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Phylogeny and classification of the Xeromelissinae (Hymenoptera: Apoidea, Colletidae) with special emphasis on the genus *Chilicola*

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Abstract. A phylogenetic analysis and classification are provided for the bee subfamily Xeromelissinae based on 248 morphological characters, many of which are novel and illustrated. A total of 47 ingroup species was included in the analysis, representing at least two divergent members from each described genus or subgenus and seven taxa which did not readily fall within previously described subgenera. Three most parsimonious trees were found (length, 1508; consistency index, 40; retention index, 70). The result shows that *Xeromelissa* renders *Chilimelissa* paraphyletic, and the 20 known *Chilimelissa* species are reassigned to *Xeromelissa*, giving the following new combinations: *X. luisa* (Toro & Moldenke) (this is the type species of *Chilimelissa*), *X. mucar* (Toro & Moldenke), *X. xanthorhina* (Toro), *X. brevimalaris* (Toro), *X. rosie* (Toro and Packer), *X. laureli* (Toro and Packer), *X. chusmiza* (Toro), *X. longipalpa* (Toro), *X. pedroi* (Toro & Moldenke), *X. australis* (Toro & Moldenke), *X. chillan* (Toro & Moldenke), *X. farellones* (Toro & Moldenke), *X. machi* (Toro), *X. minuta* (Toro & Moldenke), *X. nortina* (Toro & Moldenke), *X. sielfeldi* (Toro & Moldenke), *X. obscura* (Toro & Moldenke), *X. irwini* (Toro & Moldenke), *X. nolanai* (Toro & Moldenke) and *X. rozeni* (Toro & Moldenke). Group support was estimated using symmetric resampling and group supported/contradicted (GC) ratios, which compare the frequency of each most parsimoniously resolved clade with the alternative arrangement that was most commonly found in resampling. Relationships among subgenera for *Chilicola* are weakly supported. By contrast, when three previously synonymized subgenera (*Stenoediscelis, Heteroediscelis* and *Oediscelisca*) are resurrected, there is good support for all subgenera (GC $\geq$ 99), except two: a paraphyletic *Oediscelis* and a polyphyletic *Anoediscelis*. Both of these subgenera became monophyletic following successive approximations character weighting. Four distinctive new subgenera are described: *Unicarinicola* Packer **subgen.n.**, *Obesicola* Packer **subgen.n.**, *Capitatiscopa* Packer **subgen.n.** and *Toroediscelis* Packer **subgen.n.**, and a revised key to the subgenera of *Chilicola* is provided.

Introduction

The subfamily Xeromelissinae comprises almost 200 species of mostly temperate climate South American bees. The group is remarkable for the extreme secondary sexual characteristics of males in many species and the extreme modification of mouthparts in both sexes of some of its constituent taxa (Fig. 1).

The subfamily was originally erected, tentatively, by Cockerell (1926) for the newly described species *Xeromelissa wilmattae* Cockerell. In 1944, Michener suggested that this species might belong to his newly described subfamily, the Chilicolinae, which at that time contained 22 species. This

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association was formalized by Toro & Michener (1975), who united the two subfamilies as the Xeromelissinae. Michener (1995) divided the Xeromelissinae into two tribes: the Chilicolini and Xeromelissini. The former contained the genera *Xenochilicola*, with three described species (Toro & Moldenke, 1979; Genaro & Packer, 2005), and *Chilicola*, with numerous subgenera and many species (Michener, 2000, 2002; Moure & Urban, 2002; Packer & Genaro, 2007). The Xeromelissini comprised two genera: the monotypic *Xeromelissa* and *Chilimelissa* with, at that time, 16 species.

The Xeromelissini was separated from the Chilicolini on the basis of four characteristics (these were presumed apomorphies and are demonstrated formally as such below): the elongate anterior tentorial impressions giving a recurved epistomal sulcus, maxillary palpus abruptly slender at segment 4, pale integumental bands on the metasomal terga and the presence of a preapical lobe on the male gonostylus. The Chilicolini could be defined on the basis of the elongate thorax and the divergent margins of the stigma basal to vein r (the former is a continuous character, difficult to code in formal analysis; the latter is shown to be plesiomorphic in the analysis that follows).

The distinction between the two tribes was cast into doubt by the discovery of a new genus and species, *Geodiscelis megacephala* Michener & Rozen (1999), which exhibits a mixture of the traits used for tribal separation: it has the strong paraocular lobe and pale tergal bands of the Xeromelissini, but the elongate thorax, unmodified maxillary palpus and basally divergent stigmal margins of the Chilicolini. Consequently, Michener & Rozen (1999) concluded that tribal classification within the subfamily was unwarranted. Subsequently, a second species of *Geodiscelis* was found (Packer, 2005), agreeing with the mixture of tribal level characteristics mentioned above, but superficially very distinctive. The status of this group of bees was thrown into deeper uncertainty by Engel (2005), who subsumed the Xeromelissinae within the subfamily Hylaeinae but without supporting data.

Of the genera included within the Xeromelissinae, only *Chilicola* has been considered sufficiently diverse (or studied in enough detail) to warrant subgeneric classification. Michener (2000) recognized seven subgenera (*Anoediscelis*, *Chilicola*, *Chilioediscelis*, *Hylaeosoma*, *Oediscelis*, *Prosopoides* and *Pseudiscelis*), subsequently adding *Oroediscelis* as an eighth (Michener, 2002). Previously, four additional subgenera had been described: *Heteroediscelis* (Toro & Moldenke, 1979), split among *Anoediscelis* (three species) and *Oediscelis* (the remaining ten); *Idioprosopis* (Meade-Waldo, 1914), now placed within *Oediscelis*; *Oediscelisca* (Moure, 1946), also subsumed within *Oediscelis*; and *Stenoediscelis* (Toro & Moldenke, 1979), placed within *Anoediscelis*. All of these changes were made by Michener (1995).

Moure & Urban (2002) provided a catalogue of the Neotropical Xeromelissinae, listing 74 species. Brooks & Michener (1999), Toro & Packer (2001), Michener (2002), Gonzalez & Michener (2004), Packer (2004a, 2005), Genaro & Packer (2005), Hinojosa-Diaz & Michener (2005), Gibbs & Packer (2006) and Packer & Genaro (2007) described additional species. The latter paper included many species not readily assignable to previously recognized subgenera, most of which are included in the analysis presented here. The total number of described species is currently 120. Many additional species await description and the total number known from collections exceeds 170. Additional collecting will certainly bring the total to well over 200.

Michener (2002) performed a phylogenetic analysis of the subgenera of *Chilicola*. The result suggested that *Xenochilicola* renders the genus *Chilicola* paraphyletic, the subgenera *Chilicola* and *Chilioediscelis* combined render *Oediscelis* paraphyletic, and *Hylaeosoma* probably renders *Anoediscelis* paraphyletic. He cautioned that his results were preliminary and did not formally alter the classification of these bees.

The present study was initiated to obtain a more robust higher level phylogeny for the Xeromelissinae from which to construct a more stable classification for these interesting little bees.

Phylogenetic methods

Choice of taxa

Because of the large size of the subfamily, exemplars were chosen from amongst the genera and subgenera. Herein, each of the genera and subgenera included by Michener (2002) is represented by at least two species, except for the monotypic genus *Xeromelissa*. The diverse genus *Chilimelissa* was represented by six species, including one species from each of the major clades within the group based on preliminary analyses (L. Packer, unpublished data). For *Chilicola*, particularly diverse subgenera, or those shown previously to be of dubious monophyly (Michener, 2002), were represented by more exemplars than those considered generally unproblematic. In particular, exemplars from groups of species placed previously in other, or additional, subgenera by earlier authors were included. For all previously described subgenera, the type species of the subgenus was included (Table 1). The second either was morphologically divergent from the type species or, if phylogenetic analyses were available (Michener, 2002; Gibbs & Packer, 2006; for *Oroediscelis* and *Chilicola* s.s., respectively), chosen to straddle the basal node. Additional species were chosen on the basis of apparently intermediate morphologies between previously named higher level groupings: for example, *C. clavillo* Packer has some features apparently intermediate between Moure's *Oediscelisca* and *Oediscelis*. In all instances, taxa were chosen on the proviso that both sexes were available for study.

Based on the results from previous phylogenetic analyses (Alexander & Michener, 1995), the following taxa were included as outgroups: two species of *Scrapter* [the two species chosen, *S. nitida* Friese and *S. heterodoxus* (Cockerell), are very divergent members of this genus (Eardley, 1996; Davies *et al.*, 2005; Davies & Brothers, 2006), which has recently been given subfamilial rank (Engel, 2005; Melo

Table 1. Classification of the Xeromelissinae according to various authors.

	Assignment by		
Species	Michener (2000, 2002)	Toro & Moldenke (1979)	Present article
G. megacephala Michener & Rozen*	*Geodiscelis*	Unknown at that time	*Geodiscelis*
G. longiceps Packer	Unknown at that time	Unknown at that time	*Geodiscelis*
X. nortina (Toro & Moldenke)	*Chilimelissa*	*Chilimelissa*	*Xeromelissa*
X. rozeni (Toro & Moldenke)	*Chilimelissa*	*Chilimelissa*	*Xeromelissa*
X. chillan (Toro & Moldenke)	*Chilimelissa*	*Chilimelissa*	*Xeromelissa*
X. australis (Toro & Moldenke)	*Chilimelissa*	*Chilimelissa*	*Xeromelissa*
X. luisa (Toro & Moldenke)	*Chilimelissa*	*Chilimelissa**	*Xeromelissa*
X. xanthorhina (Toro)	*Chilimelissa*	*Chilimelissa*	*Xeromelissa*
X. wilmattae Cockerell*	*Xeromelissa*	*Xeromelissa*	*Xeromelissa*
Xn. mamigna Toro & Moldenke*	*Xenochilicola*	*Xenochilicola*	*Xenochilicola*
Xn. diminuta Toro & Moldenke	*Xenochilicola*	*Xenochilicola*	*Xenochilicola*
C. herbsti (Friese)	*C.* (*Anoediscelis*)	*C.* (*Anoediscelis*)	*C.* (*Anoediscelis*)*
C. plebeia Spinola	*C.* (*Anoediscelis*)	*C.* (*Anoediscelis*)	*C.* (*Anoediscelis*)
C. ashmeadi (Crawford)	*C.* (*Anoediscelis*)	*C.* (*Anoediscelis*)	*C.* (*Anoediscelis*)?
C. paramo Gonzalez & Michener	Unknown at that time	Unknown at that time	*C.* (*Anoediscelis*)?
C. unicarinata Packer	Unknown at that time	Unknown at that time	*C.* (*Unicarinicola*)*
C. biguttata Packer	Unknown at that time	Unknown at that time	*C.* (*Capitatiscopa*)*
C. friesei Moure	*C.* (*Oediscelis*)	Not treated	*C.* (*Oediscelisca*)*
C. tricarinata Packer	Unknown at that time	Unknown at that time	*C.* (*Oediscelisca*)
C. clavillo Packer	Unknown at that time	Unknown at that time	*C.* (*Oediscelisca*)
C. inermis (Friese)	*C.* (*Anoediscelis*)	*C.* (*Stenoediscelis*)	*C.* (*Stenoediscelis*)*
C. mailen Toro & Moldenke	*C.* (*Anoediscelis*)	*C.* (*Stenoediscelis*)	*C.* (*Stenoediscelis*)
C. olmue Toro & Moldenke	*C.* (*Anoediscelis*)	*C.* (*Heteroediscelis*)	*C.* (*Toroediscelis*)*
C. tregualemu Packer	Unknown at that time	Unknown at that time	*C.* (*Toroediscelis*)
C. obesifrons Packer	Unknown at that time	Unknown at that time	*C.* (*Obesicola*)*
C. catinipunctata Packer	Unknown at that time	Unknown at that time	*C.* (*Obesicola*)
C. longiceps (Ashmead)	*C.* (*Hylaeosoma*)	Not treated	*C.* (*Hylaeosoma*)*
C. polita Michener	*C.* (*Hylaeosoma*)	Not treated	*C.* (*Hylaeosoma*)
C. rostrata Friese	*C.* (*Pseudiscelis*)	Not treated	*C.* (*Pseudiscelis*)*
C. nanula Packer	Unknown at that time	Unknown at that time	*C.* (*Pseudiscelis*)
C. prosopoides Friese	*C.* (*Prosopoides*)	Not treated	*C.* (*Prosopoides*)*
C. granulosa Packer	Unknown at that time	Unknown at that time	*C.* (*Prosopoides*)
C. brzoskai Michener	*C.* (*Oroediscelis*)	Unknown at that time	*C.* (*Oroediscelis*)
C. styliventris Friese	*C.* (*Oroediscelis*)	Not treated	*C.* (*Oroediscelis*)*
C. rubriventris Spinola*	*C.* (*Chilicola*)	*C.* (*Chilicola*)	*C.* (*Chilicola*)*
C. venticola Packer	*C.* (*Chilicola*)	*C.* (*Chilicola*)	*C.* (*Chilicola*)
C. andina Toro & Moldenke	*C.* (*Chilioediscelis*)	*C.* (*Chilioediscelis*)	*C.* (*Chilioediscelis*)*
C. araucana Toro & Moldenke	*C.* (*Chilioediscelis*)	*C.* (*Chilioediscelis*)	*C.* (*Chilioediscelis*)
C. anomalipes Packer	Unknown at that time	Unknown at that time	*C.* (*Chilioediscelis*)
C. vernalis (Philippi)	*C.* (*Oediscelis*)	*C.* (*Oediscelis*)	*C.* (*Oediscelis*)*
C. lonco Toro & Moldenke	*C.* (*Oediscelis*)	*C.* (*Oediscelis*)	*C.* (*Oediscelis*)
C. solervicensis Toro & Moldenke	*C.* (*Oediscelis*)	*C.* (*Idioprosopis*)	*C.* (*Oediscelis*)
C. chalcidiformis Toro & Moldenke	*C.* (*Oediscelis*)	*C.* (*Idioprosopis*)*	*C.* (*Oediscelis*)
C. hahni Herbst	*C.* (*Oediscelis*)	Subgenus unassigned	*C.* (*Oediscelis*)
C. setosicornis Packer	Unknown at that time	Unknown at that time	*C.* (*Oediscelis*)
C. mantagua Toro & Moldenke	*C.* (*Oediscelis*)	*C.* (*Heteroediscelis*)	*C.* (*Heteroediscelis*)*
C. neffi Toro & Moldenke	*C.* (*Oediscelis*)	*C.* (*Heteroediscelis*)	*C.* (*Heteroediscelis*)

Type species of accepted genera are indicated by an asterisk in the first column; type species of accepted subgenera of *Chilicola* are similarly indicated in the last column; type species of the one currently synonymized genus and one subgenus of *Chilicola* are given in the third column.

& Gonçalves, 2005)]; three representatives of the subfamily Hylaeinae [*Meroglossa impressifrons* (Smith), *Palaeorhiza perviridis* (Cockerell) and *Hyleoides concinna* (Fabricius)]; and two of the Euryglossinae [*Euryglossa adelaidae* Cockerell and *Euhesma halictoides* (Rayment)]. *Colletes cunicularius* L. was used as a more distant outgroup to root the entire tree. Thus, no assumptions were made concerning outgroup relationships or, indeed, ingroup monophyly, other than the choice of *Colletes* as outgroup to all the remaining taxa. All ingroup and outgroup exemplars and localities for the specimens studied are listed in Table S1 (see 'Supplementary material').

Character selection and specimen preparation

Previous studies that have described potentially useful characters include Toro & Moldenke (1979), Alexander & Michener (1995), Michener (2000, 2002), Michener & Rozen (1999), Packer (2003) and Gibbs & Packer (2006). Information provided in these papers served as the basis for some character choice, although often with somewhat different state delimitations. The morphological terminology follows Michener (1944, 2000, 2002), with some additional terms from Prentice (1998), Packer (2003) and Packer & Genaro (2007).

Whole specimens were cleared in KOH and stored in glycerin when sufficient material was available. For rarer species, only male and female genitalia and the mouthparts and sting apparatus of females were cleared. Some characters observed in cleared material could not be scored in rarer species; for example, features of the prosternum and mesophragma. Some others, such as certain features of the forecoxa, could be seen in rare material only by relaxing the specimen for manipulation.

