Phylogenetic relationships among bumble bees (*Bombus* Latr.): a reappraisal of morphological evidence

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Abstract. Cladistic analyses of morphological characters of adult bumble bees show significantly higher congruence among characters of the male genitalia than among other characters of males and females. Phylogenetic interpretations of groups supported by the combined morphological evidence (even with minimal assumptions) include (1) that the earliest diverging species belong to the paraphyletic subgenus *Mendacibombus*, together with *Bombus nevadensis* and *B.confusus*; (2) that, in contrast, species of the subgenus *Bombus* (sensu stricto) share a relatively recent common ancestor with *B.pressus* and *B.rufipes*; and (3) that *Psithyrus* (the social parasites) is a monophyletic group, and the sister-group of *B.persicus*. For genus-group nomenclature a single genus *Bombus* (sensu lato) is recommended, to include *Psithyrus* as another subgenus. Names for sections and for groups of subgenera are synonymized with subgeneric names.

Introduction

Bumble bees attract biologists because, like butterflies, they are particularly large and colourful insects of those temperate regions where biologists have been most active. These bees have become popular for behavioural and ecological studies, many of which would benefit from an understanding of phylogenetic relationships.

Bumble bees are widespread among alpine, temperate and arctic environments of the northern continents (Fig. 1). In the southern hemisphere they are native only in the East Indies and South America. Regional richness of the (approximately) 250 species peaks in the mountains bordering Tibet to the east (Gansu, Sichuan) and in the mountains of central Asia (Tien Shan). Species richness is otherwise high in the southern mountains of Eurasia, in the north-temperate mixed forest zone of the Holarctic Region, and in the mountains of the northern Neotropical Region. This pattern is far from a simple latitudinal gradient. It is also apparently far from a global equilibrium, as shown by the 'successful' introduction of European species into the southern hemisphere in New Zealand (Gurr, 1957), Tasmania (Cardale, 1993) and Chile (Arretz & Macfarlane, 1982). For mountains within temperate regions, species richness peaks in meadows around the upper forest and subalpine zones (Pittioni, 1937; Rasmont, 1988; Williams, 1991).

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Adult bumble bees feed mainly on nectar, which provides energy for flight, whereas the larvae are fed on a mixture of pollen and honey, which provides their requirements for growth (e.g. Alford, 1975; Heinrich, 1979; Morse, 1982; Plowright & Laverty, 1984). Almost all species are generalists in their choice of food plants, visiting a broad range of remunerative flowers. They also show unusually well-developed endothermy, which is facultative when foraging (Heinrich, 1993). Most species are social, but unlike other highly social long-tongued bees, they can avoid predictable, long periods of adverse conditions through diapause by solitary queens. Only a few species from the tropics of South America (Sakagami, 1976) and South-East Asia (Michener & Amir, 1977) have colonies that may persist for more than a year. Some species, the 'cuckoo' bumble bees, have specialized in parasitizing colonies of other bumble bee species (reviewed by Alford, 1975; Fisher, 1987).

Elucidation of phylogenetic relationships among bumble bees is not entirely straightforward, because the different species are morphologically 'monotonous' (Michener, 1990), particularly among the females. This is evident from keys to identification, for which authors are often obliged to depend heavily on characters of colour (e.g. Özbek, 1983; Thorp *et al.*, 1983; Prŷs-Jones & Corbet, 1987; Laverty & Harder, 1988; Labougle, 1990; Starr, 1992), despite the difficulties presented by regional convergences in colour patterns (Plowright & Owen, 1980; Williams, 1991). Indeed, although Dahlbom (1832) and Lepeletier (1832) had separated socially parasitic bumble bees from the truly social species, the first detailed, formal classific-
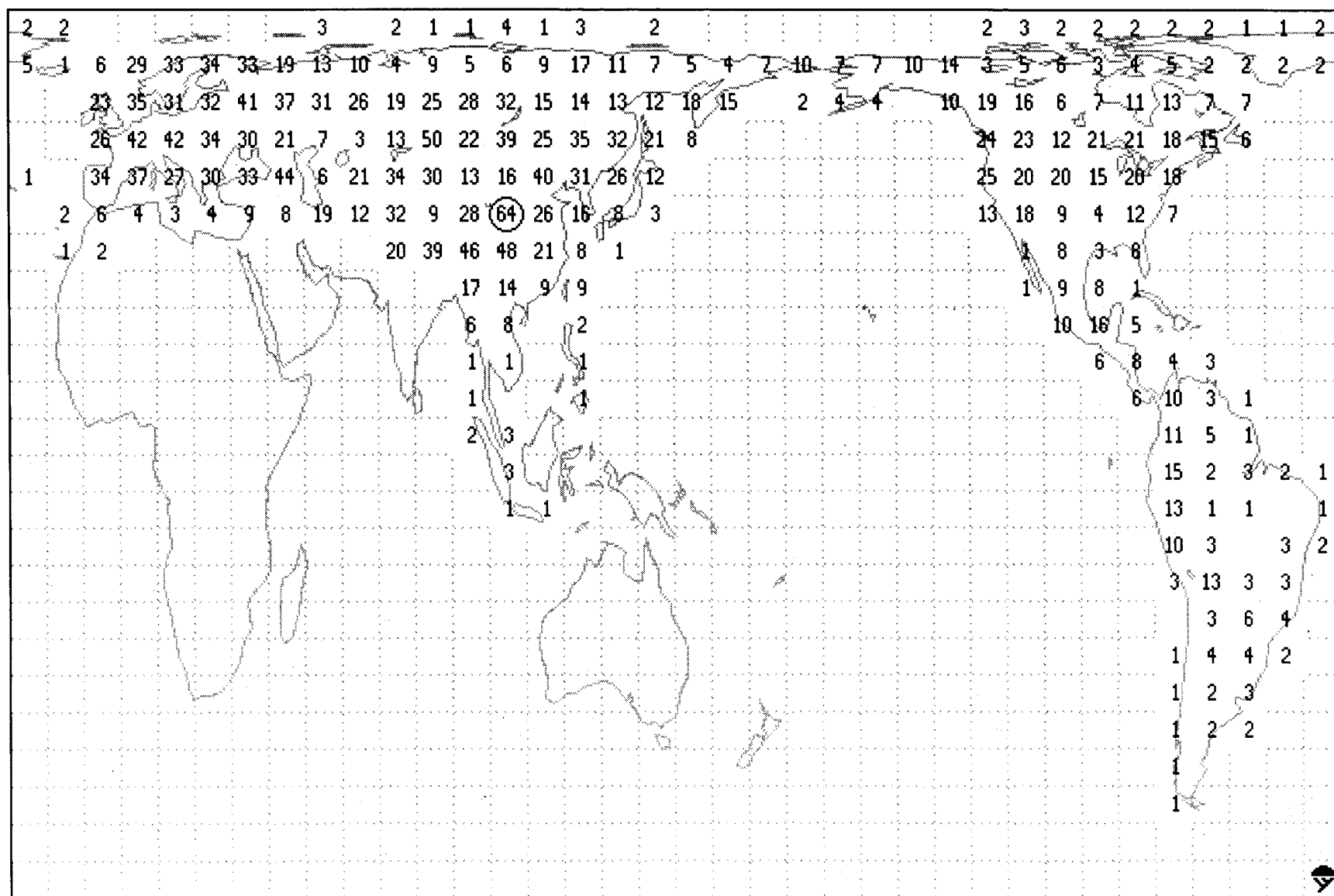
Fig. 1. Maps of indigenous species richness for regional faunas of all bumble bees world-wide: (a) from specimens in collections and literature records (Williams, 1993, with additional unpublished distribution records provided from China by S.-f. Wang and J. Yao, and from South America by G. Chavarría), shown as numbers of species; and (b) the same but with a limited interpolation of disjunct species distributions, by known gross habitat association where suitable habitat is known to have been extensive in each grid cell between disjunct records (interpolation increases the total number of records by less than 10%, most of which are in the Russian arctic), richness shown by logarithmic grey-scale intensities in classes of
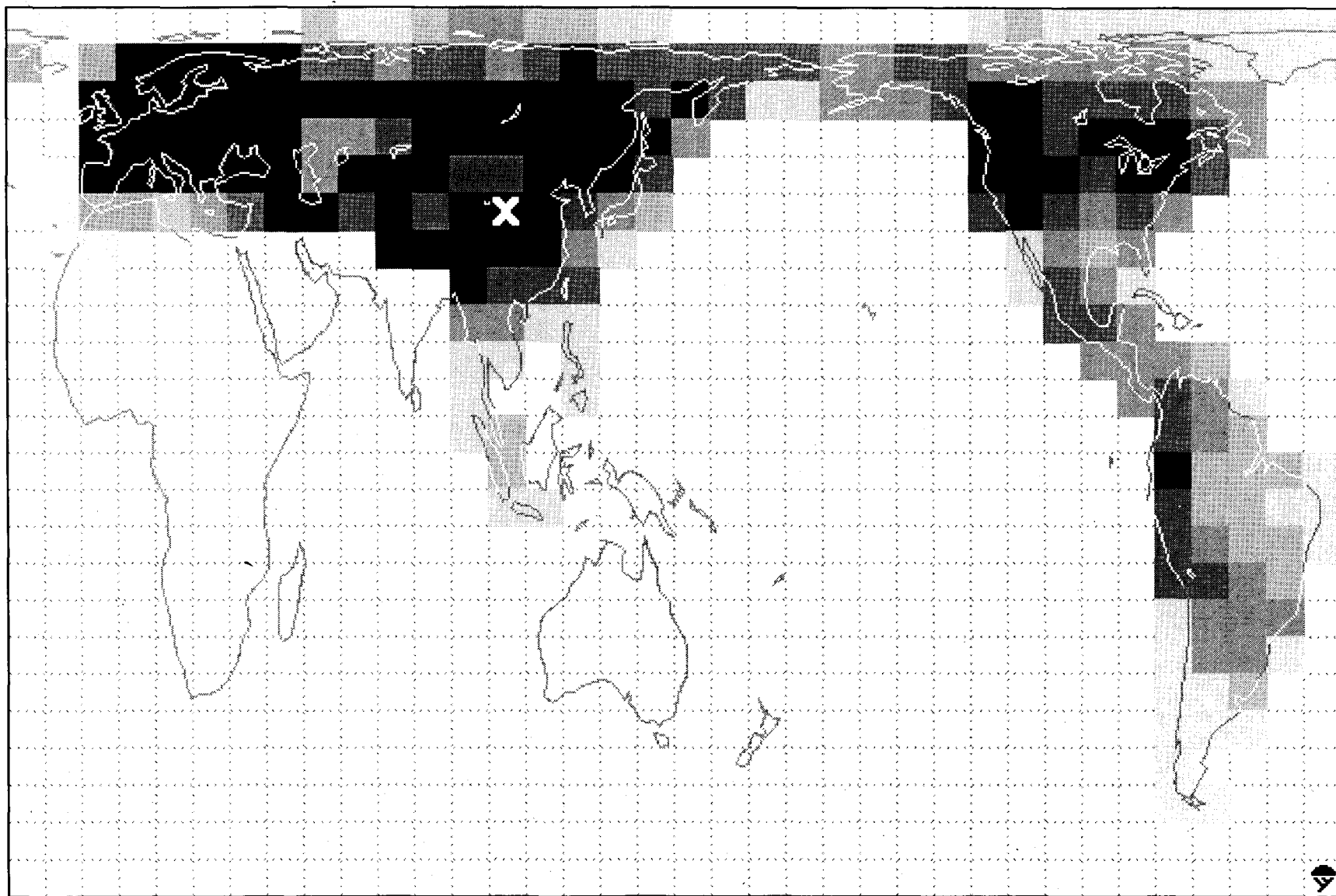
approximately equal size by the frequency of values between minimum (light grey) and maximum (black with white 'X'), with white for no indigenous presence records. The map is an equal-area projection (grid-cell area *c.* 611,000 km^2 for intervals of 10° longitude), plotted using a coarse-scale version of WORLDMAP software (Williams, 1992). The species list is a current estimate based on an unpublished catalogue (see Appendix 1).

