and Schuh (2011).

This is the only grouping within the Phylinae with a transantarctic distribution. Its diversity is greatest in Australia and New Zealand, with the Australian taxa showing much greater morphological diversity than the New Zealand taxa. The South American taxa placed in Exocarporina are limited in number and are restricted in distribution to Chile and adjacent Argentina. Whereas described diversity in the Leucophoropterini (Menard and Schuh, 2011) and Pilophorini (Schuh and Menard, 2011) in Australia can be judged to be representative of the actual diversity of the fauna, many genera remain to be described from the continent and their tribal assignments remain to be determined. *Campylomma* Reuter (Nasocorini) is widely distributed in the Old World, including Australia, and unlike taxa here placed in the Exocarporina and those that remain to be described, it is virtually novel in not being endemic to the continent. See *Hypseloecus* Reuter, Pilophorini; *Sejanus* Distant, Leucophoropterina.

***Ampimpacoris*** Weirauch and Schuh, 2011 (Neotropical: Northwestern Argentina; 1 sp.)

This taxon was treated as being closely related to *Wallabicoris* by Weirauch and Schuh (2011), and is therefore included in the Exocarporina. *Ampimpacoris* is distinctive within the subtribe in being ant mimetic and showing strong sexual dimorphism.

\****Ancoraphylus*** Weirauch, 2007 (Australian: Australia; 4 spp.)

See comments under *Polyozus*.

***Araucanophylus*** Carvalho, 1984 (Neotropical: Chile; 2 spp.)

This taxon was treated as closely related to *Xiphoides* Eyles and Schuh by Weirauch and Schuh (2011), and is therefore included in the Exocarporina.

***Basileobius*** Eyles and Schuh, 2003 (Australian: New Zealand; 1 sp.)

This taxon is related to *Xiphoides* on the basis of male genitalic structure and therefore is included in the Exocarporina (see also comments under *Xiphoidellus*).

***Chiloephyllus*** Carvalho, 1984 (Neotropical: Chile; 1 sp.)

We place this taxon in the Exocarporina based on the endosoma forming a single coil as also seen in *Araucanophylus* and its occurrence in southern Chile. Although this taxon was not discussed by Weirauch and Schuh (2011), we believe many of the arguments they made for the relationships of *Araucanophylus* also apply to *Chiloephyllus*.

***Cyrtodiridius*** Eyles and Schuh, 2003 (Australian: New Zealand; 1 sp.)

This taxon is related to *Xiphoides* on the basis of male genitalic structure and therefore is included in the Exocarporina (see also comments under *Xiphoidellus*).

\****Exocarporis*** Weirauch, 2007 (Australian: Australia; 3 spp.)

See comments under *Polyozus*.

***Gonzalezinus*** Carvalho, 1981 (Neotropical: Central Chile; 2 spp.)

This genus shares many of the attributes found in *Araucanophylus*. We are therefore assigning it to the Exocarporina, on the basis of morphology and geography.

***Halormus*** Eyles and Schuh, 2003 (Australian: New Zealand; 1 sp.)

This taxon is related to *Xiphoides* on the basis of male genitalic structure and is therefore included in the Exocarporina (see also comments under *Xiphoidellus*).

***Harpagophylus*** Schuh and Weirauch, 2010 (Australian: Australia; 5 spp.)

See comments under *Melaleucoides*.

**Jiwarli** Soto and Weirauch, 2007 (Australian: Australia; 4 spp.)

On the basis of morphology Schuh and Weirauch (2010) treated this taxon as a member of the clade containing *Melaleuroides* and *Polyozus*. We therefore include *Jiwarli* in the Exocarpocorina.

**Leptidolon** Reuter, 1904, (Australian: Australia; 1 sp.)

This taxon has remained unstudied since its original description. The holotype is deposited in the Museum Victoria. Our initial examination of the specimen indicates that *Leptidolon* is a member of the Exocarpocorina.

**Mecenopa** Eyles and Schuh, 2003 (Australian: New Zealand; 1 sp.)

Related to *Xiphoides* on the basis of male genitalic structure and therefore included in the Exocarpocorina (see also comments under *Xiphoidellus*).

\***Melaleuroides** Schuh and Weirauch, 2010 (Australian: Australia; 18 spp.)

Along with *Harpagophylus* and *Thryptomenomiris*, the taxon was treated as related to *Polyozus* and *Jiwarli* Soto and Weirauch by Schuh and Weirauch (2010) on the basis of morphology, including the similarities in the endosoma seen in *Melaleuroides* and *Polyozus*. We therefore include this taxon in the Exocarpocorina. *Melaleuroides*, *Harpagophylus*, and *Thryptomenomiris* are novel among Australian taxa in having fleshy recurved parempodia of a type similar to that seen in *Moissonia* and some other taxa within the Phylinae.