An exhaustive search was made for useful characters from all parts of the body of both males and females. In many instances, variation was similar between the two sexes, and such characters were coded solely for males. Sexually dimorphic characteristics, such as male and female genitalia, were scored only for the appropriate sex. Variation between taxa in mouthparts was sometimes more distinct for females, and so these variables were coded only for females.

Phylogenetic analysis

The data matrix (Table S2, see 'Supplementary material') was entered into WINCLADA (Nixon, 1999) for preliminary exploration. The final analyses were made with TNT (Goloboff *et al*., 2003b) with the default options, except as noted below. Ratchet, sectorial, drift and tree fusing with 'collapse trees after search' and 'find minimal length' set to ten found the same most parsimonious trees. Successive approximations character weighting was employed using the rescaled consistency index as a weight. Symmetrical resampling (Goloboff *et al*., 2003a) was performed on unweighted results with 10 000 iterations and a probability of character weight change (up or down) of 33%. Symmetric resampling allows the estimation of group support without being biased by differential character (or character state) weights, which affect the results obtained with jackknifing and bootstrapping (see Goloboff *et al*., 2003a). Support is indicated on the cladograms using group supported/contradicted (GC) ratios. For a particular node, this 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 favoured in all resampled matrices) to maximum support (the original grouping found in all resampled matrices) (Goloboff *et al*., 2003a). For comparison, bootstrap values were calculated using the standard (with replacement) option as implemented in TNT, again with 10 000 replications.

Descriptions

The following abbreviations are used in the taxonomic and character descriptions: F, S and T followed by a number, flagellomeres and metasomal sterna and terga, respectively; LOL, longitudinal diameter of the lateral ocellus; i and d, puncture density (for example, i = 2d denotes that the puncture interspaces are twice the puncture diameters). Items italicized in the descriptions are unique amongst the subgenera of *Chilicola*.

Results

Two hundred and forty-eight characters were coded (Appendix 1). These came from all parts of the adult body (Table 2), and neither mouthparts nor male terminalia dominate the dataset.

Phylogenetic analysis yielded three most parsimonious trees with a length of 1508 steps, consistency index (CI) of 40 and retention index (RI) of 70. A strict consensus of these three is shown in Fig. 1. Successive approximations character weighting stabilized after two rounds to give a tree of length 45 122, CI of 60 and RI of 81 (Fig. 2). Generic level relationships amongst ingroup taxa were identical between weighted and unweighted results, and the differences between the two involved minor rearrangements amongst well-supported subgenera within *Chilicola* (exceptions to this are discussed below).

The presence of a fovea to the prementum is a strong character state linking all but *Colletes*; this feature, although considerably reduced in Euryglossinae, is unique amongst the bees. The strongest synapomorphy uniting the Xeromelissinae with the Hylaeinae and Euryglossinae is the presence of a specialized area at the apex of S5 in females, also a feature unknown elsewhere amongst the bees.

The unweighted tree has the Euryglossinae as a weakly supported sister to the Xeromelissinae. The weighted tree unites

Table 2. Number and proportion of different character systems used in the phylogenetic analysis, by sex.

	Male	Female	Total (%)
Coloration	24	5	29 (11.6)
Pubescence	16	12	28 (11.2)
Sculpture	18	5	23 (9.2)
Head structure	22	9	31 (12.9)
Mouthparts	7	34	41 (16.9)
Mesosoma	40	12	52 (20.9)
Metasoma	8	7	15 (6.0)
Genitalia	23	5	28 (11.2)
Combined secondary sexual characteristics of males			38 (15.2)

the Euryglossinae with the Hylaeinae, and has the Xeromelissinae as sister to the two combined. Support for a monophyletic Xeromelissinae is strong, indicated by, amongst other character states: stipes deepest near to the base; suspensorium inserted interstitially in the lateral wall of the prementum; prementum with an internal thickening for approximately the apical one-quarter of its length; and hind wing Cu-a evanescent with tubular portion restricted to a small angulation on vein M.

The Xeromelissinae contains two large, weakly supported clades: one is the genus *Chilicola* alone, supported by a posteriorly convex median portion of the S2 gradulus and membranous lobes to the penis valve in males (secondarily lost in some species), and an elongate apodemal region of the seventh hemitergite and a corbiculate sternal scopa (reversed in one subgenus – *Chilioediscelis*) in females. The other clade has *Xenochilicola* as sister to a clade with *Geodiscelis* leading to *Xeromelissa* via a paraphyletic *Chilimelissa*. This clade is supported by appressed dense pubescence on the lower paraocular area in males and episternal groove posteroventrally orientated in both sexes. The unexpected grouping of *Xenochilicola* with *Geodiscelis* and *Xeromelissa* receives low support, and constraining *Xenochilicola* + *Chilicola* as monophyletic results in three trees one step longer than in the unconstrained analysis. The consensus of these three trees is less resolved than in Fig. 1, but successive approximations (constraint removed after initial weighting) yields the same topology as the weighted result based on the unconstrained analysis (Fig. 2).

All genera are monophyletic with the exception of *Chilimelissa*. Characters which support the nesting of *X. wilmattae* deep within *Chilimelissa* include the presence of a mesotarsal rake and a deep cardo in females, maxillary palpomere 1 sharply concave mesally in both sexes and details of the male hind leg and genitalia. The reduction in the number of labial palpomeres to three is an unusual characteristic amongst the bees, and *X. wilmattae* shares this with *X. xanthorhina* (Toro & Moldenke) (and several additional species not included in the analysis). As a result, all 20 described species of *Chilimelissa* currently known are reassigned here to *Xeromelissa*. These new combinations are as follows: *X. luisa* (Toro & Moldenke) (this is the type species of *Chilimelissa*), *X. australis* (Toro & Moldenke), *X. brevimalaris* (Toro), *X. chillan* (Toro & Moldenke), *X. chusmiza* (Toro), *X. farellones* (Toro & Moldenke), *X. irwini* (Toro & Moldenke), *X. laureli* (Toro and Packer), *X. longipalpa* (Toro), *X. machi* (Toro), *X. minuta* (Toro & Moldenke), *X. mucar* (Toro & Moldenke), *X. nolanai* (Toro & Moldenke), *X. nortina* (Toro & Moldenke), *X. obscura* (Toro & Moldenke), *X. pedroi* (Toro & Moldenke), *X. rosie* (Toro and Packer), *X. rozeni* (Toro & Moldenke), *X. sielfeldi* (Toro & Moldenke) and *X. xanthorhina* (Toro).

The sister group relationship between *Geodiscelis* and *Xeromelissa* (as now understood) is well supported: synapomorphies uniting the two genera include epistomal sulcus recurved, labrum elongate and membranous lobe on the inner margin of the gonoforceps in males present.

Most of the subgenera of *Chilicola* accepted by Michener (1995, 2002) are monophyletic and strongly supported, with GC values of either 99 or 100, with the exception of the type subgenus (GC = 89) and *Oediscelis* and *Anoediscelis*. *Oediscelis* is both polyphyletic and paraphyletic, but becomes only paraphyletic if Toro & Moldenke's *Heteroediscelis* and Moure's *Oediscelisca* are removed from it. Thus defined, it becomes monophyletic in the weighted analysis. The situation with *Anoediscelis* is similar: in the unweighted analysis it remains non-monophyletic, even when two well-supported groups are removed from it – Toro & Moldenke's subgenus *Stenoediscelis* and *Toroediscelis* Packer **subgen.n.**, described below. The weighted tree suggests a monophyletic *Anoediscelis* (once the aforementioned two subgenera are removed), albeit rather weakly supported (GC = 37). Although the characters that separate (*C. herbsti* + *C. plebeia*) and (*C. ashmeadi* + *C. paramo*) in the unweighted analysis are not convincing, neither are those that unite them in the weighted tree.

Four of the nodes in Fig. 1 received negative GC values and one had a value of zero. All nodes with negative GC values were unstable to successive approximations character weighting; the node with a value of unity was also unstable to weighting, although that with GC = 0 was returned in the weighted analysis. The nodes that were poorly supported by GC values in the unweighted analysis represent parts of the topology that are not locally parsimonious in alternative pseudoreplicate matrices. Thus, there are other resolutions of these particular nodes that, in the pseudoreplicates, are almost as parsimonious as the results shown; nonetheless, the topology of Fig. 1 remains the globally most parsimonious result with the raw data.

Three previously described, but subsequently synonymized, subgenera should be reinstated (*Stenoediscelis*, *Heteroediscelis* and *Oediscelisca*) and four additional subgenera warrant description. Comparison of the various recent classifications of the Xeromelissinae with that accepted here is provided in Table 1.

Subgenus Stenoediscelis *Toro & Moldenke 1979*

Type species. *Chilicola inermis* (Friese, 1906).

Diagnosis. Each of the following characteristics is unique amongst the Xeromelissinae. Parascutal carina notched. Female mandible with subapical tooth attaining or almost attaining mandibular apex, obtuse angulation present on inner surface of mandible basal to subapical tooth. Male hind basitarsus outwardly concave, otherwise unmodified. Male S7 with lunate to L-shaped ventral lobe.

Additional species. *C. mailen* Toro & Moldenke, 1979, *C. denisii* Packer, 2007.

Comments. There are numerous additional species in this subgenus from Argentina and at least one more to be described from Chile; all share the diagnostic features noted above.

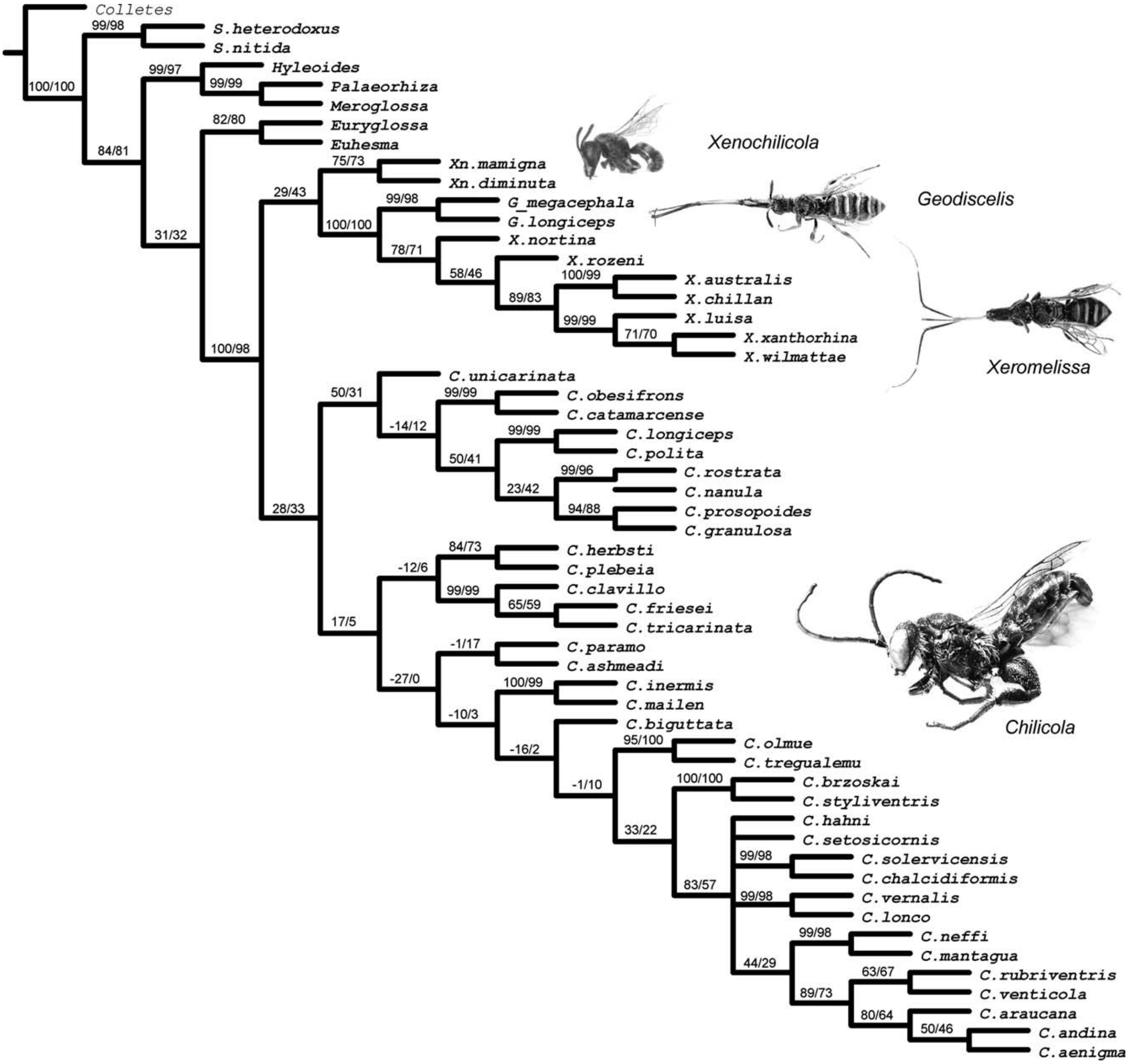

Fig. 1. Most parsimonious tree for the data matrix presented in Table S2. Group supported/contradicted (GC) ratios and bootstrap values are shown above the internodes, with the GC value preceding '/'. The exemplars of xeromelissine genera shown are, from top to bottom: *Xenochilicola diminuta* male, *Geodiscelis longiceps* female, *Xeromelissa rozeni* female and *Chilicola vernalis* male. It should be noted that the other species of *Geodiscelis* and *Xeromelissa* do not have such elongate heads and not all *Chilicola* males have such modified hind legs.

Subgenus Heteroediscelis *Toro & Moldenke 1979*

Type species. *Chilicola mantagua* Toro & Moldenke 1979.

Diagnosis. Readily diagnosable only in males: S1 with robust, ventrally directed process longer than broad, subparallel to obtusely truncate apex (other *Chilicola* with a process to S1 have it narrowing to pointed apex in profile). Amongst *Chilicola* subgenera with elongate anterior tentorial pits, only *Heteroediscelis* males lack membranous lobes to the penis valve.

Additional species. *C. diaguita* Toro & Moldenke 1979, *C. valparaiso* Toro & Moldenke 1979, *C. neffi* Toro & Moldenke 1979, *C. vicugna* Toro & Moldenke 1979, *C. deserticola* Toro & Moldenke 1979, *C. mavida* Toro & Moldenke 1979, *C. vina* Toro & Moldenke 1979, *C. travesia* Toro & Moldenke 1979, *C. erithropoda* Toro & Moldenke 1979.

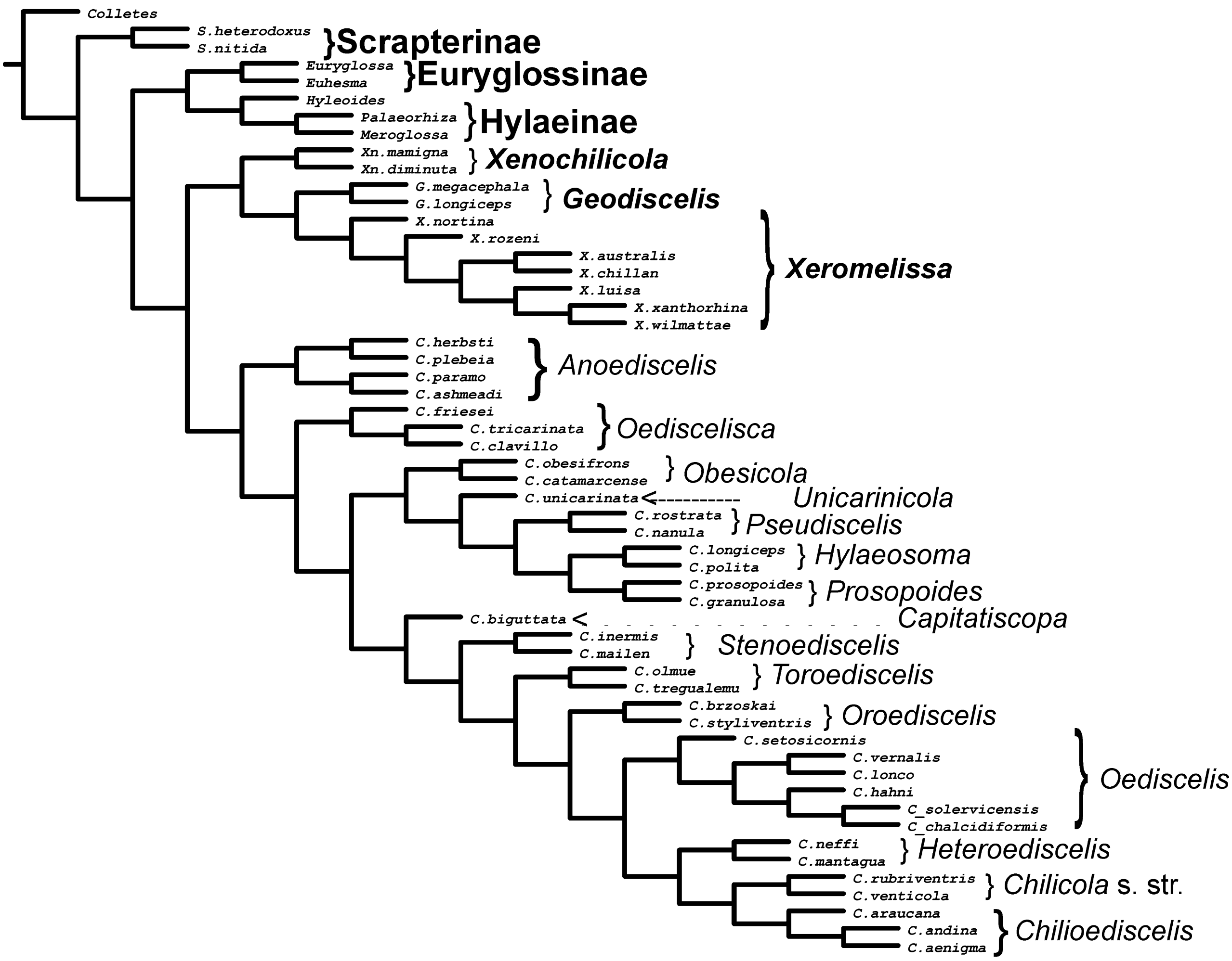

Fig. 2. Most parsimonious tree for the weighted analysis.

