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Phylogenetic systematics and a revised generic classification of anthidiine bees
(Hymenoptera: Megachilidae)

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Abstract

The bee tribe Anthidiini (Hymenoptera: Megachilidae) is a large, cosmopolitan group of solitary bees that exhibit intriguing nesting behavior. We present the first molecular-based phylogenetic analysis of relationships within Anthidiini using model-based methods and a large, multi-locus dataset (five nuclear genes, 5081 base pairs), as well as a combined analysis using our molecular dataset in conjunction with a previously published morphological matrix. We discuss the evolution of nesting behavior in Anthidiini and the relationship between nesting material and female mandibular morphology. Following an examination of the morphological characters historically used to recognize anthidiine genera, we recommend the use of a molecular-based phylogenetic backbone to define taxonomic groups prior to the assignment of diagnostic morphological characters for these groups. Finally, our results reveal the paraphyly of numerous genera and have significant consequences for anthidiine classification. In order to promote a classification system based on stable, monophyletic clades, we hereby make the following changes to Michener's (2007) classification: The subgenera *Afranthidium* (*Zosteranthidium*) Michener and Griswold, 1994, *Afranthidium* (*Branthidium*) Pasteels, 1969 and *Afranthidium* (*Immanthidium*) Pasteels, 1969 are moved into the genus *Pseudoanthidium*, thus forming the new combinations *Pseudoanthidium* (*Zosteranthidium*), *Pseudoanthidium* (*Branthidium*), and *Pseudoanthidium* (*Immanthidium*). The genus *Neanthidium* Pasteels, 1969 is also moved into the genus *Pseudoanthidium*, thus forming the new combination *Pseudoanthidium* (*Neanthidium*). Based on morphological characters shared with our new definition of the genus *Pseudoanthidium*, the subgenus *Afranthidium* (*Mesanthidiellum*) Pasteels, 1969 and the

genus *Gnathanthidium* Pasteels, 1969 are also moved into the genus *Pseudoanthidium*, thus forming the new combinations *Pseudoanthidium* (*Mesanthidiellum*) and *Pseudoanthidium* (*Gnathanthidium*).

Keywords: Megachilidae, Anthidiini, phylogenetics, integrative systematics, nesting behavior

1. Introduction

The megachilid tribe Anthidiini (Apoidea, Megachilidae) includes approximately 870 described species (Ascher and Pickering 2015) and is widely distributed on all continents except Australia, where only one genus is native, and in the Caribbean and Antarctica, where it is absent (Michener 1979). They are broad, robust bees and are usually easily distinguished from other megachilids by their dark cuticula and striking yellow, white, or red integumental markings (Michener 2007).

Anthidiine bees exhibit fascinating nesting behavior. Some build their nests in preexisting cavities, such as pithy plant stems, empty snail shells, or abandoned insect galleries (Müller et al. 1997; Xambeu 1896; Ferton 1911; Fabre 1891; Grandi 1934; Pasteels 1977; Claude-Joseph 1926); others build exposed nests on the surfaces of rocks, trees, or other structures (Gess and Gess 2007; Ferton 1901; Pasteels 1977; Westrich 1989; Muller 1931; Müller et al. 1997); several lineages excavate their own burrows in soil (O'Brien 2007; Evans 1993; Micheli 1935; Maneval 1936; Pasteels 1977; Müller et al. 1997). The French naturalist, Jean-Henri Fabre, described the “resinous

70 putty” and “felted cotton” typical of anthidiine nests (Fabre 1914). Fabre’s descriptions
71 highlight an intriguing aspect of their nesting biology: unlike members of the megachilid
72 tribes Osmiini and Megachilini, whose primary nest-building materials may include leaf
73 pieces, mud, pebbles, resin, flower petals, and masticated leaf pulp, the preferred *materia*
74 *prima* of Anthidiini is almost exclusively limited to one of two principal sources: plant
75 resins and plant fibers. These materials may be supplemented with pebbles, leaf strips,
76 grains of sand, animal fur, snail shell fragments and bits of bark or other debris
77 (Michener 2007).

78
79 Fabre was among the first to classify Anthidiini into two broad groups based on
80 primary nest-building material (Fabre 1891). He recognized *les résiniers*, those
81 anthidiines that use plant resins to build their nest cells, as a separate group from *les*
82 *cotonniers*, or those anthidiines that use plant fibers to build their nest cells. Michener’s
83 (2007) suprageneric classification also divided Anthidiini into two groups: Series A
84 includes 23 non-parasitic genera in which females have three or four rounded or blunt
85 mandibular teeth separated by shallow concavities, while Series B includes eight genera
86 with five or more sharp teeth separated by acute V-shaped notches. While Michener’s
87 groups are based on mandibular dentition and Fabre’s groups are based on nesting
88 behavior, Michener’s Series A coincides with *les résiniers* of Fabre and his Series B
89 coincides with *les cotonniers* of Fabre, implying a relationship between female
90 mandibular dentition and choice of nesting material (Perez 1879, 1889; Pasteels 1977).

91
92 The conspicuous morphological diversity of anthidiine bees has inspired multiple

classification systems, with some authors preferring to divide the tribe into many small genera and other authors preferring fewer, much larger, genera. Pasteels' 1969 classification of Old World Anthidiini includes 46 genera and Urban and Moure's (2012) classification of neotropical Anthidiini includes 39 genera. While the genera presented by Michener (2007) are more inclusive than those of either Pasteels (1969) or Urban and Moure (2012), he also favors a system of multiple, small genera: his 2007 classification divides worldwide Anthidiini into 37 genera.

In contrast, Warncke's (1980) classification of Palaearctic anthidiines recognizes only two genera: *Anthidium*, which encompasses all non-parasitic anthidiines, and *Stelis*, which includes the parasitic anthidiines (for comparison, Michener's (2007) classification recognizes ten non-parasitic Palaearctic genera). Warncke (1980) justified his classification, noting that "*Anthidium* differs in many groups but no group has developed a new characteristic. It seems not right to split it [the genus *Anthidium*] in many genera (for example Pasteels 1969)." Michener (2007) objects, arguing that Warncke's system groups together very different forms into what is likely a paraphyletic group.

Despite the fascinating natural history of Anthidiini and the general lack of consensus regarding the assignment of anthidiine species to genera, there has been no treatment of the phylogenetic relationships among worldwide lineages of anthidiine bees and the evolutionary history of the tribe remains largely unknown. The only existing cladistic analysis of Anthidiini was presented by Müller (1996); it included only non-cleptoparasitic western Palaearctic anthidiines, however, making it difficult to assess

relationships on a world-wide basis. In this paper we reconstruct the evolutionary history of the tribe Anthidiini using model-based methods and a large, multi-locus dataset, as well as a combined dataset consisting of both molecular and morphological characters. We offer the first molecular-based phylogenetic hypothesis of relationships within the tribe and discuss the impact of our results on anthidiine classification. We also examine the utility of morphological characters historically used to recognize taxa. Finally, we propose a generic-level revision of Anthidiini.

2. Materials and methods

2.1 Taxon sampling

For molecular analyses, we sampled extensively within the tribe Anthidiini, choosing 123 representative species from 28 genera and 69 subgenera (Table 1). We chose 38 outgroup taxa representing all other megachilid tribes, as well as all other families of bees. Collection localities and DNA voucher numbers are listed in Table 1. Voucher specimens are deposited in the Cornell University Insect Collection, in the collection at the USDA-ARS Bee Biology and Systematics Laboratory at Utah State University, and in the Litman-Praz insect collection in Neuchâtel, Switzerland.

For combined molecular-morphological analyses, we used our molecular dataset together with a subset of the taxa present in the megachilid morphological matrix published by Gonzalez et al. (2012). We used all of the anthidiines included by Gonzalez et al. (2012) (27 genera in total), as well as 26 of their outgroup genera that overlapped with the outgroup taxa present in our molecular dataset. A total of 53 taxa were thus

represented by morphological data in our combined analyses. In cases where a subgenus in the morphological matrix was represented by a different species than the species for the same subgenus in the molecular matrix, we created a chimeric taxon labeled to subgenus. Use of the morphological dataset allowed us to include four anthidiine genera for which fresh specimens for molecular analyses were unavailable: *Gnathanthidium*, *Anthidioma*, *Indanthidium* and *Xenostelis*. The ingroup for our combined analysis thus includes 32 genera, or 89% of generic-level diversity for the tribe.

2.2 Dataset and alignment

We sequenced a total of 5081 base pairs from four nuclear protein-coding genes (CAD, 879 base pairs; NAK, 1488 base pairs; LW-rhodopsin, 672 base pairs; and EF1-alpha, F2 copy, 750 base pairs) and one nuclear ribosomal gene (28S, 1292 base pairs). All DNA extraction and sequencing protocols follow Danforth et al. (1999). PCR primers and conditions for CAD, NAK, LW-rhodopsin, and 28S were identical to those listed in Table S3 from Litman et al. (2011). For EF1-alpha, we used the forward primer HaF2for1 (5' GGG YAA AGG WTC CTT CAA RTA TGC 3') together with an anthidiine-specific reverse primer, F2RevAnth (5' AAT CAG CAG CRC CYT TCG GTG G 3'). The PCR conditions for this set of primers were 45s@94°C /45s@58°C /1m@72°C, run for 36 cycles; the PCR runs were preceded by 5 minutes at 94°C and followed by 7 minutes at 72°C.

Sequencing was performed at the Cornell University Life Sciences Core Laboratories Center using an Applied Biosystems 3730xl DNA analyzer and at the

University of Neuchâtel using an Applied Biosystems 3500 DNA analyzer. Sequences were edited using Sequencher version 5.3 sequence analysis software (Gene Codes Corporation 2015). Alignments were performed using MAFFT (Kato and Standley 2013) and then adjusted by eye in MacClade (Maddison and Maddison 2005); all introns were removed from protein-coding genes. The ribosomal gene 28S was aligned by secondary structure following Kjer (1995), using the 28S secondary structure model of *Apis mellifera* (Gillespie et al. 2006); unalignable regions were removed. New sequence data are archived in GenBank and all DNA accession numbers are listed in Table 2.

2.3 Test for nucleotide compositional bias

Nucleotide compositional bias has been cited as a source of error in phylogenetic reconstruction (Ho and Jermiin 2004; Jermiin et al. 2004; Praz and Packer 2014), namely by causing lineages sharing a similar bias to cluster together due to convergent evolution rather than shared ancestry (Sheffield 2013). RY recoding (in which each nucleotide is recoded simply as either as a purine or pyrimidine) has been proposed as a means of eliminating this bias, namely by homogenizing nucleotide frequencies among taxa (Woese et al. 1991). In order to test for nucleotide compositional bias, we divided our dataset into fourteen partitions, one for each of the three codon positions of each protein coding gene, as well as two partitions corresponding to the stem and loop regions of 28S. Each partition was tested individually using the “Base/AA frequencies” command in PAUP* 4.0a142 (X86) (Swofford 2003), which implements a chi-square test for nucleotide heterogeneity among taxa. The test was restricted to ingroup taxa. We found the third codon position of NAK to exhibit a significant compositional bias ($P < 0.001$)

and thus this partition was recoded (i.e. all A's and T's were replaced by G's and C's, respectively; Thomas et al. 2013). The recoding effectively removed the bias from the partition ($P = 1.00$ after recoding and subsequent reanalysis in PAUP) and the recoded partition was used in all subsequent analyses. We compared this recoding method with another method in which all purines were replaced by "0" and all pyrimidines by "1". In both maximum likelihood and Bayesian analyses, topologies, branch lengths and node support values using this binary recoding method were highly congruent with the results of the first recoding method (differences were restricted to weakly supported nodes, which were not implicated in taxonomic changes). Only results using the first recoding method are presented.

2.4 Partitioning regime and model-testing

We used the same fourteen partitions described above (using the recoded third position of NAK) and performed a greedy search using the BIC metric in PartitionFinder v1.1.0 (Lanfear et al. 2012) to establish a partitioning regime and determine appropriate models of nucleotide substitution. We ran the analysis twice, once to find models adapted for use in RAxML and once to find models adapted for use in MrBayes. Nine partitions were suggested for RAxML (best models in parentheses): the third position of NAK (GTR+I+G); the first position of opsin (GTR+I+G); the second position of opsin (GTR+I+G); the stem region of 28S (GTR+I+G); the first positions of CAD, EF1-alpha and NAK (GTR+I+G); the third positions of CAD and opsin (GTR+I+G); the second position of CAD and the loops region of 28S (GTR+I+G); the second positions of EF1-alpha and NAK (GTR+I+G); and the third position of EF1-alpha (GTR+I+G). Ten

partitions were suggested for the MrBayes analysis (best model in parentheses): the first positions of CAD, EF1-alpha, and NAK (GTR+I+G); the second position of CAD and the loops region of 28S (HKY+I+G); the third position of CAD (GTR+I+G); the second positions of EF1-alpha and NAK (GTR+I+G); the third position of EF1-alpha (HKY+I+G); the first position of opsin (HKY+I+G); the second position of opsin (SYM+I+G); the third position of opsin (SYM+I+G); the third position of NAK (HKY+I+G); and the stems region of 28S (HKY+I+G).

Both the alpha parameter of the gamma distribution and 'I' (i.e. the parameter that allows for an estimation of invariant sites) account for near-zero rates of nucleotide substitution in maximum likelihood and Bayesian analyses. The inevitable correlation between these two parameters makes it impossible to optimize them independently of one another and may be a source of error in parameter estimation (Yang 2006 and references therein; Stamatakis 2014). Following the remarks of Yang (2006) and Stamatakis (2014), we excluded the 'I' parameter from all models also including the gamma distribution, despite the recommendations of PartitionFinder. Thus for all nine models cited for the RAxML analysis and all ten models cited for the MrBayes analysis, the 'I' parameter was eliminated and the gamma distribution retained.

We used the same partitions as described above in combined molecular-morphological analyses, plus an additional partition for morphological data. In RAxML analyses, the morphological partition was modeled using the multi-state option with a GTR model (-K GTR). In MrBayes, we used a Lewis model.

