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Dual origins of social parasitism in North American *Dialictus* (Hymenoptera: Halictidae) confirmed using a phylogenetic approach

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Abstract

The bee subgenus *Dialictus* (Halictidae: *Lasioglossum*) displays a large array of behaviours including solitary behaviour, eusociality, and social parasitism. Socially parasitic *Dialictus* share a suite of morphological traits; these could result from shared ancestry, but given their functional significance, could also have resulted from adaptive convergence. A combined morphological and molecular phylogenetic approach was used to test for monophyly of North American socially parasitic *Dialictus*. Two data sets were used in the phylogenetic analyses. First, short mitochondrial DNA sequences from previous taxonomic studies of North American *Dialictus*, including six social parasites, were used because of the broad taxon sampling they provide. These data were analysed in combination with a set of 40 morphological characters, including a large proportion of characters associated with social parasitism. Phylogenetic analysis of the combined DNA barcode and morphology data set resolves two distinct lineages of social parasite. The second data set was based on three genes (cytochrome *c* oxidase subunit 1, elongation factor 1α, and long-wavelength rhodopsin), but with sparser taxon sampling, including one representative from each putative social parasite-lineage. This also supported dual origins of social parasitism among North American *Dialictus*. The evolution of social parasitism is discussed.

Brood parasitism, including kleptoparasitism and social parasitism, is a common life-history trait among bees and has been recorded from four bee families: Apidae, Colletidae, Halictidae, and Megachilidae (Wcislo and Cane, 1996; Rozen, 2000, 2001, 2003; Daly and Magnacca, 2003; Michener, 2007). Most brood parasitic bees are kleptoparasites (Rozen, 2000), which lay eggs in the nest of a host bee and usually do not remain in the nest. Hosts of kleptoparasites are most often solitary species but also include some social halictines and euglossines (Sick et al., 1994; Augusto and Garofalo, 1998). Social parasites differ because they invade the host's nest and become part of the colony, usually replacing the queen in some fashion (Fisher, 1984; Batra et al., 1993; Wcislo, 1997). Social parasitism in bees has arisen independently in bumble bees (multiple times, Hines and Cameron, 2010), allodapines (multiple times, Smith et al., 2007; Tierney et al., 2008), and the halictine genera *Lasioglossum* (Wcislo, 1997; this paper), *Microsphecodes* (Eickwort and Eickwort, 1972), *Sphecodes* (Knerer, 1973) and possibly *Megalopta* (Biani and Wcislo, 2007).

Emery's rule in bees

Social parasites are often closely related to or are sister species of their hosts: respectively, the loose and strict forms of Emery's rule (Wilson, 1971; Bourke and Franks, 1991; Smith et al., 2007). A close relationship of host and parasite is expected if parasites originate as intra-specific 'cheaters' (Starr, 1979; West-Eberhard, 1986) or if inherited similarities between closely related species facilitate inter-specific manipulation (Wilson, 1971; Carlin, 1988; Lowe et al. 2002). Intra-specific parasitism and nest usurpation have been recorded for

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halictines (Plateaux-Quénu 1960; Knerer, 1973; Packer, 1986; Smith and Weller 1989), apids (Plowright and Laverty, 1984; Birmingham et al., 2004; Lopez-Vaamonde et al., 2004), and megachilids (Eickwort, 1975; reviewed in Wcislo, 1987; Field, 1992; Beekman and Oldroyd 2008). Emery's rule applies to some socially parasitic bees in the strict (e.g. *Braunsapis*; Smith et al., 2007) or loose (e.g. *Bombus*; Hines and Cameron, 2010) forms, but not others (e.g. *Microsphecodes* and *Sphecodes* each of which parasitize distantly related species—*Sphecodes* attacks bees in at least three different families, Michener, 1978). Extinction, speciation, and host switching can confound phylogenetic patterns obscuring evidence of the origins of social parasitism (Smith et al., 2007). For example, the strict form of Emery's rule cannot be detected if speciation events have occurred within either the host or the parasite lineage. Lineages of social parasite that arose more recently are less likely to have undergone these confounding effects and are therefore more suitable for understanding the origins of social parasitism. Social behaviour in the halictines arose much later than in most other social hymenopterans (approximately 20–22 million years before present; Brady et al., 2006), which suggests that halictine social parasites might be an ideal group for studying evolution of the behaviour.

Brood parasitic halictines

Michener (1978) reviewed the brood parasitic halictines and estimated five independent origins. Since then several new halictine brood parasites, apparently recently derived from their hosts, have been found (Pauly, 1984, 1997; Engel et al., 1997; Gibbs, 2009b). The large genus *Lasioglossum* (*sensu* Danforth et al., 2008), with > 1750 described species (Ascher and Pickering, 2011), is believed to have multiple origins of brood parasitism (Gibbs, 2009b). In Samoa, two species of the subgenus *Echthralictus* are believed to be derived from the subgenus *Homalictus* (Michener, 1978). New Caledonia has a brood parasitic species presumably derived from the subgenus *Chilalictus* (A. Pauly, K. Walker, J. Munzinger, B. Donovan, unpublished data). In Africa, the *Afrodialictus* group of the subgenus *Dialictus* (*sensu* Michener, 2007; Gibbs, 2010) is believed to have given rise to two brood parasites: *Lasioglossum synavei* Pauly (1984); Arduser and Michener, 1987) and *Lasioglossum ereptor* Gibbs (2009b). Finally, in North America, several species of social parasite, formerly classified separately as the genus, or subgenus (of *Lasioglossum*), *Paralictus*, are believed to have been derived from related nest-building *Dialictus* (Danforth et al., 2003). The number of known socially parasitic *Dialictus* in North America has expanded recently from five (Mitchell, 1960) to 12 (Table 1; Gibbs, 2010, 2011). Most of these novel species are extremely rare in collections and some are only known from one or a few specimens. Social parasitism has been confirmed for two species of *Dialictus* in North America (Wcislo, 1997) and is inferred for the remaining brood parasites based on eusociality of their presumed nest-building *Dialictus* hosts (Michener, 1974; see below).

