

A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae)

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ABSTRACT. The cladistic method is used to classify sixty species of bumble bees by characters of the male genitalia selected for their functional importance. A system of three genera is recommended, preserving the holophyletic groups *Mendacibombus* Skorikov, *Psithyrus* Lepeletier and *Bombus* Latreille, with the retention of the named subgroups of *Bombus* in subgeneric status. A new subgenus *Brachycephalibombus* is recognized in order to avoid paraphyletic groupings. The phylogenetic interpretation of the cladogram is considered and biogeographic problems discussed.

Introduction

The approximately 291 species of bumble bees (Bombini) have most frequently been placed in two genera, *Bombus* Latreille (1802a, b) for the 'true' bumble bees and *Psithyrus* Lepeletier (1832) for the cleptoparasitic or 'cuckoo' bumble bees. Within each of these genera, groups of species have been recognized, originally by similarities in the colour patterns of the pubescence on the body (Dalla Torre, 1880, 1882) and later by similarities in details of the structure of the male genitalia (Radoszkowsky, 1884). The latter proved to remain more constant within species and so this approach has been refined over the intervening century and used to define many subgenera (Robertson, 1903; Vogt, 1911; Ball, 1914; Skorikov, 1914a, b, 1922, 1933, 1938; Krüger, 1917, 1920; Frison, 1927, 1930, 1935; Quilis-Pérez, 1927; Richards, 1929b; Reinig, 1930; Popov, 1931; Pittioni, 1939, 1949; Franklin, 1954; Tkalců, 1972; Thorp *et al.*, 1983; Laverty *et al.*, 1985). Richards (1968) provided

a summary of the subgeneric system, including keys and documentation of synonymy (but see Yarrow, 1971), which has been widely accepted.

Many authors have expressed opinions concerning the similarities between these various groups of bumble bees or their evolutionary history (e.g. Sladen, 1912; Franklin, 1912, 1913, 1954; Krüger, 1917, 1920; Skorikov, 1922; Frison, 1927; Plath, 1927, 1934; Richards, 1927b, 1929a, 1968; Kruseman, 1952; Yarrow, 1954; Milliron, 1961, 1971; Hobbs, 1964; Tkalců, 1972, 1974a; Pekkarinen *et al.*, 1979; Ito, 1983). The fossil record (Zeuner & Manning, 1976) is too fragmentary to contribute much information directly as to their history. The present paper is an expansion of work carried out in 1980 arising from my interest in phylogeny, in which the cladistic method was applied to bumble bees for the first time. It is a preliminary investigation including only about 20% of the world fauna, but is designed so that the results could contribute to the classification of all the bumble bees, to be elaborated and resolved as further species are included and the significance of new characters becomes clarified.

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<i>Hortobombus</i> Vogt, 1911: 56	Peru	BMNH
<i>Pyrobombus</i> Dalla Torre, 1880: 40	England	PHW
	Norway	PHW
	Japan	BMNH, PHW
<i>Laesobombus</i> Krüger, 1920: 350	Spain	BMNH, PHW
<i>Melanobombus</i> Dalla Torre, 1880: 40	England	PHW
<i>Lapponicobombus</i> Quilis-Pérez, 1927: 19	Sweden	BMNH
<i>Mendacibombus</i> Skorikov, 1914a: 125	Italy	BMNH
<i>Mucidobombus</i> Krüger, 1920: 350	Spain	BMNH
<i>Chromobombus</i> Dalla Torre, 1880: 40	England	PHW
<i>Bombus</i> Robertson, 1903: 176	USA	PHW
	Mexico	BMNH, PHW
<i>Agrobombus</i> Vogt, 1911: 52	England	PHW
<i>Rhodobombus</i> Dalla Torre, 1880: 40	Austria	BMNH
<i>Pratobombus</i> Vogt, 1911: 49	England	PHW
<i>Pressibombus</i> Frison, 1935: 342	India	BMNH
<i>Robustobombus</i> Skorikov, 1922: 157	Colombia	BMNH
<i>Rubicundobombus</i> Skorikov, 1922: 154	Ecuador	BMNH, PHW
<i>Rufipeditobombus</i> Skorikov, 1922: 156	Java	PHW
<i>Rufocinctobombus</i> Frison, 1927: 78	USA	PHW
[<i>Kozlovibombus</i> Skorikov, 1922: 152]	India	BMNH, PHW
<i>Psithyrus</i> Lepeletier, 1832: 373	England	PHW
<i>Senexitobombus</i> Frison, 1930: 3	Sumatra	BMNH
<i>Sibiricobombus</i> Vogt, 1911: 60	China	BMNH
[<i>Nobilibombus</i> Skorikov, 1933: 62]	India	BMNH
<i>Poecilobombus</i> Dalla Torre, 1882: 23	USA	PHW
<i>Kallobombus</i> Dalla Torre, 1880: 40	England	PHW
<i>Subterraneobombus</i> Vogt, 1911: 62	England	PHW
<i>Thoracobombus</i> Dalla Torre, 1880: 40	Sweden	PHW
<i>Bombus</i> Latreille, 1802a: 437	USSR	BMNH*
<i>Tricornibombus</i> Skorikov, 1922: 151	Costa Rica	BMNH*
<i>Volucellobombus</i> Skorikov, 1922: 149	Norway	PHW*
<i>Alpigenobombus</i> Skorikov, 1914a: 128		PHW
<i>handlirshi</i> Friese, 1903: 255 [<i>Bombus</i>]		
<i>hortorum</i> Linnaeus, 1761: 424 [<i>Apis</i>]		
<i>hypnorum</i> Linnaeus, 1758: 579 [<i>Apis</i>]		
<i>ignitus</i> Smith, 1869: 207 [<i>Bombus</i>]		
<i>laesus</i> Morawitz, 1875: 3 [<i>Bombus</i>]		
<i>lapidarius</i> Linnaeus, 1758: 579 [<i>Apis</i>]		
<i>laponicus</i> Fabricius, 1793: 318 [<i>Apis</i>]		
<i>mendax</i> Gerstaecker, 1869: 323 [<i>Bombus</i>]		
<i>mucidus</i> Gerstaecker, 1869: 324 [<i>Bombus</i>]		
<i>muscorum</i> Linnaeus, 1758: 579 [<i>Apis</i>] nec auct.		
<i>nevadensis</i> Cresson, 1874: 102 [<i>Bombus</i>]		
<i>nigrodorsalis</i> Franklin, 1907: 90 [<i>Bombus</i>]		
<i>pascuorum</i> Scopoli, 1793: 306 [<i>Apis</i>]		
<i>pomorum</i> Panzer, 1805: 86 [<i>Bremus</i>]		
<i>pratorem</i> Linnaeus, 1761: 424 [<i>Apis</i>]		
<i>pressus</i> Frison, 1935: 342 [<i>Bremus</i>]		
<i>robustus</i> Smith, 1854: 400 [<i>Bombus</i>]		
<i>rubicundus</i> Smith, 1854: 400 [<i>Bombus</i>]		
<i>rufipes</i> Lepeletier, 1836: 473 [<i>Bombus</i>]		
<i>rufocinctus</i> Cresson, 1863: 106 [<i>Bombus</i>]		
<i>rufofasciatus</i> Smith, 1852: 48 [<i>Bombus</i>]		
<i>rupestris</i> Fabricius, 1793: 320 [<i>Apis</i>]		
<i>senex</i> Vollenhaven, 1873: 229 [<i>Bombus</i>]		
<i>sibiricus</i> Fabricius, 1781: 478 [<i>Apis</i>]		
<i>sikkimi</i> Friese, 1918: 82 [<i>Bombus</i>]		
<i>sitkensis</i> Nylander, 1848: 235 [<i>Bombus</i>]		
<i>soroensis</i> Fabricius, 1776: 246 [<i>Apis</i>]		
<i>subterraneus</i> Linnaeus, 1758: 579 [<i>Apis</i>]		
<i>sybarum</i> Linnaeus, 1761: 425 [<i>Apis</i>]		
<i>terrestris</i> Linnaeus, 1758: 578 [<i>Apis</i>] nec auct.		
<i>tricornis</i> Radoszkowsky, 1888: 319 [<i>Bombus</i>]		
<i>volucelloides</i> Gribodo, 1892: 119 [<i>Bombus</i>]		
<i>wurfleni</i> Radoszkowsky, 1859: 482 [<i>Bombus</i>]		