ation of bumble bees was also made on the basis of colour pattern by von Dalla Torre (1880, 1882). Later, it was discovered that there are many easily observed and more consistent characters among the male genitalia, which can be used to group species (Schmiedeknecht, 1882; Radoszkowski, 1884). These characters were also found to show congruence with some of the characters of females and phylogenetic interpretations of the groups followed (Krüger, 1917). Elaboration of this system of groups in a synoptic review by Skorikov (1922) provided the basis for the classification of bumble bees that is still in widest use today (for a list of groups see, for example, Ito, 1985; Williams, 1985; for keys to groups see Richards, 1968). In parallel to these morphological studies, there have also been classifications of bumble bees using characters of nest structure and associated behaviour (e.g. Smith, 1876; Sladen, 1912; Plath, 1934; Hobbs, 1964; Haas, 1976; Sakagami, 1976). Unfortunately, this behavioural information is still completely lacking for many species and some characters may vary greatly within those species where they are known (Plowright, 1977). For a review of classifications of bumble bees, see Ito (1985).

Renewed interest in phylogeny has been stimulated by the possibility of applying the more explicit methods of phenetics (e.g. Plowright & Stephen, 1973; Ito, 1985) and cladistics (Ito & Sakagami, 1985; Williams, 1985) in the search for 'natural' classifications. Apart from morphological and behavioural data, there is also a growing wealth of new information from molecular techniques (e.g. Stephen & Cheldelin, 1973; Pekkarinen, 1979; Pekkarinen *et al.*, 1979; Obrecht & Scholl, 1981; Pamilo *et al.*, 1987; Scholl & Obrecht, 1988).

Here, I reassess some of the morphological evidence from adults for groupings of bumble bees made in an earlier study (Williams, 1985). The aim is to provide better information for comparison and combination in forthcoming studies of morphological, behavioural and molecular evidence (S. Cameron, in prep.; G. Chavarría, in prep.; A. Scholl and E. Obrecht, in prep.).

Methods

This study focuses on analysis of character variation among forty-eight species of bumble bees, although during its course 227 species (>90% of all known bumble bees) were examined in both sexes (Appendix 1). The forty-eight species include representatives of each of the subgenera of the genus *Bombus* Latreille recognized by Richards (1968). Also included are two of the socially parasitic bumble bees, *B.insularis* and *B.sylvestris*, together with other species considered particularly distinctive in previous studies: *B.macgregori* (Labougle & Ayala, 1985); *B.lapponicus*, *B.festivus*, *B.brachycephalus*, *B.haueri* and *B.handlirschi* (Williams, 1985); *B.convexus*, *B.sporadicus*, *B.morawitzi* and *B.simillimus* (Williams, 1991).

All material examined had been stored as dried and pinned specimens. Male specimens were partially rehydrated (relaxed) in a humid box, their genital capsules

were extracted, and then re-dried with the gonocoxites opened slightly to give clear views of the penis valves from the side.

Genealogical relationships are likely to be inferred most reliably from classifications that have been constructed using cladistic methods (Wiley, 1981; Farris, 1983; Forey *et al.*, 1992). Cladistics recognizes groups by homologies (equivalent in this sense to synapomorphies), which can be identified by tests of conjunction (single occurrence within the same organism), topological correspondence (similarity of position) and congruence (Patterson, 1982). The first two of these criteria were applied by inspection of specimens when coding characters. Congruence among these data was examined by applying the parsimony criterion as implemented in the HENNIG86 software (Farris, 1988).

HENNIG86 disregards polarity assignments for character changes when building trees, which are rooted at the outgroup node only at the time of tree plotting. For this study, the relationship between outgroups and ingroup was assumed to be as reported by Cameron (1993) and Roig-Alsina & Michener (1993) (Xylocopini, (Euglossini, Bombini)), using *Lestis bombylans* (Xylocopini) and *Eufriesea pulchra* (Euglossini) to represent two outgroups and ignoring the Meliponini. Morphological terminology and homologies of parts of the male genitalia of bumble bees with those of other bees follow Williams (1985, 1991).

Three analyses of character congruence were carried out. Initially, multistate characters were analysed as nonadditive (unordered) states. Because many terminal taxa were included (precluding exhaustive enumeration of possible trees), shortest trees were sought using the heuristic options *mh** (to build multiple trees, adding terminals in different sequences and then swapping branches locally, retaining only one tree for each starting tree), *bb** (for global branch swapping on trees supplied by mh*) and *nelsen* (for strict consensus trees from sets of shortest trees supplied by bb*). For a second analysis, the multistate coding was used to explore logical dependencies between complex character states by analysing with additive (ordered) states. In a third analysis, individual characters with low congruence were then identified by the successive weighting procedure (Farris, 1988; Carpenter *et al.*, 1993), using the options *mh**; *bb**; *xs w*; *cc* (where xs with the w option sets a character's weight according to its fit to the trees supplied by bb*) iteratively until weights remained constant. An association of characters of the male genitalia with higher weights than expected by chance was tested by simulating 10,000 random draws without replacement from among all of the observed weights.

Results

A total of forty-four morphological characters of adult bumble bees are identified in this study (Appendix 2). Of these characters, half (characters 0–21) are the result of reappraisal of homologies from a previous study of male genitalia (Williams, 1985). The remaining characters are coded to summarize some of the other more apparent
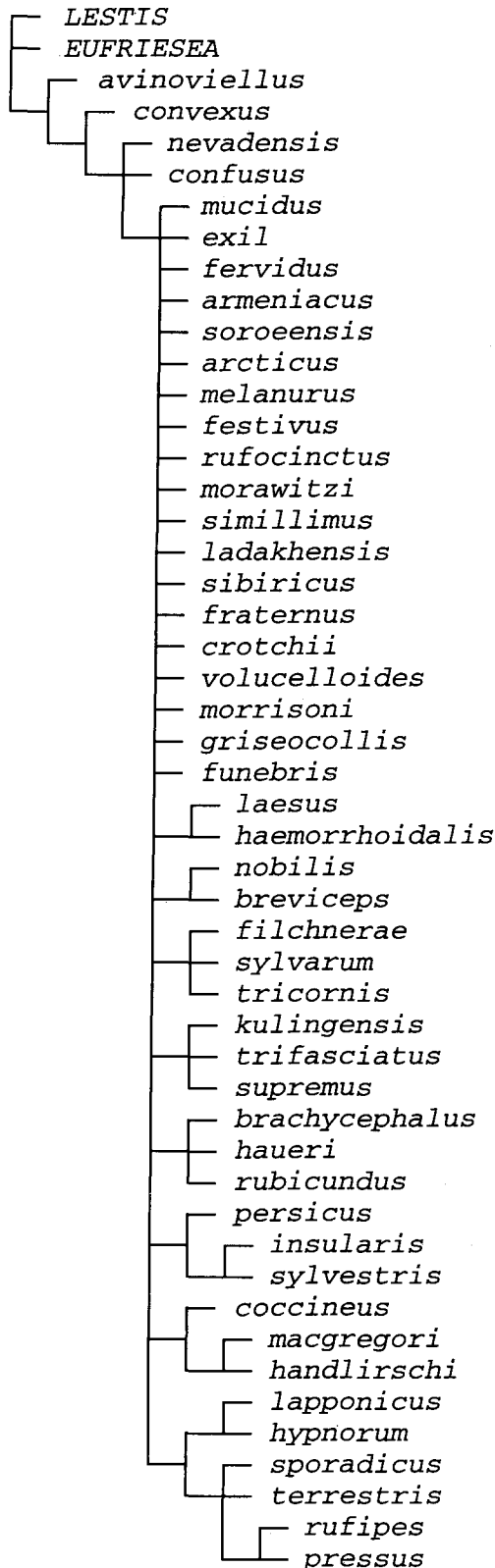
Fig. 2. Strict consensus tree summarizing common groups among the 1887 retained equally shortest trees for the data in Table 1 with all character states analysed nonadditively.

