



## 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 *Afrantheidium* (*Zosterantheidium*) Michener and Griswold, 1994, *Afrantheidium* (*Brantheidium*) Pasteels, 1969 and *Afrantheidium* (*Immantheidium*) Pasteels, 1969 are moved into the genus *Pseudoantheidium*, thus forming the new combinations *Pseudoantheidium* (*Zosterantheidium*), *Pseudoantheidium* (*Brantheidium*), and *Pseudoantheidium* (*Immantheidium*). The genus *Neantheidium* Pasteels, 1969 is also moved into the genus *Pseudoantheidium*, thus forming the new combination *Pseudoantheidium* (*Neantheidium*).

Based on morphological characters shared with our new definition of the genus *Pseudoantheidium*, the subgenus *Afrantheidium* (*Mesanthidiellum*) Pasteels, 1969 and the genus *Gnathantheidium* Pasteels, 1969 are also moved into the genus *Pseudoantheidium*, thus forming the new combinations *Pseudoantheidium* (*Mesanthidiellum*) and *Pseudoantheidium* (*Gnathantheidium*).

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### 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; Xamheu, 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 putty” and “felted cotton” typical of anthidiine nests (Fabre, 1914). Fabre's descriptions highlight an intriguing aspect of their nesting biology: unlike members of the megachilid tribes Osmiini and Megachilini, whose primary nest-building materials may include leaf pieces, mud, pebbles, resin, flower petals, and masticated leaf pulp, the preferred *materia prima* of Anthidiini is almost exclusively limited

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to one of two principal sources: plant resins and plant fibers. These materials may be supplemented with pebbles, leaf strips, grains of sand, animal fur, snail shell fragments and bits of bark or other debris (Michener, 2007).

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

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 47 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 western 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 nine non-parasitic western 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 (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 45 s@94 °C/45 s@58 °C/1 m@72 °C, run for 36 cycles; the PCR runs were preceded by 5 min at 94 °C and followed by 7 min 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 (Katoh 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 Jermini, 2004; Jermini 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 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

**Table 1**

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

| 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 Eksteenfontein, 9.x.2008                           |
| <i>Afranthidium (Capanthidium) poecilodontum</i>      | 1612           | SOUTH AFRICA: NCP, 10 km E Nabapeep, 15.x.2008                                |
| <i>Afranthidium (Capanthidium) schulthessi</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) cardueae</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, 12 km N Kuruman, 09.iii. 2010                              |
| <i>Afranthidium sp. nov.</i>                          | cp179          | SOUTH AFRICA: Barcode 4484 A03  |
| <i>Afrostellis sp.</i>                                | 1645           | SOUTH AFRICA: NCP, 1 km 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) absonulum</i>         | 1635           | SOUTH AFRICA: KZN, Kulene Experimental Farm, 09–12.iii.2002                   |
| <i>Anthidiellum (Pycnanthidium) sp.</i>               | 1647           | SOUTH AFRICA: ECP,W Bavianskloof 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, 3.2 km 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) tumericum</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>Euasps abdominalis</i>                             | 1627           | SOUTH AFRICA: NP, 14 km E Vivo, 17.iii.2002                                   |
| <i>Euasps 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: Guaira, Res. de Recursos, Manejados 24.i.2007                       |
| <i>Hypanthidium (Hypanthidium) obscurius</i>          | sc171          | PARAGUAY: Paraguari, M. Nat. Achahay, 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, 01.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 Bavianskloof P.P., 27.ii.2010                             |
| <i>Paranthidium (Paranthidium) jugatorium</i>         | 495            | USA: NY, Tompkins Co., Ithaca, 31.vii.1997                                    |
| <i>Paranthidium (Rapanthidium) sp.</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) micrurum</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                                 |

(continued on next page)

Table 1 (continued)

| Taxon   | Voucher number | Collection locality   |
|---|----------------|---|
| <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, Margoon 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: Hohstenn, 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</i> group sp. B           | 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: Hohstenn, 26.v.2005  |
| <i>Stelis (Stelis) aff. robertsoni</i>                  | 1408           | USA: CA, Mariposa Co. Yosemite Valley, 05.vii.2006                              |
| <i>Stelis (Stelis) semirubia</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          | LEWNI 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) perditia</i>                | cp505          | USA: CA, San Benito Co., 2.0 km NNW McCabe Canyon, 12.v.2011                    |
| <b>Outgroup</b>   |                |   |
| <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 florissomne</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                                  |

Table 1 (continued)

| Taxon                              | Voucher number | Collection locality                                    |
|------------------------------------|----------------|--|
| <i>Neofidelia profuga</i>          | 802            | CHILE: Atacama Prov., 5 km N Inca-havas, 03.x.1999     |
| <i>Noteriades</i> sp.              | 1580           | THAILAND: Chiang Mai, 24.iii.2007                      |
| <i>Ochreriades 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                |

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 (Figs. 1 and 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

