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Integrative taxonomy identifies new (and old) species in the *Lasioglossum (Dialictus) tegulare* (Robertson) species group (Hymenoptera, Halictidae)

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Abstract

An integrative taxonomic approach that utilizes the DNA barcode region of cytochrome *c* oxidase subunit 1 in conjunction with traditional morphological approaches identifies five distinct species previously recognized as *Lasioglossum (Dialictus) tegulare* (Robertson). Differences in DNA sequences and congruent, albeit minor, morphological variation support separation of *L. tegulare* into five species. Unique nucleotide substitution patterns for each species allows for character-based diagnostics using DNA barcodes. The names *L. ellisiae* (Sandhouse) and *L. lepidii* (Graenicher) are removed from synonymy. Two new species, *L. puteulanum* Gibbs **sp. n.** and *L. carlinvillense* Gibbs **sp. n.**, are described. A key is provided, which permits the identification of both males and females. The utility of the DNA barcode region as part of an integrative taxonomic framework is discussed.

Key words: Cryptic species, integrative taxonomy, DNA barcodes, *Lasioglossum*, *Dialictus*, Halictidae

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Introduction

Several methods for automated species identification using quantitative approaches have been proposed (Gaston & O'Neill 2004) but none has garnered the attention of DNA barcoding. DNA barcoding is a new method that promises to speed taxonomic progress and allow identification of specimens even without taxonomic expertise (Hebert *et al.* 2003a). DNA barcoding employs a short strand of a standard gene to identify species. A 657-bp fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) is the chosen standard for animals (Hebert *et al.* 2003a). DNA barcoding has incited much controversy in the taxonomic community and has been both lauded and denounced in the literature (*e.g.* Trewick 2008 and references therein).

Integrative taxonomic approaches that combine morphological, molecular and other types of data are the best methods for describing species (Dayrat 2005; Page *et al.* 2005; DeSalle *et al*. 2005). Morphological and molecular data have complementary strengths (Hillis 1987; Hillis & Wiens 2000) and in combination can overcome weaknesses of single datasets alone (*e.g.* Wahlberg *et al*. 2005). Molecular evidence can provide an independent test of morphological assessments of species identity and vice versa (Page *et al.* 2005). Multiple sources of data (*e.g.* morphology, DNA, geography) are needed to test and corroborate hypothetical species limits (DeSalle *et al*. 2005).

DNA barcoding efforts provide molecular data that may aid in discovering cryptic species (Hebert *et al*. 2004; Yassin *et al*. 2007) but these findings should be incorporated into an integrative taxonomic framework (Dayrat 2005; DeSalle *et al*. 2005). Confounding factors such as incomplete lineage sorting or diversifying selection acting on morphological traits can result in closely related species that cannot be differentiated by a single piece of molecular evidence (Avise 2000; Funk & Omland 2003). In this respect, the DNA barcode region does not differ from other candidate genes. DNA barcoding efforts are novel relative to other molecular methods by virtue of the standardization and taxonomic breadth for which DNA sequence data is being made available. One advantage of selecting the DNA barcode region for integrative taxonomic purposes over other genes is that the data can be used both for alpha taxonomy and for species identification.

The importance of bees as pollinators (Buchmann & Nabhan 1996; Klein *et al*. 2007) and their potential as ecosystem monitors (Zayed *et al*. 2004) makes their study of particular importance. The large number of bee species (>19,000 valid species-names worldwide [Ascher *et al.* 2008]) with many highly speciose genera and subgenera makes species recognition difficult. In many cases, cryptic species, caste differentiation and sexual dimorphism add to the puzzle (Sandhouse 1924; Knerer & Atwood 1962; Janjic & Packer 2001; Pilgrim & Pitts 2006; Sheffield & Westby 2007). Molecular evidence, such as DNA barcodes, may not only differentiate cryptic species (Carman & Packer 1997; Packer & Taylor 1997; Danforth *et al.* 1998; Hebert *et al*. 2004; Witt *et al*. 2006; see Avise 2000, 2004 for further examples) but also associate queens, workers, larval stages and dimorphic sexes (Pilgrim & Pitts 2006; Gibbs *in press*) that would otherwise be misidentified (or not identified further than subgenus) based on morphology alone.

The subgenus *Dialictus* (Halictidae: *Lasioglossum*) is one of the most taxonomically difficult groups amongst the bees. In North America, *Dialictus* are both speciose (over 270 currently recognized names) and the most commonly collected subgenus of bee (MacKay & Knerer 1979; Eickwort 1988; Grixti & Packer 2006; Campbell *et al.* 2007). *Dialictus* are also notoriously difficult to identify to species because they are "morphologically monotonous" (Packer 1997; Michener 2007). In most cases, only very subtle differences can be used to differentiate closely related species. Identification is further complicated by the existence of castes in the many eusocial species (reviewed in Michener 1974; Packer 1993; Yanega 1997). In bee diversity studies many *Dialictus* cannot be identified to the species level (*e.g.* Giles & Ascher 2006) preventing more in depth study of sociobiology, biodiversity and pollination biology. The extreme similarity between species may be due in part to a recent origin and rapid diversification of the speciose lineage containing *Dialictus*, likely to have started 20–22 million years ago (Brady *et al*. 2006). Very little taxonomic progress has been made on this group in the last forty years (Mitchell 1960; Knerer & Atwood 1966), and there is much work to be done.

The nominal species *Lasioglossum tegulare* (Robertson), widespread in eastern North America, is one of

the few currently recognized species of *Dialictus* that is easy to identify. As the name suggests, this species has a distinctive tegula (Fig. 1), which is remarkable for its size, shape and punctation. Two additional species from the eastern United States, *L. marinum* (Crawford) and *L. surianae* (Mitchell), have similar tegulae but are easily distinguished morphologically from *L. tegulare*. The microsculpture of *L. tegulare*, as well as its size and colouration, differ from *L. marinum* and the two are not close relatives (Gibbs, unpublished data). *Lasioglossum surianae* has distinct colouration patterns that easily distinguish it from *L. tegulare*. The presence of the elongate tegula was not mentioned in Mitchell's (1960) key or description of *L. surianae* but inspection of the holotype clearly shows this character. *Lasioglossum marinum* is a sand dune specialist uncommonly collected outside of coastal areas from Florida to Massachusetts (Graenicher 1927; Moure & Hurd 1987), while *L. surianae* is only known from the Florida Keys (Mitchell 1960) and the Bahamas. The *L. tegulare* species group extends into South America but will require considerable additional study. Two other species with large tegulae, *L. ellisiae* (Sandhouse) and *L. lepidii* (Graenicher), have been described from eastern North America but were synonymized with *L. tegulare* (Mitchell 1960).

Easily recognized species may not be examined in as great detail as taxa known to belong to difficult species complexes and may be a repository for cryptic species (Packer & Taylor 1997). I report the existence of cryptic species within the "species" *L. tegulare* identified through reciprocal illumination from DNA barcodes and morphology. Previous DNA barcode studies have usually used phenetic methods (Prendini 2005) and left putative new species for future workers to describe (*e.g.* Hebert *et al*. 2004). In this study I apply more phylogenetically rigorous parsimony and Bayesian methods to study patterns in the molecular evidence. I also provide detailed morphological description of the new species. The taxonomic limits of *L. tegulare* are revised with the description of two new cryptic species, *L. puteulanum* Gibbs **sp. n.** and *L. carlinvillense* Gibbs **sp. n.** and the removal of the names *L. ellisiae* and *L. lepidii* from synonymy.

Materials and methods

DNA extraction, PCR and sequencing were done at the Canadian Centre for DNA Barcoding at Guelph University (Guelph, Ontario) using standard protocols described elsewhere (Hebert *et al.* 2003b) and available online at http://www.dnabarcoding.ca/pa/ge/research/protocols. Universal primers for amplifying the DNA barcode sequence for insects (LCO1490 and HCO2198; Folmer *et al.* 2004 or the variants LEPF and LEPR; Hebert *et al*. 2004) were used. DNA barcodes were generated from *L. tegulare* specimens throughout its range (ON to FL). Two alternate outgroups were used, *L. (Hemihalictus) lustrans* (Cockerell) and *L. (Evylaeus) quebecense* (Crawford) based on a higher level phylogeny for *Lasioglossum* (Danforth *et al.* 2003). The outgroups belong to the acarinate *Evylaeus* and carinate *Evylaeus* groups respectively (Danforth *et al*. 2003). *Lasioglossum marinum* and *L. surianae* were included to compare the relationships of the *L. tegulare* species group to other eastern species with enlarged tegulae. Sequences from *L. vierecki* were included based on the results of previous studies (Danforth *et al.* 2003), wherein *L. vierecki* appears in the sister clade of the *tegulare* species group. Only those sequences that were greater than 600bp with at most one ambiguous base pair were included in the phylogenetic analysis.

DNA barcode sequences were uploaded to BOLD: the barcode of life data system (Ratnasingham & Hebert 2007). The analytical system within BOLD was used to generate a neighbour-joining (NJ) tree based on a Kimura-2 parameter model of base substitution (Kimura 1980).

To determine if the patterns observed in the NJ tree were robust to more rigorous methods, sequences were input into TNT (Goloboff *et al*. 2003a) for parsimony-based phylogenetic analyses. A driven search was performed 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 (Goloboff *et al*. 2003b) was performed on the results using groups from the tree with a 33% probability of changing the weights (up or down) for 10000 replicates. Support values are indicated on the tree using ratio of groups supported or contradicted (GC). For each node, the difference between the frequency of the group and

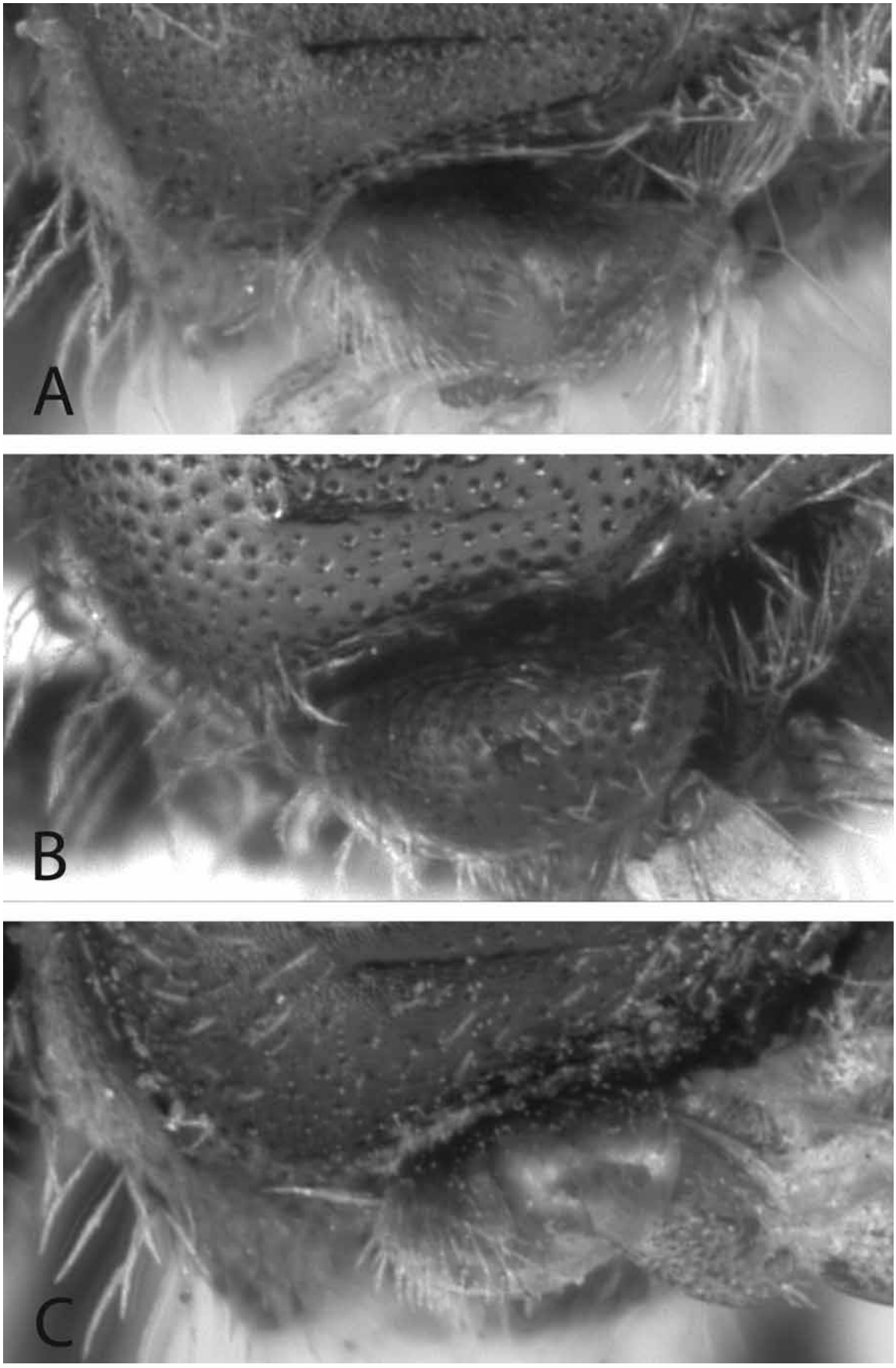

FIGURE 1. Dorsal views of enlarged and punctate tegulae from a *L. tegulare* species group (A) female, (B) male. (C) A tegula from a typical *L. (Dialictus)* species.

the most frequent alternate arrangement is calculated. GC values range from -100 to +100, indicating maximum contradiction (alternate arrangement is found in all resampled matrices) to maximum support (group found in all resampled matrices).

A Bayesian phylogenetic analysis was performed using MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001) on the DNA barcode dataset. The data were partitioned by codon position. The general time reversible model (GTR) of evolution was applied with the rate of evolutionary change based on a gamma distribution. Four chains were run simultaneously. The analysis was continued until the standard deviation of split frequencies decreased to a suitable level (below 0.01). In total, 2,000,000 generations were run with trees sampled from every fiftieth generation for a total of 40,000 trees. The unstable "burn-in" region was removed by deleting the initial 25% of trees in the analysis.

Species descriptions are included for the cryptic species identified using integrative taxonomy. Descriptions follow the format used in Toro and Moldenke (1979) and are subdivided into sections on colouration, pubescence, surface sculpture and structure. The subsections themselves proceed from the anterior to posterior of the specimen. Terminology for structures and surface sculpture largely follow Michener (2007) and Harris (1979), respectively. Additional terminology related to the propodeum is based on Murao and Tadauchi (2007) as follows: The term 'lateral slope' refers to the dorsal surface of the propodeum laterad of the metapostnotum. The term 'oblique carina' refers to the carina that separates the lateral slope from the posterior surface. The appressed hairs on the declivous surface of the first tergum, when present, are referred to as the acarinarial fan. Measurements and abbreviations follow Gibbs and Packer (2006). The following abbreviations are used: IOC—interocellar distance, OOC—ocellocular distance, UOD—upper ocular distance, LOD—lower ocular distance, i—interspace, d—puncture diameter (these are used in conjunction to give a relative measure of puncture density), and OD—median ocellar diameter (this abbreviation is primarily used to give a relative measure of hair length). The OD for each species is approximately 0.12 mm. Individual terga, sterna and flagellomeres are referred to by the letter T, S, and F, respectively, followed by the appropriate number. Relative size measurements are given in ratios based on eyepiece graticule units. This is meant to prevent the use of unwieldy measurements in standard units. Ratios based on measurements of individual body parts were taken from the type specimen. Head, body and forewing length and head breadth were measured from additional specimens but values from the holotype are given before parentheses. A dichotomous key is included.

The following abbreviations are used for institutions in which specimens examined are deposited: ANSP: Academy of Natural Sciences, Philadelphia, PA; CUIC: Cornell University Insect Collection, Ithaca, NY; INHS: Illinois Natural History Survey, Champaign, IL; SEMC: Kansas University Natural History Museum (Snow Entomological Collection), Lawrence, KS; NMNH: National Museum of Natural History, Washington, DC; PCYU: Packer's Apoidea Collection at York University, Toronto, ON; UWGB: University of Wisconsin, Green Bay (Richter Museum of Natural History), WI. DNA barcoded specimens used in the phylogenetic analysis are annotated as such and for new species are designated as paratypes.

Results

The DNA barcode region of COI was sequenced from specimens identified based on morphology as *Lasioglossum tegulare*. Unexpectedly high levels of sequence divergence were noted among specimens of *L. tegulare*. A more comprehensive study of morphology and more thorough sampling of DNA barcode sequences provided evidence of a species complex previously misinterpreted as a single species.

I obtained seventy-one DNA barcode sequences of lengths 604–658bp, with no more than a single ambiguous base pair per sequence. All sequences are publicly available on BOLD (LTEG project) and GenBank (accession numbers FJ663058–FJ663128) (Table 1). All sequences from the *L. tegulare* species complex lacked indels, in-frame stop codons, non-synonymous mutations and each had a highly similar GC% (25.18, SE = 0.053, min = 24.06, max = 25.9) with an extreme AT-bias in the third codon position (95.43, SE

= 0.1, min = 94.05, max = 96.69). These characteristics are inconsistent with amplification of nuclear pseudogenes (Song *et al*. 2008).

TABLE 1. *Lasioglossum* species included in this study with BOLD process ID and GenBank accession numbers. Numbers in brackets indicate ambiguous base pairs.

Subgenus	Species	BOLD Process ID	Genbank Accession Numbers	Length (bp)	State or Province
Evylaeus	*quebecense*	DLII816-07	FJ663099	658	VA
Hemihalictus	*lustrans*	DIAL511-06	FJ663075	658	NC
Dialictus	*marinum*	DIAL746-06	FJ663076	614	VA
		DIAL747-06	FJ663077	658	VA
		DIAL748-06	FJ663078	658	VA
		DIAL749-06	FJ663079	658	VA
		DIAL763-06	FJ663080	658	VA
		DLII418-07	FJ663081	645	VA
		DLII685-07	FJ663082	657	MD
	vierecki	DIAL033-06	FJ663128	619	MD
		DIAL034-06	FJ663127	624	MD
		DIAL035-06	FJ663119	619	MN
		DIAL121-06	FJ663120	658	MB
		DIAL358-06	FJ663121	614	IN
		DIAL370-06	FJ663122	614	NY
		DIAL479-06	FJ663123	622	NC
		DIAL480-06	FJ663124	658	SC
		DIAL484-06	FJ663125	658	SC
		DIAL915-06	FJ663126	654	ON
	surianae	BEECB173-07	FJ663100	632	Bahamas
	tegulare	DIAL091-06	FJ663102	658	VA
		DIAL366-06	FJ663109	614	NY
		DIAL367-06	FJ663110	614	VA
		DIAL485-06	FJ663111	658	WV
		DIAL490-06	FJ663112	658	WV
		DIAL493-06	FJ663113	658[1]	WV
		DIAL495-06	FJ663114	658	NC
		DIAL518-06	FJ663115	658	SC
		DIAL683-06	FJ663103	658	DC
		DIAL684-06	FJ663104	658	DC
		DIAL742-06	FJ663105	614	VA
		DIAL743-06	FJ663106	658	VA
		DIAL744-06	FJ663107	618	VA
		DIAL745-06	FJ663108	604	VA
		DIAL824-06	FJ663116	653	VA

to be continued.