**Pimeleocoris** Eyles and Schuh, 2003 (Australian: New Zealand; 3 spp.)

This taxon is related to *Xiphoides* on the basis of male genitalic structure and therefore is included in the Exocarpocorina (see also comments under *Xiphoidellus*).

\***Polyozus** Eyles and Schuh, 2003 (Australian: New Zealand; 9 spp.)

Along with *Ancorophylus* and *Exocarpocoris*, this taxon was treated as a member of a monophyletic group by Weirauch (2007) on the basis of male and female genitalic morphology.

**Thryptomenomiris** Schuh and Weirauch, 2010 (Australian: Australia; 2 spp.)

See comments under *Melaleuroides*.

\***Wallabicoris** Schuh and Pedraza, 2010 (Australian: Australia; 37 spp.)

**Xiphoidellus** Weirauch and Schuh, 2011 (Australian: Australia; 6 spp.)

*Xiphoidellus* was related to *Wallabicoris* by Schuh and Pedraza (2010) on the basis of morphology and 16S mDNA sequence data. It was treated as related to *Araucanophylus* by Schuh and Weirauch (2010) on the basis of morphology. Because of the overlapping schemes of relationships in these papers, we treat *Xiphoidellus* as belonging to the Exocarpocorina.

**Xiphoides** Eyles and Schuh, 2003 (Australian: New Zealand; 6 spp.)

*Xiphoides* is related to *Xiphoidellus* and *Araucanophylus* on the basis of male genitalic structure and we therefore include it in the Exocarpocorina (see also comments under *Xiphoidellus*).

Subtribe Semiina Knight, 1923 (type genus: *Semium* Reuter, 1976)

DIAGNOSIS: Genera in this subtribe are unique in having relatively derived forms of the male genitalia and relatively typical phylinae external morphologies or an extremely simplified, tubular endosoma and relatively autapomorphic external morphology relative to other Phylinae.



nae, such as a reduced, slitlike scent gland and thickened, rodlike parempodia. Females have a relatively wide cuneus compared to other Phylinae (Menard et al., 2013), associated with reduced wings if forewings are present at all in females.

DISCUSSION: This grouping is based on the analysis of Menard et al. (2013), which brought together a substantial amount of sequence data for members of a group of taxa that had for the most part been of problematic placement because of their varied facies and disparate distributions.

\***Criocoris** Fieber, 1858 (Holarctic; 13 spp.)

The endosoma in members of this Holarctic genus is structurally simple and not unlike that seen in *Nicholia*.

\***Hoplomachidea** Reuter, 1909 (Western Nearctic; 1 sp.)

We place this taxon in the Semiini, Semiina based on the analytic results of Menard et al. (2013). This taxon nonetheless shares some attributes with the Cremnorrhina, such as the expanded base of the claw with a somewhat enlarged free pulvillus extending from it, the strongly projecting frons and clypeus, the erect black setae on the dorsum, and the rather heavily sclerotized endosoma. We have concluded that even though the name and some morphological attributes suggest an affinity with *Hoplomachus*, these two taxa are not members of the same clade with the Phylinae.

\***Karoocapsus** Schuh, 1974 (Ethiopian: South Africa; 8 spp.)

Schuh (1974) placed this taxon in the Leucophoropterini and the basis of its simple endosoma and mimetic characteristics. The analysis of Menard et al. (2013), on the basis of DNA sequence data and morphology, consistently groups *Karoocapsus* with *Tytthus*, which Schuh (1974) also placed in the Leucophoropterini, but in the analysis of Menard et al. (2013) neither of those taxa group with *Leucophoptera*, *Sejanus*, and other members of the Leucophoroptera.

**Monocris** V. Putshkov, 1974 (Palearctic: Iraq, Turkmenistan; 2 spp.)

This taxon was originally described from Turkmenistan and recorded as feeding on *Salsola* (Chenopodiaceae). Linnavuori (1988) described a second species from Iraq as also feeding on Chenopodiaceae. *Monocris* has the anterior margin of the pronotum somewhat less strongly and uniformly depressed than in *Semium* and *Nicholia*, but the scent-gland evaporatory area is slitlike as in both of those genera, a condition not seen elsewhere in the Phylinae. Also, the endosoma is simple, as is the case in both *Nicholia* and *Semium*. We therefore place *Monocris* in the Semiina.

**Monospatha** Eyles and Schuh, 2003

This monotypic New Zealand taxon was originally placed in the Phylini. We transfer it to the Semiina based on the similarity of structure of the endosoma to that seen in *Pseudostenarus*, with an apical secondary gonopore and a free "arm" extending from the base of the endosoma.