Methods and Materials

The cladistic method is employed here for the classification of species into groups defined from their possession of shared, derived character states (Hennig, 1981), or synapomorphies. It is assumed here that this method reflects evolutionary change, in the form of modification of characters and divergence of species.

Selection of taxonomic units

The multitude of described specific and subspecific taxa has been studied extensively during the development of the subgeneric system (*op. cit.*). Because the subgeneric system is based on characters of the male genitalia, then variation in genital structures will *a priori* be lesser within than between subgenera. Therefore subgeneric type-species, supplemented by the other known divergent forms, should constitute a representative collection of operational taxonomic units (O.T.U.s, see Table 1).

The integrity of the various subgenera is supported by the congruence of many character states in the descriptions provided by Richards (1968), using characters not only of males but also of females. Furthermore, the results of an analysis of female wing venation measurements (wing venation was not considered by Richards, 1968) by Plowright & Stephen (1973) similarly imply that these groups are unlikely to be artificial.

Selection of characters

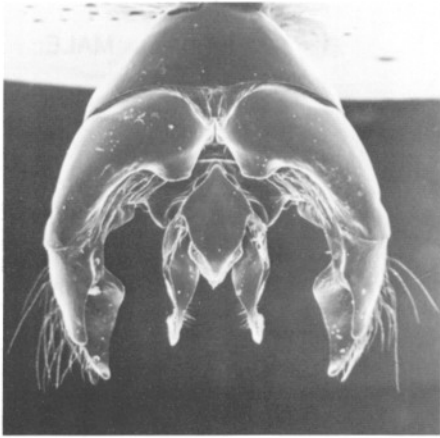
Female bumble bees are morphologically relatively homogeneous between species, whereas males present numerous multi-state characters, especially in their genitalia (Richards, 1927b), suitable for phenetic analysis. Because of the limited variation encountered in male genital characters within species, they have a long history of use in systematics, with the result that much of the interspecific variation is probably now known.

The terminology for component structures of the male genitalia proposed by Michener (1944) from studies of homology is preferred (but see Michener, 1958), although this is modified for bumble bees following a study of the Euglossini (Williams, in prep.). Despite

arguments to the contrary by Snodgrass (1941), who apparently did not examine the euglossines, I believe that the 'laciniae' of bumble bees are homologous with the volsellae of other bees, but have become greatly enlarged and extended distally, ventrad to the gonostylus, a state which represents a major synapomorphy of the monophyletic (*sensu* Hennig, 1981) Bombini. An example of the genitalia of a male bumble bee is illustrated in Figs. 1 and 2. The terminology adopted is presented in Figs. 3 and 4. A guide for the conversion of the terms used by Richards (1968) in his key to the subgenera is included as Table 2.

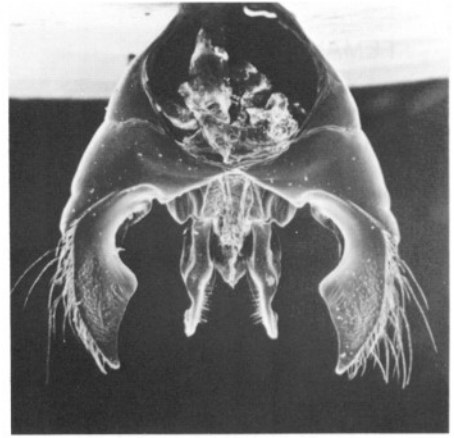
The male genitalia consist essentially of a pair of gonoforceps for clasping the female and an intromittent organ. There are two hypotheses for the function and observed elaborations in the details of these structures. They have been regarded as a lock and key, species isolating mechanism (see Richards, 1927b), although this is doubtful because sibling species have been defined by almost identical male genitalia, supported by close similarity in female characters. Pairing between members of such anatomically similar populations is probably prevented by other isolating mechanisms such as species-specific pheromones acting as behavioural releasers, or separation of preferred mating sites in space or time (Svensson, 1980). Nevertheless, the genitalia may have become elaborated as more general locking devices to prevent interruption during copulation by other, competing, conspecific males (Richards, 1927a; Parker, 1970).

Copulating pairs are rarely encountered and there are few accounts of the mechanics of copulation between bumble bees in the literature. However, a single pair *in copulo* of *B. (Melanobombus) lapidarius* was found in the collection of the British Museum (Natural History) and a diagram showing a partial dissection is presented in Fig. 5. The salient points are that the female is locked with her sting assembly pulled posteriorly and dorsally away from the male (cf. Fig. 7 in Holm, 1964) by at least three points of contact, presumably prior to intromission: the volsellae clasp the membranes at the sting base from above and the gonostyli hold the rami of the valvulae with an opposing action so that the sting base is effectively gripped from above and



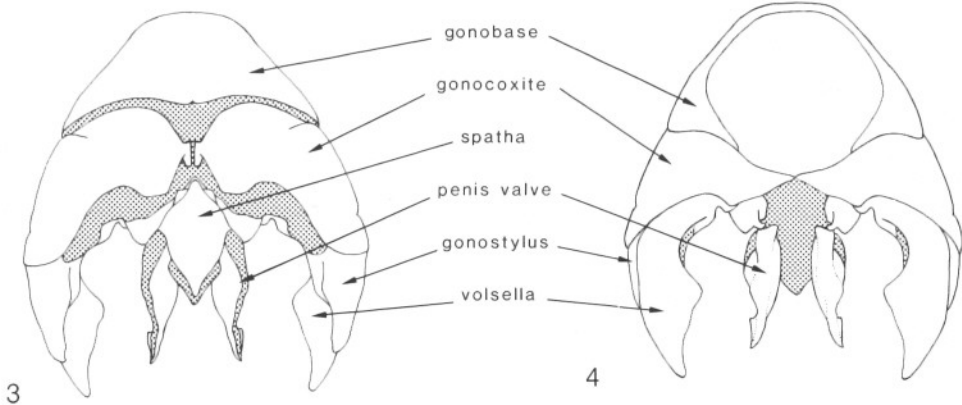
1

500µm



2

500µm



3

4

FIGS. 1-4. Scanning electron micrographs of the dorsal (1) and ventral (2) aspects of the male genital capsule of *Mendacibombus avinoviellus*, with diagrams of the dorsal (3) and ventral (4) aspects of the same. Unshaded areas are shaded in the diagrams.

