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Australian *Lasioglossum* + *Homalictus* form a monophyletic group: resolving the "Australian enigma"

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Abstract -- The bee genus *Lasioglossum* includes over 1000 species of bees distributed on all continents except Antarctica. *Lasioglossum* is a major component of the bee fauna in the Holarctic, Ethiopian, and Oriental regions, and is an important group for investigating the evolution of social behavior in bees. Given its cosmopolitan distribution, the historical biogeography of the genus is of considerable interest. We reconstructed phylogenetic relationships among the subgenera and species within *Lasioglossum* s.s. using DNA sequence data from a slowly evolving nuclear gene, EF-1α. The entire data set includes over 1604 aligned nucleotide sites (including three exons plus two introns) for 89 species (17 outgroups plus 72 ingroups). Parsimony and maximum likelihood analyses provide strong evidence that the primarily Indoaustralian subgenera (*Homalictus*, *Chilalictus*, *Parasphecodes*) form a monophyletic group. Bootstrap support for the Australian clade ranged from 73% to 77% (depending on the method of analysis). Monophyly of the Australian *Lasioglossum* suggests that a single colonization event (via Southeast Asia and New Guinea) gave rise to a lineage of over 350 native Indoaustralian bees. We discuss the implications of Australian monophyly for resolving the "Australian enigma" -- similarity in social behavior among the Australian halictine bees relative to Holarctic groups.

[Key words: biogeography, phylogeny, maximum likelihood, elongation factor-1α, social evolution]

The Australian bee fauna is remarkable in many ways. Over half of the species of Australian bees belong to one family (Colletidae), which is commonly considered to be the most plesiomorphic of bees (Alexander & Michener, 1995). In addition, major families in other parts of the world are absent in Australia (Andrenidae and Melittidae), and Australia is surprisingly depauperate in parasitic bees (Wcislo, 1988). While the endemic Australian Colletidae (Euryglossinae) and Stenotritidae, and the predominantly Australian Paracolletini and Hylaeinae may represent groups that became isolated on Australia during the breakup of Gondwana in the Mesozoic, many other groups of bees have clearly colonized Australia from the north via Southeast Asia and New Guinea (Michener, 1979a). Numerous independent colonization events have occurred within the bee family Halictidae because several distantly related genera now occupy parts of Australia: *Nomioides* Schenck (Nomioidinae, 1 sp., Yeates & Exley, 1986), *Lipotriches* Gerstaecker (=*Nomia* Latreille; Nomiinae, approximately 70 spp., Cardale, 1993 and Michener 2000), *Sphecodes* Latreille (Halictinae, 2 sp., Cardale, 1993), *Pachyhalictus* Cockerell (Halictinae, 2 spp., Walker, 1993, 1996), *Lasioglossum* Curtis (Halictinae, many species, Michener, 1965; Walker, 1995), and *Homalictus* Cockerell (Halictinae, many species; Walker, 1986, 1997). By far the largest groups of Indoaustralian halictid bees are in the related genera *Lasioglossum* and *Homalictus*, which together account for nearly 350 species of Australian halictine bees.

The genus *Lasioglossum* includes over 1000 species worldwide with numerous subgenera and species groups recognized. The subgeneric groupings within *Lasioglossum* are treated by some authors as separate genera (see Krombein, *et al.*, 1979; Moure & Hurd, 1987) because they comprise such large and diverse taxa. Others treat *Lasioglossum* as a genus consisting of many subgenera

(Ebmer, 1987; Michener, 2000). For the purposes of this paper, we will refer to the genus *Lasioglossum* and its numerous subgenera (e.g., the *Lasioglossum* subgenus *Chilalictus* is referred to below as *L.* (*Chilalictus*), the *Lasioglossum* subgenus *Parasphecodes* as *L.* (*Paraphecodes*), and so on for all subgenera listed in Table 1).

Michener (2000) divided the subgenera of *Lasioglossum* into two groups: the *Hemihalictus* series, which includes all subgenera with a weakened 1st r-m cross vein in females, and the *Lasioglossum* series, which includes all subgenera with a completely sclerotized 1st r-m cross vein (Table 1). Six of the eight subgenera within the *Lasioglossum* series consist predominantly or exclusively of endemic Australian species: *Australictus*, *Callalictus*, *Chilalictus*, *Glossalictus*, *Parasphecodes*, and *Pseudochilalictus* (Table 1).

While *Homalictus* (plus the cleptoparasitic derivative, *Echthralictus* Perkins & Cheesman, found in Samoa [Perkins & Cheesman, 1928; Michener, 1965, 1978a]) has not recently been considered a subgenus of *Lasioglossum* (Michener, 2000), both morphological characters (*Lasioglossum sensu lato* and *Homalictus* share weakened 2r-m and 2m-cu cross veins in females (see Fig. 1 in Danforth, 1999)) and molecular data presented below indicate that *Homalictus* arises from within *Lasioglossum*. We have therefore chosen to refer to *Homalictus* as a subgenus of *Lasioglossum* throughout this paper. While *Homalictus* has its center of diversity in Australia, many species occur in New Guinea (Pauly, 1986; Michener, 1980a) and the group occurs as far north as Sri Lanka and southeast Asia and thence southward and eastward to Indonesia (Pauly, 1980), the Philippines (Cockerell, 1919; Michener, 1980b), and the islands of Fiji (Michener, 1979b) and Samoa, however all the available evidence suggests that *Homalictus* has its origins in Australia (Michener, 1979a).

Members of Indoaustralian *Lasioglossum* and *Homalictus* are

distinct both behaviorally and, to a lesser extent, morphologically, from their Holarctic relatives in the genus *Lasioglossum*. First, like most Australian bees, they primarily visit plants in the family Myrtaceae (such as *Melaleuca* and *Eucalyptus*; Walker, 1986 and Michener, 1965) for pollen and nectar. Other important sources of pollen and nectar include plants in the families Mimosaceae (such as *Acacia*), Proteaceae (such as *Banksia*), and Papilionaceae (Berhhardt & Walker, 1984, 1985; Bernhardt, 1987; Walker, 1986), and, to a lesser extent, Amaranthaceae, Asteraceae, Lamiaceae, Dilleniaceae, Frankeniaceae, Goodeniaceae, Haemodoraceae, Haloragaceae, Myoporaceae, Portulacaceae, Rutaceae, Solanaceae, Sterculiaceae, and Xanthorrhoeaceae (T. Houston, pers. comm.). Australian halictines are generally considered narrowly polylectic, in that most species restrict pollen foraging to Myrtaceae but will visit a diverse array of genera depending on locality. Nevertheless, a number of species are clearly oligolectic. *Lasioglossum* (*Chilalictus*) *megacephalum* is restricted to Goodeniaceae, *L.* (*Chilalictus*) *frankenia* is oligolectic on *Frankenia* (Frankeniaceae), and numerous species of *Chilalictus* are oligolectic on *Wahlenbergia* (Campanulaceae) (Walker, 1995). Only two subgenera of Holarctic *Lasioglossum*, *Hemihalictus* (Daly, 1961) and *Sphecodogastra* (McGinley, 2000), are known to be oligolectic.

More importantly, the Australian *Lasioglossum* and *Homalictus* have a unique array of behavioral attributes that distinguishes them from *Lasioglossum* in other parts of the world (Michener, 1960; Knerer & Schwarz, 1976, 1978). All species studied to date exhibit either solitary or communal nesting behavior (Michener, 1960, 1974), such that multiple females share a nest but do not cooperate in cell provisioning or show reproductive division of labor. Michener (1960) conducted a broad survey of species in *Homalictus*, *Chilalictus* and *Parasphecodes* by dissecting females

collected on flowers. For virtually all species examined, 100% of females are fertilized. Such results provide strong, though indirect, evidence that these species are not eusocial. More detailed studies involving nest excavations and dissections of foraging and resident females have been conducted on additional species, including *L.* (*Chilalictus*) *lanarium* (Knerer & Schwarz, 1978), *L.* (*Chilalictus*) *cognatum* (as *L.* [*Chilalictus*] *inclinans*, Knerer & Schwarz, 1978), *L.* (*Chilalictus*) *platycephalum* (as *L.* [*Chilalictus*] *mesembryanthemiellum*, Knerer & Schwarz, 1978; McConnell-Garner & Kukuk, 1997), *L.* (*Chilalictus*) *leai* (as *Halictus leai*, Cardale & Turner, 1966), and *L.* (*Chilalictus*) *hemichalceum* (Rayment, 1955; Houston, 1970; Kukuk, 1992; Kukuk & Schwarz, 1987, 1988; Kukuk & Crozier, 1990; Kukuk & Sage, 1994; Ward & Kukuk, 1998). In all cases, nests contained multiple, reproductively active females, and in some cases there was evidence of overlap in generations. Nests may be huge in some species, such as *Homalictus urbanus*, which has up to 160 females per nest (T. Houston obs., cited in Walker, 1986).