**Myrmicopsella** Poppius, 1914, **incertae sedis** (Ethiopian: Madagascar, 1 sp.)

Schuh (1974) placed *Myrmicopsella* in the Leucophoropterini, indicating that this taxon known only from the holotype female was probably most closely related to *Karoocapsus*. *Myrmicopsella* was subsequently placed in the Phylini incertae sedis by Menard and Schuh

(2011). We transfer *Myrmicopsella* to the Semiini, Semiina on the assumption that it is indeed related to *Karoocapsus*, as the habitus suggests, but nonetheless treat that placement as incertae sedis.

**Nicholia** Knight, 1929 (Nearctic: American Southwest and Mexico; 2 spp.)

*Lapazphylus* Carvalho and Costa, 1992, **new synonymy**

We here place *Nicholia* Knight in the Semiina because of the very similar slitlike structure of the evaporatory area of the metathoracic scent gland to that seen in *Semium* and the apparent lack of any “mushroom bodies” to serve as an evaporatorium. The anterior margin of the pronotum in *Nicholia* is not nearly as broad and flat as that in *Semium*, but is nonetheless weakly expanded.

*Lapazphylus* was placed in the Hallodapini by its authors (Carvalho and Costa, 1992) because of their perception that it possessed a pronotal collar. Our comparison of the illustrations of *Lapazphylus lapazensis* Carvalho and Costa, provided as part of the original description, and of genitalic and other morphology of a congener from Durango, Mexico, with specimens of *Nicholia eriogoni* Knight indicates that *Lapazphylus* is synonymous with *Nicholia* **new synonymy**; *Lapazphylus* possesses the weak pronotal collar, the slitlike scent-gland opening, and the elongate, slender endosoma with a very small, slender, secondary gonopore.

\***Parapseudosthenarus** Schuh, 1974 (Ethiopian: South Africa; 3 spp.)

See comments under *Pseudosthenarus*.

\***Pseudosthenarus** Poppius, 1914 (Ethiopian: Namaqualand; 11 spp.)

Schuh (1974) placed this taxon and its sister group *Parapseudosthenarus* Schuh (Schuh and Salas, 2011) in the Phylini. The nondescript general morphology, and the novel structure of the endosoma and left paramere, gave no clear indication of more restricted affinities. The analyses of Menard et al. (2013) consistently group these two genera and also groups them with several other genera with distributions both inside and outside of South Africa.

**Rakula** Odhiambo, 1967 (Ethiopian: Gabon; 1 sp.)

Odhiambo (1967) compared *Rakula* with *Psallus*, *Sthenarus*, and *Pseudosthenarus*. Linnavuori (1993a) compared it with *Atractotomus*. We believe the most convincing argument for relationships of *Rakula* is with the *Pseudosthenarus* group of genera (see Schuh and Salas, 2011) because of the overall black coloration, the presence of shining setae on the dorsum, the short labium, and the form of the endosoma in the male, which based on illustrations from Odhiambo (1967) is short, flat, and has a large apical secondary gonopore. If our hypothesis is correct, then the inflated second antennal segment is simply autapomorphic in the *Rakula*.

\***Semium** Reuter, 1876 (Nearctic: Southwest United States and Mexico; 5 spp.)

Knight (1923) erected a new tribe to contain only *Semium* and placed it in the Orthotylinae (Orthotylini) on the basis of parempodial structure. Kelton (1959) moved *Semium* to the Phylinae: Phylini on the basis of male genitalic structure. The anterior pronotal margin is depressed and collarlike, the metathoracic scent gland is slitlike without an evaporatory area, and the endosoma is simple, similar to the situation seen in *Nicholia* and *Monocris*.

***Thoth*** Linnavuori, 1993a, (Ethiopian: West Africa; 5 spp.)

This taxon was said to be related to *Yotvata* and *Comsidolon* by Linnavuori (1993a), who divided *Thoth* into three species groups based on the form of the endosoma and the left paramere. Considering the extreme variation seen in these structures we suggest that the group might not be monophyletic. We are also not convinced that the comparisons with *Compsidolon* and *Yotvata* are particularly useful in understanding the tribal placement of *Thoth*, because we have placed these two genera in different subtribes. The structure of the endosoma in *T. mundane* Linnavuori would appear to suggest a relationship with *Darfuromma*, whereas the tube-shaped endosoma with the apically placed secondary gonopore, modified left paramere, coloration, and vestiture of the type species, *T. punctipes* Linnavuori, may indicate relation to *Pseudosthenarus*. On this basis, we place *Thoth* in the Semiina.

\****Tytthus*** Fieber, 1864 (Cosmopolitan; 24 spp.)

See comments under *Karoocapsus*. The revision of Henry (2012) presented up-to-date information on the taxonomy and biology of this taxon, including the description of several new species.

