

Phylogeny of the Xeromelissinae (Hymenoptera: Colletidae) Based upon Morphology and Molecules*

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Abstract – We present the results of a combined analysis of 248 morphological characters and sequences from 3 genes for 29 species of Xeromelissinae and 7 outgroup taxa including representatives of the colletid subfamilies Colletinae, Euryglossinae, Hylaeinae, Paracolletinae, and Scrapterinae. The paracolletine genus *Trichocolletes* was used to root the tree. The results agree with most of those obtained in an earlier, entirely morphological analysis. Noteworthy are (1) the paraphyly of *Chilimelissa* in relation to *Xeromelissa*, and (2) the lack of sister group relationship between Hylaeinae and Xeromelissinae. Other than minor rearrangements resulting from swapping adjacent nodes, the only major difference is the placement of one species of *Chilicola*, *C. aenigma*, which no longer groups within *C. (Chilioediscelis)*, but instead appears to be closer to *Xenochilicola*. The influence upon phylogenetic results caused by highly morphologically autapomorphic taxa is discussed.

bee / Colletidae / phylogeny / Neotropical / Xeromelissinae

1. INTRODUCTION

Xeromelissinae is a subfamily of Colletidae of moderate size (approximately 200 species) all of which are restricted to the New World. As the name implies, these bees are generally found in xeric habitats, mostly in temperate areas of southern South America. Xeromelissinae bees are typically small to minute, and generally slender.

The taxonomy of Xeromelissinae has had a complex history, summarized by Packer (2008). No tribal divisions are currently accepted within the subfamily: the previous tribal level classification having been dispensed with by Michener and Rozen (1999).

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There are four currently recognized genera, the phylogenetic relationships among which, according to Packer's (2008) analysis of a large number of morphological characters, are summarized in Figure 1.

Only *Chilicola* has been considered large and/or diverse enough to warrant division into subgenera, of which there are now fifteen. *Chilimelissa*, as commonly recognized (e.g. Michener, 2000) is comparatively speciose and diverse, although no formal subdivision into subgenera has yet been made as phylogenetic analysis of it remains incomplete. *Xenochilicola* comprises three species, and *Xeromelissa* is monotypic and only includes *X. wilmattae* Cockerell. Packer (2008) found *Xeromelissa* to render *Chilimelissa* paraphyletic, and as a consequence proposed a revised generic classification for Xeromelissinae.

The purpose of the present paper is to test Packer's classification of the Xeromelissinae

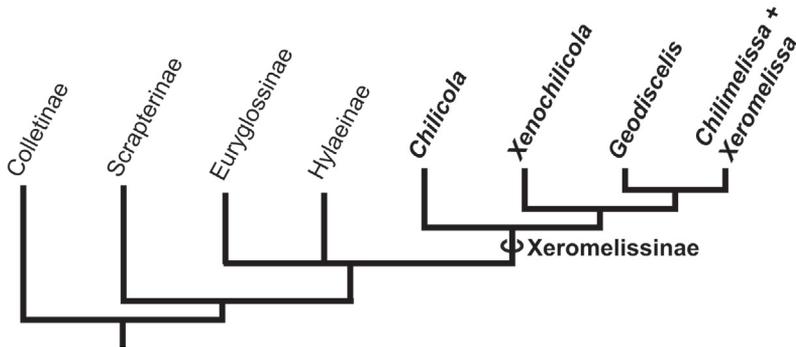


Figure 1. Summary of phylogenetic relationships among xeromelissinae genera according to the analysis of the morphological data set by Packer (2008: Figs. 1 and 2).

by comparing results among morphological, molecular and total evidence analyses.

2. METHODS

2.1. Taxon sampling

Different taxa were available in a form suitable for DNA sequencing than were used in the previous morphological analysis. Consequently, there are fewer representative subgenera of *Chilicola*, but more species of *Chilimelissa*, than in the earlier study and the remaining two genera are represented by only a single species each. *Chilicola* is abbreviated as “Cc.”, *Chilimelissa* as “Cm.”, and *Colletes* as “Co.”. There are also differences in the outgroups used for molecular and morphological analyses. In some cases (such as *Hylaeus affinis* (Smith)), the same outgroups available for DNA were scored for the morphological characters. In others, only congeners could be used, with the result that *Colletes cunicularius* L., *Scapter nitida* Friese, *Euhesma halictoides* (Rayment), and *Callohesma calliopsiformis* (Cockerell) were used for morphology whereas *Co. bicolor* Smith, *S. niger* Lepeletier and Serville, *E. crabronica* (Cockerell), *E. platyrhina* (Cockerell), and *Ca. calliopsella* (Cockerell) were sequenced. Packer (2008) used *Colletes* to root the entire tree (which included representatives of three other subfamilies related to the Xeromelissinae – Hylaeinae, Euryglossinae, and Scapterinae¹). Here

¹The choice of usage of Scapterinae Melo and Gonçalves over Scapterinae Ascher and Engel is discussed in Appendix 1 (online material).

we use the paracolletine genus *Trichocolletes* to root the entire tree, including *Colletes*. This decision is based upon results of a higher level phylogeny of the entire Colletidae (Almeida, 2007).

In instances where only one sex is known for a species that was used in the molecular data set, that sex was coded for the morphological characters and a closely related species was used for the other sex. This was necessary twice: females of *Chilicola tricarinatoides* Packer and males of *Cc. liliana* Packer are unknown. Females of *Cc. tricarinata* Packer and males of *Cc. olmue* Toro and Moldenke, respectively, were used in their place. Similarly, there are a few cases where the species that was sequenced was very closely related to one that was studied morphologically, these taxa were combined in the total evidence analysis. Thus *Cc. unicarinata* Packer and *Cc. chubutense* Packer; *Cc. andina* Toro and Moldenke and *Cc. araucana* Toro and Moldenke; *Cc. mantagua* Toro and Moldenke and *Cc. vicugna* Toro and Moldenke; *Cc. brzoskai* Michener and *Cc. (Oroediscelis) sp.* were used for morphological and molecular data, respectively.

In total, 36 taxa were included in the analyses, 7 representing outgroups. The complete list of taxa and their provenances are provided in Table S1 (online material).

2.2. Morphological characters

We simply scored all exemplars for the same characters as were used by Packer (2008) and do not reiterate the characters or their states here. In cases where additional character states were required for

the different suite of species used, these are described in Appendix 2 (online material). Similarly, we only present the data matrix for those taxa not included in the previous analysis (Appendix 3: online material).