TABLE 1. (continued)

Subgenus	Species	BOLD Process ID	Genbank Accession Numbers	Length (bp)	State or Province
		DIAL1050-06	FJ663117	658	SC
		DIAL1051-06	FJ663118	658	SC
		DLII468-07	FJ663101	645	MD
	ellisiae	BEECB213-07	FJ663069	658	MN
		BEECB221-07	FJ663068	658	MN
		DIAL356-06	FJ663063	586	IN
		DIAL476-06	FJ663064	658	IN
		DIAL653-06	FJ663061	658	ON
		DIAL654-06	FJ663062	658	ON
		DIAL888-06	FJ663065	658	NC
		DIAL918-06	FJ663067	654	ON
		DIAL1089-06	FJ663066	658	NC
		DLII031-06	FJ663070	645	ON
		DLII833-07	FJ663071	658	MA
	lepidii	DIAL863-06	FJ663072	655	FL
		DIAL865-06	FJ663073	658	FL
		DIAL867-06	FJ663074	658	FL
	puteulanum	DIAL027-06	FJ663083	614	FL
		DIAL028-06	FJ663084	615	FL
		DIAL029-06	FJ663085	615	FL
		DIAL473-06	FJ663086	658[1]	FL
		DIAL487-06	FJ663087	658[1]	NC
		DIAL496-06	FJ663088	644	SC
		DIAL498-06	FJ663089	658	SC
		DIAL501-06	FJ663090	658[1]	SC
		DIAL513-06	FJ663091	658[1]	FL
		DIAL514-06	FJ663092	658[1]	FL
		DIAL866-06	FJ663093	622	FL
		DLII435-07	FJ663094	645	SC
		DLII465-07	FJ663095	619	SC
		DLII472-07	FJ663096	635	FL
		DLII474-07	FJ663097	619	FL
		DLII696-07	FJ663098	611	FL
	carlinvillense	DIAL728-06	FJ663058	658	IL
		DIAL832-06	FJ663059	636	IL
		DIAL837-06	FJ663060	658	IL

A neighbour-joining tree of the seventy barcode sequences shows deep divergences within the nominal species *L. tegulare* (Fig. 2). The five putative species, previously known as *L. tegulare*, each form a distinct

cluster within the tree. Pair-wise sequence divergences between species are summarized in Table 2. The average pair-wise sequence divergence among the five species was 3.06%. *Lasioglossum puteulanum* and *L. tegulare* were found to have the most similar DNA barcodes. The minimum sequence divergence between this species pair was only 1.7%. The maximum intraspecific divergence was 0.9%, slightly more than half (0.53) the minimum interspecific value. A clear distinction can then be made between intra- and interspecific variation.

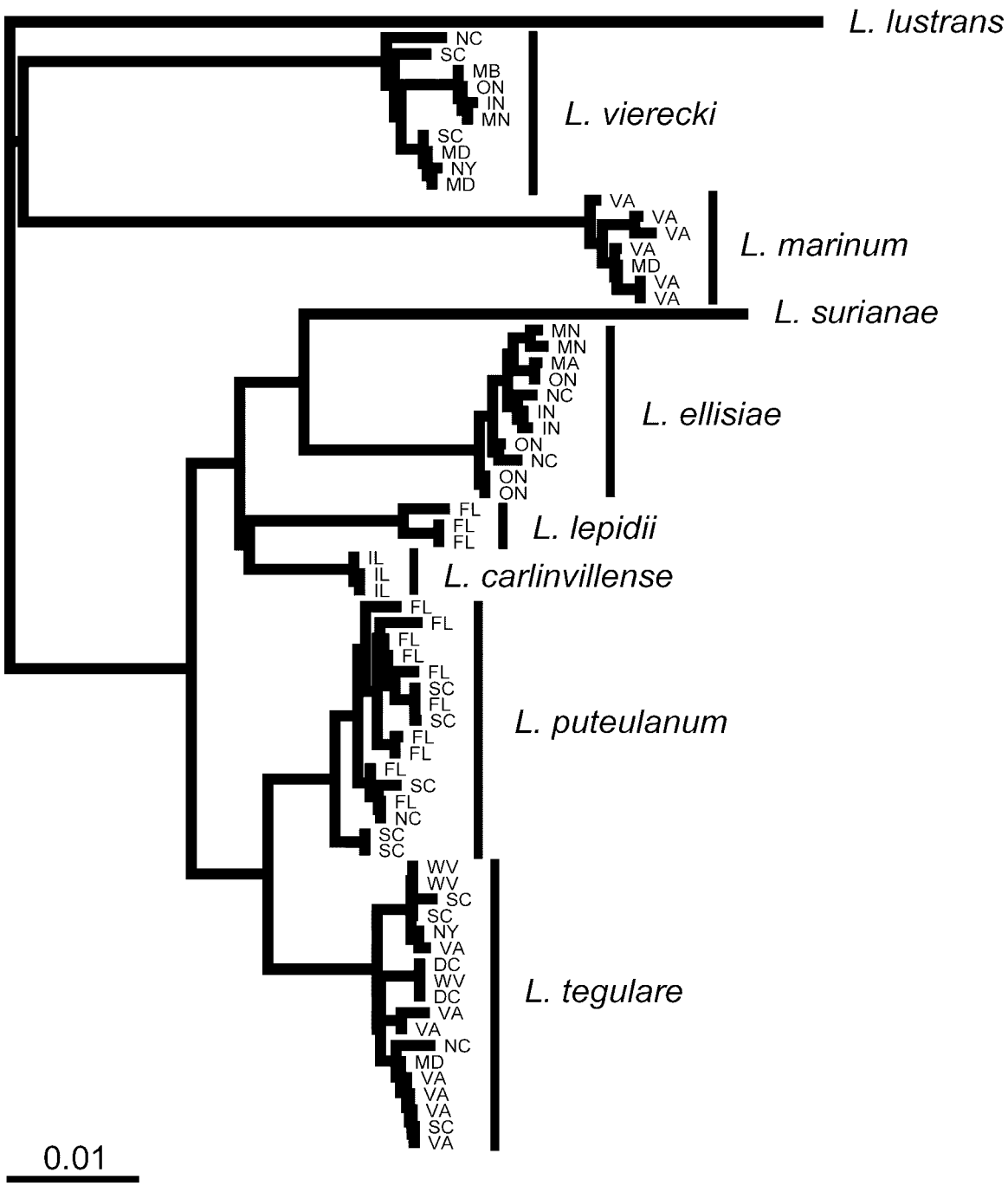

FIGURE 2. Neighbour-joining tree based on DNA barcode sequences implemented using the analytical tools in BOLD with *L. lustrans* as the outgroup. Individual sequences are marked with the standard two letter abbreviation for the province or state of origin.

The parsimony analyses for the two alternative outgroups, *L. lustrans* and *L. quebecense*, found 525 and 268 equally most parsimonious trees of length 238 and 255 steps, respectively, after sampling more than 11 billion rearrangements each. A strict consensus of the equally most parsimonious trees from each analysis

collapsed many nodes but each putative species resolved as a distinct monophyletic unit (Fig. 3). The strict consensus trees of the two parsimony analyses differed in only one node of the *L. vierecki* clade that was collapsed or resolved when the outgroup was *L. lustrans* or *L. quebecense*, respectively. Symmetric resampling showed very strong support (GC value >95 or >93) for all putative species except *L. puteulanum* (GC value 52 or 67).

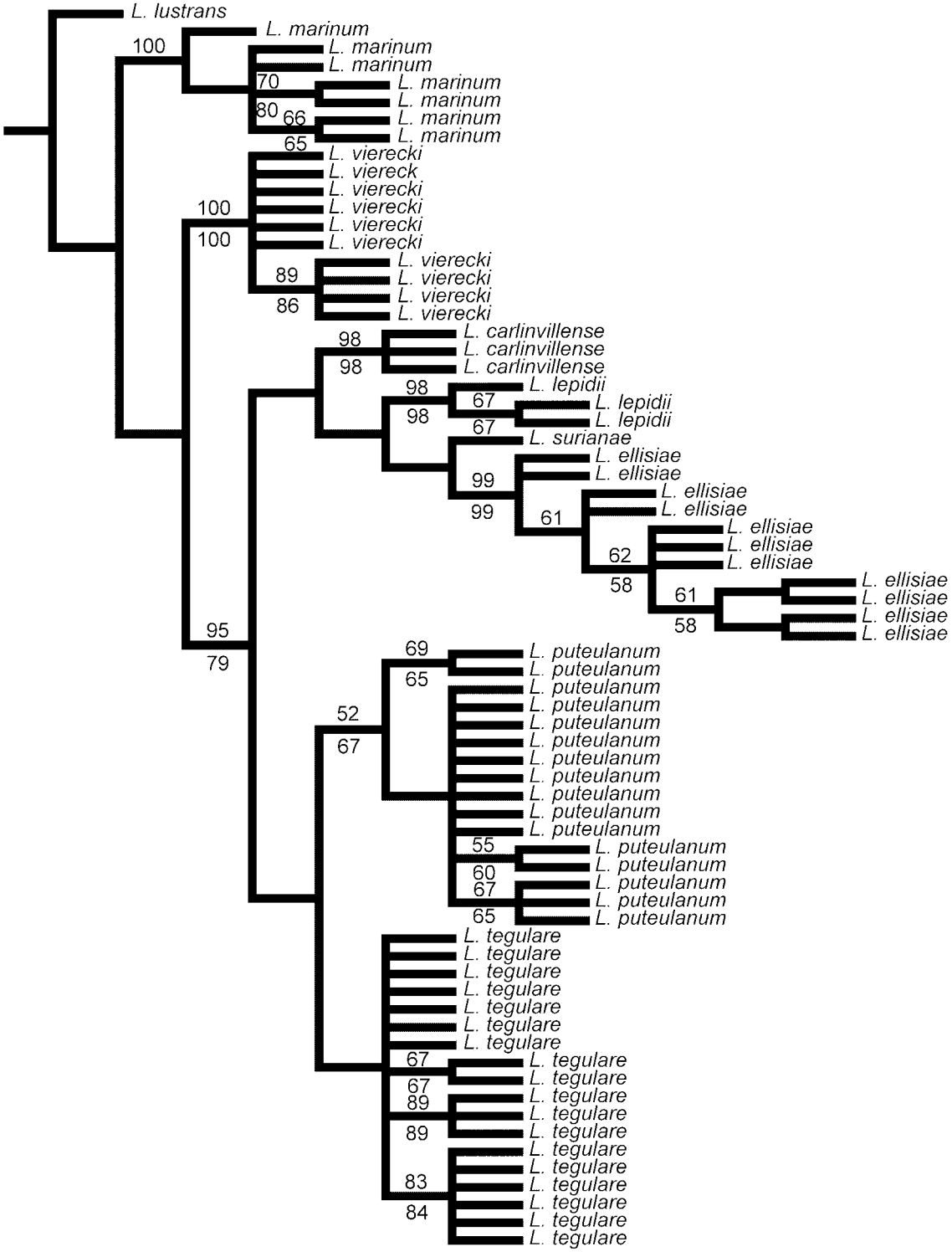

FIGURE 3. Strict consensus of 525 equally most parsimonious trees (length = 238) found with *L. lustrans* set as the outgroup. Numbers at nodes indicate GC values (Goloboff *et al*., 2003b) greater than 50 after 10000 replicates using default setting traditional searches with TNT for each replicate (Goloboff *et al*., 2003a). Upper and lower GC values are from analyses with the outgroup as *L. lustrans* and *L. quebecense*, respectively.

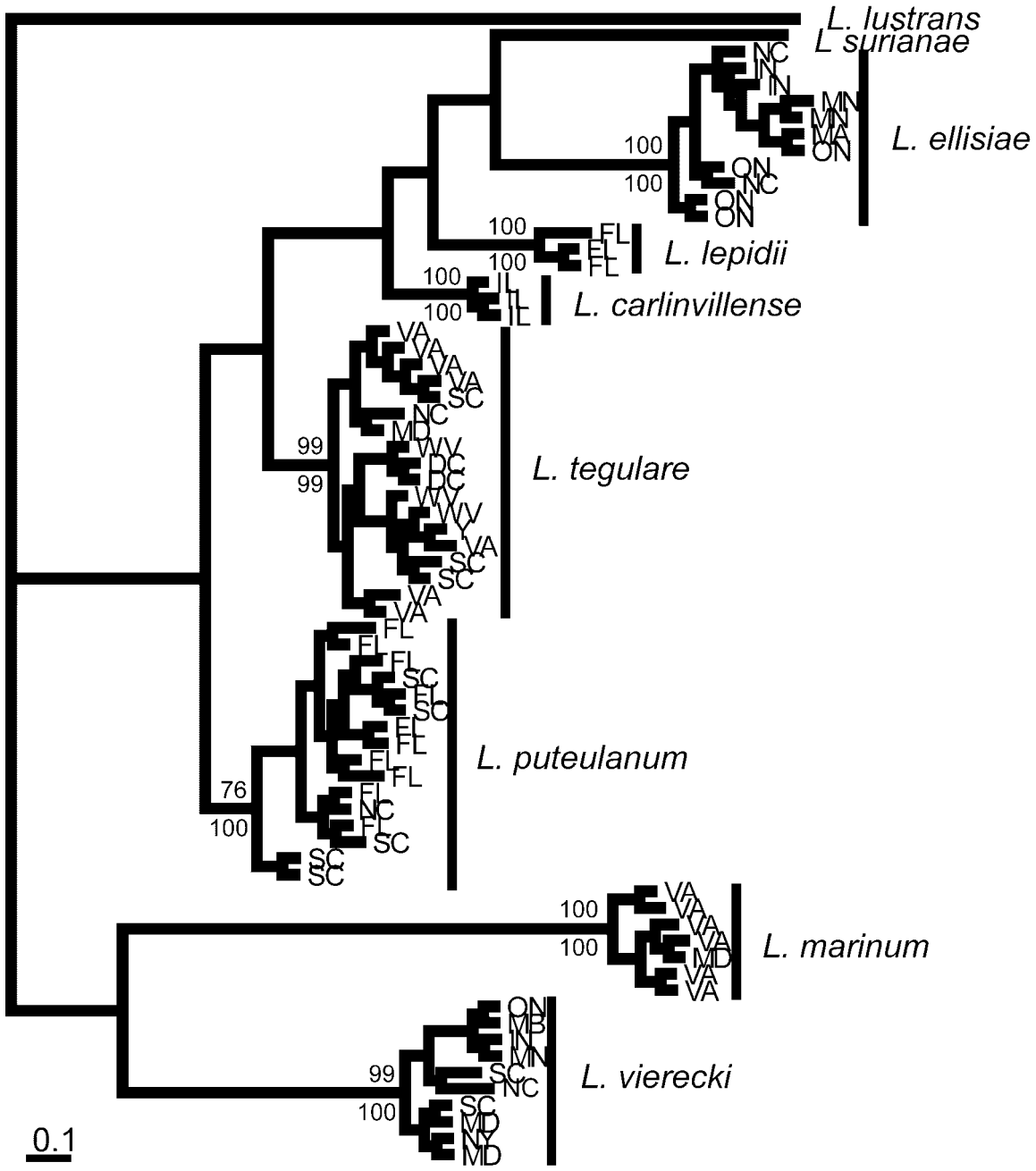

FIGURE 4. Most probable tree based on Bayesian analysis using *L. lustrans* as the outgroup. Numbers at basal node of each species indicate posterior probabilities. Upper and lower probabilities are from analyses with the outgroup as *L. lustrans* and *L. quebecense*, respectively.

TABLE 2. Summary of pair-wise sequence differences. Upper triangle indicates minimum percent pair-wise sequence divergence between species. Numbers on diagonal indicate maximum intraspecific sequence diversity. Lower triangle indicates number of sites that do not share nucleotides in common between species pairs.

Species	*L. tegulare*	*L. ellisiae*	*L. lepidii*	*L. puteulanum*	*L. carlinvillense*
L. tegulare	0.9	3.9	3.4	1.7	2.7
L. ellisiae	22	0.8	3.6	3.6	3.5
L. lepidii	17	22	0.6	3.3	2.3
L. puteulanum	8	17	17	0.8	2.6
L. carlinvillense	14	22	14	15	0.0

TABLE 3. Invariant nucleotides not shared by other members of the *L. tegulare* species complex. Nucleotide position is given relative to the full length COI gene of *Apis mellifera*. Nucleotides present in other species of the complex (often invariant) are given in order of frequency.

Species	# of unique substitutions	Nucleotide Position (relative to *Apis*)	Invariant nucleotide	Most common nucleotide in other species
L. tegulare	2	159	C	T
		258	T	A,G
L. ellisiae	7	75	T	A,G
		210	T	A
		324	C	T
		354	A	T
		357	A	T
		558	T	A
		615	C	T
L. lepidii	4	414	A	T,C
		594	G	A
		636	C	T
		666	G	A
L. puteulanum	2	96	A	T
		381	C	T
L. carlinvillense	3	255	C	T
		414	C	T,A
		621	C	T
L. surianae	13	57	A	T
		147	C	T
		162	C	T
		165	C	T
		318	C	A
		330	G	A
		363	G	A
		400	C	T
		441	C	A
		459	C	T
		465	C	T
		516	C	T
		537	C	T
		606	T	A

The results of the Bayesian analyses are largely congruent with the parsimony trees. Each of the putative species forms a distinct monophyletic group with high posterior probability (99–100) for all putative species except *L. puteulanum* (76) (Fig. 4). One important difference between the Bayesian trees and the previous

results is the relative position of the *L. puteulanum* clade. In both the NJ and parsimony trees, *L. puteulanum* is sister group to *L. tegulare s. str.* (Figs. 2, 3). In contrast, *L. puteulanum* appears as a basal branch and sister group to the remaining species in the complex in the Bayesian result (Fig. 4). The node supporting the joint *L. tegulare s. str.* and *L. puteulanum* clade had low support (GC value 38 or 49) in the parsimony tree.

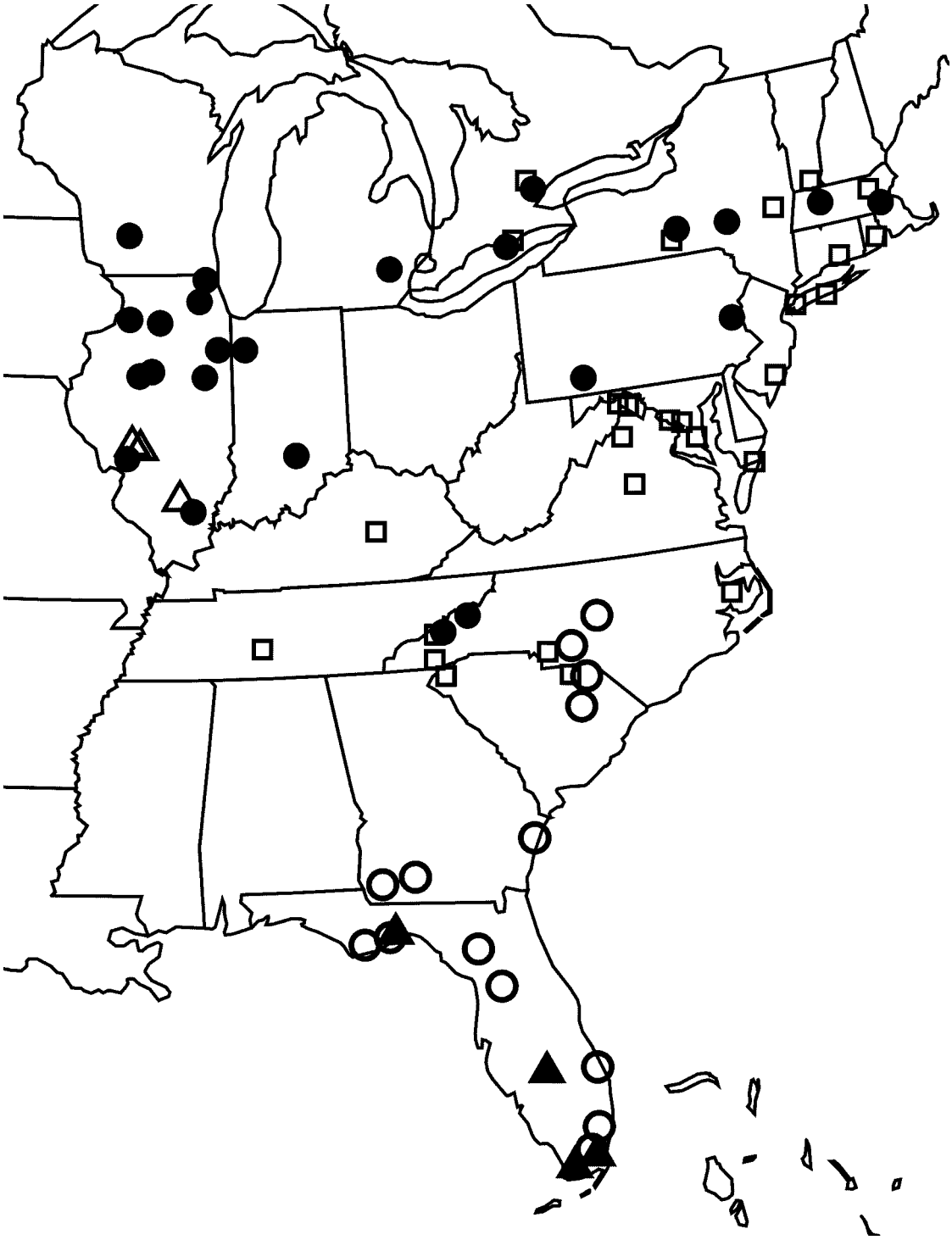

FIGURE 5. Distribution map of *L. tegulare* species group east of the Mississippi (excluding *L. surianae*). Open squares = *L. tegulare*; black circles = *L. ellisiae*; black triangles = *L. lepidii*; open circles = *L. puteulanum*; open triangles = *L. lepidii*.