Comments. There is at least one additional species in this endemic Chilean group.

Subgenus Oediscelisca *Moure 1946*

Type species. *Chilicola friesei* Ducke 1907.

Diagnosis. The combination of hind femur massively expanded and anterior tentorial pit punctiform is diagnostic for males. The membranous kidney-shaped ventral lobes to S7 and details of the apical process of S8 are also diagnostic. Females cannot currently be readily differentiated from those of *Anoediscelis*.

Additional species. *C. dalmeidai* Moure 1946, *C. tricarinata* Packer 2007, *C. tricarinatoides* Packer 2007, *C. clavillo* Packer 2007.

Comments. Numerous additional species in this group require description; all have an expanded hind femur and modified hind tibia in males. The tibial modifications are extremely varied. The subgenus is known from described species from Argentina and Brazil; some additional undescribed species extend the range into Bolivia.

Obesicola Packer ***subgen.n***.

Type species. *Chilicola obesifrons* Packer 2007.

Diagnosis. *Obesicola* is differentiated from other *Chilicola* by the coarsely punctate to foveolate thoracic dorsum and pronotal collar moderately long with sides not strongly convergent anteriorly but angulate at anterolateral corners (Fig. 7A, see Appendix 1) (other subgenera with elongate pronota – *Pseudiscelis*, *Prosopoides* and some species of *Hylaeosoma* – have anterolateral corners rounded and lateral margins convergent anteriorly). The lack of distinct emargination on the inner eye margins and the frons usually somewhat expanded around the median ocellus and mesad of the upper eye, with both expanded areas comparatively impunctate but with strongly imbricate microsculpture (Fig. 7A, B, see Appendix 1), are shared only with some species of *Prosopoides*.

Description

Small bees, body length, 3–4.5 mm.

Colour. Black. Male with yellow on labrum, mandible, clypeus and lower paraocular area, and antenna; flagellum mostly orange; legs marked with yellow–orange. Female lacking yellow markings and with reduced areas of orange on legs.

Surface sculpture. Microsculpture strongly imbricate, appearing granular, especially on frontal swellings. Punctation coarse for size of insect, especially on mesoscutum, which is often foveolate. Punctures mostly lacking on swollen areas of frons. Dorsal surface of propodeum with disc slightly depressed, with weak, irregular median carina, weakly rugoso-reticulate on either side. Metasomal terga with weak granular microsculpture, almost impunctate.

Pubescence. Short and sparse, not especially plumose. Males lacking long erect hairs on gena and metasomal sterna. Female with corbiculate S2, hairs with short branches on anterior side of rhachis. Both sexes lacking apicolateral hair patches on metasomal terga.

Structure. *Head*. Slightly longer than broad. Labrum twice as broad as long. Subapical tooth not attaining apex of mandible. Malar space linear. Epistomal sulcus expanded below anterior tentorial pit almost to laterally reflexed portion of sulcus, pit not separated from sulcus. Frons usually with swellings around median ocellus and between lateral ocellus and compound eye. Facial fovea broadly oval, shiny and distinct in female, smaller and less distinct in male. Inner margin of compound eye not emarginate (see Appendix 1), strongly convergent below, UOD at least 2LOD in males, at least 1.5LOD in females. Head somewhat produced above compound eye, upper ocular tangent passing below lower margin of median ocellus. Male antenna short, F2 especially short, four times broader than long, antenna otherwise unmodified.

Mesosoma. Pronotal collar long, medially 0.5–0.7× as long as scape and at least 1.5× LOL, *lateral margin straight to slightly concave forming right angled or slightly acute anterolateral angles*. Pre-episternal groove complete, sharply curved anteriorly below. Propodeum elongate, dorsal surface as long as posterior depth and subequal to length of scutellum. Male hind leg unmodified except tibia slightly expanded, lacking angles or carinae. Hind tibial spurs unmodified, hind tarsal claws bifurcate. Stigmal perpendicular crossing near apex of second submarginal cell.

Metasoma. Male metasomal sterna unmodified. *Male terminalia*. S7 with two pairs of lateral lobes, *apical pair broad, membranous, pigmented except for basal and apical extremities*; basal pair very small, narrow with acute dorsolaterally orientated angulation. S8 with apical process elongate, widest at apex, slightly emarginate apically. Penis valve with pair of subapical dorsally orientated membranous lobes. Gonostylus not clearly demarcated from gonoforceps.

Etymology. The subgeneric name is based on the generic and specific epithets of the type species, *C. obesifrons*, the species name of which refers to the swellings on the frons.

Additional species. *C. catamarcense* Packer 2007.

Comments. In addition to these two species, there are at least four more ranging from Bolivia in the north to Neuquen Province in Argentina in the south.

Capitatiscopa Packer ***subgen.n.***

Type species. *Chilicola biguttata* Packer 2007.

Diagnosis. The large areas of yellow on the face (clypeus, most of the supraclypeal area, lower paraocular area to antennal socket, mandible), combined with the mostly black labrum, are unique amongst *Chilicola* (all others with considerable yellow on the lower face also have an entirely yellow labrum). The blunt or capitate metasomal scopal hairs of the females are also unique. Because only one species is known from this subgenus, only characters that are generally of importance in the subgeneric differentiation within *Chilicola* are considered below.

Description

Colour. Black. Male with following parts yellow: mandible (except apex, red–brown), clypeus, supraclypeal and paraocular areas, legs with extensive yellow markings. Female with yellow spot adjacent to anterior tentorial pit, legs with yellow markings considerably reduced in comparison with male.

Surface sculpture. Microsculpture imbricate. Punctures generally small and moderately dense, on mesoscutum $i < d$. Dorsal surface of propodeum with few, strong, radiating striae. Metasomal terga with few, small, shallow and obscure punctures.

Pubescence. White, somewhat woolly. Male with genal beard and lacking patches of erect hair on metasomal sterna. Female with strongly capitate hairs on front tibia and tarsus, *corbicula of S2 with hairs unbranched, blunt or capitate*. Both sexes lacking apicolateral hair patches on metasomal terga.

Structure. *Head*. Round. Malar space linear. Clypeus slightly broader than long, slightly protuberant in profile. Paraocular lobe absent, epistomal sulcus beneath anterior tentorial pit expanded into a groove, pit appearing comma-shaped. Supraclypeal area strongly protuberant above. Facial fovea absent but represented in female by an area bearing woolly hairs. Eye emarginate, strongly converging below, vertex not strongly developed above summits of eyes, upper ocular tangent passing through middle of median ocellus.

Mesosoma. Pronotal collar short, medial length subequal to LOL. Pre-episternal groove distinct and complete. Dorsal surface of propodeum less than 1.5× as long as metanotum, shorter than scutellum. Legs of male unmodified, lacking swellings, angles or carinae, hind tibia gradually expanding towards apex, attaining mid-length of trochanter when folded. Hind tibial spurs unmodified. Hind tarsal claws bifurcate. Stigmal perpendicular traversing second submarginal cell near middle or closer to base.

Metasoma. Sterna without modifications. *Male terminalia*. S7 with two pairs of lateral lobes, ventral lobe broad and membranous, outer margin concave and posterior margin curved dorsally; dorsal lobe elongate, narrowing apically from broad base (see Appendix 1). S8 apical process very large, emarginate apically, broadest subapically (see Appendix 1). Foramen of gonobase very large. Gonostylus very broad, clearly demarcated from gonocoxite, not flattened or markedly concave beneath. No inner membranous lobes to gonocoxite. Penis valve with pair of long, broadly based membranous lobes.

Etymology. The name refers to the capitate or blunt scopal hairs of the female.

Included species. So far, only the type species of the subgenus is known although males of some superficially similar species remain to be described; the females of these additional forms have not been detected.

Comments. A distinctive species that does not readily fall into any of the other named subgenera.

Unicarinicola Packer ***subgen.n.***

Type species. *Chilicola unicarinata* Packer 2007.

Diagnosis. Amongst males of *Chilicola*, the following character states are unique: ocellocular distance less than LOL; single oblique carina on inner surface of hind tibia which is otherwise very narrow in dorsal view with abrupt expansion towards apex; no long hairs on lateral surface of propodeum; overall form of S7 and dorsal lobe with numerous long hairs. For females: branches on scopal hairs of S2 restricted to apex of anterior surface of rhachis and orange marks on lower paraocular area (the latter are found rarely elsewhere in *Chilicola*). The ocellocular character does not work for females, as some *Chilicola* (*Oediscelisca*) have a similarly short ocellocular distance.

Description

Colour. Black. Male with extensive yellow or whitish markings on face, entire area below antennae pale; flagellum orange; legs marked with yellow–orange. Female with ill-defined orange markings on lower face, legs entirely brown to entirely orange.

Surface sculpture. Microsculpture generally weak. Punctation small, generally sparse, especially shallow and obscure on metasoma.

Pubescence. Short and sparse, not especially plumose. Males with long erect hairs on gena and with posterolateral patches of elongate hair on metasomal sterna. Female with corbiculate S2, hairs with short branches on anterior side of rhachis only towards apex. Both sexes lacking apicolateral hair patches on metasomal terga.

Structure. *Head*. Longer than broad. Labrum twice as broad as long. Subapical tooth not attaining apex of mandible. Malar space linear. Epistomal sulcus expanded below anterior tentorial pit almost to laterally reflexed portion of sulcus, pit not separated from sulcus. Frons without unusual swellings or depressions, facial fovea absent. Inner margin of compound eye emarginate. Head slightly produced above compound eye, upper ocular tangent crossing lower tangent of median ocellus. Male antenna moderately long, most flagellomeres longer than broad, otherwise unmodified.

Mesosoma. Pronotal collar short, medially 0.75× LOL. Anterolateral corners of pronotum rounded. Pre-episternal groove complete. Propodeum elongate, dorsal surface at least 1.5× metanotum to longer than scutellum. *Hind leg of male unmodified except for tibia slightly expanded at apex with one oblique carina on inner surface near mid-length*. Hind tibial spurs unmodified, hind tarsal claws bifurcate. Stigmal perpendicular crossing near middle of second submarginal cell.

Metasoma. Male metasomal sterna unmodified. *Male terminalia*. *S7 with one pair of long lateral lobes bearing very long setae*, ventral lobe very short. S8 apical process large, widest at truncate apex. Penis valve with one or two subapical dorsally orientated membranous lobes arising from considerably expanded apical portion of valve, *penis valve microserrate laterally*. Gonostylus not clearly demarcated from gonoforceps.

Etymology. The subgeneric name is based on the specific epithet for the type species, which itself refers to the single oblique carina on the inner surface of the hind tibia in the male.

Additional species. *C. chubutense* Packer 2007.

Comments. Undescribed species in this subgenus are known from Bolivia and Argentina. The range of morphological variation in this subgenus is comparatively slight.

Toroediscelis Packer ***subgen.n.***

Type species. *Chilicola olmue* Toro & Moldenke 1979, by original designation.

Diagnosis. The presence of one or more small angulations on otherwise unmodified hind trochanter is sufficient to diagnose males (except *C. orophila*). Ventral lobes to male S7 absent and dorsal lobes bearing transverse hair row are also diagnostic. For females, the combination of anterior tentorial pit expanded below, hind tibial spurs unmodified, metasomal terga with apicolateral patches of white tomentum, stigmal perpendicular interstitial with first recurrent vein and dorsal surface of propodeum rugulose is diagnostic.

Description

Smallish bees, body length, 4–7 mm.

Colour. Black with yellow markings more restricted than in other subgenera to entirely absent.

Surface sculpture. Microsculpture strongly imbricate, surface of head and mesosoma mostly dull. Punctation strong, crowded on frons in male, sparser in female. Dorsal surface of propodeum rugulose.

Pubescence. Mostly short and sparse, not especially plumose. Males lack long erect hairs on metasomal sterna sometimes with apical patch of long hairs on outer surface of hind tibia. Female S2 corbiculate, hairs with numerous short branches on anterior side of rhachis. Apicolateral hair patches on metasomal terga present.

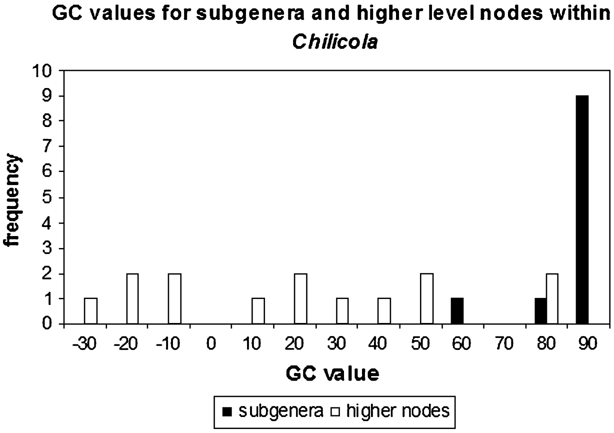

Fig. 3. Histogram of group supported/contradicted (GC) ratios for nodes within *Chilicola*. Subgeneric support is shown by filled bars, and higher level support by open bars. Results for *Anoedisceli*s and *Oediscelis* are not included (see text).