TABLE 2. Equivalence of terminologies for components of the male genitalia.

Michener (1944)	Richards (1968)	This paper	Abbreviation
Gonobase	Cardo	Gonobase	GB
Gonocoxite	Stipes	Gonocoxite	GC
Squama	Squama	Gonostylus	GS
Gonostylus	Lacinia	Volsella	VS
Spatha	Spatha	Spatha	PS
Penis valve	Sagitta	Penis valve	PV

below; while the sixth metasomal sternite (hypopygium) is locked between the parapepial processes of the gonocoxites and the base of the spatha, ensuring protrusion of the sting assembly and presumably access to the female gono-

pore. Kopelke (1982) describes how the penis valves are also anchored among the weakly sclerotized folds which lie between the rami of the second valvulae. Confirmation of these functions and the determination of the signifi-

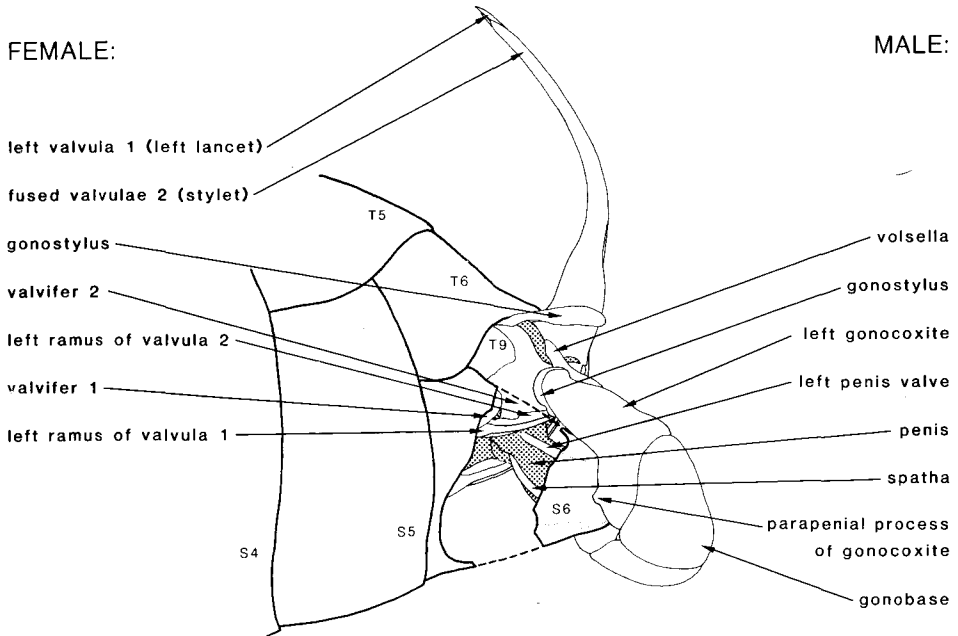


FIG. 5. Diagram of the left ventrolateral aspect of the apex of the metasoma from a female of *Bombus lapidarius*, in copulo, with sternite 6 partially dissected away. Numbers refer to the segmental sclerites of the female metasoma and unsclerotized areas are shaded.

cance of modifications to the 'inner projections from the sting-sheath' (Richards, 1927b) must await future studies of paired bees, for example using sudden freezing by dropping them into liquid nitrogen for subsequent dissection or sectioning.

Only genital components considered to be of crucial functional importance to successful copulation were examined when selecting characters for inclusion in this study. The rationale is that selection is expected to act on such characters of the genitalia so that major structural changes could only persist in the population in the unlikely event that they were accompanied by the requisite reciprocal changes in the anatomy of the other sex. Therefore these structures should be more conservative than others which do not have to 'fit' in order to allow successful copulation. Intraspecific interference competition between males for mates might favour any slight modification in the direction of increasing complexity if this would improve performance at clasping the female. Such a character suite is then particularly suitable for analysis by the cladistic method because it is more likely to obey the divergence model of evolution that this method assumes. Thus examination for data

collection was restricted to the valves of the intromittent penis, the clasping apices of the gonoforceps and those areas believed to function in locking the sixth sternite of the female.

Data collection

The sources of the material examined for data collection are indicated in Table 1. Genital capsules were dissected out, softened in water, re-set and dried in air as shown in Figs. 1 and 2, before being glued to card points. Selected structures were examined from all aspects, drawn and subsequently re-examined for character state coding using a Wild M5A binocular microscope with a drawing tube attachment, at a magnification of $\times 50$.

Polarity of evolutionary change

Decisions regarding topographic similarity between characters and the dependent state changes are illustrated in Fig. 6. Little intra-specific variation was found in the characters selected for coding. Polarities of character state transitions are established using the out-group comparison technique (Bishop, 1982). Elsewhere (Williams, in prep.) I examine rela-

tionships between the currently accepted genera of the Bombinae (Bombini + sister-group Euglossini) based on characters of the male genitalia and suggest probable character states for the common ancestor of modern bumble bees. Figs. 1 and 2 illustrate many of these character states which are suggested to be ancestral (plesiomorphic) for bumble bees from the results of this work.

Character state trees

Trees representing state transitions were postulated separately for each of the 14 selected (non-metric) characters.

1. Ventro-basal angles of the penis valves (PV-a: 13 states). These mark the bases of the laterally compressed blades of the penis valves in the plesiomorphic state. Elaborated states generally show development as basally directed hooks, which could possibly lock inside the inner projections of the sting sheath. Secondary reductions appear to have occurred, principally in those groups with complex hooked heads to the penis valves. Development of the basal angles is also variously accompanied by lateral or ventral flanges to support them, or flexion of the penis valve shafts to exaggerate them.

2. Interio-basal shelves of the penis valves (PV-b: 2 states). Strongly developed only in *Mendacibombus*, possibly to preserve the rigidity of the laterally compressed penis valves, or to support or direct the erectile penis during intromission.

3. Shafts of the penis valves (PV-c: 2 states). Only the apomorphic dorso-ventral widening of these structures (e.g. *Cocci-neobombus*) is included here, possibly a device in these species, with dorso-ventrally compressed heads to the penis valves, analogous to the interio-basal shelves of *Mendacibombus*.