The tree topologies among the various analyses are all largely congruent with some minor variation among the within species relationships. All analyses agree that the putative species are monophyletic. Choice

of outgroup had no effect on the species-level topology. The relative positions of *L. marinum* and *L. vierecki* in each analysis support the hypothesis that *L. marinum* does not belong to the *L. tegulare* species group and evolved an elongate tegula independently. The position of the *L. surianae* sequence in each analysis renders the *L. tegulare s. l.* sequences paraphyletic. The paraphyletic pattern of the DNA barcode sequences from the nominal species *L. tegulare* and the congruent pattern of morphology and DNA are consistent with the presence of cryptic species in *L. tegulare* (Funk & Omland 2003).

Each of the five species (and also *L. surianae*) has unique invariant nucleotide substitutions not shared by other members of the *L. tegulare* species complex (Table 3). The number of unique substitutions ranges from two to seven among the five species examined here. These substitutions could be used as diagnostic characters for identifying these species. The possibility of DNA-based identification of these species is therefore not limited to distance-based methods.

Morphological comparison of the five putative cryptic species and *L. surianae* found subtle differences among individuals belonging to different clades in the DNA barcode-phylogenies. Proper association of dimorphic sexes was possible by virtue of the DNA barcode data. Division of *L. tegulare* into multiple species is justified by the analysis of the DNA sequence data and morphological study. Partial corroboration also comes from the geographical distributions of the species that occupy incompletely overlapping ranges (Fig. 5). By comparison to type material, it was found that two of these species correspond with the previously synonymised names *L. ellisiae* and *L. lepidii*. The remaining cryptic species are described herein.

Lasioglossum (Dialictus) tegulare species group

Diagnosis. Members of the *L. tegulare* group can be distinguished from most other *Dialictus* by the presence of an enlarged and punctate tegula. In North America, there are two exceptions; *L. marinum* and *L. megastictum* (Cockerell) both have enlarged tegula but additional morphological data do not support a close relationship to *L. tegulare* (Gibbs, unpublished data). Both of these latter species are larger than members of the *tegulare* group and have dense punctation on the mesoscutum. In contrast, species within the *tegulare* group are small to at most medium-sized *Dialictus* and have close but distinctly separated punctures on the central disc of the mesoscutum. In addition, *L. marinum* has metallic reflections on the metasoma that are absent in the *tegulare* group. *Lasioglossum megastictum* lacks punctures on the mesepisternum that are a common feature of many *tegulare* group species.

Description. Small to medium sized (3.5–6.1 mm); andreniform; head and mesosoma dull metallic; metasoma dark brown to piceous, rarely ferruginous (as in *L. hunteri* [Crawford]); mesoscutum punctation close but distinctly separated on centre of disc; mesepisternum often distinctly punctate; tegula enlarged forming posterior angle often coarsely punctate; basal vein arched; 2nd and 3rd submarginal crossveins (1rs-m and 2rs-m) and 2nd recurrent vein (2m-cu) weak.

Lasioglossum (Dialictus) tegulare (Robertson), comb. n.
(Figures 6A–D, 7A–C)

Halictus tegularis Robertson, 1890: 318. ♀ ♂.
Chloralictus tegularis: Robertson, 1902: 248 (key).
Halictus (Chloralictus) tegularis: Viereck, 1916: 706 (key).
Lasioglossum (Chloralictus) tegulare: Michener, 1951: 1118 (catalogue).
Dialictus tegularis Mitchell, 1960: 423 (♀ ♂ redescriptions).

Diagnosis. Females of *L. tegulare* can be recognized by the following combination of characters: head and mesosoma pale to golden green, paraocular area with sparse, subappressed hairs which do not obscure the surface, distinct microsculpture between punctures of mesoscutum and mesepisternum, and three or four teeth

on the inner hind tibial spur (not including apex of rachis). Females of *L. puteulanum* have the head and mesosoma deep blue. Females of *L. lepidii* have dense subappressed hairs on the paraocular area which obscure the surface adjacent to the inner eye margin and lower paraocular area. Females of *L. ellisiae* have the integument of the mesoscutum (particularly adjacent to parapsidal lines) and mesepisternum smooth, with at most faint microsculpture which gives these areas a shiny appearance. Females of *L. carlinvillense* have only two teeth on the inner hind tibial spur.

Males of *L. tegulare* can be recognized by the following combination of characters: ventral surface of flagellum pale, appressed hairs of face mostly limited to paraocular areas and not obscuring clypeus, and T2–T3 punctures uniformly dense on disc basal to the premarginal line. Males of *L. ellisiae* have the ventral surface of the flagellum dark to ferruginous and T2–T3 punctures dense on basal half but sparse approaching premarginal line. Males of *L. lepidii* have the ventral surface of the flagellum bright yellow and appressed hairs of the face dense, obscuring the majority of the clypeus. Males of *L. puteulanum* have appressed hairs more uniformly distributed on face with less than half of the clypeal surface obscured.

Redescription. Female. Length: 4.7 (4.0–4.9) mm, fore wing length: 3.3 (2.8–3.5) mm head width: 1.4 (1.2–1.4) mm, head length: 1.3 (1.1–1.3) mm, n=20

Colouration. Head and mesosoma dull metallic pale green except the following: labrum brown-piceous; mandible base brown, apex red; clypeus brown, golden metallic above; supraclypeal area lighter green to golden; antennae brown, ventral surface of flagellomeres ruddy-brown except F8–F10 ventral surface testaceous; mesoscutum green to golden green; tegula piceous with central area ferruginous; legs brown, fore medio- and distitarsi reddish, apex of mid and hind distitarsi testaceous; wing venation and pterostigma testaceous-brown; wings faintly dusky; propodeum with green to blue reflections; metasoma piceous-brown; marginal zones of terga and sterna light brown.

Pubescence. Lower paraocular area with sparse, subappressed, plumose hairs; head and mesosoma with sparse, erect, plumose hairs (1–1.5OD), longer on metanotum and ventral surface of mesosoma (2OD); posterolateral margin of pronotum and pronotal lobe with dense, appressed tomentum; dense scopa on hind femur; propodeal lateral surface hairs (2OD) with long branches; acarinarial appressed fan complete; terga with sparse, erect hairs (1–2OD), more abundant on ventrolaterally reflexed portions; T3–T5 ventrolaterally reflexed areas with few erect hairs longer (2.5–3OD); T2–T3 basolateral areas and T4 dorsal surface with sparse appressed, plumose hairs; sterna with long, posteriorly oriented hairs emerging from apical half of disc (2–3OD); S1–S4 hairs with long branches.

Surface sculpture. Clypeus glabrate except upper margin imbricate, punctures moderately coarse (i=1–2d), fine above (i=d); supraclypeal area smooth and shining below, imbricate above, punctures fine (i=1–1.5d); lower paraocular area imbricate, glabrate below, punctures moderately coarse and deep ($i \leq d$); upper paraocular and frontal areas with punctures fine and shallow becoming reticulate centrally; gena lineolate, punctures fine and obscure; mesoscutum and mesoscutellum tessellate between fine punctures; mesoscutal punctures well spaced but not sparse in anteromedial and submedial areas (i=1–1.5d), dense on remainder of disc ($i \leq d$); mesoscutellum densely punctate medially and along margins, submedial area impunctate; pre-episternum rugulose; mesepisternum scabriculous, closely and coarsely punctate($i \leq d$), punctures finer and more obscure below, hypoepimeral area punctulate; tegula finely punctate (i=1–1.5d), more sparsely punctate centrally; metapostnotum with anastomozing rugae, median stria reaching posterior margin, lateral striae coarser and more regular extending onto anterior half of lateral slope; posterior half of lateral slope dull due to microsculpture; lateral surface of propodeum scabriculous to tessellate with few, deep punctures ($i \geq 2d$); metasoma coriarious with very fine obscure punctures, evenly spaced on T1–T4 (i=1.5d); anteriorly directed surface of T1 and dorsolateral portions anterior to premarginal line impunctate.

Structure. Head slightly broader than long; eyes convergent below (UOD:LOD = 1.25:1.0); clypeus protruding about one half below lower ocular tangent; distance from antennal sockets to clypeus, shorter than clypeus; antennal sockets distinctly nearer to each other than to inner eye margin; frontal line carinate ending 2OD from median ocellus; OOC less than IOC (1.0:1.5); eye wider than gena in lateral view; hypostomal carinae parallel; mesoscutum length to width (1.0:1.3); ratio of lengths of mesoscutellum: metanotum: dorsal

surface of propodeum (1.8:1.0:1.4); tegula elongate, angulate posteromedially; inner hind tibial spur pectinate with three subapical teeth; oblique propodeal carina weakly evident, not contiguous with lateral carina.

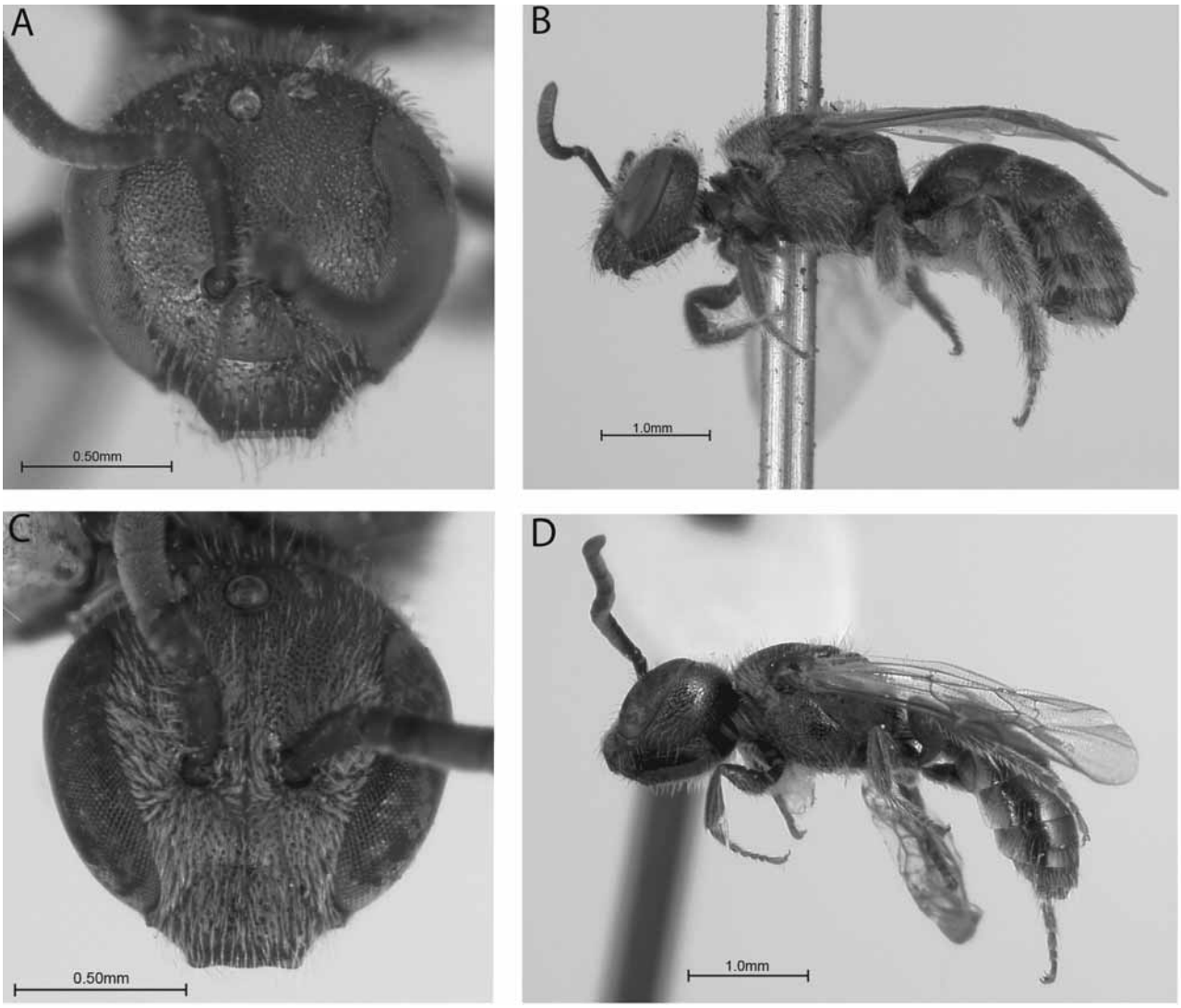

FIGURE 6. *Lasioglossum tegulare* A) face of female holotype; B) lateral habitus of female holotype; C) face of male; D) lateral habitus of male.

Male. Length: 3.8 mm, fore wing length: 2.75 mm, head length: 1.1 mm, head width: 1.1 mm

Colouration. Head and mesosoma dull metallic green with faint golden reflections except gena with blue reflections; mesepisternum bluish-green below; propodeum bluish; the following parts dark brown-piceous: labrum; mandible except apex reddened; lower clypeus; antenna, lighter basally, F1–F3 testaceous ventrally; tegula; wing venation and pterostigma brown; wings hyaline, apex faintly dusky; metasoma.

Pubescence. Inter-antennal area and paraocular area from mandible base to emarginated portion of eye with subappressed hairs; head, mesosoma, anteriorly directed surface of T1 and ventrolaterally reflexed portions of terga with sparse, erect hairs (1.5–2OD); T1–T4 with short laterally oriented setae; sterna with erect hairs, densest on S4–S5.

Surface sculpture. Head and mesosoma glabrate and shining; clypeus (i≤d), supraclypeal area (i=1–1.5d) and lower paraocular area (i=d) punctation fine and deep; upper paraocular area and frons reticulate; gena faintly imbricate-lineolate with obscure punctures; mesoscutum imbricate anteromedially; mesoscutal punctures on disc between parapsidal lines well spaced (i≤1.5d), close laterally (i<d); mesoscutellum punctures close on margins and medial line (i<d), well spaced elsewhere (i=1.5d); pre-episternum rugulose;

mesepisternum punctures moderately coarse and deep (i=d); metapostnotum irregularly striate, laterally striations extending onto anterior half of lateral slope; lateral and posterior propodeal surfaces shiny-imbricate with deep, moderately fine punctures (i=1–1.5d); terga smooth, very faintly coriarious; terga punctures fine but deep and distinct (i=1–1.5d), apically impressed areas impunctate; anteriorly directed surface of T1 largely impunctate.

Structure. Face length subequal to breadth; eyes convergent below (UOD:LOD = 1.5:1.0); clypeus protruding slightly more than one half below lower ocular tangent; antennal sockets slightly nearer to each other than to inner eye margin; frontal line carinate ending less than 2OD from median ocellus; OOC less than IOC; eye wider than gena from lateral view; hypostomal carinae parallel; pedicel subequal in length to F1; F2–F10 length 1.5 times breadth, F11 longer; ratio of lengths of mesoscutellum: metanotum: dorsal surface of propodeum (1.9:1.0:1.6); tegula enlarged, posterior margin not strongly angled; propodeal carina not evident between dorsal and posterior surfaces; metasoma narrow relative to female.

Terminalia. Median lobe of S7 narrow and elongate, sides subparallel, apex rounded (Fig. 7A); apical margin of S8 weakly convex (Fig. 7B); genitalia as shown in Fig. 7C; gonostylus with few erect dorsal hairs near base; retrorse lobes elongate, attenuated apically, covered with fine setae.

Range. Vermont to South Carolina, west to Ontario, Kentucky and Tennessee.

Specimens examined. Holotype, USA, CONNECTICUT: HOLOTYPE ♀, N. Haven, 6.vi.1878, (WH Patton) (ANSP); RHODE ISLAND: 2 ♀, Newport Co., N41.4969 W71.3678, 22.vii.2005, (P Ostenton); MASSACHUSETTS: 1 ♀, Middlesex Co., Harvard:Oxbow NWR, Wallace Rd., 28.v.2006, (MF Veit); 1 ♀, Middlesex Co., Dunstable, sandpit 0.1mi E of airport, 29.iv.2006, (MF Veit) (PCYU); VERMONT: Windham Co., N42.4969 W71.3678, 22.vii.2005, (P Ostenton) (PCYU); NEW YORK: 1 ♀, Suffolk Co., 6.ix.2005, (SW Droege) [Barcoded]; 1 ♀, Suffolk Co., N41.13403 W72.3247, 8.ix.2005, (SW Droege); 1 ♀, Suffolk Co., 8.ix.2005, (SW Droege); 1 ♀, Suffolk Co., N41.05132 W71.9519, 7.ix.2005, (SW Droege); 2 ♀, Suffolk Co., 6.ix.2005, (SW Droege); (PCYU); 3 ♂, Tompkins Co., Buttermilk Falls S.P., Ithaca, 7.x.1967, (G & K Eickwort); 1 ♀, Tompkins Co., 6-mile Creek, SE Ithaca Reservoir, 25.v.1968, (G & K Eickwort); 1 ♂, Tompkins Co., Michigan Hollow, gravel pit, 5mi S of Danby, 7.ix.1968, (G & K Eickwort); 1 ♀, Albany Co., Partridge Run St. Game Area, 5mi N Rensselaerville, 6.vi.1970, (G & K Eickwort); 1 ♀, Albany Co., Rensselaerville, 28.vii.1970, (G & K Eickwort); 1 ♀, Albany Co., Rensselaerville, Huyck Reserve, 12.vi.1969, (G & K Eickwort); 1 ♂, Albany Co., Colonie, 20.viii.1969, (G & K Eickwort); 1 ♀, Cayuga Co., Fair Haven Beach S.P., 8.vi.1968, (G & K Eickwort); 1 ♀, Ludlowville, 6.vi.1968, (LL Pechuman); 1 ♂ & 3 ♀, Nassau Co., Jones Beach S.P., 31.vii.1974, (GC Eickwort); 1 ♂ & 1 ♀, Nassau Co., Jones Beach S.P., 26.vi.1976, (G Eickwort); 7 ♂, Nassau Co., Hempstead Lake S.P., 4–6.vii.1974, (GC Eickwort); 2 ♀, Nassau Co., Kennedy Wildlife Sanct., Tobay Beach, 18.vi.1989, (GC Eickwort); 1 ♀, Nassau Co., Tobay Beach, 24–26.vi.1976, (GC Eickwort); 1 ♂, Nassau Co., Floral Pk., 4.vii.1982, (D Yanega); 1 ♀, Montauk, 4.v.1947, (R Latham); 1 ♀, 3-mile Har., 6.vi.1941, (R Latham); 1 ♂, Van Cortland Pk., 20.vii.1913 (CUIC); 1 ♂, Queens Co., Floral Pk., Long I., 6.viii.1983, (D Yanega) (SEMC); NEW JERSEY: 1 ♀, Atlantic Co., 39 35'N 74 46'W, 21.vii.2003, (B Ahlstrom) (PCYU); 1 ♂, Weymouth, 26.vii.1923; 1 ♀, San Isle Junction, "May,25" (CUIC); 1 ♂, Ramsey, 10.vii.1913 (SEMC); MARYLAND: Camp Springs, 11.v.10, (JC Crawford); 1 ♀, Cabin John, 16.iv.1915, (JC Crawford); 1 ♀, Pr. George's Co., N38.9764 W76.7491 20.vii.2002, (S Kolski); 1 ♀, Pr. George's Co., N38.9591 W76.734 20.viii.2004, (S Kolski); 1 ♀, Pr. George's Co., N39.002 W76.7505 20.viii.2004, (S Kolski); 3 ♀, Pr. George's Co., N38.9977 W76.7573 30.ix–1x,2004, (S Kolski); 4 ♀, Anne Arundel Co., N38.7839 W76.7014, B Hollister (SEMC); 1 ♀, Calvert Co., N38.536 W76.518, 7.vii.2006, (M Gates); 1 ♀, Talbot Co., N38.8 W76.283, 7–8.v.2005, (W Steiner); 1 ♀, Caroline Co., N38.9194 W75.8279, 13.v.2007, (M Price); 1 ♂, Wicomico Co., N38.2909 W75.5364, 12.vi.2004, (SW Droege); 1 ♂, Anne Arundel Co., N38.7839 W76.7014, 21.ix.2004, (B Hollister); 1 ♂, Pr. George's Co., N38.9893 W76.7322, 20.vii.2004, (S Kolski); 1 ♂ & 1 ♀, Pr. George's Co., N38.9123 W76.755, 12–13.viii.2003, (Haramis & Archer); 2 ♀, Pr. George's Co., N38.9123 W76.755, 13–14.viii.2003, (Haramis & Archer); 1 ♀, Pr. George's Co., N38.9123 W76.755, 28–29.viii.2003, (Haramis & Archer); 1 ♀, Pr. George's Co., N38.9123 W76.755, 26–27.viii.2003, (Haramis & Archer); 2 ♀, Pr. George's Co., N38.9123 W76.755, 14–15.viii.2003, (Haramis