Among the more remarkable aspects of communal Australian *Lasioglossum* is that they defend their nests by plugging the nest entrance with the metasoma (Rayment, 1935; Michener, 1960; P. Kukuk pers. comm.; BND pers. obs.) while showing low levels of aggression towards conspecifics (Kukuk & Crozier, 1990; Kukuk, 1992; Kukuk & Sage, 1994). Molecular genetic studies indicate that nestmates in communal *Chilalictus* are unrelated (Kukuk & Sage, 1994) as one would expect for communal (as opposed to eusocial) species. Communal nesting is rare in the Holarctic groups of *Lasioglossum*. Species in the nominate subgenus, *Lasioglossum* s.s., have been observed by numerous authors to be solitary, while most species in the *Hemihalictus* series are primitively eusocial (e.g., numerous species of *Dialictus* and *Evylaeus*; see Michener [1990], Packer [1993], Yanega [1997], and Wcislo [1997] for reviews).

At least one species of Australian *Lasioglossum* (*L.* [*Chilalictus*] *hemichalceum*) shows discrete male dimorphism while male positive head allometry is widespread in the subgenus *Chilalictus* (Walker, 1995). Large-headed males in *L.* (*Chilalictus*) *hemichalceum* have been interpreted as guards (Houston, 1970; Kukuk & Schwarz, 1988).

Nest architecture in the Australian *Lasioglossum* and *Homalictus* is also distinct from their Holarctic relatives. All Australian *Lasioglossum* and *Homalictus* construct cells either in series (e.g., in *Homalictus* and some *Chilalictus*) or in clusters (some *Chilalictus*) (Knerer & Schwarz, 1976). Holarctic *Lasioglossum* typically construct sessile cells off of a central nest tunnel, as in *L.* (*Evylaeus*) *marginatum*, *L.* (*Evylaeus*) *malachurum*, and many species of *L.* (*Dialictus*), although some species (*L.* [*Evylaeus*] *duplex*) construct cells in clusters (Michener, 1974).

This unique suite of social attributes present in the Australian *Lasioglossum* and *Homalictus* was referred to by Knerer & Schwarz (1976) as the "Australian enigma." They presumed that the social behavior of the Australian halictines was convergently evolved, perhaps in response to heavy ant predation on ground-nesting bees, or in response to mutillid wasp attack (Rayment citations, in Michener, 1960). The classification of Australian halictine bees would not have suggested a common ancestral origin for Australian *Lasioglossum* and *Homalictus*, since *Homalictus* was considered a distinct genus, and even the Australian subgenera of *Lasioglossum* are not obviously monophyletic based on morphology (Michener, 1965). In addition, there is substantial morphological diversity among the Australian subgenera of *Lasioglossum*. Within *Chilalictus* alone there are small, metallic greenish species that superficially resemble North American *Dialictus* (in fact they were classified as such [using the synonymous name *Chloralictus*] prior to Michener's 1965 study), small black species similar to

Northern Hemisphere *Evylaeus*, and large species with metasomal hair bands and imbricate mesosomal sculpturing that resemble Northern Hemisphere *Lasioglossum* s.s.

We sought to test the hypothesis that the Australian subgenera of *Lasioglossum* plus *Homalictus* form a monophyletic group by analyzing a large nucleotide data set for a diverse array of species within *Lasioglossum* and *Homalictus* plus outgroups. If the Indoaustralian *Lasioglossum* + *Homalictus* form a monophyletic group, we would conclude that the unique social attributes of the Australian halictine bees are derived from a common ancestor which also had those traits, rather than through convergent evolution in social behavior. Likewise, monophyly would suggest a single colonization of Australia in the distant past, rather than multiple, recent colonizations.

We chose a nuclear, protein-coding gene, elongation factor-1α (EF-1α), for this study. EF-1α encodes an enzyme involved in the GTP-dependent binding of charged tRNAs to the acceptor site of the ribosome during translation (Maroni, 1993). Previous cladistic analyses of EF-1α sequence data have found that this gene provides useful phylogenetic information across a wide range of divergence times (Friedlander et al., 1992, 1994). Within insects, EF-1α has been shown to recover higher-level relationships in the moth subfamily Heliothinae (Cho et al., 1995), the moth superfamily Noctuoidea (Mitchell et al., 1997), and the bee genus *Halictus* (Danforth et al., 1999).

MATERIALS AND METHODS

Bees for this study were collected by the first author or generously provided by colleagues (see Acknowledgements). Specimens used for sequencing were primarily preserved in 95% EtOH but recently collected pinned specimens (less than five years old) and frozen specimens were also used. Outgroup and

ingroup taxa included in this study, locality data, specimen voucher numbers, and GenBank accession numbers are listed in Table 2.

DNA extractions followed standard protocols detailed in Danforth (1999). Two sets of PCR products were used to generate the data set. Initially, primers were designed based on a comparison of published *Drosophila* (Hovemann et al., 1988), *Apis* (Walldorf & Hovemann, 1990), and moth (Cho et al., 1995) sequences. Primers that initially amplified at least some halictid species included For1-deg, For3 and Cho10 (all primer sequences are listed in Danforth et. al, 1999). Based on initial comparisons of the F1 and F2 copies of EF-1α in halictid bees, we developed a new, F2-specific, reverse primer (F2-Rev1). For the downstream (3') end of EF-1α we used primers For3/Cho10. These primers amplify both EF-1α copies, however the presence of a roughly 200-250 bp intron in the F2 copy allows these PCR products to be separated on low-melting point agarose gels. Only the F2 copy was included in the present analysis.

PCR amplifications were carried out following standard protocols (Palumbi, 1996), with the following cycle conditions: 94°C, 1 min denaturation; 50-56°C, 1 min annealing; 72°C, 1 min to 1 min 20 sec extension. Prior to sequencing PCR products were either gel-purified in low-melting point agarose gels (FMC, Rockland, Maine) overnight at 4°C, or directly using the Promega (Madison, Wisconsin) Wizard PCR Preps DNA Purification kit.

For manual sequencing we used ^{33}P-labelled dideoxy chain termination reactions (Thermo Sequenase radiolabelled terminator cycle sequencing kit; Amersham Inc, Cleveland, Ohio) and standard 8% polyacrylamide gel electrophoresis, as indicated in the Amersham product manual.

Automated sequencing of PCR products was performed on an ABI 377 automated sequencer available through the Cornell Automated Sequencing Facility. Overall we sequenced EF-1α F2 in 89 species,

three of which were represented by more than one locality (giving a total of 92 OTUs). The region analyzed below corresponds with positions 196 to 1266 in the coding region of the insect EF-1α gene (Danforth & Ji, 1998), meaning our data set spans 77% of the 1386 bp coding region (Walldorf & Hovemann, 1990). As in the previous report (Danforth & Ji, 1998), we found two introns within the region analyzed (at locations 753/754 and 1029/1030).

Taxon sampling

While it was not possible to obtain representatives of all *Lasioglossum* subgenera, this study includes species from all the major subgenera. Of the eighteen widely recognized subgeneric groupings (five of which are monotypic), we included at least one member of nine of these groups and have sampled extensively within the three major North American and European subgenera *Dialictus*, *Evylaeus*, and *Lasioglossum s.s.*, as well as two major Australian subgenera, *Chilalictus* (Walker, 1995) and *Parasphecodes*. For the subgenus *Evylaeus* we included representatives of several species groups (as defined by Ebmer, 1995, 1997). Among the acarinate *Evylaeus* (as defined in Ebmer, 1997) we included representatives of the *morio*, *brevicorne*, *lucidulum/tarsatum*, *politum*, and *puncticolle* species groups. Among the carinate *Evylaeus* (as defined in Ebmer, 1995) we included representatives of the *calceatum*, *fulvicorne/fratellum*, *interruptum*, *laticeps*, *malachurum*, *marginatum*, and *pauxillum* species groups. The only large species groups that are missing from our data set are the *marginellum*, *punctatissimum*, and *trincinctum* groups. This paper focusses on the relationships among the *Lasioglossum* series of subgenera. A later paper (Danforth, in prep.) will focus on the subgeneric and species-group relationships within the *Hemihalictus* series.

Parsimony analysis

Phylogenetic analyses of nucleotide and amino acid sequences were performed using a beta test version of PAUP* (PAUP v. 4.0b2, Swofford, 1999). For equal weights parsimony analyses we used heuristic search with TBR branch swapping, random addition sequence for taxa, and fifty replicates per search. Bootstrap analysis (Felsenstein, 1985) was used to evaluate branch support on parsimony trees. Bootstrap values were calculated based on 100 replicates with ten random sequence additions per replicate and maxtrees set at 200.