Structure. *Head*. Slightly longer than broad to 1.2× longer. Labrum 2–3× broader than long. Subapical tooth

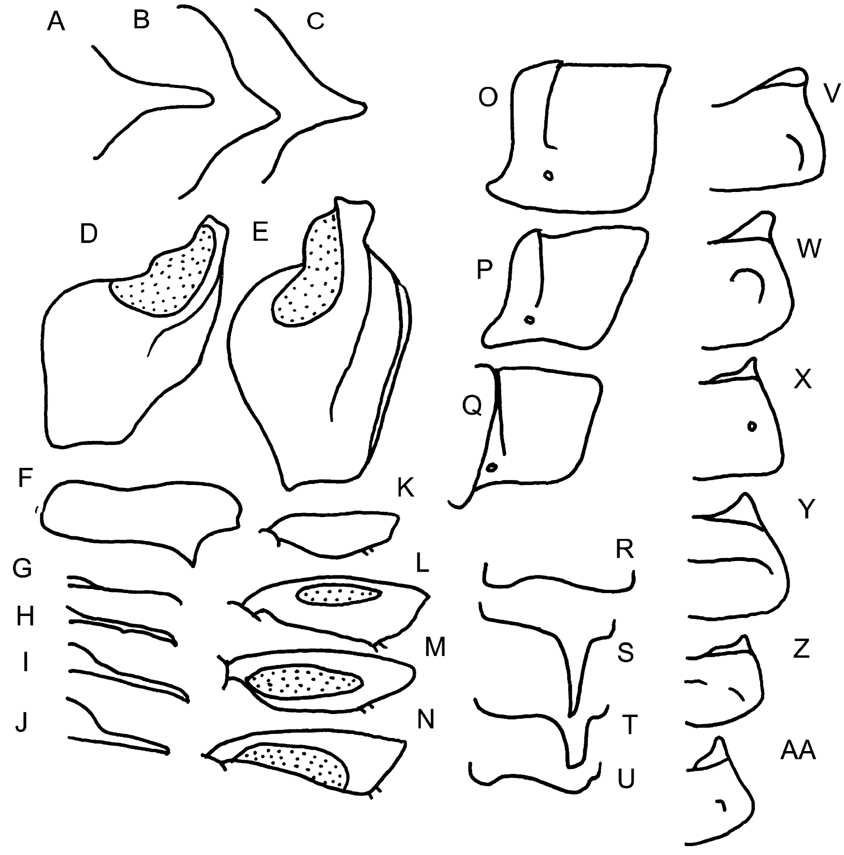

Fig. 4. Drawings of character states for male Xeromelissinae as indicated in the text. A–C, Ventral surface of prosternum, left half: A, *Chilicola* (*C.*) *herbsti* 94-0, 95-0; B, *Xeromelissa* (*X.*) *australis* 94-1, 95-1; C, *X. xanthorhina* 95-2. D, E, Posterolateral view of forecoxa, stippling denotes basal foramen: D, *X. xanthorhina* 97-1, 98-1, 99-1; E, *C. plebeia* 97-0, 98-2, 99-0. F, Forefemur of *X. australis* 101-1. G–J, Mesophragma and anterior margin of mesoscutum in dorsal view: G, *Xenochilicola* (*Xn.*) *mamigna* 107-0; H, *X. chillan* 107-1; I, *X. nortina* 107-2; J, *Geodiscelis longiceps* 107-3. K–N, Foretibia, internal surface, stippling indicates glabrous area: K, *X. nortina* 102-0, 103-0; L, *C. neffi* 102-1, 103-2; M, *Palaeorhiza perviridis* 102-2, 103-1; N, *X. chillan* 102-3, 103-3. O–Q, Lateral view of T2: O, *Xn. diminuta* 130-0; P, *X. nortina* 130-1; Q, *Meroglossa impressifrons*, 130-2. R–U, Lateral view of S1: R, *C. olmue* 131-0; S, *C. rubriventris* 131-1; T, *C. neffi* 131-2; U, *C. vernalis* 131-3. V–AA, Ventral view of left half of S3: V, *Xn. diminuta* 134-1; W, *C. plebeia* 134-2; X, *C. biguttata* 134-3; Y, *C. brzoskai* 134-4; Z, *C. vernalis* 134-5; AA, *C. unicarinata* 134-7.

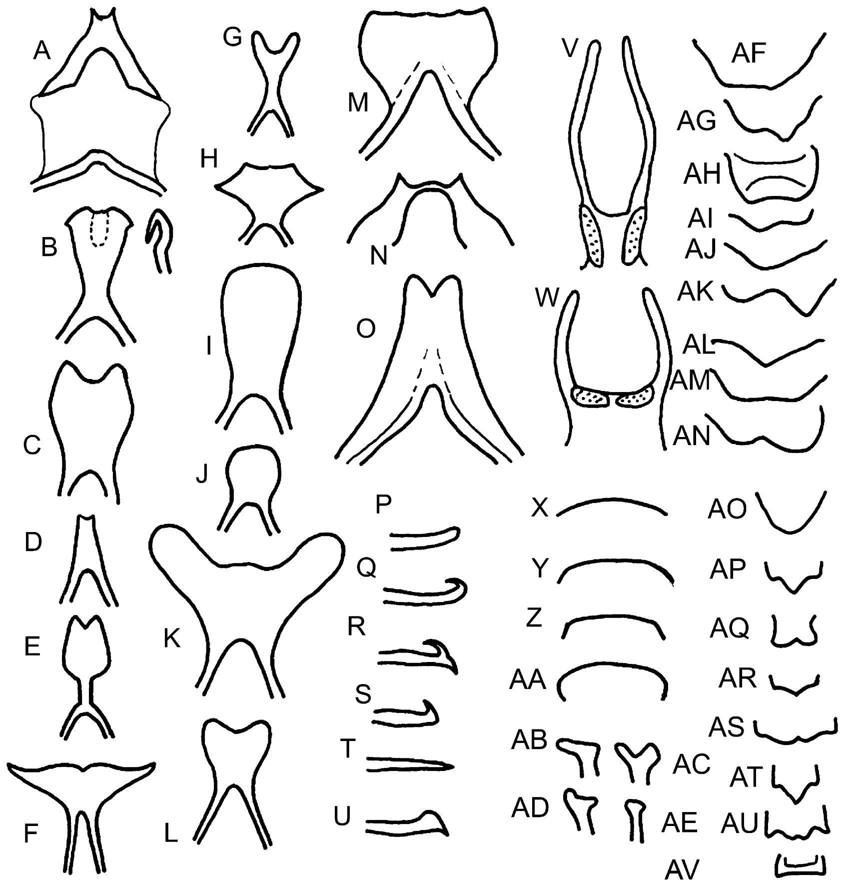

Fig. 5. Drawings of character states for Xeromelissinae. A–O, Male, disc of S7: A, *Colletes* (*Co.*) *cunicularius* 143-0; B, *Xeromelissa* (*X.*) *wilmattae* 143-1; C, *Chilicola* (*C.*) *plebeia* 143-2; D, *C. unicarinata* 143-3; E, *C. biguttata* 143-4; F, *C. venticola* 143-5; G, *C. obesifrons* 143-6; H, *C. paramo* 143-7; I, *C. hahni* 143-8; J, *C. prosopoides* 143-9; K, *Hyleoides* (*H.*) *concinna* 143-A; L, *Palaeorhiza* (*P.*) *perviridis* 143-B; M, *Meroglossa impressifrons* 143-C; N, *Euryglossa* (*E.*) *adelaidae* 143-D; O, *Scrapter* (*S.*) *heterodoxus* 143-E. P–U, Female lateral view of apex of pharyngeal rod: P, *H. concinna* 183-0; Q, *Xenochilicola* (*Xn.*) *diminuta* 183-1; R, *X. australis* 183-2; S, *C. chalcidiformis* 183-3; T, *Geodiscelis* (*G.*) *longiceps* 183-4; U, *Co. cunicularius* 183-5. V, W, Dorsal view of pharynx: V, *P. perviridis* 184-0, 187–0; W, *E. adelaidae* 184-1, 187-1. X–AA, Apical view of clypeus, ventral margin: X, *Co. cunicularius* 216-0; Y, *C. herbsti* 216-1; Z, *C. biguttata* 216-2; AA, *X. australis* 216-3. AB–AE, Base of cardo: AB, *P. perviridis* 190-0; AC, *S. nitida* 190-1; AD, *C. herbsti* 190-2; AE, *X. australis* 190-3. AF–AN, Apical scale of propodeum: AF, *Co. cunicularius* 225-0; AG, *S. nitida* 225-1; AH, *P. perviridis* 225-2; AI, *X. australis* 225-3; AJ, *X. wilmattae* 225-4; AK, *C. plebeia* 225-5; AL, *C. longiceps* 225-6; AM, *C. biguttata* 225-7; AN, *C. brzoskai* 225-8. AO–AV, Posterior margin of metasternum in ventral view: AO, *Co. cunicularius* 226-0; AP, *G. megacephala* 226-3; AQ, *X. xanthorhina* 226-4; AR, *C. mailen* 226-5; AS, *X. rozeni* 226-6; AT, *C. araucana* 226-7; AU, *C. vernalis* 226-8; AV, *C. longiceps* 226-9.

not attaining apex of mandible. Malar space linear to very short. Epistomal sulcus expanded below anterior tentorial pit almost to laterally reflexed portion of sulcus, pit not separated from sulcus. Frons sometimes with weak supra-antennal depressions; facial fovea absent, although sometimes represented by somewhat shiny area in female. Inner margin of compound eye emarginate (see Appendix 1) strongly convergent below. Head somewhat produced above compound eye, upper ocular tangent passing below lower margin of median ocellus. Male antenna elongate, most flagellomeres approximately 1.5× longer than broad (see Appendix 1), otherwise unmodified.

Mesosoma. Pronotal collar moderately long, 1.5× LOL, anterolateral corner rounded. Pre-episternal groove complete. Propodeum short, dorsal surface longer than metanotum but markedly shorter than scutellum. Male with spinose hind trochanter (except in *C. orophila*), femur somewhat swollen, hind tibia somewhat modified in some species. Hind tibial spurs unmodified, hind tarsal claws bifurcate. Stigmal perpendicular crossing near or basal to middle of second submarginal cell.

Metasoma. Male metasomal sterna unmodified. *Male terminalia.* S7 with one pair of lateral lobes (except in

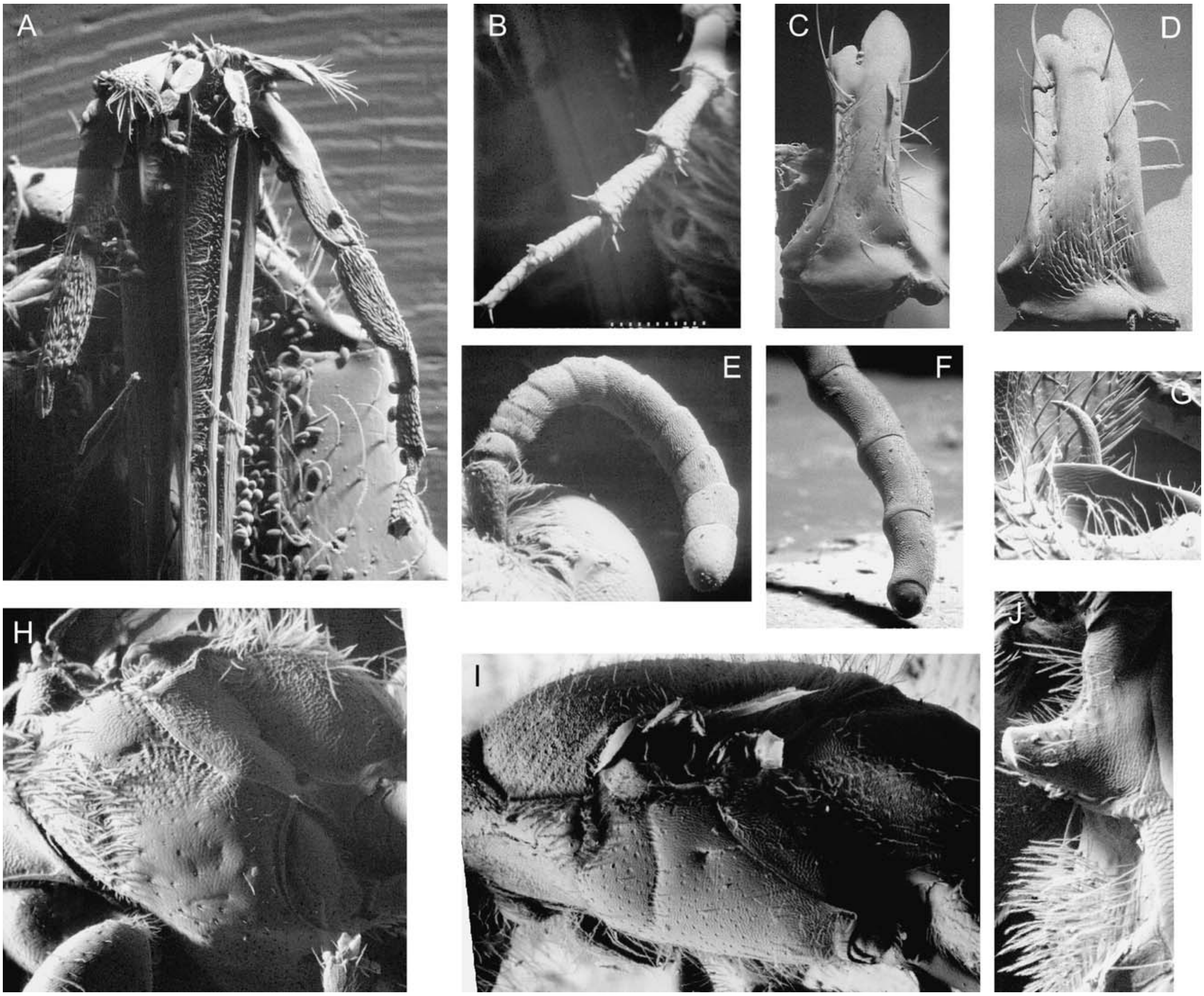

Fig. 6. Scanning electron micrographs of character states for Xeromelissinae. A, Ventral view of head of female *Xeromelissa australis* to show mouthparts 199-1, 202-2, 208-3. B, Maxillary palp of female *Chilicola neffi* 199-0, 202-0. C, Mandible of female *X. australis* 64-1, 65-1. D, Mandible of female *C. neffi* 64-0, 65-0. E, Antenna of male *C. australis* 86-2, 87-0, 88-0. F, Apex of antenna of male *C. vernalis* 87-1, 88-1. G, Apex of hind tibia of male *C. rubriventris* 123-5, 125-1. H, Lateral view of mesosoma of male *C. australis* 110-1. I, Lateral view of mesosoma of female *C. mailen* 110-0. J, Lateral view of S1 and S2 of male *C. neffi* 37-2, 131-2.

C. orophila) bearing transverse row or apical patch of hairs. S8 apical process elongate, widest at or close to apex, emarginate apically. Penis valve with pair of subapical dorsally orientated membranous lobes. Gonostylus clearly demarcated from gonoforceps.

Etymology. The name is based on Toro, in honour of the late Haroldo Toro, in recognition of his seminal studies of the bees of Chile in general, and of the Xeromelissinae in particular, and *Oediscelis*, the second oldest higher level name within the Xeromelissinae.

Additional species. *C. minor* (Philippi) 1866, *C. orophila* Toro & Moldenke 1979, *C. tregualemu* Packer 2007.

Comments. The inclusion of *C. orophila* within this subgenus is provisional. This subgenus is endemic to southern Chile.