variation among male and female adult bumble bees. Seven characters are taken from the head, thorax and abdomen of males. Fifteen characters are taken from the head, thorax and abdomen (none from the genitalia) of females. No attempt was made to examine the prosternum, sting or internal structures (e.g. Richards, 1927), because destructive examination had to be avoided for specimens of rare species. Intraspecific variation presented no insurmountable problems for coding. Some of the character states are reasonably discrete among the material examined, such as whether or not the basal keel of the female mandible reaches the distal margin (character 33) (Williams, 1991: figs 31–34). Others can be measured, such as the ratio of oculo-malar distance to the breadth of the mandible at its base (Williams, 1991: fig. 15). Ratios describe shape, in this case related to the length of the female head. Binary states could then be discriminated from a bimodality in the frequency distribution of shape ratios (character 34). But variation in some characters is more subtle, such as whether gastral sternum II bears a transverse ridge (character 40) (Ito & Sakagami, 1985: figs 1–3), so that coding of states was more subjective. In this situation, alternative coding schemes would have different consequences for character optimization and tree shape, although these are not explored here.

When all forty-four coded characters (Table 1) were included in the congruence analysis nonadditively, more than 1887 shortest trees (exhausting the storage capacity of HENNIG86, so that the number and topology of trees beyond the 1887th retained tree remains unknowable) of length 129 steps were found (consistency index 0.48). The groups shared by these 1887 retained trees can be summarized by a strict consensus tree (Fig. 2).

Twelve of the characters were coded in multiple states. Nine of these characters have states that can be arranged additively by logical links such as size. When these nine multistate characters (6, 7, 10, 13, 18, 19, 29, 36, 40, italicized in Appendix 2) were analysed additively, the number of equally shortest trees found by HENNIG86 was reduced to 939 trees of length 132 steps (consistency index 0.47) (shared groups shown in Fig. 3).

Congruency was explored further using the successive weighting procedure. When the forty-four characters were analysed iteratively with the nine multistate characters accepted as additive, the character weights stabilized to constant values after two rounds of iteration (Table 1), and just sixteen equally shortest trees were found (consistency index 0.83) (Fig. 4). The only weights of value zero were given to the non-genitalia characters 26, 27 and 34. The observed sum of weights for the twenty-two male genitalia characters was then compared with the distribution of sums of twenty-two weights by 10,000 random draws from among all forty-four weights and found to be significantly higher than expected by chance ($P < 0.01$).