2.3. Choice of molecular data

Molecular data were collected from three gene loci that have been providing robust results for insect phylogenetic studies (Danforth, 1999; Danforth et al., 2004). Elongation factor-1 alpha, F2 copy (EF-1 α) and the large subunit 28S rRNA locus (28S rRNA), regions D1–D5 were chosen to resolve deeper relationships among outgroup and ingroup taxa, and within Xeromelissinae as well. These genes have been used to successfully recover Tertiary to Cretaceous age divergences in bee phylogenies (e.g., Danforth et al., 1999, 2004, 2006a, b). EF-1 α has been the most widely used nuclear protein-coding gene for insect phylogenetics (see Danforth et al., 2004, pp. 310–311 for comments on this gene) The third gene sampled was cytochrome oxidase 1 (COI), a mitochondrial protein-coding gene known for its utility in species-level phylogenetic studies of insects (e.g. Danforth, 1999).

Primer information for each gene is presented in Table S2 (online material).

2.4. DNA extraction, PCR, and sequencing

Genomic DNA was extracted using phenol-chloroform protocols (Doyle and Doyle, 1990, adapted by Danforth, 1999) but without use of liquid nitrogen and RNase. Tissue was taken from the thoracic musculature and/or legs depending on the rarity and size of available specimens. The phenol-chloroform-isoamyl alcohol stage was performed in Phase-Lock Gel® 2.0 mL Eppendorf tubes to facilitate the separation of phenol from the remainder and thus increase the final DNA yield. PCR amplifications of the genes listed above were done for 35 cycles under the following conditions: an initial denaturation at 94 °C for 60 s, followed by 35 cycles under the following conditions: an initial denaturation at 94 °C for 90 s, followed by 35 cycles of denaturation at 94 °C, annealing at 48–58 °C, and extension at 72 °C – specific conditions for each locus amplified are listed in Table S2. Prior to sequencing, most PCR products were gel-purified in

low melting point agarose gels (FMC, Rockland, Maine) overnight at 4 °C. DNA was recovered from gel slices using the Promega Wizard PCR Preps DNA Purification kit. Gel purification was unnecessary for PCR products that produced a single product: both fragments of 28S rRNA and the upstream 1100 bp fragment of EF-1 α . Automatic DNA sequencing was performed using the Applied Biosystems Automated 3730 DNA Analyzer employing Big Dye Terminator chemistry and AmpliTaq-FS DNA Polymerase at Cornell University Life Sciences Core Laboratories Center.

2.5. Data analysis

2.5.1. Alignment

Alignments were generated using similarity calculated at the nucleotide level (“-n”) with DIALIGN 2.2 (Morgenstern, 1999) and corrected manually for obvious alignment errors using MacClade v. 4.08 OSX (Maddison and Maddison, 2005) and Winclada 1.00.08 (Nixon, 2002). For EF-1 α , the honey bee (*Apis mellifera*) sequence was used to establish reading frames and intron/exon boundaries. In cases where multiple sequences were available for the same species, the sequences were merged after being resolved in the same clade in preliminary analyses and resulting partial polymorphisms were kept as such.

2.5.2. Phylogenetic analyses using parsimony

Raw data files were edited with Winclada (Nixon, 2002) and this program was used to export to TNT version 1.1 (Goloboff et al., 2004). Sequence indels were treated as missing data. Ratchet, sectorial, drift and tree fusing with “collapse trees after search” and “find minimal length” set to 10 found the same most parsimonious trees. Symmetrical resampling (Goloboff et al., 2003) was performed on unweighted results with 10 000 iterations and a probability of character weight change (up or down) of 33%. Symmetric resampling allows estimation of group support without being biased by differential character (or character state) weights, which affect results obtained with jackknifing and bootstrapping (see Goloboff et al., 2003). Support is indicated on the cladograms using GC (Group supported/Contradicted). For a particular node, this

Table I. Overview of the datasets.

	Number of characters	Informative characters	Total information	Information/number of characters
EF-1 α exons	1098	267	1416	1.29
EF-1 α introns	586	240	1345	2.30
28S rRNA	1565	135	655	0.38
COI	663	257	1490	2.24
molecular combined	3912	899	4906	1.24
morphology	248	425	2143	8.61
COMBINED	4160	1324	7049	1.68

calculates the difference between the frequency of the group and the most frequently found contradictory arrangement. GC values can vary from -100 to $+100$, representing maximum contradiction (the alternative grouping is favored in all resampled matrices) to maximum support (the original grouping found in all resampled matrices) (Goloboff et al., 2003).

2.5.3. Bayesian phylogenetics

The best-fit model of evolution for each of the four partitions (introns and exons of EF-1 α , 28S rRNA, and COI) was statistically tested. Decision theory (DT), Akaike information content (AIC), and Bayesian information content (BIC) were employed to seek for a balance between model complexity and its suitability for each data partition. Two computer programs were used to shed light on the most appropriate model(s) for the data: (1) DT-ModSel (Minin et al., 2003 – DT model selection) and (2) MrAIC.pl 2.2 (Nylander, 2004 – AIC and BIC).

Bayesian searches were conducted with the serial version of MrBayes 3.1.2 (Altekar et al., 2004; Huelsenbeck and Ronquist, 2005) through the Computational Biology Service Unit at the Cornell Theory Center. Searches were run for 3×10^6 generations on two sets of 10 chains each. The initial 2000 trees were discarded after examining the variation in log likelihood scores over time. Convergence was also assessed using the potential scale factor for the parameters. A partitioned model for the four loci (exons and introns of EF-1 α treated separately) of the concatenated dataset was applied using the following unlinked models: (1) EF-1 α , exons: HKY+I+G; (2) EF-1 α , introns: GTR+I+G; (3) 28S rRNA: SYM+I+G; (4) COI: GTR+G+SSI.

3. RESULTS

3.1. Data set

GenBank accession numbers for all sequences used in this study are presented in Table S3 (Supplementary Materials).

The complete combined matrix contained 4160 characters: 3912 molecular and 248 morphological. The information content (*sensu* Farris) was higher for the morphological component as was the mean relative information of its constituent characters, i.e. information/number of characters (Tab. I). Information of a character is a quantity defined as its maximum number of steps minus its minimum number of steps (this is also the denominator for the retention index [Farris, 1989]).

3.2. Phylogenetic results

The morphological data gave nine most parsimonious trees of length 1215, $ci = 46$ and $ri = 69$ (strict consensus shown in Fig. 2). All of the unresolved nodes are within the clade formed by *Chilimelissa* and *Xeromelissa*. This is not so surprising considering that the main objective of the original morphological data matrix was to assess generic level relationships within the subfamily and subgeneric relationships within *Chilicola* – a more extensive suite of characters for *Chilimelissa* would likely result in greater resolution. The new result is entirely congruent with the previous analysis.