Discussion

Phylogenetic analysis of a large data matrix for 47 members of the Xeromelissinae and eight outgroup taxa produced three equally most parsimonious trees. The consensus of these has genera outside of *Chilicola* and subgenera within it mostly strongly supported, but the relationships amongst subgenera are mostly weakly supported. Indeed, GC values show very different distributions for nodes that represent

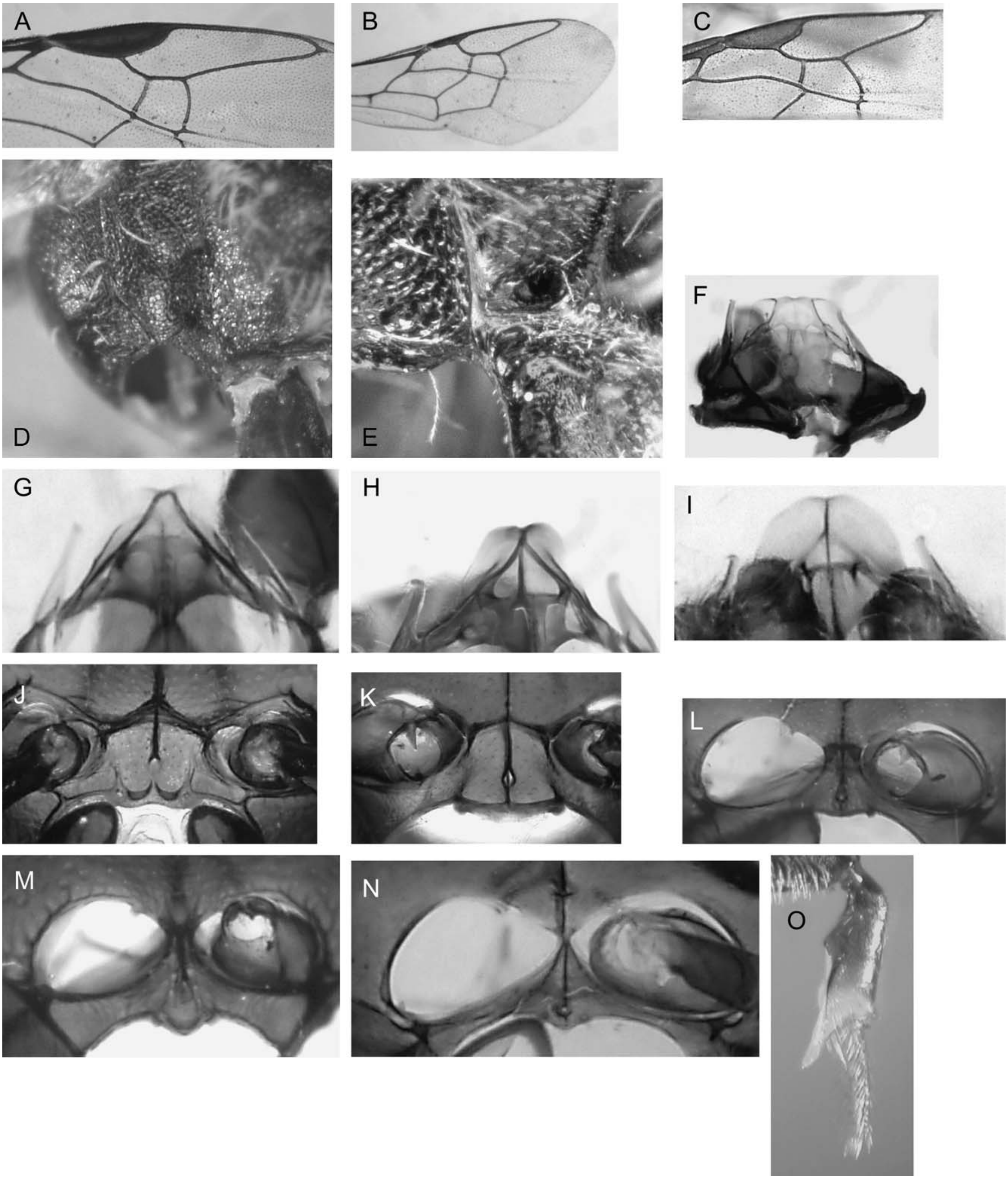

Fig. 7. Microphotographs of character states of Xeromelissinae and select outgroup exemplars. A, Subapical portion of forewing of *Chilicola plebeia* 231-2, 233-0. B, Forewing of *C. aenigma* 231-1. C, Subapical portion of forewing of *Euryglossa adelaidae* 231-0, 233-2. D, Lateral view of mesosoma of *Xeromelissa* (*X.*) *australis* 114-1. E, Lateral view of lower portion of metapleuron of *Scrapter heterodoxus* 114-0. F–I, Prosternal apophyses: F, *Xenochilicola diminuta* 93-1, 96-0; G, *C. herbsti* 96-1; H, *C. plebeia* 96-2; I, *C. aenigma* 96-3. J–N, Metasterna, ventral view: J, *Hylaeus* sp. 116-0, 226-2; K, *C. rubriventris* 116-1, 226-1; L, *C. olmue* 116-2; M, *C. herbsti* 116-3; N, *X. rozeni* 116-4. O, Hind tibia of male *C. friesei* 123-8.

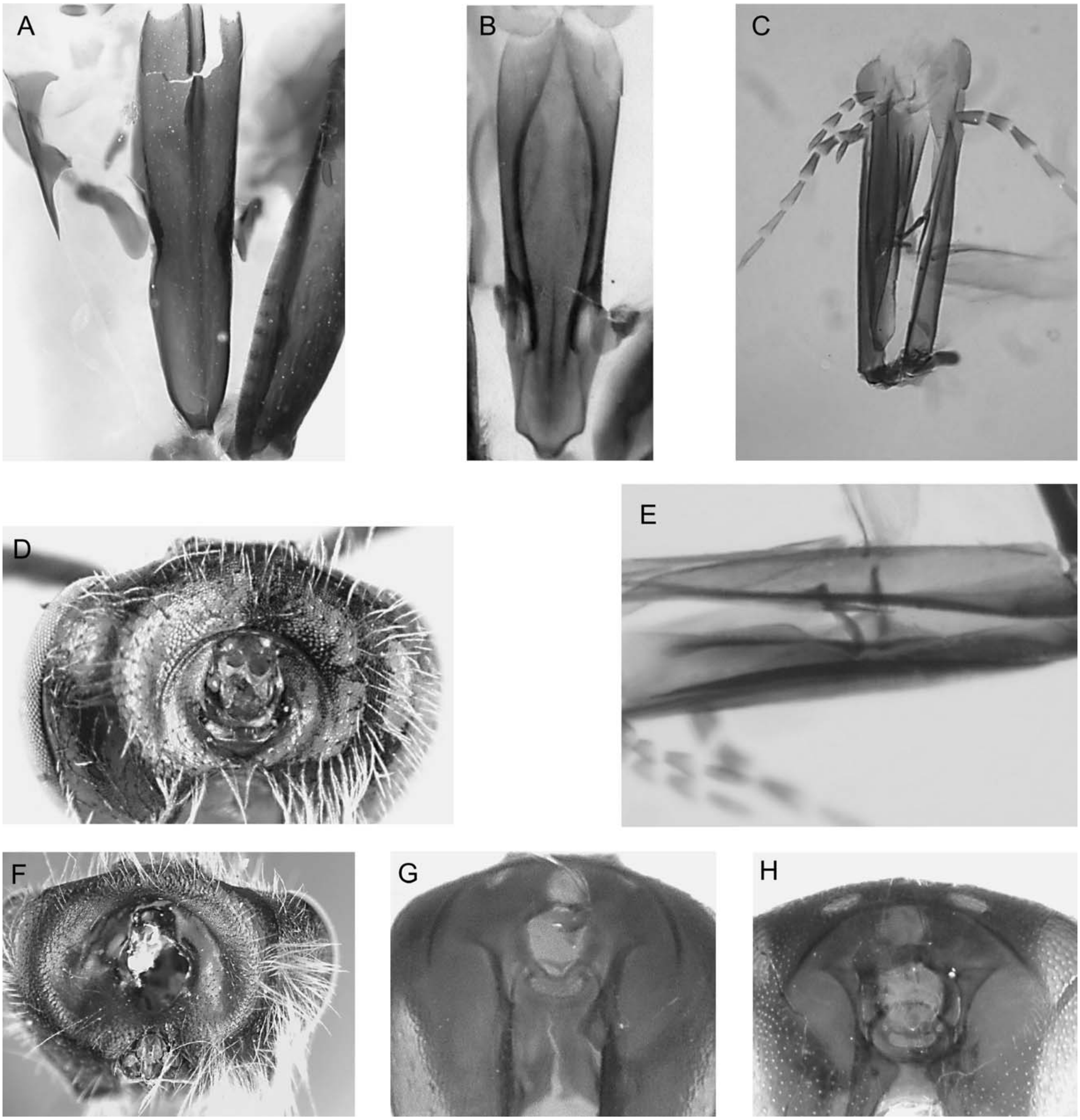

Fig. 8. Microphotographs of character states of Xeromelissinae and select outgroup exemplars. A–C and E, Prementa: A, *Colletes cunicularius* 205-0, 208-0, 210-0; B, *Scrapter heterodoxus* 205-2, 208-2, 210-1; C and E, *C. herbsti* 205-1, 208-1, 210-2; D, and F–H. Posterior views of head capsules: D, *Euhesma halictoides* 83-4, 84-1; F, *S. heterodoxus* 83-0, 84-0; G, *C. granulosa* 83-1, 84-3; H, *Xeromelissa wilmattae* 83-2, 84-2.

subgenera vs. those that represent groups of subgenera (Fig. 3). Of the latter, only (*Chilicola* + *Chilioediscelis*) receives more support (GC = 99) than the least well-supported subgenus (exceptions noted below) in the unweighted analysis (*Chilicola* s.s., GC = 89).

High support at the subgeneric level perhaps is surprising, given that exemplars were chosen to maximize the variation within subgenera. Low higher level nodal support is not so surprising, considering that taxa that exhibited unusual combinations of character states were chosen particularly for inclusion. This pattern of character state change might be explained by an early initial radiation within *Chilicola*, followed by anagenesis, high extinction rates, or both, prior to divergence leading to the extant members of the subgenera.

All subgenera accepted here (Table 1) are considered to be well supported, with the exception of *Anoediscelis* and *Oedisecelis*. Both subgenera became monophyletic only in the weighted analysis, and further research is needed on these taxa for the establishment of a stable classification within the genus.

The results of the phylogenetic analysis do not support the subdivision of the Xeromelissinae into two tribes: although [*Geodiscelis* + *Xeromelissa*] is a well-supported clade, *Xenochilicola* is removed from grouping with them to become sister to *Chilicola* by increasing the tree length by only one step. Consequently, I agree with Michener & Rozen's (1999) suggestion to dispense with tribal level classification within the subfamily. Engel's (2005) suggestion that the Xeromelissinae be subsumed within the Hylaeinae is refuted with the data at hand: in neither unweighted nor weighted analyses are these two taxa sister groups.

Supplementary material

The data matrix (Table S2) and list of the taxa used in the phylogenetic analysis, locality of the samples and museological provenance (Table S1) are available online at: www.blackwell-synergy.com under DOI reference: doi:10.1111/j.1365-3113.2007.00398.x.

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Appendix 1

Characters are divided into those scored for males and those scored for females. In many instances, characters scored for males also apply to females. Some characters scored for females also hold for males. Within each sex, characters are listed according to categories of colour, pubescence, surface sculpture and structure. Figure references are given for character states in many instances. They are capitalized for those illustrated herein (Figs 4–8), and lower case for those published elsewhere. Figures are of one of the species included herein wherever possible, or are congeneric and of the same sex, unless otherwise indicated by prefacing the author name by 'e.g.' Polymorphic binary characters are indicated by an X; polymorphic multistate characters are indicated by an X followed by the character states observed.

Characters scored from males

Colour (note that pale coloration here generally means yellow, although it may be white or pale orange).

1. *Labrum*: (0) dark (Gibbs & Packer, 2006: fig. 9A); (1) pale or pale marked (Gibbs & Packer, 2006: fig. 9B, C); (X) polymorphic.
2. *Mandible*: (0) black or dark brown (Gibbs & Packer, 2006: fig. 9A); (1) pale at least near base (Gibbs & Packer, 2006: fig. 9B, C).
3. *Clypeus*: (0) entirely dark (Gibbs & Packer, 2006: fig. 9F); (1) with pale central mark or entirely pale (Gibbs & Packer, 2006: fig. 9G, H); (2) pale laterally.
4. *Paraocular area*: (0) dark (Gibbs & Packer, 2006: fig. 9F); (1) partly pale (Gibbs & Packer, 2006: fig. 9 G); (2) entirely pale (Gibbs & Packer, 2006: fig. 9H).
5. *Malar area*: (0) dark; (1) pale marked.
6. *Genal area*: (0) dark; (1) yellow ventrally; (2) with yellow stripe.
7. *Supraclypeal area*: (0) dark (Gibbs & Packer, 2006: fig. 4C); (1) with some pale (Packer & Genaro, 2007: fig. 9A); (2) entirely pale (Toro & Moldenke, 1979: fig. 289).
8. *Scape*: (0) dark (Gibbs & Packer, 2006: fig. 3C); (1) anterior surface partly pale (Gibbs & Packer, 2006: fig. 1C); (2) entirely pale; (3) testaceous; (X) polymorphic (01).
9. *Pedicel*: (0) dark (Gibbs & Packer, 2006: fig. 3C); (1) at least anterior surface mostly pale (Packer & Genaro, 2007: fig. 2); (2) testaceous.
10. *Flagellum*: (0) dark (Gibbs & Packer, 2006: fig. 9K); (1) at least anterior surface of most flagellomeres pale (Gibbs & Packer, 2006: fig. 9L).
11. *Forecoxa*: (0) dark; (1) with some pale.
12. *Foretrochanter*: (0) dark; (1) with pale; (2) entirely pale.
13. *Forefemur*: (0) dark; (1) with some pale; (2) mostly pale; (3) entirely pale.
14. *Foretibia*: (0) dark; (1) pale anteriorly; (2) mostly pale; (3) entirely pale.
15. *Foretarsus*: (0) dark; (1) pale; (2) only basitarsus pale.
16. *Pronotal lobe*: (0) dark (Gibbs & Packer, 2006: fig. 10 A); (1) with pale marking (Gibbs & Packer, 2006: fig. 10B).
17. *Collar of pronotum*: (0) dark; (1) with pale marking.
18. *Pale mark on tegula*: (0) absent (Gibbs & Packer, 2006: fig. 10C); (1) spot (Gibbs & Packer, 2006: fig. 10D); (2) on posterior rim.

19. *Background of tegula*: (0) dark (Gibbs & Packer, 2006: fig. 10C); (1) testaceous; (2) translucent pale (Gibbs & Packer, 2006: fig. 10D).
20. *Anterior mesepisternal area*: (0) entirely dark; (1) pale marked.
21. *Mesepisternum anterior to mesocoxa*: (0) dark; (1) pale marked.
22. *Mesaxilla*: (0) dark; (1) pale marked.
23. *Wing veins*: (0) brown to black; (1) testaceous to cream.
24. *Metasoma*: (0) dark; (1) yellow apical bands; (2) yellow subapical bands; (3) mostly red; (4) broad orange bands on some terga; (5) orange basolaterally on some terga.

Pubescence.

25. *Hypostoma, dorsal to hypostomal carina*: (0) with hairs not forming a row; (1) forming a distinct row; (2) devoid of hairs.
26. *Appressed dense hairs on lower face and anteriorly on mesoscutum, covering surface or almost so*: (0) absent; (1) present.
27. *Mostly scale-like*: (0) no; (1) yes (Packer, 2005: fig. 1).
28. *Forebasitarsus with stiff bristles*: (0) no; (1) yes.
29. *Hair density on metanotum*: (0) sparse; (1) dense, obscuring surface.
30. *Metatibia with upwardly curved hairs on outer surface*: (0) absent; (1) present.
31. *Metatibia with apical hair tuft on outer surface*: (0) absent; (1) present (Michener, 2002: fig. 22g).
32. *Tergal hair bands*: (0) absent; (1) present apically (Gibbs & Packer, 2006: fig. 12F); (2) terga covered in long hair.
33. *Terga with short posterolaterally directed silvery hairs*: (0) absent; (1) present.
34. *Terga with basal bands of appressed hairs:* (0) absent; (1) present (Packer, 2005: fig. 1).
35. *Base of T2*: (0) lacking specialized hairs; (1) with dense semi-erect hairs; (2) with moderately long (< MOD) erect hairs of even length; (3) with long posteriorly directed hairs; (4) with long (≥ MOD) hairs uneven in length.
36. *S1*: (0) hairs extensive; (1) hairs only basally.
37. *S2 with specialized hair patch*: (0) absent; (1) present with apices forming concave surface (Fig. 6J); (2) present with apices forming convex surface; (3) present with hairs apically scrolled; (4) present as apicolateral tuft; (5) present as subapical row of posteriorly directed hairs; (6) apicolateral hair patch.
38. *S4*: (0) hairs similar to those of S3; (1) hairs long and erect; (2) with a dense apical row.
39. *S5*: (0) hairs similar to those of S3; (1) with hair pencil; (2) short, dense and fine; (3) apicolateral tufts.
40. *S6*: (0) unspecialized; (1) with a few long hairs (Gonzalez & Michener, 2004: fig. 4); (2) with lateral tufts (Genaro & Packer, 2005: fig. 14); (3) with posteromedially directed lateral short hair patch; (4) subapical row of posteriorly directed hairs; (5) velvety apical patch with anterior-most hairs anteriorly directed; (6) moderately long medially directed hairs covering almost entire surface; (7) dense apicolateral patch; (8) woolly erect hairs laterally.

Surface sculpture.