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

| Taxa  | 28S      | EF1-alpha | CAD      | Opsin    | NAK      |
|---|----------|-----------|----------|----------|----------|
| <b>Ingroup</b>  |          |           |          |          |          |
| <i>Afranthidium (Afranthidium) karoense</i>           | HQ996039 | HQ995698  | HQ995847 | HQ995770 | HQ995942 |
| <i>Afranthidium (Capanthidium) capicola</i>           | KU976218 | KX060937  | KX060879 | KX060813 | KU976158 |
| <i>Afranthidium (Capanthidium) rubellulum</i>         | KU976229 | KX060947  | KX060889 | KX060824 | KU976169 |
| <i>Afranthidium (Capanthidium) schultzei</i>          | KU976230 | Missing   | KX060890 | KX060825 | KU976170 |
| <i>Afranthidium (Capanthidium) poecilodontum</i>      | KU976227 | KX060945  | KX060887 | KX060822 | KU976167 |
| <i>Afranthidium (Domanthidium) abdominale</i>         | KU976216 | KX060936  | KX060877 | KX060811 | KU976156 |
| <i>Afranthidium (Mesanthidium) alternans</i>          | KU976217 | Missing   | KX060878 | KX060812 | KU976157 |
| <i>Afranthidium (Mesanthidium) carduele</i>           | KU976219 | KX060938  | KX060875 | KX060814 | KU976159 |
| <i>Afranthidium (Nigranthidium) sp.</i>               | KU976226 | KX060935  | KX060886 | KX060821 | KU976166 |
| <i>Afranthidium (Nigranthidium) sp. nov. 1</i>        | KU976225 | KX060944  | KX060885 | KX060820 | KU976165 |
| <i>Afranthidium (Oranthidium) folliculosum</i>        | KU976220 | KX060939  | KX060880 | KX060815 | KU976160 |
| <i>Afranthidium sp. nov.</i>                          | KU976232 | KX060949  | KX060876 | KX060827 | KU976172 |
| <i>Afrostelis sp.</i>                                 | JX869660 | JX869701  | JX869625 | JX869733 | JX869767 |
| <i>Anthidiellum (Anthidiellum) strigatum</i>          | KU976237 | KX060954  | KX060896 | KX060832 | KU976177 |
| <i>Anthidiellum (Chloranthidiellum) sp. nov. 1</i>    | KU976234 | KX060951  | KX060892 | KX060829 | Missing  |
| <i>Anthidiellum (Loyolanthidium) robertsoni</i>       | KU976235 | KX060952  | KX060894 | KX060830 | KU976175 |
| <i>Anthidiellum (Pycnanthidium) absolum</i>           | KU976233 | KX060950  | KX060893 | KX060828 | KU976174 |
| <i>Anthidiellum (Pycnanthidium) sp.</i>               | KU976236 | KX060953  | KX060895 | KX060831 | KU976176 |
| <i>Anthidium (Anthidium) chilense</i>                 | KU976238 | KX060955  | KX060897 | KX060833 | KU976178 |
| <i>Anthidium (Anthidium) cockerelli</i>               | KU976239 | KX060956  | KX060898 | KX060834 | KU976179 |
| <i>Anthidium (Anthidium) colliguayanum</i>            | KU976240 | KX060957  | KX060899 | KX060835 | KU976180 |
| <i>Anthidium (Anthidium) deceptum</i>                 | KU976242 | KX060959  | KX060901 | KX060837 | KU976182 |
| <i>Anthidium (Anthidium) illustre</i>                 | HQ996040 | HQ995699  | HQ995848 | HQ995771 | HQ995943 |
| <i>Anthidium (Anthidium) porterae</i>                 | GU244846 | GU244996  | Missing  | AF344619 | GU245158 |
| <i>Anthidium (Anthidium) punctatum</i>                | KU976246 | KX060963  | KX060904 | KX060841 | KU976186 |
| <i>Anthidium (Gulanthidium) sp.</i>                   | KU976244 | KX060961  | Missing  | KX060839 | KU976184 |
| <i>Anthidium (Proanthidium) oblongatum</i>            | KU976245 | KX060962  | KX060903 | KX060840 | KU976185 |
| <i>Anthidium (Severanthidium) cordiforme</i>          | KU976241 | KX060958  | KX060900 | KX060836 | KU976181 |
| <i>Anthidium (Turkanthidium) gratum</i>               | KU976243 | KX060960  | KX060902 | KX060838 | KU976183 |
| <i>Anthidium (Turkanthidium) unicum</i>               | KU976247 | KX060964  | KX060905 | KX060842 | KU976187 |
| <i>Anthodioctes (Anthodioctes) mapiensis</i>          | HQ996041 | HQ995700  | HQ995849 | HQ995772 | HQ995944 |
| <i>Anthodioctes (Bothranthidium) lauroi</i>           | KU976248 | KX060965  | Missing  | KX060843 | KU976188 |
| <i>Austrostelis catamarcensis</i>                     | JX869661 | JX869702  | JX869626 | JX869734 | JX869768 |
| <i>Aztecantidium tenochtitlanicum</i>                 | KU976249 | Missing   | KX060906 | KX060844 | KU976189 |
| <i>Bathanthidium (Manthidium) binghami</i>            | HQ996044 | HQ995703  | HQ995852 | HQ995775 | HQ995947 |