Discussion

All attempts to estimate phylogeny are limited by the

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┌─ LESTIS
├─ EUFRIESEA
│   ┌─ avinoviellus
└───┤   ┌─ convexus
    └───┤   ┌─ nevadensis
        └───┤   ┌─ confusus
            └───┤   ┌─ mucidus
                └───┼─ exil
                    ├─ fervidus
                    ├─ armeniacus
                    ├─ soroeensis
                    ├─ arcticus
                    ├─ melanurus
                    │   ┌─ laesus
                    ├───┴─ haemorrhoidalis
                    │   ┌─ filchnerae
                    ├───┼─ sylvarum
                    │   └─ tricornis
                    │   ┌─ kulingensis
                    ├───┼─ trifasciatus
                    │   └─ supremus
                    │   ┌─ persicus
                    ├───┤   ┌─ insularis
                    │   └───┴─ sylvestris
                    │   ┌─ nobilis
                    └───┤   ┌─ breviceps
                        └───┤           ┌─ rufipes
                            │           ├─ pressus
                            │       ┌───┼─ sporadicus
                            │       │   └─ terrestris
                            │   ┌───┤   ┌─ hypnorum
                            │   │   └───┴─ lapponicus
                            └───┤   ┌─ festivus
                                └───┤   ┌─ rufocinctus
                                    └───┤   ┌─ morawitzi
                                        └───┤   ┌─ simillimus
                                            └───┴─ ladakhensis
                                            ┌─ sibiricus
                                        ┌───┤   ┌─ fraternus
                                        └───┤   ┌─ crotchii
                                            └───┤   ┌─ volucelloides
                                                └───┤   ┌─ morrisoni
                                                    └───┼─ griseocollis
                                                        ├─ funebris
                                                        │   ┌─ brachycephalus
                                                        ├───┼─ haueri
                                                        │   └─ rubicundus
                                                        └───┤   ┌─ coccineus
                                                            └───┤   ┌─ macgregori
                                                                └───┴─ handlirschi
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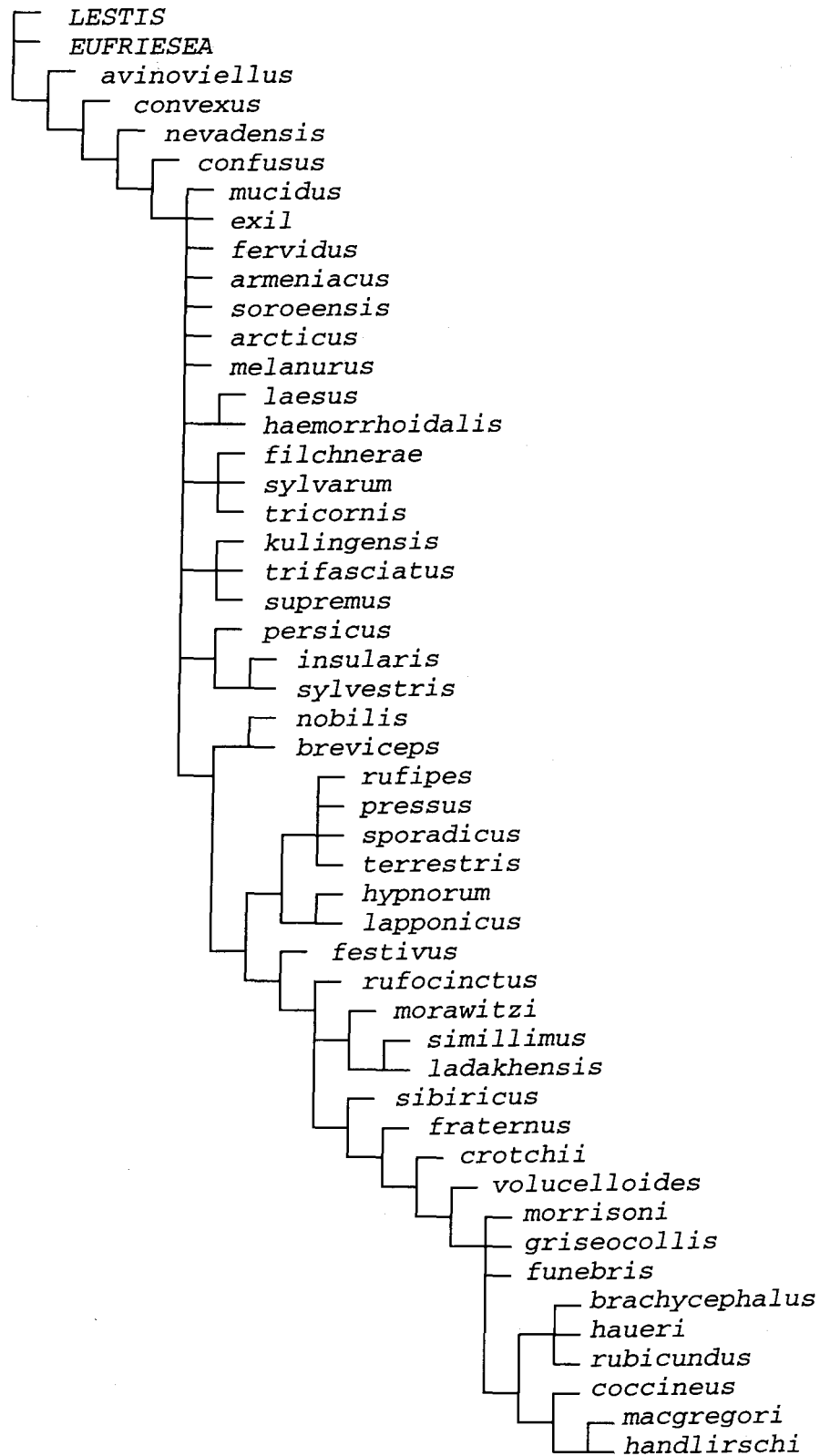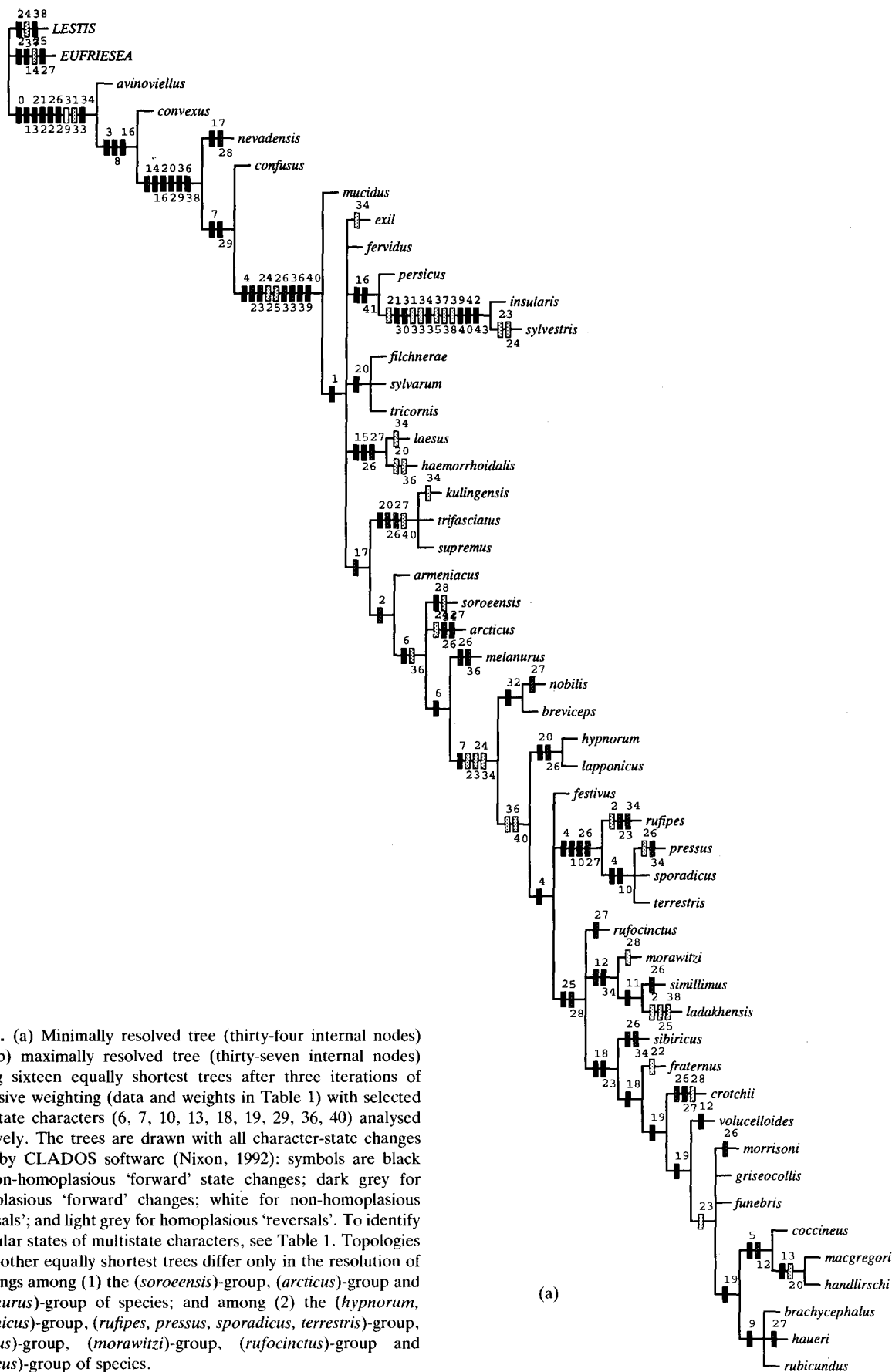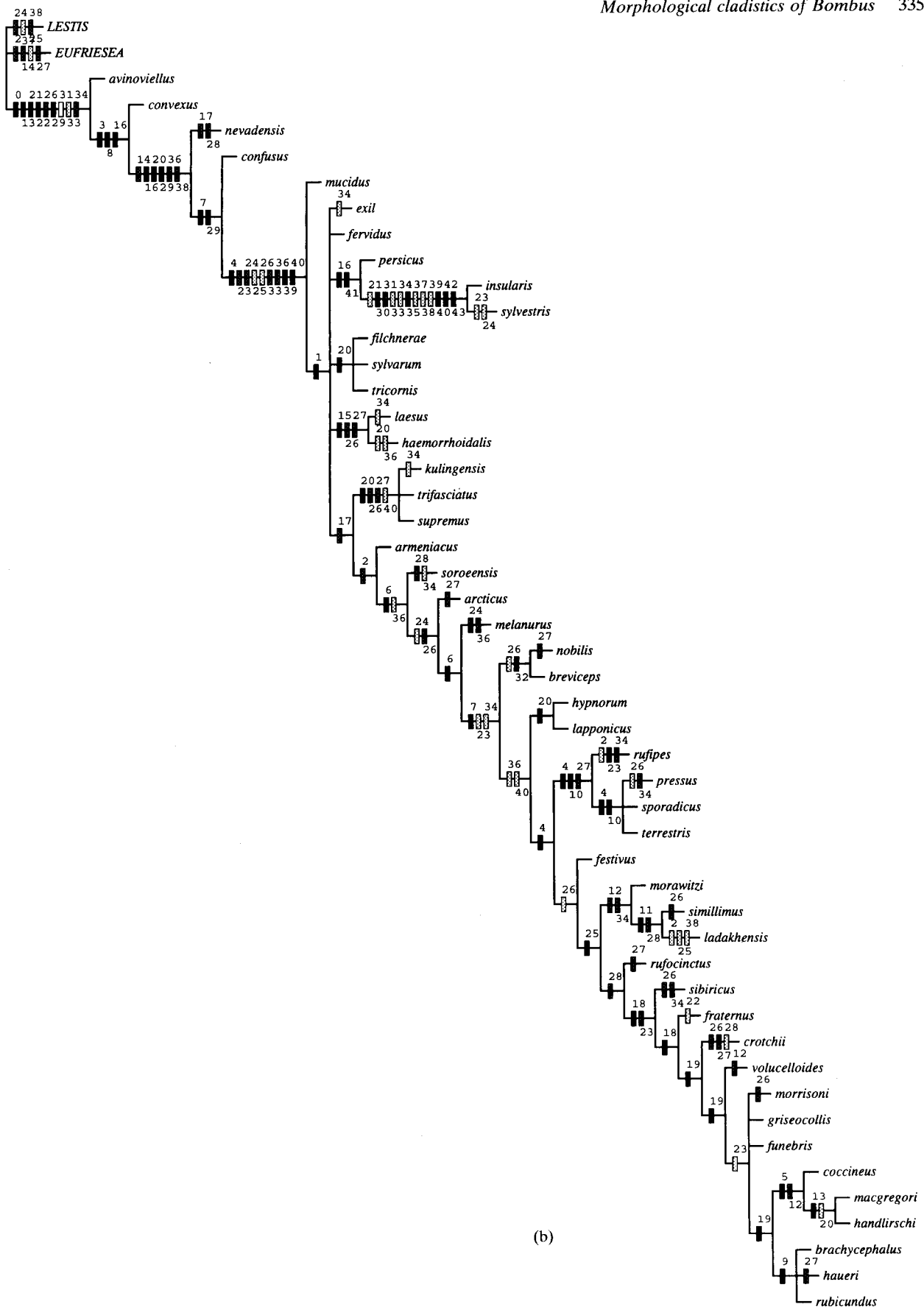
Fig. 3. Strict consensus tree summarizing common groups among the 939 equally shortest trees for the data in Table 1 with states of the selected multistate characters (6, 7, 10, 13, 18, 19, 29, 36, 40) analysed additively.

Table 1. Character matrix for bee taxa examined. Ingroup taxa (lower case) are listed in Appendix 1, characters are listed by their numbers in Appendix 2. Dashes are used for dependent states that are logically unobservable. Character weights from iterations 2 and 3 of successive weighting are shown at the bottom of the table.

Taxa	Characters 111 0123456789012	1111111 3456789	22 01	2222 2345	22 67	2 8	2333333 9012345	3333 6789	4444 0123
LESTIS	00000-000000-	00-----	00	0011	00	0	0010100	0010	0000
EUFRIESEA	00100-000000-	01-----	00	0000	01	0	0010100	0100	0000
avinoviellus	10000-000000-	1000-00	01	1001	10	0	1000010	0100	0000
convexus	10010-001000-	1001000	01	1001	10	0	1000010	0100	0000
nevadensis	10010-001000-	1102100	11	1001	10	1	2000010	1110	0000
confusus	10010-011000-	1102000	11	1001	10	0	3000010	1110	0000
mucidus	100110011000-	1102000	11	1110	00	0	3000110	2111	1000
persicus	110110011000-	1103000	11	1110	00	0	3000110	2111	1100
insularis	110110011000-	1103000	10	1110	00	0	3110001	2000	2111
sylvestris	110110011000-	1103000	10	1000	00	0	3110001	2000	2111
laesus	110110011000-	1112000	11	1110	11	0	3000100	2111	1000
haemorrhoidalis	110110011000-	1112000	01	1110	11	0	3000110	0111	1000
exil	110110011000-	1102000	11	1110	00	0	3000100	2111	1000
filchnerae	110110011000-	1102000	21	1110	00	0	3000110	2111	1000
sylvarum	110110011000-	1102000	21	1110	00	0	3000110	2111	1000
tricornis	110110011000-	1102000	21	1110	00	0	3000110	2111	1000
fervidus	110110011000-	1102000	11	1110	00	0	3000110	2111	1000
kulingensis	110110011000-	1102100	31	1110	11	0	3000100	2111	0000
trifasciatus	110110011000-	1102100	31	1110	11	0	3000100	2111	0000
supremus	110110011000-	1102100	31	1110	11	0	3000110	2111	0000
armeniacus	111110011000-	1102100	11	1110	00	0	3000110	2111	1000
soroeensis	111110111000-	1102100	11	1110	00	1	3000100	1111	1000
arcticus	111110111000-	1102100	11	1100	11	0	3000110	1111	1000
melanurus	1111102110000	1102100	11	1110	10	0	3000110	2111	1000
nobilis	1111102210000	1102100	11	1000	01	0	3001100	1111	1000
breviceps	1111102210000	1102100	11	1000	00	0	3001100	1111	1000
hypnorum	1111102210000	1102100	41	1000	10	0	3000100	0111	0000
lapponicus	1111102210000	1102100	41	1000	10	0	3000100	0111	0000
festivus	1111202210000	1102100	11	1000	00	0	3000100	0111	0000
rufipes	1101302210100	1102100	11	1100	11	0	3000110	0111	0000
pressus	1111402210200	1102100	11	1000	01	0	3000110	0111	0000
sporadicus	1111402210200	1102100	11	1000	11	0	3000100	0111	0000
terrestris	1111402210200	1102100	11	1000	11	0	3000100	0111	0000
rufocinctus	1111202210000	1102100	11	1001	01	1	3000100	0111	0000
morawitzi	1111202210001	1102100	11	1001	00	0	3000110	0111	0000
simillimus	1111202210011	1102100	11	1001	10	1	3000110	0111	0000
ladakhensis	1101202210011	1102100	11	1000	00	1	3000110	0101	0000
sibiricus	1111202210000	1102110	11	1101	10	1	3000110	0111	0000
fraternus	1111202210000	1102120	11	0101	00	1	3000100	0111	0000
crotchii	1111202210000	1102121	11	1101	11	0	3000100	0111	0000
volucelloides	1111202210001	1102122	11	1101	00	1	3000100	0111	0000
morrisoni	1111202210000	1102122	11	1001	10	1	3000100	0111	0000
griseocollis	1111202210000	1102122	11	1001	00	1	3000100	0111	0000
funebris	111120221000-	1102122	11	1001	00	1	3000100	0111	0000
brachycephalus	1111202211000	1102123	11	1001	00	1	3000100	0111	0000
haueri	1111202211000	1102123	11	1001	01	1	3000100	0111	0000
rubicundus	111120221100-	1102123	11	1001	00	1	3000100	0111	0000
coccineus	1111212210001	1102123	11	1001	00	1	3000100	0111	0000
macgregori	1111212210001	2102123	01	1001	00	1	3000100	0111	0000
handlirschi	1111212210001	2102123	01	1001	00	1	3000100	0111	0000
Weights	11 111111111	1 11 11					11 1 1		111
	0020000000002	0200400	53	2112	00	1	0030200	2214	4000

