

Research Article

Atypical Wing Venation in *Dialictus* and *Hemihalictus* and Its Implications for Subgeneric Classification of *Lasioglossum*

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The subgeneric classification of hundreds of species in *Lasioglossum* Curtis *sensu lato* is currently unstable due to differing opinions on the suitability of wing venation characters for differentiating subgenera. The subgenera *Dialictus* Robertson and *Hemihalictus* were both originally defined primarily by the forewing having two submarginal cells. I present examples of variation in submarginal cell number in the type species of these two subgenera: *L. (Dialictus) anomalum* (Robertson) and *L. (Hemihalictus) lustrans* (Cockerell). These results suggest that submarginal cell number is insufficient for recognizing subgenera in *Lasioglossum*. The variability of this character is used to refute the classification proposed by some authors that *Chloralictus* Robertson, but not *Dialictus*, be synonymised with *Evyllaesus* Robertson.

1. Introduction

Lasioglossum Curtis *sensu lato* (Apoidea: Halictidae) is the largest genus of bees with over 1700 described species [1]. This cosmopolitan genus includes many commonly collected bees which can, in both temperate and tropical areas, dominate the bee fauna in terms of number of individuals (see [2] for Ontario, [3] for Louisiana, [4] for North Carolina, and [5] for Maryland, Chihuahuan desert, and Columbia plateau, Ngo et al. in prep. for Costa Rica). In addition, the behaviourally diverse *Lasioglossum s.l.* has been the focus of numerous sociobiological studies (reviewed in [6–9]) and is an ideal group for studying the evolution of social behaviour [10].

There are competing classifications currently in use within *Lasioglossum s.l.* [11–15] that result in unstable nomenclature for many species and confusion among researchers [16]. These classifications depend on whether wing venation characters are sufficient to recognise genus-group names in *Lasioglossum s.l.* The utility of these characters is examined in an attempt to provide support for a more stable classificatory system. Stable classification and nomenclature for these important bees are highly desirable to facilitate continued study and communication of results.

Lasioglossum s.l. has been subdivided into two “series” based on the strength of the distal veins of the forewing [11, 17]. The *Lasioglossum* series has the outermost veins, 2rs-m, 2m-cu, and the second abscissa of M weak; the *Hemihalictus* series has an additional weakened vein, 1rs-m. In some cases 1rs-m is absent resulting in two rather than three submarginal cells (Figure 1). The *Hemihalictus* series, at least, seems to be a monophyletic group [17, 18] and likely resulted as a transition from an ancestral strong vein state with the state seen in the *Lasioglossum* series as a possible intermediate. The *Hemihalictus* series consists of more than half (>900) of the species in the genus *Lasioglossum*, including those under consideration in this paper.

The presence or absence of vein 1rs-m has been used to recognise genus-group names for taxa included in the *Hemihalictus* series (see [11, 13, 14, 19–25], and [16] for a complete list of genus-group names). In competing classifications, several hundred species in the *Hemihalictus* series are classified as either *Dialictus* Robertson or *Evyllaesus* Robertson depending on the status of the genus-group name *Chloralictus* Robertson [11, 13]. *Chloralictus* was formerly in common use for many species [23] but now is conventionally treated as a junior synonym of either *Dialictus* [11, 15, 24, 26]

or *Evylaeus* [12–14]. *Hemihalictus* Cockerell is the oldest name in the *Hemihalictus* series but has only ever been applied to a single species, *L. lustrans* (Cockerell).

These four genus-group names were first erected based primarily on differences in wing venation and colouration (Table 1) [20, 21]. *Dialictus* and *Chloralictus*, as originally defined, both have metallic colouration but differ in their number of submarginal cells: *Dialictus* has two (vein 1rs-m absent) and *Chloralictus* has three (vein 1rs-m present). *Hemihalictus* and *Evylaeus* have a similar relationship; both are nonmetallic but have two and three submarginal cells, respectively. The presence or absence of metallic colouration is now widely regarded as a poor character for recognising genus-group names in these bees because it can vary within species and among closely related species (see [11, 27, 28]). As a result *Dialictus* s.l. (+*Chloralictus*) and *Evylaeus* s.s. both include species with and without metallic colouration [11, 28]. Mitchell [26] was the first to treat *Chloralictus* as a junior synonym of *Dialictus*. Individuals from many species of *Chloralictus* and *Dialictus* s.s. may have vein 1rs-m present in one wing and absent in the other [29]. At least two metallic species not closely related to the type species of *Dialictus*, *L. anomalum* (Robertson), are known to be polymorphic for the presence or absence of vein 1rs-m, *L. parvum* (Cockerell) [30] and *L. asteris* (Mitchell) [15]. *Lasioglossum parvum* belongs to the *L. tegulare* species-group of Gibbs [31] whereas *L. asteris* is a social parasite [32] only distantly related to the aforementioned groups (see [18], Gibbs unpublished data). Mitchell [26] considered the absence of vein 1rs-m to be an unreliable character for these bees. Many subsequent authors have followed his classification (e.g., [11, 15, 24, 31, 33, 34]).