| <i>Benanthis madagascariensis</i>                     | HQ996045 | HQ995704  | HQ995853 | HQ995776 | HQ995948 |
| <i>Cyphanthidium intermedium</i>                      | KU976250 | KX060966  | KX060907 | KX060845 | KU976190 |
| <i>Dianthidium (Adanthidium) arizonicum</i>           | HQ996046 | HQ995705  | HQ995854 | HQ995777 | HQ995949 |
| <i>Dianthidium (Dianthidium) subparvum</i>            | GU244843 | GU244993  | KX060909 | KX060847 | GU245155 |
| <i>Dianthidium (Mecanthidium) macrurum</i>            | KU976251 | KX060967  | KX060908 | KX060846 | KU976191 |
| <i>Duckeantidium thielei</i>                          | HQ996047 | HQ995706  | HQ995855 | HQ995778 | HQ995950 |
| <i>Eoanthidium (Clistanthidium) turnericum</i>        | HQ996048 | HQ995707  | HQ995856 | HQ995779 | HQ995951 |
| <i>Eoanthidium (Eoanthidium) clypeare</i>             | KU976252 | KX060968  | KX060910 | KX060848 | KU976192 |
| <i>Epanthidium (Epanthidium) bicoloratum</i>          | HQ996049 | HQ995708  | HQ995857 | HQ995780 | HQ995952 |
| <i>Euaspiis abdominalis</i>                           | JX869662 | JX869703  | JX869627 | JX869735 | JX869769 |
| <i>Euaspiis polynesia</i>                             | JX869663 | JX869704  | JX869628 | JX869736 | JX869770 |
| <i>Hoplostelis bivittata</i>                          | JX869671 | JX869705  | Missing  | JX869737 | JX869771 |
| <i>Hypanthidioides (Saranthidium) marginata</i>       | HQ996050 | HQ995709  | HQ995858 | HQ995781 | HQ995953 |
| <i>Hypanthidium (Hypanthidium) obscurus</i>           | HQ996051 | HQ995710  | HQ995859 | HQ995782 | HQ995954 |
| <i>Icteranthidium ferrugineum</i>                     | HQ996052 | HQ995711  | HQ995860 | HQ995783 | HQ995955 |
| <i>Notanthidium (Allanthidium) rodolphi</i>           | KU976254 | KX060969  | KX060912 | KX060849 | KU976193 |
| <i>Notanthidium (Notanthidium) steloides</i>          | HQ996053 | HQ995712  | HQ995861 | HQ995784 | HQ995956 |
| <i>Pachyanthidium (Ausanthidium) ausense</i>          | KU976255 | KX060970  | KX060913 | KX060850 | KU976194 |
| <i>Pachyanthidium (Pachyanthidium) bicolor</i>        | KU976256 | Missing   | KX060914 | KX060851 | KU976195 |
| <i>Pachyanthidium (Pachyanthidium) cordatum</i>       | KU976257 | KX060971  | KX060915 | KX060852 | KU976196 |
| <i>Pachyanthidium (Trichanthidium) benguelense</i>    | HQ996054 | HQ995713  | HQ995862 | HQ995785 | HQ995957 |
| <i>Pachyanthidium (Trichanthidium) sp.</i>            | KU976258 | KX060972  | KX060916 | KX060853 | KU976197 |
| <i>Paranthidium (Paranthidium) jugatorium</i>         | GU244844 | GU244994  | HQ995863 | HQ995786 | GU245156 |
| <i>Paranthidium (Rapanthidium) sp. nov. 2</i>         | KU976259 | KX060973  | KX060917 | KX060854 | KU976198 |
| <i>Plesianthidium (Carinanthidium) cariniventre</i>   | KU976261 | KX060975  | KX060919 | KX060856 | KU976200 |
| <i>Plesianthidium (Spinanthidiellum) rufocaudatum</i> | KU976262 | KX060976  | KX060920 | KX060857 | KU976201 |
| <i>Plesianthidium (Spinanthidiellum) volkmanni</i>    | KU976263 | KX060977  | KX060921 | KX060858 | KU976202 |
| <i>Plesianthidium (Spinanthidium) calescens</i>       | KU976260 | KX060974  | KX060918 | KX060855 | KU976199 |
| <i>Plesianthidium (Spinanthidium) trachusiforme</i>   | KU976264 | KX060978  | KX060922 | KX060859 | KU976203 |
| <i>Pseudoanthidium (Branthidium) micrurum</i>         | KU976223 | KX060942  | KX060883 | KX060818 | KU976163 |
| <i>Pseudoanthidium (Branthidium) minutulum</i>        | KU976224 | KX060943  | KX060884 | KX060819 | KU976164 |
| <i>Pseudoanthidium (Exanthidium) eximium</i>          | KU976265 | KX060980  | KX060923 | KX060860 | KU976204 |
| <i>Pseudoanthidium (Immanthidium) immaculatum</i>     | KU976221 | KX060940  | KX060881 | KX060816 | KU976161 |
| <i>Pseudoanthidium (Immanthidium) junodi</i>          | KU976222 | KX060941  | KX060882 | KX060817 | KU976162 |
| <i>Pseudoanthidium (Immanthidium) repetitum</i>       | KU976228 | KX060946  | KX060888 | KX060823 | KU976168 |
| <i>Pseudoanthidium (Immanthidium) sjoestedti</i>      | KU976231 | KX060948  | KX060891 | KX060826 | KU976171 |
| <i>Pseudoanthidium (Micranthidium) sp.</i>            | KU976268 | KX060982  | KX060926 | KX060862 | KU976206 |
| <i>Pseudoanthidium (Micranthidium) sp. nov. 3</i>     | KU976267 | Missing   | KX060925 | KX060864 | Missing  |

