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Original article

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

Eduardo A.B. ALMEIDA[1,3], Laurence PACKER[2], Bryan N. DANFORTH[1]

[1] Comstock Hall, Department of Entomology, Cornell University, Ithaca, NY, 14853 USA
[2] Department of Biology, York University, Toronto, Ontario, M3J 1P3, Canada
[3] Current address: Departamento de Zoologia, Universidade Federal do Paraná, Cx. Postal 19020, CEP: 81531-980, Curitiba, P.R. Brazil

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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. Xeromelissine 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). 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

Corresponding author: Eduardo A.B. Almeida, eabalmeida@gmail.com
* Manuscript editor: Bryan Danforth
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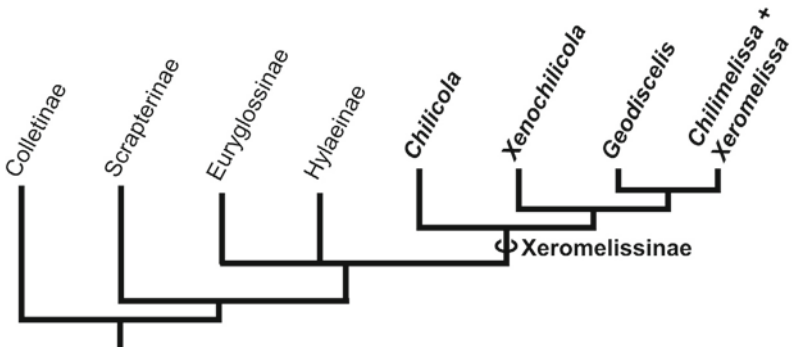

Figure 1. Summary of phylogenetic relationships among xeromelissinae genera according to the analysis of the morphological data set by Packer (2008: Figs. 1 and 2).

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., *Scrapter 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 Scrapterinae[1]). Here 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

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

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-1α) 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-1α 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-1α. 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-1α, 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-1a exons	1098	267	1416	1.29
EF-1a 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-1α, 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-1α treated separately) of the concatenated dataset was applied using the following unlinked models: (1) EF-1α, exons: HKY+I+G; (2) EF-1α, 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

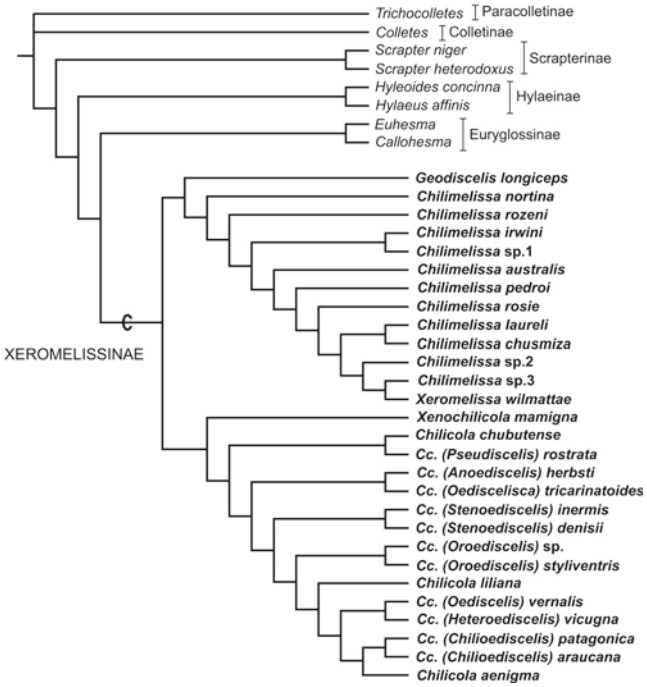

Figure 2. Strict consensus cladogram of the nine most parsimonious trees based on the morphological matrix analyzed with equal weights; tree length = 1215, ci = 46, ri = 69. Species of Xeromelissinae are marked in bold; names of colletid subfamilies sampled as outgroups for the analysis are provided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

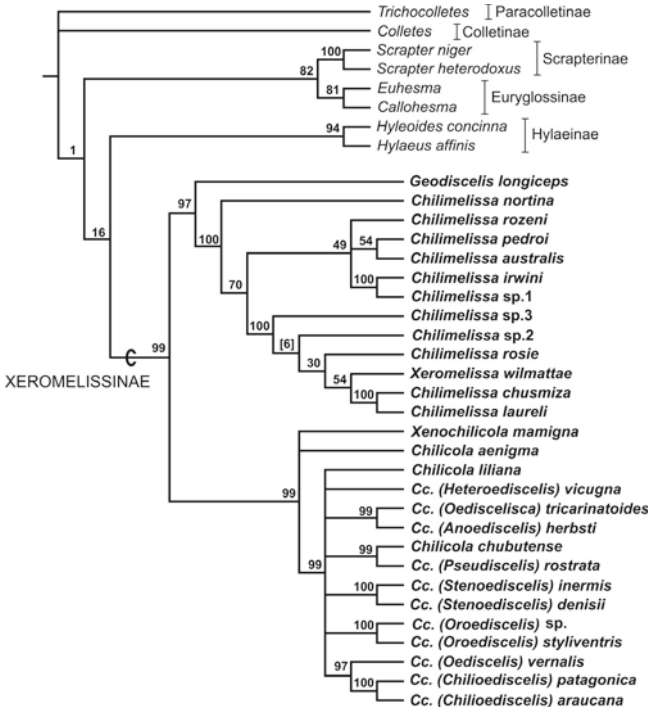

Figure 3. Strict consensus cladogram of the eight most parsimonious trees based on the molecular matrix analyzed with equal weights; tree length = 3703, ci = 49, ri = 62. Numerals represent GC support values calculated from 10000 replications using TNT (P = 33). Species of Xeromelissinae are marked in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