In contrast, Ebmer [13, 25, 27] has argued that the presence or absence of vein 1rs-m is sufficient to classify *Dialictus* and *Chloralictus* as separate subgenera. As such, *Chloralictus* is then considered by him to be a junior synonym of *Evylaeus* because colour is not considered a reliable character [27]. The classification espoused by Ebmer [13, 25] is followed by others [12, 14] and results in a paraphyletic *Evylaeus* (+*Chloralictus*) [18, 35] because *Dialictus sensu* Ebmer [13], Pesenko et al. [12] and Murao and Tadauchi [14] is derived from within it (see [18]; Gibbs unpublished data). Ebmer [13] explicitly rejects a strict cladistic classification for these bees. Thus, the classification set forth by Ebmer [13, 25], and used by many Old World authors, depends solely on the reliability of the presence or absence of vein 1rs-m for separating *Dialictus* from *Chloralictus*.

The genus-group name *Hemihalictus* has only ever been applied to a single species, *L. lustrans*, a solitary oligolege on *Pyrrhopappus* DC [36] and related Asteraceae in the tribe Cichorieae (M. Arduser *in litt.*). *Hemihalictus* renders *Dialictus* s.l. paraphyletic [18] but has never been treated as a synonym because it has priority over all other names in the *Hemihalictus* series [11, 16] and would require hundreds of name changes if the synonymy was applied. *Hemihalictus* is characterized by the lack of vein 1rs-m, nonmetallic integument, serrate inner hind tibial spurs of females, and short flagellomeres in males. The flagellomere character is also seen in some *Dialictus* s.l. (e.g., *L. pectorale* (Smith))

as well as some *Evylaeus* s.s. (e.g., *L. marginatum* (Brullé)), and the hind tibial spur character is similar to those of some *Evylaeus* s.s. (e.g., *L. laeve* (Kirby) and *L. lineare* (Schenck); see [12] for variation in hind tibial spurs). All of the species in the preceding sentence would be considered *Evylaeus* in some classifications [13, 24, 26, 27].

Variation in the wing venation of *L. anomalum*, the type species of *Dialictus*, and *L. lustrans*, the type species of *Hemihalictus*, is described herein based on large-scale taxonomic studies of *Dialictus* s.l. [15, 31, 37]. The implications of this variation for the subgeneric classification of *Lasioglossum* s.l. are discussed.

2. Methods

My revisionary studies of North American *Dialictus* s.l., which include the type species of both *Dialictus* and *Chloralictus*, have involved the examination of many tens of thousands of specimens [15]. In addition to morphology, my studies have included a molecular component for aiding taxonomic study [15, 31, 37–39]. A database of over three thousand homologous DNA sequences (DNA barcodes) for *Lasioglossum* s.l. is currently stored on the Barcode of Life Data Systems [40] and GenBank.

DNA barcoding, the use of a standard gene fragment for species-level identification [41], was used to verify the identity of some of the specimens described herein. The standard fragment used for animals is 658 bp on the 5' end of cytochrome *c* oxidase subunit 1 [42]. Sequencing was performed at the Canadian Centre for DNA Barcoding at the University of Guelph (Guelph, Ontario). DNA was extracted from a single dried leg (or in some cases two legs) using automated extraction protocols for 96-well plates [43]. One of two primer pairs was used to amplify the DNA barcode region (LCO1490 and HCO2198 [44] or the variants LepF1 and LepR1; [45]). Samples that failed to amplify were then reattempted using internal primer pairs (LepF1 and C_AntMr1D-RonIIdg_R [46] and LepR1/MLepF1; [47]). PCR and sequencing reactions followed standard Canadian Centre for DNA Barcoding protocols [48]. Sequences were uploaded to the Barcode of Life Data Systems [40].

3. Results

Seven individuals of *Lasioglossum* (*Dialictus*) *anomalum* with atypical wing venation were examined (Table 2). Six of these had vein 1rs-m present in one wing but absent in the other. The final specimen, collected in Guelph, Ontario, Canada, approximately 900 km Northeast of the type locality in Carlinville, Illinois, had vein 1rs-m present in both wings (Figure 2) resulting in wing venation typical of *Chloralictus* and *Evylaeus*. The specimens are otherwise morphologically identical to *L. anomalum*. The DNA barcode sequences of the Ontario and Michigan specimens matched DNA barcode sequences of *L. anomalum* individuals with vein 1rs-m absent in both wings sampled throughout its range, including approximately 300 km from the type locality (Figure 3). A

TABLE 1: Characteristics of *Hemihalictus*, *Dialictus*, *Evylaeus*, and *Chloralictus* type species.