Fig. 4. (a) Minimally resolved tree (thirty-four internal nodes) and (b) maximally resolved tree (thirty-seven internal nodes) among sixteen equally shortest trees after three iterations of successive weighting (data and weights in Table 1) with selected multistate characters (6, 7, 10, 13, 18, 19, 29, 36, 40) analysed additively. The trees are drawn with all character-state changes fitted by CLADOS software (Nixon, 1992): symbols are black for non-homoplasious 'forward' state changes; dark grey for homoplasious 'forward' changes; white for non-homoplasious 'reversals'; and light grey for homoplasious 'reversals'. To identify particular states of multistate characters, see Table 1. Topologies of the other equally shortest trees differ only in the resolution of groupings among (1) the (*soroeensis*)-group, (*arcticus*)-group and (*melanurus*)-group of species; and among (2) the (*hypnorum, lapponicus*)-group, (*rufipes, pressus, sporadicus, terrestris*)-group, (*festivus*)-group, (*morawitzi*)-group, (*rufocinctus*)-group and (*sibiricus*)-group of species.

(a)

(b)

same problems of discovering homologies, whether they deal with (for example) aligning molecular sequences, gel electrophoresis bands or with morphology (Patterson et al., 1993). The best estimate of the phylogenetic tree is likely to be among the shortest trees that are based on total evidence from combining as many good characters as possible (e.g. Kluge & Wolfe, 1993). However, the data for all forty-four morphological characters in this study show only moderate congruency (consistency index 0.48), which results in large numbers of equally shortest trees (more than 1887, out of a possible 10^{33} trees), which in turn share few common groups (summarized in Fig. 2).

It is generally claimed that only one phylogenetic tree can truly describe the history of a group. Choosing among so many possible trees in search of the best estimate of this phylogenetic tree can only be achieved, in the absence of more data, by making further assumptions. For example, nine characters are coded in multiple classes distinguished by properties such as size (italicized in Appendix 2). Additive analysis of these states implies that extreme size classes are linked logically via the intermediate size classes. If the additive relationship among states of multistate characters is accepted as realistic, then the best estimate of the phylogenetic tree is likely to be among the 939 trees summarized in Fig. 3. Consensus trees such as this should not be interpreted as 'the phylogenetic tree' of bumble bees, because the strict consensus topology is not represented among the 939 shortest trees built directly from the additive data (this is demonstrated by the greater consensus tree length of 155 steps as compared to 132 steps required for the individual trees). However, Fig. 3 does summarize the groups consistent with all of the shortest trees supported by the available morphological evidence, and some of these groups are particularly likely to reflect relationships by ancestry.

If it is accepted that not all characters provide equally strong evidence of relationship, then the successive weighting procedure may be useful to discriminate the more congruent from the less congruent characters. This has been seen (at least by some) as the only cladistically justified form of weighting, employing a posteriori and recursively the inference of congruency derived from comparison among all characters in the data set to give higher weights to the more generally congruent characters (Carpenter et al., 1993). The present results show congruency to be higher among characters of the male genitalia than among other characters of male and female morphology. Some possible evolutionary explanations for particularly high congruence among characters of the male genitalia were discussed by Williams (1985, 1991). However, just because a few characters show particularly high congruence, they should not in consequence be advocated as the sole source of evidence for better estimates of the actual phylogeny. Trees built exclusively from these highly selected characters are merely more successful as summaries of this one part of the data.

The trees in Fig. 4 still include evidence from most characters other than those of the male genitalia and, if the assumptions behind both additive states and successive weighting of characters are accepted, represent just two among sixteen best estimates of bumble bee phylogeny. Among the alternative shortest trees there are no truly 'wild card' species that appear in many very different positions. The differences among these sixteen trees lie in the resolution of grouping among (1) the (soroeensis)-group, (arcticus)-group and (melanurus)-group of species, and among (2) the (hypnorum, lapponicus)-group, (rufipes, pressus, sporadicus, terrestris)-group, (festivus)-group, (morawitzi)-group, (rufocinctus)-group and (sibiricus)-group of species. Alternatively, this can be viewed as uncertain positions for B.soroeensis, B.festivus and B.rufocinctus on these trees. Of the thirty-four to thirty-seven internal nodes in each of these trees, only nine are supported by more than a single, non-homoplasious character-state change.

Low congruence for characters could be the result of errors in identifying homologies. This might be corrected by further study, perhaps by greater resolution in the coding of character states. For example, because this study follows earlier work focusing on characters of the male genitalia (Williams, 1985), it might be argued that more time in total has been spent in elucidating homologies of genitalia and that this is sufficient to explain the apparently higher congruence. Yet female bumble bees are more frequent in the field and in collections and are often more difficult to identify. In consequence, if there had been any difference in the investment of effort between the sexes, then greater effort might actually have been invested in the search for characters and homologies among females.

Another explanation for low congruence could follow from the observation that some characters are more difficult to code than others. Some of the most difficult characters for coding are among the non-genitalia characters (Appendix 2: characters 24, 26, 27, 28, 36, 40). However, three of the seven characters with lowest congruence (Table 1: characters 23, 34, 38) are not in this set and so are not as easily explained in this way.

Alternatively, incongruent characters could represent homoplasious suites of traits that have been more labile during the evolution of bumble bees. For example, male eye size (character 25), antennal length (character 23) and beard (character 22) are all related to mate-searching behaviour, which in turn may be related in part to habitat structure (Williams, 1991). This morphology and behaviour may differ strongly among even closely related species. Similarly, the shape of the oculo-malar area (character 34) is related to proboscis length (Medler, 1962), which is related in turn to variation in feeding constraints and behaviour governing flower choice (reviewed by e.g. Morse, 1982). Although sometimes less variable among closely related species than mate-searching behaviour, the ability to reach deep nectaries directly could have conferred selective advantages in even distantly related groups of bumble bees (e.g. B.supremus and B.sibiricus). Yet other apparently homoplasious structures, such as male corbiculae (characters 26, 27) (Sakagami & Ito, 1981) and the female mid-basitarsal spine (character 36), are not known to have any present functions.

Some groups are shared by all of the trees in Figs 2–4 and so permit relatively robust inferences. These groups are compared below with results from other studies.

B.sporadicus and B.terrestris

The trees in Figs 2–4 differ most strikingly from some of the most recent classifications of bumble bees (Ito, 1985; Pamilo *et al.*, 1987; Scholl & Obrecht, 1988) in the grouping of *B.sporadicus*, *B.terrestris* and closely similar species (i.e. the subgenus *Bombus* sensu stricto) with other species. These other studies are essentially phenetic and recognize that species of *Bombus* s.str. are particularly dissimilar from other bumble bees, both in the morphology of their male genitalia and in their enzyme mobilities.