The molecular data yields eight most parsimonious trees with length of 3703 steps, $ci = 49$ and $ri = 62$ (strict consensus shown in Fig. 3). While the relationships among

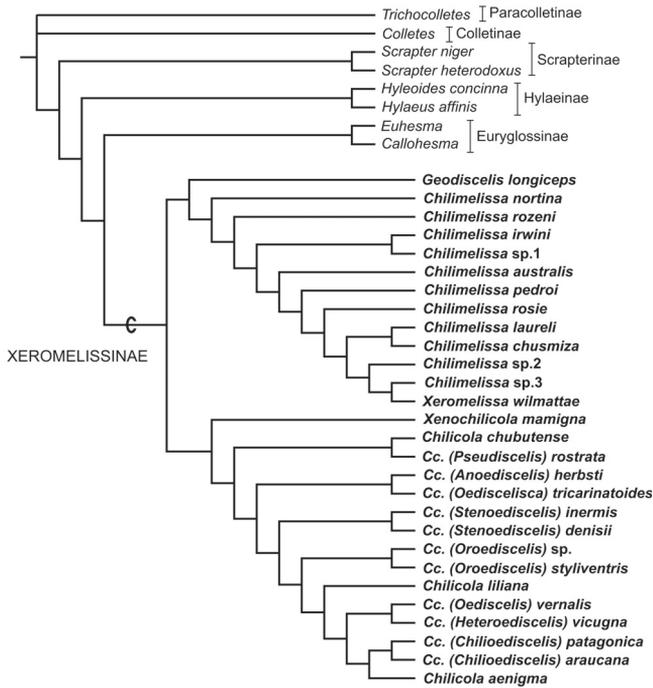


Figure 2. Strict consensus cladogram of the nine most parsimonious trees based on the morphological matrix analyzed with equal weights; tree length = 1215, ci = 46, ri = 69. Species of Xeromelissinae are marked in bold; names of colletid subfamilies sampled as outgroups for the analysis are provided after the species names.

the genera of Xeromelissinae remain congruent with those of the morphological analysis (Fig. 2), the phylogenetic pattern among outgroups and subgenera of *Chilicola* are different. In particular, the molecular data place the euryglossines with the scapterines, which is congruent with previous molecular analyses (Almeida, 2007). *Chilicola* does not appear as monophyletic here, with *Xenochilicola mamigna*, *Chilicola aenigma*, and the clade comprised by the remaining *Chilicola* species forming a trichotomy. Many of the subgenera of *Chilicola* are also in unexpected relationships. Within the clade consisting of *Chilimelissa* and *Xeromelissa*, however, the pattern is congruent with that of the previously published result (Packer, 2008), except that *Cm. rozeni* and *Cm. australis* are now in a clade (along with three species not previously included) separate from other *Chilimelissa*. The Bayesian analysis of the molecular data does not support the monophyly of *Chilicola*

either: *Xenochilicola mamigna* and *Chilicola aenigma* form a clade, sister to the remaining *Chilicola* species (Fig. 4).

The total evidence analysis resulted in three equally most parsimonious trees with length of 4963 steps, ci = 48, ri = 63 (strict consensus shown in Fig. 5). This analysis reverses most of the unusual features of the results from molecular data to less unexpected patterns. The subfamily level result is (Paracolletinae, Colletinae (Scapterinae (Hylaeinae (Euryglossinae + Xeromelissinae)))). Relationships among the genera are identical to that found in the morphological cladistic analysis and the Bayesian molecular analysis, except for the placement of *Cc. aenigma*.

4. DISCUSSION

Our results are largely in good agreement with the purely morphological analysis of

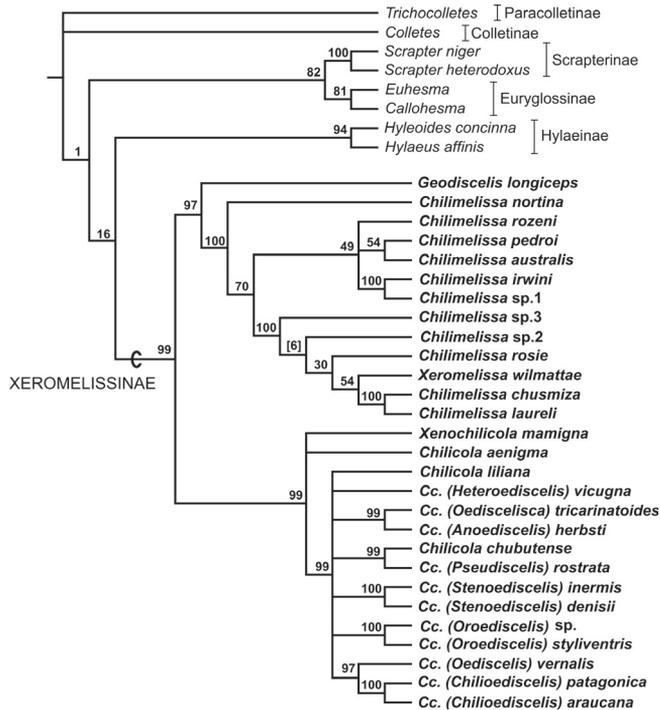


Figure 3. Strict consensus cladogram of the eight most parsimonious trees based on the molecular matrix analyzed with equal weights; tree length = 3703, ci = 49, ri = 62. Numerals represent GC support values calculated from 10000 replications using TNT (P = 33). Species of Xeromelissinae are marked in bold; names of colletid subfamilies sampled as outgroups for the analysis are provided after the species names.

Packer (2008). The relationships among the outgroups in our combined analysis is identical to that found in the earlier study, with one exception: the generic relationships among the ingroup are the same and the subgeneric (*Chilicola*) and species (*Xeromelissa*) phylogenetic patterns are mostly congruent.

The following points of some classificatory import can be stated more firmly than previously on the basis of the combined data:

- (i) Our combined data argue against Engel's (2005) suggestion that Euryglossinae and Hylaeinae are sister groups. A larger study of colletid subfamily relationships (Almeida, 2007), as well as a recent study of family-level relationships in bees (Danforth et al., 2006b), strongly suggests that Xeromelissinae is sister to Hylaeinae.
- (ii) The synonymization of *Chilimelissa* with *Xeromelissa* (Packer, 2008), the latter rendering the former paraphyletic. All

datasets tested (morphological, molecular, and combined), regardless of the kind of phylogenetic analysis performed, strongly support the paraphyly of *Chilimelissa* in relation to *Xeromelissa*. This change is being made formally by Packer (2008).

- (iii) The resurrection of the subgenus *Oediscelisca* from synonymy with *Oediscelis*, from which it is distantly located on the cladogram. It also groups with *Anoediscelis* as in the earlier study and the resurrection is made formally in Packer (2008).
- (iv) The erection of the new subgenus for *Chilicola liliana* Packer, *Cc. olmue* Toro and Moldenke, and their relatives (see Packer, 2008).
- (v) The resurrection of *Heteroediscelis* as a subgenus distinct from *Oediscelis* (Packer, 2008).

