A phylogenetic analysis of western European species of the *Lasioglossum leucozonium* species-group (Hymenoptera: Halictidae): sociobiological and taxonomic implications

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Abstract: A data matrix of 81 characters for 23 species of the subgenus *Lasioglossum* sensu Michener (1999) is analysed cladistically with the primary purpose of obtaining a phylogeny for western European species of the *Lasioglossum leucozonium* group. Outgroup taxa were chosen on the basis of published species groupings for Old World species and a phylogeny for the New World species. Outgroup resolution was poor but results for the ingroup were consistent and indicate that (*i*) the social behaviour recorded for *L. aegyptiellum* is nested within a solitary background and therefore represents an origin of sociality independent of all others within the Halictidae, (*ii*) the monotypic subgenus *Sericohalictus* is a derived member of the *leucozonium* species-group, and (*iii*) *L. laevigatum* is not a member of this group.

Résumé : Une matrice de données de 81 caractères observés chez 23 espèces du sous-genre *Lasioglossum* sensu Michener (1999) a été soumise à une analyse cladistique dont le but principal était d'obtenir une phylogénie des espèces du groupe *L. leucozonium* d'Europe de l'ouest. Les groupes externes ont été choisis d'après les regroupements reconnus d'espèces de l'Ancien monde et d'après une phylogénie des espèces du Nouveau Monde. Les résultats relatifs au groupe externe ont été médiocres, mais ceux relatifs au groupe interne étaient cohérents et indiquent que (*i*) le comportement social attribué à *L. aegyptiellum* est issu de moeurs solitaires et l'origine de son type de vie sociale est donc divergent de celui de tous les autres Halictidae, (*ii*) le sous-genre monotypique *Sericohalictus* est un membre évolué à partir du groupe d'espèces *leucozonium* et (*iii*) *L. laevigatum* n'appartient pas à ce groupe.

[Traduit par la Rédaction]

Introduction

Lasioglossum is a huge genus found in every continent except Antarctica. It has been described as morphologically monotonous (Michener 1999); nonetheless, it has been broken up into many subgenera the number and delimitations of which differ with each researcher who has published on the group in recent years (Warncke 1975; Pesenko 1986; Ebmer 1988; Michener 1999). Given the enormous number of species involved and the great diversity of opinions concerning their grouping, anyone tempted to perform a phylogenetic analysis of this group might be considered hopelessly optimistic at best, or downright crazy at worst. Nonetheless, phylogenetic analyses of these bees are of particular importance because of the considerable interest in social evolution within the group (e.g., Wcislo 1997). *Lasioglossum* contains the greatest diversity of social behaviour among the bees, with all named types of social organisation represented except advanced eusociality, and colony sizes range from a few individuals to hundreds. Additionally, a large number of species are polymorphic for social and solitary behaviour (Packer 1997). Consequently, it is crucial to be able to place this behavioural diversity within a phylogenetic context in order to establish the polarity of behavioural character states (Wenzel 1992).

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Packer (1997) surveyed the evidence for the direction of evolutionary change among eusocial and solitary behaviours within the Halictidae. In most cases a change from social to solitary behaviour within the genera or subgenera for which appropriate data were available was more parsimonious than hypotheses of recent origins of sociality. One exception seemed to be *Lasioglossum* (*Lasioglossum*) *aegyptiellum*, a species that, based upon meagre evidence (Knerer in Ebmer 1976), appears to be eusocial (Packer 1997). In the absence of any phylogenetic hypotheses concerning Old World *Lasioglossum*, Packer (1997) took the short cut of adding this species to the phylogeny for New World *Lasioglossum* (s.str.) proposed by McGinley (1986), which contained the two Holarctic members of the *leucozonium* group. This demonstrated that *L. aegyptiellum*'s social behaviour was probably derived from solitary ancestry. Clearly, a more convincing analysis is desirable and this is the primary objective of the present paper.

The genus *Lasioglossum* is characterised by a weakened vein 2r-m in the forewing of females. In several of the larger subgenera within the group, the venation is further reduced, so that only the first recurrent vein remains strong; this is the case in, for example, *Evylaeus*, *Sphecodogastra*, and *Dialictus*. The group referred to as *Lasioglossum* (*Lasioglossum*) by Michener (1999), McGinley (1986), and Ebmer

Table 1. List of ingroup and outgroup taxa.

	Subgenus sensu Pesenko or node of McGinley	Localities	Sociality	Reference
Ingroup				
L. aegyptiellum (Strand)	*Leuchalictus*	France, Spain, Greece	Eusocial?	Packer 1997
L. albocinctum (Lucas)	*Leuchalictus*	France, Italy	Unknown	
L. discum (Smith)	*Leuchalictus*	Greece, Turkey, USSR	Unknown	
L. laevigatum (Kirby)	*Leuchalictus*	U.K., France	Solitary	Stoeckhert 1933
L. leucozonium (Schrank)	*Leuchalictus*	U.K., Canada	Solitary	Atwood 1933; Stoeckhert 1933
L. majus (Nylander)	*Leuchalictus*	Austria	Solitary	Malyshev 1936[*]
L. zonulum (Smith)	*Leuchalictus*	U.K., Canada, U.S.A.	Solitary	Stoeckhert 1933
Outgroup				
L. anhypops McGinley	Node 6	U.S.A.	Unknown	
L. clavipes (Dours)	*Lucasiellus*	Sardinia, Algeria	Solitary	Sakagami and Maeta 1990
L. costulatum (Kriechbaumer)	*Ebmeria*	Austria, Bulgaria, Morocco	Solitary	Stoeckhert 1933
L. equestre (Morawitz)	*Fahrhalictus*	Tadjikistan	Unknown	
L. fuscipenne (Smith)	Node 1	Canada	Solitary?	
L. lativentre (Schenck)	*Pallhalictus*	U.K., Italy	Unknown	
L. manitouellum (Cockerell)	Node 12	U.S.A.	Unknown	
L. pallens (Brullé)	*Pallhalictus*	France, Turkey	Solitary	Sakagami and Maeta 1990
L. pavonotum (Cockerell)	Node 5	U.S.A.	Unknown	
L. prasinum (Smith)	*Lasioglossum*	U.K.	Solitary?	
L. sexnotatum (Kirby)	*Lasioglossum*	Austria	Solitary	Stoeckhert 1933[†]
L. subfasciatum (Imhof)	*Lasioglossum*	Italy	Unknown	
L. subopacum (Smith)	*Sericohalictus*	China	Unknown	
L. timberlakei McGinley	Node 4	U.S.A.	Unknown	
L. titusi (Crawford)	Node 1	U.S.A.	Unknown	
L. xanthopus (Kirby)	*Lasioglossum*	U.K., Tadjikistan	Solitary?	