Origins of brood parasitism in bees

The evolution of brood parasitism in bees has resulted in numerous morphological convergences

Table 1
List of North American socially parasitic *Lasioglossum (Dialictus)* with known host data and range

Parasite	Host	Source	Range
ascheri Gibbs			NY
cephalotes (Dalla Torre)	*zephyrum* (Smith)	Robertson, 1901 (near nest)	IA, IL, NY
curculum Gibbs			MD, WV
furunculum Gibbs			MA
izawsum	? *katherineae* Gibbs	Gibbs, 2011	MA, PA
lionotum (Sandhouse)	*imitatum* (Smith)	Wcislo, 1997 (in nest)	AL, CO, DC, MD, MO, NJ, NY, VA, WV, ON
michiganense (Mitchell)			DC, IL, MI, NC, NY, ON
platyparium (Robertson)			DC, GA, IL, KS, MD, NC, PA, WV, WI, ON
rozeni Gibbs			IL, MA, MD, NY, VA, WV
simplex (Robertson)	? *versatum* (Robertson) or *trigeminum* Gibbs	Michener, 1978 (in nest?)	IA, IL, KS, MD, VA
sitocleptum Gibbs			AZ, CO, AB, SK
wheeleri (Mitchell)			MA

Ranges are based on examined material (Gibbs, 2010, 2011).

AL, Alabama; AZ, Arizona; CO, Colorado; DC, District of Columbia; GA, Georgia; IA, Iowa; IL, Illinois; KS, Kansas; MA, Massachusetts; MD, Maryland; MI, Michigan; MO, Missouri; NC, North Carolina; NJ, New Jersey; NY, New York; PA, Pennsylvania; VA, Virginia; WI, Wisconsin; WV, West Viriginia; AB, Alberta; ON, Ontario; SK, Saskatchewan.

across parasitic taxa. These include loss or reduction of structures related to nest-building (e.g. basitibial plate, penicillus, pygidial plate) and pollen collecting (e.g. mesofemoral brush, scopa), and enhanced features related to aggression and defence (e.g. enlarged mandible, strengthened integument) (Michener, 1970, 1978). Convergence of adaptive morphologies associated with parasitism can wreak havoc with morphology-based phylogenetic analyses (Roig-Alsina and Michener, 1993). The number of estimated lineages of brood parasites in bees has varied substantially as a result of convergent evolution either in morphology or in molecules (Alexander, 1990; Michener, 2007; Straka and Bogusch, 2007; Cardinal et al., 2010). Even within the family Apidae, the estimated number of independent origins of kleptoparasitism has ranged from four (Cardinal et al., 2010) to 11 (Rozen, 2000). Adaptive convergent evolution may be particularly misleading in phylogenetic analyses of taxa with limited morphological variability such as the halictine bees. It is also possible that physiological differences associated with parasitism could result in biochemical convergence. Nonetheless, a phylogeny of these parasites is necessary for understanding the evolution of social parasitism in *Dialictus* and may throw light on its origin in other taxa.

Morphological modifications of brood parasites

The varying degrees of apparent morphological adaptation to a parasitic existence found among *Dialictus* (as *Paralictus*) led Michener (1978) and Danforth and Wcislo (1999) to suggest the possibility of polyphyletic origins for these bees. *Dialictus* includes the least modified of the halictine brood parasites (Michener, 1978; Arduser and Michener, 1987; Gibbs, 2009b), but they still share numerous morphological traits associated with brood parasitism (Michener, 1978; Table 2). The most conspicuous modifications of these social parasites are found on the head (Figs 1 and 2). The mandibles are elongate with a preapical tooth that is either reduced in size or absent entirely. The gena is often greatly enlarged to accommodate large mandibular adductor muscles (Fig. 2b). These modifications probably increase effectiveness in confrontations with the host. In some parasitic *Dialictus*, the mandible and gena are only slightly larger than in related nest-building species (Fig. 1d).

Lasioglossum, in general (and *Dialictus* in particular), is notorious for being morphologically monotonous (Michener, 1974), with few morphological differences among species. Consequently, a morphology-based phylogeny would be a poor test for convergent morphologies in parasitic *Dialictus* because the suite of traits shared by parasites, if coded independently, would be expected to overwhelm the relatively few characters that vary among nest-building species.

Table 2
Suite of traits associated with social parasitism in North American *Dialictus*

Structure	Modification	Variability
Head shape	Wide	
Labrum	Flat and broad, dorsal keel absent	
Mandibular tooth	Absent or reduced in size	Presence, size
Gena	Wide	Unmodified
Pronotal shape	Dorsolateral ridge carinate	Carina absent in *L. simplex*
Mid-femoral brush	Reduced	
Scopa	Reduced	
Basitibial plate	Reduced	Carina, size
Tibial spur	Branches short	
Penicillus	Reduced	
Pygidial region	Reduced	

Recent revisions of North American *Dialictus* have incorporated short mitochondrial sequences (commonly referred to as DNA barcodes). DNA barcodes are standardized gene fragments (Hebert and Gregory, 2005) that have been an effective tool in the study of the taxonomy of *Dialictus* (Gibbs, 2009a,c, 2010, 2011) and other organisms (see references in Golding et al., 2009) as well as having numerous additional uses (Miller et al., 2005; Wong and Hanner, 2008; Sheffield et al., 2009). A multi-locus phylogeny of *Lasioglossum* including a single parasitic *Dialictus* but with much sparser taxon sampling than now available from DNA barcodes is available (Danforth et al., 2003). Inclusion of additional parasitic species to this data set provides a second test for the monophyly of parasitic *Dialictus*.

Methods

Morphological data set

Morphological characters were coded for 85 taxa for which DNA barcode data were available (Appendix 2). We attempted to limit coding of non-independent characters in the data set. For example, characters based on microsculpture and punctation, often the only means of distinguishing closely related *Dialictus* species, could have been coded from multiple areas of the insect, but instead were limited to three clearly independent characters (based upon character state distributions among taxa) each. Exempted from this coarse-grained approach was a suite of characters related to social parasitism. These, despite reasons to believe the contrary (Wcislo, 1999), were coded and treated as if they were independent to ensure that the adaptations for social parasitism would strongly favour monophyly of