4. Form of the heads of the penis valves (PV-d: 24 states). Defined by an outer flange, often with fine teeth, these are straight in the plesiomorphic state. Apomorphic states include pronounced exteriobasal barbs and, more commonly, an inward inflexion of the dorsoventrally compressed apices as broadly reflexed hooks, which may anchor against folds of the unsclerotized areas inside the female sting base, thus causing the 'copulatory scars' (Cumber, 1949). They probably do not

penetrate the female genital tract deeply enough (Kopelke, 1982) to be involved in the removal of sperm from previous matings during the prolonged copulatory period (cf. Waage, 1979). Secondary reduction of these broad hooks is suggested to have occurred in at least five groups independently (*Bombus* s.str., *Funebribombus*, *Separatobombus*, *Brachycephalibombus* nov., *Rubicundobombus*).

5. Development of teeth on the heads of the penis valves (PV-e: 3 states). These are often basally directed barbs, but only occasionally are they very large.

6. Loss of teeth on the heads of the penis valves (PV-f: 2 states).

7. Form of the gonostyli (GS-a: 33 states). These are simple, somewhat flattened plates in the plesiomorphic state. Apomorphic states entail the development of interio-basal processes, which presumably fit around the rami as part of the clasping action. If these processes fit between the rami of the first valvulae in some species and apply an outwardly directed force, the gonostyli could also function in spreading the sting assembly and exposing the gonopore for intromission.

8. Setae of the gonostyli (GS-b: 2 states). The possession of setae by the gonostyli is plesiomorphic for the Bombinae. However, it is suggested that its suppression is plesiomorphic within the Bombini and that it reappears as an apomorphy in the 'cuckoo' bumble bees.

9. Form of the volsellae (VS-a: 27 states). It is proposed that the volsellae enlarged during the evolution of the stem-group to the bumble bees, so that they became produced apically and contacted the sting base laterally during pairing, subsequently becoming important in the clasping function of the genitalia. Elaborations are suggested to have proceeded via the acquisition of pronounced double hooks on their inner margins which grip the sting base, to more elongated structures on which the hooks assumed a more terminal position.

10. Setae of the volsellae (VS-b: 2 states). The interio-ventral faces possess subapical areas of variable extent marked by pronounced sculpturing and dense setae (even in the Euglossini), which may be of sensory function in the coordination of copulation.

11. Interio-ventral ridges of the volsellae (VS-c: 7 states). These do not occur in all bumble bees, but when present usually form

the inner and apical boundaries to the densely setose areas described above. Their form may be correlated with that of the female sting base laterally and could serve to increase the contact area of sensory function, while also strengthening the volsellae for their clasping function.

12. Basal process of spatha (PS-a: 7 states). Strongly developed only in the Bombini, this is broad in the plesiomorphic state but has become elongated and greatly narrowed in several groups. During copulation this process presses into the concavity formed in the apical angle of the inner (dorsal) surface of the sixth metasomal sternite of the female.

13. Baso-lateral depressions of spatha (PS-b: 3 states). These effectively narrow the spatha further in the region for insertion into the female sternite, perhaps increasing the area of contact and improving the lock. Their greatest development accompanies a general narrowing of the spatha and could be related to a narrowing of the apex of the sixth metasomal sternite of the females or to the extension of the dorso-lateral margins near the apex of this sternite.

14. Parapenial processes of the gonocoxites (GC-a: 5 states). Variation in these structures, just as for the characters of the spatha, is not distinctly discontinuous. Therefore only the more extreme departures from the general form have been coded. The greatest development of these processes is exhibited by the 'cuckoo' bumble bees, the females of which possess a pair of callosities ventro-laterally on the sixth metasomal sternite.

Data processing

The character state trees were tested for compatibility (as discussed by LeQuesne, 1982). Calculations were carried out by the Cambridge IBM 3081 computer using a directed version of the CLINCH program described by Estabrook *et al.* (1977). This procedure was used to examine characters represented in the data, in order to identify cases of incompatibility. The coding of incompatible characters could then be reconsidered.

Results

Of the 14 character state trees proposed, a

maximum of 10 (character trees 1, 2, 3, 4, 5, 7, 8, 9, 10, and 11 above) are found to be compatible. These include 115 out of the total of 132 character states which had been coded.

Within the single composite character state tree composed by CLINCH from this maximal clique of 10 compatible component character trees, 46 groups are distinguished among the 60 taxonomic units entered, linked by 32 hypothetical ancestors. Fig. 6 is a representation of this composite tree with diagrams at the appropriate branches to illustrate the character state transitions from the component trees.

Discussion

A number of divergent and subgeneric type-species were not available for direct examination here (Table 1), although descriptions and drawings of the male genitalia have been published for many of these so that it is possible to suggest where their affinities probably lie among the species selected for consideration in the present study. Thus *P. (Ashtonipsithyrus) ashtoni* Cresson and *P. (Eopsithyrus) tibetanus* (Morawitz) are closely similar to *P. bohemicus* and *P. decoomani* respectively (Franklin, 1913; Bischoff, 1936), while *P. (Ceratopsithyrus) Pittioni*, 1949: 271) *klapperichi* Pittioni exhibits no character states remarkable for *Psithyrus* s.l. and resembles species of *Psithyrus* s.str. in its genitalia (Pittioni, 1949). *B. (Exilobombus) Skorikov*, 1922: 150) *exul* Skorikov appears to be most similar to *B. mucidus* and *B. (Adventoribombus) Skorikov*, 1922: 150) *filchnerae* Vogt (= *Agrabombus adventor* Skorikov, synonymized by Tkalců, 1974b) closely similar to *B. pascuorum* (Tkalců, 1974b). The identity of *B. (Nobilibombus) nobilis* Friese remains in doubt, but this species was assumed to be similar to *B. sikkimi* by Richards (1968) for his redescription of the subgeneric characters. The genitalia of *B. (Obertobombus) Reinig*, 1930: 107) *oberti* Morawitz were figured by Reinig (1930) and Skorikov (1931) from which it appears to be most closely similar to *B. sibiricus*, although it does differ by the curious form of the volsellae. The males of *B. (Tanguticobombus) Pittioni*, 1939: 201) *tanguticus* Morawitz are apparently still unknown,

although this species was tentatively placed in *Melanobombus* by Richards (1968). *B. (Kozlovibombus) kozlovi* Skorikov uniquely shared this subgenus (Skorikov, 1922) with *B. rufofasciatus* (= *B. prshewalskyi* Morawitz, synonymized by Richards, 1930) and is assumed to resemble it in character states of the male genitalia. The male of *B. haueri* Handlirsch is known from a single specimen, the genitalia of which were illustrated by Milliron (1973b). I believe that this species agrees most closely with *B. brachycephalus* and is therefore quite distinct from *B. dentatus* Handlirsch to which Milliron suggested a close relationship, but which approximates *B. wurfleini* amongst the species considered here by the present interpretation of characters. *Pseudobombus* Steiner (1957: 10) is a *nomen nudum*.