Note: Species listed as "solitary?" here recorded as at least not "annual eusocial," based upon unpublished phenological data. This does not preclude them from being "delayed eusocial" or "semisocial" (Packer 1993). These species were not optimised as being solitary in the production of Fig. 4.

[*] In Sakagami and Michener (1962).

[†] Listed as *Halictus nitidus* Panzer in the original.

(1988) has been broken down into further subgenera by Warncke (1975) and Pesenko (1986). Given the huge size of the subgenus sensu Michener, a thorough phylogenetic analysis is clearly a matter for the future. Nonetheless, the work of other researchers does help with the current objective because much of the variation within the group may be captured by including representatives from the additional named groups (Pesenko 1986) or clades (McGinley 1986) for outgroup analysis.

Materials and methods

Systematic background and choice of outgroup taxa

The group of interest is the western European component of the *L. leucozonium* species-group. Warncke (1975) suggested subgeneric rank for this species-group, coining the name *Leuchalictus* for them. In his subgeneric description he noted that females of *Leuchalictus* are similar to those of *Inhalictus* Warncke, another newly described subgenus, but with the basal hair bands of the abdominal terga not interrupted medially. However, the species listed under *Inhalictus* do not form a cohesive group, as they contain some species with the second recurrent vein strong as in the subgenus *Lasioglossum* sensu Michener (for example, the species *L. laevigatum* and *L. costulatum*) and some with this vein weak (such as *L. interruptus* and *L. puncticolle*). The latter are referred to by all other authors as belonging to either *Evylaeus* or *Dialictus*. Warncke stated that the males of *Leuchalictus* have a dense patch of hairs on the sixth sternum and lack a retrorse lobe to the gonostylus. The former seems to be a unique feature of the group, whereas the retrorse lobe on the gonostylus has been lost, presumably independently, in some species-groups of the subgenus *Evylaeus* sensu authors. Pesenko's (1986) treatment of the subgenus *Lasioglossum* sensu Michener did not intermix species of *Evylaeus* with *Lasioglossum*, but included *L. laevigatum* as a species of *Leuchalictus* despite the fact that this species lacks both of the characters of this group that Warncke listed for males. Presumably this was because Pesenko's treatment was of females only. Thus, according to these authors, either six or seven species in the *leucozonium* group (depending upon whether or not *L. laevigatum* is included) are found in western Europe (Pesenko 1986; Ebmer 1988; Table 1), two of which, *L. leucozonium* and *L. zonulum*, are Holarctic.

Considering the huge number of *Lasioglossum* species outside the group being investigated, it was not possible to examine more than a small proportion. Outgroup exemplars were chosen on the basis of previous studies of the diversity within *Lasioglossum*. Pesenko (1986) divided Old World members of the subgenus *Lasioglossum* sensu Michener into eight named subgenera. Exemplars of all but two monotypic subgenera among the eight were available for study; the exceptions were *L. acuticrista* and *L. dynastes*, which were placed in the new subgenera *Lophalictus* and *Bluethgenia*, respectively (Pesenko 1986). McGinley (1986) did not subdivide New World *Lasioglossum* species into additional subgenera but did provide a phylogeny based on 26 characters. The two Holarctic species *L. leucozonium* and *L. zonulum* were hypothesised to form a clade that itself arose from a basal polytomy of five branches. Representatives from all four of the additional clades were included among the outgroup taxa. The entire suite of 16 outgroup species used here is listed in Table 1.

Data collection and character analysis

Subtle characters of cuticular sculpturing were observed, using white tissue paper to diffuse the light. It was sometimes necessary to shave portions of a bee in order to observe characters that underlie the pubescence. This was particularly true for details of facial sculpture and the form of the dorsal surface of the pronotum. In a few species it was necessary to remove pubescence from the area around the basitibial plate or inner hind tibial spur. Male genitalia were removed and boiled in 10% KOH before being neutralised in 5% acetic acid and stored in glycerine.

More effort was expended in analysing characters that seemed to vary within the ingroup than in attempting to discover an exhaustive amount of variation among the outgroup taxa. Nonetheless, many characters were included that were monomorphic in the ingroup but that might aid phylogenetic resolution of the outgroup. Some resolution of outgroup relationships is necessary if adequate resolution of the ingroup is to be achieved (Nixon and Carpenter 1993). In total, 16 characters, invariant within the ingroup but variable among outgroup taxa, were included; this number increases to 29 if *L. laevigatum* is not considered a member of the ingroup. Characters that showed only autapomorphic variation in an outgroup species were not included in the data set.

The characters used and explanations of their coding are provided in the Appendix. Terminology generally follows that of McGinley (1986). Most multistate characters were treated as unordered except for relative proportion characters in which the evolution from one to the opposite extreme character state would almost certainly have taken place through intermediate stages, or the intermediate state was probably ancestral, with evolutionary change in both directions. For example, flagellar segment 1 shorter than broad would presumably become longer than broad through an intermediate stage of being as broad as long (character 50). Some less obviously metric characters were treated similarly; for example, the median dorsal suture of the gonobase (character 74) was divided into three states and treated as an ordered character, as it was expected that evolution between the two extremes (absent and strongly developed) would have occurred through the intermediate state (weakly developed). Danforth and Eickwort (1997) followed an identical procedure in coding multistate characters for augochlorine bees.

One character that seemed to be important for resolving ingroup relationships was the form of the pubesence on the sixth sternum of males (character 63), the presence of this patch being one of the defining features of the group according to Warncke (1975). This patch occurred in a variety of complex patterns (see the account in the Appendix) that seemed to be readily associable into a linear transformation series. However, it was not possible to suggest a character state for any of the outgroup taxa for this because they all lack any modified patches of hair in this region, and within the ingroup it was not possible, a priori, to assign an ancestral state. Ingroup variation in this character was coded as shown in the Appendix, but with the outgroup intially coded as unknown. The results of a preliminary phylogenetic analysis treating it as an unordered character suggested a linear transformation series through states 1 through 4. Consequently, further analyses coded the outgroup taxa as state 0 and treated the character as an ordered transformation series.