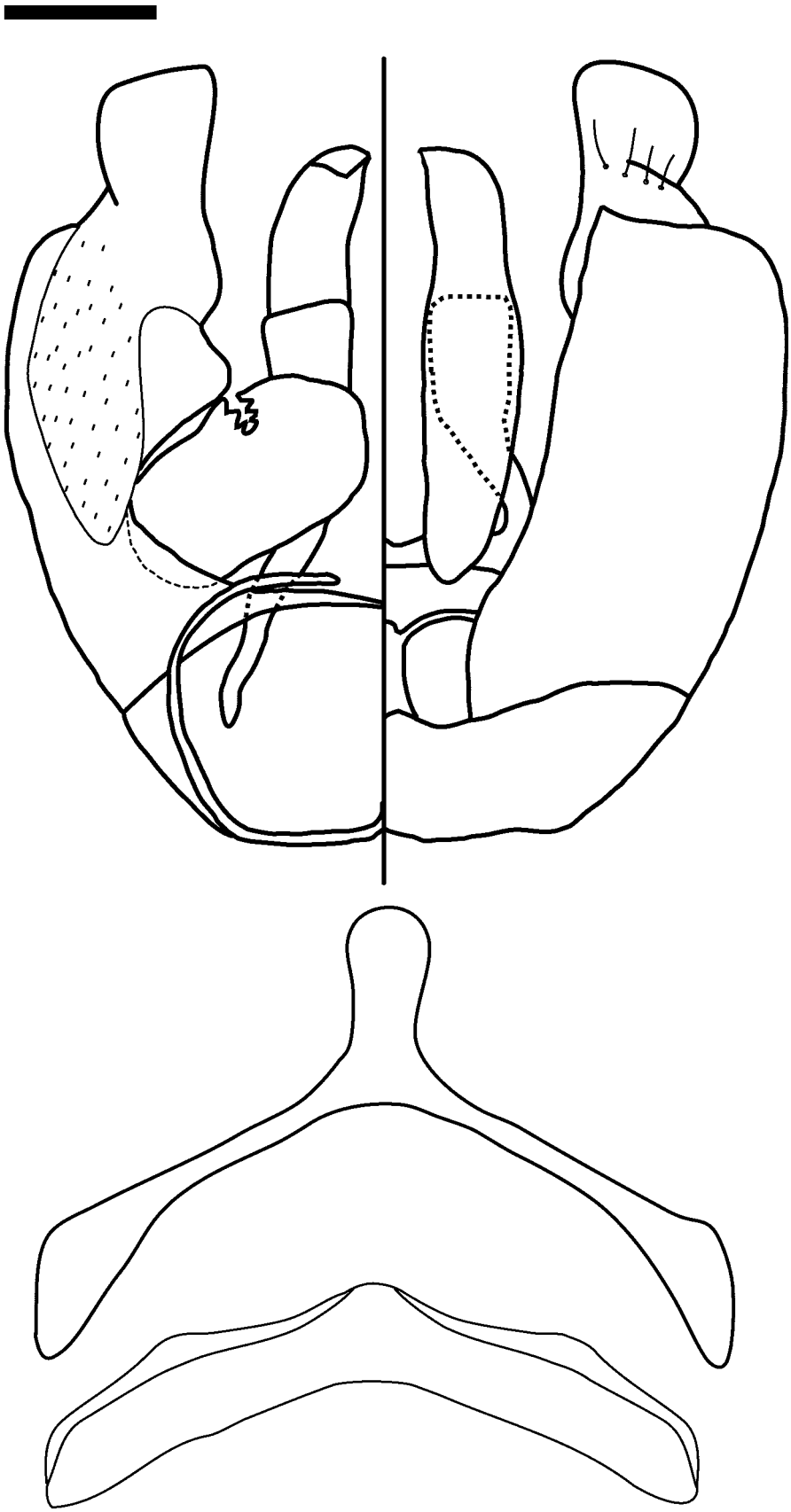

FIGURE 7. *Lasioglossum tegulare* terminal structures of male. Diagram of genitalia with ventral and dorsal sides pictured on left and right, respectively (above), diagram of S7 (middle) and diagram of S8 (below).

& Archer); 1 ♀, Pr. George's Co., N38.9959 W76.7886, 2.ix.2004, S Na; 1 ♀, Caroline Co., N39.1098 W75.7724, 7.iv.2005, (SW Droege) (PCYU); 6 ♀, Prince Georges Co., Temple Hills, 22.viii.1976, (GC Eickwort) (CUIC); WASHINGTON, D.C.: 2 ♀, N38.931 W77.116, 24.vi.2006, Pascarella; 1 ♂, N77.034 W38.885, 18–19.x.2004, (E Keto); 1 ♂, N38.9463 W77.0344, 16.vi.2004, (SW Droege); 1 ♀, N38.8871 W77.0128, 1.ix.2005, (NB Staff); 1 ♀, Mall, N38.8912 W777.0242, 16.viii.2006, (SW Droege); 1 ♂, N38.891 W77.0308, 15–16.vii.2004, (C Osborn); 1 ♂, N38.879 W77.0333, 13–14.vii.2004, (C Osborn); 1 ♂, N77.0261 W38.8694, 4–5.x.2004, (E Keto) (PCYU); VIRGINIA: 3 ♀, Assateague I., N37.9625 W75.3108, 30.vi–1.vii.2006, (SW Droege) [Barcoded]; 1 ♀, Assateague I., N37.9576 W75.3147, 30.vi–1.vii.2006, (SW Droege); 1 ♀, Assateague I., N37.9377 W75.3177, 30.vi–1.vii.2006, (SW Droege) [Barcoded]; 1 ♀, Assateague I., N37.9486 W75.3136, 2.vii.2006, (SW Droege); 1 ♀, Assateague I., N37.9086 W75.3564, 1–2.vii.2006, (SW Droege); 1 ♀, Virginia Beach, N36.917 W75.3564, 16–17.vi.2007, (W Steiner); 1 ♀, Fluvanna Co., N37.753 W78.162, 2.x.2004, (SW Droege) [Barcoded]; 1 ♀, Accomack Co., N37.938 W75.318, 30.vi–1.vii.2006, (SW Droege); 1 ♀, Hwy 340, 10km N of Shenandoah, N38.564 W78.606, 7.vi.2005, (A Zayed) [Barcoded] (PCYU); 2 ♀, Clarke Co., Blandy Exp. Farm E Boyce, 12–14.vi.1986, (JK Liebherr) (CUIC); WEST VIRGINIA: 2 ♀, Hampshire Co., N39.346 W78.403, 29–30.v.2004, (SW Droege) [Barcoded]; 1 ♀, Hampshire Co., N39.351 W78.509, 29–30.v.2004, (SW Droege) [Barcoded]; 1 ♂, Hampshire Co., N39.2334 W78.6843, 11.vii.2002, (SW Droege); 1 ♂, Hampshire Co., N39.31 W78.54, 11.vii.2002, (SW Droege); 1 ♂, Hampshire Co., N39.3012 W78.4358, 11.vii.2002, (SW Droege); 1 ♂, Hampshire Co., N39.4401 W78.4872, 7.vii.2002, (SW Droege); 1 ♂, Hampshire Co., N39.2886 W78.4819, 11.vii.2002, (SW Droege) (PCYU); 1 ♀, Hampshire Co., N39.415 W78.5012, 7.vii.2002, (SW Droege); 1 ♀, Hampshire Co., N39.333 W78.4585, 6.vii.2002, (SW Droege) (SEMC); KENTUCKY: 15 ♀, Wayne Co., N39.924 W84.8715, 23–24.vii.2007, (SW Droege); 1 ♀, Laurel Co., N37.1528 W84.1167, 27.vii.2007, (SW Droege) (PCYU); TENNESSEE: 1 ♀, Rutherford Co., N35.8275 W86.2912, 20.vii.2007, (D Green); 1 ♀, Rutherford Co., N35.8197 W86.3159, 20.vii.2007, (D Green) (PCYU); NORTH CAROLINA: 1 ♀, Union Co., N34.984 W80.449, ix–x.2003, (R Jackowski) [Barcoded]; 1 ♀, Great Smoky Mountains National Park, Cataloochee overlook, N35.54 W83.06, 6.viii.2006, (J Gibbs); 1 ♂, Highlands, 22.vii.1958, (TB Mitchell); 1 ♀, Pettigrew S.P., 27.v.1959, (TB Mitchell) (PCYU); 6 ♂ & 1 ♀, Beutenmuller, Black Mts., viii.1912; SOUTH CAROLINA: 1 ♂ & 1 ♀, Okanee Co., near Walhalla, N34.813 W83.137, 9.viii.2006, (J Gibbs) [Barcoded]; 1 ♀, Chesterfield Co., N34.637 N80.176, 18–19.v.2006, (SW Droege); 5 ♀, Chesterfield Co., N34.55 W80.26, 2007, (L Housh) (PCYU); GEORGIA: 2 ♀, Athens, 15.vi.1909, (JC Bradley); 1 ♂, Cobb Co., Lost Mount, 13.vii.1913; 1 ♂, Rabun Bald, 4000–4800ft, 21.viii.1913; CANADA, ONTARIO, 1 ♂, Norfolk, N42.6497 W80.5729, 11.viii.2007, (A Taylor); 5 ♀, Norfolk, N42.6493 W80.5687, 11.vi.2007; 1 ♂, Caledon, Gschwendtner property, N43.8148 W79.9768, 18.ix.2003, (J Grixti) (PCYU).

Type depository. ANSP.

Etymology. No explanation is given for the name in the original description but the species was undoubtedly named for the remarkable shape of the tegula.

Comments. The range of *L. tegulare* is evidently more restricted than previously reported (Moure & Hurd 1987). Northwestern and southeastern records likely correspond to one or other of the species described below. Some records from Texas could be misidentifications of *L. coactum* (Cresson), which differs in having deeply impressed marginal zones of T1 and T2 in both sexes.

Lasioglossum (Dialictus) ellisiae **(Sandhouse), comb. n.**
(Figures 8A–D)

Halictus (Chloralictus) ellisiae Sandhouse, 1924: 11. ♀.
Lasioglossum (Chloralictus) ellisiae: Michener, 1951: 1113 (catalogue).
Dialictus tegularis Mitchell, 1960: 423 (synonymy).

Diagnosis. Females of *L. ellisiae* are unique in having the integument of the mesoscutum (especially adjacent to the parapsidal lines) and mesepisternum smoother and more reflective than those of other species of the *tegulare* group in eastern North America. The remaining four species each have the integument in these areas roughened and dulled due to microsculpture. Females of *L. ellisiae* can be further distinguished by the following characters: head and mesosoma primarily bluish-green, paraocular area with sparse subappressed hairs, and inner hind tibial spur with 3 or 4 teeth (not including apex of rachis). Females of *L. puteulanum* are deep blue in colour. Females of *L. lepidii* have dense subappressed hairs on the paraocular area which obscure the surface adjacent to the inner eye margin and lower paraocular area. Females of *L. carlinvillense* have only 2 teeth on the inner hind tibial spur.

Males of *L. ellisiae* can be distinguished from the other species by the sparsely punctate zones of T2 and T3 anterior of the premarginal line. The males of *L. tegulare, L. lepidii,* and *L. puteulanum* all have uniformly dense punctation basal to the premarginal lines of T2 and T3.

Redescription. Female. Length: 5.25 (4.6–5.5) mm, fore wing length: 3.5 (3.1–3.7) mm, head length: 1.3 (1.1–1.4) mm, head width: 1.4 (1.2–1.4) mm, n=9

Colouration. Head and mesosoma dull metallic bluish-green except the following: mandible base brown-piceous, apex red; clypeus brown-piceous below, golden above; supraclypeal area green below, gold above; antenna brown-piceous, ventral surface brown, F8–F10 ruddy brown to testaceous; mesoscutum green with gold reflections; tegula brown-piceous, central area ferruginous; legs brown-piceous, fore, medio- and distitarsi reddish, mid and hind distitarsi ruddy brown; wing venation and pterostigma testaceous-brown; wings very faintly dusky; propodeum bluer than mesoscutum; metasoma brown-piceous.

Pubescence. Head and mesosoma with sparse, erect, plumose hairs (1–1.5OD), longer on metanotum and ventral pleura (2OD); posterolateral margin of pronotum and pronotal lobe with dense, appressed tomentum; dense scopa on hind femur; lateral surface of propodeum with long branched hairs (2OD); acarinarial appressed fan complete; terga with sparse, erect hairs (1–2OD), more abundant on ventrolaterally reflexed areas; T3–T5 ventrolaterally reflexed areas with few, erect hairs (2.5–3OD); T2–T3 basolateral portions and T4 dorsal surface with sparse appressed, plumose hairs; sterna with long, posteriorly oriented hairs emerging from apical half of disc (2–3OD); S1–T4 hairs with long branches.

Surface sculpture. Clypeus glabrate except upper margin imbricate, punctures moderately coarse below (i=1–1.5d), fine above (i=d); supraclypeal area smooth and shining, margins imbricate, punctures fine, irregularly spaced (i=1–4d); lower paraocular area imbricate, smooth and shining below, punctures moderately coarse and deep (i≤d); upper paraocular area and frons punctures fine, reticulate; gena lineolate, punctures fine and obscure; mesoscutum and mesoscutellum tessellate, shiny between tegula and parapsidal line and posteriorly; mesoscutum punctures fine, well spaced but not sparse in medial/submedial area (i=1–1.5d), dense on remainder of disc and along median line (i≤d); mesoscutellum densely punctate with small impunctate submedial area; pre-episternum scabriculous; mesepisternum punctures coarse above, finer below (i≤d), interspaces imbricate and shiny; hypoepimeral area reticulate; tegula finely punctate (i=1–2d), central area more sparsely punctate; metapostnotum medial area with anastomozing rugae, median striae incomplete, lateral striations more regular extending onto lateral slope; posterior surface of propodeum imbricate, with sparse, obscure punctures (i=2d); metasoma coriarious; terga with very fine punctures, more widely spaced and obscure on apical half of T1–T4 (i=1.5–2.5d); anteriorly directed surface of T1 and dorsolateral portions basal to premarginal line impunctate.

Structure. Face slightly broader than long; eyes convergent below (UOD:LOD = 1.2:1.0); clypeus protruding about one half below lower ocular tangent; distance from antennal sockets to clypeus less than length of clypeus; distance between antennal sockets half distance of socket to inner eye margin; frontal line carinate ending 2OD from median ocellus; OOC less than IOC (1.0:1.2); eye wider than gena from lateral view; hypostomal carinae parallel; mesoscutum length to width (1.0:1.1); ratio of lengths of mesoscutellum: metanotum: dorsal surface of propodeum (1.7:1.0:1.5); tegula elongate with posterior margin angled posteromedially; oblique propodeal carina weakly evident, not contiguous with lateral carina.

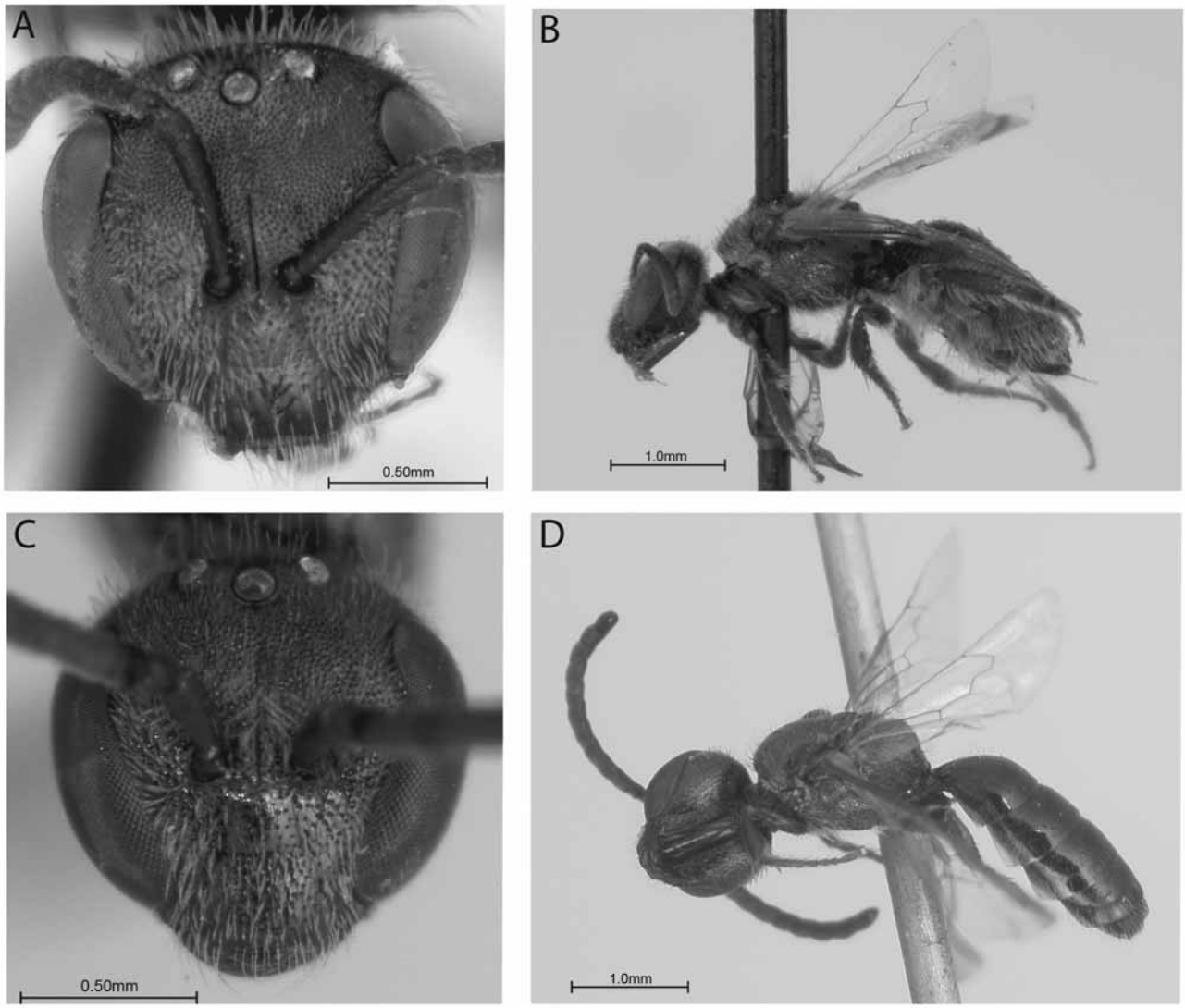

FIGURE 8. *Lasioglossum ellisiae* A) face of female holotype; B) lateral habitus of female holotype; C) face of male; D) lateral habitus of male.