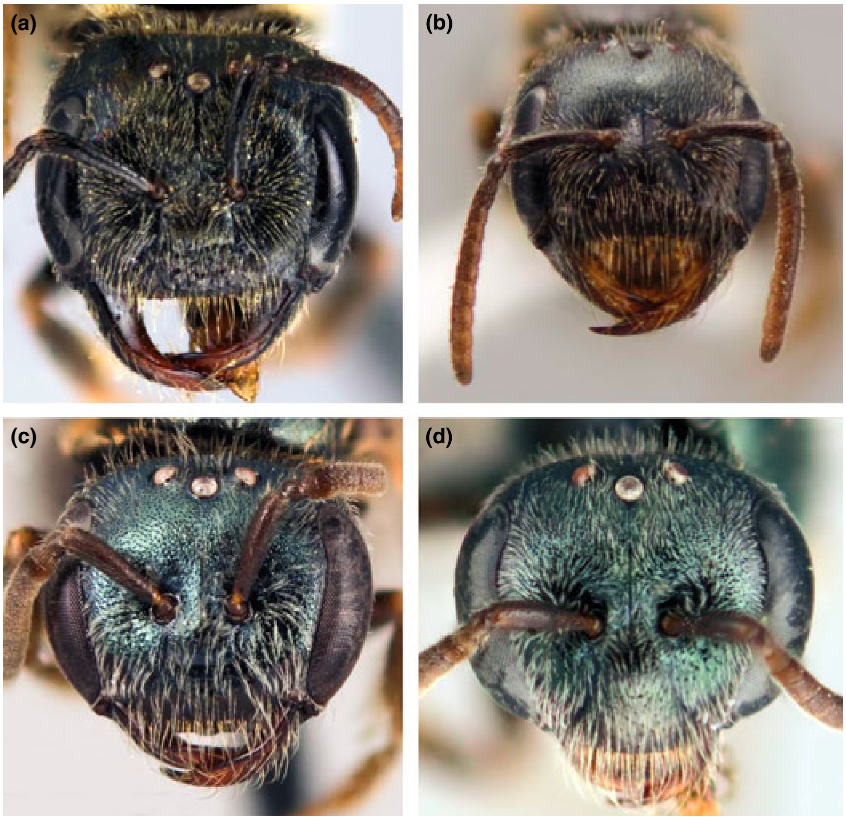

Fig. 1. Heads of socially parasitic *Dialictus*: (a) *L. cephalotes*, (b) *L. lionotum*, (c) *L. platyparium*, (d) *L. simplex*. Modified from Gibbs (2010, 2011).

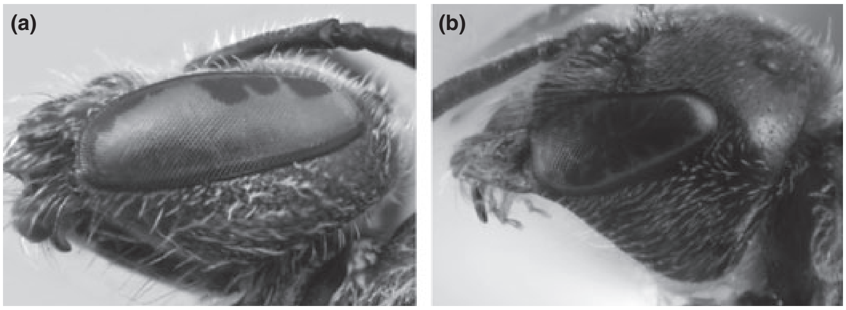

Fig. 2. Genal widths of *Dialictus*: (a) normal, (b) enlarged. Modified from Gibbs (2010).

the social parasites. A high proportion of adaptations for social parasitism in the morphological data set will provide a strong refutation of the monophyly hypothesis if the combined morphology and molecular data suggest polyphyly.

Mitochondrial DNA data set

A short fragment (654 bp) of the mitochondrial gene cytochrome *c* oxidase subunit 1 (COI) was sequenced as part of ongoing taxonomic studies of *Dialictus* (Gibbs, 2009a,b, 2010, 2011). Sequencing was performed at the Canadian Centre for DNA Barcoding at the University of Guelph (Guelph, Ontario) using methods that have been described in detail elsewhere (Hajibabaei et al., 2005; Ivanova et al., 2006; see Gibbs, 2009a,c). Sequences were uploaded to the Barcode of Life Data Systems (BOLD; Ratnasingham and Hebert, 2007) and GenBank.

COI sequences from 85 *Lasioglossum* species were downloaded from BOLD (Appendix 1). The majority of species chosen were metallic North American *Dialictus* (as defined by Michener, 2007; Gibbs, 2010) from which the parasitic species are derived (Michener, 1978;

Danforth et al., 2003). Non-parasitic species were selected to provide taxonomic breadth but weighted towards eastern North America where the majority of parasitic taxa occur (Table 1; Mitchell, 1960; Gibbs, 2011). Six social parasites were included: all five species classified by some previous authors as *Paralictus* (e.g. Mitchell, 1960; Moure and Hurd, 1987), and one newly described species (Gibbs, 2011). Based on previous phylogenetic studies (Danforth et al., 2003), two putative outgroup taxa were included, *Lasioglossum* (*Hemihalictus*) *lustrans* (Cockerell) and the non-metallic *Lasioglossum* (*Dialictus*) *villosulum* (Kirby). *Lasioglossum* (*Evylaeus*) *truncatum* (Robertson) was used to root the tree. Sequences were primarily > 650 bp in length. For the sake of taxonomic diversity, a few specimens with shorter sequence length were also included.

Multi-locus DNA data set

For the multi-locus analysis, sequence data for COI, elongation factor 1α (EF1α)—F2 copy, and long-wavelength rhodopsin (opsin) were downloaded from GenBank for all species of *Lasioglossum* with data for all three genes (see Danforth et al., 2003) with taxonomy updated based on Gibbs (2010) (Appendix 3). GenBank sequences for these genes were also downloaded for an outgroup taxon, *Halictus quadricinctus* (Fabricius). All three genes were sequenced from the parasitic species *Lasioglossum platyparium* (Robertson) and the type species of *Dialictus*, *Lasioglossum anomalum* (Robertson), using the primers and methods listed in Danforth et al. (2003). Sequencing was done using the Applied Biosystems 3130xL DNA Sequencer at the Core Molecular Biology and DNA Sequencing Facility at York University.

Each gene was aligned separately using default settings of ClustalX (Thompson et al., 1997). Alignments were concatenated and compared with reference sequences from *Apis mellifera* L. to determine reading frames and exon/intron boundaries using MESQUITE (Maddison and Maddison, 2010). Analyses were performed on the unmodified ClustalX alignment and a modified alignment was made by eye. Ambiguously aligned portions of the EF1α and opsin introns were excluded from the modified alignment.