2.5 Phylogenetic analyses

We performed maximum likelihood phylogenetic analyses using RAxML v.8.1.11 (sequential version raxmlHPC, Stamatakis 2006) hosted by the Cipres Science Gateway (Miller et al. 2010). We ran 1000 bootstrap replicates using the rapid bootstrap analysis and then calculated the best-scoring maximum likelihood tree based on the original alignment for both molecular and combined molecular-morphological analyses. We also used MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003), hosted by the Cornell University BRC Bioinformatics Facility, to perform Bayesian phylogenetic analyses. For molecular analyses in MrBayes, we ran six independent analyses for a total of 72 million generations; for mixed molecular-morphological analyses, we ran four independent analyses for a total of 160 million generations. We used Tracer (Rambaut et al. 2014) to evaluate stationarity and determine an appropriate burnin.

3. Results

3.1 Molecular analyses

Maximum likelihood and Bayesian analyses of molecular data yield well-resolved, congruent phylogenies (Figures 1, S1). Our results support the monophyly of Michener's Series B but his Series A is paraphyletic, with the genus *Trachusa* forming a strongly supported monophyletic clade, sister to the rest of Anthidiini (sister relationship supported by 100% maximum likelihood (ML) bootstrap support; 97% posterior probability). Our phylogeny demonstrates that anthidiine bees fall into five major

suprageneric clades; given the behavioral differences exhibited by these five clades, we present them as a replacement for Michener's Series A and Series B (Table 3). These clades are: (1) the *Trachusa* group (100% ML bootstrap; 100% posterior probability); (2) the *Anthidium* group (100% ML bootstrap; 99% posterior probability); (3) the *Anthodioctes* group (100% ML bootstrap; 99% posterior probability); (4) the *Dianthidium* group (84% ML bootstrap; 95% posterior probability); and (5) the *Stelis* group (98% ML bootstrap; 100% posterior probability). The *Anthidium* group, which corresponds to Michener's Series B, are those anthidiines that use plant fibers in nest construction. The *Trachusa*, *Anthodioctes*, and *Dianthidium* groups, all included in Michener's Series A, represent those bees that use resin in nest construction (with the exception of the cleptoparasitic genera *Hoplostelis* and *Austrostelis* in the *Anthodioctes* group). The *Stelis* group, also included in Michener's Series A, is exclusively cleptoparasitic.

The descriptions of two genera not included in the phylogeny, *Trachusoides* and *Apianthidium*, suggest a close phylogenetic relationship with *Trachusa*; in order to accommodate the likely future addition of these genera to the *Trachusa* group, we choose to refer to this clade as the *Trachusa* group (and not simply as the genus *Trachusa*). The genus name *Hoplostelis* Dominique, 1898 is the oldest in the *Anthodioctes* group; we prefer to name the group, however, for a genus whose behavior is representative of the group in general. For this reason, we name the group after the oldest available non-cleptoparasitic genus name in the group, *Anthodioctes* Holmberg, 1903.

While Michener (2007) included the genus *Aspidosmia* in his Series A, both molecular and morphological data refute the placement of this genus in the tribe Anthidiini (Litman et al. 2011; Gonzalez et al. 2012). A recent paper officially removed *Aspidosmia* from Anthidiini and placed it in its own tribe, Aspidosmiini (Gonzalez et al. 2012). *Aspidosmia* is thus excluded from our classification of Anthidiini.

The results of our phylogenetic analyses challenge the current classification of anthidiine bees, primarily because many genera and several subgenera emerge as paraphyletic. The *Anthidium* group includes the genera *Serapista*, *Anthidium*, *Afranthidium*, *Pseudoanthidium*, *Neanthidium*, *Anthidioma*, *Indanthidium* and *Gnathanthidium* (the last three genera represented here only by morphological data). The central and southern African genus *Serapista* is strongly supported as monophyletic (100% ML bootstrap support; 100% posterior probability) and is moderately well-supported as the sister clade to the rest of the *Anthidium* group (63% ML bootstrap; 98% posterior probability). The remaining members of the *Anthidium* group form three clades. One of these clades is the genus *Anthidium*, strongly supported as monophyletic in both ML and Bayesian analyses (100% ML bootstrap support; 100% posterior probability).

The second clade contains most but not all subgenera of the genus *Afranthidium* (i.e. *Afranthidium*, *Oranthidium*, *Domanthidium*, *Capanthidium*, *Mesanthidium*, and *Nigranthidium*). This clade is strongly supported in both ML and Bayesian analyses (95% ML bootstrap; 100% posterior probability). The subgenera *Afranthidium* (*Capanthidium*), *Afr.* (*Mesanthidium*), and *Afr.* (*Nigranthidium*) are paraphyletic.

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301 The third clade contains all members of *Pseudoanthidium*, three subgenera of
302 *Afranthidium* (*Immanthidium*, *Branthidium* and *Zosteranthidium*) and the genus
303 *Neanthidium*. This clade is strongly supported in both ML and Bayesian analyses (96%
304 ML bootstrap; 99% posterior probability).

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306 The *Anthodioctes* group consists of the Central and South American genera
307 *Aztecanthidium*, *Notanthidium*, *Epanthidium*, *Anthodioctes*, *Hoplostelis*, *Austrostelis*,
308 *Hypanthidium*, *Hypanthidioides*, and *Duckeanthidium*; these genera form a strongly
309 supported monophyletic clade sister to the *Dianthidium* group + the *Stelis* group.
310 *Hoplostelis* is strongly supported as the sister taxon to *Austrostelis* in both Bayesian and
311 ML analyses (100% ML bootstrap; 100% posterior probability); *Anthodioctes*
312 (*Bothranthidium*) *lauroi* is strongly supported as the sister taxon to *Hoplostelis* +
313 *Austrostelis* (100% ML bootstrap; 92% posterior probability). A sister-group relationship
314 between *Hypanthidium* and *Duckeanthidium* is moderately supported in ML analyses
315 (71% ML bootstrap) and strongly supported in Bayesian analyses (100% posterior
316 probability). While Bayesian analyses recover highly resolved relationships for other
317 clades in the group, ML analyses suggest that all other phylogenetic relationships within
318 this group are unclear.

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320 In the *Dianthidium* clade, the Asian genus *Bathanthidium* is the sister taxon to a
321 clade consisting of the Central and North American genera *Paranthidium* and
322 *Dianthidium*. These three genera are a strongly supported monophyletic group (96% ML

bootstrap; 96% posterior probability) which is sister to a clade containing the genera *Rhodanthidium*, *Icteranthidium*, *Eoanthidium*, *Anthidiellum*, *Pachyanthidium*, *Benanthis*, *Cyphanthidium* and *Plesianthidium* (96% ML bootstrap; 100% posterior probability), all eastern hemisphere taxa with the exception of *Anthidiellum*, which is widespread in both hemispheres; this sister group relationship is well-supported in ML analyses (84% ML bootstrap) and strongly supported in Bayesian analyses (95% posterior probability). These eleven genera together form the *Dianthidium* group. The subgenus *Anthidiellum* (*Pycnanthidium*) is strongly supported as monophyletic (100% ML bootstrap; 100% posterior probability); this subgenus, together with the genera *Eoanthidium* and *Benanthis*, are well supported as monophyletic in ML analyses (87% ML bootstrap) and strongly supported in Bayesian analyses (100% posterior probability). The subgenera *Pachyanthidium* (*Trichanthidium*) and *Pachyanthidium* (*Pachyanthidium*) are each strongly supported as monophyletic, although the genus *Pachyanthidium* is paraphyletic. The genera *Anthidiellum* and *Plesianthidium* are also paraphyletic in both Bayesian and ML analyses. *Plesianthidium* (*Spinanthidiellum*) and all members of *Pachyanthidium* and *Anthidiellum* (with the exception of subgenus *Pycnanthidium*) together constitute a well-supported clade (73% ML bootstrap support; 100% posterior probability). The genus *Rhodanthidium* is paraphyletic in both ML and Bayesian analyses, although node support is low.

The genera *Stelis*, *Euaspis* and *Afrostellis* form the strongly supported *Stelis* group. The lineages *Stelis* (*Stelidomorpha*) *nasuta*, *Stelis* (*Heterostelis*) *ruficornis*, *Stelis* (*Heterostelis*) *annulata*, *Stelis* *rozeni*, *Afrostellis*, and *Euaspis* form a weakly supported

clade at the base of the *Stelis* group (51% ML bootstrap; 89% posterior probability).
Stelis (Heterostelis) hurdi, *Stelis (Heterostelis) anthidioides* and the three species of *Stelis (Dolichostelis)* present in our phylogeny form a monophyletic group, sister to *Stelis (Malanthidium) + Stelis (Protostelis) + Stelis (Stelis)*. The subgenus *Stelis (Stelis)* is strongly supported as monophyletic (95% ML bootstrap; 100% posterior probability), as are the subgenera *Stelis (Dolichostelis)* (100% ML bootstrap; 100% posterior probability) and *Stelis (Malanthidium)* (99% ML bootstrap; 100% posterior probability). *Stelis (Heterostelis)* is paraphyletic.

3.2 Combined molecular-morphological analyses

We used combined molecular-morphological analyses to tentatively place four rare genera missing from our molecular dataset. No taxonomic changes were made based on these analyses. In the absence of molecular data for these taxa, however, the use of morphological data gives an idea of the placement of these four genera in the context of a molecular-based phylogenetic backbone.

Maximum likelihood and Bayesian analyses of combined data are presented in Figure S2 and S3. In ML analyses of combined data, *Indanthidium crenulaticauda* forms a polytomy with *Afranthidium* and *Anthidium*. In Bayesian analyses, combined data weakly support *Indanthidium crenulaticauda* as the sister group to the genus *Serapista* (<50% posterior probability). *Anthidioma chalicodomoides* is in a polytomy with the genus *Anthidium* in ML analyses; in Bayesian analyses, *Anthidioma chalicodomoides* is nested within the subgenus *Anthidium (Anthidium)* (59% posterior probability). In ML

analyses, combined data place *Gnathanthidium prionognathum* in a polytomy with *Pseudoanthidium* (*Micranthidium*) and *Afranthidium* (*Immanthidium*). In Bayesian analyses, combined data weakly support *Gnathanthidium prionognathum* as the sister taxon to *Pseudoanthidium* (*Micranthidium*) (<50% posterior probability). Finally, Bayesian analyses of combined data weakly support the placement of *Xenostelis polychroma* within the subgenus *Stelis* (*Stelis*). In ML analyses of combined data, *Xenostelis polychroma* is weakly supported as the sister taxon to Anthidiini (<50% ML bootstrap).

4. Discussion

4.1 The Trachusa group

Griswold and Michener (1988) placed the New World subgenera *Heteranthidium*, *Legnanthidium*, *Trachusomimus*, and *Ulanthidium* into the genus *Trachusa*; Michener and Griswold (1994b) later added the Old World subgenera *Archianthidium*, *Congotrachusa*, *Massanthidium*, *Metatrachusa*, *Orthanthidium*, and *Paraanthidium*. The genus *Trachusa* thus includes eleven subgenera and is identifiable by a number of synapomorphies, including the lateral ocellus closer to the eye than to the posterior margin of the vertex (although equidistant in *T. (Heteranthidium) larreae* and *bequaerti*, and *T. (Metatrachusa)*) (Griswold and Michener 1988; Michener 2007); a median ocellus whose anterior margin is closer to the antennal bases than to the posterior margin of the vertex (or equidistant) (Griswold and Michener 1988); fore- and mid-tibial spines produced as blunt, obtuse projections that extend along the tibial surface as carinae (Griswold and Michener 1988); vein cu-v of the hind wing oblique and one-half the

length of the second abscissa of M+Cu (vein cu-v oblique but less than one-half the length of M+Cu in *T. (Metatrachusa)*) (Michener 2007); and a small male T7 curved under the abdomen so that its dorsal surface faces ventrally (Michener 2007).

The position of *Trachusa* as sister to the rest of Anthidiini is supported by a series of characters that are plesiomorphic with respect to other anthidiines, including fine punctation and the general absence of carinae, sulci, and propodeal pits (Michener 1948; but see subgenera *Orthanthidium* and *Paraanthidium*, Michener 2007, both of which have a carinate omaulus and carinate or lamellate pronotal lobes). The six subgenera present in our phylogeny together form a strongly supported monophyletic group (Figures 1, S1-S3); the future addition of the remaining subgenera to our phylogeny will clarify whether the genus as it is currently defined is monophyletic.

4.2 The Anthidium group

In the genus *Anthidium*, our results support the recent synonymization of *Anthidium* (*Callanthidium*) with the subgenus *Anthidium* (*Anthidium*) (Gonzalez and Griswold 2013): *Anthidium illustre*, formerly placed in the subgenus *Callanthidium*, is clearly nested within the subgenus *Anthidium*.

In the *Afranthidium* clade, the subgenera *Afr. (Capanthidium)*, *Afr. (Mesanthidium)*, and *Afr. (Nigranthidium)* are all paraphyletic (Figures 1, S1-S3). Michener (2007) may have unintentionally predicted the paraphyly of *Afr. (Capanthidium)*, when he described the marked differences in male genitalia within the subgenus as either “parallel-sided” (as

in *Afr. capicola*) or “paddle-shaped” (as in *Afr. rubellulum*). *Afranthidium* (*Capanthidium*) *capicola* is strongly supported as the sister taxon to a clade consisting of *Afr. (Mesanthidium) carduele*, *Afr. (Mesanthidium) alternans* and *Afr. (Capanthidium) schulthessi*; *Afr. (Capanthidium) rubellulum*, on the other hand is more closely related to *Afr. (Nigranthidium) sp. nov. 1*. Furthermore, *Afr. (Capanthidium) poecilodontum*, described as “anomalous” by Michener (2007) due to distinctive wing venation shared with *Afr. (Nigranthidium) concolor*, is strongly supported as the sister taxon to *Afr. (Nigranthidium) sp.* A simple solution would be to synonymize *Afr. (Capanthidium)*, *Afr. (Mesanthidium)*, and *Afr. (Nigranthidium)*. We prefer, however, to defer a final decision regarding these subgenera until further taxa may be included in the phylogeny and a more informed taxonomic decision may be made.

Combined molecular-morphological data place three genera represented only by morphological data within the *Anthidium* group (Figures S2, S3). Michener (2007) likened *Gnathanthidium prionognathum* to the subgenus *Pseudoanthidium* (*Micranthidium*), based on the almost lamellate preoccipital ridge, pronotal lobe, omarus, and scutellar truncation, the absence of lateral teeth on male T6 and T7, and the bilobed male T7. Our results indeed suggest a close relationship between the genus *Gnathanthidium* and the subgenera *P. (Micranthidium)* and *P. (Immanthidium)*.