Male. Length: 4.0–4.3 mm, fore wing length: 3.1 mm, head length: 1.2 mm, head width: 1.2–1.3 mm, n=2

Colouration. Head and mesosoma dark metallic blue except lower paraocular area and medial areas of mesoscutum and mesoscutellum with golden-green reflections; the following dark brown-piceous: labrum; mandible except apex red; lower clypeus; antenna; tegula except central area ferruginous; legs except medio- and distitarsi brown; metasoma; wing venation and pterostigma brown; wings hyaline except apex faintly dusky.

Pubescence. Paraocular area and interantennal area with sparse, subappressed hairs; sparse longer erect hairs on head, mesosoma, anteriorly directed surface of T1 and ventrolaterally reflexed portions of terga (1.5–2OD), longest on metanotum; T1–T4 with short laterally oriented setae; sterna with erect hairs, densest on S4–S5.

Surface sculpture. Head and mesosoma smooth and shining; clypeus (i≤d), supraclypeal area (i=1–2d), and lower paraocular area (i=d) punctation moderately fine and deep; upper paraocular area and frons reticulate (i≤d); gena shining, imbricate-lineolate, obscurely punctate; mesoscutum imbricate anteromedially; mesoscutal punctures moderately coarse and deep, well spaced on disc between parapsidal lines (i≤1.5d), closer laterally (i<d) and anterolaterally (i≤0.5d); mesoscutellum punctures close on margins and medial line

(i≤d), impunctate submedially; pre-episternum reticulate; mesepisternum punctures moderately coarse and deep (i=d); metapostnotum incompletely striate, lateral striations extending onto anterior half of lateral slope; posterior half of lateral slopes and lateral surface of propodeum scabriculous, punctures obscure but deep, moderately fine (i=1–1.5d); posterior surface of propodeum smooth with distinct punctures (i=1–2d); terga smooth, very faintly coriarious; terga with fine but distinct punctures on basal half (i=1–1.5d), apical half sparsely punctate except on premarginal line; anteriorly directed surface of T1 largely impunctate.

Structure. Face length subequal to breadth; eyes convergent below (UOD:LOD = 6.6:4.3); clypeus protruding slightly more than one half below lower ocular tangent; distance between antennal sockets equal to distance to inner eye margin; frontal line carinate ending 1.5OD from median ocellus; OOC less than IOC; eye wider than gena from lateral view; hypostomal carinae parallel; pedicel subequal in length to F1; F2–F10 length 1.5 times breadth, F1 very slightly longer than F2; ratio of lengths of mesoscutellum: metanotum: dorsal surface of propodeum (2.1:1.5:1.6); tegula enlarged, posterior margin not strongly angled; propodeal carina not evident between dorsal and posterior surfaces; metasoma narrow relative to female.

Terminalia. As in *L. tegulare* see Fig. 7A–C.

Range. From the southern Appalachian Mountains north to Ontario and Massachusetts and west to Minnesota.

Specimens examined. USA, MASSACHUSETTS: HOLOTYPE ♀, Forest Hills, 5.viii.1901, (WM Wheeler) (NMNH); 1 ♂, Franklin Co., 0.86mi SSW of W. Hawley, 19.vii.2006, (MF Veit) [Barcoded]; 1 ♀, Middlesex Co., 0.2mi S of Townsend Gravel Pit, 27.v.2006, (MF Veit); 2 ♀, Middlesex Co., 0.1mi E of Airport, 29.iv.2006, (MF Veit) (PCYU); NEW YORK: 1 ♂, Tompkins Co., Cornell U. campus, Ithaca, 22.vii.1971, (G & K Eickwort); 1 ♀, Cornell U. campus, Ithaca, 9.vii.1987; (GC Eickwort); 2 ♂, Tompkins Co., Ithaca vicinity, inlet, 5.viii.1976, (G & K Eickwort); 1 ♀, Tompkins Co., Ithaca vicinity, inlet, 04.vi.1976, (G & K Eickwort); 1 ♀, Tompkins Co., Ithaca vicinity, inlet, 14.vi.1976, (G & K Eickwort); 1 ♀, Tompkins Co., Ithaca vicinity, inlet, 21.v.1984, (G & K Eickwort); 1 ♀, Tompkins Co., Ithaca vicinity, 21.v.1984, (G & K Eickwort); 1 ♀, Otsego Co., East Worchester, 22.vi.1971, (G & K Eickwort); 1 ♀, Van Natta's Dam, Ithaca, 23.v.1937, Babiy; 2 ♂, Van Natta's Dam, Ithaca, 14.viii.1931, (PP Babiy); 1 ♂, Ithaca 10.viii.1916; 1 ♀, Ithaca, 22.vi.1936; 1 ♀, Ithaca, 2.v.1915; 1 ♀, Ithaca, 6.vii.1947, (C Robinson); 1 ♂, Ithaca, 22.vi.1936; 1 ♀, Ithaca, v.1913; 1 ♂, Ithaca, 20.vi.1962; 1 ♂, Otsego Co., East Worchester, 13.viii.1968, (G & K Eickwort); 1 ♀, Tompkins Co., Ithaca, Monkey Run, 26.iv.1986, (GC Eickwort); 2 ♀, Tompkins Co., Monkey Run, 1.vi.1984, (B Alexander); 1 ♂, Tompkins Co., Michigan Hollow gravel pit, 5mi S of Danby, 7.ix.1968, (G & K Eickwort); 4 ♂, Tompkins Co., Buttermilk Falls S.P., Ithaca, 7.x.1967, (G & K Eickwort); 1 ♂, Tompkins Co., Taughannock Falls S.P., Ithaca, 7.x.1967, (G & K Eickwort); 1 ♀, Tompkins Co., Taughannock Falls S.P., Ithaca, 5.vi.1976, (G & K Eickwort); 1 ♂, Tompkins Co., 1mi S McLean, 23.vi.1975, (MJ & CA Tauber); 4 ♀, Ontario Co., Selkirk Shores S.P., 12.vi.1976, (GC Eickwort); 1 ♂, Tompkins Co., Dryden, 18.viii.1968, (G & K Eickwort); 1 ♀, Tompkins Co., Robert H. Treman S.P., Ithaca, 14.viii.1971, (G & K Eickwort); 4 ♂, Nassau Co., Hempstead Lake S.P., 4–6.vii.1974, (GC Eickwort); 1 ♂, Albany Co., 2mi NW Westerlo, 6.vii.1969, (GC Eickwort); 2 ♂, Schuyler Co., ear Reynoldsville, 17.vii.1976, (GC Eickwort); 1 ♀, Greene Co., Stony Clove Creek, 42 8'00, 74 15'10, 412m, 28.vi.1978, (TL McCabe); 2 ♀, Cayuga Co., Fair Haven Beach S.P., 27.v.1984, (GC Eickwort); 1 ♀, Seneca Co., Junius Ponds, 6mi NW Waterloo, 24.vi.1986, (GC Eickwort); 1 ♀, Seneca Co., Junius Ponds, 6mi NW Waterloo, 12.viii.1986, (GC Eickwort) (CUIC); 1 ♀, NY, Tompkins Co. 6-mile creek, SE. Ithaca Reservoir, 25.v.1968, (G & K Eickwort) (CUIC); PENNSYLVANIA: 1 ♀, Stroud Co., Stroudsburg, 14.vii.1976, (RJ Pollack); 1 ♂, Lehigh Gap River, 19.vii.1903, (JC Bradley); 1 ♂, Roberts, viii.1905, (JC Bradley) (CUIC); NORTH CAROLINA: 1 ♂, Great Smoky Mountain National Park, Cataloochee overlook, N35.54 W83.06, 6.viii.2006, (J Gibbs) [Barcoded]; 1 ♀, S. of Bryson City, Bryson City Rd. & Queen Branch Rd., N35.284 W83.487, 8.viii.06, (J Gibbs) [Barcoded]; MICHIGAN: Washtenau Co., Ann Arbor, ix.1976, (RW Carlson) (SEMC); INDIANA: 1 ♀, Jackson Co., N38.88 W86.056, 26.vii.2003, (SW Droege) [Barcoded]; 2(1) ♀, Jasper Co., Nipsco, blue pan trap, 16.vii.2003, (RP Jean) [Barcoded] (PCYU); ILLINOIS: 3 ♀, Bureau Co., 3mi NW of LaMoille, 13.v.1970, on *Salix*, (Laberge & Molina); 1 ♀, Champaign Co., Brownfield Woods, Urbana, 29–31.iii.1968, (Laberge & Ribble); 1 ♀,

Whiteside Co., Morrison, 10.vii.1968, (JC Marlin); 1 ♀, Mason Co., Bath, 2.vii.1968, (JC Marlin); 1 ♀, Mason State Forest, 2.vi.1966, (WJ Knee); 1 ♀, McHenry Co., Chain O' Lakes St. Pk., 22.vi.1967, (Laberge & Ribble); 1 ♀, Lake Co., 2 mi NW Volo, 22.vi.1967, (Laberge & Ribble); 1 ♀, Long L., "bog, smtwd." 11.viii.1906; 10 ♀, Algonquin, 16.vi.1909, (Nason); 2 ♀, Algonquin, 24.vi.1909, (Nason); 1 ♀, Woodford Co., 9mi N East Peoria, 7.viii.1968, (JC Marlin); 1 ♂, Macoupin Co., Plainview, 22.vii.1915 (INHS); 1 ♀, Kankakee Co., Hooper Br, 2.vii.2003, (RP Jean) (PCYU); WISCONSIN: 1 ♀, Sauk Co., Spring Green Preserve, N43.19785 W90.05904, 23.vii.2006, (A Wolf) (UWGB); MINNESOTA: 2 ♀, Clay Co., 3mi E & 2mi S of Felton, N47.047 W96.438, blue and yellow pan traps, 21.vii.2006, (RL Andres) (PCYU); CANADA, ONTARIO: 1 ♀, Norfolk Co., Pterophylla Plant Nursery, N42.384 W80.344, malaise trap, 13–22.viii.2006, (PJ Carson) [Barcoded]; 2 ♀, Toronto, York University, N43.775 W79.504, 24.v.2006, (J Gibbs) [Barcoded]; 1 ♀, Toronto, Ulster St. parquette, N43.659 W79.413, x.2006, (J Gibbs); 1 ♀, Haldimane-Norfolk Co., Nixon W Pr, 11.v.1998, H Douglas; 1 ♀, Haldimane-Norfolk Co., Nixon W Pr, 28.v.1998, (H Douglas) (PCYU).

Etymology. This species was named for Marion Durbin Ellis who described a number of *Dialictus* and other bee species.

Type depository. NMNH Cat. No. 26400.

Comments. Specimens that could be attributed to this species extend its range into the great plains of the United States. Additional western species that could be mistaken for *L. ellisiae* may co-occur in this area. Further study will be needed to test species boundaries of the western fauna and to determine the western range limits of *L. ellisiae*.

Lasioglossum (Dialictus) lepidii (Graenicher), comb. n.

(Figures 9A–D)

Halictus (Chloralictus) lepidii Graenicher, 1927: 204. ♀ ♂.
Lasioglossum (Chloralictus) lepidii: Michener, 1951: 1114 (catalogue).
Dialictus tegularis Mitchell, 1960: 423 (synonymy).

Diagnosis. Females of *L. lepidii* can be distinguished by the following combination of characters: head and mesosoma pale to golden green, paraocular area partially obscured by appressed hairs along inner eye margin, distinct microsculpture between punctures of mesoscutum and mesepisternum, and three teeth on the inner hind tibial spur (not including apex of rachis). Females of *L. puteulanum* have the head and mesosoma deep blue. Females of *L. tegulare* have sparse subappressed hairs on the paraocular area which do not obscure the surface. Females of *L. ellisiae* have the integument of the mesoscutum (particularly adjacent to parapsidal lines) and mesepisternum smooth, with at most faint microsculpture which gives these areas a shiny appearance. Females of *L. carlinvillense* have only two teeth on the inner hind tibial spur.

Males of *L. lepidii* are unique among these species in having dense, appressed hairs that obscure large areas of the face including the paraocular area, clypeus and frons. Males of other species have more limited tomentum on the face often only obscuring the paraocular area and never obscuring the frons.

Redescription. Female. Length: 4.3 (4.3–4.9) mm, fore wing length: 3 (3.0–3.2) mm, head length: 1.3 mm, head width: 1.3 (1.3–1.4) mm, n=2

Colouration. Head and metasoma dull metallic blue-green; mandible base brown, apex red: clypeus brown below, golden-green above; supraclypeal area golden-green; lower paraocular area brown-piceous below; antennae brown, apical flagellomeres orange-yellow ventrally; mesoscutum green with hints of gold; tegula brown-piceous, central area ferruginous; legs brown-piceous, fore medio- and distitarsi testaceous, mid and hind medio- and distitarsi ruddy brown; wing venation and pterostigma testaceous-brown; wings faintly dusky; dorsal surface of propodeum blue; metasoma brown-piceous.

Pubescence. Head and mesosoma with sparse, erect, plumose hairs (1–1.5OD), longer on metanotum and ventral pleura (2OD); mid to lower paraocular area with appressed tomentum; posterolateral margin of

pronotum and pronotal lobe with dense, appressed tomentum; dense scopa on hind femur; lateral surface of propodeum with long branched hairs (2OD); acarinarial appressed fan complete; terga with sparse erect hairs (1–2OD), more abundant on ventrolaterally reflexed portions; T3–T5 ventrolaterally reflexed areas with hairs longer (2.5–3OD); T2–T3 basolateral portions and T4 dorsal surface with sparse appressed, plumose hairs; sterna with long, posteriorly oriented hairs emerging from apical half of disc (2–3OD); S1–S4 hairs with long branches.

Surface sculpture. Clypeus glabrate below, upper margin imbricate, punctures moderately coarse below (i=1–2d), fine above (i=d);; supraclypeal area smooth, margins imbricate, punctures fine, irregularly spaced (i=1–1.5d); lower paraocular area imbricate, glabrate below, punctures moderately fine (i≤d); upper paraocular area and frons punctures fine and reticulate; gena lineolate with obscure punctures; mesoscutum and mesoscutellum tessellate; mesoscutum punctures fine, well spaced but not sparse in anteromedial and submedial area (i=1–1.5d), dense on remainder of disc (i≤d); mesoscutellum finely and densely punctate with small impunctate sublateral region; pre-episternum rugulose; mesepisternum finely scabriculous with moderately coarse and deep punctures, punctures finer and more obscure below (i≤d), posterior mesepisternum without evident punctures; hypoepimeral area reticulate; tegula very finely punctate (i=1–2d); metapostnotum medial area with anastomozing rugae; median line not evident; lateral striations more regular, partially extending onto anterior half of lateral slopes; posterior half of lateral smooth and shining; posterior surface of propodeum terga imbricate-tessellate with sparse punctures (i=2d); metasoma coriarious; terga with very fine obscure punctures, more widely spaced on apical half of T1–T4 (i=1.5–2.5d); anteriorly directed surface of T1 and dorsolateral portions anterior to premarginal line impunctate.

Structure. Face slightly broader than long; eyes convergent below (UOD:LOD = 7:5.5); clypeus protruding about one half below lower ocular tangent; distance from antennal sockets to clypeus, less than length of clypeus; distance between antennal sockets almost half distance of socket to inner eye margin; frontal line carinate ending 2–2.5OD from median ocellus; OOC less than IOC (1.5:2.0); eye wider than gena from lateral view; hypostomal carinae parallel; mesoscutum length to width (6.9:8.0); median line of mesoscutum relatively deep anteriorly; ratio of lengths of mesoscutellum: metanotum: dorsal surface of propodeum (2.5:1.5:1.9); tegula elongate with posterior margin projecting posteromedially; oblique propodeal carina weakly evident, not contiguous with lateral carina.

Male. Length: 4.0–4.3 mm, fore wing length: 2.7–3.1 mm, head length: 1.1–1.3 mm, head width: 1.1–1.3 mm, n=2

Colouration. Head and mesosoma dull metallic green except supraclypeal area with bluish tint; pre-episternum and hypoepimeral area golden-green; mesepisternum and propodeum blue; the following parts dark brown-piceous: labrum; mandible except apical half yellow to red; lower clypeus; antenna except F1–F11 bright testaceous-yellow ventrally; tegula except central area ferruginous; legs except medio- and distitarsi of legs testaceous, hind mediotarsi strongly infused with brown; metasoma; wing venation and pterostigma brown; wing subhyaline.

Pubescence. Face below level of eye emargination with dense, white tomentum, less dense on clypeus and lower supraclypeal area; face and gena with sparse, erect hairs (1.5OD); pronotal lobe posteriolateral margin with dense tomentum; remainder of mesosoma with sparse, erect hairs (1–1.5OD), more dense and long on margin of metanotum (2OD); terga ventrolaterally oriented portions with sparse, erect hairs (1.5OD); T1–T4 with laterally oriented setae; sterna with erect hairs, densest on S4–S5.

Surface sculpture. Head and mesosoma smooth and shining; clypeus (i≤d), supraclypeal area (i=1.5d) and lower paraocular area (i=d) punctation fine and deep; upper paraocular area and frons densely reticulate (i≤d); gena shining, imbricate-lineolate with obscure punctures; mesoscutum, mesoscutellum and mesepisternum shiny glabrate; mesoscutum imbricate anteromedially; mesoscutum punctures moderately fine and deep, disc between parapsidal lines well spaced (i=1–2d), closer laterally (i<d) and anterolaterally (i≤0.5d); mesoscutellum punctation dense on margins (i≤0.5d), more widely spaced on disc (i=0.5–2d); pre-episternum densely punctate; hypoepimeral area subreticulate with deep, moderately fine punctures; mesepisternum punctures moderately coarse and deep (i=d); metapostnotum irregularly striate, striations laterad extending

onto lateral slope; lateral surface of propodeum scabriculous with obscure but moderately fine and deep and close punctures (i=1–1.5d); posterior surface of propodeum smoother with distinct punctures (i=1–2d); metasoma faintly coriarious; terga with fine but distinct punctures (i=1–1.5d), apical impressed areas impunctate; anteriorly directed surface of T1 largely impunctate.