Tribe PILOPHORINI Douglas and Scott, 1876 (type genus: *Pilophorus* Hahn, 1826)

DIAGNOSIS: Parempodia recurved, either capitate or distinctly fleshy; vestiture with usually at least some elongate-lanceolate setae, these frequently dense and sometimes grouped into distinct patches, and the posterior margin of the vertex upturned (Menard et al., 2013).

DISCUSSION: This taxon was the subject of a morphology-based phylogenetic analysis by Schuh (1991). The concept of Pilophorini, as presented here, is broadened beyond that of Schuh (1974, 1991) to include *Lasiolabops* Poppius and *Dilatops* Weirauch. This concept is supported by the total-evidence analysis of Menard et al. (2013). See also discussion of *Lalyocoris* Linnavuori (Phylini, Phylina).

***Alepidiella*** Poppius, 1914 (Eastern Nearctic; 1 sp.)

***Aloea*** Linnavuori, 1975 (Ethiopian/Arabian Peninsula; 8 spp.)

***Dilatops*** Weirauch, 2006c, (Australia, New Caledonia; 2 spp.)

We are placing *Dilatops* in the Lasiolabopina in recognition of its similarities with *Lasiolabops* listed by Weirauch (2006c), including the apparent association of both groups with the genus *Ficus* (Moraceae).

***Druthmarus*** Distant, 1909 (Oriental; 4 spp.)

***Ethatractus*** Linnavuori, 1975 (Ethiopian; 3 spp.)

***Hypseloecus*** Reuter, 1891 (Paleotropical/Australian; 24 spp.)

***Lasiolabops*** Poppius, 1914 (Paleotropical; 4 spp.)

This taxon was placed in the Leucophoropterini by Schuh (1984) and Weirauch (2006). The analysis of Menard et al. (2013) placed it as a member of the Pilophorini. The form of the flattened lanceolate setae corroborates this placement, although the sculpture of the setae differs from that seen in all other Pilophorini, as does the form of the parempodia and the endosoma.

*Neoambonea* Schuh, 1974 (Ethiopian; 7 spp.)

*Parambonea* Schuh, 1974 (Ethiopian: South Africa; 1 sp.)

*Parasthenaridea* Miller, 1937 (Oriental: Malaya; 1 sp.)

*Pherolepis* Kulik, 1968 (Eastern Palearctic; 7 spp.)

*Pilophorus* Hahn, 1826 (Holarctic/Oriental; 106 spp.)

*Pseudambonea* Schuh, 1974 (Ethiopian: South Africa; 1 sp.)

*Randallophorus* Henry, 2013 (Neotropical: Paraguay; 1 sp.)

This taxon appears to be closely related to *Sthenaridea* based on general appearance and the structure of the endosoma.

*Spinolosus* Zou, 1985 (Oriental: Southern China; 1 sp.)

*Sthenaridea* Reuter, 1885 (Circumtropical; 21 spp.)

Tribe LEUCOPHOROPTERINI Schuh, 1974 (type genus: *Leucophoropera* Poppius, 1921)

DIAGNOSIS: Diagnosed by the second antennal segment being significantly thicker than antennal segments 3 and 4, the relatively wide vertex in females, the presence of ridges on the dorsal surface of the phallosome, the vestibulum of the female genitalia lying flat against the rami and not projecting anteriorly, and the triangular shape of the vestibular plates.

DISCUSSION: Arguments for the monophyly of the broadened concept of Leucophoropterini as presented here come from the total-evidence POY analysis of Menard et al. (2013).

Tuxedoina, **new subtribe** (type genus: *Tuxedo* Schuh, 2001)

DIAGNOSIS: Taxa in this lineage share morphological similarities in the endosoma, having a relatively simple, small, S shape, and with overlapping of the lateral straps at the apex, a weakly developed secondary gonopore, the left and right parameres being of nearly equivalent size, and the base of the ovipositor having a dorsal extension to the posterior wall in females.

DISCUSSION: The total-evidence POY analysis of Menard et al. (2013) indicates that the similarity of appearance and coloration of members of the Tuxedoina and Leucophoropterina is not simply superficial but the result of a common progenitor.

*Ephippicoris* Poppius, 1912 (Palearctic: Iran, Turkey, Turkestan; 1 sp.)

This taxon was most recently mentioned in the literature by Linnavuori (2010) when he recorded it from Iran as occurring on *Populus*. We have examined specimens originally from the collections of the Zoological Institute, St. Petersburg. They have attributes of coloration, sexual dimorphism, and male genitalic morphology found in *Tuxedo*, and we therefore place *Ephippicoris* in the Tuxedoina.