The differences between the two sets of results are largely minor, involving swapping

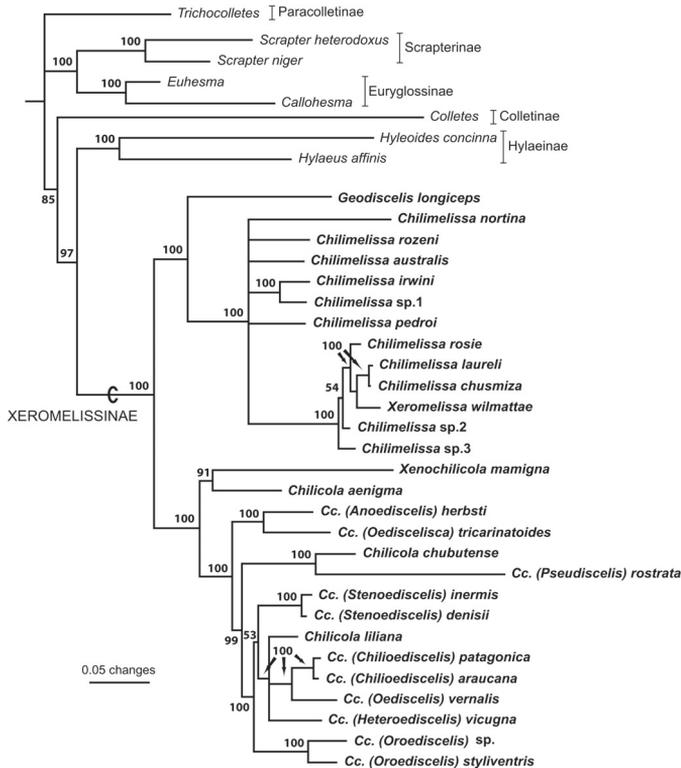


Figure 4. Bayesian majority-rule phylogram based on partitioned model with parameters estimated separately for (1) exons of EF1 α , (2) introns of EF1 α , (3) 28S rRNA, and (4) COI. Branch support is given by posterior probabilities, derived from 58 000 trees; the first 2000 trees were discarded. (harmonic mean: $-\ln L = 22713.90$). Species of Xeromelissinae are marked in bold; names of colletid subfamilies sampled as outgroups for the analysis are provided after the species names.

subgenera of *Chilicola* on adjacent nodes. Thus, the following pairs exchange places in the combined analysis in comparison to the previously published result: *Oediscelis* and *Heteroediscelis*; [*Oediscelisca* + *Anoediscelis*] and [*Cc.chubutense* + *Pseudiscelis*]; *Oroediscelis* and *Cc. liliana* (Fig. 6²). Two aspects of the current result suggest more important differences from Packer's (2008) study. The first is that *Xenochilicola* becomes sister taxon

to *Chilicola* rather than to [*Geodiscelis* + (*Chilimelissa* + *Xeromelissa*)] (Fig. 6). This possibility was mentioned by Packer (2008) who showed that the pattern suggested here was, with the original data, actually only one step longer than the most parsimonious result obtained by morphology alone. The closer relationship of *Xenochilicola* to *Chilicola* had already been suggested by the classification in which Xeromelissinae was subdivided into Chilicolini and Xeromelissini (e.g. Michener, 1995), and by the analysis by Toro and Moldenke (1979).

² *Cc. chubutense* is used here to represent the taxon represented by *Cc. unicarinata* by Packer (2008); and, similarly, *Cc. liliana* corresponds to the taxon represented by *Cc. olmue* by Packer (2008), in each case we use a very closely related species that is available for molecular analysis. The morphological data were recoded as required.

The other major difference is more surprising. Packer (2008) found that *Cc. aenigma* was nested within the subgenus *Chilioediscelis*; the combined data place it as sister

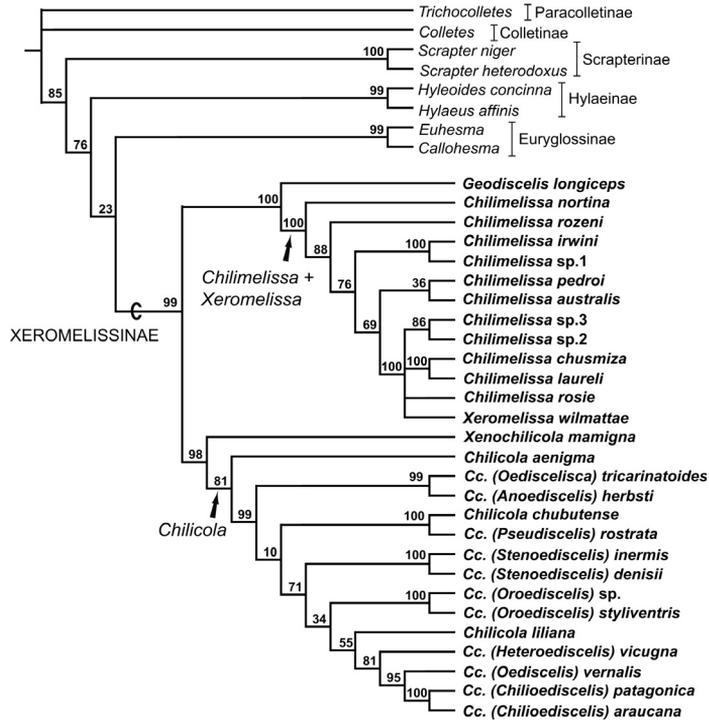


Figure 5. Strict consensus cladogram of the three most parsimonious trees inferred from a combined data set composed of 248 morphological characters and molecular data from three gene loci: EF-1 α , 28S rRNA, and COL.; tree length = 4963, ci = 48, ri = 63. Numerals represent GC support values calculated from 10000 replications using TNT (P = 33). Species of Xeromelissinae are marked in bold; names of colletid subfamilies sampled as outgroups for the analysis are provided after the species names.

to all remaining *Chilicola* (Fig. 2) and the molecular data alone suggest that it is sister to *Xenochilicola mamigna* (Fig. 4). In the morphological analysis (Fig. 2), the grouping of this species within *Cc. (Chilioedisdiscelis)* was supported most strongly by (1) the robust and curved hind tibial spurs; (2) the reduced inner tooth on the hind tarsal claws; and (3) the absence of corbiculate structure of the female sternal scopa. These all appeared as robust synapomorphic evidence for monophyly of the subgenus *Cc. (Chilioedisdiscelis)* including *Cc. aenigma* in the original morphological analysis. However, *Cc. aenigma* is a highly autapomorphic species with numerous unique states, particularly of the male genitalia, that could not be homologized with those of any other exemplar included in the study. Furthermore, it lacked some of the synapomorphies that united *Cc. (Chilioedisdiscelis)* with related

subgenera, particularly those of the male hind leg, which are considerably modified in related taxa but are not sexually dimorphic (other than for the scopal hairs) in *Cc. aenigma*. Assuming the close relationship of this species to *Xenochilicola* to be correct, it is possible to see some similarities between some of the unique states for *Cc. aenigma* and those found to be synapomorphic for the two species of *Xenochilicola* included in the morphological study. Resolution of this discrepancy will require reanalysis of the morphological traits of these bees, gathering additional molecular data and incorporation into the data matrix of a recently discovered Patagonian bee species that superficially appears somewhat intermediate between *Cc. aenigma* and *Xenochilicola* (Genaro and Packer, unpublished data).