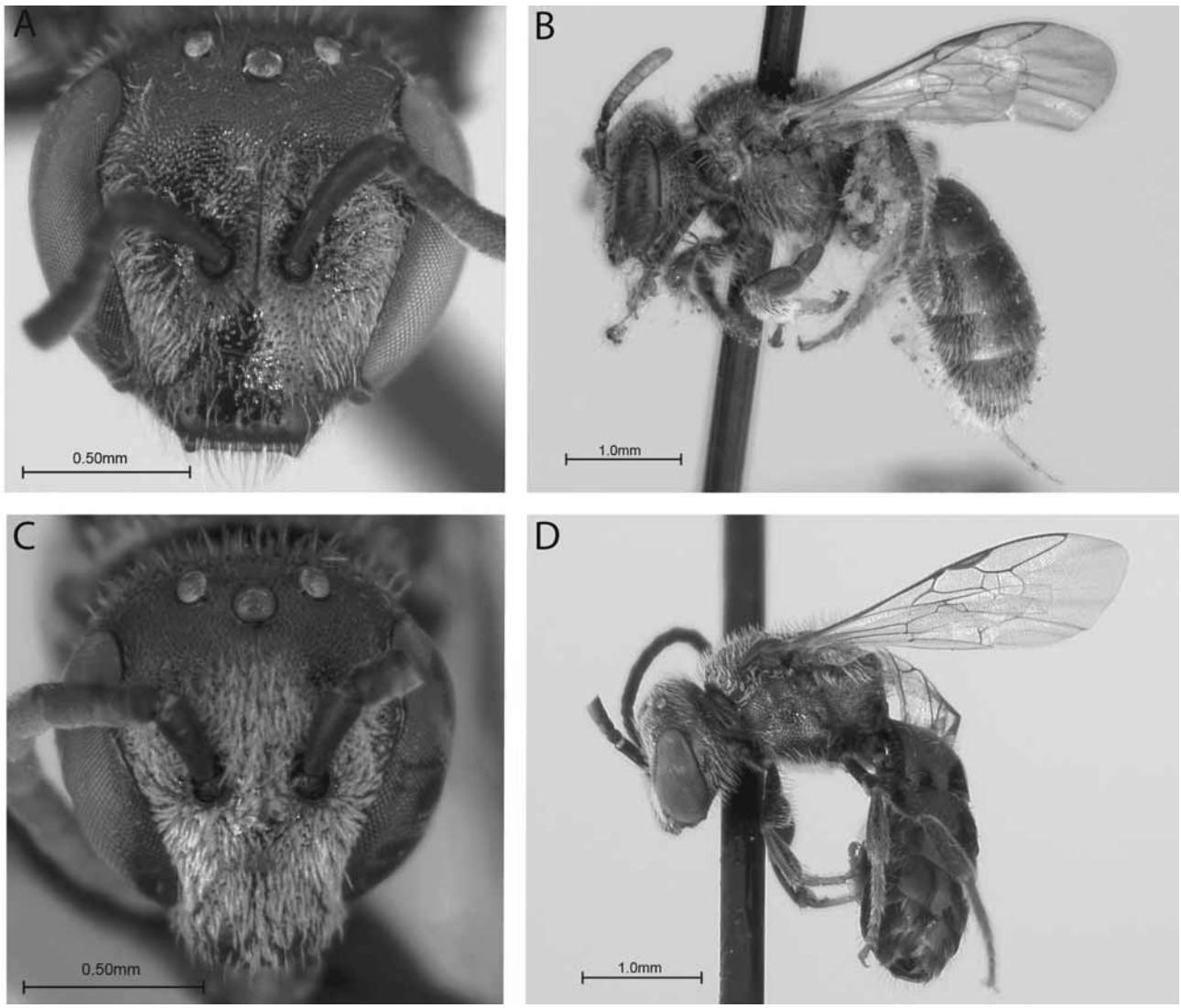

FIGURE 9. *Lasioglossum lepidii* A) face of female; B) lateral habitus of female holotype; C) face of male; D) lateral habitus of male.

Structure. Face as long as broad; eyes convergent below (UOD:LOD = 6.5:4.0); carina of frontal line ending less than 2OD from median ocellus; OOC distinctly less than IOC; eye wider than gena from lateral view; hypostomal carinae parallel; pedicel subequal in length to F1; F2–F10 length 1.5 times breadth, F1 very slightly longer than F2; ratio of lengths of mesoscutellum: metanotum: dorsal surface of propodeum (2.1:1.2:1.5); tegula enlarged, posterior margin not strongly angled; propodeal carina weak on lateral portions of margin between dorsal and posterior surfaces; metasoma narrow relative to female.

Terminalia. As in *L. tegulare* see Fig. 7A–C

Range. Florida.

Specimens examined. USA, FLORIDA, HOLOTYPE ♀, South Miami, 20.iv.1927 (NMNH); 1 ♂, Miami, 4.v.1927, (S Graenicher); 1 ♀, Miami, 22.vi.192?, (S Graenicher); Highlands Co., Highlands Hammock St. Pk., 13.iv.1964, (GC Eickwort); 1 ♀, Islamorada, 12.iv.1966, G Eickwort; (SEMC); 1 ♀ and 2 ♂, Westchester, Miami, 31.viii.2005, (JA Genaro) [Barcoded]; 1 ♀, Westchester, Miami, 31.viii.2005, (JA

Genaro) (PCYU); 3 ♀, Wakulla Co., 2mi N of Mack's Landing, Aalachicola Nat. For. 21.v.1981, (GC Eickwort et al.); 2 ♀, Wakulla Co., Ochlockones River S.P. 21.v.1981, (GC Eickwort et al.); 1 ♂ & 2 ♀, Collier Co., Seminole S.P. 25–26.v.1978, (NF & JB Johnson); 1 ♀, Archbold Biol. Stat., Lk. Placid, Highlands Co., 2.iv.1984, (B Alexander); 3 ♂ & 2 ♀, Monroe Co., Key Largo (city), 22.iii.1987, (Eickwort & Spielholz); 4 ♂ & 3 ♀, Monroe Co., Bahia Honda Key, Bahia Honda St. Rec. Area, 25.iii.1987, (Eickwort & Spielholz); 1 ♂ & 3 ♀, Monroe Co., Key Largo, Pennekamp S.P., 22.iii.1987, (Eickwort & Spielholz); 1 ♂, Monroe Co., Key Largo (east end), 22.iii.1987, (Eickwort & Spielholz); 2 ♂ & 4 ♀, Monroe Co., Long Key, Long Key St. rec. Area, 23.iii.1987, (Eickwort & Spielholz); 1 ♂, Dade Co., Redlands, 21.iii.1987, (Eickwort & Spielholz); 2 ♀, Broward Co., Hallandale Beach, 10.xii.1985, (GC Eickwort); 1 ♀, Leon Co., Tall Timbers Res. Stat., 3mi E Iamonia, 30.iii.1986, (B Alexander); 1 ♀, Pinellas Co., Ft. Desoto. Co. Pk, 1.vi.1978, (NF & JB Johnson); 1 ♂, Wakulla Co., Sopchoppy, 1.iv.1981, (LL Pechuman) (CUIC).

Etymology. No explanation for the name is given in the original description but likely refers to the flowers of *Lepidium virginicum* L. that (among others) the original specimens were collected from.

Type depository. NMNH Cat. No. 41800.

Comments. In some cases, species from Caribbean islands are known to also occur in Florida. Dr. Julio Genaro, the expert on Caribbean Apoidea, is unaware of any species matching the description of this species in the neighbouring islands (J.A. Genaro; personal communication).

***Lasioglossum (Dialictus) puteulanum* Gibbs, sp. n.**
(Figures 10A–D)

Diagnosis. Females of *L. puteulanum* are unique among these species in having the head and mesosoma distinctly blue, whereas other species are typically pale or golden green to at most faintly bluish-green. The head is on average slightly longer (often longer than wide) (ratio = 0.95: 1.10) and the clypeus protrudes giving the face a more triangular appearance than other species. In contrast, females of other species often have the head wider than long (ratio = 0.85: 1.0) with a much rounder appearance of the face.

The males of *L. puteulanum* can be recognized by the following combination of characters: head and mesosoma blue, ventral surface of flagellum pale, appressed hairs of face mostly limited to paraocular areas and only partially obscuring clypeus, and T2–T3 punctures uniformly dense on disc basal to the premarginal line. Males of *L. ellisiae* have the ventral surface of the flagellum dark to ferruginous and T2–T3 punctures dense on basal half but sparse approaching premarginal line. Males of *L. lepidii* have the ventral surface of the flagellum bright yellow and appressed hairs of the face dense, obscuring the majority of the clypeus and frons. The subappressed hairs of the face of *L. tegulare* are usually limited to the lower paraocular area but are more evenly distributed across the face in *L. puteulanum*.

Description. Female. Length: 5.2 (4.3–5.5) mm, fore wing length: 3.6 (2.9–3.6) mm, head length: 1.4 (1.2–1.4) mm, head width: 1.4 (1.2–1.4) mm, n=10

Colouration. Head and mesosoma dull metallic blue except the following: mandible base brown, apex red: clypeus brown brown-piceous below; lower paraocular area below piceous-brown; antennae brown-piceous, flagellum ventral surface paler, F8–F10 orange-yellow ventrally; mesoscutum pale blue; tegula piceous, central area ferruginous; legs brown-piceous, medio- and distitarsi ruddy brown; wing venation and pterostigma testaceous-brown; wings very faintly dusky; metasoma brown-piceous.

Pubescence. Head and mesosoma with sparse, erect, plumose hairs (1–1.5OD), longer on metanotum and ventral pleura (2OD); mid to lower paraocular area with appressed tomentum; posterolateral margin of pronotum and pronotal lobe with dense, appressed tomentum; dense scopa on hind femur; lateral surface of propodeum with long branched hairs (2OD); acarinarial appressed fan complete; terga with sparse, erect hairs (1–2OD), more abundant on ventrolaterally reflexed portions; T3–T5 ventrolaterally reflexed areas with few erect hairs (2.5–3OD); T2–T3 basolateral portions and T4 dorsal surface with sparse appressed, plumose hairs; sterna with long, posteriorly oriented hairs emerging from apical half of disc (2–3OD); S1–S4 hairs

with long branches.

Surface sculpture. Clypeus glabrate below, upper margin imbricate, punctures moderately coarse below (i=1–2d), fine above (i=d); supraclypeal area imbricate, punctures fine, well spaced but not sparse (i=1–2d); lower paraocular imbricate, glabrate below, area punctures moderately coarse and deep (i≤d); upper paraocular area and frons punctures fine and reticulate; gena lineolate with obscure punctures; mesoscutum and mesoscutellum tessellate; mesoscutum punctures fine, well spaced but not sparse in anteromedial and submedial areas (i=1–1.5d), dense on remainder of disc (i≤d); mesoscutellum punctures fine and dense, sublateral region punctures sparser (i=1.5d); pre-episternum rugulose; mesepisternum scabriculous with moderately coarse and deep punctures, punctures finer and more obscure below (i≤d), hypoepimeral area reticulate; tegula very finely and deeply punctate (i=1–2d), central area punctures less dense; metapostnotum submedial surface with incomplete anastomozing rugae, medial line complete, lateral striations more coarse and regular extending onto anterior half of lateral slope, posterior surface of lateral slope imbricate; posterior surface of propodeum terga imbricate-tessellate with sparse punctures (i=2d); metasoma faintly coriarious; terga with very fine, obscure punctures, more widely spaced on apical half of T1–T4 (i=1.5–2d); anteriorly directed surface of T1 and dorsolateral portions anterior to premarginal line impunctate.

Structure. Face as broad as long; eyes convergent below (UOD:LOD = 7.2:6.0); clypeus protruding much more than one half below lower ocular tangent; distance from antennal sockets to clypeus, less than length of clypeus; distance between antennal sockets half distance of socket to inner eye margin; frontal line carinate ending less than 2OD from median ocellus; OOC less than IOC (1.6:2.1); eye wider than gena from lateral view; hypostomal carinae parallel; mesoscutum length to width (7.7:9.0); ratio of lengths of mesoscutellum: metanotum: dorsal surface of propodeum (2.5:1.6:2.1); tegula elongate with posterior margin angled posteriomedially; hind tibial spur pectinate with 4 subapical teeth, smallest tooth often difficult to see; oblique propodeal carina weakly evident, not contiguous with lateral carina.

Male. Length: 4.0–4.6 mm, forewing length: 2.9–3.1 mm, head width: 1.1–1.3 mm, head length: 1.1–1.3 mm, n=4

Colouration. Head and mesosoma deep metallic blue except metepisternum and propodeum with purplish tints; the following parts dark brown-piceous: labrum; mandible except apex red; lower clypeus; antenna except flagellomeres testaceous ventrally; tegula; legs except tarsi light brown; tegula; wing venation and pterostigma brown; wings subhyaline; metasoma brown.

Pubescence. Face with short, appressed hairs below level of eye emargination, dense only on lower paraocular area; head and mesosoma with sparse, erect hairs, longest on gena and metanotum (1–2OD); terga ventrolaterally oriented portions with sparse, erect hairs (1–1.5OD); T1–T4 with laterally oriented setae; sterna with erect hairs, densest on S4–S5.

Surface sculpture. Face weakly imbricate; clypeus punctation fine and deep (i≤d); supraclypeal area punctation shallower (i=1–1.5d); paraocular area punctation coarser; frons reticulate; gena shining, imbricate-lineolate with obscure punctures; mesoscutum, mesoscutellum and mesepisternum glabrate and shining, mesoscutum imbricate anteromedially; mesoscutum punctures moderately fine and deep, shallower anteromedially (i≤d), submedially well spaced but not sparse (i=1d), close laterally (i<d) and anterolaterally (i≤d); mesoscutellum well spaced on medial line (i=1.5d) with bare submedial area; pre-episternum rugulose; mesepisternal punctures moderately coarse and deep (i≤d); dorsal surface of propodeum with rugae not reaching margin; posterior surface of propodeum shiny-imbricate with fine, sparse punctures (i=2–4d); terga smooth, very faintly coriarious; terga finely punctate (i=1.5–2d) except apically impressed areas impunctate; anteriorly directed surface of T1 largely impunctate.

Structure. Face longer than broad; eyes convergent below (UOD:LOD = 6.3:4.5); clypeus protruding slightly more than one half below lower ocular tangent; antennal sockets slightly nearer to each other than to inner eye margin; carina of frontal line ending more than 2OD from median ocellus; OOC slightly less than IOC (1.5:2.0); eye wider than gena from lateral view; hypostomal carinae parallel; pedicel subequal in length to F1; F2–F10 length 1.5 times breadth, F11 longer; ratio of lengths of mesoscutellum: metanotum: dorsal surface of propodeum (2:1:1.1:1.8); tegula enlarged, posterior margin strongly angled; propodeal carina not

evident between dorsal and posterior surfaces; metasoma narrow relative to female.

Terminalia. As in *L. tegulare* see Fig. 7A–C.

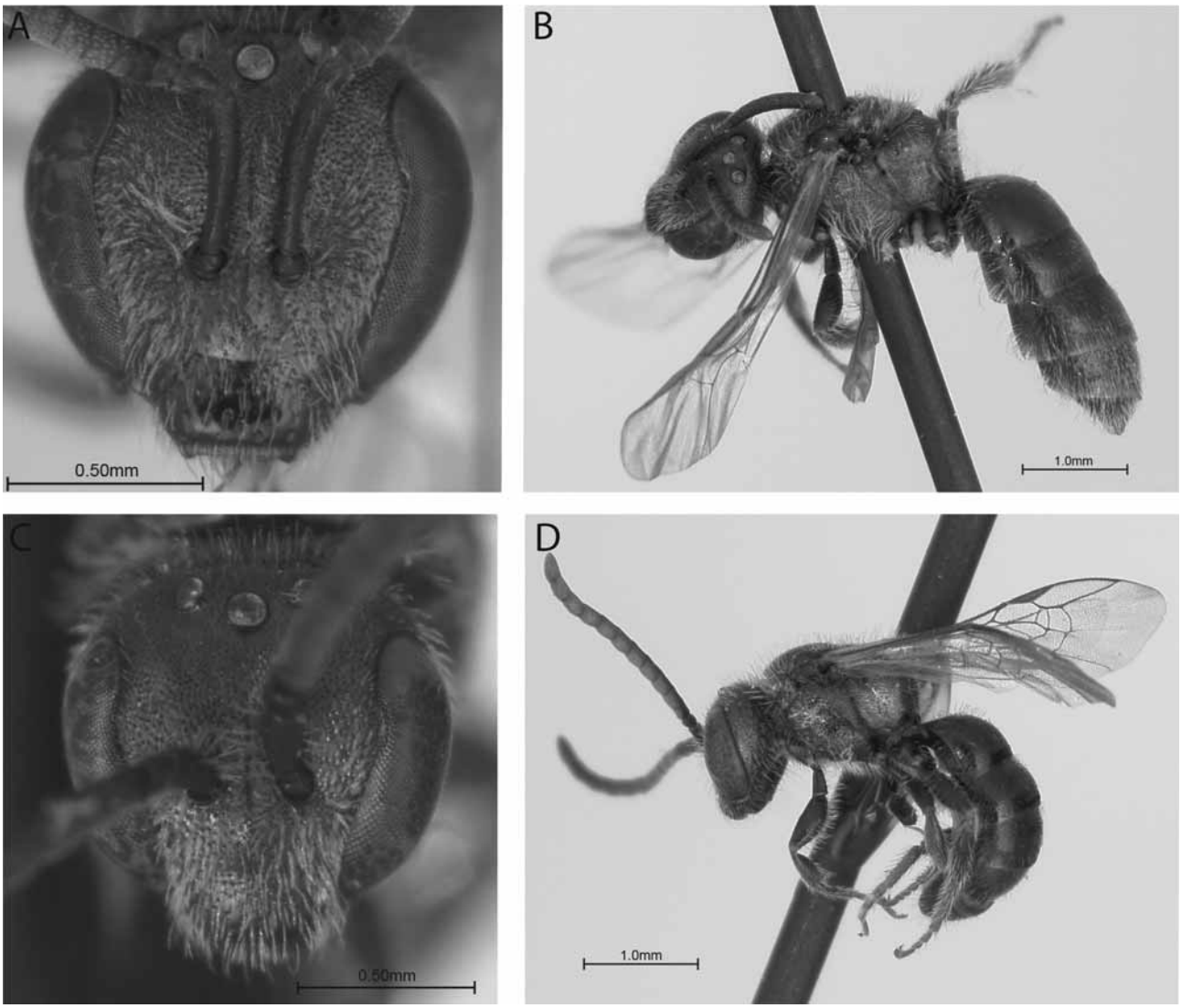

FIGURE 10. *Lasioglossum puteulanum* A) face of female holotype; B) lateral habitus of female holotype; C) face of male; D) lateral habitus of male.

Range. Coastal plain of North Carolina to Florida

Specimens examined. USA, FLORIDA, HOLOTYPE ♀, Palm Beach Co., N26.34889 W80.2756, 25.i.2005, (SW Droege) [Barcoded]; 1 ♀, collected with holotype [Barcoded]; 1 ♀, Miami, Westchester, 31.viii.2006, (JA Genaro) [Barcoded]; 1 ♀, Hendry Co., N26.3121 W81.2354, 27.i.2005, (SW Droege) [Barcoded]; 1 ♂, Broward Co., N26.30345 W80.20219, 25.i.2005, S.W. Droege [Barcoded]; 3 ♀ & 2 ♂, Broward Co., N26.107 W80.264, 27.i.2005, (SW Droege) [Barcoded]; 13 ♀, Martin Co., N27.083 W80.1442, 4.vi.2007, (SW Droege); 8 ♀, Martin Co., N27.1008 W80.152, 4.vi.2007, (SW Droege); 2 ♂, Martin Co., N27.081 W80.1416, 4.vi.2007, (SW Droege); (PCYU); 1 ♀, Inverness, (C Robertson) (INHS); 3 ♂, Gainesville, 6.v.1955, (HE & MA Evans); 1 ♂, Brighton, 19.iv.1937, (JC Bradley); 1 ♂, Crescent City, 1–3.v.1955, (HE & MA Evans); 4 ♂, Wakulla Co., 2mi N of Mack's Landing, Apalachicola Nat. For. 21.v.1981, (GC Eickwort et al.); 1 ♀, Wakulla Co., Ochlockones River S.P. 21.v.1981, (GC Eickwort et al.); 1 ♂ & 1 ♀, Collier Co., Seminole S.P. 25–26.v.1978, NF&JB Johnson; 1 ♀, Archbold Biol. Stat., Lk. Placid, Highlands Co., 2.iv.1984, (B Alexander); 3 ♂, Monroe Co., Key Largo (city), 22.iii.1987, (Eickwort & Spielholz); 1 ♀, Monroe Co., Key Largo, Pennekamp S.P., 22.iii.1987, (Eickwort & Spielholz); 1 ♂, Monroe

Co., Big Pine Key, Key Deer NW Ref., 25.iii.1987, (Eickwort & Spielholz); 1 ♂ & 4 ♀, Broward Co., Broward Beach S.P., Fort Lauderdale, 9.xii.1985, (GC Eickwort); 15 ♀, Broward Co., Hallandale Beach, 10.xii.1985, (GC Eickwort); 1 ♀, Leon Co., Tall Timbers Res. Stat. 3mi W Iamonia, 30.iii.1986, (B Alexander); 1 ♀, Dade Co., Matherson Hammock Co. Pk. 20–21.iii.1987, (Eickwort & Spielholz) (CUIC); 3 ♂ & 1 ♀, Highlands Co., Hghlds., Hammock S.P., 14.iv.1964, (GC Eickwort); 1 ♀, Liberty Co., Torreya S.P., 6.iv.1964, (GC Eickwort); 2 ♀, Franklin Co., coast 10mi S of Panacea, 7.iv.1964, (GC Eickwort); 7 ♀, Broward Co., Hollywood, 13.xii.1985, (CD Michener); 1 ♂, Collins, Seminole S.P., 13.iv.1986, (GC Eickwort) (SEMC); GEORGIA, 1 ♂, Bainbridge, vii.1909; 2 ♀, Coquitt Co., Reed Bingham S.P., 22.v.1981, (GC Eickwort et al.); 1 ♀, Colquitt Co., Reed Bingham S.P., 23.v.1981, (GC Eickwort et al.); 1 ♀, Colquitt Co., Murphy, 5.iv.1981, (LL Pechuman) (CUIC); SOUTH CAROLINA, 1 ♀, C. Sandhills NWR, N34.547 W80.177, 6–7.ix.2005, (SW Droege) [Barcoded]; 1 ♂, C. Sandhills NWR, N34.56 W80.256, 6.ix.2006, (SW Droege); 2 ♀, Chesterfield Co., N34.623 W80.19, 18–19.v.2006, (SW Droege); 1 ♀, Chesterfield Co., N34.637 W80.176, (SW Droege) [Barcoded] (PCYU); NORTH CAROLINA, 1 ♀, Moore Co., N35.284 W79.314, 19.v.2006, (SW Droege) [Barcoded] (PCYU); 1 ♂, Raleigh, 16.vii.1948, (MW Wing); 1 ♂, Wake Co., 10.vii.1949, (MW Wing) (CUIC); 1 ♂, TENNESSEE, 4.vi.1918 (CUIC).