\**Pseudophylus* Yasunaga, 1999, Palearctic: Japan, Eastern Russia; 1 sp.)

\**Tuxedo* Schuh, 2001 (Western Nearctic; 7 spp.)

Members of this taxon closely resemble species of *Sejanus* (Leucophoropterina) (Schuh, 1984, 2004a; Menard and Schuh, 2011), in size, coloration, and the rather simple structure of the endosoma.

Subtribe Leucophoroptera Schuh, 1974 (type genus: *Leucophoroptera* Poppius, 1921)

DIAGNOSIS: The Leucophoroptera is united by the C-shaped phallosome, the lack of sclerotization between the dorsal and ventral labiate plates, the presence of an anterior sclerite on the entrance of the vestibulum, and the extremely small size of the male genitalia relative to the size of the abdomen.

DISCUSSION: Synapomorphies hypothesized for the Leucophoroptera sensu Schuh (1974) and reviewed in Menard and Schuh (2011) are those listed above as diagnostic and are present in the majority of the members of this subtribe. The possession of a relatively small endosoma and small pygophore relative to the size of the abdomen is not unique to members of the Leucophoroptera, but is also found in the Pilophorini, the sister group to the Leucophoroptera (Menard et al., 2013). Members of some genera in the Leucophoroptera (*Ausejanus* Menard, *Aitkenia* Carvalho and Gross) have an anterior sclerite on the surface of the vestibulum, which is not present in any other lineages of Phylinae thus far examined.

- Abuyogocoris* Schuh, 1984 (Oriental: New Guinea; 4 spp.)  
*Aitkenia* Carvalho and Gross, 1982 (Australian: Australia; 2 spp.)  
*Arafuramiris* Schuh, 1984 (Oriental: New Guinea; Northern Australia; 7 spp.)  
*Ausejanus* Menard and Schuh, 2011 (Australian: Australia; 18 spp.)  
*Austrodapus* Menard and Schuh, 2011 (Australian: Australia; 1 sp.)  
*Biomiris* Schuh, 1984 (Oriental: New Guinea; Northern Australia; 6 spp.)  
*Blesingia* Carvalho and Gross, 1982 (Oriental: New Guinea, Solomon Islands; Australian: Australia; 7 spp.)  
*Collessicoris* Carvalho and Gross, 1982 (Australian: Australia; 1 sp.)  
*Ctypomiris* Schuh, 1984 (Oriental: New Guinea, Solomon Islands; 3 spp.)  
*Gulacapsus* Schuh, 1984 (Oriental: New Guinea; Australian: Australia; 4 spp.)  
*Johnstonsonius* Menard and Schuh, 2011 (Oriental: New Guinea; 1 sp.)  
*Leucophoroptera* Poppius, 1921 (Australian: Australia; 5 spp.)  
*Missanos* Menard and Schuh, 2011 (Oriental: New Guinea; 1 sp.)  
*Neaitkenia* Menard and Schuh, 2011 (Australian: Australia; 2 spp.)  
*Neoleucophoroptera* Menard and Schuh, 2011 (Oriental: New Ireland, Solomon Islands; 2 spp.)  
*Papuanimimus* Schuh, 1984 (Oriental: New Guinea; 2 spp.)  
*Papuanmiroides* Menard and Schuh, 2011 (Oriental: New Guinea; 1 sp.)  
*Pseudohallodapocoris* Schuh, 1984 (Oriental: New Guinea; 3 spp.)  
*Sejanus* Distant, 1910 (Oriental/Australian; ~40 spp.)  
*Solomonomimus* Schuh, 1984 (Oriental: Solomon Islands; 1 sp.)  
*Transleucophoroptera* Menard and Schuh, 2011 (Oriental: Philippine Islands; 1 sp.)  
*Trichocephalocapsus* Schuh, 1984 (Oriental: New Guinea; 2 spp.)  
*Waterhouseana* Carvalho, 1973 (Oriental: New Guinea; 2 spp.)