Because our data set includes non-coding intron sequences, we inferred insertion/deletion mutations in the two included introns. However, it was possible to align the intron regions with little difficulty and gaps were generally short (from 1 to 4 bp in length). When analyzing the introns we employed gap coding methods developed by Hervé Sauquet and described in Danforth et al. (1999). This method of gap coding assigns individual indel mutations (of whatever length) a weight equal to a single nucleotide substitution while at the same time retaining information on sequence variation within indels. We report below only the analyses based on this gap coding method, but other methods (coding gaps as missing data and as a fifth state) gave similar results. Alignments for both the original and the recoded data sets are available from the corresponding author.

Maximum likelihood analysis

For the maximum likelihood (ML) analyses we initially used the equal weights parsimony trees obtained based on the gap-coded matrix to estimate the log likelihood of each tree under 20 distinct models of sequence evolution (Sullivan & Swofford, 1997; Frati et al., 1997; Huelsenbeck & Crandall, 1997). The four basic models were Jukes-Cantor (JC), Kimura two-parameter (K2P), Hasegawa-Kishino-Yano (HKY) and the General Time Reversible (GTR) model (Swofford, et al., 1996). Within each model we had five

methods of accounting for rate heterogeneity: no rate heterogeneity, gamma distributed rates (G), proportion of invariant sites (I), gamma + invariant sites (I+G), and site-specific rates (SSR; where each codon position plus introns were assigned a different rate). Using site-specific rates was appropriate in this case, because rate catagories could be identified *a priori* and because there were clear differences in rates among sites (see below).

Once likelihoods were calculated based on equal weights parsimony trees, we then performed branch swapping using appropriate ML models with a series of increasingly exhaustive branch swapping algorithms, in the following order: NNI, SPR(1), SPR(2), TBR(1), and TBR(2). Before each round of branch swapping the ML parameters were re-estimated based on the trees currently in memory and applied to the next round of branch swapping. The parameter estimates resulting from this search algorithm are discussed below. In all cases our branch swapping algorithms converged on the same tree irrespective of the model selected (see below).

For the ML analyses we excluded the following taxa in order to reduce search time: *L.* (*Parasphecodes*) *olgae* (Ctsp153), *L.* (*Lasioglossum*) *albocinctum*, L. (*Lasioglossum*) *leucozonium* (Lale133), *L.* (*Dialictus*) *imitatum*, *L.* (*Evylaeus*) *albipes* (Eval104), *L.* (*Evylaeus*) *comagenense*, *L.* (*Evylaeus*) *duplex*, and *L.* (*Sphecodogastra*) *oenotherae*. These sequences were all very similar to other sequences in the data set, either because they represented additional specimens of the same species, or because they are closely related to another species in the data set.

RESULTS

Alignment

The 92 sequences were aligned using MegAlign in the

Lasergene software package (DNASTAR Inc., Madison, Wisconsin). *Apis mellifera* (Walldorf & Hovemann, 1990) was included as a reference to determine the reading frame of the sequences. The region analyzed consists of two introns and three exons, as judged by comparison with the *Apis* coding sequence. Intron/exon junctions were universally AG/GT or AG/GA motifs.

Together the three exons represent 1,074 bp of aligned sequence with no insertion/deletion (indel) mutations observed. Intron 1 (positions 559-844) includes 286 aligned nucleotide sites (with 11 gap coded characters), and intron 2 (positions 1121-1364) includes 244 total aligned nucleotides (with 11 gap coded characters). The entire data set includes 1604 aligned nucleotide sites plus 22 numerical characters representing gap-coded variation. For the purposes of the analysis below we deleted two regions. First, we deleted an A/T rich insertion (positions 597-659) in intron 1 that was impossible to align and present in only 21 species (this proved to be a synapomorphic insertion, see below). Second, a 9 bp region (positions 1542-1550) in exon 3 that was subject to compression on manual sequencing gels was deleted.

Base composition

The overall base composition and the base composition broken down by character partition is shown in Table 3. Overall the base composition was only slightly A/T-biased (55%). The A/T bias was most significant in introns, where A and T accounted for 65% of the nucleotides. There was no significant heterogeneity among taxa in the proportion of bases based on a chi-square test (Table 3).

Phylogenetic analysis

In all analyses presented below we included 17 outgroup taxa in the following halictine genera: *Halictus* Latreille,

Agapostemon Guérin-Méneville, *Pseudagapostemon* Schrottky, *Sphecodes* Latreille and *Mexalictus* Eickwort, *Augochlora* Smith, *Augochloropsis* Cockerell, *Megalopta* Smith, and *Neocorynura* Schrottky (Table 2).

Equal weights parsimony analyses. -- Fig. 1 shows a strict consensus tree of the 336 equally parsimonious trees obtained based on an analysis of the entire data set (exons+introns). Two major clades within *Lasioglossum* are evident, supporting Michener's division of the genus into the *Hemihalictus* and *Lasioglossum* series (Table 1; Michener, 2000). Among the subgenera of the *Lasioglossum* series there were three major clades. First, the basal branch includes species of *Lasioglossum* s.s. from Europe and N. America, including *L.*(*L.*) *laevigatum*, *L.*(*L.*) *lativentre*, *L.*(*L.*) *sexnotatum* (European species) plus *L.*(*L.*) *pavonotum*, *L.*(*L.*) *fuscipenne*, *L.*(*L.*) *desertum*, *L.*(*L.*) *coriaceum*, *L.*(*L.*) *sisymbrii*, and *L.*(*L.*) *titusi* (all North American species). Most of the species included in this group have a weakly sculptured propodeal dorsal area that is long in relation to the metanotum. Second, the branch including *L.*(*L.*) *leucozonium* and *L.*(*L.*) *zonulum* (both of which occur in North America and Europe) and the exclusively Palaearctic species, *L.*(*L.*) *discum*, *L.*(*L.*) *callizonium*, *L.*(*L.*) *majus*, and *L.* (*L.*) *albocinctum*. These species (plus *L.*(*L.*) *aegyptiellum* and *L.*(*L.*) *subopacum*) are referred to as the *Lasioglossum leucozonium* species group (see Packer, 2000). The *leucozonium* group is united by at least four morphological characters (Packer, 2000), including (1) a patch of erect setae on the male S6 (Packer's character 63), (2) a flattened apical gonostylus (Packer's character 76), (3) ventral retrorse lobes of the gonostylus lacking (Packer's character 78), and (4) relatively short and coarsely sculptured propodeal dorsal area in females. Sister to the *leucozonium* group is a lineage of Indoaustralian subgenera

and species, including *Parasphecodes*, *Homalictus*, *Chilalictus*, and Australian species tentatively placed in a new subgenus (*L.* [Subgen. Nov. N.] NDA(1)-A; K. Walker, pers. comm.). This group will be referred to below as the "Australian clade" (Fig. 1).

Within the *Hemihalictus* series relationships among species are reasonably well resolved. Our EF-1α data set recovers a monophyletic subgenus *Dialictus*, places the subgenera *Hemihalictus* and *Sudila* in the "acarinate *Evylaeus*", and recovers monophyly of the *Evylaeus calceatum* group. Relationships within the *Hemihalictus* series imply that *Evylaeus* is paraphyletic with respect to several other subgenera included in this study (including *Dialictus*, *Hemihalictus*, *Sudila*, *Sphecodogastra*, and *Paralictus*). Based on the equal weights parsimony analysis neither the carinate nor the acarinate *Evylaeus* are monophyletic (Fig. 1).

Clades that are well supported by bootstrap values include *Lasioglossum* s.l. (97%), the *Lasioglossum* series of subgenera (95%), the *Hemihalictus* series of subgenera (100%), the *Lasioglossum leucozonium* group (100%), the *leucozonium* group + Australian clade (100%), and the Australian clade (76%) (Fig. 2). Interestingly, the A/T rich insertion in intron 1 (positions 597-659) proved to be a unique and unreversed synapomorphy of the *leucozonium* group plus the Australian clade, providing strong support for the monophyly of this group. Bootstrap support for the Australian clade varied from 73% to 77%, depending on how gaps were treated in the parsimony analysis. Six characters support Australian monophyly and all are third position transitions.

The EF-1α data provide strong support for Australian monophyly, and for the inclusion of *Homalictus* within *Lasioglossum* (see above). Relationships within the *Hemihalictus* series are well-resolved, and many higher-level groupings are clearly recovered by the EF-1α data, including monophyly of

Dialictus, close relationship between *Dialictus* and the acarinate *Evylaeus*, and clear resolution within the carinate *Evylaeus*.

Inclusion of introns in the parsimony analysis is crucial to reconstructing relationships within *Lasioglossum*. While exons account for roughly twice the number of nucleotide sites sequenced, they account for only half of the parsimony informative sites (Table 4). Virtually all of the variation in exons (86.4%) is in third position silent sites. As a result, the total number of parsimony informative amino acid changes was very small (Table 4).