Indanthidium crenulicauda exhibits a suite of characters that makes it difficult to assess its phylogenetic affinities based on morphological data alone. Like the genus *Anthidium*, its yellow tergal bands are divided into four spots each, yet it differs from

Anthidium in the punctuation and shape of the depressed marginal zone in the male T5 (Michener and Griswold 1994b). *Indanthidium* has arcuate subantennal sutures, as does the genus *Pseudoanthidium*; unlike *Pseudoanthidium*, however, males lack combs on S1-S6 (Michener and Griswold 1994b). *Indanthidium* is unique in the shape of the male T7 and in its one-segmented maxillary palpi (Michener and Griswold 1994b). Maximum likelihood analyses of combined data place *Indanthidium* in a polytomy with the genera *Anthidium* and *Afranthidium* (Figure S2), while Bayesian analyses place it as the sister taxon to the genus *Serapista* (Figure S3). The actual phylogenetic position of *Indanthidium* may only be revealed upon the addition of genetic data.

The genus *Anthidioma* is a rare, southern African bee lacking the carinae and maculations found in most anthidiines and known only from female specimens. While certain morphological characters are shared between *Anthidioma*, *Afranthidium* (*Afranthidium*) and *Afranthidium* (*Oranthidium*) (Michener 2007), our analyses suggest a closer phylogenetic relationship between *Anthidioma* and the genus *Anthidium* (Figures S2, S3). Determining the phylogenetic position of *Anthidioma* may be facilitated by an evaluation of male morphological characters, thus far unknown, as well as the addition of genetic data.

4.3 The *Anthodiocetes* group

The majority of the *Anthodiocetes* group are notable for the presence of juxtantennal carinae (only absent in *Hypanthidium*, *Notanthidium*, and *Aztecanthidium*) and postspiracular pits on the propodeum (only absent in *Notanthidium*, and

461 *Aztecanthidium*), characters rare elsewhere in Anthidiini. Juxtantennal carinae are absent
462 in the *Trachusa* and *Anthidium* groups, rare in the *Dianthidium* group (only some
463 *Dianthidium* and *Eoanthidium*), and found only in *Euaspidis* and *Larinostelis* in the *Stelis*
464 group; postspiracular pits are likewise absent in the *Trachusa* and *Anthidium* groups,
465 present only in *Bathanthidium* and some *Anthidiellum* in the *Dianthidium* group and
466 occur sporadically in the *Stelis* group: all *Afrostelis*, *Euaspidis*, *Larinostelis*, *S. rozeni*, *S.*
467 (*Protostelis*), *S. (Dolichostelis)*, and some *S. (Malanthidium)*, *S. (Heterostelis)*, *S. (Stelis)*.

469 Relationships in the *Anthodioctes* group are generally weakly supported, with the
470 exception of the clade consisting of (*Hoplostelis*+*Austrostelis*)+*Anthodioctes*
471 (*Bothranthidium*). *Hoplostelis* was originally proposed by Pérez as a subgenus of *Stelis*
472 (see Griswold and Michener 1988) but has long been recognized as a distinct genus
473 (Griswold and Michener 1988); it differs from New World *Stelis* by the presence of
474 distinct foveae between the scutum and scutellum, the short, transverse scutellum, the
475 presence of a single spine on fore- and mid-tibiae, the apicolateral tooth of the male sixth
476 sternite, and the quadridentate female mandible (Griswold and Michener 1988).
477 *Hoplostelis* also lacks the distinctive clubbed gonostylus of male *Stelis* (Griswold and
478 Michener 1988). Our results clearly indicate the monophyly of the clade
479 *Hoplostelis*+*Austrostelis* and thus strongly support two independent origins of
480 cleptoparasitism in Anthidiini, one in the *Hoplostelis*+*Austrostelis* clade and the second
481 in the *Stelis* clade (Figures 1, S1-S3).

482
483 The genus *Austrostelis* was originally recognized as a subgenus of *Hoplostelis*

(Michener and Griswold 1994a); the presence, however, of unique morphological characters which clearly distinguish it from other members of *Hoplostelis*, including the sparse punctation of T1 and T6, the elongate body form, and the unmodified female mandible, have caused it to be recognized as a unique genus (Michener 2007). Although our analyses support the possibility that *Austrostelis* and *Hoplostelis* are two distinct genera, only the inclusion of other species from both genera will clarify whether the genera are reciprocally monophyletic.

While the majority of the *Anthodiocetes* group are nest-building bees, both *Hoplostelis* and *Austrostelis* are cleptoparasites. Hosts of *Hoplostelis* are bees of the tribe Euglossini, while hosts of *Austrostelis catamarcensis* include *Epanthidium tigrinum* (Zanella and Ferreira 2005) and, possibly, members of the genus *Hypanthidioides* (Michener and Griswold 1994a). While the cleptoparasitic strategy of *Austrostelis* is not known, adult female *Hoplostelis* invade nest cells that have already been closed by the host and then kill the host's larvae; the cleptoparasitic larvae develop on the pollen collected by the host bee for her own offspring (Bennett 1966). Given the preference of both *Austrostelis* and *Hoplostelis* for resin-nesting hosts, the affinity of cleptoparasites of closed host nests for closely related hosts (Litman et al. 2013 and references therein), and the close phylogenetic relationship between *Austrostelis*, *Hoplostelis* and the subgenus *Anthodiocetes* (*Bothranthidium*) *lauroi*, we predict that *Anthodiocetes* (*Bothranthidium*) may eventually be revealed as a host for other species of *Austrostelis*.

Two nest-building genera, *Notanthidium* and *Anthodiocetes*, are revealed as

paraphyletic, although node support values, especially in the case of *Notanthidium*, are weak. If the addition of further data indeed supports the paraphyly of these genera, it may be more appropriate to recognize current subgenera (as per Michener 2007) as genera, as proposed by Urban and Moure (2012).

4.4 *The Dianthidium group*

The subgenus *Dianthidium* (*Mecanthidium*) was originally described in the genus *Paranthidium* (Michener 1942). Although Michener (1942) did not specify the characters that he felt allied the subgenus *Mecanthidium* with the genus *Paranthidium*, his 1948 key grouped together the members of *Paranthidium* based on the structure of the apical margin of the female mandible and the shape of the male T7 (Michener 1948). Griswold and Michener (1988) later moved *Mecanthidium* into the genus *Dianthidium*, due to the tridentate mandible shared between the subgenus *Mecanthidium* and the rest of the genus *Dianthidium*, and in contrast to the quadridentate mandible of *Paranthidium* (Griswold and Michener 1988). Our results strongly support the sister relationship between *Dianthidium* and *Paranthidium* and confirm the phylogenetic affinity of the subgenus *Mecanthidium* with the genus *Dianthidium*. Although Michener (2007) suggests that *Bathanthidium* (*Manthidium*) may be more appropriately placed in the subgenus *Anthidiellum* (*Ranthidiellum*), our results confirm a close phylogenetic relationship between *Bathanthidium*, *Paranthidium*, and *Dianthidium*.

Branch support is low in the rest of the *Dianthidium* group and paraphyly is rife, revealing an incoherence between existing anthidiine classification (as per Michener 2007) and the underlying phylogenetic relationships among taxa. The genus *Plesianthidium* emerges in two distinct clades, *Plesianthidium* (*Spinanthidiellum*) and (*Plesianthidium* (*Spinanthidium*) + *Plesianthidium* (*Carinanthidium*)), although the latter clade is only moderately well-supported in maximum likelihood analyses (Figures 1, S1-S3). *Plesianthidium* (*Spinanthidiellum*) exhibits certain morphological characters that distinguish it from other subgenera of *Plesianthidium*, including a carinate preoccipital ridge, an angled scutellum and a weakly trifid T7. It is thus perhaps unsurprising that *Plesianthidium* (*Spinanthidiellum*) forms a monophyletic group not closely related to the other subgenera of *Plesianthidium* present in our phylogeny.

Examination of the clade *Pachyanthidium* + *Anthidiellum* (minus *Pycnanthidium*) + *Plesianthidium* (*Spinanthidiellum*) reveals a number of shared morphological characters. All have a very short mesepisternum ventrally, a broadly rectangular scutellum with a truncate posterior margin and a lamellate preoccipital margin (except carinate in *Anthidiellum* s. str.), characters not found in other members of the *Dianthidium* group. In addition, the omaulus is complete (not interrupted ventrally) in all but *Spinanthidiellum* and the pronotal lobe is lamellate (except carinate in *Spinanthidiellum*); among related taxa, these characters are found only in some *Anthidiellum* (*Pycnanthidium*). The wide, thin heads with narrow genae are distinctive. Members of this clade could be combined within the genus *Anthidiellum* with recognition of all subgenera represented in the clade. In this case, however, the status of several rare

tropical Asian subgenera presently in *Anthidiellum* would remain unclear, as they do not share the combination of characters outlined above.

4.5 The *Stelis* group

This exclusively cleptoparasitic group encompasses the greatest diversity in integumental coloration of any of the groups. Background color ranges from black to red to metallic blue or green, with or without white to yellow to red markings. It also has the greatest diversity in the shape of the female sixth tergum and sternum. Structures often appear patterned after their host. For example, *Stelis* (*Heterostelis*) has an expanded mid tibia, as does its host, *Trachusa*. *Stelis* (*Dolichostelis*) is slender and elongate like its host, *Megachile* (*Chelostomoides*), likely an adaptation to the stem-nesting habit of *M.* (*Chelostomoides*). *Stelis* (*Protostelis*) has a pattern of yellow maculations, laterally expanded axillae and the broad scutellum of its host, *Anthidiellum s. str.*; and *S. (S.) montana* and related species are the solid blue-green of their hosts, *Osmia*.

Our results confirm that the cleptoparasitic genera *Stelis*, *Afrostellis*, and *Euaspis* together form a strongly supported monophyletic clade (Litman et al. 2013). The weakly supported phylogenetic position of *Afrostellis* and *Euaspis* within the genus *Stelis*, however, makes it unclear whether one or both of these genera render the genus *Stelis* paraphyletic (either genus could be nested within the *Stelis*-clade or, alternatively, could represent the sister group to the rest of the clade).

The genus *Afrostelis* is morphologically distinct from *Stelis* in its highly modified thorax and unique male genitalia (Cockerell 1931, Michener and Griswold 1994b). Like *Stelis*, however, it exhibits two apical spines on its fore- and mid-tibiae and some have theorized that *Afrostelis* may be a specialized derivative of *Stelis* (Michener and Griswold 1994b). The genitalia of male *Euaspis* differ from those of *Stelis*: although the male gonostylus is slender at the base (as in *Stelis*), the distal end of the gonostylus is rounded and flattened (Viereck 1924), rather than angulate and broadened, as in *Stelis*. Like *Stelis*, however, *Euaspis* has two apical spines on its fore- and mid-tibiae. Michener (2007) proposed a possible derivation of *Euaspis* from a “*Pachyanthidium*-like ancestor” and suggested that morphological similarities between *Euaspis* and *Stelis* were possible convergences due to a shared cleptoparasitic lifestyle.

Our results confirm the close phylogenetic relationship between *Afrostelis*, *Euaspis*, and *Stelis* and suggest that *Afrostelis* and *Euaspis* may well be derived from within *Stelis*. In this case, both genera may eventually be assigned subgeneric rank within the genus *Stelis*. Given, however, the uncertain phylogenetic position of *Euaspis* and *Afrostelis* with regard to *Stelis*, as well as the unique suite of morphological characters exhibited by each of these taxa, we prefer for the present to recognize three distinct genera, as per Michener (2007).

The taxonomic assignment of *Stelis rozeni* to the genus *Stelis* was described as “provisional” by Griswold and Parker (2003), based on the numerous morphological differences between *S. rozeni* and other members of the genus, the difficulty associated

with its assignment to subgenus, and the fact that males of the species were then unknown. A male has subsequently been found; the genitalia are unlike those of *Afrostelis*, *Euaspis* and other *Stelis* (T. Griswold, personal communication). Our results soundly confirm the affinity of *Stelis rozeni* with the *Stelis* clade; like *Euaspis* and *Afrostelis*, however, *Stelis rozeni* may either be nested within the *Stelis* clade or sister to the rest of the clade. For the moment, we maintain its assignment to the genus *Stelis*, although future clarification of phylogenetic relationships at the base of the *Stelis* clade may eventually support placement in another genus.

Despite the paraphyly of the subgenus *Stelis* (*Heterostelis*), all known host associations are with the resin-nesting genus *Trachusa*: *Stelis annulata* on *Trachusa* (*Paraanthidium*) *interrupta* (Amiet et al. 2004), *Stelis gigantea* on *Trachusa* (*Archianthidium*) *pubescens* (suspected association, Warncke 1992), *Stelis hurdi* on *Trachusa* (*Trachusomimus*) *perdita* (Thorp 1966), *Stelis anthidioides* on *Trachusa* (*Heteranthidium*) *timberlakei* (Timberlake 1941) and *Stelis manni* on *Trachusa* (*Ulanthidium*) *manni* (suspected association, Thorp 1966). Furthermore, both Old and New World members of *Stelis* (*Heterostelis*) belong to early-branching clades in the *Stelis* group where almost all known host associations are with resin-nesting bees. Old World *Stelis* (*Heterostelis*) are found in the same clade with *Afrostelis*, a parasite of *Heriades* (Taylor 1965), and *Euaspis*, a parasite of resin-nesting *Megachile* (Iwata 1976). New World *Stelis* (*Heterostelis*) are in the same clade as *Stelis* (*Dolichostelis*), also parasites of resin-nesting *Megachile* (Krombien 1967, Parker et al. 1987). *Stelis* (*Protostelis*) *signata*, sister to the subgenus *Stelis* (*Stelis*), also exclusively favors a resin-

nesting host, *Anthidiellum strigatum* (Müller et al. 1997). Given the paraphyly of *Stelis* (*Heterostelis*) and the phylogenetic placement of members of this subgenus, as well as the apparent preference of early branching lineages of the *Stelis* group for resin-nesting hosts, the preference of *Trachusa* as a host in both Old and New World species of *Stelis* (*Heterostelis*) most likely reflects an ancestral preference of the *Stelis* group for resin-nesting hosts. A revision of the subgenus *Stelis* (*Heterostelis*) is needed.