Phylogenetic analysis

The computer program Hennig86 (Farris 1988) was used for phylogenetic analysis. Relationships among the outgroup taxa and the ingroup were estimated simultaneously (Nixon and Carpenter 1993). Because of the large number of taxa and characters involved, the mh* bb* routine was used. Multiple analyses were performed, the sequence of outgroups in the input matrix being varied to increase the chances that all "islands" of most parsimonious trees were found (Maddison 1991; Danforth and Eickwort 1997).

Sequences used were outgroups in alphabetical order, reversed alphabetical order, North American species first, European species first, and several "random" sequences obtained by moving blocks of outgroup species around in the data matrix. In addition to computer runs with all 17 outgroup taxa used in the outgroup suite, subsets of outgroups were also used: all North American outgroup species, all European outgroup species, and the members of each one of Pesenko's named subgenera or McGinley's clades separately.

Whenever multiple equally parsimonious trees were found, successive-approximations character weighting was performed (Carpenter 1988). This is a routine that uses the goodness of fit of each character on all equally parsimonious trees as the weight for that character in subsequent analysis. This procedure is repeated until stability in tree lengths and associated statistics is achieved. In this manner the number of equally parsimonious trees may be reduced using a method that relies only upon information available in the data being analysed (Wenzel 1997). However, given the great diversity and lack of resolution among the outgroup species in the different analyses, it is probable that characters which are useful in resolving ingroup relationships will receive a low weight with successive-approximations character weighting simply because they exhibit homoplasy in the poorly resolved outgroup. Consequently, a hypothetical ancestral character state suite was obtained from the outgroup node (Maddison et al. 1984) of the Nelson (strict) consensus of all most parsimonious trees in the unweighted analysis with outgroup taxa entered in alphabetical order but with New World species entered before Old World ones. This hypothetical ancestor was considered the outgroup in a reanalysis that, because of the great reduction in number of taxa, was performed using the ie* routine, guaranteed to find all most parsimonious trees (Farris 1988). Although it is preferable to analyse all outgroup and ingroup taxa simultaneously (Nixon and Carpenter 1993), the results obtained here revealed too poor a resolution of outgroups for any confidence to be placed in their phylogenetic pattern and this is why reanalysis with a hypothetical ancestor was performed.

The figures were generated using MacClade version 3 (Maddison and Maddison 1992).

Results

The data matrix of 81 characters for the 23 taxa is presented in Table 2. All sequences and combinations of outgroup taxa produced four trees that were 382 steps long with a consistency index (CI) of 33 and a retention index (RI) of 54. The low CI suggests that the data contain considerable ambiguity (Sanderson and Donoghue 1989).

All analyses placed *L. subopacum* as a member of the *leucozonium* group and *L. laevigatum* not as a member of this group. Resolution of the ingroup taxa was always the same, although the topology among outgroups varied according to the taxa used and the input sequence. A Nelson (strict) consensus of the four most parsimonious trees showed much ambiguity in outgroup interrelationships but completely resolved the ingroup (Fig. 1). Successive-approximations character weighting invariably resulted in three most parsimonious trees with a length of 516, CI of 57, and RI of 77. However, the Nelson consensus of these trees (Fig. 2) shows a polytomy in the ingroup.

Table 2. Data matrix used in the analysis.

Character		1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	88
number	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	01
aegyptiellum	010102011	0032110011	1200001123	0100101100	0010100001	0002101021	0101122000	0101112000	02
albocinctum	011110011	0031211001	1120110211	0100121000	0001100001	1101112121	0012122100	0101111001	02
discum	010102011	0032111011	2200001123	0100101100	0000100001	0002101021	0101122000	0101112000	02
leucozonium	000110011	0030110011	1121110112	0000111110	0000100001	1001001121	0001121000	0101112000	02
majus	011010011	0021102011	2210020222	0120111000	0001000001	1011121021	0013122010	0101111000	02
zonulum	000012011	0022112011	1220020222	0120110000	0001100001	1011111121	0014121010	0101111000	02
laevigatum	011111000	0010011011	1100010013	0100010002	0100001000	0100000000	0220011301	1011100010	11
anhypops	001102011	0020111101	0110200000	0021010100	0001100101	1011000010	0200111300	1000200110	02
clavipes	001111101	0010020001	0021010102	1000110100	1100101002	1010002011	1010021300	0101200110	10
costulatum	000010000	1010012001	1110200023	0000001102	0100010001	0012001000	0220011011	1010200110	01
equestre	001012001	1010112000	1100200200	0001011001	1101110011	1001001000	02101?1300	1010200110	12
fuscipenne	001112000	0010122001	1110200011	1000011100	0001000001	0001000111	0020011301	1010200110	12
lativentre	000011000	0010122001	1121110102	0000021102	0000100011	0000002100	0120011300	1010200012	12
manitouellum	001112001	0010011101	0031210100	0020110111	0001000101	1011001111	0210011301	1000200110	02
pallens	001012010	1000021001	0121210102	1000001101	2000100011	0001001111	0020011301	1010200111	12
pavonotum	101013001	0020111001	1121210102	1010001100	1000101001	1010002111	0220021300	1010200110	12
prasinum	101112011	0120211001	1121110002	1010001100	1000000001	0000002021	0220012200	1200100112	13
sexnotatum	001012001	1010110001	1111210001	1010101102	0001100000	0010100111	1100011000	0101200011	10
subopacum	010110011	0021113011	1321110222	0100121110	0001100001	0011101121	0001122000	0101012000	02
subfasciatum	000110001	1020110000	0121210101	1000011100	0001100011	0000101111	1110011302	1010200111	11
timberlakei	002112001	1000021011	1110200123	0011011000	1001001011	0011000021	0020011001	1020110010	11
titusi	002012101	0100020011	1100200112	0020101100	0000101002	2001000011	0220001301	0011110110	11
xanthopus	001101001	1030211000	0010110101	1001011101	1100100001	1000000000	0020021302	1010100110	12
ancestor*	00111?001	0010110001	1121?10102	1000111100	0000100001	?0?0?01111	10?0021?00	0101200?10	1?