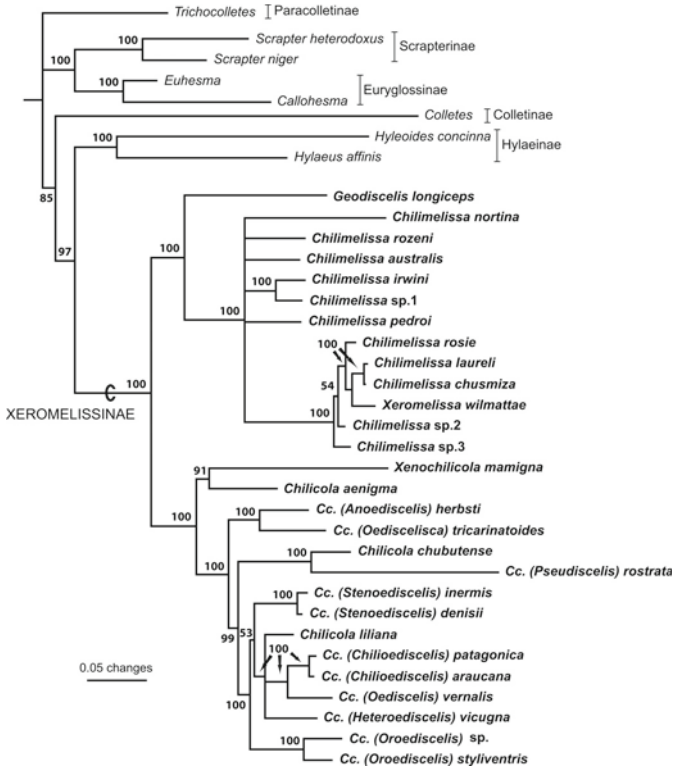

Figure 4. Bayesian majority-rule phylogram based on partitioned model with parameters estimated separately for (1) exons of EF1α, (2) introns of EF1α, (3) 28S rRNA, and (4) COI. Branch support is given by posterior probabilities. derived from 58 000 trees; the first 2000 trees were discarded. (harmonic mean: –lnL = 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. 6[2]). 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).

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

[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.

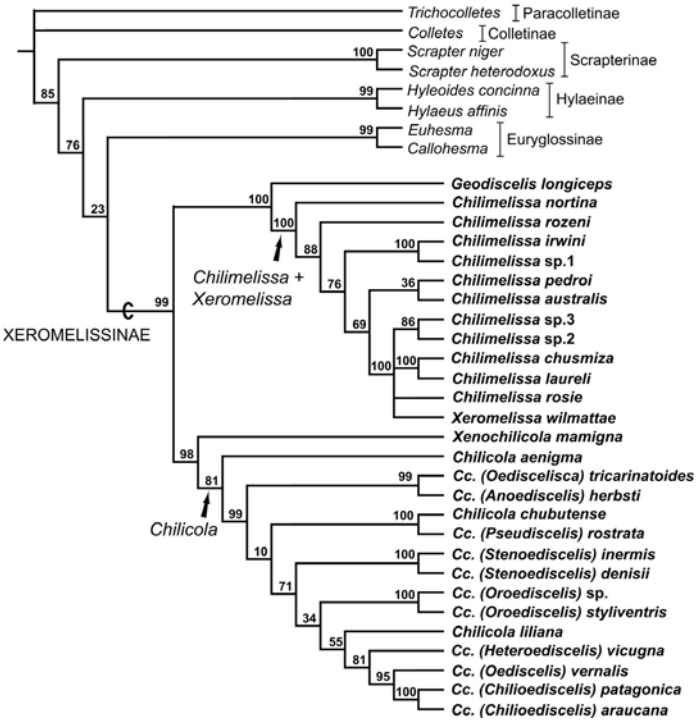

Figure 5. Strict consensus cladogram of the three most parsimonious trees inferred from a combined data set composed of 248 morphological characters and molecular data from three gene loci: EF-1α, 28S rRNA, and COI.; tree length = 4963, ci = 48, ri = 63. Numerals represent GC support values calculated 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.* (*Chilioediscelis*) 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.* (*Chiloediscelis*) 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.* (*Chilioediscelis*) 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

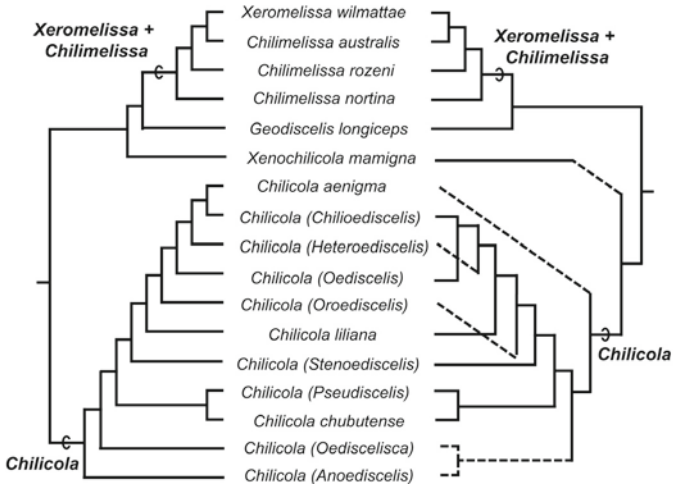

Figure 6. Summaries of phylogenetic hypotheses relationships within Xeromelissinae inferred from a morphological dataset by Packer (2008: Fig. 2): cladogram on the left; and the result of the combined matrix formed by molecular and morphological data of the present study (abridged from Fig. 5): cladogram 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 Scrapterinae 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 herrühten, 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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