These results suggest an interesting contrast to the long branch problem that is well

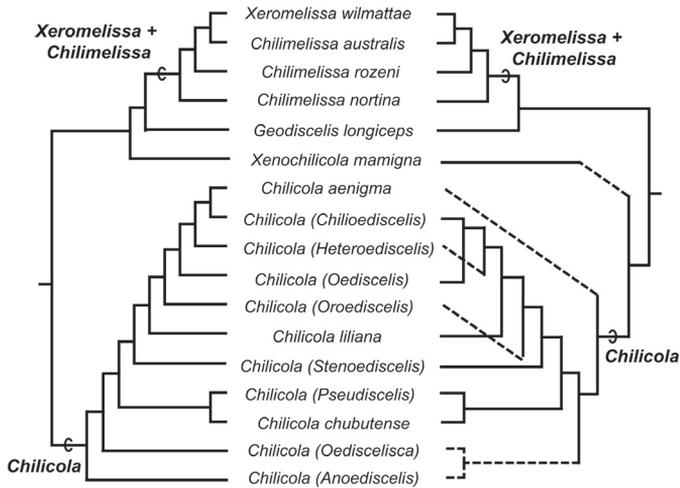


Figure 6. Summaries of phylogenetic hypotheses relationships within Xeromelissinae inferred from a morphological dataset by Packer (2008: Fig. 2): cladogram on the left; and the result of the combined matrix formed by molecular and morphological data of the present study (abridged from Fig. 5): cladogram on the right. Dashed lines represent incongruence between the two trees. Species of *Chilimelissa*, *Geodiscelis*, *Xenochilicola*, and *Xeromelissa* and subgenera of *Chilicola* missing from one of the original studies were removed from the summary cladograms, while preserving the relationships among the remaining taxa. *Chilicola liliana* and *Cc. chubutense* are included in the present study to represent two newly described subgenera (see Packer, 2008 and comments in the text).

known to dog molecular phylogenetic analyses (reviewed by Bergsten, 2005). Here we have a morphologically highly autapomorphic species that came out nested deeply within the phylogeny in, what we now believe to be, the wrong position, as a result of sharing a few convergences. This cautions against accepting the phylogenetic position of morphologically outlying taxa uncritically. An alternative interpretation is that the molecular data is responsible for the attraction of *Cc. aenigma* to be sister of *Xenochilicola* (Figs. 3, 4) or to the base of the *Chilicola*-clade (Fig. 5). The relatively long branch of *Xenochilicola mamigna* (Fig. 4) reflects many autapomorphies, which is the typical cause of the long-branch attraction phenomenon.

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Une phylogénie des Xeromelissinae (Hymenoptera : Colletidae) basée sur les caractères morphologiques et moléculaires.

Colletidae / abeille / phylogénie / Xeromelissinae / région néotropicale

Zusammenfassung – Eine Phylogenie der Xeromelissinae (Hymenoptera: Colletidae),

basierend auf morphologischen und molekularen Merkmalen. Die Xeromelissinae bilden eine Subfamilie der Colletidae. Sie umfasst etwa 200 Art mittelgrosser Bienen, die in ihrer Verbreitung alle auf die Neue Welt bechränkt sind. Wie der Namen bereits besagt, handelt es sich hierbei um Bienen, die im allgemeinen in Trockenhabitaten vorkommen, vor allem im südlichen Südamerika. Xeromelissinen sind typischerweise klein bis sehr klein und im allgemeinen von schlanker Gestalt. In der vorliegenden Arbeit präsentieren wir die Ergebnisse einer kombinierten Analyse von 248 morphologischen Merkmalen und den Sequenzen von drei Genen. Die Analyse umfasst 29 Arten, die alle Genera der Xeromelissinae repräsentieren, sowie 7 Taxa mit Vertretern der Colletiden-Subfamilien Colletinae, Euryglossinae, Hylaeinae, Paracolletinae und Scapterinae als Aussengruppen. Der molekulare Datensatz bestand aus den Sequenzen von zwei Kerngenen (Elongationsfaktor 1 alpha (F2-Kopie) und 28S rRNA) und einem mitochondrialen Gen (Cytochromoxidase 1). Die Wurzel des Stammbaums wurde mithilfe der Merkmale des Genus *Trichocolletes* (Paracolletinae) definiert. Die Ergebnisse stimmen in den meisten Punkten mit den Befunden einer früheren Analyse überein. Bemerkenswert sind (1) die Paraphylie von *Chilimelissa* in Bezug zu *Xeromelissa* und (2) das Fehlen einer Schwestergruppenbeziehung zwischen Hylaeinae und Xeromelissinae. Ausser kleineren Veränderungen in der Stammbaumtopologie, die aus der Verschiebung benachbarter Knotenpunkte herrühren, lag der einzige grössere Unterschied in der Positionierung einer Art des Genus *Chilicola*, *C. aenigma*. Diese gruppierte nicht mehr innerhalb von *C. (Chilioediscelis)*, sondern erschien enger verwandt mit *Xenochilicola*. Neben diesen Ergebnissen diskutieren wir den Einfluss von morphologisch stark autapomorphen Taxa mit wenigen gemeinsamen Merkmalen auf die phylogenetischen Beziehungen mit anderweitig weniger aussergewöhnlichen Arten.

Biene / Colletidae / Phylogenie / neotropisch / Xeromelissinae

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Online Material

APPENDIX 1.