Note: For a list of characters and character states see the Appendix. For previous taxonomy and social behaviour of the species see Table 1.
*See the text for an explanation of the derivation of these character states.

Fig. 1. Strict consensus phylogeny of four equally parsimonious trees obtained for 23 *Lasioglossum* sensu Michener species used in the analysis (Table 1). Branch lengths are proportional to the number of unambiguous character state changes. Note that outgroup relationships are highly variable depending upon the order of addition of taxa or the subset of outgroups used; nonetheless, the resolution of the *L. leucozonium* group was the same in all analyses. Characters undergoing unambiguous changes are mapped onto the tree; unique changes are indicated by a solid circle adjacent to the character number. The star in this figure and Figs. 2 and 4 indicates the origin of the *L. leucozonium* species group.

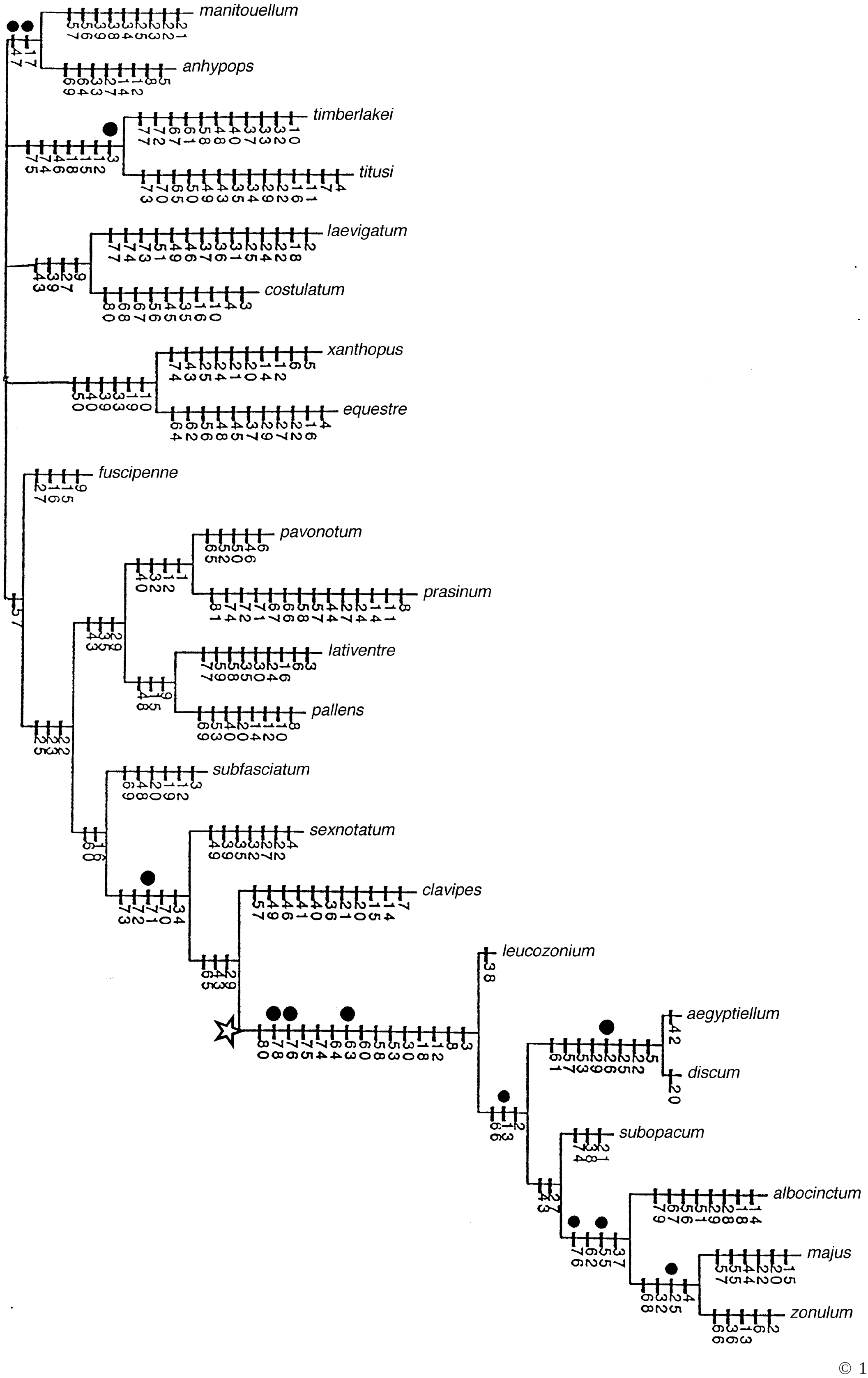
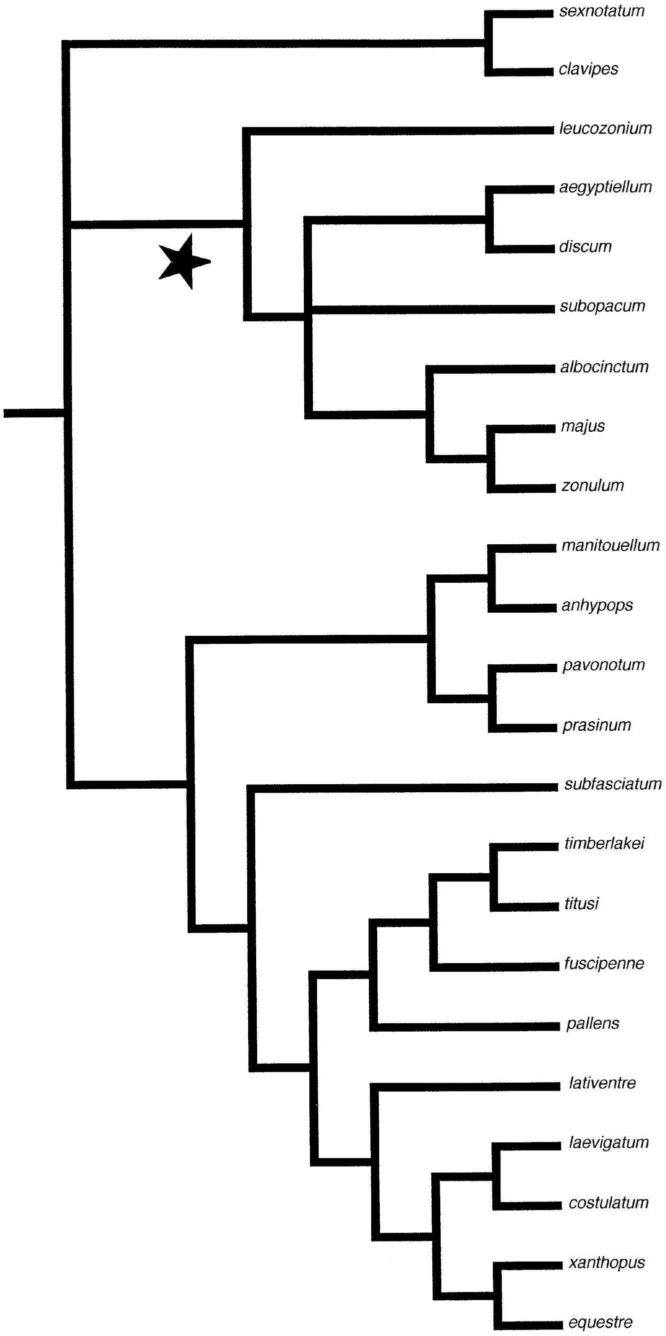