Systematics

A primary objective, when proposing a classificatory system, is assumed to be stability; ideally, novel characters would be compatible and could be included without consequent modification of the system. Thus it should be 'predictive' and also not unique to each author. Given the results of the hierarchical groupings in Fig. 6 and the stability criterion, it is recommended that the use of the generic name *Psithyrus* is continued for the holophyletic group of 'cuckoo' bumble bees (including the type-species *Apis rupestris* Fab. by designation of Curtis, 1833: 468) and the genus *Bombus* retained for their large, holophyletic, sister group, following the suppression of *Bremus* (Hemming, 1939, 1954). *Apis terrestris* Linnaeus has been accepted (Hemming, 1939, 1954). *Apis terrestris* Linnaeus has been accepted (Hemming, 1954) as the type-species of *Bombus* by designation of Latreille, 1802b: 385, despite the designation of *Apis terrestris* 'F.' by Latreille, 1802a: 437, which would have appeared to have had priority (Griffin in Richards, 1935). However, *A. terrestris* 'F.' is clearly a reference to the same entity as *A. terrestris* Linnaeus because Latreille's publications follow almost identical text. The identity of *A. terrestris* Linnaeus (Løken, 1973; Day, 1979) affects the citation of synonymy for this species but has no effect on the application of generic or subgeneric names.

However, in order to avoid an 'unnatural',

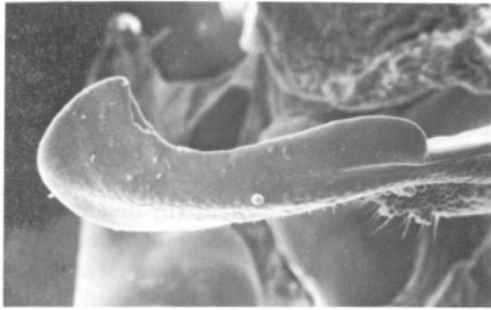
paraphyletic genus *Bombus*, the genus *Mendacibombus* Skorikov (1914a: 125) must then be resurrected. The isolated position of *Mendacibombus* was also recognized by Skorikov (1922), Tkalcû (1972) and Ito (1983). *Mendacibombus* species are restricted to higher altitudes and are predominantly Asian, with only the type-species, *M. mendax* (by designation of Sandhouse, 1942: 572), being found as far west as the Alps, where the many unusual aspects of its natural history have been described by Haas (1976). Females of this genus also possess many distinct character states (Richards, 1968) which can be used to separate them from species of the genus *Bombus* in the sense proposed here.

It is anticipated that this trigeneric system will pose few problems in identification for the non-specialist and yet be of 'predictive' value when considering the behaviour of the species. The genus *Bombus* cannot be divided into a small number of large groups compatible with the composite tree and holophyly (Fig. 6), but only many, mostly small groups of species. It is therefore suggested that the subgeneric system be retained essentially as delimited by Richards (1968), because it is proving to be of some 'predictive' value to the specialist (e.g. Sakagami, 1976). As a result of this preliminary investigation only one modification is necessary. *B. brachycephalus* cannot be included in any available subgenus holophyletically, unless the concept of *Robustobombus* be greatly broadened to encompass the distinctly divergent species *B. rubicundus*, *B. coccineus*, *B. baeri* Vachal and *B. handlirschi*. Therefore it is considered necessary to propose the recognition of a single new subgenus within the genus *Bombus*.

Brachycephalibombus subgen.n.

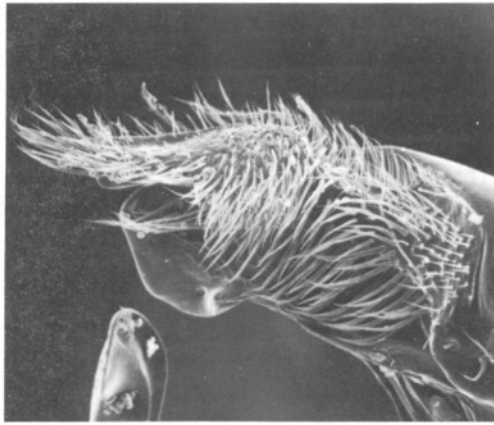
Type-species: *Bombus brachycephalus* Handlirsch, 1888: 244.

This subgenus is defined by two apomorphic character states of the male genitalia (Fig. 6): (A) the heads of the penis valves possess distinct interio-basal angles and are elongated with the apex turned inwards towards the mid line of the body, but only in a weakly scythe-like form (Fig. 7); (B) the volsellae, when viewed from an interio-ventral aspect, are apically truncated and without interiorly



7

100µm



8

200µm

FIGS. 7-8. Scanning electron micrograph of (7) the dorso-posterior aspect of the head of the right penis valve and (8) ventral aspect of the right volsella of *Bombus brachycephalus*.

directed hooks or processes, with the subapical area being strongly expanded laterally (Fig. 8).

This subgenus includes the type-species and very probably *B. haueri*. The position of *B. brachycephalus* on the composite tree (Fig. 6) shows that in respect of certain characters it is transitional between the North American *B. crotchii* and the South American *B. robustus*. Both *B. brachycephalus* and *B. haueri* occur in the mountains of Mexico, although the distribution of *B. brachycephalus* extends as far south as Honduras (Milliron, 1973b).

No subgenera are necessitated in *Mendacibombus*. Little support is provided for the continued use of the subgenera of *Psithyrus*, because their type-species are much more

closely similar to each other, in the characters examined here, than is general between the subgenera of *Bombus*. Furthermore the results of Plowright & Stephen's (1973) classification of species did not support the conventional groupings. This genus should be revised, especially now that more material is available from Eastern Asia, because it would be interesting to compare the phylogeny of the 'cuckoos' with that of their hosts. In this connection it is noted that there do not appear to be any records of *Psithyrus* species from the nests of *Mendacibombus* species.

The characters employed in this investigation have yielded a moderately asymmetric branching pattern in the composite tree, which does not permit the definition of a small number of large holophyletic groups within the genus *Bombus*. For example, Krüger's (1917) 'section' *Anodontobombus* includes *M. mendax*, *B. confusus*, *B. alpinus*, *B. soroensis* and presumably all the descendants of hypothetical ancestor 15 (Fig. 6), to which Richards (1968) added his subgenus *Orientalibombus*. This 'section' would therefore appear to be polyphyletic, a result which might be expected from homoplasy when such a large group of species is defined primarily by the possession of a single, reduced, character state. Similarly the 'sections' *Odontobombus* Krüger (1917), *Uncobombus* Krüger (1917), *Sulcobombus* Krüger (1917) and *Boopobombus* Frison (1927) are not holophyletic according to the present results, a conclusion that had also been reached concerning *Boopobombus* by Franklin (1954), Milliron (1961) and Plowright & Stephen (1973). These 'sections' have continued to be used by some recent authors because, as applied only to the restricted subset of species that are both widespread and abundant in Europe or North America, they do correlate with behavioural characters (e.g. Plath, 1927, 1934).