Table 2 (continued)

| Taxa  | 28S      | EF1-alpha | CAD      | Opsin    | NAK       |
|---|----------|-----------|----------|----------|-----------|
| <i>Pseudoanthidium (Neanthidium) octodentatum</i>       | KU976253 | KX060983  | KX060911 | KX060863 | Missing   |
| <i>Pseudoanthidium (Pseudoanthidium) scapulare</i>      | HQ996055 | HQ995714  | HQ995864 | HQ995787 | HQ995958  |
| <i>Pseudoanthidium (Royanthidium) melanurum</i>         | KU976266 | KX060981  | KX060924 | KX060861 | KU976205  |
| <i>Pseudoanthidium (Tuberanthidium) tuberculiferum</i>  | KU976269 | KX060979  | KX060927 | KX060865 | KU976207  |
| <i>Pseudoanthidium (Zosteranthidium) tergofasciatum</i> | KU976270 | Missing   | Missing  | KX060866 | KU976173  |
| <i>Rhodanthidium (Asianthidium) caturigense</i>         | KU976271 | KX060984  | KX060928 | KX060867 | KU976208  |
| <i>Rhodanthidium (Meganthidium) superbum</i>            | KU976272 | KX060985  | Missing  | KX060868 | KU976209  |
| <i>Rhodanthidium (Rhodanthidium) septemdentatum</i>     | HQ996056 | HQ995715  | HQ995865 | HQ995788 | HQ995959  |
| <i>Serapista rufipes</i>                                | HQ996057 | HQ995716  | HQ995866 | HQ995789 | HQ995960  |
| <i>Serapista soni</i>                                   | KU976273 | KX060986  | KX060929 | KX060869 | KU976210  |
| <i>Stelis (Dolichostelis) laticincta</i>                | JX869686 | JX869719  | JX869644 | JX869752 | JX869785  |
| <i>Stelis (Dolichostelis) perpulchra</i>                | JX869692 | JX869725  | JX869650 | JX869758 | JX869791  |
| <i>Stelis (Dolichostelis) rudbeckiarum</i>              | JX869694 | JX869727  | JX869653 | JX869761 | JX869794  |
| <i>Stelis (Heterostelis) annulata</i>                   | JX869673 | JX869707  | JX869630 | JX869739 | JX869773  |
| <i>Stelis (Heterostelis) anthidioides</i>               | JX869674 | Missing   | JX869631 | Missing  | Missing   |
| <i>Stelis (Heterostelis) hurdi</i>                      | JX869682 | JX869714  | JX869639 | JX869747 | JX869780  |
| <i>Stelis (Heterostelis) ruficornis</i>                 | JX869695 | Missing   | JX869654 | Missing  | JX869795  |
| <i>Stelis (Malanthidium) sp. 1</i>                      | JX869698 | JX869730  | JX869657 | JX869764 | JX869798  |
| <i>Stelis (Malanthidium) sp. 2</i>                      | JX869700 | JX869732  | JX869659 | JX869766 | JX869800  |
| <i>Stelis (Protostelis) signata</i>                     | JX869697 | JX869729  | JX869656 | JX869763 | JX869797  |
| <i>Stelis (Stelidomorpha) nasuta</i>                    | JX869688 | JX869721  | JX869646 | JX869754 | JX869787  |
| <i>Stelis (Stelis) anthocopae</i>                       | JX869675 | JX869708  | JX869632 | JX869740 | JX869774  |
| <i>Stelis (Stelis) anthracina</i>                       | JX869676 | JX869709  | JX869633 | JX869741 | JX869775  |
| <i>Stelis (Stelis) broemelingi</i>                      | JX869677 | Missing   | JX869634 | JX869742 | Missing   |
| <i>Stelis (Stelis) calliphorina</i>                     | JX869678 | JX869710  | JX869635 | JX869743 | JX869776  |
| <i>Stelis (Stelis) carnifex</i>                         | JX869679 | JX869711  | JX869636 | JX869744 | JX869777  |
| <i>Stelis (Stelis) foederalis group sp. B</i>           | JX869680 | JX869712  | JX869637 | JX869745 | JX869778  |
| <i>Stelis (Stelis) holocyanea</i>                       | JX869681 | JX869713  | JX869638 | JX869746 | JX869779  |
| <i>Stelis (Stelis) interrupta</i>                       | Missing  | JX869715  | JX869640 | JX869748 | JX869781  |
| <i>Stelis (Stelis) joanae</i>                           | JX869683 | JX869716  | JX869641 | JX869749 | JX869782  |
| <i>Stelis (Stelis) lamelliterga</i>                     | JX869684 | JX869717  | JX869642 | JX869750 | JX869783  |
| <i>Stelis (Stelis) lateralis</i>                        | JX869685 | JX869718  | JX869643 | JX869751 | JX869784  |
| <i>Stelis (Stelis) linsleyi</i>                         | Missing  | GU245002  | JX875064 | GU245312 | GU245162  |
| <i>Stelis (Stelis) monticola</i>                        | JX869687 | JX869720  | JX869645 | JX869753 | JX869786  |
| <i>Stelis (Stelis) occidentalis</i>                     | JX869689 | JX869722  | JX869647 | JX869755 | JX869788  |
| <i>Stelis (Stelis) paiute</i>                           | HQ996058 | HQ995717  | HQ995867 | HQ995790 | HQ995961  |
| <i>Stelis (Stelis) palmarum</i>                         | JX869690 | JX869723  | JX869648 | JX869756 | JX869789  |
| <i>Stelis (Stelis) pavonina</i>                         | JX869691 | JX869724  | JX869649 | JX869757 | JX869790  |
| <i>Stelis (Stelis) punctulatissima</i>                  | JX869693 | JX869726  | JX869651 | JX869759 | JX869792  |
| <i>Stelis (Stelis) aff. robertsoni</i>                  | JX869672 | JX869706  | JX869629 | JX869738 | JX869772  |
| <i>Stelis (Stelis) semirubra</i>                        | JX869696 | JX869728  | JX869655 | JX869762 | JX869796  |
| <i>Stelis (Stelis) subcaerulea</i>                      | JX869699 | JX869731  | JX869658 | JX869765 | JX869799  |
| <i>Stelis rozeni</i>                                    | Missing  | Missing   | JX869652 | JX869760 | JX869793  |
| <i>Trachusa (Archianthidium) pubescens</i>              | HQ996059 | HQ995718  | HQ995868 | HQ995791 | HQ995962  |
| <i>Trachusa (Congotrachusa) schoutedeni</i>             | KU976275 | Missing   | KX060931 | KX060871 | KU976212  |
| <i>Trachusa (Heteranthidium) cordaticeps</i>            | KU976276 | KX060988  | KX060932 | KX060872 | KU976213  |
| <i>Trachusa (Heteranthidium) larreae</i>                | GU244842 | HQ995719  | HQ995869 | HQ995792 | GU245154  |
| <i>Trachusa (Paraanthidium) interrupta</i>              | KU976277 | KX060989  | KX060933 | KX060873 | KU976214  |
| <i>Trachusa (Trachusa) byssina</i>                      | KU976274 | KX060987  | KX060930 | KX060870 | KU976211  |
| <i>Trachusa (Trachusomimus) perdita</i>                 | KU976278 | KX060990  | KX060934 | KX060874 | KU976215  |
| <b>Outgroup</b>   |          |           |          |          |           |
| <i>Afroheriades primus</i>                              | HQ996092 | EU851532  | HQ995902 | EU851638 | HQ995995  |
| <i>Anthophora montana</i>                               | HQ996012 | AY585107  | DQ067177 | AF344616 | HQ995919  |
| <i>Apis mellifera</i>                                   | AY703551 | AF015267  | DQ067178 | AMU26026 | XM_623142 |
| <i>Ashmeadiella aridula</i>                             | GU244858 | EU851535  | HQ995903 | EU851641 | GU245171  |
| <i>Aspidosmia arnoldi</i>                               | HQ996042 | HQ995701  | HQ995850 | HQ995773 | HQ995945  |
| <i>Aspidosmia volkmanni</i>                             | HQ996043 | HQ995702  | HQ995851 | HQ995774 | HQ995946  |
| <i>Bombus ardens</i>                                    | HM750237 | AF492964  | EU184803 | AF493031 | EU184741  |
| <i>Ceratina calcarata</i>                               | HQ996011 | AY585108  | DQ067190 | AF344620 | GU245213  |
| <i>Chelostoma florisomne</i>                            | HQ996094 | EU851546  | HQ995905 | EU851652 | HQ995997  |
| <i>Coelioxys afra</i>                                   | HQ996060 | EU851528  | HQ995870 | EU851634 | HQ995963  |
| <i>Colletes inaequalis</i>                              | HQ996017 | AY363004  | DQ067139 | DQ115542 | EF646387  |
| <i>Ctenoplectra albolimbata</i>                         | HQ996013 | AY585118  | EU122060 | DQ116677 | EF646391  |
| <i>Dasyopoda argentata</i>                              | AY654518 | AY585148  | DQ067161 | DQ116680 | EF646418  |
| <i>Dioxys moesta</i>                                    | HQ996037 | HQ995696  | HQ995845 | HQ995768 | HQ995940  |
| <i>Epicharis analis</i>                                 | GU244759 | GU244920  | Missing  | GU245241 | GU245064  |
| <i>Fidelia major</i>                                    | HQ996027 | DQ141113  | HQ995833 | EU851628 | HQ995931  |
| <i>Haetosmia brachyura</i>                              | HQ996095 | HQ995748  | HQ995906 | HQ995822 | HQ995998  |
| <i>Heriades crucifer</i>                                | GU244855 | EU851555  | DQ067194 | EU851661 | GU245168  |
| <i>Hoplitis adunca</i>                                  | HQ996097 | EU851572  | EU851572 | EU851678 | HQ996000  |
| <i>Lithurgus chrysurus</i>                              | HQ996031 | EU851523  | HQ995837 | EU851629 | HQ995934  |
| <i>Macropis nuda</i>                                    | HQ996008 | AY585155  | DQ067171 | DQ116686 | HQ995917  |
| <i>Megachile bombiformis</i>                            | HQ996076 | HQ995733  | HQ995886 | HQ995806 | HQ995979  |
| <i>Meganomia binghami</i>                               | HQ996010 | DQ141114  | DQ067169 | DQ116689 | EF646406  |