Fig. 2. Strict consensus of the three trees that resulted from successive-approximations character weighting from the initial analysis that resulted in Fig. 1. Note that the ingroup shows a polytomy in this figure but that it was completely resolved using unweighted data (Fig. 1).



Use of the character state suite from the hypothetical ancestor of the *leucozonium* group from Fig. 1 as outgroup yielded the phylogeny shown in Fig. 3. This tree has a length of 94 steps, CI of 76, and RI of 67, and was stable to successive-approximations character weighting. Note that this tree has exactly the same topology of ingroups as in the strict consensus of four equally parsimonious trees based upon unweighted characters (Fig. 1).

Based upon the complete analysis using all outgroup taxa, nonhomoplasious synapomorphies that unite the *leucozonium* group as constituted here (i.e., including *subopacum* but excluding *laevigatum*) are all characters of the male genitalia or last visible sternum: patch of erect hairs on S6 present (character 63), apical gonostylus flattened (76), and retrorse lobe of gonostylus absent (78).

Within the ingroup, the clade uniting all species except *leucozonium* is supported by one nonhomoplasious synapomorphy: preoccipital ridge present (13). The species-pair *aegyptiellum* and *discum* is united by having a punctate metanotum (26). The clade *majus* plus *zonulum* is supported by having the scutellum with a comparatively impunctate patch on each side (25), and this species-pair shares with *albocinctum* the apomorphic character states of lateral margins of the transverse carina of T7 in the male produced into angulations (55) and the gonostylus wedge-shaped (76). The transformation series of ever-increasing complexity of the hair pattern of the male S6 (63) provides support for the clades *albocinctum* + (*majus* + *zonulum*) and *majus* + *zonulum*.

The species-pair *L. clavipes* and *L. sexnotatum* formed the sister-group to the *leucozonium* group in most analyses. One nonhomoplasious synapomorphy united these two species with the *leucozonium* group in most analyses: gonobase convex in profile (71). When these two taxa only were included as the outgroup in a reduced data matrix analysed by the ie* routine, the same resolution of ingroup taxa as shown in Fig. 3 was obtained. The statistics for the tree resulting from this reduced data matrix are a length of 132, CI of 71, and RI of 64.

Resolution among other outgroup taxa was poor. The two species with metallic coloration (*pavonotum* and *prasinum*) were united on the basis of this one unique synapomorphy (1) despite being morphologically very different. The two North American species *titusi* and *timberlakei* were united by the nonhomoplasious synapomorphy of sparse clypeal punctation (3). In agreement with McGinley's (1986) analysis, the two North American species *anhypops* and *manitouellum* were united by two nonhomoplasious synapomorphies: the presence of a carinate lower pronotal ridge (character 17) and the male clypeus impunctate and broadly concave (character 47). Other groupings shown in Fig. 1 were the result of character-state changes that occurred homoplasiously elsewhere on the tree.

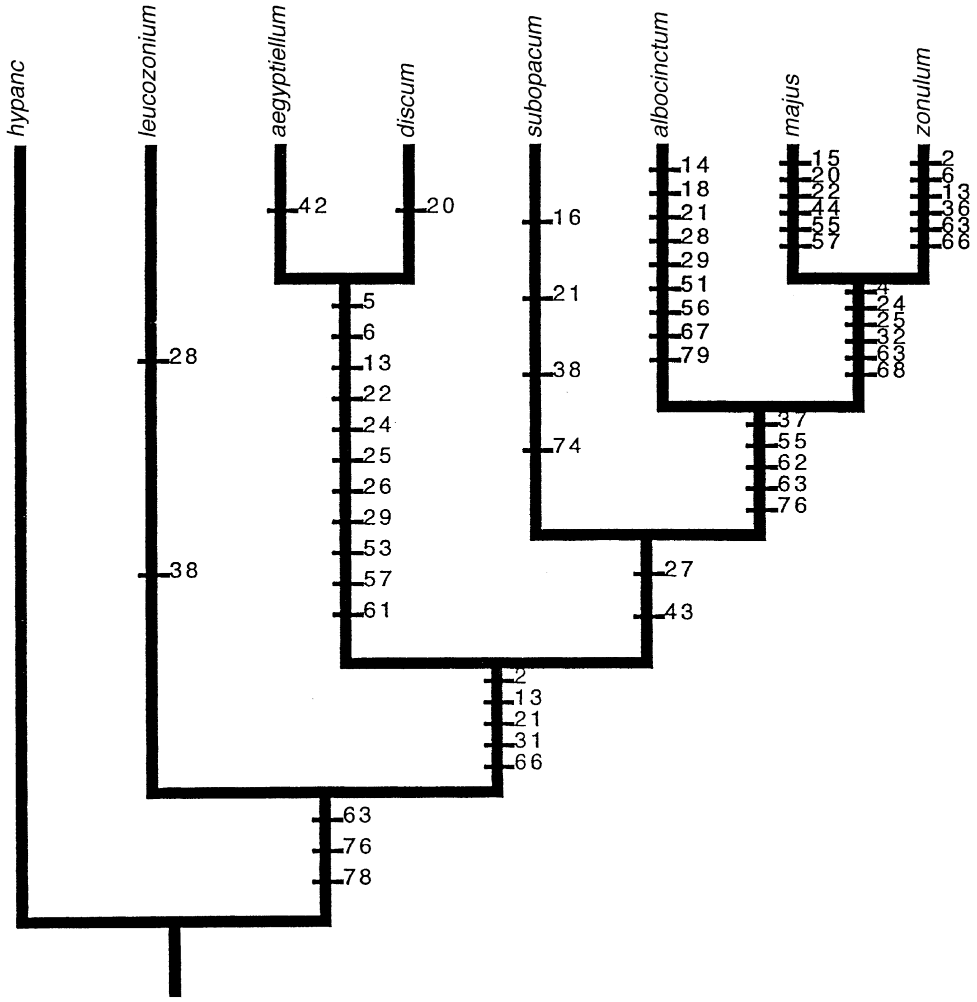
The solitary/social nature of the species with known behaviour is shown in Table 1. When this variation is plotted onto the preferred phylogenetic hypothesis (Fig. 4), or indeed any of the other trees resulting from the various analyses, it becomes clear that social behaviour in *L. aegyptiellum* is derived from solitary ancestry.