Polygeneric systems for the classification of bumble bees have been proposed more recently by Milliron (1961, 1971) and Tkalců (1972) based on ideas of polyphyletic origins for bumble bees, but have proved controversial (Richards, 1968; Tkalců, 1972, 1974a, b; Plowright & Stephen, 1973; Sakagami, 1976; Ito, 1983). Although characters of the male genitalia were taken into account in their construction, neither of these schemes is compatible

with the present composite character state tree if the criterion of holophyly is to be conserved.

Phylogeny

The cladistic method results in hierarchical classifications of taxa which should reflect their phylogeny if the character state changes during evolution are divergent. A divergence model clearly is not entirely adequate because incompatibilities between component character state trees demonstrate that homoplasy does occur. Acceptance of the tree inferred from the maximal clique implies acceptance of the minimization of homoplasy as a criterion of goodness-of-fit of the tree to the data. Critiques of the parsimony approach are provided by Panchen (1982) and Friday (1982). The composite character state tree can therefore only be used to derive an *estimate* of the relationships by relative antiquity of common ancestry between taxa. This estimate provides a basis for subsequent improvement and elaboration, as further characters and all extant taxa can be included.

Incompatibilities arising from parallel reductions of complex characters, such as (6) the lateral teeth on the heads of the penis valves, might be expected to occur by suppressions of gene expression (Gauld & Mound, 1982). Similarly, parsimony would dictate that the relatively simple modifications by narrowing of the structures (12, 13, 14) believed to function in locking the sixth metasomal sternite of the female have occurred in parallel on probably four occasions. Of the 77 branches in the composite tree, 52 depend on single character synapomorphies and further characters would be highly desirable to improve confidence in these groupings (see Panchen, 1982). Two trichotomies also exist in the composite tree without known transitions in the selected characters for their resolution.

All the taxonomic units selected for this investigation are represented by modern species and no extant species is considered to be genetically directly ancestral to any other. Therefore in the situation where one extant group is connected directly to another in the composite character state tree, it merely implies that character state transitions were not discovered which allow both groups to be distinguished from their common ancestor.

This situation is better represented by the introduction of dashed lines (e.g. Estabrook *et al.*, 1977) to separate extant groups from their ancestors. This permits the presentation of the composite character state tree as a cladogram in Fig. 9, summarizing the postulated relationships between the species studied and the recommended classification system.

A cladogram also differs from a phylogenetic tree in that the cladogram represents the rank order of divergence of character states and does not indicate speciation events directly. Neither does it contain any information on the history of action by selective forces, an issue that remains for speculation.

It has been widely accepted that the Apoidea arose in association with the angiosperms during the Cretaceous (e.g. Skorikov, 1922; Milliron, 1971; Michener, 1979; Ito, 1983; Culliney, 1983; Crepet *in Real*, 1983), from c. 100 million years (Ma) before the present. South America is the modern centre of diversity for the long proboscis bees (Michener, 1979), in which the glossa has become greatly elongated (Michener & Greenberg, 1980). This condition may have imposed fewer constraints on evolutionary increases in body size (Harder, 1983), for which the *Bombinae* are exemplary. The sister group to the *Bombini*, the *Euglossini* (Winston & Michener, 1977; Kimsey, 1984; Williams, *in prep.*), is more or less restricted to the tropical lowland areas of South and Central America (Kimsey, 1982). This contrasts markedly with the present distributions of the majority of bumble bee species, which combine large body size with a particularly long, dense, insulating pubescence (May & Casey, 1983). In Northern Europe and North America bumble bees have been collected at all altitudes from sea level up to the alpine zone (Løken, 1973; Milliron, 1971, 1973a, b), but at lower latitudes in the Himalayan region they have only been found at higher altitudes, for example between 1550 and 4900 m in Kashmir (*pers. obs.*) and 1000 m up to 5600 m, above the 'Rhumbu' [=Khumbu] Glacier, in Nepal (BMNH collection). A trend towards a maximum number of species at mid northern latitudes is shown for the fauna of the New World by Stiles (1979), with only *B. (Fervidobombus) transversalis* (Olivier) being widespread in the tropical lowland forests of the Amazonian region (Millir-

on, 1973a). This association with montane and north temperate environments is very likely to be related to their unusually well developed, facultative endothermy (see Heinrich, 1979).

Estimates of the number of species per subgenus, compiled with reference to Milliron (1971, 1973a, b), Reinig (1981) and a preliminary catalogue of the world species (in prep.), are included in Fig. 9 with a breakdown by the principal continents inhabited. The numbers of both subgenera and species tend to decrease away from Asia, through Europe and North America to South America. The overlaps in both subgenera and species between Asia and Europe are considerable: there are no European endemic subgenera, whilst the number of species common to both of these areas (38 spp.) is likely to have been underestimated, owing to the problems of species definition with morphologically similar populations that are highly polymorphic with respect to colour. Those species present in both Europe and North America (6 spp.) are widespread holarctic, often circumpolar (K. W. Richards, 1973), whereas those present in both North and South America (5 spp.), as delimited by the northern border of Mexico, are predominantly North American and penetrate south only as far as Central America.

Bumble bees would not be expected to disperse over long distances (Ito & Sakagami, 1980) and oceans should constitute particularly effective isolating barriers between faunas. It is therefore inferred from their present distributions that the initial diversification of bumble bees may have been centred on the mountains of Asia where there are still relatively few other groups of long proboscis bees (Michener, 1979) as potential competitors, and to which most species of *Mendacibombus* remain restricted. This primary speciation probably took place early in the Caenozoic Era, since fossil bees attributed to *Bombus* s.l. (Zeuner & Manning, 1976) occur in Oligocene (38–26 Ma) deposits. These records are not of sufficient quantity or quality to allow the direct reconstruction of the history of the group, but in conjunction with evidence from studies of continental palaeomagnetism, ocean floor magnetic anomalies, fossil floras and fossil mammal assemblages for available land routes, they do permit speculation as to the history of dispersal by bumble bees. Hence during much

of the Eocene Period (54–38 Ma) the northern continents apparently enjoyed warm climates (Wolfe, 1978) and Asia was isolated from both Europe and North America by seas (McKenna, 1975), although following the terminal Eocene event, c. 40 Ma, the Oligocene climate was cooler (Wolfe, 1978) and land connections became established between the northern continents (McKenna, 1975). These may have allowed ancestral bumble bees to disperse from Asia into Europe and North America and thus leave the observed fossil evidence. The much more recent rise of the mountains from Southern Asia into Europe (Smith *et al.*, 1981) has provided corridors of lower resistance for the dispersal of highland bumble bees, in addition to the lowland forms, from Asia into Europe. In contrast, the dispersal route from Asia into North America was far to the north, via Beringia (McKenna, 1975), and more dependant on low sea levels. Why then are the earlier-diverging 'true' bumble bees represented in the New World only by the species of *Fervidobombus*? In the Old World these subgenera of *Bombus* are absent or relatively poorly represented at higher altitudes in the mountains of Southern Asia (pers. obs.) and at higher latitudes (Skorikov, 1922, 1931). It is possible that the climate of Beringia acted as a selective barrier to dispersal by these, perhaps less cold tolerant, species. It is otherwise difficult to credit predation or competition with the selective extinction of all their former representatives in the New World. During succeeding periods the ancestral *Fervidobombus* and the descendants of hypothetical ancestor 13 (of the *Separatobombus* group [a term intended solely as a device to identify a holophyletic group for the purposes of the present discussion and *not* to establish a new taxonomic rank]) would have speciated in North America, while the descendants of hypothetical ancestors 22 (*Megabombus* group), 16 (*Sibiricobombus* group) and the ancestor of the *Festivobombus* group speciated principally among the mountains of Southern Asia. Thus it was probably here that the ancestor of the phenetically strongly divergent (Milliron, 1961, 1971; Tkalců, 1972; Sakagami, 1976; Ito, 1983) subgenus *Bombus* s.str. arose relatively recently. Cool temperate elements of this and other subgenera such as *Alpinobombus*, *Subterraneobombus*, *Cullumanobombus*