Xenostelis polychroma is known from a single female specimen collected on the island of Socotra. Bayesian analyses of combined data place *Xenostelis* within the subgenus *Stelis* (*Stelis*), while maximum likelihood analyses place *Xenostelis* as sister to the rest of Anthidiini; the latter placement is likely the result of male characters that are unknown and thus uncoded in the morphological matrix. *Xenostelis* exhibits two apical spines on fore- and mid-tibiae, as does *Stelis*; the enlarged tegulae of *Xenostelis*, however, are similar to those of *Afrostellis*. Michener (2007) speculates that *Xenostelis* may in fact be a synonym or a subgenus of *Afrostellis*. While we can neither confirm nor refute this hypothesis, we believe that *Xenostelis* is a close relative of the *Stelis* group. Morphology of the male genitalia, as well as the addition of DNA sequence data, will be fundamental to understanding the phylogenetic placement of *Xenostelis*.

4.6 Generic level revision of the Anthidium group

The phylogenetic hypothesis presented here not only clarifies evolutionary relationships among anthidiine bees but also serves as a framework on which to base an improved classification of the tribe. While a revision of the generic-level classification of

the *Anthodiocetes* and *Dianthidium* groups is much-needed, a combination of missing subgenera, particularly in the *Anthodiocetes* group, and weak node support prevent us from proposing such a revision in the present paper. We focus instead on a generic level revision of the *Anthidium* group, a monophyletic group for which we have excellent taxon sampling and in which consistently high internal node support allows us to propose a classification system based on a strongly-supported phylogenetic backbone.

A recent paper outlined a series of priority criteria for taxonomic revisions, among them monophyly, clade stability, and phenotypic diagnosability (Vences et al. 2013). We used these criteria as guidelines for a revised classification and considered the following three options for our revision of the *Anthidium* group:

1. Placement of the entire *Anthidium* group in the genus *Anthidium*

In this scenario, current genera in the *Anthidium* group would become subgenera of the genus *Anthidium*. This option, however, clearly groups together radically different forms. While Michener (2007) argues that maintaining extremely large, diverse genera such as *Andrena*, *Lasioglossum* and *Megachile* makes it easier for biologists to recognize taxa, other authors prefer to divide such large genera into multiple, smaller genera (e.g. Mitchell (1960), Hurd (1979), Moure and Hurd (1987) for *Lasioglossum*; Mitchell (1980) for *Megachile*; Urban and Moure (2012) for anthidiine genera; and Moure et al. (2012) for paracolletine genera).

2. Maintenance of the genus *Serapista* and placement of other species into the genus *Anthidium*

The four species in the genus *Serapista* are distributed throughout most of sub-Saharan Africa (Michener 2007). Morphologically, they are dramatically different from other species of wool carder bees, characterized by their dark integument marked by patches of white appressed squamose pubescence. In this classification system, *Serapista* would remain a unique genus, while the remaining species of the *Anthidium* group would be placed in the genus *Anthidium*. This option, however, also creates a hugely diverse genus *Anthidium*, evoking the same issues as the first option.

3. Maintenance of the system proposed by Michener (2007), incorporating changes in light of new phylogenetic results

Michener (2007) divides the *Anthidium* group into eight genera: *Anthidioma*, *Afranthidium*, *Anthidium*, *Gnathanthidium*, *Indanthidium*, *Neanthidium*, *Pseudoanthidium*, and *Serapista*. According to our results, multiple subgenera of *Afranthidium* and the genus *Neanthidium* and *Gnathanthidium* would be moved into the genus *Pseudoanthidium*. The genera *Anthidium* and *Serapista* would remain unchanged. Two genera of uncertain taxonomic affinity, *Anthidioma* and *Indanthidium*, would maintain their generic-level status until (and if) future studies suggest otherwise.

A fourth possibility was the system proposed by Pasteels (1969). Pasteels (1969) divided the Old World members of the *Anthidium* group into nineteen genera (and this system only includes the Old World taxa described up until 1969). Although Pasteels' classification proposes genera that are generally supported as monophyletic by our results, it creates large numbers of very small genera that are only minimally different

689 from one another, calling into question their utility. We thus excluded this classification
690 from consideration.

691
692 Of the three options considered, only the third option takes an existing
693 classification in widespread use (Michener, 2007) and implements only as many changes
694 as necessary to ensure the monophyly of all genera. The decision to represent taxonomic
695 diversity at the generic level or the sub-generic level is clearly subjective. We prefer the
696 third option because it places species into genera that reflect the diversity of the species
697 therein, without creating large numbers of needlessly small genera. We thus retain the
698 classification system proposed by Michener (2007) and hereby make the following
699 changes.

700
701 We move the subgenera *Afranthidium* (*Zosteranthidium*), *Afranthidium*
702 (*Branthidium*), *Afranthidium* (*Immanthidium*) and the genus *Neanthidium* into the genus
703 *Pseudoanthidium*. These form the new combinations *Pseudoanthidium*
704 (*Zosteranthidium*), *P. (Branthidium)*, *P. (Immanthidium)* and *P. (Neanthidium)*.

705 Interestingly, the genus *Afranthidium* comes out twice in the key to Old World genera of
706 Anthidiini (Michener and Griswold 1994b; Michener 2007). The subgenera that
707 correspond to the second occurrence of *Afranthidium* in the key are those in which the
708 premarginal zone is not depressed and the punctuation of this zone is not finer than the
709 basal zone. These subgenera are here assigned to *Pseudoanthidium*. Based on the
710 morphological traits associated with our new definition of *Pseudoanthidium* (outlined
711 below), we also include the genus *Gnathanthidium* and the subgenus *Afranthidium*

712 (*Mesanthidiellum*) in *Pseudoanthidium*. These form the new combinations
713 *Pseudoanthidium* (*Gnathanthidium*) and *P.* (*Mesanthidiellum*).
714

715 The genus *Afranthidium*, as now defined, thus includes the subgenera
716 *Afranthidium*, *Capanthidium*, *Domanthidium*, *Mesanthidium*, *Nigranthidium*,
717 *Oranthidium* and *Xenanthidium*. The genus *Pseudoanthidium* now includes the subgenera
718 *Branthidium*, *Exanthidium*, *Gnathanthidium*, *Immanthidium*, *Mesanthidiellum*,
719 *Micranthidium*, *Neanthidium*, *Pseudoanthidium*, *Royanthidium*, *Semicarinella*,
720 *Tuberanthidium* and *Zosteranthidium*.
721

722 With its expanded diversity, 60 described species in twelve subgenera plus
723 numerous undescribed species, it is not surprising that universal characters distinguishing
724 *Pseudoanthidium* from *Afranthidium* are not abundant. Nevertheless, a suite of characters
725 not or rarely found in *Afranthidium*, as here redefined, does exist for *Pseudoanthidium*:
726 punctuation of terga similar in diameter and density across the surface, without distinct
727 apical depressed zone; apical margins of terga broadly impunctate (several puncture
728 widths) (except *Royanthidium*); pronotal lobe at least narrowly lamellate (except
729 *Zosteranthidium*, *Immanthidium*; also occurs in *Afranthidium* subgenus *Mesanthidium*);
730 hind tibia tuberculate (except *Micranthidium*, *Immanthidium*, *Zosteranthidium*);
731 propodeum shagreened (except *Micranthidium*, *Immanthidium*, *Pseudoanthidium*,
732 *Royanthidium*, *Exanthidium*, some *Branthidium*); male sixth tergite without lateral spine
733 (except some *Exanthidium*); male seventh tergite emarginate medially (except some
734 *Micranthidium* and *Pseudoanthidium*; also occurs in *Afranthidium* subgenus

735 *Nigranthidium*); male third sternum with modified hairs (except *Royanthidium*,
736 *Mesanthidiellum*, *Gnathanthidium*, *Branthidium*); female clypeal apical margin covered
737 with dense pubescence (except *Micranthidium*, *Zosteranthidium*, *Immanthidium*,
738 *Royanthidium*, *Exanthidium*). As now constituted, *Pseudoanthidium* typically has a
739 blocky head and rather circular metasoma in cross-section.

740

741 The newly constrained *Afranthidium* is now recognized by the depressed, densely
742 and more finely punctate apical zone of the terga, the generally more flat metasoma in
743 cross-section, and the presence of a lateral spine on the sixth tergite of the male.

744

745 No changes are made to the genera *Serapista*, *Anthidium*, *Anthidioma*, or
746 *Indanthidium*.

747

748 4.7 The evolution of morphological characters - implications for classification

749

750 Many characters appear in multiple anthidiine genera and subgenera, apparently
751 without phylogenetic pattern. Males from diverse genera, for example, exhibit apical
752 marginal combs on sternites three, four or five. Such combs are present in genera from all
753 five suprageneric anthidiine groups, including members of *Trachusa* (on S4 and S5,
754 depending on subgenera), *Pseudoanthidium* (on S5 in *Pseudoanthidium*
755 (*Pseudoanthidium*) and *P.* (*Royanthidium*)), *Pachyanthidium* (on S4 and S5),
756 *Hypanthidioides* (S3 and S5, depending on subgenus), *Plesianthidium* (S4 and S5,
757 depending on subgenus), *Bathanthidium* (S4 and S5, depending on subgenus),

Dianthidium (S5), *Paranthidium* (S4, S5 and sometimes S3), *Notanthidium* (S4), and *Stelis* (S4); sternal combs are absent in other members of many of these genera, including *Trachusa*, *Pseudoanthidium*, *Plesianthidium*, *Dianthidium*, *Paranthidium*, *Notanthidium*, and *Hypanthidioides*, and in all *Afranthidium*, *Anthidium*, *Eoanthidium*, *Duckeanthidium*, *Cyphanthidium*, *Epanthidium*, *Hypanthidium* and *Anthodioctes*. The appearance of sternal combs not only varies within genera but also within species: male *Trachusa* (*Heteranthidium*) *occidentalis* have been found both with and without combs on the fourth sternum (Brooks and Griswold 1988).

Other characters that appear in diverse lineages are a strongly carinate or lamellate omaulus, seen in *Anthidiellum*, *Pachyanthidium*, *Pseudoanthidium* (*Micranthidium* and *Gnathanthidium*), *Anthidium* (*Severanthidium* and *Gulanthidium*); juxtantennal carinae, seen in most *Anthodioctes* group genera plus *Eoanthidium*, *Epanthidium*, *Euaspis* and *Larinostelis*; and a complete or partial preoccipital carina, seen in *Afranthidium* (*Mesanthidiellum*), *Anthidium* (subgenera *Severanthidium* and *Turkanthidium*), *Aztecanthidium*, *Anthodioctes*, *Afrostelis*, *Euaspis*, *Gnathanthidium*, *Icteranthidium*, *Pachyanthidium*, *Plesianthidium* (*Spinanthidiellum*), and various subgenera of *Pseudoanthidium* and *Anthidiellum*. Omaular and preoccipital carinae occur sporadically in other bees; omaular carinae are found in members of Colletidae, non-anthidiine Megachilidae and Apidae, while juxtantennal carinae are found in non-anthidiine Megachilidae. These various carinae have likely evolved in parallel and may serve to protect vulnerable areas of the body, such as the neck and antennal bases (Michener 2007).

781

782 Such traits have either evolved multiple times in parallel or are plesiomorphies that
783 have been lost in multiple lineages within the tribe Anthidiini. While potentially useful
784 for the diagnosis of taxonomic groups, they are not appropriate for the character-based
785 definition of groups. The historical use of such characters to define anthidiine taxa may at
786 least partially explain the lack of coherence between our phylogeny and the current
787 classification. We thus strongly recommend the use of a robust, molecular-based
788 phylogenetic backbone for the definition of taxonomic groups, followed by a subsequent
789 decision regarding which morphological characters are appropriate for the diagnosis of
790 these groups.

791

792 *4.8 Mandibular morphology and nesting behavior*

793

794 A correlation has long been suggested between nest-building material and
795 anthidiine mandibular dentition (Perez 1879, 1889; Pasteels 1977). Female anthidiines
796 building nests of resin, including the *Trachusa*, *Anthodiocetes*, and *Dianthidium* groups,
797 have three or four blunt mandibular teeth separated by shallow concavities that they use
798 to collect chunks of resin. In contrast, female anthidiines using plant fibers in nest
799 construction, such as those in the *Anthidium* group, have five or more sharp teeth
800 separated by V-shaped notches (Michener 2007).

801

802 The theory that mandibles exhibiting many, sharp teeth are adapted to harvesting
803 fibers from plants may be supported by the unusual nesting behavior of some members of

the genera *Rhodanthidium* and *Pachyanthidium*, both members of the *Dianthidium* group. The nest cells of *Rhodanthidium* (*Asianthidium*) *caturigense* are built of two distinct layers: an outer layer woven of plant fibers and an inner layer built of resin (Pasteels 1977). While most female members of the genus *Rhodanthidium* do not include plant fibers in their nests and exhibit extremely reduced dentition, amounting to little more than a straight margin on the mandible, *R. caturigense* has four distinct mandibular teeth separated by V-shaped notches.

Members of the subgenus *Pachyanthidium* (*Pachyanthidium*) build nest cells of resin mixed together with plant fibers (Michener 1968; Gueinzus 1858). While other subgenera of *Pachyanthidium* exhibit mandibular dentition similar to that of other resin-nesting anthidiines, members of the subgenus *Pachyanthidium* exhibit mandibular dentition consistent with that of plant fiber-nesting anthidiines. Thus the dentition seen in both *R. caturigense* and members of the subgenus *Pachyanthidium*, unique among members of the *Dianthidium* group and among resin-nesting anthidiines in general, support the theory that mandibles with multiple, sharp teeth are an adaptation for the manipulation of plant fibers. The phylogenetic position of these two species, nested deeply within the *Dianthidium* group and not closely related to one another, may imply that the combination of including plant fibers in nest construction and mandibles with multiple, sharp teeth are either a convergence shared with members of the *Anthidium* group, or a plesiomorphy retained from an early common ancestor of the *Anthidium*, *Anthodioctes*, and *Dianthidium* groups.