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## INDEX

- Abuyogocoris*, 59  
*Acrorrhinium*, 6  
*Acrotelus*, 44  
*Adelphophylus*, 27  
*Adenostomocoris*, 10  
 Aeolocorini, 5  
*Aeolocoris*, 6  
*Agrametra*, 10  
*Agraptocoris*, 28  
*Aitkenia*, 59  
*Alepidiella*, 58  
*Alloeomimus*, 6  
*Alloeotarsus*, 44  
*Alnopsallus*, 28  
*Aloea*, 58  
*Alvarengamiris*, 28  
*Amazonophilus*, 28  
*Amblytylus*, 22  
*Americodema*, 44  
*Ampimpacoris*, 54  
*Anapsallus*, 28  
*Ancoraphylus*, 54  
*Angelopsallus*, 44  
*Anomalocornis*, 28  
*Anonychiella*, 18  
*Antepia*, 44  
*Aphaenophyes*, 18  
*Arafuramiris*, 60  
*Araucanophylus*, 54  
*Arctostaphylocoris*, 11  
*Arizonapsallus*, 45  
*Arlemiris*, 29  
*Artchawakomius*, 6  
*Asciodema*, 45  
*Aspidacanthus*, 6  
 Atomomophoraria, 10  
*Atomophora*, 11  
*Atomoscelis*, 11  
*Atractotomimus*, 18  
*Atractotomoidea*, 11  
*Atractotomus*, 11  
*Auchenocrepis*, 19  
*Aurantiocoris*, 8  
 Aurillocorini, 5  
*Aurillocoris*, 6  
*Ausejanus*, 60  
*Austrodapus*, 60  
*Austropsallus*, 25  
*Azizus*, 6  
*Badezorus*, 11  
*Basileobius*, 54  
*Beckocoris*, 12  
*Bergmiris*, 12  
*Bibundiella*, 6  
*Bicurvicoris*, 29  
*Biromiris*, 60  
*Bisulcopsallus*, 45  
*Blesingia*, 60  
*Boopidella*, 6  
 Boopidocoraria, 9  
*Boopidocoris*, 12  
*Botocudomiris*, 29  
*Brachyarthrum*, 45  
*Brachyceratocoris*, 22  
*Brachycranella*, 29  
*Brendaphylus*, 19  
*Caiganga*, 12  
*Calidroides*, 22  
 Camptotylaria, 18  
*Camptotylidea*, 12  
*Camptotylus*, 19  
*Camptozorus*, 19  
*Campylomma*, 12  
*Capecapsus*, 25  
*Cariniocoris*, 45  
*Carinogulus*, 6  
*Ceratopsallus*, 45  
*Cercocarpopsallus*, 45  
*Chaetocapsus*, 6  
*Chiloephylus*, 54  
*Chinacapsus*, 12  
 Chlamydatini, 9  
*Chlamydatius*, 13  
*Chlamyopsallus*, 13  
*Chlorillus*, 45  
*Chrysochnoodes*, 19  
*Clapmarius*, 6  
*Cleotomiris*, 6  
*Cleotomiroides*, 6  
 Coatonocapsina, 25  
*Coatonocapsus*, 25  
*Collessicoris*, 60  
*Compsidolon*, 45  
*Compsonannus*, 19  
*Conostethus*, 30  
*Coquillettia*, 22  
*Crassicornus*, 30  
*Crassomiris*, 46  
 Cremnocephalaria, 5  
*Cremnocephalus*, 6

- Cremnorrhina, 21  
 CREMNORRHINI, 21  
*Cremnorrhinus*, 22  
*Criocoris*, 56  
*Ctypomiris*, 60  
*Cyrtodiridius*, 54  
*Cyrtopeltocoris*, 6  
*Dacota*, 22  
*Damioscea*, 46  
*Daretagela*, 30  
*Darfuromma*, 31  
*Dasycapsus*, 46  
*Decomia*, 9  
 DECOMIINI, 8  
*Decomioides*, 9  
*Denticulophallus*, 23  
*Dignaiia*, 31  
*Dilatops*, 58  
*Diocoris*, 6  
*Dominiquella*, 31  
*Druthmarus*, 58  
*Ectagela*, 31  
 Ectagelini, 27  
*Ellacapsus*, 31  
*Eminoculus*, 6  
*Ephippicoris*, 59  
*Eremophylus*, 32  
 Eroticoridae, 5  
*Ethatractus*, 58  
*Ethelastia*, 23  
*Euderon*, 23  
*Eumecotarsus*, 19  
*Europiella*, 46  
*Eurycolpus*, 46  
*Eurycranella*, 20  
 EXAERETINI, 18  
*Excentricoris*, 23  
 Exocarpocorina, 53  
*Exocarpocoris*, 54  
*Farsiana*, 32  
*Formicopsella*, 7  
*Frotaphylus*, 20  
*Galbinocoris*, 46  
*Gampsodema*, 7  
*Gediocoris*, 32  
*Ghazalocoris*, 32  
*Glaphyrocoris*, 7  
*Glaucopterum*, 46  
*Gonoporomiris*, 20  
*Gonzalezinus*, 54  
*Gressittocapsus*, 32  
*Guentherocoris*, 23  
*Gulacapsus*, 60  
*Hadrodapus*, 7  
*Hadrophyes*, 20  
 HALLODAPINI, 5  
*Hallodapomimus*, 7  
*Hallodapus*, 7  
*Halormus*, 54  
*Hamatophylus*, 46  
*Hambletoniola*, 13  
*Harpagophylus*, 54  
*Harpocera*, 23  
 Harpoceridae, 21  
*Helenocoris*, 13  
*Heterocapillus*, 25  
*Hirtopsallus*, 13  
*Hoplomachidea*, 56  
*Hoplomachus*, 46  
*Hyalopsallus*, 20  
*Hypseloecus*, 58  
*Icodema*, 33  
*Ifephyllus*, 7  
*Indatractus*, 33  
*Insulaphylus*, 46  
*Insulopus*, 13  
*Izyaius*, 33  
*Jiwarli*, 55  
*Johnstonsonius*, 60  
*Josifovius*, 46  
*Juniperia*, 33  
*Kapoetius*, 7  
*Karocris*, 13  
*Karoocapsus*, 56  
*Kasumiphylus*, 13  
*Keltonia*, 27  
 Keltoniina, 26  
*Kmentophylus*, 46  
*Knightensis*, 33  
*Knightomiroides*, 13  
*Knightophylina*, 47  
*Knightopiella*, 47  
*Knightopsallus*, 47  
*Laemocoris*, 7  
*Lalyocoris*, 34  
*Lamprosthenarus*, 14  
*Lapazphylus*, 57  
*Larinocerus*, 14  
*Lasiolabopella*, 34  
*Lasiolabops*, 58  
*Lattinophylus*, 14  
*Leaina*, 7  
*Lepidargyrus*, 34  
*Lepidocapsus*, 34