Discussion

Phylogeny and behaviour

Application of the phylogenetic approach to problems in evolutionary biology is becoming commonplace (Coddington 1988; Brooks and McLennan 1991; Grandcolas 1997). This is because evolutionary arguments often involve ad hoc assumptions about the direction of evolutionary change, and

Fig. 3. Most parsimonious tree for the ingroup species, using a hypothetical ancestor as the outgroup. The character-state suite for this ancestor was obtained from the outgroup node of a strict consensus of all most parsimonious trees in an unweighted analysis. See the text for further details.



when these are tested using parsimony they often turn out to be false (Packer 1997).

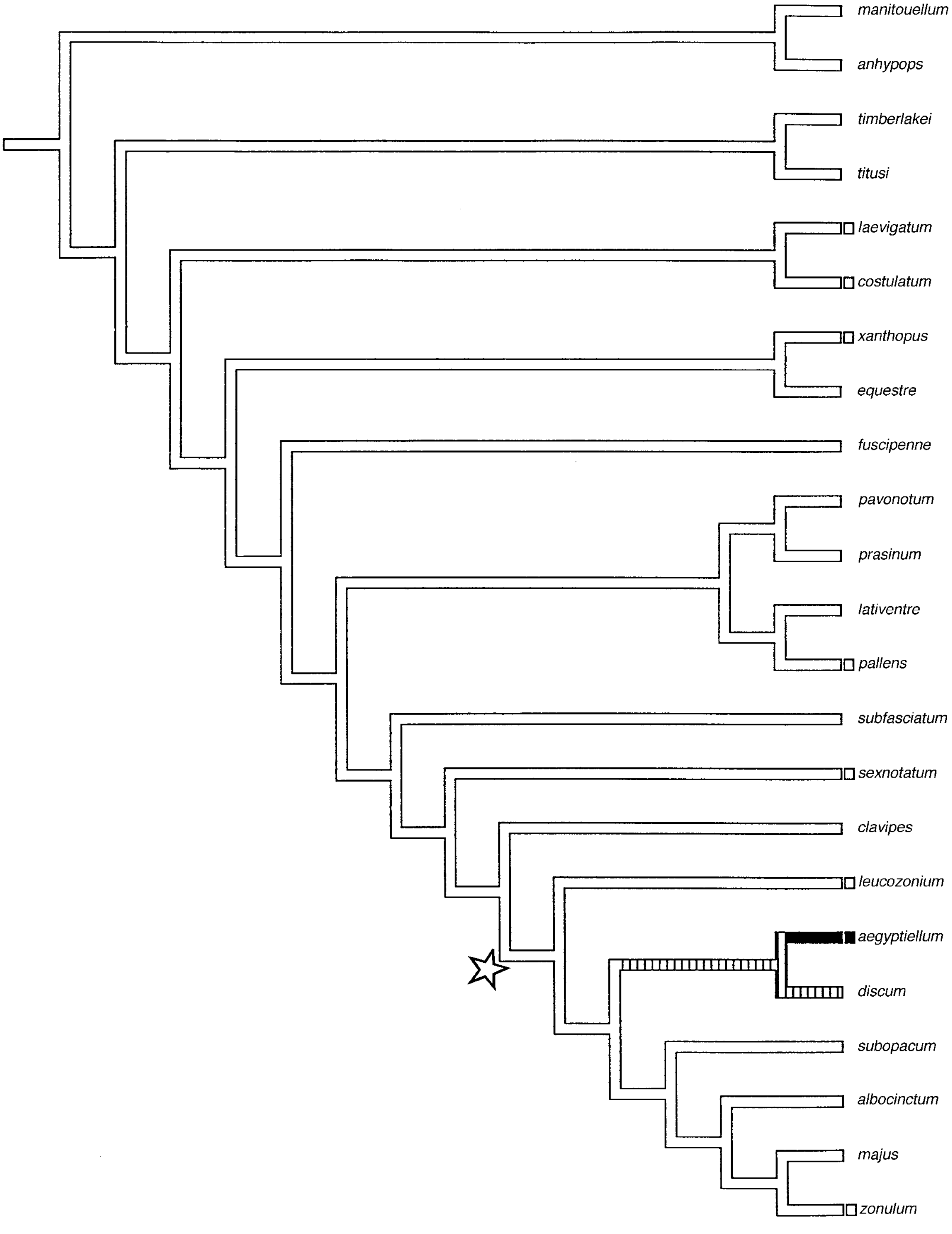
Eusociality appears to have arisen within the halictine bees many times independently. Yet this statement is based upon the assumption that within genera or subgenera which contain both solitary and social species, the direction of evolutionary change has been from solitary to social. Phylogenetic analysis indicates that in most instances it is easier to document the reverse: solitary behaviour arising from a social ancestry (Danforth and Eickwort 1997; Packer 1997). This suggests the importance of making a higher level phylogenetic analysis of halictine bees to document whether the taxa that appear to have social behaviour as an ancestral character state form a monophyletic group with sociality as an ancestral condition. Danforth and Eickwort (1997) indicated that eusociality within the Augochlorini is shared ancestrally by the only three genera in the tribe known to exhibit eusociality; a similar analysis is badly needed for the Halictini.