Maximum likelihood analyses. -- We applied ML to our data for two reasons. First, there is substantial rate heterogeneity among sites. For coding sequences alone (exons) there are large differences among first, second, and third positions (with third positions evolving an order of magnitude faster than second positions). With the inclusion of non-coding introns there is an additional source of rate heterogeneity in that the introns evolve considerably faster than exons overall. Second, there is clear evidence of transition/transversion bias. Depending on the model of sequence evolution selected, transitions occur at a rate 3.67 to 4.12 times that of transversions, indicating that character state transformations within positions are not all equally probable.

As expected, the log likelihoods increased with increasingly complex models (Fig. 3). Allowing for variable transition/transversion ratios and accounting for rate heterogeneity among sites improved the likelihood scores considerably, however including empirical base frequencies (HKY) as opposed to equal base frequencies (K2P) did not improve the likelihood score as judged by the likelihood ratio test ($-2 \ln \Lambda = -9.42$, df = 3, ns; Huelsenbeck & Crandall, 1997). We chose to use the K2P model with site-specific rates because this was the

simplest model that substantially improved the likelihood scores, and because search times under this model were shorter on the Power Mac G3 computer used for the ML analysis.

Branch swapping led to only slight increases in -Ln likelihood (from 15370.82 to 15361.75), indicating that the parsimony trees come very close to the tree topologies estimated under ML. In an analysis of the entire data set (exons and introns) we obtained one tree (-Ln likelihood = 15361.75; Fig. 4). We also performed branch swapping under more complex models (e.g., HKY+SSR and GTR+SSR). In either case we obtained the same final tree topology as obtained with the simpler model (K2P+SSR). Estimates of the relative rate of substitution indicated that third positions evolve at roughly the same rate as introns, and both introns and third positions evolve roughly an order of magnitude faster than either first or second positions: introns, 1.64; nt1, 0.17; nt2, 0.06; nt3, 1.93 (based on the K2P+SSR model).

The tree topology obtained using likelihood (Fig. 4) recovers many of the same higher nodes as the consensus of equally parsimonious trees (Fig. 1) and the 50% bootstrap consensus tree (Fig. 2). Based on ML we recovered monophyletic *Hemihalictus* and *Lasioglossum* series, a monophyletic *leucozonium* group, a monophyletic Australian clade, and a sister group relationship between the *leucozonium* group and the Australian clade.

DISCUSSION

Phylogenetic results

While we were unable to include representatives of all the Australian subgenera, it is likely that the Australian subgenera that were not included (*Callalictus*, *Pseudochilalictus*, and *Australictus*) are closely related to those that were included in

our analysis. Species of *Australictus* and *Callalictus* are similar morphologically to species of *Parasphecodes*. The relationship of *Pseudochilalictus* (a monotypic subgenus) to the other subgenera is not clear, but *Pseudochilalictus* may be closely related to *Parasphecodes* (possibly rendering *Parasphecodes* paraphyletic; K. Walker, pers. comm.)

The results presented above provide strong and unambiguous support for monophyly of *Homalictus* plus the Australian *Lasioglossum* irrespective of the data partitions analyzed, the methods used for coding gaps, or the methods of analysis (parsimony vs. likelihood). While this hypothesis is novel, it is not incompatible with any morphological characters.

Biogeographic implications

The sister group relationship implied by these data between the *Lasioglossum leucozonium* group and the Australian clade makes sense biogeographically. The subgenus *Lasioglossum* is widespread across the Palaearctic from western Europe to Japan and southward to southeast Asia. The *leucozonium* group is also widespread across the Palearctic region. The genus *Lasioglossum* (like *Halictus*, a closely related genus) is primarily a northern Hemisphere group. The Australian clade represents the only major radiation of *Lasioglossum* in the southern Hemisphere.

The presence of species of *Homalictus* outside of Australia is likely due to dispersal from Australia, rather than the reverse, as suggested by Michener (1979a), since the majority of species are Australian endemics.

The results presented here for Australian halictine bees parallel the results for bird higher level relationships as determined by DNA-DNA hybridization studies (Sibley & Ahlquist, 1985, 1990; Sibley, Ahlquist, & Monroe, 1988). The major lineage of passerine birds of the world (the oscines, Suborder Passeres) is composed of two large, monophyletic, sister clades: the

Parvorder Corvida and the Parvorder Passerida. These two lineages are estimated to have diverged in the Eocene or Oligocene, according to molecular clock estimates from DNA-DNA hybridization (Sibley & Ahlquist, 1990). The three major superfamilies within the Corvida include the Menuroidea (31 spp.), the Meliphagoidea (276 spp.) and the Corvoidea (794 spp.). Relationships implied by the DNA hybridization studies place the Meliphagoidea and Corvoidea as sister groups (Sibley, Ahlquist & Monroe, 1988). Within the Parvorder Passerida there are three recognized superfamilies: Muscicapoidea (610 spp.), Sylvioidea (1195 spp.), and Passeroidea (1651 spp.), and the Sylvioidea and Passeroidea are sister groups. When one considers the zoogeographic distributions of these groups, it is clear that virtually all of the families within the Parvorder Corvida are endemic to Australia or share a common ancestor that was originally Austro-Papuan. Two of the corvid superfamilies are exclusively Australian (Menuroidea and Meliphagoidea), and the majority of families within the Corvoidea are Austro-Papuan endemics. Derived members of the Parvorder Corvida have dispersed from Australia to other parts of the world, including Eurasia, N. America, and S. America. Groups that have dispersed from Australia or that have been derived from Australian ancestors include the Families Irenidae, Laniidae, Vireonidae, and three subfamilies within the family Corvidae (Corvinae, Aegithininae, and Malaconotinae).

While there are representatives of the Parvorder Passerida in Australia, these are recent colonists from groups with origins in Eurasia and Africa (Sibley & Ahlquist, 1990). Because of the distinction between the two Parvorders, Sibley & Ahlquist distinguish between the "old endemics" (including Australian members of the Parvorder Corvida) and the "new endemics" (including the Australian members of the Parvorder Passerida). Of the 700 species of Austro-Papuan passerines, 400 (57%) are "old endemics." The recognition of Australian endemism in the Corvida

resolved many problems in bird phylogeny because convergent evolution among members of the two Parvorders had obscured the true phylogenetic affinities in many cases.

Our results for halictine bees parallel those of Sibley and Ahlquist for birds. A major radiation within Australia has given rise to an endemic fauna (400 species in the passerine birds and over 350 species of halictine bees) that shows convergent features with relatives from other parts of the world. As with Australian passerines, halictine bees that originated in Australia have given rise to descendants now present in neighboring regions, including Sri Lanka, southeast Asia, New Guinea, the Philippines (*Homalictus*), and Samoa (*Echthralictus*). That the Australian *Lasioglossum* + *Homalictus* form a monophyletic group helps resolve many questions in halictid bee social evolution and biogeography. Other major Australian radiations include the marsupial mammals (Archer, 1981) and the plant family Myrtaceae (Beadle, 1981).

Evidence of Australian monophyly among *Lasioglossum* subgenera also helps resolve the "Australian enigma" posed by Knerer & Schwarz (1976). Similarity among the Australian *Lasioglossum* in flower associations, nest architecture, and sociality (with most Australian *Lasioglossum* being communal rather than eusocial) is likely due to common ancestry rather than convergent evolution. Ecological factors such as mutillid parasitism and ant predation may have favored communal associations among nestmates in the early Australian colonists.

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Table 1. Classification of the subgenera of *Lasioglossum* (modified slightly from Michener, 2000).

Subgenus (no. species)	Distribution
Lasioglossum series	
Ctenonomia Cameron (>100)	Paleotropical (mostly SE Asia)
Lasioglossum Curtis s.s. (>150)[a]	Holarctic and Mesoamerican
Australictus Michener (10)	Australia (widespread)
Callalictus Michener (8)	Australia (VIC, SA, NSW, QLD)
Chilalictus Michener (134)	Australia (widespread) & New Caledonia (1 sp.)
Glossalictus Michener (1)	Australia (WA)
Parasphecodes Smith (92)	Australia (widespread) & New Guinea
Pseudochilalictus Michener (1)	Australia (NSW & QLD)
Homalictus Cockerell (94)[b]	Indoaustralia (widespread)
Echthralictus Perkins & Cheesman (2)[b, c]	Samoa
Hemihalictus series	
Acanthalictus Cockerell (1)	Siberia
Austrevylaeus Michener (9)	Australia & New Zealand
Dialictus Robertson (>300)[a]	Nearctic/Neotropical
Evylaeus Robertson (>100)[a]	Holarctic/Neotropical

Hemihalictus Cockerell (1)	Nearctic
Paradialictus Pauly (1)	Africa (Zaire)
Paralictus Robertson (3)[c]	Nearctic
Sellalictus Pauly (11)	Africa (Zaire to Cape Prov.)
Sphecodogastra Ashmead (8)	Nearctic
Sudila Cameron (6)	Sri Lanka and Malaysia

[a] Indicates subgenera with both solitary and eusocial species.