Type depository. PCYU

Etymology. The specific epithet refers to the blue colouration of the head and mesosoma.

Comments. This species may be extremely difficult to differentiate from *L. tegulare* in areas where their ranges overlap. The blue colouration characteristic of this species should be sufficient to identify most individuals; however, colouration is sometimes variable in *Dialictus* and can be affected by preservation methods. Species identification of questionable specimens is possible using DNA barcodes.

***Lasioglossum (Dialictus) carlinvillense* Gibbs, sp. n.**
(Figures 11A–D)

Diagnosis. This species is smaller in body size than other species. The inner hind tibial spur of the female is unique in having only two subapical teeth as opposed to the three or four teeth in the other species. The male is unknown.

Description. Female. Length: 4.3 (4.3–4.5) mm, fore wing length: 2.7 (2.7) mm, head width: 1.2 (1.2–1.3) mm, head length: 1.2 (1.2) mm, n=3

Colouration. Head and mesosoma dull metallic bluish-green except the following: labrum brown-piceous, mandible base brown, apex red; clypeus brown, golden above; supraclypeal area bronzed above; antennae brown-piceous except ventral surface of flagellomeres brown, F8–F10 testaceous ventrally; gena blue; mesoscutum green to golden green; tegula piceous with central area ferruginous; legs brown-piceous, medio- and distitarsi ferruginous; wing venation and pterostigma testaceous; wings faintly dusky; propodeum darker with blue reflections; metasoma piceous-brown; apical portions of terga and sterna light brown.

Pubescence. Lower paraocular area with sparse, subappressed, plumose hairs; head and mesosoma with sparse, erect, plumose hairs (1–1.5OD), longer on metanotum and ventral pleura (2OD); posterolateral margin of pronotum and pronotal lobe with dense, appressed tomentum; dense scopa on hind femur; propodeal lateral surface hairs (2OD) with long branches; acarinarial appressed fan complete; terga with sparse, erect hairs (1–2OD), more abundant on ventrolaterally reflexed portions; T3–T5 ventrolaterally reflexed areas with few erect hairs (2.5–3OD); T2–T3 basolateral portions and T4 dorsal surface with sparse appressed, plumose hairs; sterna with long, posteriorly oriented hairs emerging from apical half of disc (2–3OD); S1–S4 hairs with long branches.

Surface sculpture. Clypeus glabrate except upper margin imbricate, punctures moderately coarse (i=1–2d), fine above (i=d); supraclypeal area smooth and shining below, imbricate above, punctures fine (i=1–1.5d); lower paraocular area imbricate, glabrate below, punctures moderately coarse and deep (i≤d); upper paraocular area and frons punctures fine and shallow becoming reticulate; gena lineolate, punctures fine

and obscure; mesoscutum and mesoscutellum tessellate between fine punctures; mesoscutum punctures well spaced but not sparse in anteromedial and submedial areas (i=1–1.5d), dense on remainder of disc (i≤d); mesoscutellum densely punctate medially and along margins with sublateral area less densely punctate (i=1–1.5d); pre-episternum rugulose; mesepisternum scabriculous, closely and coarsely punctate (i≤d), punctures finer and more obscure below, hypoepimeral area reticulate; tegula finely punctate (i=1–1.5d), central area more sparsely punctate; metapostnotum with irregular striations, median striation reaching margin, lateral striations extending onto anterior half of lateral slope; posterior half of lateral slope dull due to microsculpture; lateral surface of propodeum tessellate with sparse punctures (i≥2d); metasoma coriarious with fine but deep punctures, evenly spaced over T1–T4 (i=1.5d) except less dense on apically impressed area; anteriorly directed surface of T1 and dorsolateral portions anterior to premarginal line impunctate.

Structure. Face broader than long to subequal; eyes convergent below (UOD:LOD = 1.2:1); clypeus protruding almost one half below lower ocular tangent; distance from antennal sockets to clypeus, shorter than clypeus; antennal sockets distinctly nearer to each other than to inner eye margin; frontal line carinate ending 2OD from median ocellus; OOC less than IOC (1.0:1.7); eye wider than gena from lateral view; hypostomal carinae parallel; mesoscutum length to width (1.0:1.3); ratio of lengths of mesoscutellum: metanotum: dorsal surface of propodeum (1.8:1.0:1.4); tegula elongate with posterior margin angled posteromedially; inner hind tibial spur pectinate with two subapical teeth; oblique propodeal carina weakly evident, not contiguous with lateral carina.

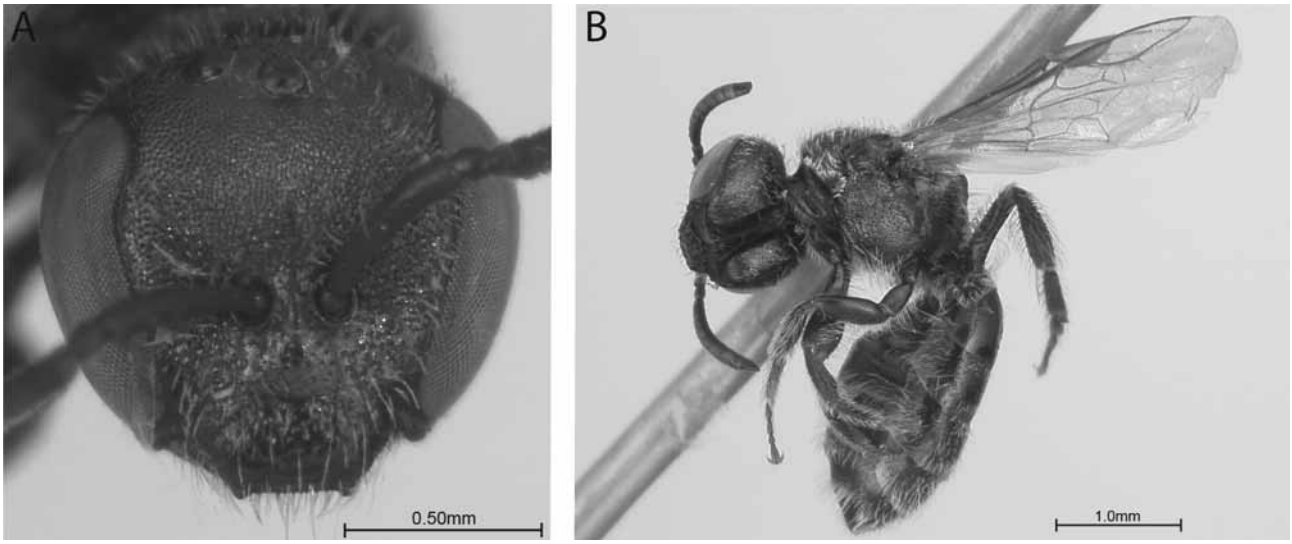

FIGURE 11. *Lasioglossum carlinvillense* A) face of female holotype; B) lateral habitus of female holotype.

Range. South-central Illinois

Specimens examined. USA, ILLINOIS: HOLOTYPE ♀, Macoupin Co., E of Carlinville, N39.2787 W89.7961, 25.vi.2006, (J Gibbs & C Sheffield) [Barcoded]; 1 ♀, Carlinville, N39.2787, W89.8898, 24.vi.2006, (J Gibbs) [Barcoded]; 1 ♀, Litchfield, N39.1484 W89.667, 25.vi.2006, (C Sheffield) [Barcoded] (PCYU); 1 ♀, Dubois, 8.viii.1917 (INHS)

Type depository. PCYU

Etymology. The specific epithet refers to the type locality and the famous collection site of Charles Robertson.

Comments. The male of this species is unknown. The known range of this species is very small. It is possible that this is a prairie species found at the eastern edge of its range.

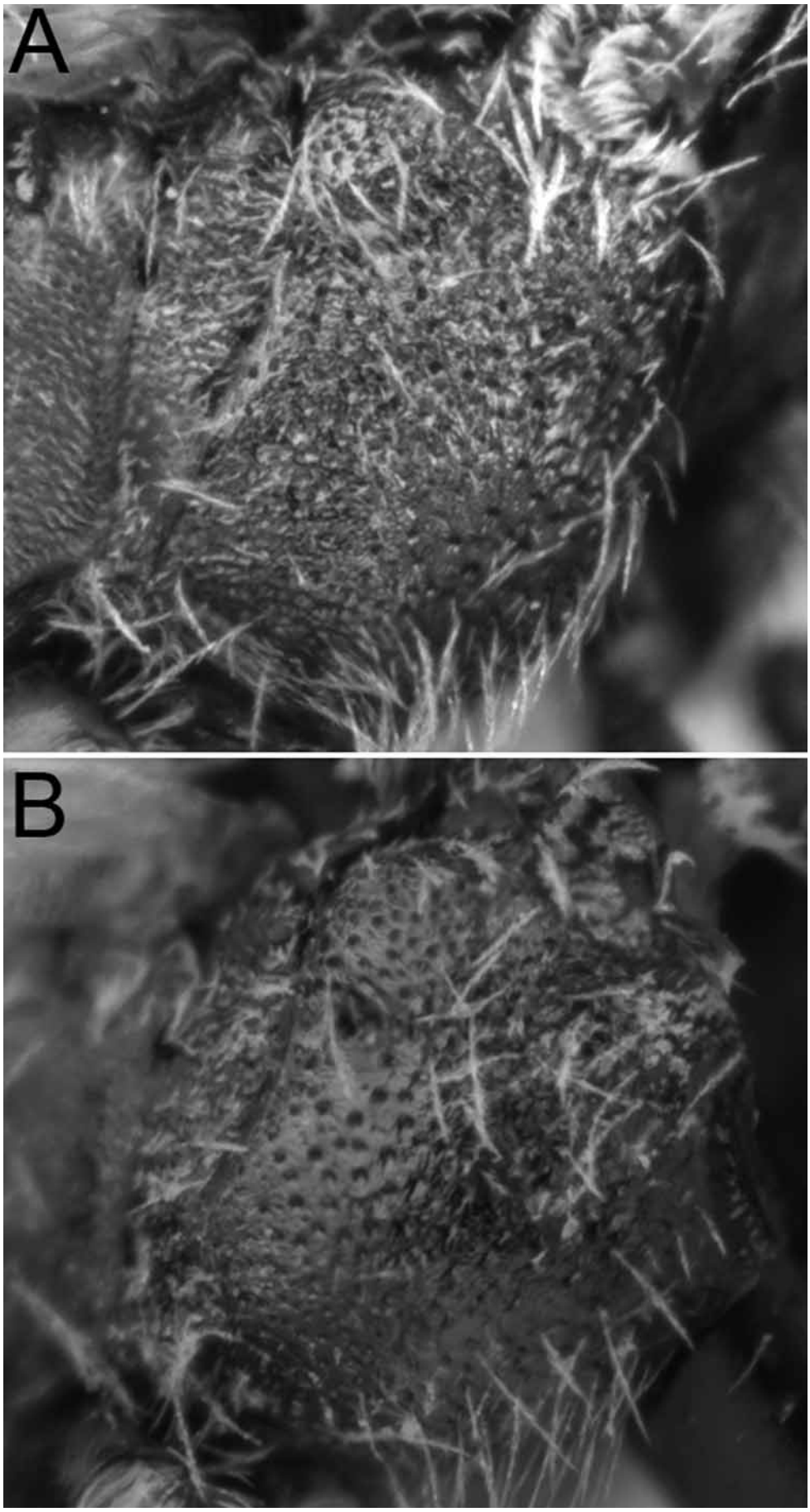

FIGURE 12. Mesepisternum of female showing microsculpture of (A) *L. tegulare* and (B) *L. ellisiae*.

FIGURE 13. Dorsal surface of the propodeum showing surface sculpture of the metapostnotum in (A) *L. lepidii* and (B) *L. tegulare*.

Key to eastern species

The following keys to species can be substituted for *L. tegulare* in couplet 6 for females and couplet 4 for males in Mitchell's (1960) key to *Dialictus*.

Key to females.

1 Integument of head and mesosoma with distinct metallic blue reflections; head slightly longer than broad to subequal (ratio = 0.95: 1.10) (Fig. 10A); clypeus protruding two thirds below suborbital tangent (Southeastern USA) ..... *L. puteulanum*
- Integument of head and mesosoma with metallic green reflections, if blue reflections present then usually restricted to pleura and propodeum; head usually broader than long (ratio = 0.85: 1.0) (*e.g.* Fig. 6A); clypeus one half below suborbital tangent 2
2 Surface of mesepisternum (Fig. 12A) and mesoscutum adjacent to parapsidal lines smooth and shining, only faint microsculpture between punctures (Northeastern USA and Southern Ontario)..... *L. ellisiae*
- Surface of mesepisternum (Fig. 12B) and mesoscutum dull and roughened due to microsculpture between punctures 3
3 Inner hind tibial spur with only two subapical teeth (Illinois)..... *L. carlinvillense*
- Inner hind tibial spur with three or four subapical teeth..... 4
4 Paraocular area with appressed hair dense, obscuring surface along inner margin of eye (Fig. 9A); metapostnotum with anastomozing rugae, medial striation not distinct (Fig. 13A) (Florida) ..... *L. lepidii*
- Paraocular area with appressed hairs sparse not obscuring surface (Fig. 6A); metapostnotum striate (Fig. 13B), if submedial striations anastomozing then long and straight medial striation distinctly visible (Northeastern USA and Southern Ontario)..... *L. tegulare*

Key to males.

1 Ventral surface of antenna dark brown to ferruginous; punctures on T2–T3 dense on basal portion of disc becoming extremely sparse and indistinct towards the impunctate apically impressed area (Fig. 14A) (Northeastern USA and Southern Ontario)..... *L. ellisiae*
- Ventral surface of antenna somewhat dull to bright yellow; punctures on T2–T3 uniformly dense from margin to impunctate apically impressed region (Fig. 14B) 2
2 Integument of face (including paraocular area, frons and majority of clypeus) obscured by white tomentum (Fig. 9C); flagellomeres bright yellow on ventral surface; antennal sockets nearer to inner eye margin than each other (ratio = 0.7); pre-episternum punctate-reticulate (Florida)..... *L. lepidii*
- Integument of face less obscured by tomentum primarily on paraocular area (never extending onto frons) (Figs. 6C, 10C); flagellomeres yellowish-brown to yellow ventrally; distance between antennal sockets and inner margin of eye subequal to distance between eye sockets (ratio = 0.9–1.0); pre-episternum rugulose..... 3
3 Head and mesosoma green to bluish; facial tomentum mostly limited to paraocular areas (Southern Ontario and Eastern USA north of Florida)..... *L. tegulare*
- Head and mesosoma blue; facial tomentum more evenly distributed on face (Southeastern USA) ..... *L. puteulanum*

Discussion

DNA barcodes are increasingly becoming a standard tool used by taxonomists (*e.g.* Van Nieukerken 2007; Pyle *et al*. 2008; Gibbs *in press*; Gibbs & Sheffield *in press*) but the method continues to be criticized in the literature (Rubinoff *et al*, 2007; Wheeler 2008). Some potential drawbacks were dismissed above for the data presented herein. The remaining criticisms of relevance to the present study are primarily i) DNA barcoding data are presented in a phenetic manner using NJ trees, ii) a short sequence of mtDNA is insufficient for the detection of new species and iii) species delimitation using % sequence divergence is arbitrary. I address these issues in turn.

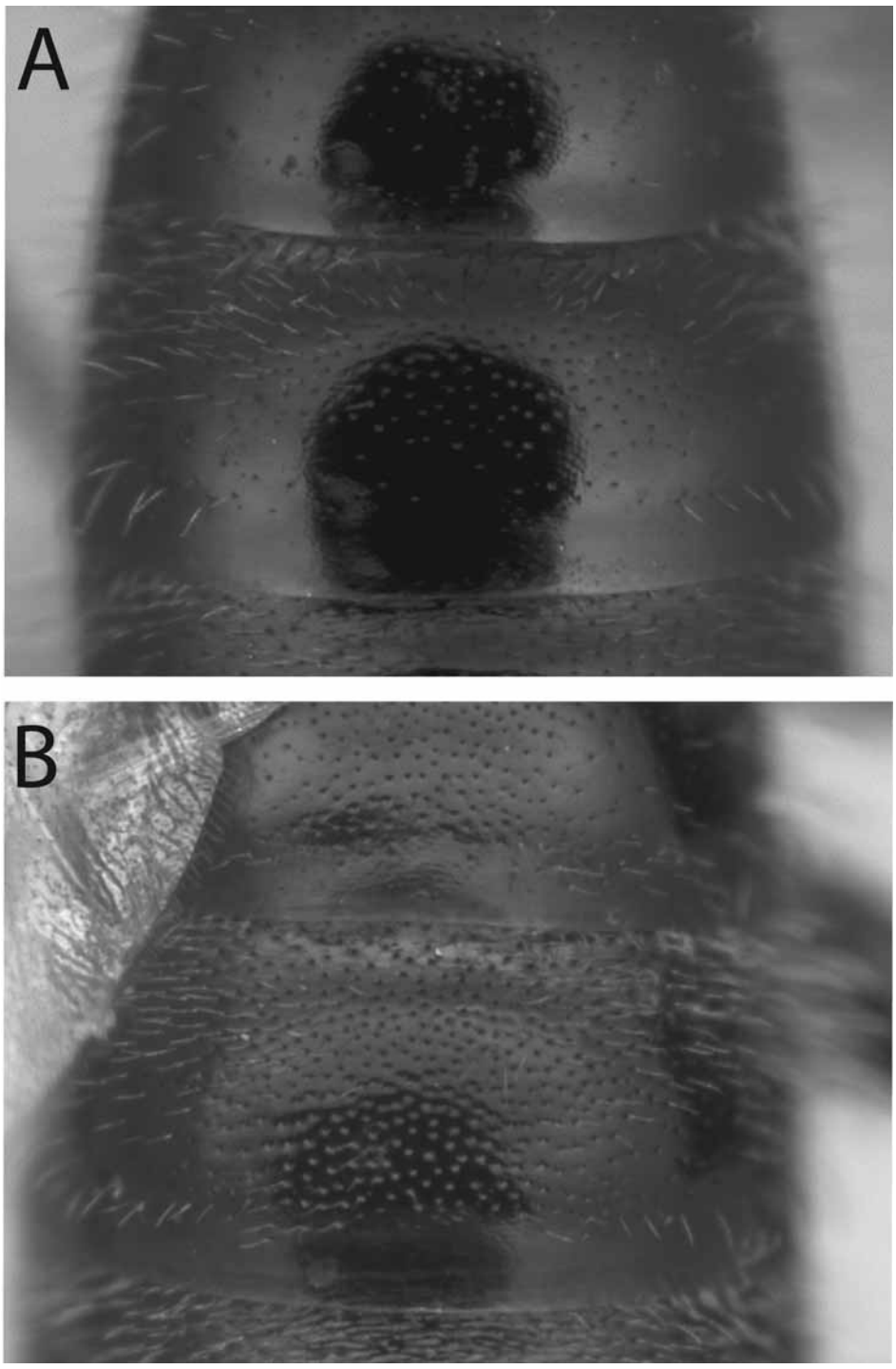

FIGURE 14. Dorsal views of male T2 showing punctation in (A) *L. ellisiae* and (B) *L. puteulanum*.