Phylogenetic analyses

We performed phylogenetic analyses of both data sets using TNT (Goloboff et al., 2003a). Characters were given equal weights and analysed with a driven search using default settings with the following exceptions: ratchet (200 iterations, up and down weight probabilities set to 10), drift (20 cycles), and 'find minimum length' set to 100. Symmetric resampling was performed on the resulting trees using 1000 replicates, with changes in probabilities set to 33, using groups from the consensus tree, and expressed using GC values (groups supported/groups contradicted) (Goloboff et al., 2003b). For each node, the GC value indicates the difference between the frequencies with which that group was found in resampled matrices versus the most frequent alternative arrangement in which the group was not found. GC values range from a maximum contradiction value of − 100 (alternative arrangement found in all resampled matrices) to a maximum support value of + 100 (group found in all resampled matrices). Bremer supports were also calculated for the resultant trees using the script 'Bremer.run' [available at: http://tnt.insectmuseum.org/images/0/08/Bremer.run (last accessed 1 August 2011)].

We repeated the TNT analyses of the multi-locus data set while using the 'force' command to constrain the social parasites as monophyletic. The number of extra steps in the constrained analysis was compared with the number of morphological characters shared by the social parasites.

Results

Morphological and mtDNA combined analyses

A parsimony-based phylogenetic analysis of the combined mitochondrial DNA (654 bp, 192 parsimony-informative) and morphological (40 characters; Appendix 2) data set resulted in 410 equally parsimonious trees [length: 1741, consistency index (CI): 0.198, retention index (RI): 0.514; Fig. 3]. Two independent lineages of social parasite separated by six internal nodes are resolved in the strict consensus tree [referred to below as the *cephalotes* (*L. cephalotes*, *L. lionotum* – previously known as *L. asteris* (Mitchell)) and *platyparium* groups (*L. platyparium*, *L. michiganense*, *L. simplex*, *L. rozeni*)]. The same two lineages were recovered when the COI data were analysed separately, indicating that the morphological data did not promote underestimation of the number of socially parasitic lineages.

The clade subtending *L. lionotum* and its host, *L. imitatum*, is supported by four morphological and six molecular synapomorphies (Fig. 4). In addition to the suite of parasitic adaptations, the *cephalotes* group is supported by two additional morphological synapomorphies not shared by the *platyparium* group and eight molecular ones. Only one morphological and two molecular synapomorphies support the clade subtending *L. simplex* and its host (Fig. 4). When the parasites were constrained as monophyletic, only the 12 morphological characters that are adaptations for parasitism supported the clade.

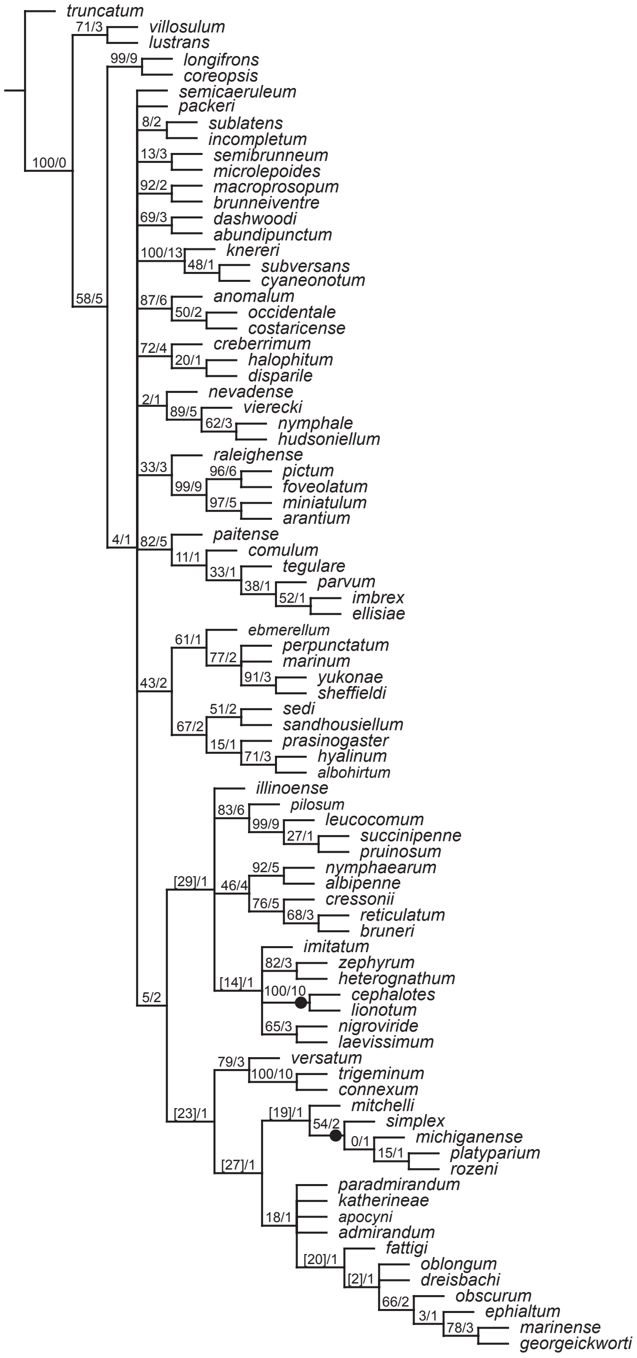

Fig. 3. Strict consensus of 410 equally most-parsimonious trees (L: 1741, CI: 0.198, RI: 0.514) based on combined data set of 192 parsimony-informative characters of COI and 40 morphological characters. Support for nodes is given in GC values (before slash) and Bremer supports (after slash). Negative GC values are given in parentheses (see text for explanation of GC values). Socially parasitic lineages are marked with a circle.