41. *Labrum*: (0) shiny; (1) dull.
42. *Labrum*: (0) impunctate; (1) sparsely punctate; (2) densely punctate.
43. *Clypeus and lower paraocular area*: (0) shiny; (1) dull.
44. *Clypeus*: (0) not deeply and distinctly punctate; (1) deeply and distinctly punctate.
45. *Paraocular area with punctures*: (0) not denser than on clypeus; (1) denser than on clypeus.
46. *Density of punctures of frons*: (0) sparse, interspaces larger than puncture diameters; (1) denser, interspaces at most subequal to puncture diameters; (2) crowded with sharp edges.
47. *Punctures of frons*: (0) round and discrete; (1) elongate in weak grooves.
48. *Size of punctures of mesoscutum*: (0) small, less than width of parapsidal line; (1) moderate in size, subequal to width of parapsidal line; (2) large, most punctures wider than parapsidal line.
49. *Depth of punctures of mesoscutum*: (0) shallow, indistinct; (1) moderately distinct; (2) deep and distinct.
50. *Density of punctures on mesoscutum*: (0) dense, interspaces less than puncture diameter; (1) interspaces approximately equal to puncture diameter; (2) sparse, interspaces greater than puncture diameter.
51. *Punctation of scutellum*: (0) not sparser than on mesoscutum; (1) sparser than on mesoscutum.
52. *Mesopleural punctation*: (0) equally dense above and below scrobal groove; (1) denser above scrobal groove; (2) sparser or absent above scrobal groove (Fig. 6I).
53. *Metapleural sculpture*: (0) similar above and below; (1) different above and below.
54. *Punctation of metapleuron*: (0) impunctate; (1) punctate; (2) rugostriate above; (3) rugose; (4) striate and punctate.
55. *Tergal punctures*: (0) distinct; (1) obscure, shallow; (2) none.
56. *T1 punctures*: (0) not dense, $i > d$; (1) dense, mostly $i \leq d$.
57. *T2 punctures*: (0) no denser than on T1; (1) denser than on T1.
58. *T2 basal area*: (0) unmodified; (1) transversely striate; (2) concave; (3) abruptly concave.

Structure.

59. *Labrum*: (0) transverse (Toro & Moldenke, 1979: fig. 7); (1) length and breadth subequal or longer than broad (Toro & Moldenke, 1979: fig. 293).
60. *Apical margin of labrum:* (0) straight; (1) strongly convex (Toro & Moldenke, 1979: fig. 293); (2) weakly convex (Toro & Moldenke, 1979: fig. 66); (3) biconcave (Toro & Moldenke, 1979: fig. 212); (4) concave medially (Toro & Moldenke, 1979: fig. 196); (5) triangular (Davies & Brothers, 2006: fig. 9); (6) apically truncate.

61. *Apical fringe of labrum*: (0) normal, not composed of strong bristles; (1) composed of strong bristles.
62. *Glossal apex*: (0) distinctly concave (e.g. Michener, 2000: fig. 46-1a); (1) very broad and weakly concave; (2) pointed (e.g. Michener, 2000: fig. 46-1i).
63. *Greatest depth of mandible in apical half*: (0) past subapical tooth; (1) basal to subapical tooth (Fig. 6D).
64. *Mandible*: (0) acetabular carina (Fig. 6D); (1) acetabular carina (Fig. 6C).
65. *Mandible base*: (0) with abductor swelling normal (Fig. 6D); (1) abductor swelling enlarged (Fig. 6C).
66. *Malar space*: (0) linear (Michener, 2000: fig. 44-2b); (1) present but not extensive (Michener, 2000: fig. 44-2e); (2) considerably longer than width of base of mandible (Michener, 2000: fig. 44-2g).
67. *Malar line*: (0) absent (Michener, 2000: fig. 44-2e); (1) present (Michener, 2000: fig. 44-2g). In taxa with a linear malar space, this character could not be assessed and was scored as inapplicable. The malar line is an extension of the epistomal sulcus (L. Packer, unpublished observations).
68. *Lateral portion of clypeus, laterad of epistomal lobe*: (0) margin rounded (Toro & Moldenke, 1979: fig. 315); (1) margin angulate (Michener, 2000: fig. 45-1b). This character can only be scored for taxa with a recurved epistomal sulcus (see character 71 below); those without a recurved sulcus were scored as inapplicable.
69. *Anterior tentorial pit*: (0) punctiform (Michener, 2000: fig. 44-2a); (1) comma-shaped (Michener, 2000: fig. 44-2c); (2) comma-shaped and deeply impressed; (3) triangular (Gibbs & Packer, 2006: fig. 3C); (4) elongate oval; (5) very long (Michener, 2000: figs 44-2f, 45-1).
70. *Epistomal sulcus*: (0) evenly convex; (1) angularly bent laterad below; (2) divergent and sinuate (Michener, 2000: fig. 44-2d); (3) recurved ventrally (Michener, 2000: fig. 45-1); (4) modified by deep depression in face (Michener, 2000: fig. 46-4i); (5) concave at mid-length, making clypeus somewhat hour-glass shaped (Michener, 2000: fig. 46-4g).
71. *Ratio of distance between outer margin of antennal socket and inner margin of compound eye to distance between inner margins of antennal sockets*: (0) > 1 (Michener, 2000: fig. 44-2f); (1) approximately equal (Michener, 2000: fig. 45-1a); (2) clearly < 1 (Michener, 2000: fig. 44-2a).
72. *Supraclypeal area in profile*: (0) angularly produced; (1) strongly convex (Michener, 2000: fig. 45-1b); (2) weakly convex or flat (Michener, 2000: fig. 45-1g); (3) modified by deep depression in paraocular region.
73. *Summit of supraclypeal area in profile:* (0) below antennal socket (Packer & Genaro, 2007: fig. 7A); (1) at lower tangent of antennal socket; (2) above lower tangent of antennal socket (Packer & Genaro, 2007: fig. 8B).
74. *Emargination of inner margin of compound eye*: (0) high up on eye; (1) near middle of eye; (2) low on eye. Species in which the inner margin of the eye is not concave were coded as inapplicable for this character; see next character.
75. *Emargination of inner margin of compound eye*: (0) long (Michener, 2000: fig. 45-2c); (1) intermediate in length (Packer, 2004a: fig. 7); (2) short (Michener, 2000: fig. 44-2d); (3) absent (Genaro & Packer, 2005: figs 1–3).
76. *Inner eye margins*: (0) parallel (Michener, 2000: fig. 46-4i); (1) slightly convergent below (Michener, 2000: fig. 45-1c); (2) strongly convergent below (Genaro & Packer, 2005: figs 1–3).
77. *Vertex*: (0) not transversely depressed behind ocellar triangle before vertex; (1) transversely concave behind ocellar triangle.
78. *Margin between vertex and occiput*: (0) rounded; (1) sharp; (2) strongly carinate to lamellate (Michener, 2000: fig. 44-2e).
79. *Head behind compound eyes*: (0) not produced (Packer & Genaro, 2007: fig. 17B); (1) produced; (2) strongly produced (Packer & Genaro, 2007: fig. 8B).
80. *Vertex in frontal view*: (0) convex (Gibbs & Packer, 2006: fig. 14J); (1) flat or concave (Gibbs & Packer, 2006: fig. 14K).
81. *Greatest length of genal area*: (0) near dorsal margin of compound eye (Michener, 2000: fig. 44-2d); (1) above middle of compound eye (Michener, 2000: fig 44-2b); (2) at middle of compound eye; (3) below middle of compound eye (Michener, 2000: fig. 45-2d).
82. *Orientation of genal area laterad of hypostomal area*: (0) ventrally produced mesad; (1) flat; (2) dorsally orientated mesad; (3) strongly dorsally orientated mesad; (4) dorsally orientated mesad only anteriorly.
83. *Occipital sulcus*: (0) strongest dorsally (Fig. 8F); (1) strongest laterally (Fig. 8G); (2) strongest dorsolaterally (Fig. 8H); (3) absent; (4) forming a strong inverted U-shaped depression (Fig. 8D).
84. *Postoccipital suture*: (0) fused medially (Fig. 8F); (1) almost fused medially (Fig. 8D); (2) clearly but not extremely widely separated (Fig. 8H); (3) extremely widely separated (Fig. 8G).
85. *F1 in profile*: (0) ventral surface divergent for its entire length, dorsal surface horizontal; (1) ventral surface abruptly divergent for basal portion only, dorsal surface horizontal; (2) ventral and lateral surfaces divergent; (3) ventral surface with a weak convexity at base; (4) ventral surface concave.
86. *Number of flagellomeres beyond F1 that are extremely short (approximately three times wider than long)*: (0) 0 (Packer & Genaro, 2007: fig. 2); (1) 1; (2) 2 or more (Fig. 6E).
87. *Flagellomeres*: (0) not dorsoventrally expanded towards apex (Fig. 6E); (1) dorsoventrally expanded towards apex (Fig. 6F). In some specimens, small membranous protrusions emerge from the apex of some flagellomeres, and it is likely that the expansions noted here house these structures, which are of unknown function.
88. *FXI*: (0) not unusually reduced (Fig. 6E); (1) reduced, oval or hemispherical (Fig. 6F).

89. *Orientation of anterior surface of pronotal collar*: (0) strongly sloping posterodorsally; (1) weakly sloping posterodorsally; (2) vertical; (3) sloping anterodorsally.
90. *Vertical pronotal carina*: (0) present; (1) absent.
91. *Length of pronotal collar medially (in cases in which the collar is not clearly separated from an anterior surface of the raised portion of the pronotum, it is taken to be that area of different sculpture that is usually, but not always, horizontal)*: (0) linear; (1) short, less than MOD (Packer & Genaro, 2007: fig. 17E); (2) of moderate length, subequal to MOD (Packer & Genaro, 2007: fig. 3E); (3) long, ≥ 2MOD (Packer & Genaro, 2007: fig. 8E).
92. *Humeral angle of pronotum*: (0) gradually rounded (Packer & Genaro, 2007: fig. 8E); (1) abruptly rounded; (2) angulate (Packer & Genaro, 2007: fig. 3E).
93. *Lateral propleural carina*: (0) weak; (1) strong forming a strong concavity posteriorly to receive trailing edge of lower lateral surface of pronotum (Fig. 7F).
94. *Probasisternum*: (0) transverse, clearly shorter than wide, with short anterior and posterior angulations (Fig. 4A); (1) diamond-shaped, at least as long as wide (Fig. 4B, C).
95. *Anterior prosternal process*: (0) narrowly angulate (Fig. 4A); (1) rounded (Fig. 4B); (2) broadly angulate (Fig. 4C).
96. *Dorsal arms of prosternal apophysis*: (0) not meeting before apex (Fig. 7F); (1) meeting more or less at apex (Fig. 7G); (2) appearing fused apically for a short distance (Fig. 7H); (3) appearing fused apically for a long distance (Fig. 7I).
97. *Basal articular forecoxal lobe*: (0) long and narrow (Fig. 4D); (1) comparatively short and broad (Fig. 4E).
98. *Longitudinal lateral carinae on forecoxa*: (0) none; (1) 1 (Fig. 4D); (2) 2 (Fig. 4E).
99. *Posterolateral forecoxal carina*: (0) far from foramen (Fig. 4E); (1) close to foramen (Fig. 4D). Taxa with no posterior lateral carina are coded as inapplicable.
100. *Longitudinal carina on mesal surface of forecoxa*: (0) present; (1) absent.
101. *Forefemur*: (0) lacking a strong ventral angle; (1) with a strong ventral angle (Fig. 4F).
102. *Shape of foretibia*: (0) widest basal to malus and gradually expanding from base to apex (Fig. 4K); (1) widest at base of malus but not gradually expanding from base to apex (Fig. 4L); (2) parallel-sided for most of length (Fig. 4M); (3) widest at base of malus, gradually expanding to apex (Fig. 4N).
103. *Glabrous patch on inner surface of foretibia*: (0) absent (Fig. 4K); (1) large, not ventrally located (Fig. 4M); (2) small (Fig. 4L); (3) large, ventrally positioned (Fig. 4N).
104. *Apex of malus*: (0) normal; (1) bent ventrally.
105. *Forebasitarsus*: (0) elongate, four times as long as broad or more; (1) less than three times as long as broad.
106. *Parascutal carina*: (0) entire; (1) notched (Packer & Genaro, 2007: fig. 13D).
107. *Mesophragma*: (0) very short, medial portion barely visible from dorsal view, lateral portions not visible (Fig. 4G); (1) short throughout (Fig. 4H); (2) of moderate length (Fig. 4I); (3) elongate (Fig. 4J).
108. *Apex of mesophragma*: (0) entire; (1) notched.
109. *Notaulus*: (0) absent; (1) linear; (2) represented by an area of crowded punctures.
110. *Orientation of episternal groove (excluding ventral portion)*: (0) vertical (Fig. 6I); (1) posteroventrally orientated (Fig. 6H).
111. *Episternal groove ventral to scrobal groove*: (0) present (Fig. 6I); (1) absent (Gibbs & Packer, 2006: fig. 13G).
112. *Lateral intercoxal area*: (0) short; (1) elongate, associated with modified hind leg; (2) elongate, not associated with hind leg modification.
113. *Lateral surface of mesosoma*: (0) moderately flat; (1) narrowed at metapleuron.
114. *Metapleural separation from mesocoxal cavity*: (0) normal, separated by clear metapseudosternal area (Fig. 7D); (1) very close or metapleuron apparently attaining mesocoxal cavity (Fig. 7E).
115. *Lower metapleural pit*: (0) at posterior margin of metapleuron (Fig. 7E); (1) near middle of metapleuron (Fig. 7D).
116. *Metasternum between mesocoxae*: (0) very wide, wider than posterior breadth (Fig. 7J); (1) wide but narrower than posterior breadth (Fig. 7K); (2) narrower, less than width of insertion of trochanter to coxa (Fig. 7L); (3) narrower than insertion of trochanter to coxa (Fig. 7M); (4) linear (Fig. 7N).
117. *Metasternum*: (0) flat; (1) curved dorsally posteriorly.
118. *Stigma*: (0) margins apically divergent (Fig. 7A); (1) parallel-sided (Fig. 7B).
119. *Number of submarginal cells*: (0) 3; (1) 2.
120. *Ratio of first to second abscissa of hind wing M + Cu:* (0) much less than 1; (1) subequal (Michener, 2000: fig. 44-1a); (2) longer than 1 (Michener, 2000: fig. 44-1b).
121. *Metatrochanter*: (0) unmodified (Toro & Moldenke, 1979: fig. 335); (1) with a short but broad projection; (2) with one or more short narrow processes (Packer & Genaro, 2007: fig. 15D); (3) with a broad, moderately long, projection (Packer & Genaro, 2007: fig. 10D); (4) with two processes joined by a carinate ridge (Packer & Genaro, 2007: fig. 16D, F); (5) with a bevelled edge; (6) with two processes of unequal length and form (Packer & Genaro, 2007: fig. 12D); (7) with a scythe-shaped process.
122. *Metafemur*: (0) unmodified, not swollen, convex ventrally (Packer & Genaro, 2007: fig. 4F); (1) swollen, flat ventrally (Packer & Genaro, 2007: fig. 9F); (2) swollen, concave ventrally (Packer & Genaro, 2007: fig. 15E); (3) very swollen, flat ventrally (Toro & Moldenke, 1979: fig. 250); (4) very swollen, concave ventrally (Packer & Genaro, 2007: fig. 16D); (5) not swollen, concave ventrally (Toro & Moldenke, 1979: fig. 356); (6) swollen apically (Toro & Moldenke, 1979:

fig. 297); (7) swollen, convex ventrally (Gonzalez & Michener, 2004: fig. 3).