Genus-group name	Type species	Date of publication	Vein 1rs-m	Integument colour	Female inner hind tibial spur	Male flagellomere length
<i>Hemihalictus</i> Robertson	<i>Panurgus lustrans</i> Cockerell	1897, p. 288	Absent	Nonmetallic	Serrate/denticulate	short
<i>Dialictus</i> Robertson	<i>Halictus anomalus</i> Robertson	1 Feb. 1902, p. 48	Absent	Metallic	Pectinate	short
<i>Evylaeus</i> Robertson	<i>Halictus arcuatus</i> Robertson*	10 Sep. 1902, p. 247	Present	Nonmetallic	Serrate/denticulate	long
<i>Chloralictus</i> Robertson	<i>Halictus cressonii</i> Robertson	10 Sep. 1902, p. 248	Present	Metallic	Pectinate	long

*Junior subjective synonym of *Halictus cinctipes* Provancher.

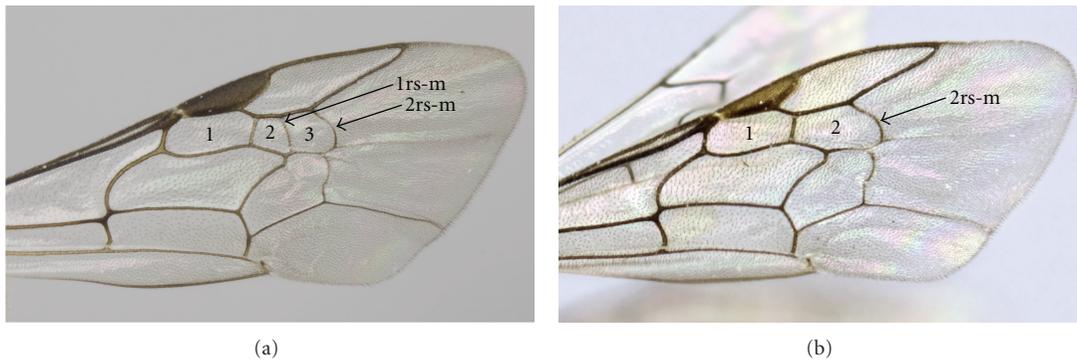


FIGURE 1: Forewing of *Lasioglossum* belonging to the *Hemihalictus* series. Numbers indicate submarginal cells. (a) Vein 1rs-m present. (b) Vein 1rs-m absent. Modified from [31].



FIGURE 2: Lateral habitus of *Lasioglossum* (*Dialictus*) *anomalum* with three submarginal cells. Bar = 1 mm.

series of *L. anomalum* collected from the same site as the Ontario specimen had vein 1rs-m absent.

A single male specimen of *L. (H.) lustrans* with vein 1rs-m present in both forewings has been examined (Figure 4). In other respects, it appears to be a normal specimen of *L. lustrans*. The identification was also verified using DNA barcodes. The locality data for this specimen is as follows: USA, Wisconsin, Marinette Co., Dunbar Barrens, N45.65149 W088.2415, 13.vii.2005 (C. Destree). A second male specimen with vein 1rs-m absent was also examined from the same locality. Both specimens are stored at the Richter Museum of Natural History, University of Wisconsin, Green Bay, Wisconsin.

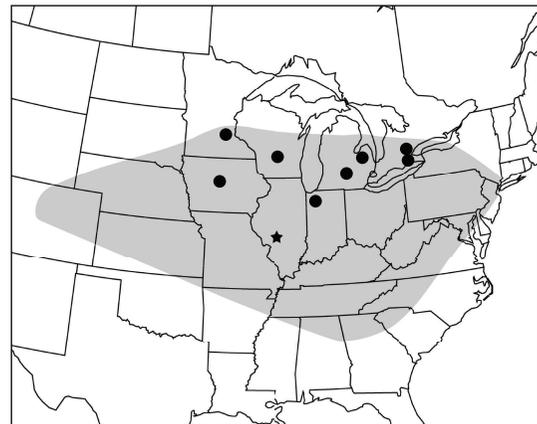


FIGURE 3: Map of *Lasioglossum anomalum* distribution in eastern North America with type locality indicated by a star. Circles indicate collection localities of DNA barcoded specimens. Modified from [31].