- Leptidolon*, 55  
*Leptomimus*, 7  
*Leptoxanthus*, 34  
*Lestonisca*, 7  
*Leucodellus*, 47  
*Leucophoroptera*, 60  
 Leucophoroptera, 59  
 LEUCOPHOROPTERINI, 59  
*Leutiola*, 23  
*Linacoris*, 7  
*Lindbergopsallus*, 14  
*Lineatopsallus*, 47  
*Lissocapsus*, 7  
*Litoxenus*, 47  
*Liviopsallus*, 35  
*Lopidodenus*, 24  
*Lopsallus*, 14  
*Lopus*, 24  
*Macrotylus*, 24  
*Maculamiris*, 47  
*Malacotes*, 48  
*Malaysiamiris*, 9  
*Malaysiamiroides*, 9  
*Malgacheocoris*, 7  
*Marrubiocoris*, 48  
*Maurodactylus*, 14  
*Mecenopa*, 55  
*Megalocoleus*, 48  
*Megalodactylus*, 20  
*Megalopsallus*, 14  
*Melaleuroides*, 55  
*Mendozaphylus*, 35  
*Millerimiris*, 38  
*Mimocoris*, 8  
*Missanos*, 60  
*Mixtecaminis*, 38  
*Moiseevichia*, 48  
*Moissonia*, 20  
*Monocris*, 56  
*Monospatha*, 56  
*Monosynamma*, 15  
*Myombea*, 8  
*Myrmicomimus*, 8  
*Myrmicopsella*, 56  
*Nanopsallus*, 48  
*Naresthus*, 15  
 NASOCORINI, 9  
*Nasocoris*, 15  
*Natalophylus*, 38  
*Neaitkenia*, 60  
*Neisopsallus*, 15  
*Neoambonea*, 59  
*Neolaemocoris*, 8  
*Neoleucophoroptera*, 60  
*Neophylus*, 15  
*Neopsallus*, 48  
*Nevadocoris*, 15  
*Nicholia*, 57  
*Nigrimiris*, 15  
*Nigrocapillocoris*, 15  
*Nubaia*, 38  
*Occidentodema*, 48  
*Oligobiella*, 15  
 Oligobiellini, 10  
*Oligotylus*, 48  
*Omocoris*, 48  
*Omphalonotus*, 8  
*Oncotyliidea*, 48  
 Oncotyliina, 43  
*Oncotylus*, 49  
*Opisthotaenia*, 49  
*Opuna*, 20  
*Orectoderus*, 24  
*Oreocapsus*, 49  
*Orthonotus*, 39  
*Orthopidea*, 16  
*Pachyxyphus*, 24  
*Pangania*, 8  
*Papuamimus*, 60  
*Papuanmiroides*, 60  
*Parachlorillus*, 49  
*Parafulvius*, 39  
*Paralaemocoris*, 8  
*Paralopus*, 24  
*Parambonea*, 59  
*Parapsallus*, 49  
*Parapsallus vitellinus*, 49  
*Parapseudosthenarus*, 57  
*Parasciodema*, 26  
*Parasthenaridea*, 59  
*Paravoruchia*, 39  
*Paredrocoris*, 49  
*Pastocoris*, 20  
*Phaeochiton*, 49  
*Phallospinophylus*, 49  
*Phaxia*, 16  
*Pherolepis*, 59  
*Phoenicocoris*, 16  
*Phoradendrepulus*, 8  
 Phylina, 27  
 PHYLINI, 26  
*Phylloidea*, 49  
*Phylus*, 39  
*Phymatopsallus*, 49