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References

- Amiet F., M. Hermann, A. Müller, R. Neumeyer. 2004. *Apidae 4*. Fauna Helvetica 9, (Centre Suisse de Cartographie de la Faune - Schweizerische Entomologische Gesellschaft, Neuchâtel) (in French, German).
- Ascher J.S., Pickering J. 2015. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species.
- Bennett F.D. 1966. Notes on the biology of *Stelis (Odontostelis) bilineolata* (Spinola), a parasite of *Euglossa cordata*. *Journal of the New York Entomological Society* 74: 72-79.
- Brooks R.W., Griswold T.L. 1988. A key to the species of *Trachusa* subgenus *Heteranthidium* with descriptions of new species from Mexico (Hymenoptera: Megachilidae, Anthidiini). *Journal of the Kansas Entomological Society* 61: 332-346.
- Claude-Joseph F. 1926. Recherches biologiques sur les Hyménoptères du Chile (Mellifères). *Annales des Sciences Naturelles, Zoologie* 10: 114-268 (in French).
- Cockerell. T.D.A. 1931. Heriadine and related bees from Liberia and the Belgian Congo. *Revue de Zoologie et de Botanique Africaines* 20: 331-341.
- Danforth B.N., Sauquet H., Packer L. 1999. Phylogeny of the bee genus *Halictus* (Hymenoptera: Halictidae) based on parsimony and likelihood analyses of nuclear EF-1 alpha sequence data. *Molecular Phylogenetics and Evolution* 13: 605-618.
- Evans H.E. 1993. Observations on the nests of *Paranthidium jugatorium perpictum*

- (Cockerell) (Hymenoptera: Megachilidae: Anthidiini). *Pan-Pacific Entomologist* **69**: 319-322.
- Fabre J.H. 1891. *Souvenirs entomologiques. Quatrième Série*. (Delagrave, Paris) (in French).
- Fabre J.H. 1914 *The Mason-bees* (Dodd, Mead and Company, Madison).
- Ferton C. 1901. Notes détachées sur l'instinct des Hyménoptères mellifères ravisseurs avec la description de quelques espèces (1re série). *Annales de la Société Entomologique de France* **70**: 83-148 (in French).
- Ferton C. 1911. Notes détachées sur l'instinct des Hyménoptères mellifères ravisseurs avec la description de quelques espèces (7e série). *Annales de la Société Entomologique de France* **80**: 351-412 (in French).
- Gene Codes Corporation, Sequencher® version 5.3 sequence analysis software, Ann Arbor, MI USA <http://www.genecodes.com>
- Gess S.K., F.W. Gess. 2007. Notes on nesting and flower visiting of some anthidiine bees (Hymenoptera: Megachilidae: Megachilinae: Anthidiini) in southern Africa. *Journal of Hymenoptera Research* **16**: 30-50.
- Gillespie J.J., J.S. Johnston, J.J. Cannone, R.R. Gutell. 2006. Characteristics of the nuclear (18S, 5.8S, 28S and 5S) and mitochondrial (12S and 16S) rRNA genes of *Apis mellifera* (Insecta: Hymenoptera): structure, organization, and retrotransposable elements. *Insect Molecular Biology*, 15(5): p. 657-86.
- Gonzalez V.H., T. Griswold, C.J. Praz, and B.N. Danforth. 2012. Phylogeny of the bee family Megachilidae (Hymenoptera: Apoidea) based on adult morphology. *Systematic Entomology*, 37: 261-286.
- Gonzalez V.H., T. L. Griswold. 2013. Wool carder bees of the genus *Anthidium* in the Western Hemisphere (Hymenoptera: Megachilidae): diversity, host plant associations, phylogeny, and biogeography. *Zoological Journal of the Linnean Society*, 168: 221-425.
- Grandi G. 1934. Contributi alla conoscenza degli Imenotteri melliferi e predatori XIII. *Bollettino del Laboratorio di Entomologia del Reale Istituto Superiore Agrario di Bologna* 7: 1-144 (in Italian).
- Griswold T.L. 1985. A generic and subgeneric revision of the *Heriades* genus-group (Hymenoptera: Megachilidae). PhD Thesis, Utah State University, Logan.
- Griswold T.L., Michener C.D. 1988. Taxonomic observations on Anthidiini of the western hemisphere (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 61: 22-45.

- Griswold T.L., Parker F.D. 2003. *Stelis rozeni*, new species, the first record of the parasitic bee genus *Stelis* from southern Africa (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 76: 282-285.
- Gueinzus W. 1858. On the habits of the hymenoptera of Natal. *Proceedings of the Entomological Society of London*, 1858-1859, pp. 9-11, In: Transactions of the Entomological Society of London, New Series V, 1858-1861.
- Ho S.Y.W., L.S. Jermin. 2004. Tracing the decay of the historical signal in biological sequence data. *Systematic Biology*, 53(4): 623-637.
- Huelsenbeck J.P., F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* 17: 754-755.
- Hurd P.D. 1979. Superfamily Apoidea, pp. 1741-2209 in K. V. Krombein, P. D. Hurd, Jr., D. R. Smith, and B. D. Burks, eds., *Catalog of Hymenoptera in America North of Mexico*, Vol. 2. Washington: Smithsonian Institution Press.
- Iwata K. 1976. *Evolution of instinct: Comparative ethology of Hymenoptera* (Amerind Publishing Co. Pvt. Ltd., New Delhi).
- Jermin L.S., S.Y.W. Ho, F. Ababneh, J. Robinson, A.W.D. Larkum. 2004. The biasing effect of compositional heterogeneity on phylogenetic estimates may be underestimated. *Systematic Biology*, 53(4): 638-643.
- Katoh K., D.M. Standley. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30:772-780.
- Kjer K. M. 1995 Use of rRNA secondary structure in phylogenetic studies to identify homologous positions: an example of alignment and data presentation from the frogs. *Molecular Phylogenetics and Evolution*, 4: 314 – 330.
- Lanfear R., B. Calcott, S.Y.W. Ho, S. Guindon. 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29(6): 1695-1701.
- Litman J.R., Eardley C.D., Danforth B.N., Praz C.J. 2011. Why do leafcutter bees cut leaves? New insights into the early evolution of bees. *Proceedings of the Royal Society B* 278: 3593-3600.
- Litman J., C.J. Praz, B.N. Danforth, T.L. Griswold, S. Cardinal. 2013. Origins, evolution, and diversification of cleptoparasitic lineages in long-tongued bees. *Evolution*, 67(10): 2982-2998.

956 Maddison D.R., Maddison W.P. 2005 *Macclade 4.08 for OSX* (Sinauer Associates, Inc.,
957 Sunderland, Massachusetts).
958

959 Maneval H. 1936. L'*Anthidium caturigense*, son nid, sa larve. *Annales de la Société*
960 *Entomologique de France* **105**: 1-5 (in French).
961

962 Micheli L. 1935. Note biologiche e morfologiche sugli Imenotteri VII. *Bollettino della*
963 *Società Veneziana di Storia Naturale*, **1**: 126-134 (in Italian).
964

965 Michener C.D. 1942. Taxonomic observations on bees with descriptions of new genera
966 and species (Hymenoptera: Apoidea). *Journal of the New York Entomological Society*
967 **50**: 273-282.
968

969 Michener C.D. 1948. The generic classification of the anthidiine bees. *American Museum*
970 *Novitates*, **1381**: 1-29.
971

972 Michener C. 1968. Nests of some African megachilid bees, with description of a new
973 *Hoplitis* (Hymenoptera, Apoidea). *Journal of the Entomological Society of Southern*
974 *Africa* **31**: 337-359.
975

976 Michener C.D. 1979. Biogeography of the bees. *Annals of the Missouri Botanical*
977 *Garden*. **66**(3): 277-347.
978

979 Michener C.D. 2000. *The Bees of the World* (The Johns Hopkins University Press,
980 Baltimore).
981

982 Michener C.D. 2007. *The Bees of the World* (The Johns Hopkins University Press,
983 Baltimore).
984

985 Michener, C.D., Griswold T.L. 1994a. The neotropical *Stelis*-like cleptoparasitic bees
986 (Hymenoptera: Megachilidae). *Proceedings of the Entomological Society of Washington*
987 **96**: 674-678.
988

989 Michener, C. D., T. L. Griswold. 1994b. The classification of old world Anthidiini.
990 *University of Kansas Science Bulletin* **55**: 299-327.
991

992 Miller M.A., W. Pfeiffer, T. Schwartz. 2010. "Creating the CIPRES Science Gateway for
993 inference of large phylogenetic trees" in *Proceedings of the Gateway Computing*
994 *Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA pp 1 - 8.
995

996 Mitchell T.B. 1960. Bees of the eastern United States. I. *Technical bulletin (North*
997 *Carolina Agricultural Experiment Station)*, **141**: 1-538.
998

999 Mitchell T.B. 1980. A Generic Revision of the Megachiline Bees of the Western
1000 Hemisphere. [ii] + 95 pp. Raleigh: Department of Entomology, North Carolina State
1001 University.

1002
1003 Moure J.S., P.D. Hurd, Jr. 1987. An Annotated Catalog of the Halictid Bees of the
1004 Western Hemisphere. vii + 405 pp. Washington, D.C.: Smithsonian Institution Press.
1005
1006 Moure J.S., V. Graf, D. Urban. 2012. Paracolletini Cockerell, 1934. In Moure, J. S.,
1007 Urban, D. & Melo, G. A. R. (Orgs). *Catalogue of Bees (Hymenoptera, Apoidea) in the*
1008 *Neotropical Region - online version*. Available at
1009 <http://www.moure.cria.org.br/catalogue>.
1010
1011 Muller M. 1931. Zur Biologie unsere Wollbienen (*Anthidium* F.). *Zeitschrift für*
1012 *wissenschaftliche Insektenbiologie* 26: 14-148 (in German).
1013
1014 Müller A. 1996. Host-plant specialization in western Palearctic anthidiine bees
1015 (Hymenoptera: Apoidea: Megachilidae). *Ecological Monographs* 66: 235-257.
1016
1017 Müller A., Krebs A., Amiet F. 1997 *Bienen. Mitteleuropäische Gattungen, Lebensweise,*
1018 *Beobachtung* (Naturbuch-Verlag, Augsburg) (in German).
1019
1020 Müller A., Topfl W., Amiet F. 1996. Collection of extrafloral trichome secretions for nest
1021 wool impregnation in the solitary bee *Anthidium manicatum*. *Naturwissenschaften* 83:
1022 230-232.
1023
1024 O'Brien M.F. 2007. Notes on *Dianthidium simile* (Cresson) (Hymenoptera:
1025 Megachilidae) in Michigan. *The Great Lakes Entomologist* 40: 23-28.
1026
1027 Parker F.D., Cane J.H., Frankie G.W., Vinson S.B. 1987. Host records and nest entry by
1028 *Dolichostelis*, a kleptoparasitic anthidiine bee (Hymenoptera: Megachilidae). *Pan-Pacific*
1029 *Entomologist* 63: 172- 177.
1030
1031 Pasteels J.J. 1969. La systématique générique et subgénérique des Anthidiinae
1032 (Hymenoptera, Apoidea, Megachilidae) de l'Ancien Monde. *Mémoires de la Société*
1033 *Royale d'Entomologie de Belgique* 31: 1-148 (in French).
1034
1035 Pasteels J.J. 1977. Une revue comparative de l'éthologie des Anthidiinae nidificateurs de
1036 l'ancien monde (Hymenoptera, Megachilidae). *Annales de la Société Entomologique de*
1037 *France* 13: 651-667 (in French).
1038
1039 Perez J. 1879. Contribution à la faune des Apiaires de France - 2e partie. *Actes de la*
1040 *Société Linnéenne de Bordeaux*: (French).
1041
1042 Perez J. 1889 *Les Abeilles* (Hachette, Paris) (French).
1043
1044 Praz C.J., L. Packer 2014. Phylogenetic position of the bee genera *Ancyla* and *Tarsalia*
1045 (Hymenoptera: Apidae): a remarkable base compositional bias and an early Paleogene
1046 geodispersal from North America to the Old World. *Molecular Phylogenetics and*
1047 *Evolution*, 81:258-270.

- Rambaut A., M.A. Suchard, D. Xie and A.J. Drummond. 2014. Tracer v1.6, Available from <http://beast.bio.ed.ac.uk/Tracer>
- Ronquist F., Huelsenbeck J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.
- Sequencher® version 5.3 sequence analysis software, 2015, Gene Codes Corporation, Ann Arbor, MI USA. <http://www.genecodes.com>
- Sheffield N.C. 2013. The interaction between base compositional heterogeneity and among-site rate variation in models of molecular evolution. *ISRN Evolutionary Biology*, Article ID 391561, 1-8.
- Stamatakis A. 2006. Raxml-vi-hpc: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688-2690.
- Stamatakis, A. 2014. The RAxML v8.1.x manual. Heidelberg Institute for Theoretical Studies, Heidelberg.
- Swofford D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0a144. Sinauer Associates, Sunderland, Massachusetts.
- Taylor, J.S. 1965. Notes on some South African bees (Hymenoptera: Colletidae, Megachilidae). *Pan- Pacific Entomologist* 41: 173-179.
- Thomas J.A., J.W.H. Trueman, A. Rambaut, J.J. Welch. 2013. Relaxed phylogenetics and the Palaeoptera problem: resolving deep ancestral splits in the insect phylogeny. *Systematic Biology*, 62(2): 285-297.
- Thorp R.W. 1966. Synopsis of the genus *Heterostelis* Timberlake (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 39: 131-146.
- Timberlake P.H. 1941. Ten new species of *Stelis* from California (Hymenoptera, Apoidea). *Journal of the New York Entomological Society* 49: 123-137.
- Urban D., J. S. Moure. 2012. Anthidiini Ashmead, 1899. In Moure, J. S., Urban, D. & Melo, G. A. R. (Orgs). *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region - online version*. Available at <http://www.moure.cria.org.br/catalogue>.
- Vences M, J.M. Guayasamin, A. Miralles, I. de la Riva. 2013. To name or not to name: Criteria to promote economy of change in Linnean classification schemes. *Zootaxa*, 3636(2): 201-244.
- Viereck H.L. 1924. The Philippine species of *Parevaspis*, a genus of bees. *Philippine Journal of Science*, 24: 745-747.