Justification for the use of *Scapterinae* Melo and Gonçalves, 2005

In 2005, two family-group names were proposed to include the African colletid genus *Scapter* Lepeletier and Serville (Ascher and Engel *in* Engel, 2005; and Melo and Gonçalves, 2005; the latter being published approximately two months earlier than the former; according to Ascher and Engel, 2006). *Scapter* used to be traditionally included in Colletinae (*sensu* Michener, 2000) or in Paracolletini (Michener, 1989). Its removal from Colletinae and placement in a subfamily of its own makes the classification more concordant with the accumulating phylogenetic evidence for lack of a close relationship between *Scapter* and remaining paracolletine bees (references in Melo and Gonçalves, 2005; Ascher and Engel *in* Engel, 2005). The two names are spelled differently, which facilitates their distinction: Melo and Gonçalves (2005) used the stem “Scapter-”, whereas Ascher and Engel (*in* Engel, 2005) picked “Scaptr-”.

Based on the Principle of Priority (ICZN, 1999: article 23.1), the name proposed by Melo and Gonçalves (2005) is to be considered the senior synonym. However, Ascher and Engel (2006) claimed that the name based on the stem “Scapter-” is not valid because Melo and Gonçalves did not comply with article 13.1 (ICZN, 1999) in providing an explicit diagnosis for the group. By accepting Ascher and Engel’s (2006) position, *Scapterini* Melo and Gonçalves is to be interpreted as *nomen nudum*. Nevertheless, Melo and Gonçalves (2005) listed various references that indirectly serve for the diagnosis of the group and,

therefore, comply with Article 13.1.2 of the Code (ICZN, 1999).

Because we believe the interpretation of this matter remains contentious and depends on the subjective interpretation of article 13.1, we prefer to remain neutral on this and adhere to the Principle of Priority, which favors the name by Melo and Gonçalves (2005). The name used throughout the paper hence is ***Scapterinae*** Melo and Gonçalves.

Finally, we would like to point out that the reason for this choice does not have to do with the adoption of a more correct spelling of the stem of the family-group name based on *Scapter*. Under the International Code of Zoological Nomenclature, stems of both names, i.e. Scapter- and Scaptr-, are equally acceptable because they were proposed after 1999 (ICZN, 1999: Article 29.4.2; and, for further discussion, see Ascher and Engel, 2006: 118).

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APPENDIX 2

Additional morphological character states

For a full description of the characters see Packer (2008: Appendix 1). An asterisk marks a state that was present in the original matrix but was redefined for current purposes.

Character #	Additional state(s)
25	6. Metasomal terga with amber submarginal zones
38	3*. S2 specialised hairs sparse
39	3. S4 with long erect hairs
40	4. S5 with long erect hairs and apical hair row
41	9. S6 with hairs
61	4*. Labrum narrowly concave apically
82	4. Genal margin mostly parallel to posterior margin of compound eye
86	5. F1 petiolate
119	2. Stigma absent
140	4*. S7 ventral lobe anteriorly directed basally, laterally directed apically
143	9. S7 dorsal lobe triangular
144	4*. S7 apical disk unique 9*. S7 apical disk unique
145	8. S8 apical lobe unique
151	3. Inner posterior margin of gonoforceps with acute process
152	5. Mesovenral lobe of gonoforceps broadly based, swollen
153	4. Membranous lobe of gonoforceps long and broadly attached
156	8. Gonostylus unique
164	3. Paraocular area with triangular pale marking
174	5. Metasomal terga with sparse apical bands of silver setae
179	4. Frontal line below broadly raised
181	9. Facial fovea broadly S-shaped
184	6*. Epipharyngeal tongs with apex unique
191	4. Basal articulation of cardo L-shaped
210	2. Premental rods of intermediate length
211	4. Prementum ventrally angularly convex
214	7. Premental lobe short, bilobed 8. Premental lobe parallel-sided basally, flared apically
226	9. Metapleural flange broadly convex

Table S1. List of species included in this study and their respective locality data.

Species	Collecting Information
<i>Trichocolletes (Trichocolletes) sp.</i>	AUSTRALIA. NSW. 53 km S Oberon. 30.xi.1999
<i>Colletes bicolor</i> Smith 1879	CHILE. Region II (Antofagasta). 16 km. N Taltal. 5.x.2002
<i>Colletes bicolor</i> Smith 1879	ARGENTINA. Tucumán. 2 km ENE Amaicha del Valle. 24.x.2004
<i>Scrapier heterodoxus</i> (Cockerell 1921)	SOUTH AFRICA. WCP. 31 km S Clanwilliam. 7.ix.2001
<i>Scrapier niger</i> Lepelletier & Serville 1825	SOUTH AFRICA. WCP. 21 km N Hermanus. 28.ix.2001
<i>Hyleoides concinna</i> (Fabricius 1775)	AUSTRALIA. Queensland. South of Eukey. 18.xii.2002
<i>Hylaeus (Prosopis) affinis</i> (Smith 1853)	USA. NY. Tompkins Co., Ithaca.
<i>Euhesma platyrhina</i> (Cockerell 1915)	AUSTRALIA. WA; Kalbarri Nat.Prk. Rd to Z-Bend, 5 km along. 08.x.2005
<i>Euhesma aff. crabronica</i> (Cockerell 1914)	AUSTRALIA. WA; Eurardy Stat. 09.x.2005
<i>Callohesma calliopsella</i> (Cockerell 1910)	AUSTRALIA. Victoria. Yan yaen. 20.xi.1999
<i>Geodiscelea longiceps</i> Packer, 2005	CHILE. Region I (Tarapacá). HWY.687, km 29. ~ 62 km ESE Pozo Almonte. 9.iv.2004
<i>Chilimelissa nortina</i> Toro & Moldenke, 1979	CHILE. Region III (Atacama). Aguas Blancas S of Toconao
<i>Chilimelissa rozeni</i> Toro & Moldenke, 1979	CHILE. Region III (Atacama). Panamerican Hwy., km 1005, NE Chanaral
<i>Chilimelissa australis</i> Toro & Moldenke, 1979	ARGENTINA. Santa Cruz. 20 km E Los Antiguos. 17.xi.2003
<i>Chilimelissa australis</i> Toro & Moldenke 1979	ARGENTINA. Santa Cruz. 20 km E Los Antiguos. 17.xi.2003
<i>Chilimelissa irwini</i> Toro & Moldenke, 1979	ARGENTINA. Santa Cruz. 25 km E Los Antiguos. 25.0m. 22.xi.2003. "pan trap"
<i>Chilimelissa pedroi</i> Toro & Moldenke, 1979	CHILE. Region II (Antofagasta). Aguas Blancas, S of Toconao
<i>Chilimelissa rosie</i> Toro & Packer, 2001	CHILE. Region II (Antofagasta). Aguas Blancas, S of Toconao
<i>Chilimelissa laureli</i> Toro & Packer, 2001	CHILE. Region I (Tarapacá). Near Zapahuira. iv.2004
<i>Chilimelissa chusmiza</i> Toro, 1981	CHILE. Region I (Tarapacá). Chusmiza. iv.2004
<i>Chilimelissa</i> sp.1 ¹	ARGENTINA. Tucumán. Los Cardones; 19 km SE Amaicha del Valle. 2765m. 17.ii.2003
<i>Chilimelissa</i> sp.2 ¹	CHILE. Region I (Tarapacá). km 46.8, 79.8 km ESE Pozo Almonte. iv.2004
<i>Chilimelissa</i> sp.3 ¹	CHILE. Region II (Antofagasta). 10 km SE Chug Chung, W of Chuquicamata. 31.x.2000
<i>Xeromelissa wilmattae</i> Cockerell, 1926	CHILE. Region II (Antofagasta). Chusmiza. iv.2004. on Malvaceae
<i>Xenochilicola mamigna</i> Toro & Moldenke 1979	CHILE. Region I (Tarapacá). HWY.687, km 50.5. ~83.5km ESE Pozo Almonte
<i>Chilicola (Aneodisceleis) herbsti</i> (Friese, 1906)	CHILE. Region IV (Coquimbo). Limari, Chañar. 04.ix.2004
<i>Chilicola chubutense</i> Packer, 2007 ²	ARGENTINA. Region IV (Coquimbo). Limari, Chañar. 04.ix.2004
<i>Chilicola (Stenoedisceleis) inermis</i> (Friese, 1906)	CHILE. Region IV (Coquimbo). Limari, Chañar. 04.ix.2004
<i>Chilicola (Stenoedisceleis) denisii</i> Packer, 2007	ARGENTINA. Santa Cruz. 20 km E Los Antiguos. 17.xi.2003