(continued on next page)

Table 2 (continued)

| Taxa                               | 28S      | EF1-alpha | CAD      | Opsin    | NAK      |
|------------------------------------|----------|-----------|----------|----------|----------|
| <i>Melitta leporina</i>            | AY654529 | AY585158  | DQ067174 | DQ116688 | EF646394 |
| <i>Melitturga clavicornis</i>      | HQ996015 | AY585104  | DQ067134 | DQ116703 | HQ995920 |
| <i>Neofidelia profuga</i>          | HQ996030 | GU244990  | HQ995836 | HQ995760 | GU245151 |
| <i>Noteriades</i> sp.              | HQ996090 | EU851589  | HQ995900 | EU851695 | HQ995993 |
| <i>Ochreeriades fasciatus</i>      | HQ996098 | EU851590  | HQ995909 | EU851696 | HQ996001 |
| <i>Osmia lignaria</i>              | GU244856 | EU851610  | HQ995910 | EU851715 | GU245169 |
| <i>Pararhophites quadratus</i>     | GU244841 | EU851522  | HQ995824 | EU851627 | GU245153 |
| <i>Promelitta alboclypeata</i>     | HQ996009 | EF594330  | Missing  | EF594379 | HQ995918 |
| <i>Protosmia humeralis</i>         | HQ996101 | EU851621  | HQ995913 | EU851726 | HQ996004 |
| <i>Pseudoheriades moricei</i>      | HQ996102 | EU851622  | HQ995914 | EU851727 | HQ996005 |
| <i>Radoszkowskiana rufiventris</i> | HQ996091 | HQ995747  | HQ995901 | HQ995821 | HQ995994 |
| <i>Rophites algirus</i>            | HQ996016 | AY585144  | DQ067159 | DQ116675 | HQ995921 |
| <i>Thyreus delumbatus</i>          | HQ996014 | AY585119  | DQ067184 | DQ116679 | HQ245118 |
| <i>Wainia eremoplana</i>           | HQ996104 | EU851626  | HQ995916 | EU851731 | HQ996007 |
| <i>Xylocopa virginica</i>          | GU244903 | GU245047  | Missing  | GU245343 | GU245220 |

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 *Austrorstelis* 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*, *Afrantheridium*, *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 mono-

phyletic in both ML and Bayesian analyses (100% ML bootstrap support; 100% posterior probability).