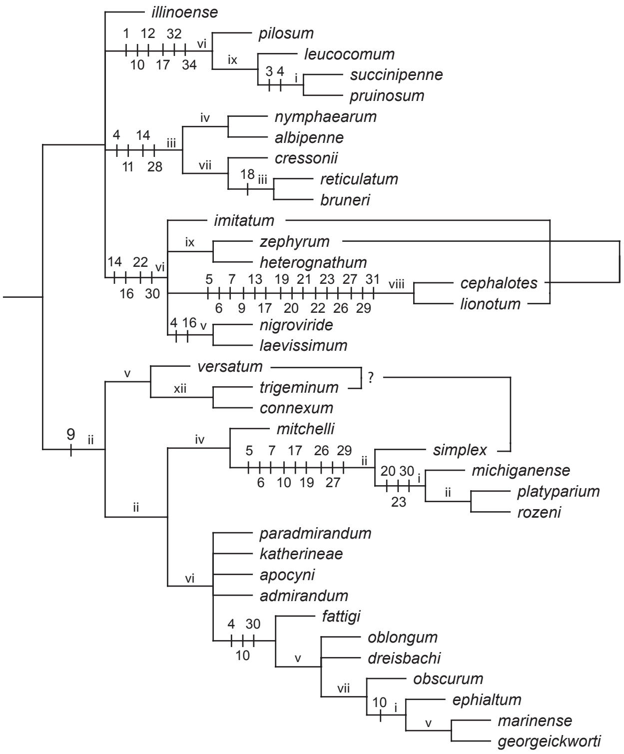

Fig. 4. Portion of the strict consensus subtending both parasitic lineages with morphological synapomorphies listed. Roman numerals indicate the number of molecular synapomorphies supporting a clade. Known host–parasite relationships are indicated by connecting lines.

Multi-locus DNA phylogenetic analyses

The three-gene data set resulted in 3448 aligned nucleotide sites (COI: 1239 bp, opsin: 685 bp, EF1α: 1524 bp) for 54 taxa using ClustalX. Ambiguously aligned regions of the introns were then excised to create a data set of 3413 bp (859 parsimony-informative), including COI (1239 bp), opsin (651 bp), and EF1α (1523 bp). Results from this modified alignment are presented below.

Two equally parsimonious trees resulted (length: 4840, CI: 0.270, RI: 0.518; Fig. 5). Analysis of the ClustalX unmodified alignment resulted in an identical consensus tree. The two social parasites included in the data set, *L. lionotum* and *L. platyparium*, are not resolved as monophyletic. High support (GC values of 94 and 99) was found for the relationships of the social parasites to their closest non-parasitic relatives (Fig. 5). The topology of the multi-locus consensus tree is congruent with the combined morphological and mtDNA consensus.

A parsimony analysis was also performed on the three-gene data set, with the two parasitic taxa constrained as monophyletic resulting in trees that were 44 steps longer (4884 steps) than the most-parsimonious ones without constraints (4840 steps). The suite of morphological characters shared between the social parasites (Table 2; Appendix 2) is therefore insufficient to support a monophyletic origin of social parasitism.

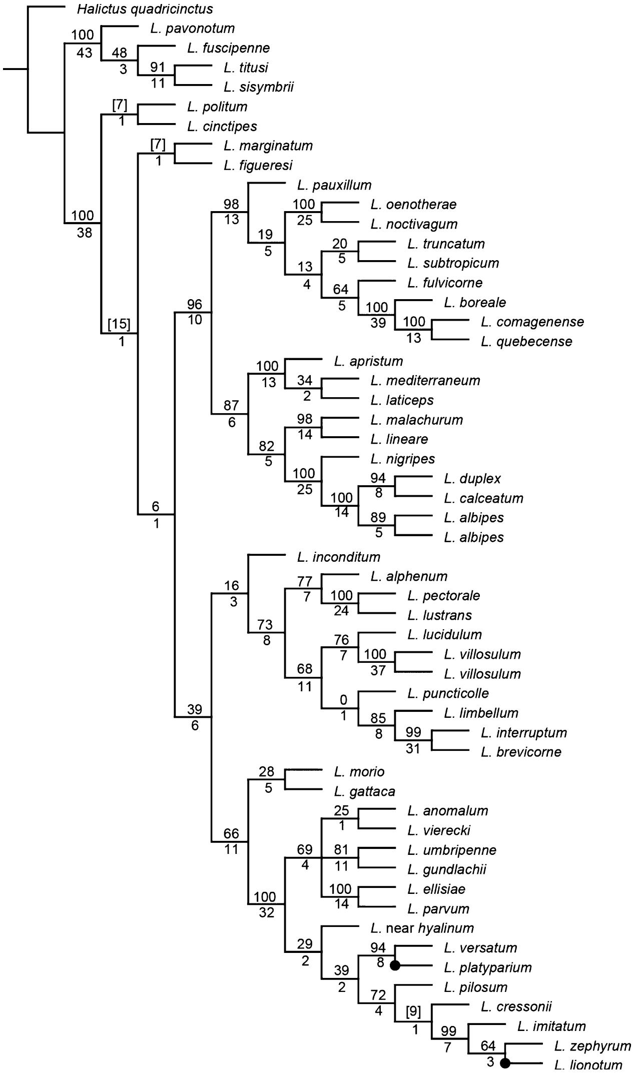

Fig. 5. Strict consensus of two equally most-parsimonious trees (L: 4840, CI: 0.270, RI: 0.518) based on 859 parsimony-informative characters from three protein-coding genes: EF1α, COI, and opsin. Support for nodes is given in GC values (above branch) and Bremer supports (below branch). Negative GC values are given in parentheses (see text for explanation of GC values). Socially parasitic lineages are marked with a circle.

Discussion

Molecular evidence does not support a monophyletic origin of social parasitism in North American *Dialictus*. Both data sets analysed here support dual origins for the social parasites sampled in this study. The suite of characters shared by the social parasites is due to convergent evolution. Brood parasitic bees in other halictines as well as more distantly related taxa share many of the same modifications found in the socially parasitic *Dialictus* (Michener, 1978, 2007) so convergent evolution resulting from parasitism is not unexpected. Many of the modifications present in brood parasitic bees are present in males of related nest-building species. The suite of characters associated with brood parasitism may be an exploitation of existing developmental pathways rather than *de novo* evolution of independent traits (Wcislo, 1999). The number of morphological character states shared between the parasitic lineages (Michener, 1978; Appendix 2), even if coded as independent rather than a single adaptive suite, is far fewer than the 44 additional steps required to constrain the social parasites as a single lineage with our multi-locus DNA data.