and some *Pyrobombus* possibly reached the Nearctic Region rather more recently, if the limited degree of morphological differentiation of the present nearctic species from their palaeartic relatives can be interpreted in this way. The subgenus *Pyrobombus* has now a continuous, wide, holarctic distribution and accounts for nearly half of the North American fauna (Fig. 9), in which the number of other subgenera of *Bombus* represented (9) is lower than in Europe (14) or Asia (22). However, although morphologically reasonably uniform, the species of *Pyrobombus* are particularly heterogeneous with respect to enzyme phenotypes (Pekkarinen *et al.*, 1979) and male 'marking' pheromones (Svensson, 1980).

Following the reconnection of North and South America at the isthmus, *c.* 3 Ma (Cox, 1974), only some species of *Fervidobombus*, the ancestral species of *Funebribombus* and descendants of hypothetical ancestor 18 (*Robustobombus* group) reached South America, possibly because tropical lowland forests presented barriers to dispersal for most bumble bees. These groups must then have evolved rapidly in isolation from other bumble bees to give rise to their morphologically strongly divergent modern descendants. The closest previous period during which there is evidence (Cox, 1974) for the availability of potential dispersal routes to South America was at the beginning of the Cenozoic Era, *c.* 70–60 Ma, when Asia was joined to Europe via North America. For bumble bees to have dispersed to South America at this time, a much earlier origin for ancestral bumble bees would have to be postulated, and the fauna of Europe might then have been expected to resemble that of North America more closely than it resembles the fauna of Asia, or at least uniquely share some species in relict, disjunct distributions. Therefore it is perhaps more likely that ancestral bumble bees did not reach South America until much later, as described above, although the common ancestors to the Bombinae may well have used these earlier land routes for dispersal.

European species of *Megabombus*, *Laesobombus*, *Bombus* s.str. and *Melanobombus* have become established in the Atlas Mountains of Africa probably quite recently, having dispersed via the Iberian Peninsula. The only bumble bee from Africa south of the Sahara is

a unique female described as *B. (Fervidobombus) abditus* (Tkalců, 1966), but which is indistinguishable from *B. brevivillus* according to Sakagami (1976) and probably represents an introduced or mislabelled individual (Michener, 1979).

The apparent success of the bumble bees in mountainous and north temperate environments, as measured by their abundance, may be attributed to their facultative endothermy. Coupled with this is the short, annual, development cycle of small colonies, which allows females to avoid predictable annual, and often long, periods of adverse conditions by hibernation with minimal energy costs. This may have proved advantageous, in comparison with the honey bees (cf. Culliney, 1983), following the decrease in mean annual temperature and more particularly the increase in mean annual range of temperatures at higher northern latitudes during the Cenozoic Era (Wolfe, 1978). In Europe, the largest number of species of bumble bees is now concentrated in the Alps, which possibly represent their refugia in the present interglacial.

Applications

The dichotomous branching pattern of the composite character state tree should allow it to be used as a key (Penny, 1982) for the identification of male bumble bees to the subgeneric level. In practice many of the more derived character states appear to have arisen by reduction from more complex states, creating difficulties at the earlier stages of such a 'key'. However, with closer acquaintance it may still be possible to use Fig. 6 as a general guide.

Bumble bees are economically important for pollination, particularly of leguminous seed crops and certain tree fruits (e.g. Free, 1970). Consequently there has long been an interest in introducing them to areas outside their natural range to increase crop yields, for example to New Zealand (Gurr, 1957, 1972), Australia (Oliff, 1895) and the Philippines (Frison, 1925). Introduction, combined with suitable management techniques, can prove very profitable (MacFarlane *et al.*, 1983). But in order to select the most effective species for trial towards this purpose, it would be advantageous to possess a model from which re-

levant behaviours and seasonal patterns of colony development could be predicted for candidate species, which occur in areas with similar climates, but about which no such data were directly available. Perhaps the most useful and interesting aspect of the phylogenetic study of bumble bees is this relationship between morphological and behavioural divergences of populations.

Acknowledgments

My thanks to Dr S. A. Corbet and Dr A. E. Friday for their help and advice. I am also very grateful to the Trustees and staff of the British Museum (Natural History) for the loan of material from the collection, and to the following who have contributed to my collection used in this investigation: Dr M. E. Archer, Miss A. O. Divers, Miss J. A. Hawkings, Dr M. Ito, Mr J. M. Labougle, Mr T. M. Laverty, Mr S. J. Martin, Dr B. Petersen (for the Zoologisk Museum, Copenhagen), Dr R. C. Plowright, Mr J. A. Stenløkk, Dr R. W. Thorp, Dr S. Wang (for the Institute of Zoology, Beijing). The work was carried out while holding a Natural Environment Research Council studentship. Valuable material was collected during the Cambridge Expedition to Kashmir, 1980, which was supported by the Mark Pryor Fund, Carl Pantin Fund (Trinity College, Cambridge), M. E. Mosely Fund and Worts Travelling Scholars Fund (University of Cambridge).