i) The use of a neighbour-joining algorithm to provide specimen identification ignores several decades of study that demonstrate the superiority of phylogenetic over phenetic philosophical criteria (Farris 1977, 1983; Hull 1988). Nevertheless, the phenetic approach is seemingly necessitated by the rapidity of NJ algorithms combined with the near impossibility of performing a rigorous phylogenetic analysis with the large number of short sequences commonly generated in DNA barcoding studies. Here I have demonstrated that rigorous phylogenetic analysis can be performed to permit diagnosis of cryptic species as both monophyletic and diagnosable entities. The latter based upon discrete characters (nucleotide substitutions), which are an improvement over phenetic distances (DeSalle *et al*. 2005; DeSalle 2005). Consequently, the rigour of

cladistic methodology can be applied to DNA barcode data when the question being addressed is of manageable size. The application of more rigorous phylogenetic analyses to DNA barcode data is becoming more frequent in the literature (Skevington *et al.* 2007; Hastings *et al.* 2008; Witt *et al.* 2008).

ii) It has been known for a long time that there are numerous species that cannot be differentiated solely on the basis of traditional morphological analysis (see Avise 2004). An example from the bees is *Halictus ligatus*, an abundant and easily recognised "species" until demonstrated to be two well differentiated species using allozymes and DNA sequence data (Carman & Packer 1997; Danforth et al. 1998, 1999). One of these cryptic species, *H. poeyi*, is found to the southeast of the Appalachian mountains, the other, *H. ligatus*, to the northwest and they are sympatric in the Piedmont region where the very high differentiation found at nuclear loci as well as mitochondrial sequence divergence is entirely maintained (Packer 1999). Despite large levels of genetic differentiation, the two species have remained resistant to morphological diagnosis. Even morphometric analysis of wing venation and male genitalia has failed to result in discrimination (Packer, unpublished data). In the results for the *L. (D.) tegulare* species complex presented here, morphological diagnosis is possible for all of the species found to be differentiated genetically. Morphological differences between these species could be (and for a long time was) mistaken for intraspecific variation without an independent dataset to test species limits (DeSalle *et al.* 2005). Consequently, a short sequence of mtDNA is useful for species discovery (*e.g.* Hebert *et al.* 2004) and can provide data of use for integrative taxonomy (Smith *et al*. 2007; Miller 2007; Padial & De La Riva 2007).

iii) Sequence divergence is an easy metric to measure but not necessarily an easy variable to interpret. While many cases of completely non-overlapping % differences between intraspecific and interspecific divergences are known, the mere fact of evolution will result in numerous instances of overlap between them (*e.g.* Meyer & Paulay 2005). Precisely the same is true of morphological analysis: usually there are sufficient differences between sister species to permit identification (though in many insects this remains possible for only one sex) but there are many cases in which differentiation is possible only through additional information, such as DNA sequence or ecological data (*e.g.* Smith *et al.* 2008). While there are rare cases of zero DNA barcode differentiation, there are many examples of zero, or almost zero, morphological differentiation between diagnosable species (Avise 2004; see also Packer *et al. in press*). In this study, I used DNA barcode data to discover genetically discrete groups of individuals for which I could then find discrete morphological differences. The level of morphological differentiation among the newly discovered or resurrected species is sometimes meagre. Nonetheless, such limited amounts of differentiation are commonly found among species in the Halictidae (Wheeler 1928; Michener 2007), as well as in many other insects (Hebert *et al*. 2004; Smith *et al*. 2006, 2008) and as noted above, genetically well-differentiated species are sometimes morphologically indistinguishable.

The issue of arbitrary levels of differentiation for the separation of organisms at the species level is just as much a problem for traditional morphological approaches as it is for DNA barcoding. The only difference is that the quantitative aspect of DNA barcoding makes the arbitrariness more obvious. Nonetheless, when individuals fall into clearly discrete clusters on an NJ tree with interspecific differentiation clearly greater than intraspecific differentiation and these clusters are robust to phylogenetic analysis, it is not unreasonable to refer to the clusters as representing species. In the cases presented here, morphological differences discriminate clades that are also diagnosable with the mtDNA sequence differences and are of similar magnitude to that found among uncontroversial species elsewhere among the bees.

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Literature cited

Ascher, J. S. *et al.* (2008) Apoidea species guide. Available from http://www.discoverlife.org/mp/20q?guide=Apoidea_species (accessed 31 December 2008)

Avise, J.C. (2000) *Phylogeography: the History and Formation of Species*. Harvard University Press, Boston, Massachusetts, viii + 447 pp.

Avise, J.C. (2004) *Molecular Markers, Natural History and Evolution*. Springer, New York, New York, 684 pp.

Brady, S.G., Sipes, S., Pearson A. & Danforth, B.N. (2006) Recent and simultaneous origins of eusociality in halictid bees. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 273, 1643–1649.

Buchmann, S.L. & Nabhan, G.P. (1996) *The Forgotten Pollinators*. Island Press, Washington, DC, xx + 292 pp.

Campbell, J.W., Hanula, J.L. & Waldrop, T.A. (2007) Effects of prescribed fire and fire surrogates on floral visiting insects of the blue ridge province in North Carolina. *Biological Conservation*, 134, 393–404.

Carman, G.M. & Packer, L. (1997) A cryptic species allied to *Halictus ligatu*s Say (Hymenoptera: Halictidae) detected by allozyme electrophoresis. *Journal of the Kansas Entomological Society*, 69,168–176.

Danforth, B.N., Mitchell, P.L. & Packer L. (1998) Mitochondrial DNA differentiation between two cryptic *Halictus* (Hymenoptera : Halictidae) species. *Annals of the Entomological Society of America*, 91, 387–391.

Danforth, B.N., Sauquet, H. & Packer, L. (1999) Phylogeny of the bee genus *Halictus* (Hymenoptera; Halictidae) based on parsimony and likelihood analyses of nuclear EF-1 alpha sequence data. *Molecular phylogenetics and Evolution*, 13, 605–618.

Danforth, B.N., Conway, L. & Ji, S.Q. (2003) Phylogeny of eusocial *Lasioglossum* reveals multiple losses of eusociality within a primitively eusocial clade of bees (Hymenoptera : Halictidae). *Systematic Biology*, 52, 23–36.

Dayrat, B. (2005) Towards integrative taxonomy. *Biological Journal of the Linnean Society*, 85, 407–415.

DeSalle, R. (2005) Species discovery versus species identification in DNA barcoding efforts: response to Rubinoff. *Conservation Biology*, 20, 1545–1547.

DeSalle, R., Egan, M.G. & Siddall, M. (2005) The unholy trinity: taxonomy, species delimitation, and DNA barcoding. *Philosophical Transactions of the Royal Society, London B-Biological Science*, 360, 1905–1916.

Eickwort, G.C. (1988) Distribution patterns and biology of West Indian sweat bees (Hymenoptera: Halictidae). *In*: Liebherr, J.K. (Ed.), *Zoogeography of Caribbean Insects*. Cornell University Press, Ithaca, pp. 231–253.

Farris, J.S. (1977) On the phenetic approach to vertebrate classification. *In*: Hecht, M.K., Goody, P., & Hecht, B.M. (Eds.), *Major Patterns in Vertebrate Evolution*. Plenum, New York, pp. 823–850.

Farris, J.S. (1983) The logical basis of phylogenetic analysis. *In*: Platnick, N.I. & Funk, V.A. (Eds.), *Advances in Cladistics 2*. Columbia University Press, New York, pp. 7–36.

Folmer O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Funk, D.J. & Omland, K.E. (2003) Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution and Systematics*, 34, 397–423.

Gaston, K. J. & O'Neill, M.A. (2004) Automated species identification: why not? *Philosophical Transactions of the Royal Society of London Series B-Biological Science*, 359, 655–667.

Gibbs, J. (*in press*) An aberrant bee of the species *Lasioglossum (Dialictus) disparile* (Cresson) with brief taxonomic notes on the species. *Journal of the Kansas Entomological Society.*

Gibbs, J. & Packer, L. (2006) Revision and phylogenetic analysis of *Chilicola sensu stricto* (Hymenoptera: Colletidae) with the description of a new species. *Zootaxa*, 1355, 1–37.

Gibbs, J. & Sheffield, C.S. (*in press*) Rapid range expansion of the wool-carder bee, *Anthidium manicatum* (Linnaeus) (Hymenoptera: Megachilidae), in North America. *Journal of the Kansas Entomological Society.*

Giles, V. & Ascher, J.S. (2006) A survey of the bees of the Black Rock Forest Preserve, New York (Hymenoptera: Apoidea). *Journal of Hymenoptera Research*, 15, 208–231.

Goloboff, P.A., Farris, J.S. & Nixon, K. (2003a) T.N.T.: Tree analysis using new technology. Program and documentation available from the authors and at www.zmuc.dk/public/phylogeny (last accessed 31 December 2008)

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J. & Szumik, C.A. (2003b) Improvements to resampling measures of group support. *Cladistics*, 19, 324–332.
Graenicher, S. (1927) Bees of the genus *Halictus* from Miami, Florida. *Psyche*, 34, 203– 208.
Grixti, J.C. & Packer, L. (2006) Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. *The Canadian Entomologist*, 138, 147–164.
Hastings, J.M., Schultheis, P.J., Whitson, M.K., Holliday, C.W., Coelho, J.R. & Mendell, A.M. (2008) DNA barcoding of New World cicada killers (Hymenoptera: Crabronidae). *Zootaxa*, 1713, 27–28.
Harris, R.A. (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology*, 28, 1–31.
Hebert, P.D.N., Cywinska, A., Ball, S.L., & deWaard, J.R. (2003a) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 313–321.
Hebert P.D.N., Ratnasingham S., & deWaard, J.R. (2003b) Barcoding animal life: cytochrome *c* oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London Series B-Biological Science*, 270, S96–S99.
Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H. & Hallwachs, W. (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator. Proceedings of the National Academy of Sciences of the United States of America*, 101, 14812–14817.
Hillis, D.M. (1987) Molecular versus morphological approaches to systematics. *Annual Review of Ecology and Systematics*, 18, 23–42.
Hillis, D.M. & Wiens, J.J. (2000) Molecules versus morphology in systematics: conflicts, artifacts, and misconceptions. *In*: Wiens, J.J. (Ed.) *Phylogenetic Analysis of Morphological Data*. Smithsonian Institution Press, Washington, D.C., pp. 1–19.
Huelsenbeck, J.P. & Ronquist, F. (2001) MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics*, 17, 754–755.
Hull, D.L. (1988) Science as a Process. University of Chicago Press, Chicago, Illinois, xiii + 586 pp.
Janjic, J. & Packer, L. (2001) New descriptions of *Halictus* (*Seladonia*) from the New World (Hymenoptera: Halictidae). *Journal of Hymenoptera Research*, 10, 55–75.
Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111–120.
Klein, A.M., Vaissière, B., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen C. & Tscharntke, T. (2007) Importance of crop pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London Series B Biological Sciences*, 274, 303–313.
Knerer, G. & Atwood, C.E. (1962) An annotated checklist of the non-parasitic Halictidae (Hymenoptera) of Ontario. *Proceedings of the Entomological Society of Ontario*, 92, 160–176,
Knerer, G. & Atwood, C.E. (1966) Additional descriptions in the genus *Dialictus* Robertson (Hymenoptera: Halictidae). *The Canadian Entomologist*, 98, 881–887.
MacKay, P.A. & Knerer, G. (1979) Seasonal occurrence and abundance in a community of wild bees from an old field habitat in southern Ontario. *The Canadian Entomologist*, 111, 367–376.
Meyer, C.P. & Paulay, G. (2005) DNA barcoding: error rates based on comprehensive sampling. *PLoS Biology*, 3, 2229–2238.
Michener, C.D. (1951) Superfamily Apoidea. *In:* Muesebeck, C.F., Krombein, K.V. & Townes, H.K. (Eds.), *Hymenoptera of America North of Mexico.* USDA Agriculture Monograph No. 2. United States Government Printing Office, Washington, D.C. pp. 1043–1255.
Michener, C.D. (1974) *The Social Behavior of the Bees*. Belknap Press, Cambridge, Massachusetts, xii + 404 pp.
Michener, C.D. (2007) *The Bees of the World, 2nd Ed.* Johns Hopkins University Press, Baltimore, Maryland, xvi + 953 pp.
Miller, S.E. (2007) DNA barcoding and the renaissance of taxonomy. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 4775–4776.
Mitchell, T.B. (1960) Bees of the Eastern United States: volume I. *N.C. Agricultural Experimental Station Technical Bulletin*, 141, 1–538.
Moure, J.S. & Hurd, P.D., Jr. (1987) *An Annotated Catalog of the Halictid Bees of the Western Hemisphere (Hymenoptera: Halictidae)*. Smithsonian Institution Press, Washington, D.C, vii + 405 pp.
Murao, R. & Tadauchi, O. (2007) A revision of the subgenus *Evylaeus* of the genus *Lasioglossum* in Japan (Hymenoptera, Halictidae) part I. *Esakia*, 47, 169–254.
Packer, L. (1993) Multiple-foundress associations in sweat bees. *In*: Keller, L. (Ed.), *Queen Number and Sociality in Insects*. Oxford University Press, New York, 214–233 pp.
Packer, L. (1997) The relevance of phylogenetic systematics to biology: Examples from medicine and behavioural ecology. *Mémoires du Muséum National d'Histoire Naturelle*, 173, 11–29.
Packer, L. (1999) The distribution of *Halictus ligatus* Say and *H. poeyi* Lep. (Hymenoptera; Halictidae) in North America. *In*: Byers, G.W.R., Hagen, R.H., & Brooks, R.W. (Eds.), *Entomological Contributions in Memory of Byron*

A. Alexander. University of Kansas Nature History Museum Special Publication, 24, pp. 81–84.
Packer, L. & Taylor, J.S. (1997) How many hidden species are there? An application of the phylogenetic species concept to genetic data for some comparatively well known bee "species". *The Canadian Entomologist*, 129, 587–594.
Packer, L., Gibbs, J., Sheffield, C. & Hanner, R. (*in press*) DNA barcoding and the mediocrity of morphology. *Molecular Ecology Resources*.
Padial, J.M. & De La Riva, I. (2007) Integrative taxonomists should use and produce DNA barcodes, *Zootaxa*, 1586, 67–68.
Page, T.J., Choy, S.C. & Hughes, J.M. (2005) The taxonomic feedback loop: symbiosis of morphology and molecules. *Biology Letters*, 1, 139–142.
Pilgrim, E.K. & Pitts, J.P. (2006) A molecular method for associating the dimorphic sexes of velvet ants (Hymenoptera: Mutillidae). *Journal of the Kansas Entomological Society*, 79, 222–230.
Prendini, L. (2005) Comment on "Identifying spiders through DNA barcodes". *Canadian Journal of Zoology*, 83, 498–504.
Pyle, R.L., Earle, J.L. & Greene, B.D. (2007) Five new species of the damselfish genus *Chromis* (Perciformes: Labroidei: Poacentridae) from deep coral reefs in the tropical western Pacific. *Zootaxa*, 1671, 3–31.
Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: the barcoding of life data system (www.barcodinglife.org). *Molecular Ecology Notes*, 7, 355–364.
Robertson, C. (1890) New North American bees of the genera *Halictus* and *Prosopis. Transactions of the American Entomological Society*, 17, 315–318.
Robertson, C. (1902) Synopsis of Halictinae. *The Canadian Entomologist*, 34, 243–250.
Rubinoff, D., Cameron, S. & Will, K. (2006) A genomic perspective on the shortcomings of mitochondrial DNA for "barcoding" identification. *Journal of Heredity*, 97, 581–594.
Sandhouse, G.A. (1924) New North American species of bees belonging to the genus *Halictus (Chloralictus)*. *Proceedings of the U.S. National Museum*, 65, 1–43.
Sheffield, C.S. & Westby, S.M. (2007) The male of *Megachile nivalis* Friese, with an updated key to members of the subgenus *Megachile* s. str. (Hymenoptera: Megachilidae) in North America. *Journal of Hymenoptera Research*, 16, 178– 191.
Skevington, J.H., Kehlmaier, C. & Ståhls, G. (2007) DNA barcoding: mixed results for big-headed flies (Diptera: Pipunculidae). *Zootaxa*, 1423, 1–26.
Smith, M.A., Woodley. N.E., Janzen, D.H., Hallwachs, W. & Hebert, P.D.N. (2006) DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies parasitoid flies (Diptera, Tachinidae) *Proceedings of the National Academy of Sciences of the United States of America*, 103, 3657–3662.
Smith, M.A., Wood, D.M., Janzen, D.H., Hallwachs, W. & Hebert, P.D.N. (2007) DNA barcodes affirm that 16 species of apparently generalist tropical parasitoid flies (Diptera, Tachinidae) are not all generalists. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 4967–4972.
Smith, M., Rodriguez, J.J., Whitfield, J.B., Deans, A.R., Janzen, D.H., Hallwachs, W. & Hebert, P.D.N. (2008) Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 12359–12364.
Song, H., Buhay, J.E., Whiting, M.F. & Crandall, K.A. (2008) Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 13486–13491.
Toro, H. & Moldenke, A. (1979) Revision de los Xeromelissinae Chilenos (Hymenoptera - Colletidae). *Anales del Museo de Historia Natural de Valparaiso*, 12, 95–182
Trewick, S.A. (2008) DNA barcoding is not enough: mismatch of taxonomy and genealogy in New Zealand grasshoppers (Orthoptera: Acrididae). *Cladistics*, 24, 240–254.
Van Nieukerken, E.J. (2007) *Acalyptris* Meyrick : revision of the *platani* and *staticis* groups in Europe and the Mediterranean (Lepidotera: Nepticulidae). *Zootaxa*, 1436, 1–48.
Viereck, H.L. (1916) The Hymenoptera, or wasp-like insects of Connecticut. *Connecticut State Geological and Natural History Survey Bulletin*, 22, 1–824, pls. I–X.
Wahlberg, N., Braby, M.F., Brower, A.V.Z., de Jong, R., Lee, M.-M., Nylin, S., Pierce, N.E., Sperling, F.A.H., Vila, R., Warren, A.D. & Zakharov, E. (2005) Synergistic effects of combining morphological and molecular data in resolving the phylogeny of butterflies and skippers. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 272, 1577–1586.
Wheeler, Q.D. (2008) Undisciplined thinking: morphology and Hennig's unfinished revolution. *Systematic Entomology*, 33, 2–7.
Wheeler, W.M. (1928) *The Social Insects: Their Origin and Evolution*, Kegan Paul, Trench, Trubner and Co., Ltd. London, xviii + 378 pp.
Witt, J.D.S., Threloff, D.L. & Hebert., P.D.N. (2006) DNA barcoding reveals extraordinary cryptic diversity in an

amphipod genus: implications for desert spring conservation. *Molecular Ecology*, 15, 3073–3082.
Yanega, D. (1997) Demography and sociality in halictine bees (Hymenoptera: Halictidae). *In*: Choe, J.C. & B.J. Crespi (Eds.), *The evolution of social behavior in insects and arachnids*. Cambridge University Press, Cambridge, U.K, pp. 293– 315.
Yassin, A., Cappy, P., Madi-Ravazzi, L., Ogereau, D. & David, J.R. (2007) DNA barcode discovers two cryptic species and two geographical radiations in the invasive drosophilid *Zaprionus indianus*. *Molecular Ecology Notes*, 8, 491–501.
Zayed, A., Roubik, D.W. & Packer, L. (2004) Use of diploid male frequency data as an indicator of pollinator decline. *Proceedings of the Royal Society of London B* (Suppl), 271, S9–S12.