Lasioglossum aegyptiellum was thought to be eusocial by Knerer (cited by Ebmer 1976), based upon observations of a single nest inhabited by several adults. The complete data for this nest were presented by Packer (1997), who concluded from a preliminary phylogenetic analysis that this species' sociality was derived from solitary ancestry. The more thorough analysis presented here supports this conclusion. If further field research corroborates the suggestion that this species is eusocial, this would be the first well-documented case of a recent origin of eusociality within any clade of bees.

Taxonomic considerations

The genus *Lasioglossum* is a huge and complex one, with a large number of subgenera regardless of which researcher's opinion is considered. By using previous treatments which outlined some of the species-groups that may occur within the subgenus *Lasioglossum* sensu Michener, it was possible to reduce the number of species incorporated into the phylogenetic analysis, making both data collection and analysis feasible within a reasonable time frame. Complete phylogenetic analysis of all species in the genus is impossible, because of both the time required to analyse the characters and the impossibility of performing a phylogenetic analysis of so many taxa. Nonetheless, two comments

Fig. 4. Behaviour of *Lasioglossum* species mapped onto the phylogeny. Behaviour is indicated in a small box beside the taxon name (the absence of a box means that behavioural information is lacking); an open box refers to solitary behaviour and a solid box to sociality. Present knowledge indicates that social behaviour arose within the lineage leading to *L. aegyptiellum*. Because the behaviour of *L. discum* is unknown, sociality may have arisen in the common ancestor of *L. aegyptiellum* and *L. discum*; consequently, the state for *L. discum* is shown as equivocal (hatched).



on previous attempts at subdivision of this group may be made.

First, Pesenko's subgenus *Sericohalictus* should be subsumed within the *Leuchalictus* group (as is also suggested by Michener 1999); it is merely a highly autapomorphic species with obvious close affinities to the *L. leucozonium* species-group. Second, the inclusion of *L. laevigatum* within the *leucozonium* group is inappropriate; it has none of this group's apomorphic characters, it lacks both male characters used in the original diagnosis of the group, and its phylogenetic position is considerably removed from the *leucozonium* species-group in all of the more resolved phylogenies obtained. Given the instability of outgroup relationships in this analysis, any serious redistribution of taxa among named groups is unwarranted at this time. The results presented here support the view that a detailed morphological phylogenetic analysis of the major groupings within *Lasioglossum* will indeed be a difficult task.

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Appendix

Characters with an asterisk are multistate ones that were treated as unordered. Characters 1–43 were observed in females, the remainder in males. Because of outgroup complexity, the states listed below do not imply plesiomorphy or apomorphy.

Sterna and terga are referred to as S and T, respectively.

1. Colour: nonmetallic (0); metallic (1).
2. Sizes of supraclypeal punctures: fairly uniform (0); of two distinct sizes intermixed (1).