1094
1095 Warncke K. 1980. Die Bienengattung *Anthidium* Fabricius, 1804, in der Westpaläarktis
1096 und im turkestanischen Becken. *Entomofauna* 1(10): 119-210 (in German).
1097
1098 Warncke K. 1992. Die westpaläarktischen Arten der Bienengattung *Stelis* Panzer, 1806
1099 (Hymenoptera, Apidae, Megachilinae). *Entomofauna* 13(22): 341-376 (in German).
1100
1101 Westrich P. 1989. *Die Wildbienen - Baden-Württembergs* (Eugen Ulmer GmbH & Co.,
1102 Stuttgart) (German).
1103
1104 Woese C.R., L. Achenbach, P. Rouviere, L. Mandelco. 1991. Archaeal phylogeny:
1105 reexamination of the phylogenetic position of *Archaeoglobus fulgidus* in light of certain
1106 composition-induced artifacts. *Systematic and Applied Microbiology* 1991, 14:364-371
1107
1108 Xamheu V. 1896. Moeurs et métamorphoses des *Anthidium oblongatum* et
1109 *septemdentatum*, Hymenoptères du group des Apides. *Bulletin de la Societe*
1110 *Entomologique de France*: 328-333 (in French).
1111
1112 Yang Z. 2006. Computational Molecular Evolution (Oxford University Press, Oxford).
1113
1114 Zanella F.C.V., A.G. Ferreira. 2005. Registro de hospedeiro de *Austrostelis* Michener &
1115 Griswold (Hymenoptera: Megachilidae) e de sua ocorrência na Caatinga. *Neotropical*
1116 *Entomology*, 34(5): 857-858.

Figure 1 Best scoring maximum likelihood tree based on analysis of molecular data. Numbers shown at nodes are maximum likelihood bootstrap values based on 1000 bootstrap replicates in RAxML. Terminals are labeled following our revised classification. Black asterisks indicate cleptoparasitic clades.

Figure S1 Maximum clade credibility tree based on nearly 60,000,000 post-burnin generations from MrBayes analysis of molecular data. Numbers shown at nodes are Bayesian posterior probabilities. Terminals are labeled following our revised classification.

Figure S2 Best scoring maximum likelihood tree based on analysis of combined molecular-morphological data. Numbers shown at nodes are maximum likelihood bootstrap values based on 1000 bootstrap replicates in RAxML. Terminals are labeled following our revised classification.

Figure S3 Maximum clade credibility tree based on 78,000,000 post-burnin generations from MrBayes analysis of combined molecular-morphological data. Numbers shown at nodes are Bayesian posterior probabilities. Terminals are labeled following our revised classification.

Table 1 Taxon list, DNA voucher numbers, collection localities and dates for specimens used in this study. Voucher numbers marked with a hyphen (“-”) indicate taxa for which sequences were downloaded from Genbank. For Genbank accession numbers, see Table 2. Taxa are labeled following our revised classification.

Table 2 GenBank accession numbers for sequences used in this study. Taxa are labeled following our revised classification.

Table 3 Revised suprageneric classification of Anthidiini based on the results of maximum likelihood and Bayesian phylogenetic analyses of molecular data. Genera included in our molecular dataset are marked in bold typeface; genera not included in our molecular dataset are marked in regular typeface and are proposed affiliations. Each genus is marked with either an “A” or a “B”, indicating whether they belong to Michener’s Series A or Series B (2000, 2007). Based on the results of prior studies, we have omitted the genus *Aspidosmia* from Anthidiini.

Figure 1

Trachusa group

© David Genoud

Anthidium group

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Anthodiocetes group

© Jessica Litman

Dianthidium group

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Stelis group

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Table 1

Taxon	Voucher number	Collection locality
<i>Afranthidium (Afranthidium) karoense</i>	1588	SOUTH AFRICA: NCP, 42 km S Eksteenfontein, 9.x.2008
<i>Afranthidium (Capanthidium) capicola</i>	1594	SOUTH AFRICA: WCP, Clanwilliam, 19.x.2008
<i>Afranthidium (Capanthidium) rubellulum</i>	1610	SOUTH AFRICA: NCP, 42 km S Eeksteenfontein, 9.x.2008
<i>Afranthidium (Capanthidium) poecilodontum</i>	1612	SOUTH AFRICA: NCP, 10 km E Nabapeep, 15.x.2008
<i>Afranthidium (Capanthidium) schultzei</i>	cp183	MOROCCO: Aksri, Paradise Valley, 15.iv.2009
<i>Afranthidium (Domanthidium) abdominale</i>	1644	SOUTH AFRICA: ECP, 42 km NW Cradock, 02.iii.2010
<i>Afranthidium (Mesanthidium) alternans</i>	cp182	MOROCCO: Guelmim, 17.iv.2009
<i>Afranthidium (Mesanthidium) carduele</i>	1596	GREECE: Lesvos, vic Pyrra, Kalloni Bay, 16.vi.2007
<i>Afranthidium (Nigranthidium) sp. nov. 1</i>	1611	SOUTH AFRICA: NCP, 10 km E Nabapeep, 15.x.2008
<i>Afranthidium (Nigranthidium) sp.</i>	1452	SOUTH AFRICA: NCP, Nabapeep, 15.x.2008
<i>Afranthidium (Oranthidium) folliculosum</i>	1640	SOUTH AFRICA: NCP, 12km N Kuruman, 09.iii. 2010
<i>Afranthidium sp.nov.</i>	cp179	SOUTH AFRICA: Barcode 4484 A03
<i>Afrostelis sp.</i>	1645	SOUTH AFRICA: NCP, 1km S Campbell, 07.iii.2010
<i>Anthidiellum (Anthidiellum) strigatum</i>	cp25	ITALY: Poggio Picenze, 01.vii.2011
<i>Anthidiellum (Loyolanthidium) robertsoni</i>	1387	USA: NV, Clark Co., E. CC Spring, 19.vii.2004
<i>Anthidiellum (Chloranthidiellum) sp. nov. 1</i>	1608	TANZANIA: Dodoma Region, 62 km E Dodoma, 3.i.2003
<i>Anthidiellum (Pycnanthidium) absconditum</i>	1635	SOUTH AFRICA: KZN, Kulene Experimental Farm, 09-12.iii.2002
<i>Anthidiellum (Pycnanthidium) sp.</i>	1647	SOUTH AFRICA: ECP, W Bavienskloof P.P., 27.ii.2010
<i>Anthidium (Anthidium) cockerelli</i>	1385	USA: NV, Clark Co., Yucca Gap, 17.v.2004
<i>Anthidium (Anthidium) chilense</i>	1625	CHILE: Coquimbo Province, 13 km E Vicuna, Rt.41, 21.x.2009
<i>Anthidium (Anthidium) colliguayanum</i>	1624	CHILE: Coquimbo Province, 13 km E Vicuna, Rt.41, 21.x.2009
<i>Anthidium (Anthidium) deceptum</i>	1642	PERU: Ica, E of Nazca, 15 km marker on Hwy 30A, 02.iv.2010
<i>Anthidium (Anthidium) illustre</i>	1384	USA: NV, Clark Co., Lovell Cyn., 16.vi.2004
<i>Anthidium (Anthidium) porterae</i>	645	USA: NM, Hidalgo Co., 20 mi S Animas, 17.ix.1999
<i>Anthidium (Anthidium) punctatum</i>	1554	SWITZERLAND: Weiach, 29.vi.2004
<i>Anthidium (Gulanthidium) sp.</i>	1637	IRAN: 13 km E Kalameh, road Busher-Shiraz, 03.vi.2009
<i>Anthidium (Proanthidium) oblongatum</i>	505	USA: NY, Tompkins Co., Ithaca, 01.vii.1999
<i>Anthidium (Severanthidium) cordiforme</i>	1628	SOUTH AFRICA: Limpopo Prov., 26 km W Messina, 18.iii.2002
<i>Anthidium (Turkenthidium) gratum</i>	1598	UZBEKISTAN: Bukara Prov., 40 km NE Gazli, 31.v. 2008
<i>Anthidium (Turkenthidium) unicum</i>	1597	UZBEKISTAN: Qarschi Prov., 25 km SE Muborak, 02.vi.2008
<i>Anthodiocetes (Anthodiocetes) mapirensis</i>	1519	BOLIVIA: La Paz, Puente Villa, 11.iii.2011
<i>Anthodiocetes (Bothranthidium) lauroi</i>	1649	BOLIVIA: La Paz, 5 km W Mapiri, 16-18.iii.2001
<i>Austrostelis catamarcensis</i>	1599	ARGENTINA: Salta Prov, Carayete, 10 km S, 24.x - 13.xi.2003
<i>Aztecanthidium tenochtitlanicum</i>	cp173	MEXICO: Jalisco, Chamela (Biol. Stat.), 20.vii.1989
<i>Bathanthidium (Manthidium) binghami</i>	1536	THAILAND: Petchabun Nam NP, 1-8.iii.2007
<i>Benanthis madagascariensis</i>	1518	MADAGASCAR: Tulear, Androy, x.2002
<i>Cyphanthidium intermedium</i>	cp174	SOUTH AFRICA: NCP, 3.2km S Augrabies, 28.i.2009
<i>Dianthidium (Adanthidium) arizonicum</i>	1386	USA: UT, Garfield Co., Escalante, 27.vi.2002
<i>Dianthidium (Dianthidium) subparvum</i>	1267	USA: UT, Cache Co., Blacksmith Fork Cyn., Left Hand Fork, 05.viii.2003
<i>Dianthidium (Mecanthidium) macrurum</i>	1648	MEXICO: Sonora, 40 km E Alamos, Rancho Palo Injerto, 30.ix.2006
<i>Duckeanthidium thielei</i>	1607	COSTA RICA: Heredia, La Selva Biol. Sta., Puerto Viejo de Sarapiquí, 5.i.1999
<i>Eoanthidium (Clistanthidium) turnericum</i>	1589	SOUTH AFRICA: NCP, Eksteenfontein, 9.x.2008
<i>Eoanthidium (Eoanthidium) clypeare</i>	1436	JORDAN: Wadi Shuyab, vi.2007
<i>Epanthidium (Epanthidium) bicoloratum</i>	1441	ARGENTINA: Catamarca, Trampasacha, 25.x -12.xi.2003
<i>Euaspiis abdominalis</i>	1627	SOUTH AFRICA: NP, 14 km E Vivo, 17.iii.2002
<i>Euaspiis polynesia</i>	1426	THAILAND: Prachup Kiri Khan Province, Pranburi District, 24.vi.2003
<i>Hoplostelis bivittata</i>	1636	PANAMA: Veraguas Province, Rancheria Island, 18.vii.2009
<i>Hypanthidioides (Saranthidium) marginata</i>	CP2	PARAGUAY: Guairá, Res. de Recursos, Manejados 24.i.2007
<i>Hypanthidium (Hypanthidium) obscurus</i>	sc171	PARAGUAY: Paraguarí, M. Nat. Acahay, 17.i.2007
<i>Icteranthidium ferrugineum</i>	1432	UZBEKISTAN: Karakalpakstan, Beruni, 25.v.2008
<i>Notanthidium (Allanthidium) rodolphi</i>	1623	CHILE: Coquimbo Province, 13 km E Vicuna, Rt.41, 21.x.2009
<i>Notanthidium (Notanthidium) steloides</i>	1542	CHILE: Region Metro, Farellones, 31.xii.2008
<i>Pachyanthidium (Ausanthidium) ausense</i>	1591	SOUTH AFRICA: NCP, Richtersveld National Park, 11.x.2008
<i>Pachyanthidium (Pachyanthidium) bicolor</i>	1606	KENYA: Coast Province, Taita Hill Discovery Centre, 13.xii.2002
<i>Pachyanthidium (Pachyanthidium) cordatum</i>	1631	SOUTH AFRICA: KZN, Ithala Nature Reserve, near Louwsburg, 07.iii.2002
<i>Pachyanthidium (Trichanthidium) benguelense</i>	1434	SOUTH AFRICA: Limpopo Prov., 27 km E Waterpoort, 07.i.2004
<i>Pachyanthidium (Trichanthidium) sp.</i>	1646	SOUTH AFRICA: ECP, W Bavienskloof P.P., 27.ii.2010
<i>Paranthidium (Paranthidium) jugatorium</i>	495	USA: NY, Tompkins Co., Ithaca, 31.vii.1997
<i>Paranthidium (Rapanthidium) sp. nov. 2</i>	1604	MEXICO: Colima, San Antonio, La Becarrera, 10.x.2008
<i>Plesianthidium (Carinanthidium) cariniventre</i>	1595	SOUTH AFRICA: WCP, Hoek se Berg, E Clanwilliam, 20.x.2008
<i>Plesianthidium (Spinanthidiellum) rufocaudatum</i>	1609	SOUTH AFRICA: NCP, Nieuwoudtville Wildflower Preserve, 18.x.2008
<i>Plesianthidium (Spinanthidiellum) volkmanni</i>	1449	SOUTH AFRICA: NCP, Eksteenfontein, 09.x.2008
<i>Plesianthidium (Spinanthidium) calescens</i>	1279	SOUTH AFRICA: WCP, 7 km W Nieuwoudtville, 9.x. 2002
<i>Plesianthidium (Spinanthidium) trachusiforme</i>	1613	SOUTH AFRICA: NCP, 10 km E Nabapeep, 15.x.2008
<i>Pseudoanthidium (Branthidium) micurum</i>	1592	SOUTH AFRICA: NCP, Richtersveld National Park, 13.x.2008
<i>Pseudoanthidium (Branthidium) minutulum</i>	1593	SOUTH AFRICA: NCP, Richtersveld National Park, 13.x.2008
<i>Pseudoanthidium (Exanthidium) eximium</i>	1600	ITALY: Piemonte, Susa, Salbertrand, 01.vii. 2006
<i>Pseudoanthidium (Immanthidium) immaculatum</i>	1629	SOUTH AFRICA: ECP, 74 km E Barkly East, 04.iii.2002
<i>Pseudoanthidium (Immanthidium) junodi</i>	1634	SOUTH AFRICA: ECP, 74 km E Barkly East, 04.iii.2002
<i>Pseudoanthidium (Immanthidium) repetitum</i>	1632	SOUTH AFRICA: Limpopo Prov., 30 km W Sibasa, 30.iii.2002
<i>Pseudoanthidium (Immanthidium) sjoestedti</i>	1633	SOUTH AFRICA: FS, Tussen Die Riviere NR, 02.iii.2002
<i>Pseudoanthidium (Micranthidium) sp. nov. 3</i>	1605	TANZANIA: Kilimanjaro Region, 19 km SE Same, 14.i.2003