4. Discussion

Ebmer [27] argued that metallic colouration was not a reliable character for recognising genus-level differences between *Evylaeus* and *Chloralictus*. To support this argument, he used the examples of *L. viride* (Brullé) and *L. morio* (Fabricius). In the case of *L. viride*, both black and metallic forms

TABLE 2: *Lasioglossum anomalum* individuals with vein 1rs-m present. PCYU: Laurence Packer’s Collection, York University (Toronto, Canada), AMNH: American Museum of Natural History (New York, USA), ARC: Albert J. Cook Arthropod Research Collection, Michigan State University (East Lansing, USA), and IRCW: University of Wisconsin–Entomology (Madison, USA).

Depository	Forewing (s) with 1rs-mPresent	Country	Province or state	Latitude (north)	Longitude (west)	Collection date
PCYU	2	CANADA	Ontario	43.5	80.31	16.viii.2007
PCYU	1	USA	Iowa	43.32472	91.13444	15.viii.2005
PCYU	1	USA	Michigan	43.61667	83.31739	16-20.vi.2008
ARC	1	USA	Michigan	43.69311	83.20706	30.vii.2009
ARC	1	USA	Michigan	43.69311	83.20706	30.vii.2009
AMNH	1	USA	New York	40.86806	73.42611	26.vii.1962
IRCW	1	USA	Wisconsin	43.28245	89.58043	5.vi.1995



FIGURE 4: Dorsal habitus of *Lasioglossum (Hemihalictus) lustrans* with three submarginal cells. Bar = 1 mm.

are known from the same locality. Morphologically they are indistinguishable and the colour variation in these two forms is considered to be a polymorphism. Colour aberrations also occur—*Halictus balticus* Blüthgen was the name given to a black specimen of the normally metallic *L. morio*. Other examples of metallic/nonmetallic polymorphism are known from *Lasioglossum* (J. Gibbs, unpublished data) and in the genus *Agapostemon* (L. Packer, unpublished observation).

The examples given herein for wing venation are analogous to those provided by Ebmer [27] for colouration. At least two species in the *Hemihalictus* series, *L. parvum* and *L. asteris*, show both the presence and absence of vein 1rs-m with a high frequency. *Lasioglossum parvum* belongs to the *L. parvum/tegulare* species group [18, 31] whereas *L. asteris* is a distantly related parasitic species [18]. Neither of these species is believed to be a close relative of *L. anomalum*, a view supported by preliminary phylogenetic analyses (J. Gibbs, unpublished data). In the *Lasioglossum* series, *L. (Ctenonomia) bakeri* Pauly was described from two individuals, each with a different number of submarginal cells [49]. Less frequent variation, such as that of the *L. anomalum* and *L. lustrans* individuals described here, fails to support the utility of this character for species-level identification, let alone genus-level classification.

Even disregarding the benefits of a cladistic classification (for discussion see [50–52]) these examples, strongly suggest that the presence or absence of vein 1rs-m is not sufficiently reliable to recognise *Dialictus* and *Chloralictus* as separate genera, subgenera or even to recognise species. *Chloralictus*

should be considered a junior synonym of *Dialictus* based on the principle of priority (Article 23.3, [53]) following Mitchell [26], Krombein [33], Hurd [54], Moure and Hurd [24], Michener [7, 11], and many others. *Chloralictus* cannot justifiably be considered a synonym of *Evylaeus* without the latter name in turn becoming a junior synonym of the older name *Dialictus*. The type species of *Evylaeus* belongs to the “carinate-*Evylaeus*” which is sufficiently different morphologically and phylogenetically [18] from *Dialictus* + *Chloralictus* to be recognised as distinct. The evidence presented here and previously [29, 30] does not support the classification used by Ebmer [13, 25] even if a phenetic classification was considered appropriate.

The subgenus *Hemihalictus* is also recognised primarily on the basis of the absence of vein 1rs-m. This name has priority over all other names in the *Hemihalictus* series, and its sole species is clearly nested within the *Dialictus s.l.* clade [17, 18, 35]. The existence of individuals with vein 1rs-m present provides additional support for considering *Hemihalictus* synonymous with *Dialictus s.l.* If this synonymy were made, the subgeneric placement of hundreds of species would change. *Hemihalictus* is an uncommonly collected, monotypic taxon. A petition to set aside the principle of priority in the case where *Hemihalictus* is considered a synonym of *Dialictus* or *Evylaeus* has been submitted to the International Commission of Zoological Nomenclature [16].

Some authors have chosen to elevate subgenera of *Lasioglossum* to the level of genus [24, 26, 27, 54, 55] which would seem unwise given the difficulty in distinguishing between these higher taxa and the probability that many *Lasioglossum* subgenera are paraphyletic [17, 18]. A subdivision of *Lasioglossum s.l.* into smaller genera may be desirable but should await a more complete phylogeny of the group to allow a stable classification [11].

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