Different degrees of morphological adaptation related to social parasitism among socially parasitic *L.* (*Dialictus*) (Table 2, Fig. 1) was considered to be possible evidence for polyphyly (Michener, 1978). The most apparent differences are the modifications of the mandible, gena, and pronotum (Fig. 1). Both species in the *cephalotes* group, *L. cephalotes* and *L. lionotum*, have each of these features strongly modified (see Michener, 1978; Gibbs, 2011). However, the *platyparium* group includes species with varying mandibular size, genal width, and pronotal shape and have the preapical mandibular tooth present or absent (Mitchell, 1960; Gibbs, 2010, 2011). All four of these features relate to the aggressive/defensive morphology of the parasites (but see Wcislo, 1999). Similar modifications sometimes occur in tandem in nest-building *Lasioglossum*, either in males [e.g. *L. hartii* (Robertson), *L. pectinatum* (Robertson)] or in females where caste differences are apparent [e.g. *L. semibrunneum* (Cockerell)]. These modifications result from competition for reproductive opportunities in the form of intra-sexual conflict between males and caste-based antagonism between females (e.g. Pabalan et al., 2000). Our results do not support separate origins of social parasitism for species in the *platyparium* group, such as *L. simplex* and *L. rozeni*, with varying degrees of morphological modification.

Host relationships and Emery's rule

Little is known of the host relationships of parasitic *Dialictus* (see Table 1; Michener, 1978; Wcislo, 1997). Both species in the *cephalotes* group are associated with eusocial hosts. *Lasioglossum lionotum* is a social parasite of *L. imitatum* (Wcislo, 1997; Fig. 4) and *L. cephalotes* is believed to be a parasite of *L. zephyrum* (Robertson, 1901, 1926; Fig. 4). As the parasites are sister taxa, the strict form of Emery's rule does not apply to the *cephalotes* group. The host species, *L. imitatum* and *L. zephyrum*, are closely related to the *cephalotes* group, supporting the loose form of Emery's rule. One could speculate that the common ancestor of the *cephalotes* group followed the strict rule, with subsequent co-speciation in both parasite and host lineages.

The *platyparium* group arises from a grade including *L. versatum* (*sensu* Gibbs, 2010), *L. trigeminum*, and the *L. viridatum* species-group. *Lasioglossum simplex*, a member of the *platyparium* group, has been reported to be a parasite of *L. versatum* (see Michener, 1966, 1978), but the species Michener (1966) studied may have been the closely related *L. trigeminum* (Gibbs, 2011) (Fig. 4). The monophyly of the parasites and the phylogenetic distance between *L. simplex* and its possible hosts is inconsistent with Emery's rule in the strict form. The common ancestor of the *platyparium* group could not have been sister taxon to a common ancestor of *L. versatum* or *L. trigeminum*.

Lasioglossum mitchelli Gibbs is the most closely related nest-building species to the *platyparium* group in the combined DNA barcode/morphology analysis. Nothing is known of its nesting behaviour, although it is probably eusocial based on phenological evidence (adult females present from April to October, males present July to October; Gibbs, 2010), size variation among females (J. Gibbs, unpublished data), and the ancestral state of *Dialictus* (Danforth et al., 2003). It has not been identified as a host of any of the parasitic taxa but based on its phylogenetic position *L. mitchelli* would be a good candidate, worthy of study.

Our results are not consistent with Emery's rule in its strict form. Both strict and loose forms of Emery's rule are known to occur in allodapine bees (Michener, 1974; Lowe and Crozier, 1997; Smith et al., 2007), and the loose form has been reported from bumble bees (Cameron et al., 2007; Hines and Cameron, 2010) and *Lasioglossum* (Danforth et al., 2003). The strict form of Emery's rule does not apply to social parasites in the allodapine genus *Macrogalea* (Smith et al., 2007). The halictine *Microsphecodes kathleenae* Eickwort and Stage is a social parasite of *L. umbripenne* (Ellis) (Eickwort and Eickwort, 1972) but belongs to a separate clade composed entirely of brood parasites (Danforth et al., 2004, 2008). The strict form of Emery's rule has been rejected for other social Hymenoptera, including Vespinae (Carpenter and Perera, 2006) and Polistinae (Choudhary et al., 1994; Carpenter, 1997), in each of which the social parasites form a monophyletic group closely related to their host taxa, as seen here for *Dialictus*. Emery's rule has been both rejected (Ward, 1996; Sumner et al., 2004) and accepted for different groups of ants (Sumner et al., 2004; Savolainen and Vepsäläinen, 2003; but see Steiner et al., 2006). In *Dialictus*, if the strict form was valid for the common ancestors of the two socially parasitic lineages, it has since been obscured by multiple subsequent speciation events and host switches. The recent discovery of seven new species of brood parasitic *Dialictus* in North America (Gibbs, 2010, 2011) highlights the need for additional study of this behaviourally diverse taxon.

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Appendix 1

GenBank accession numbers for COI sequences used in combined morphological and molecular analysis. Taxonomy based on Gibbs (2010, 2011). See Danforth et al. (2003) for additional GenBank accessions.