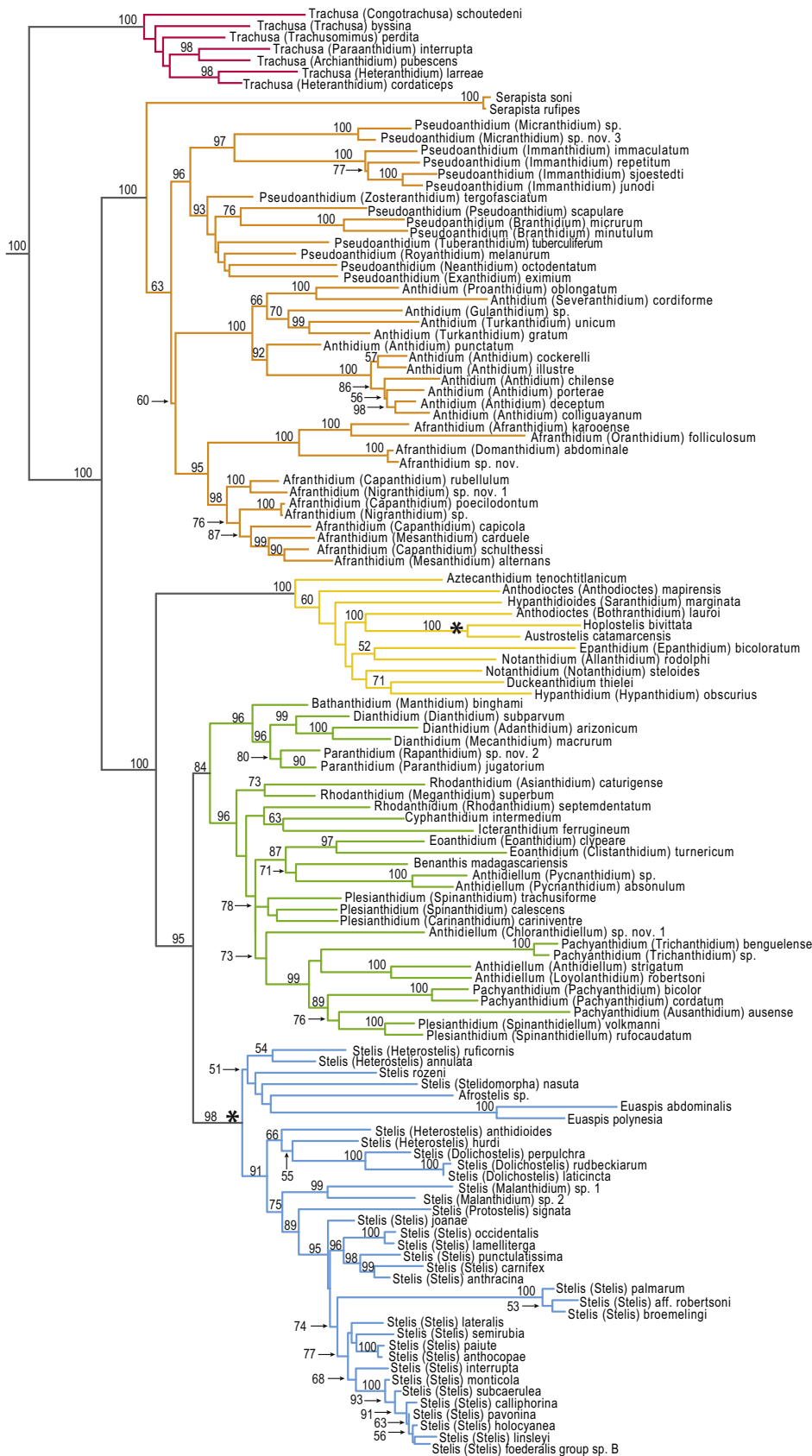
The second clade contains most but not all subgenera of the genus *Afrantheridium* (i.e. *Afrantheridium*, *Orantheridium*, *Domantheridium*, *Capantheridium*, *Mesanthidium*, and *Nigrantheridium*). This clade is strongly supported in both ML and Bayesian analyses (95% ML bootstrap; 100% posterior probability).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

The third clade contains all members of *Pseudoanthidium*, three subgenera of *Afrantheridium* (*Immantheridium*, *Brantheridium* and *Zosteranthidium*) and the genus *Neanthidium*. This clade is strongly supported in both ML and Bayesian analyses (96% ML bootstrap; 99% posterior probability).

The *Anthodioctes* group consists of the Central and South American genera *Aztecantidium*, *Notanthidium*, *Epantheridium*, *Anthodioctes*, *Hoplostelis*, *Austrorstelis*, *Hypantheridium*, *Hypantherioides*, and *Duckeantidium*; these genera form a strongly supported monophyletic clade sister to the *Dianthidium* group + the *Stelis* group. *Hoplostelis* is strongly supported as the sister taxon to *Austrorstelis* in both Bayesian and ML analyses (100% ML bootstrap; 100% posterior probability); *Anthodioctes* (*Bothrantheridium*) *lauroi* is strongly supported as the sister taxon to *Hoplostelis* + *Austrorstelis* (100% ML bootstrap; 92% posterior probability). A sister-group relationship between *Hypantheridium* and *Duckeantidium* is moderately supported in ML analyses (71% ML bootstrap) and strongly supported in Bayesian analyses (100% posterior probability). While Bayesian analyses recover highly resolved relationships for other clades in the group, ML analyses suggest that all other phylogenetic relationships within this group are unclear.