Table S1. Cont.

Species	Collecting Information
<i>Chilicola liliiana</i> Packer, 2007 ³	ARGENTINA. Santa Cruz. 56 km S Perito Moreno. 23.xi.2003
<i>Chilicola (Pseudiscelis) rostrata</i> (Friese, 1906)	ARGENTINA. Tucumán. Los Cardones; 19 km SE Amaicha del Valle. 2765m. 17.ii.2003
<i>Chilicola (Oroediscelis) sp.</i>	BOLIVIA. La Paz. Sorata, env. 3100 m. 20.iv.1997 (open shrub). "s.s. B-04"
<i>Chilicola (Oroediscelis) styliventris</i> (Friese, 1908)	PERU. Junin Dept. Tarma. 22.x.1999
<i>Chilicola (Chiltoediscelis) patagonica</i> Toro & Moldenke, 1979	ARGENTINA. Santa Cruz. 25 km S Los Antiguos. 22.xi.2003
<i>Chilicola (Chiltoediscelis) araucana</i> Toro & Moldenke, 1979	ARGENTINA. Santa Cruz. 23 km E Las Heras. 16.xi.2003.
<i>Chilicola aenigma</i> Packer, 2007	ARGENTINA. Santa Cruz. 20 km E Los Antiguos. 17.xi.2003
<i>Chilicola aenigma</i> Packer, 2007	ARGENTINA. Santa Cruz. 25 km S Los Antiguos. 22.xi.2003
<i>Chilicola (Oediscelis) vernalis</i> (Philippi 1866)	CHILE. Region IV (Coquimbo). Parque Nacional Fray Jorge. 12.iv.2000
<i>Chilicola (Heteroediscelis) vicugna</i> Toro & Moldenke, 1979	CHILE. Region IV (Coquimbo). Elqui, Pangué. 11-30.ix.2004
<i>Chilicola (Oediscelis) tricarinatoides</i> Packer, 2007	ARGENTINA. Chubut. 8 km S Rada Tilly. 30m. 24.xi.2003

¹ Descriptions of these three species are given by: Packer (in press) New descriptions of *Xeromelissa* (Hymenoptera: Apoidea: Colletidae), Zootaxa.].

² *Chilicola chubutense* is used here to represent the taxon represented by *Cc. unicarinata* by Packer L. (2008) [Packer L. (2008) Phylogeny and classification of the Xeromelissinae (Hymenoptera: Apoidea, Colletidae) with special emphasis upon the genus *Chilicola*, Syst. Entomol., in press, published article online: 6 September, 2007: doi: 10.1111/j.1365-3113.2007.00398.x].

³ *Chilicola liliiana* is used here to represent the taxon represented by *Cc. olmue* by Packer (2008).

Table S2. Primer sequences for EF-1a, 28S rRNA, and COI used for PCR assays of bees.

Locus	Primer	Sequence	Reference
EF-1a (F2 copy) ^a	HaF2For1	5'-GGG YAA AGG WTC CTT CAA RTA TGC -3'	Danforth et al., 1999
	For3rho	5'-GGY GAC AAY GTT GTT TTY AAY G -3'	Danforth et al., 1999
	F2-rev1	5'-A ATC AGC AGC ACC TTT AGG TGG -3'	Danforth et al., 1999
	Cho10-Rev(mod)	5'-AC RGC VAC KGT YTG HCK CAF GTC -3'	Danforth et al., 1999
28S rRNA ^b	A-28S-For	5'-CCC CCT GAA TTT AAG CAT AT-3'	Ward and Brady, 2003
	Bel28S-For (D2-3665F)	5'-AGA GAG AGT TCA AGA GTA CG TG -3'	Belshaw and Quicke, 1997
	Mar28S-Rev (D3-4283R)	5'-TAG TTC ACC ATC TTT CGG GTC CC -3'	Mardulyn and Whitfield, 1999
	28SD4-Rev (D5-4749R)	5'-GTT ACA CAC TCC TTA GCG GA -3'	Danforth et al., 2006a
	LCO	5'-GGTCAAACAATCAATAAAGATATTGG -3'	Folmers et al., 1994
COI ^c	LCO Hym	5'-CAAATCATAAAGATATTGG -3'	Schulmeister et al., 2004
	LCO bee1 FOR	5'-TCWACMAATCAWAAARAYATTGG -3'	original primer sequence
	HCO	5'-TAAACTTCAGGGTGACCAAAAATCA -3'	Folmers et al., 1994
	HCO extA hym	5'-GAAAGTTATATTTTAAATTTACCTGG -3'	Schulmeister et al., 2004
	HCO extB hym rev	5'-CCTATTGAWARAAACATARTGAAAATG -3'	Schulmeister et al., 2004
	HCO out hym rev	5'-CCAGGTAAAATTAATAATATAAACTTC -3'	Schulmeister et al., 2004
	HCO outout hym rev	5'-GTAAATATATGRTGDGCTC -3'	Schulmeister et al., 2004
	HCO (mod A)	5'-ATABACTTCWGGRTGWCCAAARAATCA -3'	original primer sequence
	HCO (mod B)	5'-ACTTCWGGRTGWCCAAARAATCAAAATAA -3'	original primer sequence

^a PCR conditions. HaF2For1 / F2-rev1: 94 °C for 1 min, 48–52 °C for 1.5 min (35 cycles); For3rho / Cho10-Rev(mod): 94 °C for 1 min, 54–56 °C for 1 min, 72 °C for 1 min (35 cycles).