Species	Locality	Length (bp)	GenBank accession no.
L. (*Evylaeus*) *truncatum* (Robertson, 1901)*	North Carolina	645[0n]	JF903561
L. (*Hemihalictus*) *lustrans* (Cockerell, 1897)*	South Carolina	658[0n]	JF903531
L. (*Dialictus*) *villosulum* (Kirby, 1802)*	France	658[0n]	JF903563
L. (*Dialictus*) *cephalotes* (Dalla Torre, 1896)†	New York	407[0n]	JF903501
L. (*Dialictus*) *lionotum* (Sandhouse, 1923)†	Maryland	635[0n]	JF903529
L. (*Dialictus*) *michiganense* (Mitchell, 1960)†	North Carolina	645[0n]	JF903534
L. (*Dialictus*) *platyparium* (Robertson, 1895)†	Maryland	657[0n]	JF903550
L. (*Dialictus*) *rozeni* Gibbs, 2011 †	Maryland	657[0n]	JF903524
L. (*Dialictus*) *simplex* (Robertson, 1901)†	Maryland	657[0n]	JF903559
L. (*Dialictus*) *abundipunctum* Gibbs, 2010	Utah	658[0n]	JF903493
L. (*Dialictus*) *admirandum* (Sandhouse, 1924)	Ontario	658[0n]	JF903494
L. (*Dialictus*) *albipenne* (Robertson, 1890)	New Brunswick	657[0n]	JF903495
L. (*Dialictus*) *albohirtum* (Crawford, 1907)	Alberta	658[0n]	JF903496
L. (*Dialictus*) *anomalum* (Robertson, 1892)	Michigan	658[0n]	JF903497
L. (*Dialictus*) *apocyni* (Mitchell, 1960)	North Carolina	654[1n]	JF903498
L. (*Dialictus*) *arantium* Gibbs, 2011	Maryland	658[0n]	GU666313
L. (*Dialictus*) *bruneri* (Crawford, 1902)	Maryland	657[0n]	JF903499
L. (*Dialictus*) *brunneiventre* (Crawford, 1907)	California	658[0n]	JF903500
L. (*Dialictus*) *comulum* (Michener, 1951)	Sonora	407[0n]	JF903502
L. (*Dialictus*) *connexum* (Cresson, 1872)	Texas	658[0n]	GU708265
L. (*Dialictus*) *coreopsis* (Robertson, 1902)	Delaware	658[0n]	JF903503
L. (*Dialictus*) *costaricense* (Crawford, 1906)	Costa Rica	645[0n]	JF903504
L. (*Dialictus*) *creberrimum* (Smith, 1853)	Mississippi	645[0n]	JF903505
L. (*Dialictus*) *cressonii* (Robertson, 1890)	North Carolina	655[0n]	JF903506
L. (*Dialictus*) *cyaneonotum* (Crawford, 1907)	California	657[0n]	JF903507
L. (*Dialictus*) *dashwoodi* Gibbs, 2010	Washington	658[0n]	JF903508
L. (*Dialictus*) *disparile* (Cresson, 1872)	North Carolina	657[0n]	JF903509
L. (*Dialictus*) *dreisbachi* (Mitchell, 1960)	Ontario	657[0n]	JF903510
L. (*Dialictus*) *ebmerellum* Gibbs, 2010	Utah	658[0n]	JF903511
L. (*Dialictus*) *ellisiae* (Sandhouse, 1924)	Ontario	658[0n]	FJ663062
L. (*Dialictus*) *ephialtum* Gibbs, 2010	Ontario	658[0n]	JF903512
L. (*Dialictus*) *fattigi* (Mitchell, 1960)	Ontario	658[0n]	JF903513
L. (*Dialictus*) *foveolatum* (Robertson, 1902)	Indiana	623[2n]	JF903514
L. (*Dialictus*) *georgeickworti* Gibbs, 2011	Virginia	657[0n]	JF903523
L. (*Dialictus*) *halophitum* (Graenicher, 1927)	Virginia	658[0n]	JF903515
L. (*Dialictus*) *heterognathum* (Mitchell, 1960)	North Carolina	658[0n]	JF903516
L. (*Dialictus*) *hudsoniellum* (Cockerell, 1919)	Utah	658[1n]	JF903517
L. (*Dialictus*) *hyalinum* (Crawford, 1907)	Utah	658[0n]	JF903518
L. (*Dialictus*) *illinoense* (Robertson, 1892)	North Carolina	657[0n]	JF903519
L. (*Dialictus*) *imbrex* Gibbs, 2010	California	658[0n]	JF903520
L. (*Dialictus*) *imitatum* (Smith, 1853)	Ontario	658[0n]	JF903521
L. (*Dialictus*) *incompletum* (Crawford, 1907)	Washington	658[0n]	JF903522
L. (*Dialictus*) *katherineae* Gibbs, 2011	Massachusetts	658[0n]	HM407358
L. (*Dialictus*) *knereri* Gibbs, 2010	British Columbia	658[0n]	JF903526
L. (*Dialictus*) *laevissimum* (Smith, 1853)	Maine	658[0n]	JF903527
L. (*Dialictus*) *leucocomum* (Lovell, 1908)	Nova Scotia	658[0n]	JF903528
L. (*Dialictus*) *longifrons* (Baker, 1906)	North Carolina	658[0n]	JF903530
L. (*Dialictus*) *macroprosopum* Gibbs, 2010	British Columbia	658[0n]	JF903532
L. (*Dialictus*) *marinense* (Michener, 1936)	British Columbia	658[0n]	JF903533
L. (*Dialictus*) *marinum* (Crawford, 1904)	Virginia	658[0n]	FJ663077
L. (*Dialictus*) *microlepoides* (Ellis, 1914)	Nevada	658[0n]	JF903535
L. (*Dialictus*) *miniatulum* (Mitchell, 1960)	Florida	658[0n]	GU666311
L. (*Dialictus*) *mitchelli* Gibbs, 2010	Illinois	658[0n]	JF903536
L. (*Dialictus*) *nevadense* (Crawford, 1907)	Utah	658[0n]	JF903537
L. (*Dialictus*) *nigroviride* (Graenicher, 1910)	Ontario	657[0n]	JF903538
L. (*Dialictus*) *nymphaearum* (Robertson, 1890)	North Carolina	645[0n]	JF903543
L. (*Dialictus*) *nymphale* (Smith, 1853)	North Carolina	658[0n]	JF903539
L. (*Dialictus*) *oblongum* (Lovell, 1905)	Virginia	658[0n]	JF903540

Appendix 1

(*Continued*)