<i>Pseudoanthidium (Micranthidium) sp.</i>	1641	GHANA: Central UCC, Valco Gardens, 01.xi.2008
<i>Pseudoanthidium (Neanthidium) octodentatum</i>	cp410	MOROCCO: Igerm, 28.iv.2003
<i>Pseudoanthidium (Pseudoanthidium) scapulare</i>	1601	ITALY: Toscana, Massa Maritima, 28.vii.2005
<i>Pseudoanthidium (Royanthidium) melanurum</i>	1438	GREECE: Kalogria, 25.v.2006
<i>Pseudoanthidium (Tuberanthidium) tuberculiferum</i>	cp782	SOUTH AFRICA: NCP, 6 km S Garies, 17.x.2008
<i>Pseudoanthidium (Zosteranthidium) tergofasciatum</i>	cp646	SOUTH AFRICA: WCP, Knersvlakte, 24.viii.2010
<i>Rhodanthidium (Asianthidium) caturigense</i>	cp23	SWITZERLAND: Valais, Euseigne, 25.vi.2011
<i>Rhodanthidium (Meganthidium) superbum</i>	1638	IRAN: Yasuj Region, Margoan Waterfall, 29.v.2009
<i>Rhodanthidium (Rhodanthidium) septemdentatum</i>	1514	GREECE: Rhodos, Stegna, 08.v.2005
<i>Serapista rufipes</i>	1450	SOUTH AFRICA: NCP, Eksteenfontein, 09.x.2008
<i>Serapista soni</i>	1626	SOUTH AFRICA: Limpopo Prov., 1 km N Vivo, 17.iii.2002
<i>Stelis (Dolichostelis) laticincta</i>	1389	USA: CA, Mariposa Co., Yosemite Valley, 27.vi.2005
<i>Stelis (Dolichostelis) perpulchra</i>	cp123	USA: NV, Clark Co., 1.5 miles NW Corn Creek Sprs., 27.v.2004
<i>Stelis (Dolichostelis) rudbeckiarum</i>	cp122	USA: UT, Garfield Co., Point Lookout, 30.vii.2002
<i>Stelis (Heterostelis) annulata</i>	cp21	ITALY: San Giovanni, 6.vii.2011
<i>Stelis (Heterostelis) anthidioides</i>	cp506	USA: CA, San Benito Co., Pinnacles Natl. Mon., Balconies Cliffs Tr., 22.vi.1998
<i>Stelis (Heterostelis) hurdi</i>	1409	USA: CA, San Benito Co., Pinnacles Natl. Mon., 22.v.1999
<i>Stelis (Heterostelis) ruficornis</i>	cp509	GREECE: Lesvos, 2.2 km SE Mystegna, 6-8.v.2004
<i>Stelis (Malanthidium) sp.1</i>	cp159	THAILAND: Barcode: 14515-H09
<i>Stelis (Malanthidium) sp. 2</i>	cp157	THAILAND: Barcode: 03767-H01
<i>Stelis (Protostelis) signata</i>	1440	SWITZERLAND: Hohtenn, 26.v.2005
<i>Stelis (Stelidomorpha) nasuta</i>	1614	GREECE: Atiiki, Athens Pref., 20 km S Athens, 15.vi.2006
<i>Stelis (Stelis) anthocopae</i>	1392	USA: NV, Clark Co., St. Thomas Gap, 12.v.2005
<i>Stelis (Stelis) anthracina</i>	1396	USA: NV, Clark Co., St. Thomas Gap, 15.iv.2005
<i>Stelis (Stelis) broemelingi</i>	1391	USA: AZ, Cochise Co., E. Apache, 29.viii.2003
<i>Stelis (Stelis) calliphorina</i>	1403	USA: CA, Mariposa Co., Moraine Dome, 06.vii.2005
<i>Stelis (Stelis) carnifex</i>	1395	USA: CA, Mariposa Co., Eagle Peak, 19.v.2006
<i>Stelis (Stelis) foederalis group sp. B</i>	1398	USA: CA, Mariposa Co., Ostrander Rocks
<i>Stelis (Stelis) holocyanea</i>	1405	USA: CA, Mariposa Co., Deer Camp, 09.viii.2006
<i>Stelis (Stelis) interrupta</i>	1406	USA: CA, Mariposa Co., Ostrander Rocks, 03.vii.2005
<i>Stelis (Stelis) joanae</i>	1410	USA: NV, Clark Co., St. Thomas Gap, 21.iv.2004
<i>Stelis (Stelis) lamelliterga</i>	1400	USA: UT, Kane Co., Kitchen Corral Spring, 29.v.2002
<i>Stelis (Stelis) lateralis</i>	1401	USA: UT, Washington Co. Rimrock Spring, 11.v.2006
<i>Stelis (Stelis) linsleyi</i>	1271	USA: CA, Madera Co., Yosemite National Park, 11.vii.2005
<i>Stelis (Stelis) monticola</i>	1402	USA: CA, Mariposa Co., Moraine Dome, 05.vi.2006
<i>Stelis (Stelis) occidentalis</i>	1399	USA: CA, Tuolumne Co., White Wolf, 08.vii.2006
<i>Stelis (Stelis) paiute</i>	1394	USA: NV, Clark Co., Jean Lake, 14.iv.2004
<i>Stelis (Stelis) palmarum</i>	1393	USA: UT, Kane Co., Paradise Cyn., 26.v.2003
<i>Stelis (Stelis) pavonina</i>	1404	USA: CA, Tuolumne Co., Mammoth Peak, 29.vii.2004
<i>Stelis (Stelis) punctulatissima</i>	1551	SWITZERLAND: Hohtenn, 26.v.2005
<i>Stelis (Stelis) aff. robertsoni</i>	1408	USA: CA, Mariposa Co. Yosemite Valley, 05.vii.2006
<i>Stelis (Stelis) semirubra</i>	1407	USA: CA, Madera Co., Parsons Peak, 02.viii.2004
<i>Stelis (Stelis) subcaerulea</i>	1397	USA: CA, Mariposa Co., Bernice Lake, 09.viii.2006
<i>Stelis rozeni</i>	1603	SOUTH AFRICA: NCP, Richtersveld National Park, 12-14.ix.2001
<i>Trachusa (Archianthidium) pubescens</i>	1533	TURKEY: Erzurum, Akören, 15 km N Hınıs, 19.vii.2003
<i>Trachusa (Congotrachusa) schoutedeni</i>	1538	REP. CONGO: Dept. Pool, Iboubikro, Lesio-Loun, 9-15.ix.2008
<i>Trachusa (Heteranthidium) cordaticeps</i>	cp133	LEWN 07-NM-1403
<i>Trachusa (Heteranthidium) larreae</i>	1142	USA: NV, Clark Co., Las Vegas Sand Dunes, 1.iv.2004
<i>Trachusa (Paraanthidium) interrupta</i>	1602	ITALY: Piemonte, Susa, 2.vii.2006
<i>Trachusa (Trachusa) byssina</i>	1558	SWITZERLAND: Splügen, 23.vii.2005
<i>Trachusa (Trachusomimus) perdita</i>	cp505	USA: CA, San Benito Co., 2.0 km NNW McCabe Canyon, 12.v.2011
Outgroup		
<i>Anthophora montana</i>	633	USA: AZ, Cochise Co., Chiricahua Mts., 14.ix.99
<i>Apis mellifera</i>	-	
<i>Aspidosmia arnoldi</i>	1544	SOUTH AFRICA: NCP, Eksteenfontein, 09.x.2008
<i>Aspidosmia volkmanni</i>	1579	SOUTH AFRICA: NCP, Richtersveld, near De Koci, 09.ix.2007
<i>Ashmeadiella aridula</i>	1270	USA: UT, Garfield Co., Long Canyon, 01.ix.2003
<i>Bombus ardens</i>	-	
<i>Ceratina calcarata</i>	656	USA: NY, Tompkins Co., Ithaca, 04.viii.1999
<i>Chelostoma florissomme</i>	1553	SWITZERLAND: Chur
<i>Coelioxys afra</i>	1549	SWITZERLAND: Weiach, 29.vi.2004
<i>Colletes inaequalis</i>	450	USA: NY, Tompkins Co., Ithaca
<i>Ctenoplectra albolimbata</i>	983	SOUTH AFRICA: KZN: 20 km NE Hluhluwe, 09-12.iii. 2002
<i>Dasygaster argentata</i>	973	FRANCE: Gard, Generac, 22.vi.2002
<i>Dioxys moesta</i>	1546	GREECE: Rhodos, Kamiros, 12.v.2005
<i>Epicharis analis</i>	-	
<i>Fideliopsis major</i>	JL005	SOUTH AFRICA: NCP, Eksteenfontein, 09.x.2008
<i>Haetosmia brachyura</i>	1428	UZBEKISTAN: Karakalpakstan, Beruni, 25.v.2008
<i>Heriades crucifer</i>	1149	USA: AZ, Cochise Co., Chiricahua Mts., 25.viii.2003
<i>Hoplitis adunca</i>	1552	ITALY: Aosta, 30.08.2004
<i>Lithurgus chrysurus</i>	1545	ITALY: Abruzzo, Massa, 20.viii.2002
<i>Macropis nuda</i>	1272	USA: NY, Rensselaer Co., Rensselaerville, 15.vii.2005
<i>Megachile bombiformis</i>	1531	SOUTH AFRICA: Limpopo Prov., 20 km E Waterpoort, 07.i.2004
<i>Meganomia binghami</i>	1021	SOUTH AFRICA: Limpopo Prov., 8.5 km N Vivo, 07.i.2004
<i>Melitta leporina</i>	-	

<i>Melitturga clavicornis</i>	959	FRANCE: Hérault, Causse de la Selle 17.vi.2002
<i>Neofidelia profuga</i>	802	CHILE: Atacama Prov., 5 km N Inca-havas, 03.x.1999
<i>Noteriades sp.</i>	1580	THAILAND: Chiang Mai, 24.iii.2007
<i>Ochrieriades fasciatus</i>	1557	JORDAN: 20 km W Amman, 24.iv.2007
<i>Osmia lignaria</i>	1265	no locality data
<i>Pararhophites quadratus</i>	1547	TUNISIA: Nefta, 28.iii.2006
<i>Promelitta alboclypeata</i>	1321	MOROCCO: Erfoud to Msissi road, 12.iv.2006
<i>Protosmia humeralis</i>	1559	JORDAN: Wadi Shu'ayb, 22.iv.2007
<i>Pseudoheriades moricei</i>	1431	ISRAEL: Negev
<i>Radoszkowskiana rufiventris</i>	1587	EGYPT: Tel el Kebir, 30°32'2"N 31°49'48"
<i>Rophites algirus</i>	968	FRANCE: Var, Entrecasteaux, 14.vi.2002
<i>Thyreus delumbatus</i>	987	SOUTH AFRICA: Limpopo Prov., 14 km E Vivo, 17.iii.2002
<i>Wainia eremoplana</i>	1548	JORDAN: Wadi el Hasa, 20.iv.2007
<i>Xylocopa virginica</i>	1153	USA: NY, Tompkins Co., Ithaca, 8.v.2001