The present reappraisal of morphological characters finds no grounds to change the interpretation of highly derived morphology of the penis valve for grouping these species with other highly derived bumble bees that was presented in Williams (1985). All of the analyses here group *B.sporadicus* and *B.terrestris* with the Oriental *B.rufipes* and *B.pressus*. Elaboration of the head of the penis valve (character 10, Fig. 5) from an inwardly recurved hook as in *B.hypnorum*, by enlargement and expansion outwards (*B.festivus*), ventrally (*B.rufipes*) and apically (*B.pressus*), appears to provide homologies for the unique, broad funnel of *B.sporadicus* and *B.terrestris*. The reduction of the ventro-lateral angle of the penis valve (Table 1, character 4) from a frequently acute angle to an obscure curve might be an homology (synapomorphy) of *B.festivus* and the *rufocinctus*-group (*B.rufocinctus* and species below it in Figs 3 and 4). The broadly rounded ventro-lateral angle of the penis valve in *B.sporadicus* and *B.terrestris* could then be a partial reduction from the strongly angled state in *B.hypnorum*. Alternatively, the rounded angle
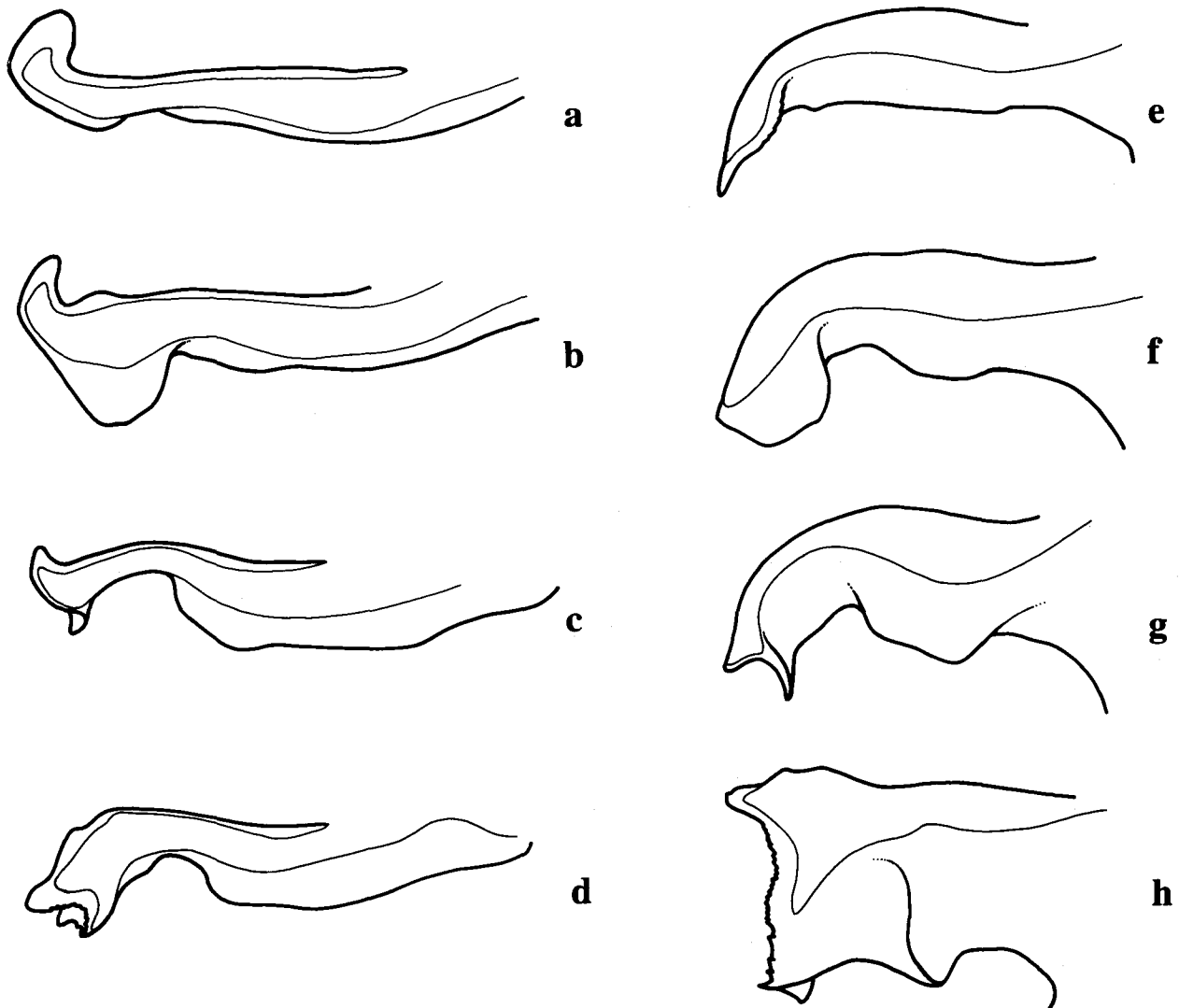
Fig. 5. Male right penis valve from postero-dorsal aspect for (a) *B.festivus*, (b) *B.rufipes*, (c) *B.pressus*, (d) *B.terrestris*; and from outer lateral aspect for (e) *B.festivus*, (f) *B.rufipes*, (g) *B.pressus* and (h) *B.terrestris*.

could be a reversal from the reduced state in *B.festivus*. For all of the congruence analyses, character 4 was analysed nonadditively, so that the fit of the character states to the trees was free to be optimized. However, even with the successive weighting analysis (Fig. 4), the shortest trees still differ in the placement of the (*rufipes, pressus, sporadicus, terrestris*)-group by this character. Consequently, more characters are required for resolution of this issue. But irrespective of the identity of the precise sister-group, the shortest trees with the other nine multistate characters analysed additively (Figs 3 and 4) all group these species together with *B.rufocinctus, B.sibiricus*, etc., but exclude *B.nobilis, B.melanurus*, etc. The phylogenetic interpretation is that species of the subgenus *Bombus* s.str. may be dissimilar to most other bumble bees, not because of slow divergence during a long independent history, but because of recent yet unusually rapid character divergence.

B.avinoviellus, B.convexus and B.nevadensis

Species of the subgenus *Mendacibombus* (represented here by *B.avinoviellus* and *B.convexus*), rather than species of the subgenus *Bombus* s.str., were inferred from a previous cladistic study (Williams, 1985) to be among the earliest diverging bumble bees that survive to the present. From an examination of all of the species of this group, Williams (1991: fig. 5; male of *B.superbus* examined more recently courtesy of S.-f. Wang and J. Yao) concluded that *Mendacibombus* is likely to be paraphyletic with respect to all other bumble bees. These conclusions are also supported here (Figs 2–4).

The relationships of the North American *B. (Bombias) nevadensis* have been problematic (Williams, 1991). On the one hand, obvious similarities to species of the paraphyletic grade '*Mendacibombus*', such as the simple, straight form of the male penis valve, may be symplesiomorphies or, in the case of enlarged male eyes, may be highly homoplasious (see above), and so not reliably informative. On the other hand, the inner projections from the male gonostylus and volsella both show possible homologies (synapomorphies) with species such as *B.arcticus* and *B.melanurus*. For example, Ito (1985) grouped *B.nevadensis* with the Eurosiberian *B.confusus*, but suggested a 'link with *Alpinobombus* group, especially the subgenus *Kallobombus*' (*B.soroeensis*). However, in the present study, additional evidence from non-genitalia morphology provides most support for a group of *B.nevadensis* with all other bumble bees excluding *Mendacibombus*, and for a group of all bumble bees excluding both *Mendacibombus* and *B.nevadensis* (Fig. 4).

Particularly low similarity between *B.nevadensis* and the other North American bumble bees (where *Mendacibombus* is not represented) has been found in phenetic studies of female wing venation (Plowright & Stephen, 1973), larval antennae (Stephen & Koontz, 1973) and enzymes (Stephen & Cheldelin, 1973). According to Rasmont (1988), *B.mendax* and *B.nevadensis* are the only species of bumble bees known to share the trait that eggs are laid in

separate cells, which then remain separate throughout the development of the larvae. Indeed, among bumble bees *B.mendax* builds very unusual nests (Haas, 1976), which show greater resemblance in structure to nests of some stingless bees (cf. Wille & Michener, 1973). In particular, the cocoons are almost completely torn down soon after the emergence of the adults, so that pollen and honey must be stored elsewhere. Unlike other bumble bees, these food reserves are held exclusively outside the wax envelope of the brood nest and the honey may be stored in hexagonally arranged cells (Haas, 1976). Unlike *B.mendax*, *B.nevadensis* does not tear down empty cocoons, and may even store food reserves in them, although reserves are often stored in discrete clumps of wax cells on the edge of the brood nest (Hobbs, 1965), therefore showing some similarity to *B.mendax*. *B.nevadensis* also shows both of the major kinds of brood-feeding behaviours known among bumble bees, being both a 'pocket maker' and a 'pollen storer' at successive stages of colony development (Hobbs, 1965; Plowright, 1977). A cladistic treatment of these behavioural traits is clearly required (G. Chavarría, in prep.).

B.insularis and B.sylvestris

The relationship of the socially parasitic bumble bees (*Psithyrus*, represented here by *B.insularis* and *B.sylvestris*) to the fully social species has been much discussed in the context of the evolution of parasitic behaviour. Despite arguments for a polyphyletic ancestry (e.g. Plath, 1922; Richards, 1927; Reinig, 1935), analogous to that of socially parasitic species among vespine social wasps (Carpenter, 1987), most recent studies of bumble bees have favoured (if phenograms are interpreted as phylogenetic estimates) a monophyletic ancestry for the socially parasitic species (Plowright & Stephen, 1973; Pekkarinen *et al.*, 1979; Ito, 1985; Williams, 1985; Pamilo *et al.*, 1987), analogous to that of socially parasitic species among social wasps of the genus *Polistes* (Carpenter *et al.*, 1993) (an exception is Obrecht & Scholl's (1981) phenogram of bumble bees, which groups *Psithyrus rupestris* separately from the rest of the *Psithyrus*, whereas Pekkarinen *et al.*'s (1979) phenogram includes *B. (Kallobombus) soroeensis* in a group of *Psithyrus* species). Phylogenetic interpretation of Figs 2–4 supports a monophyletic ancestry for *Psithyrus*. However, species of at least some other subgenera have apparently become obligate social parasites (*B. (Thoracobombus) inexspectatus*, see Yarrow, 1970) or at least frequently facultative social parasites (*B. (Alpinobombus) hyperboreus* [a junior synonym of *B.arcticus* (Quenzel)], see Richards, 1973) independently.