Species	Locality	Length (bp)	GenBank accession no.
L. (*Dialictus*) *obscurum* (Robertson, 1892)	North Carolina	654[0n]	JF903541
L. (*Dialictus*) *occidentale* (Crawford, 1902)	Manitoba	658[0n]	JF903542
L. (*Dialictus*) *packeri* Gibbs, 2010	Saskatchewan	658[0n]	JF903544
L. (*Dialictus*) *paitense* (Cockerell, 1926)	Peru	658[0n]	HQ558059
L. (*Dialictus*) *paradmirandum* (Knerer & Atwood, 1966)	Wisconsin	657[0n]	JF903545
L. (*Dialictus*) *parvum* (Cresson, 1865)	Cuba	658[0n]	JF903546
L. (*Dialictus*) *perpunctatum* (Ellis, 1913)	Manitoba	658[0n]	JF903547
L. (*Dialictus*) *pictum* (Crawford, 1902)	Manitoba	658[0n]	JF903548
L. (*Dialictus*) *pilosum* (Smith, 1853)	North Carolina	658[1n]	JF903549
L. (*Dialictus*) *prasinogaster* Gibbs, 2010	Alberta	658[0n]	JF903551
L. (*Dialictus*) *pruinosum* (Robertson, 1892)	Utah	658[0n]	JF903552
L. (*Dialictus*) *raleighense* (Crawford, 1932)	Georgia	658[0n]	JF903553
L. (*Dialictus*) *reticulatum* (Robertson, 1892)	Mississippi	645[0n]	JF903554
L. (*Dialictus*) *sandhousiellum* Gibbs, 2010	British Columbia	658[0n]	HM407455
L. (*Dialictus*) *sedi* Gibbs, 2010	Colorado	658[0n]	JF903555
L. (*Dialictus*) *semibrunneum* (Cockerell, 1895)	Arizona	658[0n]	JF903556
L. (*Dialictus*) *semicaeruleum* (Cockerell, 1895)	Utah	657[0n]	JF903557
L. (*Dialictus*) *sheffieldi* Gibbs, 2010	Nova Scotia	657[0n]	JF903558
L. (*Dialictus*) *sublatens* (Cockerell, 1926)	Peru	658[0n]	HM407456
L. (*Dialictus*) *subversans* (Mitchell, 1960)	Nova Scotia	658[0n]	GU666297
L. (*Dialictus*) *succinipenne* (Sandhouse, 1924)	Alberta	620[0n]	JF903560
L. (*Dialictus*) *tegulare* (Robertson, 1890)	Virginia	658[0n]	FJ663106
L. (*Dialictus*) *trigeminum* Gibbs, 2011	North Carolina	657[0n]	JF903525
L. (*Dialictus*) *versatum* (Robertson, 1902)	North Carolina	658[0n]	JF903562
L. (*Dialictus*) *vierecki* (Crawford, 1904)	South Carolina	658[0n]	FJ663124
L. (*Dialictus*) *yukonae* Gibbs, 2010	Yukon Territory	658[0n]	JF903564
L. (*Dialictus*) *zephyrum* (Smith, 1853)	West Virginia	657[0n]	JF903565

*Outgroup taxon.

†Social parasite.

Appendix 2

List of morphological characters used in phylogenetic analyses. Character states associated with social parasitism are marked with an asterisk. All specimens deposited at Cornell University Insect Collection and Packer Collection, York University.

Code from females

0. Head and mesosoma, colour: (0) black, (1) metallic.
1. Metasomal terga, colour: (0) black, (1) metallic.
2. Clypeus, colour: (0) black, (1) testaceous.
3. Flagellum ventral surface, colour: (0) brown, to slightly ferruginous at apex, (2) testaceous.
4. Tegula, colour: (0) brown, (1) testaceous or ferruginous, (2) pale yellow.
5. Mesotibial and mesofemoral combs: (0) strong, (1) reduced*.
6. Scopa: (0) strong, (1) reduced*.
7. Penicillus: (0) strong, (1) reduced*.
8. Metasomal tergum 1, acarinarial appressed hair fan: (0) absent, (1) present.
9. Metasomal tergum 2, acarinarial fan completion: (0) open medially, (1) closed medially.
10. Metasomal terga, tomentum: (0) dense, (1) moderately dense, (2) basal patches, (3) absent.
11. Head and mesosoma, microsculpture: (0) fine, (1) coarse.
12. Mesoscutum, punctation: (0) dense throughout, (1) sparse medially, (2) sparse throughout.
13. Mesepisternum, punctation: (0) absent or indistinct, (1) present, dense, (1) present, sparse.
14. Mesepisternum, sculpture: (0) polished, (1) tessellate or imbricate, (2) rugulose or strigate, (3) rugose.
15. Tegula, punctation: (0) fine, indistinct; (1) coarse, distinct.
16. Metapostnotum, sculpture: (0) smooth, rugae if present limited to basal half, (1) rugae weak, faint on tessellate background, (2) rugae strong, distinct.
17. Face, length: (0) short, (1) long, (2) very long.
18. Hypostomal carinae: (0) parallel, (1) divergent.
19. Labrum, apical process: (0) narrow, dorsal keel present, (1) wide, dorsal keel absent*.
20.Mandible, length: (0) short, reaching opposing clypeal angle (1) elongate, surpassing opposing clypeal angle*.
21. Mandible, tooth: (0) present, (1) reduced or absent*.
22. Gena, width: (0) narrower than eye, (1) wider than eye, (2) enormous*.
23. Pronotum, dorsolateral shape: (0) broadly rounded, (1) sharply angled*.
24. Tegula, shape: (0) ovoid, (1) elongate, with posterior angle.
25. Forewing, vein 1rs-m: (0) present, (1) absent.
26. Basitibial plate: (0) normal (1) reduced*.
27. Inner metatibial spur: (0) serrate, (1) pectinate, branches short, (2) pectinate, branches long.
28. Propodeum, lateral carina: (0) reaching dorsal margin, (1) not reaching dorsal margin.
29. Tergum 5, pseudopygidial area: (0) well defined, (1) poorly defined*.

Coded from males

30. Face, pubescence: (0) sparse, not obscuring integument except on lower paraocular area, (1) moderately dense, partially obscuring

integument on face, (2) very dense, obscuring most of integument on face.
31. Flagellomere, length: (0) long (length more than 1.5 × width), (1) short (length < 1.5 × width).
32. Clypeus distal margin, colour: (0) yellow-testaceous, (1) brown-black.
33. Metabasitarsus, colour: (0) yellow-testeaceous, (1) brown-reddish brown.
34. Metasomal tergum 2, punctures of apical impressed area: (0) present, (1) absent.
35. Metasomal sterna, pubescence: (0) hairs relatively short, (1) hairs very long, scopa-like.
36. Gonocoxa, shape: (0) inner dorsal margin parallel basally, strongly divergent in apical half, (1) inner dorsal margin, weakly divergent over entire length.
37. Gonostylus, shape: (0) very long, (1) short, (2) long, (3) large, round.
38. Gonostylus, setae: (0) long, plumose, (1) short, simple, (2) long, medially directed.
39. Penis valve, shape: (0) normal, (1) narrow.

Appendix 3

Updated taxonomy for *Lasioglossum* (*Dialictus*) species on GenBank.

Current name based on Gibbs (2010, 2011)	Name on GenBank based on Danforth et al. (2003)
Lasioglossum ellisiae (Sandhouse, 1924)	*Lasioglossum tegulare* (Robertson, 1890)
Lasioglossum lionotum (Sandhouse, 1923)	*Lasioglossum asteris* (Mitchell, 1960)
Lasioglossum versatum (Robertson, 1902)	*Lasioglossum rohweri* (Ellis, 1915)
Lasioglossum near *hyalinum* (undescribed)	*Lasioglossum hyalinum* (Crawford, 1907)