[b] Previously not considered as part of *Lasioglossum*.

[c] Indicates socially parasitic subgenera.

Table 2 -- Taxa included in this study, collecting localities, specimen voucher codes, and GenBank Accession numbers.

Species	Locality	Voucher Code[a]	GenBank Accession
Outgroup taxa:			
Augochlora pura (Say)	Ithaca, New York, USA	Aupu333	AF140314
Augochloropsis metallica (Fabricius)	Ithaca, New York, USA	Aume334	AF140315
Megalopta genalis Meade-Waldo	Smithsonian Tropical Res. Station, Republic of Panamá	Mgge247	AF140316
Neocorynura discolor (Smith)	Colombia	Ncdi249	AF140317
Agapostemon kohliellus (Vachal)	Dominican Republic	Agko12	AF140318
Agapostemon sericeus (Forster)	Ithaca, New York, USA	Agse162	AF140319
Agapostemon tyleri (Cockerell)	Portal, Arizona, USA	Agty230	AF140320
Agapostemon virescens (Fabricius)	Ithaca, NY, USA	Agvr161	AF140321
Pseudagapostemon brasiliensis Cure	Minas Gerais, Brazil	Psbr347	AF140323
Halictus (*Halictus*) *farinosus* Smith	Logan, Utah, USA	Hafa25	AF140332
Halictus (*Halictus*) *ligatus* Say	Rock Hill, South Carolina, USA	Hali(c)	AF140300
Halictus (*Halictus*) *poeyi* Lepeletier	Rock Hill, South Carolina, USA	Hapo(d)	AF140303
Halictus (*Halictus*) *rubicundus* (Christ)	Missoula, Montana, USA	Haru32	AF140335
Halictus (*Seladonia*) *confusus* Smith	Junius Ponds, New York, USA	Haco301	AF140304
Mexalictus arizonensis Eickwort	Miller canyon, Arizona, USA	Mxaz97	AF140322
Sphecodes minor Robertson	Sydney, Nova Scotia, Canada	Spmi21	AF140324
Sphecodes ranunculi Robertson	Ithaca, New York, USA	Spra337	AF140325
Ingroup taxa:			
L. (*Chilalictus*) *convexum* (Smith)	Cobboboonee S.F., Victoria, Australia	Chcv156	AF264790

L. (*Chilalictus*) *conspicuum* (Smith)	Cobboboonee S.F., Victoria, Australia	Chcs155	AF264789
L. (*Chilalictus*) *cognatum* (Smith)	Cobboboonee S.F., Victoria, Australia	Chcg317	AF264788
L. (*Chilalictus*) *erythrurum* (Cockerell)	6km E. SA/WA border, S. Australia	Chey308	AF264791
L. (*Chilalictus*) *florale* (Smith)	6km E. SA/WA border, S. Australia	Chfl320	AF264792
L. (*Chilalictus*) *lanarium* (Smith)	Cobboboonee S.F., Victoria, Australia	Chla316	AF264793
L. (*Chilalictus*) *mediopolitum* (Ckll.)	6km E. SA/WA border, S. Australia	Chmd291	AF264794
L. (*Chilalictus*) *mirandum* (Cockerell)	Bluff Knoll, Stirling Range NP, W. Australia, Australia	Chmi319	AF264795
L. (*Chilalictus*) *parasphecodum* (Walker)	6km E. SA/WA border, S. Australia	Chps318	AF26496
L. (*Chilalictus*) *supralucens* (Cockerell)	Bluff Knoll, Stirling Range NP, W. Australia, Australia	Chsu295	AF26497
L. (*Dialictus*) *cressonii* (Robertson)	Ontario, Canada	Dicr66	AF264801
L. ("*Dialictus*") *figueresi* Wcislo	Republic of Panamá	Difi341	AF264802
L. (*Dialictus*) *gundlachii* (Baker)	Puerto Rico	Digu48	AF264803
L. (*Dialictus*) *hyalinum* (Crawford)	Mt. Lemmon, Arizona, USA	Diha277	AF264804
L. (*Dialictus*) *imitatum* (Smith)	Ithaca, New York, USA	Diim27	AF264805
L. (*Dialictus*) *parvum* (Cresson)	Puerto Rico	Dipa7	AF264806
L. (*Dialictus*) *pilosum* (Smith)	Junius Ponds, New York, USA	Dipi71	AF264807
L. (*Dialictus*) *rohweri* (Ellis)	Junius Ponds, New York, USA	Dirh79	AF264808
L. (*Dialictus*) *tegulare* (Robertson)	Junius Ponds, New York, USA	Ditg81	AF264809
L. (*Dialictus*) *umbripenne* (Ellis)	Republic of Panamá	Dium322	AF264810
L. (*Dialictus*) *vierecki* (Crawford)	Junius Ponds, New York, USA	Divi67	AF264811
L. (*Dialictus*) *zephyrum* (Smith)	Junius Ponds, New York, USA	Dizp74	AF264812
L. (*Evylaeus*) *albipes* (Fabricius)	Les Eyzies, Dordogne, France (social)	Eval99	AF264814
L. (*Evylaeus*) *albipes* (Fabricius)	Longemer & Col de la Schlucht, Vosges, France (solitary)	Eval104	AF264813

L. (*Evylaeus*) *apristum* (Vachal)	Mt.Sanbe, Shimane Prefecture, Japan	Evap145	AF264815
L. (*Evylaeus*) *boreale* Svensson	Inuvik, NWT, Canada	Evbo262	AF264816
L. (*Evylaeus*) *calceatum* (Scopoli)	Les Eyzies, Dordogne, France	Evca105	AF264817
L. (*Evylaeus*) *cinctipes* (Provancher)	Ithaca, New York, USA	Evci311	AF264818
L. (*Evylaeus*) *comagenense* Knerer & Atwood	Sydney, Nova Scotia, Canada	Evco255	AF264819
L. (*Evylaeus*) *duplex* (Dalla Torre)	Sendai, Miyagi Prefecture, Japan	Evdu142	AF264820
L. (*Evylaeus*) *fulvicorne* (Kirby)	Ventoux, Vaucluse, France	Evfu310	AF264821
L. (*Evylaeus*) *gattaca* Danforth & Wcislo	Chiriquí Province, Republic of Panamá	Evsp324	AF264834
L. (*Evylaeus*) *laticeps* (Schenck)	Les Eyzies, Dordogne, France	Evla117	AF264822
L. (*Evylaeus*) *lineare* (Schenck)	Pont-Saint-Vincent, Meurthe et Moselle, France	Evli137	AF264823
L. (*Evylaeus*) *marginatum* (Brullé)	Les Eyzies, Dordogne, France	Evmg108	AF264825
L. (*Evylaeus*) *malachurum* (Kirby)	Les Eyzies, Dordogne, France	Evml111	AF264826
L. (*Evylaeus*) *mediterraneum* (Blûthgen)	Les Eyzies, Dordogne, France	Evme289	AF264824
L. (*Evylaeus*) *morio* (Fabricius)	Les Eyzies, Dordogne, France	Evmo148	AF264827
L. (*Evylaeus*) *nigripes* (Lepeletier)	Beaumont du Ventoux, Vaucluse, France	Evng129	AF264828
L. (*Evylaeus*) *pauxillum* (Schenck)	Vienna, Austria	Evpa131	AF264829
L. (*Evylaeus*) *pectorale* (Smith)	Florida, USA	Evpe10	AF264830
L. (*Evylaeus*) *politum* (Schenck)	Les Eyzies, Dordogne, France	Evpo122	AF264831
L. (*Evylaeus*) *puncticolle* (Morawitz)	Les Eyzies, Dordogne, France	Evpu128	AF264832
L. (*Evylaeus*) *quebecense* (Crawford)	no locality data	Evqu325	AF264833
L. (*Evylaeus*) *subtropicum* Sakagami	Iriomote Is., Okinawa Prefecture, Japan	Evsu139	AF264835
L. (*Evylaeus*) *truncatum* (Robertson)	Ithaca, New York, USA	Evtr312	AF264836
L. (*Evylaeus*) *villosulum* (Kirby)	Les Eyzies, Dordogne, France	Evvi125	AF264837
L. (*Hemihalictus*) *lustrans* (Cockerell)	Bastrop, Texas, USA	Helu186	AF264838