Likely sister-groups to *Psithyrus* were identified as *B. (Fervidobombus) dahlbomii* or *B. (Orientalibombus) funerarius* by Ito & Sakagami (1985), and as *B. (Eversmannibombus) eversmanniellus* (a junior synonym of *B.persicus*) by Williams (1985). Ito (1985) had also concluded that the most phenetically similar groups to *Psithyrus* are *Eversmannibombus* and *Mucidobombus*.

The conclusion favouring the Middle-Eastern *B. (Eversmannibombus) persicus* is also supported here (Figs 2–4).

Genus-group names

Use of a single genus, *Bombus* Latreille, is recommended for all bumble bees. The social parasites, *Psithyrus* Lepeletier, may be included within *Bombus* as a single subgenus (Williams, 1991).

Since Lepeletier (1832), *Psithyrus* has been recognized as a genus separate from the rest of the bumble bees, which have often been placed in a single genus *Bombus* (but see e.g. Skorikov, 1922; Milliron, 1961; Tkalcù, 1972). Most recent studies have shown (if phenograms are interpreted as phylogenetic estimates) this traditional concept of the genus *Bombus*, which includes *Mendacibombus* but not *Psithyrus*, to be paraphyletic (Plowright & Stephen, 1973; Obrecht & Scholl, 1981; Ito, 1985; Williams, 1985; Pamilo *et al.*, 1987), and so recognizable only by phenetic similarity (an exception is Pekkarinen *et al.*'s (1979) phenogram, which places the *Psithyrus* species as a 'sister-group' to the other bumble bees, but includes within the *Psithyrus* group the species *B. (Kallobombus) soroeensis*). Williams (1985) attempted to conserve monophyletic genera *Psithyrus* and *Bombus* by recognizing a genus *Mendacibombus*. However, further study of all of the species of *Mendacibombus* showed that it is likely to be paraphyletic with respect to all other bumble bees, with the consequence that perhaps another nine genera (mostly for single species) might be required as a minimum to maintain strict monophyly of bumble bee genera alongside a genus *Psithyrus* (Williams, 1991). The present study also supports paraphyly of *Mendacibombus* (Figs 2–4, see discussion of *B.avinoviellus*, *B.convexus* and *B.nevadensis*). Williams (1991) recommended a pragmatic solution, recognizing a single genus, *Bombus*, for all bumble bees, including *Psithyrus* as a subgenus. This was a return to an emphasis of the more widely shared characters and the more distant affinities for the generic concept, encouraged particularly by the opinion of Michener (1990) that bumble bees are 'morphologically monotonous' in comparison with variation among species within closely related groups like Euglossini (orchid bees) or Meliponini (stingless bees). Furthermore, the subgenera within the former genus *Psithyrus* have been considered less distinct than the other subgenera of *Bombus* (Pittioni, 1939; Ito, 1985; Williams, 1985; Michener, 1990), and may be treated as synonyms of *Psithyrus* (Milliron, 1961; Williams, 1991). Unfortunately, treating *Psithyrus* as a subgenus does bring a few names in the species group originally ascribed to the genus *Psithyrus* into secondary homonymy with names in the genus *Bombus* (e.g. *Psithyrus norvegicus* Sparre-Schneider, 1917, becomes a junior homonym in *Bombus* of *Bombus lapponicus* var. *norvegicus* Friese, 1911 [deemed subspecific following ICZN, 1985: Article 45 g(ii)], see Appendix 1). However, the advantage of a single genus for all bumble bees is that it recognizes a group for which the evidence of monophyly is particularly strong, so that nomenclature is most likely to remain stable in the future.

Within the genus *Bombus*, the established subgeneric names (e.g. Richards, 1968) may be found convenient by some specialists who wish to label assemblages of more closely similar species. Unfortunately, Richards's concepts of the bumble bee subgenera did not always communicate ideas of phylogenetic relationship well, because some of these assemblages now appear to be paraphyletic (e.g. *Mendacibombus*), or even polyphyletic (e.g. *Sibiricobombus* in the sense of Richards, 1968, includes *Obertobombus*, whereas he placed *B. (Sibiricobombus) flaviventris* in *Subterraneobombus*, see Appendix 1 and Williams, 1991). Of course, all subgeneric names for bumble bees may be treated simply as synonyms of *Bombus* (sensu lato) and ignored by those who wish to do so. But when a comprehensive cladistic revision is available, then perhaps the nomenclature of the more reliably monophyletic species-groups could be revised, if the system is still found to be useful.

The names *Odontobombus* Krüger (1917), *Anodontobombus* Krüger (1917), *Uncobombus* Vogt in Krüger (1917), *Sulcobombus* Krüger (1917) and *Boopobombus* Frison (1927) were originally proposed for sections or for groups of subgenera of the genus *Bombus*, but must now be treated as subgeneric names (ICZN, 1985: Article 10e). The section *Odontobombus* was considered by Milliron (1961) to be equivalent to his concept of the subgenus *Megabombus* Dalla Torre. The type-species of *Odontobombus* is designated here as the originally included species *Bombus argillaceus* (Scopoli) to fix the identity of *Odontobombus* as a junior synonym of *Megabombus* in accordance with Milliron's action (**syn.n.**). The section *Anodontobombus* was considered by Milliron (1961) to be synonymous with the subgenus *Pyrobombus* Dalla Torre. The type-species of *Anodontobombus* was designated by Williams (1991) as the originally included species *Bombus hypnorum* (Linnaeus) to fix the identity of *Anodontobombus* as a junior synonym of *Pyrobombus* in accordance with Milliron's action. The group name *Uncobombus* was also considered by Milliron (1961) to correspond to *Pyrobombus* Dalla Torre. The type-species of *Uncobombus* was designated by Williams (1991) as the originally included species *Bombus hypnorum* (Linnaeus) to fix the identity of *Anodontobombus* as a junior synonym of *Pyrobombus* in accordance with Milliron's action. The group name *Sulcobombus* had its type-species designated by Sandhouse (1943) as *Bombus confusus* Schenck, effectively making it a junior synonym of *Confusibombus* Ball (Richards, 1968). The section *Boopobombus* was stated by Frison to include those forms considered by Franklin (1913) to belong to the subgenus *Bombias* Robertson. The type-species of *Boopobombus* is designated here as the originally included species *Bremus auricomus* (Robertson) (=*Bombus auricomus*) to fix the identity of *Boopobombus* as a junior synonym of *Bombias* in accordance with Frison's statement (**syn.n.**).

The present study is far from exhaustive, even for morphological characters. But with the rapidly growing availability of molecular information as a source of further

data for combination, it is possible to hope for a better resolution of at least some of the problems in the near future.

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Appendix 1

List of ingroup taxa examined (species of the genus *Bombus* s.l.). Taxa in bold type are those examined in detail for this study (Table 1), preceded by a subgeneric assignment in parentheses. The sequence and grouping of these species follows that in the consensus tree of the sixteen shortest trees from the additive successive weighting analysis. Each taxon in bold type is followed by other bumblebee taxa for which both sexes have been examined and which share the most character states (no cladistic inference should be drawn without including all of these species in an analysis). Oldest available names are used insofar as these are known (from a catalogue of >3000 names, unpublished). Where these differ from names in common use, the latter are placed in brackets (current usage of *B.muscorum* and *B.terrestris* is maintained following ICZN, 1985: Article 80). This is done merely to clarify identity in the face of current nomenclatural problems and no formal nomenclatural action should be inferred.

(Mendacibombus) **avinoviellus** (Skorikov); *mendax, makarjini, superbus, himalayanus, marussinus, turkestanicus, defector, handlirschianus, shaposhnikovi*

(Mendacibombus) **convexus** Wang [= *lugubris*]; *waltoni*

(Bombias) **nevadensis** Cresson

(Confusibombus) **confusus** Schenck

(Mucidobombus) **mucidus** Gerstaecker

(Eversmannibombus) **persicus** Radoszkowski [= *eversmanniellus*]

(Psithyrus) **insularis** (Smith), **sylvestris** (Lepeletier); *citrinus, intrudens* [= *variabilis*], *suckleyi, vestalis, perezi, ashtoni, bohemicus, coreanus, barbutellus, maxillosus, cornutus, expolitus, turneri, tibetanus, chinensis, novus, branickii, rupestris, ferganicus, morawitzianus, campestris, pieli, transbaicalicus* [= *norvegicus*], *fernaldae, flavidus, skorikovi, quadricolor*

(Laesobombus) **laesus** Morawitz, *(Orientalibombus)* **haemorrhoidalis** Smith; *funerarius, braccatus*

(Exilobombus) **exil** (Skorikov)

(Thoracobombus) **filchnerae** Vogt [= *adventor*], **sylvarum** (Linnaeus), *(Tricornibombus)* **tricornis** Radoszkowski; *(Thoracobombus) muscorum, anachoreta, opulentus, zonatus, humilis, deuteronymus, schrencki, honshuensis, impetuosus, potanini, remotus, pseudobaicalensis, hedini, ruderarius, inexspectatus, veteranus, mlokosievitzii, pascuorum* [= *agrorum* (Fabricius)], *(Tricornibombus) atripes, imitator*

(Fervidobombus) **fervidus** (Fabricius); *pensylvanicus* [= *pennsylvanicus*], *excellens, dahlbomii, morio, diligens, opifex, bellicosus, pullatus, weisi* [= *nigrodorsalis*], *medius, steindachneri, brasiliensis, niger* [= *atratus*], *transversalis, mexicanus, brevivillus, digressus*

(Senexibombus) **kulingensis** Cockerell, *(Diversobombus)* **trifasciatus** Smith, *(Megabombus)* **supremus** Morawitz; *(Senexibombus) bicoloratus, senex, irisanensis, (Diversobombus) longipes, diversus, ussurensis, (Megabombus) gerstaeckeri, consobrinus, czerskii, yezoensis, koreanus, sushkini, hortorum, portchinsky, ruderatus, argillaceus,* *securus, religiosus*