123. *Metatibia*: (0) unmodified or weakly modified (Packer & Genaro, 2007: figs 3G, 9F); (1) gradually expanded to apex (Packer & Genaro, 2007: fig. 16D); (2) with a single carina on inner surface, otherwise unmodified (Packer & Genaro, 2007: fig. 5F); (3) produced apicoventrally (Packer & Genaro, 2007: fig. 15F); (4) swollen with pronounced crests (Michener, 2002: figs 31c, 32b); (5) very robust with deep subapical concavity (Fig. 6G) (Gibbs & Packer, 2006: fig. 15D); (6) considerably expanded, deepest apically, lacking deep concavity (Toro & Moldenke, 1979: fig. 228); (7) expanded with inner surface flat and surrounded by a carina (Toro, 1981: fig. 4); (8) flattened blade extending beyond insertion of basitibia (Fig. 7O); (9) expanded for apical one-third to one-quarter, three strong carinae ventrally (Packer & Genaro, 2007: fig. 10D–F); (A) triangular with oblique concavity ventrally (Packer & Genaro, 2007: fig. 12D, E).
124. *Metatibia*: (0) shorter than metafemur; (1) longer than metafemur.
125. *Metatibial spurs*: (0) unmodified (Gibbs & Packer, 2006: fig. 15E); (1) strongly sclerotized and curved (Fig. 6G).
126. *Metabasitarsus*: (0) unmodified (Packer & Genaro, 2007: fig. 10D); (1) with ventral swelling (Michener, 2002: fig. 32a); (2) outwardly concave (Packer & Genaro, 2007: fig. 13E).
127. *Dorsal surface of propodeum*: (0) very short, at most subequal in length to metanotum; (1) moderately long, longer than metanotum but not as long as scutellum; (2) long, subequal in length to scutellum.
128. *Propodeum in profile*: (0) dorsal and posterior surfaces forming a gradual curve; (1) angulate.
129. *T1*: (0) unmodified, approximately as broad as long; (1) narrow, longer than apical breadth such that metasoma appears subpetiolate.
130. *T2 gradulus*: (0) posteriorly bent at lateral extremity (Fig. 4O); (1) straight and directed towards spiracle (Fig. 4P); (2) straight and directed posterior to spiracle (Fig. 4Q).
131. *S1*: (0) unmodified (Fig. 4R); (1) with a process tapering to apex in profile (Fig. 4S); (2) with a process parallel-sided to obliquely truncate apex in profile (Figs 4S, 6J); (3) swollen apicoventrally (Fig. 4U).
132. *Lateral posteriorly orientated extensions of gradulus of S2*: (0) absent; (1) short; (2) long.
133. *S2 gradulus medially*: (0) straight; (1) bowed posteriorly; (2) absent.
134. *Gradulus or gradular marks on S3–S6*: (0) absent; (1) elongate, comma-shaped on S3 and S4 (Fig. 4V); (2) U-shaped on S3 and S4 (Fig. 4W); (3) very small, circular or semicircular (Fig. 4X); (4) entire on S3 and S4 (Fig. 4Y); (5) separated into medial and lateral portions (Fig. 4Z); (6) absent on S3 and S4, small on S5 and/or S6; (7) L-shaped on S3, small on S4 and S5; (8) S3–S5 with lateral angular portions only (Fig. 4AA).
135. *S4*: (0) unmodified; (1) with a pair of longitudinal swellings; (2) with a pair of processes, triangular to elongate (Michener, 2002: fig. 21).
136. *S5*: (0) unmodified; (1) apex deeply concave (Genaro & Packer, 2005: fig. 14).
137. *S7, ventral lobes*: (0) absent (Packer & Genaro, 2007: fig. 15G); (1) present (Packer & Genaro, 2007: fig. 16G).
138. *S7, ventral lobes with pigmented bands*: (0) absent; (1) present (Packer & Genaro, 2007: fig. 3H).
139. *S7 ventral lobes*: (0) membranous, kidney shaped, laterally directed (Michener, 2002: fig. 5c); (1) reduced to small swellings (Genaro & Packer, 2005: fig. 15); (2) crescentic (Toro & Moldenke, 1979: fig. 210); (3) not long, outer margin concave, posteriorly acute (Packer & Genaro, 2007: fig. 16G); (4) quadrate (Toro & Moldenke, 1979: fig. 229); (5) elongate, posteriorly directed and acutely pointed (Packer & Genaro, 2007: fig. 7H); (6) complex, folded and convoluted (Michener, 2002: figs 31b, 34d); (7) reduced to short flange (Packer & Genaro, 2007: fig. 5H); (8) membranous, anterolaterally directed (Toro & Moldenke, 1979: fig. 299); (9) posterolaterally directed, broad at base, pointed at apex (Gibbs & Packer, 2006: fig. 6G); (A) cleaver-shaped, narrow basally, quadrately expanded apically and with a posteriorly directed subbasal triangular process (Toro & Moldenke, 1979: fig. 345); (B) bifid (Gonzalez & Michener, 2004: fig. 5); (C) short with a quadrate ventral process (Packer & Genaro, 2007: fig. 17J); (D) transverse, rectangular (Michener, 2000: fig. 46-8k); (E) short, lateral extremity weakly concave (Michener, 2000: fig. 46-8i); (F) anterolaterally directed, short, sclerotized and rounded (Michener, 2000: fig. 46-8f).
140. *S7 dorsal lobes*: (0) absent (Packer, 2005: fig. 3); (1) present (Gibbs & Packer, 2006: fig. 6G).
141. *S7 dorsal lobe setation*: (0) none (Michener, 2002: fig. 34d); (1) apical row or pencil of normal hairs (Michener, 2002: fig. 5c); (2) apical patch or row of capitate hairs (Packer & Genaro, 2007: fig. 7H); (3) marginal row of laterally directed long hairs (Packer & Genaro, 2007: fig. 5G); (4) transverse row (Packer & Genaro, 2007: fig. 15G); (5) covered in short hairs (Toro & Moldenke, 1979: fig. 299); (6) with a tuft of hairs and a row of hairs; (7) with a basal tuft of hairs and an apical row (Toro & Moldenke, 1979: fig. 72); (8) with an anterior row of hairs on apical half (Packer & Genaro, 2007: fig. 9H); (9) with a basal tuft (Michener, 2000: fig. 46-8f).
142. *S7 dorsal lobe shape*: (0) digitiform (Toro & Moldenke, 1979: fig. 299); (1) elongate, laterally directed, strap-like (Michener, 2002: fig. 5c); (2) conical (Toro & Moldenke, 1979: fig. 345); (3) expanded, posteriorly concave, with a digitiform medial process; (4) approximately forming an equilateral triangle (Toro & Moldenke, 1979: fig. 194); (5) elongate, sclerotized, longitudinally orientated (Packer & Genaro, 2007; fig. 5G); (6) broad basally, abruptly narrowed apically (Michener, 2002: fig. 31b); (7) narrow, sclerotized and anteriorly directed; (8) reduced to a small thorn

(Packer & Genaro, 2007: fig. 3H); (9) elongate, curved posteriorly such that the dorsal lobes combined form a flattened W (Gibbs & Packer, 2006; fig. 6G); (A) short, laterally directed, oval and membranous (Toro & Moldenke, 1979: fig. 360).

143. *S7 apical disc*: (0) arrowhead shaped (Fig. 5A); (1) narrow, apex folded anteroventrally (Fig. 5B); (2) laterally convex, concave apically (Fig. 5C); (3) narrowed to shallowly concave apex (Fig. 5D); (4) tulip-shaped (Fig. 5E); (5) greatly expanded posterolaterally (Fig. 5F); (6) with narrow posteriorly directed processes (Fig. 5G); (7) angularly expanded laterally before apex (Fig. 5H); (8) elongate, subparallel sided to broadly rounded apex (Fig. 5I); (9) broad and short (Fig. 5J); (A) broadly expanded to rounded lobes apically (Fig. 5K); (B) cordiform (Fig. 5L); (C) lateral margins strongly convex outwardly, apex broadly truncate (Fig. 5M); (D) reduced to a narrow bridge uniting the two halves of the sternum (Fig. 5N); (E) narrowed to bilobate apex (Fig. 5O). Taxa for which this structure was too small or membranous to see clearly were coded as unknown.
144. *S8 apical process*: (0) elongate, broadened towards apex (Eardley, 1996: fig. 48); (1) narrowed and cylindrical towards apex (Packer, 2005: fig. 4); (2) narrowed to apex (Genaro & Packer, 2005: fig. 16); (3) divergent towards blunt or moderately concave apex (Michener, 2002: fig. 5c); (4) short, rounded (Toro & Moldenke, 1979: fig. 342); (5) elongate, almost parallel-sided, apex truncate; (6) long and narrow with bifurcate apex (e.g. Michener, 2002: fig. 17c); (7) short, converging from base to apex (Packer & Genaro, 2007: fig. 17K); (8) membranous, sinuate laterally, apex angularly excised, apicolaterally pointed (Packer & Genaro, 2007: fig. 10H).
145. *Junction between apical and lateral process of S8*: (0) indistinct (Eardley, 1996: fig. 48); (1) approximately right angular (Michener, 2000: fig. 46-8h); (2) broadly concave (Genaro & Packer, 2005: fig. 11); (3) deeply concave (Gibbs & Packer, 2006: fig. 6H); (4) narrowly but not deeply concave (Packer, 2005: fig. 4); (5) angularly excised (Toro & Moldenke, 1979: fig. 324).
146. *Apicoventral margin of gonobase*: (0) unmodified (Packer, 2005: fig. 5); (1) with a broad process (Gonzalez & Michener, 2004: fig. 7); (2) with a narrow process; (3) broadly triangular.
147. A*nterodorsal margin of gonobase*: (0) unmodified (Packer, 2005: fig. 5); (1) deeply concave (Genaro & Packer, 2005: fig. 17).
148. *Depth of gonoforceps*: (0) normal; (1) flattened.
149. *Internal basal ridge of gonoforceps*: (0) absent; (1) present. This is an internal ridge that extends posteriorly from the anterolateral corner of the dorsal surface of the gonoforceps.
150. *Inner margin of gonoforceps posteriorly*: (0) unmodified (Gibbs & Packer, 2006: fig. 6H); (1) angulate (Packer, 2005: fig. 5); (2) produced to a posteriorly orientated triangular process (Eardley, 1996: fig. 49).
151. *Mesoventral lobe of gonoforceps*: (0) absent (Michener, 2000: fig. 46-8g); (1) flat, medially directed (Toro, 1981: fig. 5); (2) swollen, broadly convex (Packer & Genaro, 2007: fig. 10I); (3) swollen, forming an obtuse or right angle (Packer, 2004a: fig. 5); (4) a swollen anteromedially directed broad lobe (Packer & Genaro, 2007: fig. 5I); (5) L-shaped with apical portion much longer than basal one (Packer & Genaro, 2007: fig. 3J); (6) acute anteriorly directed somewhat flattened lobe; (7) strongly sclerotized, posteromedially directed, apex pointed (Eardley, 1996: fig. 49); (8) acute, not flattened, anteromedially directed lobe (Gonzalez & Michener, 2004: fig. 7); (9) forming a large, somewhat membranous plate. This lobe is usually positioned so as to approximate the apex of the volsella; in state 1, it seems to be formed solely from the ventral sheet of the gonocoxite; in the others, it is more three dimensional and composed of the ventral and mesal surfaces.
152. *Mesal posteriorly directed lobe at base of gonostylus*: (0) absent (Gibbs & Packer, 2006: fig. 1I); (1) present, short, membranous (Toro, 1981: fig. 5); (2) present, membranous, long (Packer, 2005: fig. 5); (3) a sclerotized flap bearing strong setae on dorsal surface (Michener, 2000: fig. 46-8d).
153. *Volsella*: (0) cuspis not covered by ventral surface of gonoforceps (Gibbs & Packer, 2006: fig. 1I); (1) cuspis mostly hidden by gonoforceps in ventral view (Toro, 1981: fig. 1).
154. *Gonostylus*: (0) not clearly demarcated from rest of gonoforceps (Gibbs & Packer, 2006: fig. 6H); (1) clearly demarcated from remainder of gonoforceps (Packer, 2005: fig. 5).
155. *Gonostylus*: (0) rounded, not curved or concave medially (Michener, 2002: fig. 5a); (1) narrow, apicomedially orientated (Toro & Moldenke, 1979: fig. 291); (2) elongate, concave medially (Packer & Genaro, 2007: fig. 15I); (3) apicomedially curved (Gibbs & Packer, 2006: fig. 6I); (4) parallel-sided; (5) short and triangular (Genaro & Packer, 2005: fig. 17); (6) narrowing to apex from broad base in lateral view, curved ventrally in lateral view (Eardley, 1996: fig. 49); (7) broadest subapically and tapering to pointed apex in dorsal view (Eardley, 1996: fig. 6); (8) a narrow, well-sclerotized, ventrally bent hook (Michener, 2000: fig. 46-8d); (9) oval; (A) arising from apical inner margin of gonocoxite and somewhat digitiform (Packer, 2005: fig. 5).
156. *Gonostylus*: (0) without robust setae; (1) with robust setae, at least at base (Michener, 2002: fig. 46-8d).
157. *Penis valve*: (0) without strongly expanded lateral shelf; (1) with strongly expanded lateral shelf; (2) with shelf lateroventrally orientated (Michener, 2002: fig. 34a).
158. *Membranous lobes of penis valve*: (0) none (e.g. Michener, 2002: fig. 14a); (1) 1 (Gonzalez & Michener, 2004: fig. 7); (2) 2 (Gibbs & Packer, 2006: fig. 1I).
159. *Penis valve with unsclerotized region ventrally*: (0) absent; (1) present.

Characters scored from females

Colour.

160. *Labrum*: (0) dark; (1) pale.
161. *Mandible*: (0) dark; (1) pale marked; (2) almost entirely pale.
162. *Clypeus*: (0) dark; (1) distinctly yellow or white marked; (2) suffused with orange–brown.
163. *Paraocular area*: (0) dark; (1) with a small yellow mark; (2) with a large pale mark.
164. *Legs*: (0) almost entirely dark; (1) narrowly pale near leg joints; (2) more extensively pale.

Pubescence.

165. *Foretibial hairs*: (0) unbranched; (1) branched.
166. *Foretibial hairs*: (0) of normal length; (1) long and sparse laterally.
167. *Foretarsal rake*: (0) absent; (1) present.
168. *Mesotrochanteral comb*: (0) absent; (1) short, felt-like; (2) long but not made up of scopa-like hairs; (3) made up of scopa-like hairs.
169. *Mesofemoral comb*: (0) absent; (1) present.
170. *Mesotarsal rake*: (0) absent; (1) weak, one long hair per tarsomere; (2) strong, more than one long hair per tarsomere (Packer, 2005: fig. 2).
171. *Metatibial ventral hairs*: (0) long and palmate; (1) simple; (2) with one branch; (3) with a few branches, not palmate; (4) short palmate; (5) branches only towards apex.
172. *Lateral surface of propodeum*: (0) short hairs above, minute below; (1) large area of moderately long hairs above, minute below; (2) small area of moderately long hairs above, short hairs below; (3) short and sparse hairs all over; (4) very long hairs above, long hairs below; (5) dense very short hairs all over.
173. *Number of metasomal terga with apicolateral hair patches*: (0) 0; (1) 1; (2) 2; (3) 3; (4) terga covered in long hairs.
174. *Prepygidial fimbria*: (0) absent; (1) present.
175. *Scopa on S2*: (0) entire (Gibbs & Packer, 2006: fig. 12 I); (1) absent medially, scopa corbiculate (Gibbs & Packer, 2006: fig. 12J); (2) absent.
176. *Hairs on S2*: (0) simple; (1) with a few long branches on anterior of rhachis; (2) numerous short anterior branches; (3) plumose; (4) with branches on posterior of rhachis only; (5) capitate or blunt; (6) with anterior branches restricted to apex of rhachis; (7) almost palmate; (8) longest branches at mid-length, all anterior; (9) most hairs with branches on anterior of rhachis, a few with branches posteriorly.

Surface sculpture.

177. *Lower face striate*: (0) no (Gibbs & Packer, 2006: fig. 12L); (1) yes (Gibbs & Packer, 2006: fig. 12K).
178. *Frontal line below*: (0) very strong, almost lamellate; (1) a groove; (2) flat; (3) carinate.
179. *Frontal line above*: (0) carinate; (1) surface too densely punctate for line to be detectable; (2) groove; (3) flat or weakly impressed.
180. *Facial fovea*: (0) absent (Gibbs & Packer, 2006: fig. 6 A); (1) very deep, broad and distinct, situated near top of inner eye margin; (2) linear (Michener, 2000: fig. 46-4h); (3) a broad shallow groove; (4) shallow, oval (Michener, 2000: fig. 44-2c); (5) defined mesally by a carina (Michener, 2000: fig. 44-2d); (6) represented by a shiny area not otherwise differentiated from rest of frons; (7) clearly depressed only laterally and dorsally, otherwise differentiated only by lack of punctures; (8) very weakly impressed.
181. *Metanotum*: (0) rugose or with crowded punctures; (1) coarsely punctate on a smooth background; (2) indistinctly punctate or impunctate on a roughened background; (3) small sparse punctures on a smooth background; (4) indistinctly punctate on a smooth background; (5) small moderately dense punctures; (6) distinct well-separated punctures.

Structure.