L. (*Homalictus*) *megastigmus* (Cockerell)	Bluff Knoll, Stirling Range NP, W. Australia, Australia	Homg360	AF264839
L. (*Homalictus*) *punctatus* (Smith)	Adelaide, S. Australia, Australia	Hopu245	AF264840
L. (*Lasioglossum*) *albocinctum* Lucas	France	Laab315	AF338386
L. (*Lasioglossum*) *callizonium* (Pérez)	Berja, Almeria Prov., Spain	Laca380	AF264841
L. (*Lasioglossum*) *coriaceum* (Smith)	no locality data	Laco15	AF264842
L. (*Lasioglossum*) *desertum* (Smith)	Rose Canyon Lake, Arizona, USA	Lade251	AF264843
L. (*Lasioglossum*) *discum* (Smith)	France	Ladi313	AF264850
L. (*Lasioglossum*) *fuscipenne* (Smith)	Michigan, USA	Lafu65	AF264844
L. (*Lasioglossum*) *laevigatum* (Kirby)	Les Eyzies, Dordogne, France	Lala23	AF264845
L. (*Lasioglossum*) *lativentre* (Schenck)	Les Eyzies, Dordogne, France	Lalt120	AF264848
L. (*Lasioglossum*) *leucozonium* (Schrank)	Les Eyzies, Dordogne, France	Lale133	AF264846
L. (*Lasioglossum*) *leucozonium* (Schrank)	Ithaca vicinity, New York, USA	Lale170	AF264847
L. (*Lasioglossum*) *majus* (Nylander)	France	Lamj314	AF264849
L. (*Lasioglossum*) *pavonotum* (Cockerell)	Point Reyes Natl. Sea Shore, California, USA	Lapa339	AF264851
L. (*Lasioglossum*) *sexnotatum* (Kirby)	Morigny-Champigny, Essonne, France	Lasx136	AF264853
L. (*Lasioglossum*) *sisymbrii* (Cockerell)	Chiricahua Mts., Arizona, USA	Lasi253	AF264852
L. (*Lasioglossum*) *titusi* (Crawford)	Twentynine Palms, California, USA	Lati167	AF264854
L. (*Lasioglossum*) *zonulum* (Smith)	Ithaca, New York, USA	Lazo284	AF264855
L. (*Paralictus*) *asteris* Mitchell	Ithaca, New York, USA	Paas30	AF264856
L. (*Parasphecodes*) *hybodinum* (Cockl.)	6km E. SA/WA border, S. Australia, Australia	Pahy299	AF264857
L. (*Parasphecodes*) *olgae* (Rayment)	Cobboboonee S.F., Victoria, Australia	Ctsp153	AF264798
L. (*Parasphecodes*) *olgae* (Rayment)	S. Australia, Australia	Ctsp397	AF264800

L. (*Parasphecodes*) sp.	Cobboboonee S.F., Victoria, Australia	Pasp160	AF264858
L. (*Sphecodogastra*) *noctivagum* Linsley & MacSwain	Monahans Sand Hills, Texas, USA	Stno258	AF264859
L. (*Sphecodogastra*) *oenotherae* (Stevens)	Ithaca, New York, USA	Stoe54	AF264860
L. (*Sudila*) *alphenum* (Cameron)	Hakgala Botanical Garden, NE District, Sri Lanka	Sual390	AF264861
L. (Subgen. Nov. N.) NDA(1)-A	Cobboboonee S.F., Victoria, Australia	Ctsp297	AF264799

[a] Voucher specimens and DNA extractions are housed in the Cornell University Insect Collection.

Table 3 -- Base composition of EF-1α sequence data.

	A	C	G	T	p-value[a]
Exon	26.5	24.7	24.2	24.5	1.0
nt1	28.7	18.2	38.3	14.8	1.0
nt2	30.2	26.1	16.2	27.5	1.0
nt3	20.7	29.8	18.1	31.3	1.0
Intron	29.5	16.0	19.0	35.5	1.0
Overall	27.4	22.2	22.7	27.6	1.0

[a] p-values refer to the probability of rejecting the null hypothesis of homogeneity among taxa in base composition.

Table 4 -- Composition of introns and exons.

	Total	Const.	Pars. Uninf.	Pars. Inf.
Exons	1074	731	63	280
nt1	358	318	14	26
nt2	358	335	11	12
nt3	358	78	38	242
Introns[a]	489	168	60	261
Amino acids	358	314	19	25

[a] Based on gap coded data set.

Figure captions

Fig. 1. Strict consensus tree based on analysis of unweighted nucleotide data; exons plus introns with indel mutations coded as described in Danforth et. al. (1999) (1540 nucleotide positions; 534 parsimony informative characters; ci = 0.3946, ri = 0.7541, length = 2477). Outgroups included *Halictus* (*Seladonia*) *confusus*, *Halictus* (*Halictus*) *farinosus*, *H.* (*H.*) *rubicundus*, *H.* (*H.*) *ligatus*, *H.* (*H.*) *poeyi*, *Agapostemon kohliellus*, *A. sericeus*, *A. tyleri*, *A. virescens*, *Pseudagapostemon brasilensis*, *Mexalictus arizonensis*, *Sphecodes minor*, *Sphecodes ranunculi*, *Augochloropsis metallica*, *Megalopta genalis*, *Augochlora pura*, and *Neocorynura discolor*.

Fig. 2. 50% bootstrap consensus tree based on analysis of unweighted nucleotide data; exons plus introns with indel mutations coded as described in Danforth et. al. (1999). Outgroups as in Fig. 1.

Fig. 3. -Ln likelihoods based on the equal weights parsimony trees for 20 models of sequence evolution. Likelihoods improved slightly with branch swapping, as described in Results. SSR refers to site-specific rates for introns, first, second, and third positions. The arrow indicates the model used for tree searching.

Fig. 4. -- Maximum likelihood analysis based on the K2P+SSR model. -Ln likelihood = 15361.75. Branch lengths are shown as proportional to character changes.