3\. Density of clypeal punctation: dense, interspaces less than diameter (0); intermediate, interspaces and punctures subequal, (1); sparse, interspaces greater than diameter of punctures (2).
4\. Punctation of apical area of clypeus: not reduced in density (0); markedly sparser than on more proximal portions (1).
5\. Surface of supraclypeus: smooth between punctures (0); tessellate or wrinkled (1).
6.* Sculpture of area immediately surrounding midocellus: punctate (0); with a smooth, impunctate area extending around entire anterior margin of ocellus (1); with smooth area lateral to midocellus only (2); smooth area anteriorly only (3).
7\. Face in profile: convex with supraclypeus raised well above level of compound eyes (0); comparatively flat (1).
8\. Impunctate area from close to epistomal area to halfway along inner margin of compound eye: absent (0); present (1).
9\. Strong lateral projection on either side of distal keel of labrum: absent (0); present (1).
10\. Basal elevation of female labrum: entire (0); notched so as to make the projection U- or V-shaped (1).
11\. Distal keel of female labrum: narrow (0); broad (1).
12\. Epistomal angle: so obtuse as to be almost straight (0); obtuse (1); forming a right angle (2); acute (3).
13\. Preoccipital ridge: absent (0); weak (1); strong (2).
14\. Head shape: wide, width (between outer margins of compound eyes) at least 10% greater than length (from clypeal margin to posterior margin of vertex) (0); round, less than 10% wider (1); elongate, head as long as wide or longer (2).
15\. Postocellar region: long, with distance from posterior margin of lateral ocelli to posterior margin of vertex longer than or equal to distance between lateral ocelli (measured from their posterior margin) (0); intermediate (1); short, at least 50% wider than long (2).
16\. Pronotal lateral angle: rounded (0); obtusely angulate (1); forming a right angle (2); acute (3).
17\. Lower portion of pronotal lateral ridge: rounded (0); carinate (1).
18\. Pronotum between apex of lateral angle and mesonotum: rounded (0); concave (1).
19\. Carinate margin between lateral angle and pronotal lobe: absent (0); present (1).
20\. Mesoscutal lip from above: convex (0); straight (1); concave (2).
21\. Mesoscutial lip in profile: gently rounded towards pronotum (0); slightly angulate (1); abruptly angled (2); acutely angled (3).
22\. Mesoscutal punctation density: sparse, interspaces wider than puncture diameter (0); intermediate interspaces and punctures subequal (1); dense, interspaces smaller than puncture diameter (2); crowded, interspaces sharply edged (3).
23\. Interspaces of mesoscutum: shiny (0); dull (1).
24.* Median scutellar impression: absent (0); broad but in posterior half only (1); narrow but complete (2).
25.* Scutellar punctation: sparse (0); dense (1); with an impunctate region on each side of disk (2).
26\. Metanotum: rugulose (0); punctate (1).
27\. Dorsal area of propodeum: long, closer in length to scutellum than to metanotum (0); intermediate, closer to metanotum in length than to scutellum (1); short, shorter than metanotum (2).
28\. Lateral propodeal carinae: short, not extending much farther than halfway up side of propodeum (0); long, extending to dorsal surface of propodeum (1); complete and extending across dorsal surface of propodeum (2).
29.* Surface of dorsal area of propodeum: smooth (0); ruguloso-striolate (1); weakly striate,with striations irregular (2); longitudinally striate, striations strong and mostly linear (3).
30\. Median apical rim of dorsal surface of propodeum: rounded (0); raised (1).
31\. Posterior margin of propodeum viewed from above: convex (0); straight or concave (1).
32.* Teeth of inner hind tibial spur: long, longer than basal breadth (0); intermediate, forming an equilateral triangle (1); short, semicircular (2).
33\. Colour of hind tibia: dark (0); orange (1).
34\. Basitibial plate: short, less than 15% of length of tibia (0); long, about 20% of length of tibia (1).
35.* Colour of hind tibial hairs: pale (0); yellowish (1); dark (2).
36\. Short, longitudinal carinae on anterolateral portions of T3 and (or) T4 (note that these appear similar to what is usually referred to as lateral gradular carinae): absent (0); present (1).
37\. First tergum: without a raised area on each side (0); with a raised area, which is usually markedly less densely punctate than adjacent regions (1).
38\. Surface of first tergum: smooth between the punctures, shiny (0); tessellate, dull (1).
39\. Basal hair band of T2: entire (0); narrowed medially (1); divided into lateral patches (2).
40\. Apical margins of terga 2–4: thick, dark (0); thinner, testaceous in colour (1); very thin, transparent (2).
41\. Apical impressed areas of T2 and T3: short, less than one-third length of tergite (0); moderately long, between one-third and one-half length of tergite (1); long, more than half as long as tergite (2).
42\. Fourth tergum: without markedly raised area (0); with area anterior to apical impression abruptly raised (1).
43\. Pubescence of T5: pale, white to orange (0); dark, brown to black (1).
44\. Apex of labrum: truncate (0); slightly convex (1).
45\. Incised and swollen basal projection of labrum: absent (0); present (1).
46\. Yellow maculation of clypeus: present (0); absent (1).
47\. Clypeus: punctate and convex across surface (0); impunctate and broadly concave (1).
48\. Mandible length: long, attaining opposing clypeal angle (0); short, not extending as far as opposing clypeal angle (1).
49\. Scape length: short, only twice as long as greatest breadth (0); intermediate, three to four times as long as wide (1); long, five times as long as wide (2).
50\. Flagellar annulus I: broader than long (0); quadrate (1); longer than broad (2).
51\. Flagellar annulus II: less than twice as long as broad (0); twice as long as broad or longer (1).
52\. Leg coloration: with extensive pale markings, all tarsi and basal maculation on tibiae pale (0); entirely dark (1).
53\. Carina on posterolateral margin of hind coxa: weak or absent (0); strongly developed, sharp (1); produced into a flange (2).
54\. Basitibial plate: weak or absent (0); strong (1).
55\. Tergum 7: with, at most, a weak transverse carina (0); carina with strong lateral angulations (1); carina triangularly produced on each side (2).
56\. Reflexed margin of T7: short, as short or shorter than scape width (0); intermediate, approximately 50% longer than width of scape (1); long, almost twice as long as scape width (2).
57\. Margin of pygidial plate: rounded (0); angulate (1).
58\. Pygidial plate: narrow (0); wide (1); very wide (2).
59\. Carinate margin of pygidial plate: weak (0); strong (1).

60. Profile of T7: not produced (0); strongly produced medially, so that pygidial plate overhangs margin of tergite (1).
61. Setae on S5: directed laterally (0); directed posteriorly (1); directed medially (2).
62. S5 apical margin: straight (0); slightly emarginate (1); strongly emarginate (2).
63.* Pubescence of S6: dense pubescent patch absent (0); with a V-shaped patch (1); pubescence in an inverted A shape (2); with the long arms of the inverted A approximated (3); with the apex of the A separated from the rest (4). This character was originally coded as unordered and then, based upon the results of phylogenetic analysis, treated as an ordered character (see the text).
64. Apical margin of S7: at least moderately wide (0); very narrow (1).
65.* Medial apodeme(s) of S7: absent (0); one present medially (1); two apodemes (often weak) present (2).
66. Medial pair of apodemes of S8: not developed (0); weak, occurring at most as slight reflexed margins (1); strong, projecting anteriorly (2).
67.* Apical margin of S8: broad and emarginate (0); broad and truncate or broadly rounded (1); narrowly rounded to pointed (2); sinuate with central and lateral projections (3).
68. S8 lateral to apical projection: concave (0); with a convex “shoulder” (1).
69. Shape of gonobase viewed from above: expanded towards apex (0); parallel-sided (1); narrowed apically (2).
70. Gonobase length: short (0); long (1).
71. Gonobase in lateral view: flat or gently curved towards gonoforceps (0); strongly convex (1); almost vertical (2).
72.* Gonobase/gonoforceps junction: smoothly continuous (0); angulate with gonoforceps abruptly broader than gonobase (1); gonobase with swollen collar just before gonoforceps (2).
73. Posterior ventral arms of gonobase: entire (0); interrupted medially (1).
74. Median longitudinal dorsal suture of gonobase: absent (0); weak (1); strong (2).
75. Gonostylus attachment: broadly based (0); arising from ventral margin of gonoforceps (1).
76.* Gonostylus shape: not flattened (0); flattened and elongate (1); flattened and wedge-shaped (2).
77. Area of gonostylus between apical stylus and retrorse lobe: unspecialised (0); at least slightly produced and usually with stronger setation (1).
78. Retrorse lobe of gonostylus: present (0); absent (1).
79.* Dorsal surface of penis valves: flat (0); slightly ridged on either side (1); with inner margin strongly produced (2).
80. Apex of penis valves: abruptly coming to a point (0); gradually narrowing to apex (1).
81.* Ventral process of penis valves in lateral view: absent (0); thin (1); broad (2); oriented medially (3).