In the *Dianthidium* clade, the Asian genus *Bathantheridium* is the sister taxon to a clade consisting of the Central and North American genera *Paranthidium* and *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*, *Icterantheridium*, *Eoanthidium*, *Anthidiellum*, *Pachyantheridium*, *Benanthis*, *Cyphantheridium* and *Plesiantheridium* (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* (*Pycnantheridium*) 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





**Trachusa group**



**Anthidium group**



**Anthodioctes group**



**Diantidium group**



**Stelis group**



**Fig. 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.

**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.

| Trachusa group          | Anthidium group            | Anthodioctes group         | Dianthidium group         | Stelis group            |
|-------------------------|----------------------------|----------------------------|---------------------------|-------------------------|
| <i>Apianthidium</i> (A) | <b>Afranthidium</b> (B)    | <b>Anthodioctes</b> (A)    | <i>Acedanthidium</i> (A)  | <b>Afrostelis</b> (A)   |
| <b>Trachusa</b> (A)     | <i>Anthidioma</i> (B)      | <b>Austrostelis</b> (A)    | <b>Anthidiellum</b> (A)   | <b>Euaspsis</b> (A)     |
| <i>Trachusoides</i> (A) | <b>Anthidium</b> (B)       | <b>Aztecanthidium</b> (A)  | <b>Bathanthidium</b> (A)  | <i>Larinostelis</i> (A) |
|                         | <i>Indanthidium</i> (B)    | <b>Duckeanthidium</b> (A)  | <b>Benanthis</b> (A)      | <b>Stelis</b> (A)       |
|                         | <b>Pseudoanthidium</b> (B) | <b>Epanthidium</b> (A)     | <b>Cyphanthidium</b> (A)  | <i>Xenostelis</i> (A)   |
|                         | <b>Serapista</b> (B)       | <b>Hoplostelis</b> (A)     | <b>Dianthidium</b> (A)    |                         |
|                         |                            | <b>Hypanthidioides</b> (A) | <b>Eoanthidium</b> (A)    |                         |
|                         |                            | <b>Hypanthidium</b> (A)    | <b>Icteranthis</b> (A)    |                         |
|                         |                            | <b>Notanthidium</b> (A)    | <b>Pachyanthidium</b> (A) |                         |
|                         |                            |                            | <b>Paranthidium</b> (A)   |                         |
|                         |                            |                            | <b>Plesianthidium</b> (A) |                         |
|                         |                            |                            | <b>Rhodanthidium</b> (A)  |                         |

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*, *Euaspsis* and *Afrostelis* form the strongly supported *Stelis* group. The lineages *Stelis* (*Stelidomorpha*) *nasuta*, *Stelis* (*Heterostelis*) *ruficornis*, *Stelis* (*Heterostelis*) *annulata*, *Stelis* *rozeni*, *Afrostelis*, and *Euaspsis* 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 Figs. S2 and S3. In ML analyses of combined data, *Indanthidium crenulicauda* forms a polytomy with *Afranthidium* and *Anthidium*. In Bayesian analyses, combined data weakly support *Indanthidium crenulicauda* 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 (Figs. 1 and 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 *Afranthurium* clade, the subgenera *Afr.* (*Capanthidium*), *Afr.* (*Mesanthidium*), and *Afr.* (*Nigranthidium*) are all paraphyletic (Figs. 1 and 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*). *Afranthurium* (*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 (Figs. S2 and S3). Michener (2007) likened *Gnathanthidium prionognathum* to the subgenus *Pseudoanthidium* (*Micranthidium*), based on the almost lamellate preoccipital ridge, pronotal lobe, ocellus, 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 crenulaticauda* 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 *Afranthurium* (Fig. S2), while Bayesian analyses place it as the sister taxon to the genus *Serapista* (Fig. 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*, *Afranthurium* (*Afranthurium*) and *Afranthurium* (*Oranthidium*) (Michener, 2007), our analyses suggest a closer phylogenetic relationship between *Anthidioma* and the genus *Anthidium* (Figs. S2 and 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 *Anthodioctes* group

The majority of the *Anthodioctes* group are notable for the presence of juxtantennal carinae (only absent in *Hypanthidium*, *Notanthidium*, and *Aztecantidium*) and postspiracular pits on the propodeum (only absent in *Notanthidium*, and *Aztecantidium*), characters rare elsewhere in Anthidiini. Juxtantennal carinae are absent in the *Trachusa* and *Anthidium* groups, rare in the *Dianthid-*

*ium* group (only some *Dianthidium* and *Eoanthidium*), and found only in *Euaspid* and *Larinostelis* in the *Stelis* group; postspiracular pits are likewise absent in the *Trachusa* and *Anthidium* groups, present only in *Bathanthidium* and some *Anthidiellum* in the *Dianthidium* group and occur sporadically in the *Stelis* group: all *Afrostelis*, *Euaspid*, *Larinostelis*, *S. rozeni*, *S.* (*Protostelis*), *S.* (*Dolichostelis*), and some *S.* (*Malanthidium*), *S.* (*Heterostelis*), *S.* (*Stelis*).

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

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 punctuation 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 *Anthodioctes* 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 *Hypanthioides* (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 *Anthodioctes* (*Bothranthidium*) *lauroi*, we predict that *Anthodioctes* (*Bothranthidium*) may eventually be revealed as a host for other species of *Austrostelis*.

Two nest-building genera, *Notanthidium* and *Anthodioctes*, 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 (Figs. 1 and 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 trifold 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 omanus 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 *Euaspsis* together form a strongly supported monophyletic clade (Litman et al., 2013). The weakly supported phylogenetic position of *Afrostellis* and *Euaspsis* 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 *Afrostellis* 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 *Afrostellis* may be a specialized derivative of *Stelis* (Michener and Griswold, 1994b). The genitalia of male *Euaspsis* 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, *Euaspsis* has two apical spines on its fore- and mid-tibiae. Michener (2007) proposed a possible derivation of *Euaspsis* from a “*Pachyanthidium*-like ancestor” and suggested that morphological similarities between *Euaspsis* and *Stelis* were possible convergences due to a shared cleptoparasitic lifestyle.