^b PCR conditions. A-28S-For Mar28S-Rev: 94 °C for 1 min, 58 °C for 1 min, 72 °C for 1.5 min (35 cycles); Bel28S-For / 28SD4-Rev: 94 °C for 1 min, 58 °C for 1 min, 72 °C for 1.5 min (35 cycles).

^c PCR conditions: 94 °C for 1 min, 48–52 °C for 1.5 min (35 cycles).

Table S3. List of species included in this study and their respective voucher numbers and GenBank accession numbers.

Species	Voucher #	EF-1alpha	28S rRNA	COI
<i>Trichocolletes (Trichocolletes) sp.</i>	Trsp708	AY585139	DQ872760	DQ872677
<i>Colletes bicolor</i> Smith 1879	EA0044	DQ884646	DQ768535	DQ872688
<i>Colletes bicolor</i> Smith 1879	EA0082	DQ884650	DQ768539	DQ872692
<i>Scapter heterodoxus</i> (Cockerell 1921)	Scht903	AY585136	DQ872773	—
<i>Scapter niger</i> Lepeletier & Serville 1825	Scng905	AY585137	DQ872774	—
<i>Hyleoides concinna</i> (Fabricius 1775)	KM268	DQ884691	DQ768601	DQ872734
<i>Hylaeus (Proxopsis) affinis</i> (Smith 1853)	KM112	DQ884672	DQ768581	—
<i>Euhesma platyrhina</i> (Cockerell 1915)	EA0148	DQ884652	DQ768541	DQ872694
<i>Euhesma aff. crabronica</i> (Cockerell 1914)	EA0155	DQ884654	DQ768543	—
<i>Callohesma calliopsella</i> (Cockerell 1910)	Euca688	AY585126	DQ872768	DQ872696
<i>Geodiscelis longiceps</i> Packer, 2005	EA0049	DQ884655	DQ768544	DQ872700
<i>Chilimelissa nortina</i> Toro & Moldenke, 1979	EA0052	DQ884657	DQ768546	DQ872702
<i>Chilimelissa rozeni</i> Toro & Moldenke, 1979	ChrZ857	AY585120	DQ872776	DQ872714
<i>Chilimelissa australis</i> Toro & Moldenke, 1979	EA0051	DQ884656	DQ768545	DQ872701
<i>Chilimelissa australis</i> Toro & Moldenke 1979	EA0141	DQ872741	DQ768555	DQ872711
<i>Chilimelissa irwini</i> Toro & Moldenke, 1979	EA0053	DQ884658	DQ768547	DQ872703
<i>Chilimelissa</i> sp. ¹	EA0138	DQ884659	DQ768554	DQ872710
<i>Chilimelissa pedroi</i> Toro & Moldenke, 1979	EA0153	DQ872742	DQ768556	DQ872712
<i>Chilimelissa rosie</i> Toro & Packer, 2001	EA0132	DQ872738	DQ768551	DQ872707
<i>Chilimelissa laureli</i> Toro & Packer, 2001	EA0133	DQ872739	DQ768552	DQ872708
<i>Chilimelissa chusmiza</i> Toro, 1981	EA0134	DQ872740	DQ768553	DQ872709
<i>Chilimelissa</i> sp. ²	EA0131	DQ872737	DQ768550	DQ872706
<i>Chilimelissa</i> sp. ³	EA0154	DQ872743	DQ768557	DQ872713
<i>Xeromelissa wilmattae</i> Cockerell, 1926	EA0054	DQ872735	DQ768548	DQ872704
<i>Xenochilicola mamigna</i> Toro & Moldenke 1979	EA0055	DQ884660	DQ768558	DQ872715
<i>Chilicola (Anoediscelis) herbsti</i> (Friese, 1906)	EA0140	DQ884663	DQ768572	DQ872729

Table S3. Cont.

Species	Voucher #	EF-1alpha	28S rRNA	COI
<i>Chilicola chubutense</i> Packer, 2007 ²	EA0067	DQ872753	DQ768568	DQ872725
<i>Chilicola (Stenoediscelis) inermis</i> (Friese, 1906)	EA0139	DQ872754	DQ768571	DQ872728
<i>Chilicola (Stenoediscelis) denisii</i> Packer, 2007	EA0058	DQ872745	DQ768560	DQ872717
<i>Chilicola lilitana</i> Packer, 2007 ³	EA0060	DQ872746	DQ768561	DQ872718
<i>Chilicola (Pseudoediscelis) rostrata</i> (Friese, 1906)	EA0137	DQ884662	DQ768570	DQ872727
<i>Chilicola (Oroediscelis) sp.</i>	EA0063	DQ872749	DQ768564	DQ872721
<i>Chilicola (Oroediscelis) styliventris</i> (Friese, 1908)	Chsp800	AY585121	DQ872780	DQ872730
<i>Chilicola (Chilioediscelis) patagonica</i> Toro & Moldenke, 1979	EA0064	DQ872750	DQ768565	DQ872722
<i>Chilicola (Chilioediscelis) araucana</i> Toro & Moldenke, 1979	EA0065	DQ872751	DQ768566	DQ872723
<i>Chilicola aenigma</i> Packer, 2007	EA0061	DQ872747	DQ768562	DQ872719
<i>Chilicola aenigma</i> Packer, 2007	EA0066	DQ872752	DQ768567	DQ872724
<i>Chilicola (Oediscelis) vernalis</i> (Philippi 1866)	EA0057	DQ872744	DQ768559	DQ872716
<i>Chilicola (Heteroediscelis) vicugna</i> Toro & Moldenke, 1979	EA0136	DQ884661	DQ768569	DQ872726
<i>Chilicola (Oediscelis) tricarinatoides</i> Packer, 2007	EA0062	DQ872748	DQ768563	DQ872720

¹ Descriptions of these three species are given by Packer (in press) [Packer L. (in press) New descriptions of *Xeromelissa* (Hymenoptera: Apoidea: Colletidae), Zootaxa].

² *Chilicola chubutense* is used here to represent the taxon represented by *Cc. unicolor* by Packer L. (2008) [Packer L. (2008) Phylogeny and classification of the Xeromelissinae (Hymenoptera: Apoidea, Colletidae) with special emphasis upon the genus *Chilicola*, Syst. Entomol., in press, published article online: 6 September, 2007: doi: 10.1111/j.1365-3113.2007.00398.x].

³ *Chilicola lilitana* is used here to represent the taxon represented by *Cc. olmue* by Packer (2008).