Fig. 1

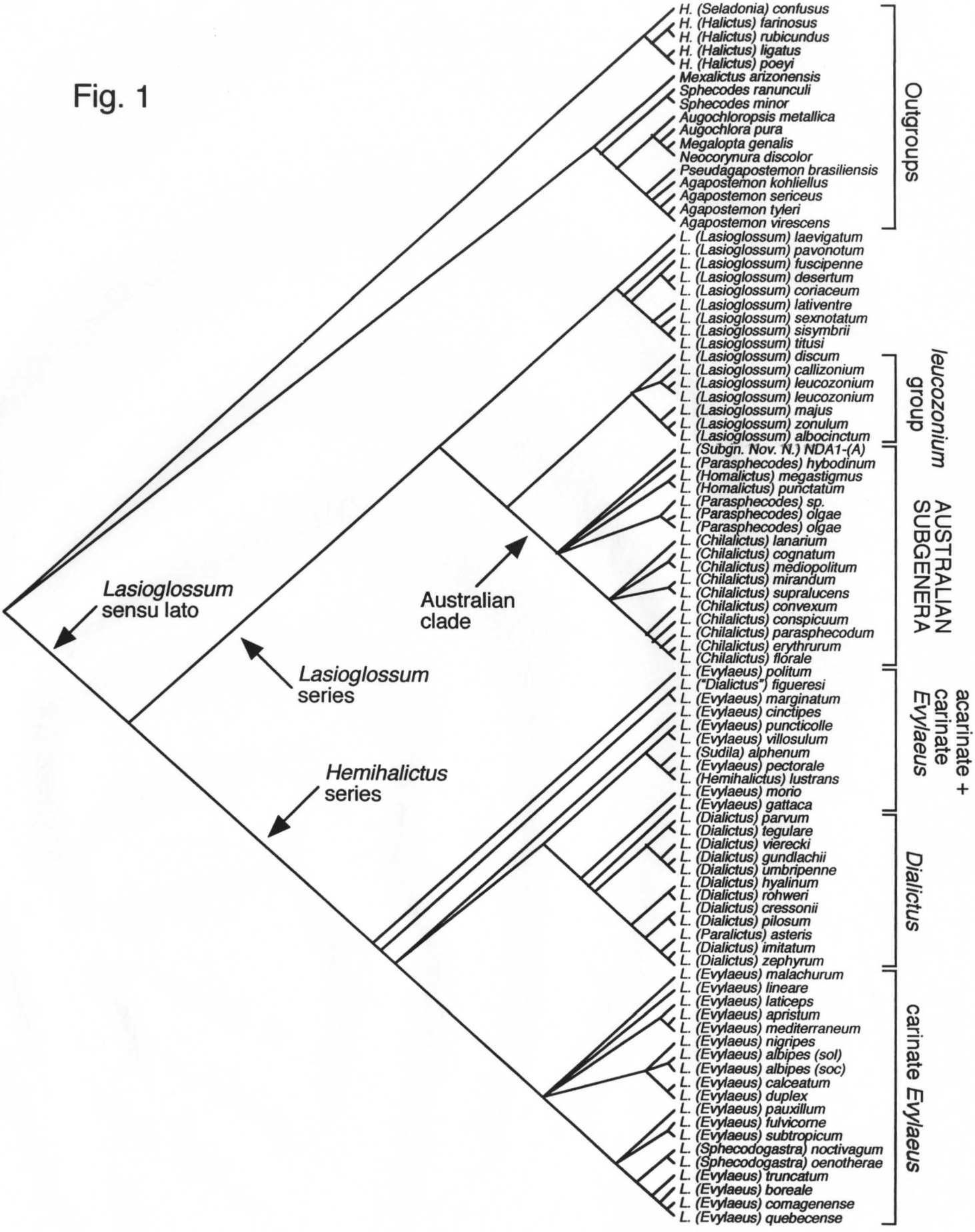
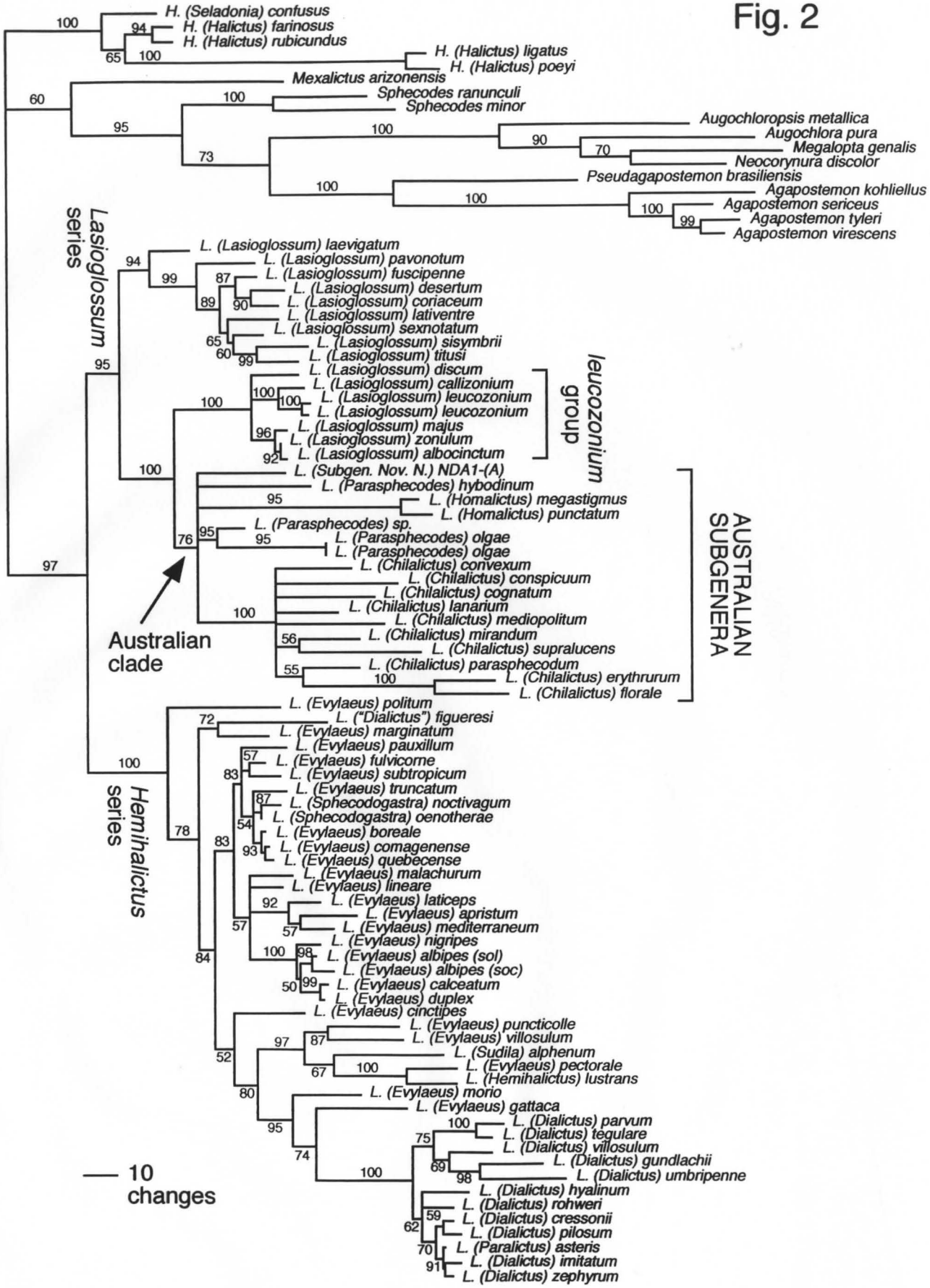

H. (Seladonia) confusus
H. (Halictus) farinosus
H. (Halictus) rubicundus
H. (Halictus) ligatus
H. (Halictus) poeyi
Mexalictus arizonensis
Sphecodes ranunculi
Sphecodes minor
Augochloropsis metallica
Augochlora pura
Megalopta genalis
Neocorynura discolor
Pseudagapostemon brasiliensis
Agapostemon kohliellus
Agapostemon sericeus
Agapostemon tyleri
Agapostemon virescens
Outgroups
L. (Lasioglossum) laevigatum
L. (Lasioglossum) pavonotum
L. (Lasioglossum) fuscipenne
L. (Lasioglossum) desertum
L. (Lasioglossum) coriaceum
L. (Lasioglossum) lativentre
L. (Lasioglossum) sexnotatum
L. (Lasioglossum) sisymbrii
L. (Lasioglossum) titusi
L. (Lasioglossum) discum
L. (Lasioglossum) callizonium
L. (Lasioglossum) leucozonium
L. (Lasioglossum) leucozonium
L. (Lasioglossum) majus
L. (Lasioglossum) zonulum
L. (Lasioglossum) albocinctum
leucozonium group
L. (Subgn. Nov. N.) NDA1-(A)
L. (Parasphecodes) hybodinum
L. (Homalictus) megastigmus
L. (Homalictus) punctatum
L. (Parasphecodes) sp.
L. (Parasphecodes) olgae
L. (Parasphecodes) olgae
L. (Chilalictus) lanarium
L. (Chilalictus) cognatum
L. (Chilalictus) mediopolitum
L. (Chilalictus) mirandum
L. (Chilalictus) supralucens
L. (Chilalictus) convexum
L. (Chilalictus) conspicuum
L. (Chilalictus) parasphecodum
L. (Chilalictus) erythrurum
L. (Chilalictus) florale
AUSTRALIAN SUBGENERA
L. (Evylaeus) politum
L. ("Dialictus") figueresi
L. (Evylaeus) marginatum
L. (Evylaeus) cinctipes
L. (Evylaeus) puncticolle
L. (Evylaeus) villosulum
L. (Sudila) alphenum
L. (Evylaeus) pectorale
L. (Hemihalictus) lustrans
L. (Evylaeus) morio
L. (Evylaeus) gattaca
acarinate + carinate Evylaeus
L. (Dialictus) parvum
L. (Dialictus) tegulare
L. (Dialictus) vierecki
L. (Dialictus) gundlachii
L. (Dialictus) umbripenne
L. (Dialictus) hyalinum
L. (Dialictus) rohweri
L. (Dialictus) cressonii
L. (Dialictus) pilosum
L. (Paralictus) asteris
L. (Dialictus) imitatum
L. (Dialictus) zephyrum
Dialictus
L. (Evylaeus) malachurum
L. (Evylaeus) lineare
L. (Evylaeus) laticeps
L. (Evylaeus) apristum
L. (Evylaeus) mediterraneum
L. (Evylaeus) nigripes
L. (Evylaeus) albipes (sol)
L. (Evylaeus) albipes (soc)
L. (Evylaeus) calceatum
L. (Evylaeus) duplex
L. (Evylaeus) pauxillum
L. (Evylaeus) fulvicorne
L. (Evylaeus) subtropicum
L. (Sphecodogastra) noctivagum
L. (Sphecodogastra) oenotherae
L. (Evylaeus) truncatum
L. (Evylaeus) boreale
L. (Evylaeus) comagenense
L. (Evylaeus) quebecense
carinate Evylaeus
Lasioglossum sensu lato
Australian clade
Lasioglossum series
Hemihalictus series