(Rhodobombus) **armeniacus** Radoszkowski; *agrorum* (Schrank) [= *mesomelas*], *pomorum*

(Kallobombus) **soroeensis** (Fabricius)

(Alpinobombus) **arcticus** (Quenzel) [= *hyperboreus*]; *balteatus, neoboreus, polaris* [= *arcticus* (Kirby)], *alpinus*

(Subterraneobombus) **melanurus** Lepeletier; *fragrans, fedtschenkoi, personatus, subterraneus, elegans* [= *distinguendus*], *appositus, borealis*

(Alpigenobombus) **nobilis** Friese, **breviceps** Smith; *kashmirensis, wurflenii, grahami*

(Pyrobombus) **hypnorum** (Linnaeus), **lapponicus** (Fabricius); *abnormis, perplexus, haematurus, subtypicus, mirus, lemniscatus, lepidus, infirmus, parthenius, luteipes, flavescens, rotundiceps, beaticola, flavus, ardens, modestus, cingulatus, brodmannicus, jonellus, pyrenaeus, biroi, frigidus, sandersoni, pleuralis* [= *flavifrons*], *centralis, vandykei, caliginosus, vagans, praticola* [= *mixtus*], *sitkensis, melanopygus, monticola, bimaculatus, impatiens, vosnesenskii, bifarius, huntii, ternarius, ephippiatus*

(Festivobombus) **festivus** Smith

(Rufipedibombus) **rufipes** Lepeletier; *eximius*

(Pressibombus) **pressus** (Frison), *(Bombus s.str.)* **sporadicus** Nylander, **terrestris** (Linnaeus); *tunicatus, franklini, affinis, ignitus, hypocrita, patagiatus, lucorum, terricola*

(Cullumanobombus) **rufocinctus** Cresson; *cullumanus, semenoviellus*

(Obertobombus) **morawitzi** Radoszkowski; *oberti*

(Melanobombus) **simillimus** Smith, **ladakhensis** Richards; *richardsiellus, pyrosoma, rufofasciatus, semenovianus, incertus, lapidarius, keriensis, sichelii*

(Sibiricobombus) **sibiricus** (Fabricius); *flaviventris, obtusus, asiaticus, niveatus, sulfureus*

(Fraternobombus) **fraternus** (Smith)

(Crotchiibombus) **crotchii** Cresson

(Robustobombus) **volucelloides** Gribodo; *robustus, tucumanus, hortulanus, butteli*

(Separatobombus) **morrisoni** Cresson

(Separatobombus) **griseocollis** (Degeer)

(Funebribombus) **funebris** Smith

(Brachycephalibombus) **brachycephalus** Handlirsch, **haueri** Handlirsch, *(Rubicundobombus)* **rubicundus** Smith

(Coccineobombus) **coccineus** Friese; *baeri*

(Dasybombus) **macgregori** Labougle & Ayala, **handlirschi** Friese

Appendix 2

List of character states, with coding. Multistate characters analysed additively are shown in italics. Characters of penis refer to penis valves unless otherwise specified.

Male penis
0. Spatha broader than long (0); spatha longer than broad (1).

1. Spatha basally broadly rounded (0); spatha basally acutely pointed (1).
2. Spatha laterally continuous with valves (0); spatha laterally overhanging valves (1).
3. Dorsal lightly sclerotized channel narrow (0); dorsal lightly sclerotized channel broad (1).
4. Shaft without a distinct ventro-lateral angle (0); shaft with an acute ventro-lateral angle near the mid-point of its length (1); shaft with only a weak trace of a ventro-lateral angle (2); shaft with ventro-lateral angle broadly rounded as a shallow convexity (3); shaft with ventro-lateral angle pronounced as a very broadly rounded right angle (4).
5. Shaft dorso-ventrally narrow or irregular in breadth (0); shaft uniformly dorso-ventrally expanded (1).
6. *Apex straight or curved outwards (0); apex curved in towards body midline (1); head broadly curved inwards (2).*
7. *Head strongly laterally compressed (0); head nearly tubular (1); head strongly dorso-ventrally flattened (2).*
8. Inner basal shelves broad (0); inner basal shelves narrow (1).
9. Inner shelves of head absent or weakly defined (0); inner shelves of head strongly marked basally by a pronounced right angle, then running parallel to shaft axis as far as recurved head (1).
10. *Head with outer shelf narrow (0); head with outer shelf extended laterally by more than the same breadth as head (1); head with outer shelf curved ventrally and then twisted towards apex, to form half of a funnel (2).*
11. Head with outer shelf narrow or broad (0); head with outer margin of shaft with straight section narrowed subapically (1).
12. Head with inner (median) margin of recurved section convex (0); head with inner margin of recurved section concave (1).

Male volsella
13. *Small irregular sclerite, not extending apically further than gonostylus (0); large clasping organ, extending apically further than gonostylus (1); entire volsella elongated and narrowed (2).*
14. Outer margin with long setae (0); outer margin without long setae (1).
15. Lateral margins subapically converging (0); lateral margins broadened immediately subapically and then truncated apically (1).
16. Inner margin without a distinct subapical process (0); inner margin with a subapical process, which is usually toothed, arising just before inner margin and projecting in towards midline of body (1); inner subapical process produced distinctly beyond inner margin, often in the form of a broad curved tongue (2); inner subapical process reduced to an indistinct curve on margin, always lacking teeth (3).
17. Inner subapical process distinctly separated from apex, often nearer midpoint of length (0); inner subapical process narrowly subapical, at least on

long axis of volsella (1).
18. *Inner ventral ridge not swollen or swelling not curved back proximally towards outer margin (0); inner ventral ridge, near the mid-point of volsellar length, pronounced at the inner edge of a coarsely sculptured area in the apical half and curved back proximally towards outer margin (1); coarsely sculptured ventral area broadened basally before an inner constriction to a narrower subapical neck, and pear-shaped (2).*
19. *Coarsely sculptured ventral area weakly defined or proximal half reaching outer margin adjacent to gonocoxite (0); proximal half of coarsely sculptured ventral area separated from outer margin by a concave, weakly sculptured area, forming a narrow shining submarginal groove (1); proximal half of coarsely sculptured ventral area separated from outer margin by a concave, weakly sculptured area, forming a submarginal groove as broad as coarsely sculptured area (2); proximal half of coarsely sculptured ventral area separated from outer margin by a broad submarginal groove with long setae (3).*

Male gonostylus
20. Inner basal corner without a distinct process (0); inner basal corner with a distinct rounded process projecting in towards midline of body (1); inner basal corner with a distinct process, distally narrowed in the form of a sharp spine (2); inner basal process with teeth (3); inner basal process twisted to ventral of inner margin (4).
21. Basal inner margin associated with setae (0); basal inner margin without associated setae (1).

Male head
22. Mandible with sparse long setae from posterior margin (0); mandible with dense long setae from posterior margin, forming 'beard' (1).
23. Antenna short, not reaching back beyond wing bases (0); antenna long, reaching back beyond wing bases (1).
24. Flagellum segments nearly straight and cylindrical (0); flagellum segments curved (1).
25. Compound eye similar in relative size to female eye (0); compound eye distinctly enlarged relative to female eye (1).

Male thorax
26. Hind tibia with outer surface uniformly convex (0); hind tibia with outer surface partially concave medially in distal third (1).
27. Hind tibia with short or long hairs over entire outer surface (0); hind tibia without even short hairs medially in distal third (1).

Male abdomen
28. Gastral sternum VII with posterior margin medially convex or irregular, but not broadly concave (0); gastral sternum VII with posterior margin medially broadly concave (1).

Female head

29. *Labrum with median longitudinal ridge (0); labrum with complete transverse ridge between two grooves (1); labrum with transverse ridge broadly interrupted medially (2); labrum with median part of transverse ridge displaced towards apex of labrum to form a projecting lamella, which reaches towards the anterior margin of the labrum (3).*

30. Labrum broadly rectangular (0); labrum broadly triangular (1).

31. Mandible distally broadly rounded (0); mandible distally pointed (1).

32. Mandible with two to four teeth (0); mandible with six teeth (1).

33. Mandible with basal keel not reaching distal margin (0); mandible with basal keel reaching distal margin (1).

34. Oculo-malar distance less than the basal breadth of mandible (0); oculo-malar distance equal to or greater than the basal breadth of mandible (1).

35. Oculo-malar area broadly rounded into the face anteriorly, the area below the eye uniformly convex (0); oculo-malar area separated from the face anteriorly by a narrowly rounded angle, the area immediately below the eye partially concave (1).

Female thorax

36. *Mid basitarsus with disto-posterior corner broadly* rounded or forming a right angle (0); mid basitarsus with acute disto-posterior corner (1); mid basitarsus with pronounced disto-posterior spine (2).

37. Hind tibia without corbicula (0); hind tibia with corbicula (1).

38. Hind tibia with disto-posterior corner forming a right angle (0); hind tibia with disto-posterior corner acute or spinosely produced (1).

39. Hind basitarsus with proximo-posterior process no longer than broad (0); hind basitarsus with proximo-posterior process longer than broad (1).

Female abdomen

40. *Gastral sternum II without transverse ridge (0); gastral sternum II with weakly rounded transverse ridge (1); gastral sternum II with strongly raised transverse ridge (2).*

41. Gastral sternum VI without subapical swellings, curving gradually dorsally (0); gastral sternum VI with paired subapical swellings, lateral areas abruptly turned dorsally (1).

42. Gastral sternum VI without lateral keels (0); gastral sternum VI with lateral keels (1).

43. Gastral segments V−VI nearly co-axial with segments I−IV (0); gastral segments V−VI curled ventrally and back towards anterior (1).