- Piceophylus*, 50  
 PILOPHORINI, 58  
*Pilophorus*, 59  
*Pimeleocoris*, 55  
*Pinomiris*, 16  
*Pinophylus*, 50  
*Placochilus*, 50  
*Plagiognathidea*, 40  
 Plagiognathina, 43  
*Plagiognathus*, 50  
*Platyscytisca*, 40  
*Platyscytus*, 40  
*Plesiodema*, 50  
*Pleuroxonotus*, 50  
*Podullahas*, 8  
*Polyozus*, 55  
*Pongocoris*, 8  
*Porophoroptera*, 40  
 Pronotocrepini, 21  
*Pronotocrepis*, 24  
*Pronototropis*, 50  
*Pruneocoris*, 16  
 Psallidae, 27  
*Psallodema*, 50  
*Psallomimus*, 16  
*Psallomorpha*, 50  
*Psallopsis*, 20  
*Psallovius*, 51  
*Psallus*, 40  
*Pseudambonea*, 59  
*Pseudatomoscelis*, 27  
*Pseudohallodapocoris*, 60  
*Pseudophylus*, 59  
*Pseudosthenarus*, 57  
*Pygovepres*, 51  
*Quercophylus*, 51  
*Quernocoris*, 51  
*Rakula*, 57  
*Randallopsallus*, 21  
*Ranzovius*, 51  
*Reuteroscopus*, 27  
*Rhinacloa*, 16  
*Rhinocapsus*, 51  
*Ribautocapsus*, 8  
*Roburocoris*, 51  
*Roudairea*, 41  
*Rubellomiris*, 51  
*Rubeospineus*, 51  
*Rubrocuneocoris*, 9  
*Ruwaba*, 8  
*Sacculifer*, 51  
*Salicarus*, 16  
*Salicopsallus*, 51  
*Sasajiophylus*, 41  
*Schaffneropsallus*, 51  
*Schuhistes*, 26  
*Sejanus*, 60  
 Semiina, 55  
 SEMIINI, 53  
*Semium*, 57  
*Shendina*, 24  
*Skukuza*, 8  
*Sohenus*, 8  
*Solenoxyphus*, 17  
*Solomonominus*, 60  
*Somalocoris*, 41  
*Spanagonicus*, 17  
*Spinolosus*, 59  
*Squamophylus*, 17  
*Stenoparia*, 51  
*Sthenaridea*, 59  
*Sthenaropsidea*, 51  
*Sthenaropsis*, 17  
*Sthenarus*, 42  
*Stibaromma*, 42  
*Stictopsallus*, 52  
*Stirophylus*, 52  
*Stoebea*, 52  
*Strophopoda*, 24  
*Syngonus*, 8  
 Systellonotaria, 5  
*Systellonotidea*, 8  
*Systellonotopsis*, 8  
*Systellonotus*, 8  
*Taeniophorus*, 17  
*Tannerocoris*, 17  
*Tapirula*, 52  
*Tapuruyunus*, 17  
*Teleorhinus*, 25  
*Thermocoris*, 52  
*Thoth*, 58  
*Thryptomenomiris*, 55  
*Thymopsallus*, 17  
*Tibiopilus*, 42  
*Ticua*, 25  
*Tijucaphylus*, 18  
*Tinicephalus*, 52  
*Tragiscocoris*, 52  
*Transleucophoroptera*, 60  
*Trevesa*, 42  
*Trichocephalocapsus*, 60  
*Trichophorella*, 8  
*Trichophthalmocapsus*, 8  
*Tunisiella*, 18

- Tuponia*, 21  
Tuponiina, 18  
*Tuxedo*, 59  
Tuxedoina, 59  
*Tytthus*, 58  
*Utopnia*, 25  
*Vanduzeeophylus*, 52  
*Vesperocoris*, 52  
*Villaverdea*, 43  
*Viscacoris*, 53  
*Vitsikamiris*, 8  
*Voruchia*, 18  
*Voruchiella*, 21  
*Wallabicoris*, 55
- Waterhouseana*, 60  
*Waupsallus*, 27  
*Widdringtoniola*, 43  
*Wygomiris*, 8  
Xenocorini, 27  
*Xiphoidellus*, 55  
*Xiphoides*, 55  
*Yotvata*, 21  
*Zakanocoris*, 43  
*Zanchiophylus*, 43  
*Zaratus*, 8  
*Zinjolopus*, 25  
*Zophocnemis*, 53

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