Fig. 2


H. (Seladonia) confusus
H. (Halictus) farinosus
H. (Halictus) rubicundus
H. (Halictus) ligatus
H. (Halictus) poeyi
Mexalictus arizonensis
Sphecodes ranunculi
Sphecodes minor
Augochloropsis metallica
Augochlora pura
Megalopta genalis
Neocorynura discolor
Pseudagapostemon brasiliensis
Agapostemon kohliellus
Agapostemon sericeus
Agapostemon tyleri
Agapostemon virescens
Lasioglossum series
L. (Lasioglossum) laevigatum
L. (Lasioglossum) pavonotum
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L. (Lasioglossum) callizonium
L. (Lasioglossum) leucozonium
L. (Lasioglossum) leucozonium
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L. (Parasphecodes) sp.
L. (Parasphecodes) olgae
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L. (Chilalictus) convexum
L. (Chilalictus) conspicuum
L. (Chilalictus) cognatum
L. (Chilalictus) lanarium
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AUSTRALIAN SUBGENERA
Australian clade
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L. (Sphecodogastra) noctivagum
L. (Sphecodogastra) oenotherae
L. (Evylaeus) boreale
L. (Evylaeus) comagenense
L. (Evylaeus) quebecense
L. (Evylaeus) malachurum
L. (Evylaeus) lineare
L. (Evylaeus) laticeps
L. (Evylaeus) apristum
L. (Evylaeus) mediterraneum
L. (Evylaeus) nigripes
L. (Evylaeus) albipes (sol)
L. (Evylaeus) albipes (soc)
L. (Evylaeus) calceatum
L. (Evylaeus) duplex
L. (Evylaeus) cinctipes
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L. (Evylaeus) villosulum
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L. (Hemihalictus) lustrans
L. (Evylaeus) morio
L. (Evylaeus) gattaca
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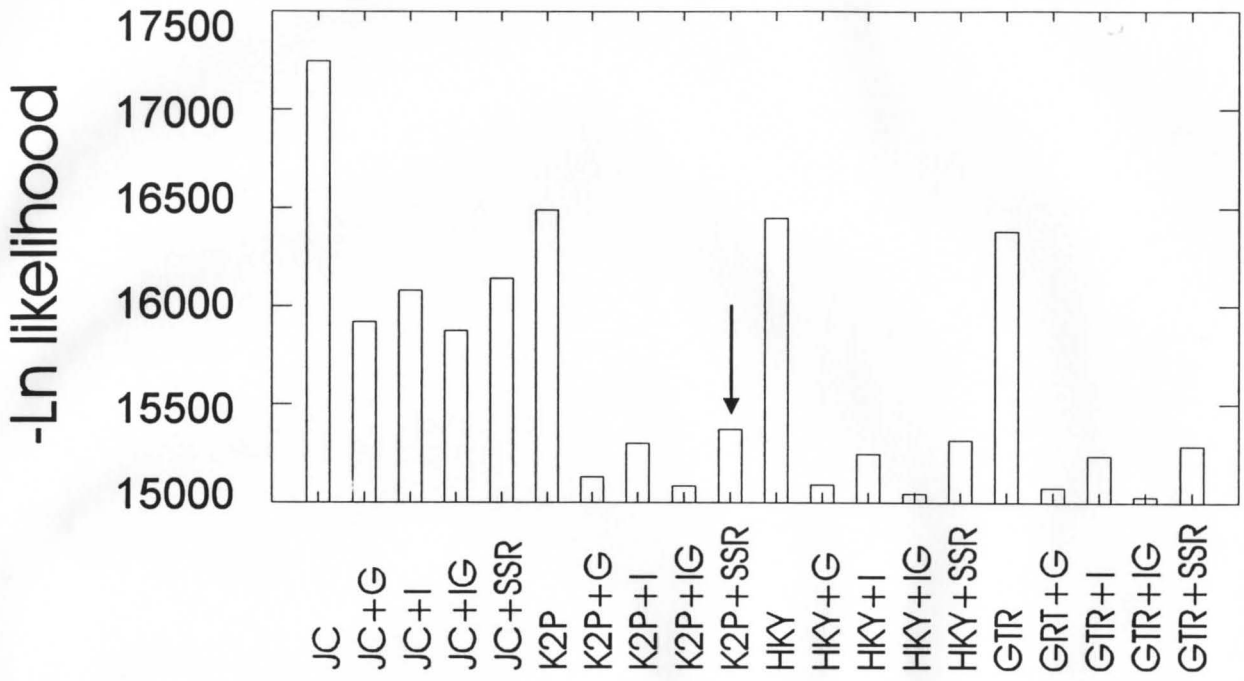
L. (Dialictus) cressonii
L. (Dialictus) pilosum
L. (Paralictus) asteris
L. (Dialictus) imitatum
L. (Dialictus) zephyrum
Hemihalictus series
10 changes

Fig. 3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17000
16500
16000
15500
15000
JC
JC+G
JC+I
JC+IG
JC+SSR
K2P
K2P+G
K2P+I
K2P+IG
K2P+SSR
HKY
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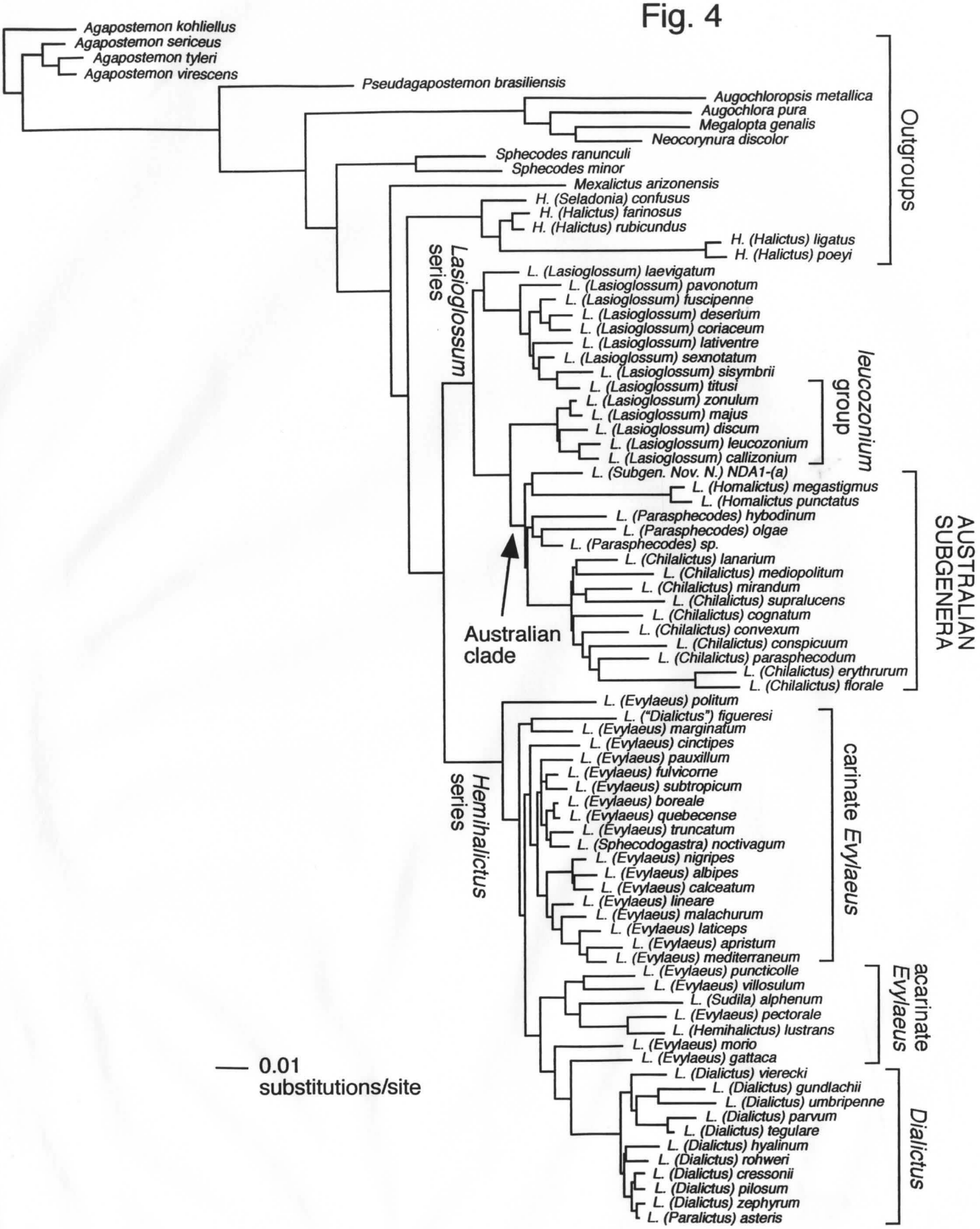
HKY+IG
HKY+SSR
GTR
GRT+G
GTR+I
GTR+IG
GTR+SSR

Fig. 4


Agapostemon kohliellus
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Agapostemon virescens
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L. (Dialictus) parvum
L. (Dialictus) tegulare
L. (Dialictus) hyalinum
L. (Dialictus) rohweri
L. (Dialictus) cressonii
L. (Dialictus) pilosum
L. (Dialictus) zephyrum
L. (Paralictus) asteris
Dialictus
0.01
substitutions/site