Our results confirm the close phylogenetic relationship between *Afrostellis*, *Euaspsis*, and *Stelis* and suggest that *Afrostellis* and *Euaspsis* 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 *Euaspsis* and *Afrostellis* 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 *Afrostellis*, *Euaspsis* and other *Stelis* (T. Griswold, personal communication). Our results soundly confirm the affinity of *Stelis rozeni* with the *Stelis* clade; like *Euaspsis* and *Afrostellis*, 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 haldi* 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 *Afrostellis*, a parasite of *Heriades* (Taylor, 1965), and *Euaspsis*, 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* (Krombein, 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 *Afrostelis*. Michener (2007) speculates that *Xenostelis* may in fact be a synonym or a subgenus of *Afrostelis*. 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 *Anthodioctes* and *Dianthidium* groups is much-needed, a combination of missing subgenera, particularly in the *Anthodioctes* 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*, *Afranthurium*, *Anthidium*, *Gnathanthidium*, *Indanthidium*, *Neanthidium*, *Pseudoanthidium*, and *Serapista*. According to our results, multiple subgenera of *Afranthurium* and the genera *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 from one another, calling into question their utility. We thus excluded this classification from consideration.

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

We move the subgenera *Afranthurium* (*Zosteranthidium*), *Afranthurium* (*Branthidium*), *Afranthurium* (*Immanthidium*) and the genus *Neanthidium* into the genus *Pseudoanthidium*. These form the new combinations *Pseudoanthidium* (*Zosteranthidium*), *P.* (*Branthidium*), *P.* (*Immanthidium*) and *P.* (*Neanthidium*). Interestingly, the genus *Afranthurium* comes out twice in the key to Old World genera of Anthidiini (Michener and Griswold, 1994b; Michener, 2007). The subgenera that correspond to the second occurrence of *Afranthurium* in the key are those in which the premarginal zone is not depressed and the punctation of this zone is not finer than the basal zone. These subgenera are here assigned to *Pseudoanthidium*. Based on the morphological traits associated with our new definition of *Pseudoanthidium* (outlined below), we also include the genus *Gnathanthidium* and the subgenus *Afranthurium* (*Mesanthidiellum*) in *Pseudoanthidium*. These form the new combinations *Pseudoanthidium* (*Gnathanthidium*) and *P.* (*Mesanthidiellum*).

The genus *Afranthurium*, as now defined, thus includes the subgenera *Afranthurium*, *Capanthidium*, *Domanthidium*, *Mesanthidium*, *Nigranthidium*, *Oranthidium* and *Xenanthidium*. The genus *Pseudoanthidium* now includes the subgenera *Branthidium*, *Exanthidium*, *Gnathanthidium*, *Immanthidium*, *Mesanthidiellum*, *Micranthidium*, *Neanthidium*, *Pseudoanthidium*, *Royanthidium*, *Semicarinella*, *Tuberanthidium* and *Zosteranthidium*.

With its expanded diversity, 60 described species in twelve subgenera plus numerous undescribed species, it is not surprising that universal characters distinguishing *Pseudoanthidium* from *Afranthurium* are not abundant. Nevertheless, a suite of characters not or rarely found in *Afranthurium*, as here redefined, does exist for *Pseudoanthidium*: punctation of terga similar in diameter and density across the surface, without distinct apical depressed zone; apical margins of terga broadly impunctate (several puncture widths) (except *Royanthidium*); pronotal lobe at least narrowly lamellate (except *Zosteranthidium*, *Immanthidium*; also occurs in *Afranthurium* subgenus *Mesanthidium*); hind tibia tuberculate (except *Micranthidium*, *Immanthidium*, *Zosteranthidium*); propodeum shagreened (except *Micranthidium*, *Immanthidium*, *Pseudoanthidium*, *Royanthidium*, *Exanthidium*, some *Branthidium*); male sixth

tergite without lateral spine (except some *Exanthidium*); male seventh tergite emarginate medially (except some *Micranthidium* and *Pseudoanthidium*; also occurs in *Afrantheidium* subgenus *Nigranthidium*); male third sternum with modified hairs (except *Royanthidium*, *Mesanthidiellum*, *Gnathanthidium*, *Branthidium*); female clypeal apical margin covered with dense pubescence (except *Micranthidium*, *Zosteranthidium*, *Immanthidium*, *Royanthidium*, *Exanthidium*). As now constituted, *Pseudoanthidium* typically has a blocky head and rather circular metasoma in cross-section.

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

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

#### 4.7. The evolution of morphological characters – implications for classification

Many characters appear in multiple anthidiine genera and subgenera, apparently without phylogenetic pattern. Males from diverse genera, for example, exhibit apical marginal combs on sternites three, four or five. Such combs are present in genera from all five suprageneric anthidiine groups, including members of *Trachusa* (on S4 and S5, depending on subgenera), *Pseudoanthidium* (on S5 in *Pseudoanthidium* (*Pseudoanthidium*) and *P.* (*Royanthidium*)), *Pachyanthidium* (on S4 and S5), *Hypanthidioides* (S3 and S5, depending on subgenus), *Plesianthidium* (S4 and S5, 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 *Afrantheidium*, *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*, *Euaspsis* and *Larinostelis*; and a complete or partial preoccipital carina, seen in *Afrantheidium* (*Mesanthidiellum*), *Anthidium* (subgenera *Severanthidium* and *Turkanthidium*), *Aztecantidium*, *Anthodioctes*, *Afrostelis*, *Euaspsis*, *Gnathanthidium*, *Icterantheidium*, *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).

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

a subsequent decision regarding which morphological characters are appropriate for the diagnosis of these groups.

#### 4.8. Mandibular morphology and nesting behavior

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

The theory that mandibles exhibiting many, sharp teeth are adapted to harvesting 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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#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ymp.2016.03.018>.

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