Table 2

Taxa	EF1-alpha	CAD	Opsin	NAK	28S
Ingroup					
<i>Afranthidium (Afranthidium) karoense</i>	HQ995698	HQ995847	HQ995770	HQ995942	HQ996039
<i>Afranthidium (Capanthidium) capicola</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Capanthidium) rubellulum</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Capanthidium) schultzei</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Capanthidium) poecilodontum</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Domanthidium) abdominale</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Mesanthidium) alternans</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Mesanthidium) carduele</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Nigranthidium) sp.</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Nigranthidium) sp. nov. 1</i>	pending	pending	pending	pending	pending
<i>Afranthidium (Oranthidium) folliculosum</i>	pending	pending	pending	pending	pending
<i>Afranthidium sp. nov.</i>	pending	pending	pending	pending	pending
<i>Afrostellis sp.</i>	JX869701	JX869625	JX869733	JX869767	JX869660
<i>Anthidiellum (Anthidiellum) strigatum</i>	pending	pending	pending	pending	pending
<i>Anthidiellum (Chloranthidiellum) sp. nov. 1</i>	pending	pending	pending	pending	pending
<i>Anthidiellum (Loyolanthidium) robertsoni</i>	pending	pending	pending	pending	pending
<i>Anthidiellum (Pycnanthidium) absonulum</i>	pending	pending	pending	pending	pending
<i>Anthidiellum (Pycnanthidium) sp.</i>	pending	pending	pending	pending	pending
<i>Anthidium (Anthidium) chilense</i>	pending	pending	pending	pending	pending
<i>Anthidium (Anthidium) cockerelli</i>	pending	pending	pending	pending	pending
<i>Anthidium (Anthidium) colliguayanum</i>	pending	pending	pending	pending	pending
<i>Anthidium (Anthidium) deceptum</i>	pending	pending	pending	pending	pending
<i>Anthidium (Anthidium) illustre</i>	HQ995699	HQ995848	HQ995771	HQ995943	HQ996040
<i>Anthidium (Anthidium) porterae</i>	GU244996	missing	AF344619	GU245158	GU244846
<i>Anthidium (Anthidium) punctatum</i>	pending	pending	pending	pending	pending
<i>Anthidium (Gulanthidium) sp.</i>	pending	pending	pending	pending	pending
<i>Anthidium (Proanthidium) oblongatum</i>	pending	pending	pending	pending	pending
<i>Anthidium (Severanthidium) cordiforme</i>	pending	pending	pending	pending	pending
<i>Anthidium (Turkanthidium) gratum</i>	pending	pending	pending	pending	pending
<i>Anthidium (Turkanthidium) unicum</i>	pending	pending	pending	pending	pending
<i>Anthodiocetes (Anthodiocetes) mapirensis</i>	HQ995700	HQ995849	HQ995772	HQ995944	HQ996041
<i>Anthodiocetes (Bothranthidium) lauroi</i>	pending	pending	pending	pending	pending
<i>Austrostelis catamarcensis</i>	JX869702	JX869626	JX869734	JX869768	JX869661
<i>Aztecantidium tenochtitlanicum</i>	pending	pending	pending	pending	pending
<i>Bathanthidium (Manthidium) binghami</i>	HQ995703	HQ995852	HQ995775	HQ995947	HQ996044
<i>Benanthis madagascariensis</i>	HQ995704	HQ995853	HQ995776	HQ995948	HQ996045
<i>Cyphanthidium intermedium</i>	pending	pending	pending	pending	pending
<i>Dianthidium (Adanthidium) arizonicum</i>	HQ995705	HQ995854	HQ995777	HQ995949	HQ996046
<i>Dianthidium (Dianthidium) subparvum</i>	pending	pending	pending	pending	pending
<i>Dianthidium (Mecanthidium) macrurum</i>	pending	pending	pending	pending	pending
<i>Duckeantidium thielei</i>	HQ995706	HQ995855	HQ995778	HQ995950	HQ996047
<i>Eoanthidium (Clistanthidium) turnericum</i>	HQ995707	HQ995856	HQ995779	HQ995951	HQ996048
<i>Eoanthidium (Eoanthidium) clypeare</i>	pending	pending	pending	pending	pending
<i>Epanthidium (Epanthidium) bicoloratum</i>	HQ995708	HQ995857	HQ995780	HQ995952	HQ996049
<i>Euaspid abdominalis</i>	JX869703	JX869627	JX869735	JX869769	JX869662
<i>Euaspid polynesia</i>	JX869704	JX869628	JX869736	JX869770	JX869663
<i>Hoplostelis bivittata</i>	JX869705	Missing	JX869737	JX869771	JX869671
<i>Hypanthidioides (Saranthidium) marginata</i>	HQ995709	HQ995858	HQ995781	HQ995953	HQ996050
<i>Hypanthidium (Hypanthidium) obscurius</i>	pending	pending	pending	pending	pending
<i>Icteranthis ferrugineum</i>	HQ995711	HQ995860	HQ995783	HQ995955	HQ996052
<i>Notanthidium (Allanthidium) rodolphi</i>	pending	pending	pending	pending	pending
<i>Notanthidium (Notanthidium) steloides</i>	HQ995712	HQ995861	HQ995784	HQ995956	HQ996053
<i>Pachyanthidium (Ausanthidium) ausense</i>	pending	pending	pending	pending	pending
<i>Pachyanthidium (Pachyanthidium) bicolor</i>	pending	pending	pending	pending	pending
<i>Pachyanthidium (Pachyanthidium) cordatum</i>	pending	pending	pending	pending	pending
<i>Pachyanthidium (Trichanthidium) benguelense</i>	HQ995713	HQ995862	HQ995785	HQ995957	HQ996054
<i>Pachyanthidium (Trichanthidium) sp.</i>	pending	pending	pending	pending	pending
<i>Paranthidium (Paranthidium) jugatorium</i>	GU244994	HQ995863	HQ995786	GU245156	GU244844
<i>Paranthidium (Rapanthidium) sp. nov. 2</i>	pending	pending	pending	pending	pending
<i>Plesianthidium (Carinanthidium) cariniventre</i>	pending	pending	pending	pending	pending
<i>Plesianthidium (Spinanthidiellum) rufocaudatum</i>	pending	pending	pending	pending	pending
<i>Plesianthidium (Spinanthidiellum) volkmanni</i>	pending	pending	pending	pending	pending
<i>Plesianthidium (Spinanthidium) calescens</i>	pending	pending	pending	pending	pending
<i>Plesianthidium (Spinanthidium) trachusiforme</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Branthidium) micrurum</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Branthidium) minutulum</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Exanthidium) eximium</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Immanthidium) immaculatum</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Immanthidium) junodi</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Immanthidium) repetitum</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Immanthidium) sjoestedti</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Micranthidium) sp.</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Micranthidium) sp. nov. 3</i>	pending	pending	pending	pending	pending

Taxa	EF1-alpha	CAD	Opsin	NAK	28S
<i>Pseudoanthidium (Neanthidium) octodentatum</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Pseudoanthidium) scapulare</i>	HQ995714	HQ995864	HQ995787	HQ995958	HQ996055
<i>Pseudoanthidium (Royanthidium) melanurum</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Tuberanthidium) tuberculiferum</i>	pending	pending	pending	pending	pending
<i>Pseudoanthidium (Zosteranthidium) tergofasciatum</i>	pending	pending	pending	pending	pending
<i>Rhodanthidium (Asianthidium) caturigense</i>	pending	pending	pending	pending	pending
<i>Rhodanthidium (Meganthidium) superbum</i>	pending	pending	pending	pending	pending
<i>Rhodanthidium (Rhodanthidium) septemdentatum</i>	HQ995715	HQ995865	HQ995788	HQ995959	HQ996056
<i>Serapista rufipes</i>	HQ995716	HQ995866	HQ995789	HQ995960	HQ996057
<i>Serapista soni</i>	pending	pending	pending	pending	pending
<i>Stelis (Dolichostelis) laticincta</i>	JX869719	JX869644	JX869752	JX869785	JX869686
<i>Stelis (Dolichostelis) perpulchra</i>	JX869725	JX869650	JX869758	JX869791	JX869692
<i>Stelis (Dolichostelis) rudbeckiarum</i>	JX869727	JX869653	JX869761	JX869794	JX869694
<i>Stelis (Heterostelis) annulata</i>	JX869707	JX869630	JX869739	JX869773	JX869673
<i>Stelis (Heterostelis) anthidioides</i>	Missing	JX869631	Missing	Missing	JX869674
<i>Stelis (Heterostelis) hurdi</i>	JX869714	JX869639	JX869747	JX869780	JX869682
<i>Stelis (Heterostelis) ruficornis</i>	Missing	JX869654	Missing	JX869795	JX869695
<i>Stelis (Malanthidium) sp. 1</i>	JX869730	JX869657	JX869764	JX869798	JX869698
<i>Stelis (Malanthidium) sp. 2</i>	JX869732	JX869659	JX869766	JX869800	JX869700
<i>Stelis (Protostelis) signata</i>	JX869729	JX869656	JX869763	JX869797	JX869697
<i>Stelis (Stelidomorpha) nasuta</i>	JX869721	JX869646	JX869754	JX869787	JX869688
<i>Stelis (Stelis) anthocopae</i>	JX869708	JX869632	JX869740	JX869774	JX869675
<i>Stelis (Stelis) anthracina</i>	JX869709	JX869633	JX869741	JX869775	JX869676
<i>Stelis (Stelis) broemelingi</i>	Missing	JX869634	JX869742	Missing	JX869677
<i>Stelis (Stelis) calliphorina</i>	JX869710	JX869635	JX869743	JX869776	JX869678
<i>Stelis (Stelis) carnifex</i>	JX869711	JX869636	JX869744	JX869777	JX869679
<i>Stelis (Stelis) foederalis group sp. B</i>	JX869712	JX869637	JX869745	JX869778	JX869680
<i>Stelis (Stelis) holocyanea</i>	JX869713	JX869638	JX869746	JX869779	JX869681
<i>Stelis (Stelis) interrupta</i>	JX869715	JX869640	JX869748	JX869781	Missing
<i>Stelis (Stelis) joanae</i>	JX869716	JX869641	JX869749	JX869782	JX869683
<i>Stelis (Stelis) lamelliterga</i>	JX869717	JX869642	JX869750	JX869783	JX869684
<i>Stelis (Stelis) lateralis</i>	JX869718	JX869643	JX869751	JX869784	JX869685
<i>Stelis (Stelis) linsleyi</i>	GU245002	JX875064	GU245312	GU245162	Missing
<i>Stelis (Stelis) monticola</i>	JX869720	JX869645	JX869753	JX869786	JX869687
<i>Stelis (Stelis) occidentalis</i>	JX869722	JX869647	JX869755	JX869788	JX869689
<i>Stelis (Stelis) paiute</i>	HQ995717	HQ995867	HQ995790	HQ995961	HQ996058
<i>Stelis (Stelis) palmarum</i>	JX869723	JX869648	JX869756	JX869789	JX869690
<i>Stelis (Stelis) pavonina</i>	JX869724	JX869649	JX869757	JX869790	JX869691
<i>Stelis (Stelis) punctulatissima</i>	JX869726	JX869651	JX869759	JX869792	JX869693
<i>Stelis (Stelis) aff. robertsoni</i>	JX869706	JX869629	JX869738	JX869772	JX869672
<i>Stelis (Stelis) semirubra</i>	JX869728	JX869655	JX869762	JX869796	JX869696
<i>Stelis (Stelis) subcaerulea</i>	JX869731	JX869658	JX869765	JX869799	JX869699
<i>Stelis rozeni</i>	Missing	JX869652	JX869760	JX869793	Missing
<i>Trachusa (Archianthidium) pubescens</i>	HQ995718	HQ995868	HQ995791	HQ995962	HQ996059
<i>Trachusa (Congotrachusa) schoutedeni</i>	pending	pending	pending	pending	pending
<i>Trachusa (Heteranthidium) cordaticeps</i>	pending	pending	pending	pending	pending
<i>Trachusa (Heteranthidium) larreae</i>	HQ995719	HQ995869	HQ995792	GU245154	GU244842
<i>Trachusa (Paraanthidium) interrupta</i>	pending	pending	pending	pending	pending
<i>Trachusa (Trachusa) byssina</i>	pending	pending	pending	pending	pending
<i>Trachusa (Trachusomimus) perdita</i>	pending	pending	pending	pending	pending
Outgroup					
<i>Anthophora montana</i>	AY585107	DQ067177	AF344616	HQ995919	HQ996012
<i>Ashmeadiella aridula</i>	EU851535	HQ995903	EU851641	GU245171	GU244858
<i>Aspidosmia arnoldi</i>	HQ995701	HQ995850	HQ995773	HQ995945	HQ996042
<i>Bombus ardens</i>	AF492964	EU184803	AF493031	EU184741	HM750237
<i>Ceratina calcarata</i>	AY585108	DQ067190	AF344620	GU245213	HQ996011
<i>Chelostoma florissomme</i>	EU851546	HQ995905	EU851652	HQ995997	HQ996094
<i>Coelioxys afra</i>	EU851528	HQ995870	EU851634	HQ995963	HQ996060
<i>Colletes inaequalis</i>	AY363004	DQ067139	DQ115542	EF646387	HQ996017
<i>Ctenoplectra albolimbata</i>	AY585118	EU122060	DQ116677	EF646391	HQ996013
<i>Dasygaster argentea</i>	AY585148	DQ067161	DQ116680	EF646418	AY654518
<i>Dioxys moesta</i>	HQ995696	HQ995845	HQ995768	HQ995940	HQ996037
<i>Epicharis analis</i>	GU244920	Missing	GU245241	GU245064	GU244759
<i>Haetosmia brachyura</i>	HQ995748	HQ995906	HQ995822	HQ995998	HQ996095
<i>Heriades crucifer</i>	EU851555	DQ067194	EU851661	GU245168	GU244855
<i>Hopliis adunca</i>	EU851572	HQ995908	EU851678	HQ996000	HQ996097
<i>Macropis nuda</i>	AY585155	DQ067171	DQ116686	HQ995917	HQ996008
<i>Megachile bombiformis</i>	HQ995733	HQ995886	HQ995806	HQ995979	HQ996076
<i>Meganomia binghami</i>	DQ141114	DQ067169	DQ116689	EF646406	HQ996010
<i>Melitta leporina</i>	AY585158	DQ067174	DQ116688	EF646394	AY654529
<i>Melitturga clavicornis</i>	AY585104	DQ067134	DQ116703	HQ995920	HQ996015
<i>Noteriades sp</i>	EU851589	HQ995900	EU851695	HQ995993	HQ996090
<i>Ochreirades fasciatus</i>	EU851590	HQ995909	EU851696	HQ996001	HQ996098
<i>Osmia lignaria</i>	EU851610	HQ995910	EU851715	GU245169	GU244856

Taxa	EF1-alpha	CAD	Opsin	NAK	28S
<i>Promelitta alboclypeata</i>	EF594330	Missing	EF594379	HQ995918	HQ996009
<i>Protosmia humeralis</i>	EU851621	HQ995913	EU851726	HQ996004	HQ996101
<i>Pseudoheriades moricei</i>	EU851622	HQ995914	EU851727	HQ996005	HQ996102
<i>Radoszkowskiana rufiventris</i>	HQ995747	HQ995901	HQ995821	HQ995994	HQ996091
<i>Rophites algirus</i>	AY585144	DQ067159	DQ116675	HQ995921	HQ996016
<i>Tetrapedia maura</i>	GU244979	Missing	GU245300	GU245145	GU244834
<i>Thyreus delumbatus</i>	AY585119	DQ067184	DQ116679	GU245118	HQ996014
<i>Wainia eremoplana</i>	EU851626	HQ995916	EU851731	HQ996007	HQ996104
<i>Xylocopa virginica</i>	GU245047	Missing	GU245343	GU245220	GU244903

Table 3

<i>Trachusa</i> group	<i>Anthidium</i> group	<i>Anthodiocetes</i> group	<i>Dianthidium</i> group	<i>Stelis</i> group
<i>Apianthidium</i> (A)	<i>Afranthurium</i> (B)	<i>Anthodiocetes</i> (A)	<i>Acedanthidium</i> (A)	<i>Afrostelis</i> (A)
<i>Trachusa</i> (A)	<i>Anthidioma</i> (B)	<i>Austrostelis</i> (A)	<i>Anthidiellum</i> (A)	<i>Euaspis</i> (A)
<i>Trachusoides</i> (A)	<i>Anthidium</i> (B)	<i>Aztecanthidium</i> (A)	<i>Bathanthidium</i> (A)	<i>Larinostelis</i> (A)
	<i>Indanthidium</i> (B)	<i>Duckeanthidium</i> (A)	<i>Benanthus</i> (A)	<i>Stelis</i> (A)
	<i>Pseudoanthidium</i> (B)	<i>Epanthidium</i> (A)	<i>Cyphanthidium</i> (A)	<i>Xenostelis</i> (A)
	<i>Serapista</i> (B)	<i>Hoplostelis</i> (A)	<i>Dianthidium</i> (A)	
		<i>Hypanthidioides</i> (A)	<i>Eoanthidium</i> (A)	
		<i>Hypanthidium</i> (A)	<i>Icteranthurium</i> (A)	
		<i>Notanthidium</i> (A)	<i>Pachyanthidium</i> (A)	
			<i>Paranthidium</i> (A)	
			<i>Plesianthidium</i> (A)	
			<i>Rhodanthidium</i> (A)	

Trachusa group

Anthidium group

Anthodiocetes group

Dianthidium group

Stelis group

100%

100%

100%

84%

98%

100%

95%

100%

100%

Node support = ML bootstrap values