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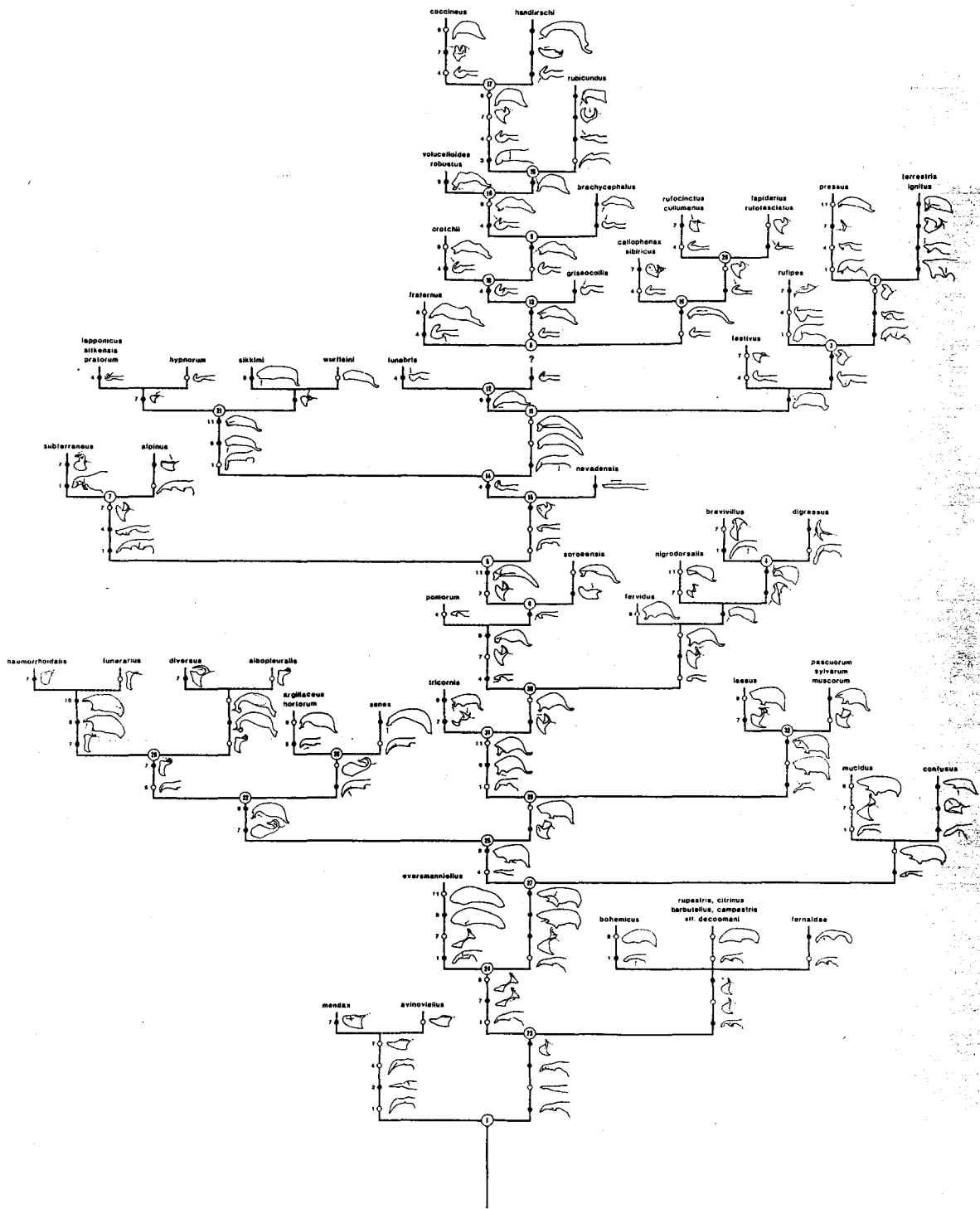
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Accepted 25 May 1984



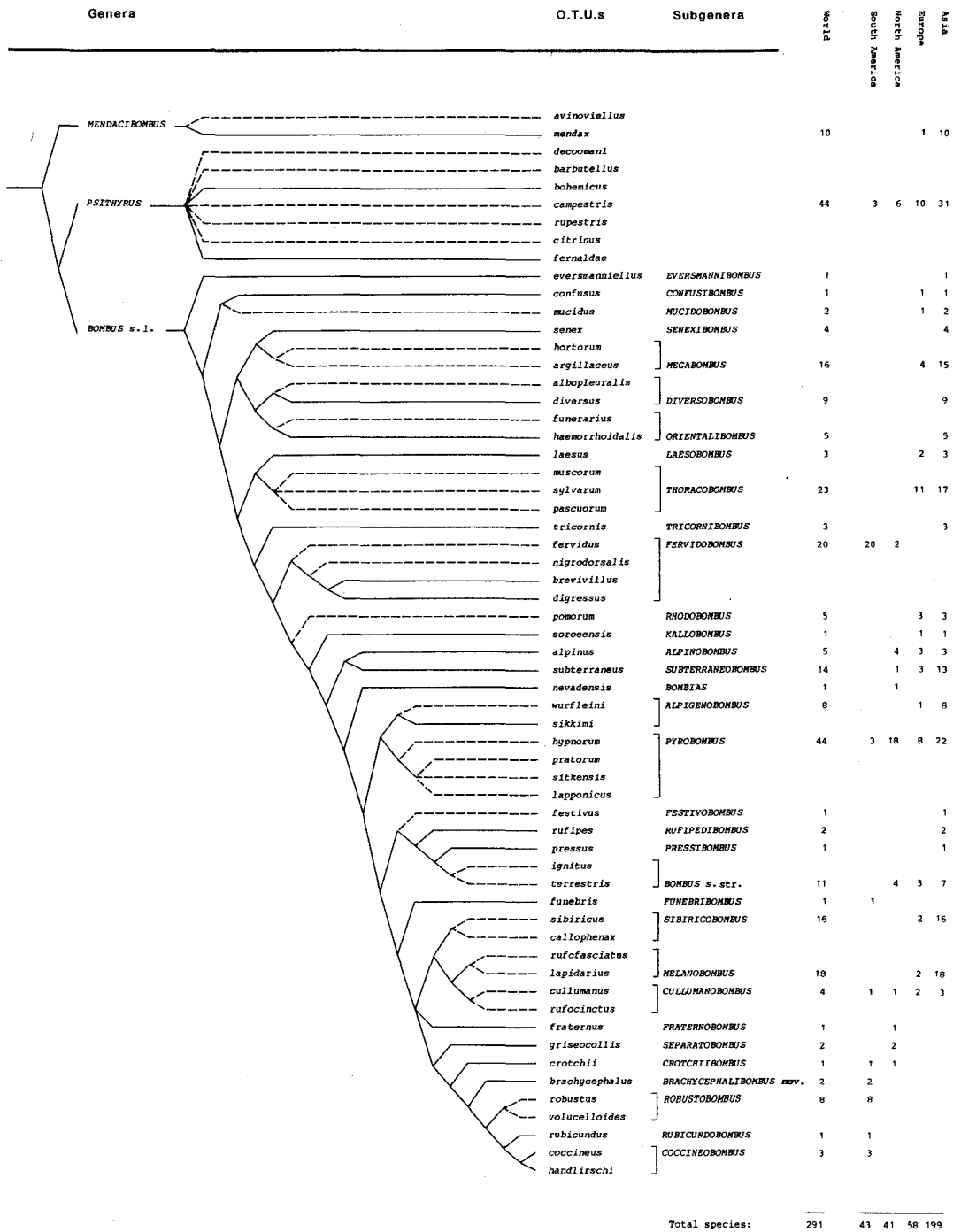


FIG. 9. Cladogram illustrating the relationships between extant taxa of the Bombini as estimated from the combined character tree, with the recommended usage of genera and subgenera. Estimates of the numbers of species in these various groups and a break-down by major regions are included to the right.