182. *Oral surface of labrum*: (0) largely sclerotized; (1) sclerotized for apical half, margin linear; (2) sclerotized for apical half, margin strongly concave.
183. *Pharyngeal rods apically*: (0) blunt (Fig. 5P); (1) recurved (Fig. 5Q); (2) with a double angulation (Fig. 5R); (3) blunt with a subapical angulation (Fig. 5 S); (4) tapered to apex (Fig. 5T); (5) with ventral expansion narrowing to apex (Fig. 5U).
184. *Space between pharyngeal rods*: (0) at least twice as long as wide (Fig. 5V); (1) at most 1.5 times as long as wide (Fig. 5W).
185. C*ross-section of pharyngeal rods*: (0) rounded; (1) laterally compressed; (2) dorsoventrally compressed.
186. *Membrane between pharyngeal rods*: (0) entirely unsclerotized; (1) with a sclerotized patch.
187. *Sensory field of the pharyngeal plate*: (0) elongate (Fig. 5V); (1) transverse (Fig. 5W).
188. *Cardo*: (0) bent near base/comparatively straight; (1) sinuate/straight; (2) straight/straight; (3) concave/concave; (4) bent/straight; (5) bent/concave for a short distance; (6) bent/sinuate; (7) sinuate/sinuate; (8) concave/straight; (9) concave/concave for a short distance. The statement before the '/' refers to the shape of the cardo in ventral view; after the '/', it refers to the lateral view.
189. *Cardo in cross-section*: (0) approximately round; (1) laterally compressed.
190. *Basal articulation of cardo*: (0) cardinal lever more strongly developed than cardinal condyle (Fig. 5AB); (1) lever and condyle equally developed (Fig. 5AD); (2) V-shaped (Fig. 5AC); (3) blunt, not or barely produced laterad or mesad (Fig. 5AE).
191. *Depth of cardo*: (0) not unusually deep at mid-length; (1) unusually deep at mid-length.
192. *Mentum*: (0) sclerotized (Michener, 2000: fig. 33-4c); (1) not sclerotized (e.g. Michener, 2000: fig. 33-4e).

193. *Lorum*: (0) broad and heavily sclerotized (e.g. Michener, 2000: fig. 33-4e); (1) neither broad nor so heavily sclerotized (e.g. Michener, 2000: fig. 33-4g).
194. *Length of lorum*: (0) not unusually short; (1) short.
195. *Stipes*: (0) not bent laterally, curved in transverse section; (1) bent mesally for most of length, L-shaped in transverse section; (2) bent mesally only towards apex.
196. *Greatest depth of stipes*: (0) far from base; (1) at most at basal one-third of length.
197. *Galeal comb*: (0) not extended (e.g. Davies & Brothers, 2006: figs 37–42); (1) extended (Michener, 2000: fig. 47-1).
198. *Number of galeal comb teeth*: (0) ~ 30; (1) 10–25 (Michener, 2000: fig. 38-18a); (2) 1–9 (Michener, 2000: fig. 38-18b); (3) none.
199. *Maxillary palpomeres abruptly shortened at fourth*: (0) no (Fig. 6B); (1) yes (Fig. 6A).
200. *Maxillary palpomere 1*: (0) cylindrical; (1) concave ventrally; (2) concave with a longitudinal carina.
201. *Maxillary palpomere 2*: (0) glabrous; (1) with many hairs not arranged in a row; (2) with a single row of hairs.
202. *Maxillary palpomere 3*: (0) not denticulate or hairy; (1) denticulate; (2) denticulate and hairy (Fig. 6A).
203. *Number of maxillary palpomeres*: (0) 6; (1) 7 (Packer & Genaro, 2007: fig. 7E); (2) variable with apical ones deciduous.
204. *Lacinia*: (0) a small, membranous, hairy lobe; (1) somewhat triangular, unevenly narrowing to pointed apex; (2) a narrow sclerotized strap; (3) an elongate triangle, shorter than galeal blade; (4) narrow and elongate, much longer than galeal blade; (5) a broad lobe with dense robust hairs.
205. *Insertion of suspensorium on prementum*: (0) laterad (Fig. 8A); (1) interstitial (Fig. 8C, E); (2) interstitial in a deep pocket that is visible in ventral view of prementum (Fig. 8B).
206. *Location of insertion of suspensorium along length of prementum*: (0) beyond half way; (1) at middle; (2) in basal third; (3) close to base.
207. *Suspensorium*: (0) not angulate at mid-length; (1) angulate.
208. *Premental fovea*: (0) absent; (1) present only apically, not carinate laterally (Davies & Brothers, 2006: fig. 25); (2) carinate with carinae converging towards apex (Fig. 8B); (3) with subparallel weak carinae (Fig. 6A); (4) with strong subparallel carinae (Fig. 8 C); (5) with strong mesally directed lamellae.
209. *Premental rods*: (0) short; (1) long (Fig. 8C).
210. *Premental median thickening*: (0) entire (Fig. 8A); (1) basal only (Fig. 8B); (2) present only for apical one-quarter (Fig. 8C); (3) absent.
211. *Lateral surface of prementum*: (0) unmodified; (1) with minute pustules.
212. *Cross-section of prementum*: (0) much broader than deep; (1) depth and breadth subequal.
213. *Premental lobe*: (0) membranous, digitiform; (1) a wedge-shaped flatted lobe, narrowest at base; (2) triangular, flattened, narrowest at base; (3) rounded and hairy; (4) flattened, parallel-sided: (5) keel-like, hairy; (6) absent.
214. *Labial palp*: (0) basal palpomere cylindrical; (1) basal palpomere concave ventrally.
215. *Number of labial palpomeres*: (0) 4; (1) 3.
216. *Apical margin of clypeus in apical view*: (0) evenly and weakly convex (Fig. 5X); (1) abruptly convex laterally (Fig. 5Y); (2) bent almost at right angles laterally (Fig. 5 Z); (3) curved around base of labrum laterally (Fig. 5AA).
217. *Clypeus in profile*: (0) not evenly convex from base to apex, although may be considerably produced; (1) evenly convex.
218. *Compound eye*: (0) elongate (Packer, 2004a: fig. 6); (1) comparatively short and broad (Michener, 2000: fig. 45-1d).
219. *Gena*: (0) of normal length; (1) elongate.
220. *Ocellocular distance*: (0) no longer than diameter of lateral ocellus (Packer & Genaro, 2007: fig. 5C); (1) longer but not twice as long as diameter of lateral ocellus (Packer & Genaro, 2007: fig. 16C); (2) twice as long as diameter of lateral ocellus (Packer & Genaro, 2007: fig. 10C).
221. *Inner eye margin*: (0) as in male; (1) less convergent below than in male; (2) divergent below.
222. *Hypostomal carina in profile*: (0) sinuate; (1) convex; (2) straight.
223. *Scape*: (0) of normal length; (1) short; (2) very short.
224. *Number of flagellomeres beyond first that are very short*: (0) none; (1) 2 (e.g. Fig. 6E); (2) 3.
225. *Apical scale of propodeum*: (0) truncate, apical margin approximately half length of flange (Fig. 5AF); (1) shallowly concave, longest posteriorly (Fig. 5AG); (2) thickened laterad (Fig. 5AH); (3) short, weakly concave, longest anteriorly (Fig. 5I); (4) convex, rounded (Fig. 5J); (5) concave, longest posteriorly (Fig. 5AK); (6) triangular (Fig. 5AL); (7) truncate, apical margin two-thirds or more of flange length (Fig. 5AM); (8) very long and rounded posteriorly (Fig. 5AN).
226. *Metasternum posteriorly*: (0) an elongate U-shape (Fig. 5AO); (1) gently convex (e.g. Fig. 7K); (2) linear or concave (e.g. Fig. 7J); (3) short triangular (Fig. 5 AP); (4) bilobate (Fig. 5AQ); (5) obtusely angulate (Fig. 5AR); (6) narrowly indented (Fig. 5AS); (7) acutely angulate (Fig. 5AT); (8) with a medial indentation (Fig. 5AU); (9) ending in a transverse ridge (Fig. 5AV).
227. *Basitibial plate*: (0) absent; (1) entire; (2) fragmented (Michener, 2000: fig. 47-5h).
228. *Hind tibial spurs*: (0) of normal length, markedly less than half as long as basitarsus; (1) half as long as basitarsus.
229. *Hind tarsal claw*: (0) with a long inner tooth (Gibbs & Packer, 2006: fig. 15G); (1) with inner tooth reduced or absent (Gibbs & Packer, 2006: fig. 15H).
230. *Ratio of length of basal vein before Cu to Rs*: (0) very short, much less than half as long (Michener, 2000: fig. 46-5a); (1) half as long or almost half as long (e.g. Michener, 2000: fig. 47-2b); (2) greater than half as long (Gonzalez & Michener, 2004: fig. 1); (3) subequal

(e.g. Michener, 2002: fig. 3d); (4) longer; (5) much longer (e.g. Michener, 2002: fig. 3c).

231. *Stigmal margin in marginal cell*: (0) angularly convex (Fig. 7C); (1) straight or concave (Fig. 7B); (2) convex but not angulate (Fig. 7A).
232. *Stigmal perpendicular*: (0) basal to first recurrent vein; (1) in basal portion of second submarginal cell (Fig. 7 C); (2) in apical half of second submarginal cell (Fig. 7A); (3) apical to second recurrent vein (e.g. Michener, 2002: fig. 3c).
233. *Intersection of recurrent veins with vein $R_s + M$*: (0) both basal to respective submarginal crossveins (e.g. Michener, 2002: fig. 3c); (1) first interstitial with first submarginal crossvein, second basal to second crossvein (Fig. 7A); (2) both in second submarginal cell (Fig. 7C); (3) second recurrent vein enters third submarginal cell.
234. *Hind wing Cu*: (0) tubular and long (Michener, 2000: fig. 46-5a); (1) tubular but short; (2) reduced to, at most, an angulation (Michener, 2000: fig. 44-1).
235. *Median longitudinal carina on dorsal surface of propodeum*: (0) absent; (1) present.
236. *Propodeum towards apex*: (0) much of morphologically dorsal surface (metapostnotum) on declivous surface; (1) depressed, with somewhat raised rim; (2) flat, posterior margin rounded; (3) flat, posterior margin truncate; (4) posterolateral surface somewhat swollen around dorsal surface.
237. *T1*: (0) with longitudinal groove; (1) lacking longitudinal groove.
238. *Pygidial plate*: (0) absent; (1) triangular; (2) lateral margin sinuate, narrow but deep.
239. *S1 apex*: (0) entire; (1) with apicomedial slit.
240. *S5 specialized area*: (0) absent; (1) present, short; (2) moderately long, U-shaped; (3) long U-shaped or triangular.
241. *S6 with apical lobe to marginal zone*: (0) present (Packer, 2004b: fig. 6D); (1) absent.
242. *S6 in apical view*: (0) plate forming an acute angle; (1) forming an obtuse angle.
243. *S6 apex*: (0) without a median spine (Gibbs & Packer, 2006: fig. 15K); (1) with a median spine (Gibbs & Packer, 2006: fig. 15L).
244. *Lateral process of T7*: (0) straight, posteriorly directed (e.g. Packer, 2003: fig. 3D); (1) straight, laterally directed (e.g. Packer, 2003: fig. 3C); (2) sinuate, posteriorly directed (Packer, 2003: fig. 3E).
245. *Shape of T7 apodemal region*: (0) broadly rounded (e.g. Packer, 2003: fig. 3C); (1) short (Aravena & Toro, 1985: fig. 8); (2) elongate (Packer, 2003: fig. 3E).
246. *T7 apodemal region*: (0) not curved mesad (Aravena & Toro, 1985: fig. 8); (1) curved mesad (Aravena & Toro, 1985: fig. 3).
247. *Ventral arms of furcula*: (0) broad (e.g. Packer, 2003: fig. 11D); (1) narrow (e.g. Packer, 2003: fig. 11E).
248. *Sting shaft*: (0) curved ventrad (e.g. Packer, 2003: fig. 11B); (1) straight (e.g. Packer, 2003: fig. 11C); (2) curved dorsad.

Appendix 2

Key to genera of Xeromelissinae and subgenera of Chilicola

1\. Epistomal lobe recurved, projecting onto clypeus; metasoma marked with yellow or white in both sexes 2
Epistomal lobe not recurved, at most forming a right angle; metasoma not marked with yellow (except in males of one Chilean species which has long apicolateral projections to S5) 3

2(1). Maxillary palps unmodified; dense squamate hairs basally on metasomal terga .... *Geodiscelis*
Maxillary palps modified, either markedly narrowed at fourth segment, extremely long, or with three well-developed segments followed by a variable number of deciduous segments; squamate hairs lacking on metasomal terga basally...... *Xeromelissa*

3(1). Dorsal surface of propodeum subequal in length to metanotum; small bees, less than 4 mm in length; male S5 deeply concave; female S2 not corbiculate .... *Xenochilicola*
Dorsal surface of propodeum usually clearly longer than metanotum, if subequal then bees clearly longer than 5 mm; male S5 not deeply concave; female S2 usually corbiculate, if not, then hind tibial spurs strongly sclerotized and curved..... *Chilicola* 4

4(3). Hind tibial spurs robust, sclerotized and strongly curved apically 5
Hind tibial spurs unmodified, sometimes dark in coloration but never robust or strongly curved apically 6

5(4). Teeth on tarsal claws considerably reduced or absent, face not markedly concave in profile but only weakly produced, female with S2 not in the form of a corbicula, female S6 lacking apical spine .... *Chilioediscelis*
Teeth on tarsal claws of normal size, face markedly concave in profile, female scopa on S2 forming a corbicula, female S6 with apical spine-like process .... *Chilicola*

6(4). Anterior tentorial pit punctiform and not situated in an elongate groove, triangular or comma-shaped depression or ventrally elongate towards apex of clypeus 7
Anterior tentorial pit not punctiform, either situated in an elongate groove formed by expansion of the epistomal sulcus beneath the pit, in a triangular or comma-shaped depression or considerably elongate towards apex of clypeus 8

7(6). Male hind leg unmodified, or if somewhat expanded (in *C. plebeia*, a Chilean species), then clypeus produced into lateral angles and mandibles considerably enlarged (females cannot be differentiated from those of the following subgenus) .... *Anoediscelis*
Male hind leg strongly modified, trochanter with an angulate process, femur considerably swollen, tibia variously modified but always at least somewhat

swollen apically; clypeus not produced into lateral angles and mandibles not enlarged (females cannot be differentiated from those of the previous subgenus) .... *Oediscelisca*

8(6). Parascutal carina notched .... *Stenoediscelis*
Parascutal carina entire 9

9(8). Anterolateral corners of pronotum sharply angulate .... *Obesicola*
Anterolateral corners of pronotum rounded, usually obtuse, if almost a right angle then clearly not sharply angulate 10

10(9). Stigmal perpendicular crossing marginal cell close to or beyond second recurrent vein ..... *Hylaeosoma*
Stigmal perpendicular crossing marginal cell more basally, near middle of second submarginal cell or interstitial with first recurrent vein 11

11(10). Male with supraclypeal area marked with yellow; female with hairs of scopa of S2 unbranched and blunt or capitate .... *Capitatiscopa*
Male with supraclypeal area entirely dark; female without blunt or capitate hairs on S2 12

12(11). Facial fovea deep and distinct and separate from inner margin of compound eye .... *Prosopoides*
Facial fovea absent although sometimes represented by an area somewhat shinier than surrounding frons, this area is not depressed or set off by raised areas from the rest of the frons 13

13(12). Pronotum elongate, medial length of collar at least one-third of anterior width of collar; maxillary palp with seven segments .... *Pseudiscelis*
Pronotum not elongate, medial length of collar at most one-quarter of anterior width of collar; maxillary palp with six segments 14

14(13). Male S4 with a pair of projections, triangular or elongate; female with dorsal surface of propodeum bearing irregular, radiating striae .... *Oroediscelis*
Male S4 unmodified, female with dorsal surface of propodeum differently sculptured, if striate then striae parallel or forming fingerprint-like pattern 15

15(14). Both sexes without apicolateral patches of white hairs on metasomal terga .... *Unicarinicola*
Both sexes with apicolateral patches of white hair at least on T1–T2 16

16(15). Male with ventral projection on S1 and/or apical flagellomere reduced to a small hemispherical nub; both sexes with stigmal perpendicular at first recurrent vein 17
Male without ventral projection on S1 and apical flagellomere of normal length; both sexes with stigmal perpendicular in middle of second submarginal cell .... *Toroediscelis*

17(16). Male with projection on S1 tapered to apex in profile or absent; male (except in *C. hahni* from central Chile) with last antennal flagellomere short, appearing hemispherical or narrowly oval; both sexes with dorsal surface of propodeum subequal in length to metanotum (except in *C. setosicornis* Packer from Northern Argentina) .... *Oediscelis*
Male with projection on S1 almost parallel sided to obliquely truncate apex; apical flagellomere subequal in length to penultimate one; both sexes with dorsal area of propodeum longer than metanotum (known only from Chile) .... *Heteroediscelis*