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Phylogenetic relationships and classification of the Vespinae (Hymenoptera: Vespidae)

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ABSTRACT. The phylogenetic relationships of the genera, subgenera and species-groups of the Vespinae are analysed using cladistic techniques. The results are used as the basis for a natural classification of these wasps. The cladogram for the four genera recognized is: *Vespa* + (*Provespa* + (*Dolichovespula* + *Vespula*)). No subgenera are recognized; all those previously described are synonymized with the appropriate genus. The synonymies of *Nyctovespa* with *Vespa* and *Rugovespula* with *Vespula* are new.

Introduction

The yellowjackets and hornets are the most familiar of wasps. Almost ubiquitous throughout the north temperate regions and oriental tropics, they are generally recognized – and feared – by laymen. The history of human knowledge of these wasps is ancient (cf. Spradbery, 1973; Edwards, 1980). The fascination engendered by their eusocial behaviour is also ancient, and so they are the subject of an ever-burgeoning number of behavioural studies. In addition to social organization, considerable current interest is focused on aspects of venom chemistry, economic injury and biological control potential (e.g. Akre & MacDonald, 1986). With the attention paid to these wasps, it might be expected that their classification would be stable, and their evolutionary relationships grasped at least in outline. But this is not the case. Great controversy currently exists; both nomenclature and classification vary from author to author, and evolutionary relationships are in dispute. Some current classifications do not follow the International Code of Zoological Nomenclature. More serious is the lack of a comprehensive phylogenetic system. As a result, paraphyletic taxa are in use, and much discussion of the evolutionary development of behaviour is misplaced. Without differentiation of features into derived and primitive states, disputes on groupings and evolutionary development are unresolvable (cf. Yamane, 1976; Greene, 1979; Matsuura & Yamane, 1984; MacDonald & Matthews, 1975, 1984). The present work is intended to redress this situation, by providing the first comprehensive cladistic treatment of supraspecific taxa in the Vespinae.

Previous treatments

The taxonomic history of the vespine genera has been reviewed by Bequaert (1930, 1932), Guiglia (1971) and Edwards (1980). I review here only recent studies dealing with evolutionary relationships, independent of taxonomy.

MacDonald & Matthews (1975, 1984) questioned the placement of *Vespula squamosa* in the *rufa* species group, or *Vespula s.str.* (Bequaert, 1932). This stance has been followed by general authors, who have regarded this species and its sister-species *sulphurea* as of uncertain place-

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ment (Edwards, 1980; Akre *et al.*, 1981). MacDonald & Matthews (1975: 1004) stated: 'Comparative nest architectural, behavioral, morphological, and electrophoretic data currently under study strongly indicate that *V.squamosa* is wrongly aligned with the *V.rufa* group'. No morphological or electrophoretic data pertinent to this question have ever been published, but MacDonald (1977) and MacDonald & Matthews (1984) listed a number of nest architecture and behavioural characters which, they suggested, showed greater similarity to the *V.vulgaris* species group (*Paravespula*). It will be shown below that these features are either plesiomorphic in Vespinae, or uninformative. MacDonald (1977) stated that the male genitalia of *squamosa* are distinctive (also mentioned by Yamane *et al.*, 1980), and MacDonald & Matthews (1984) cited a study by Kugler *et al.* (1976) showing seven ovarioles per ovary in *squamosa* (versus six in most other vespines) as also indicating wrong placement of *squamosa* in the *rufa* group. These traits, of course, are autapomorphies, and such unique characters are irrelevant to the placement of the species – they only show that it is monophyletic. Synapomorphies uniting the *squamosa* and *rufa* groups are presented below.

Yamane (1976) presented a cladogram for vespine subgenera; however, it did not include *Provespa* or the parasitic subgenera (viz *Vespula* (only with *austriaca*), and *Pseudovespula*). This latter omission is unimportant, as recognition of subgenera for the parasitic species renders other subgenera paraphyletic, as discussed below. Yamane (1976: Table 3) listed fifteen characters used in the construction of his tree, and differentiated these into primitive and derived states. He upheld the monophyly of *Vespula* + *Dolichovespula*, and *Dolichovespula*, but could not determine whether *Allovespula* was the sister-group of *Paravespula* or *Dolichovespula*. As developed below, the polarity of two of Yamane's characters was incorrectly inferred, and there are no grounds for grouping *Allovespula* with *Dolichovespula* (done on the basis of grey, pliable nest paper). Yamane's cladogram also showed the interrelationships of the subgenera of *Dolichovespula* as: *Metavespula* + (*Boreovespula* + *Dolichovespula*). The latter two taxa were grouped by three characters, and single autapomorphies were noted for each of them. The polarity of one of these characters (tyloides) is also incorrectly inferred, and the states of the other two characters associating *Boreovespula* and *Dolichovespula* are also true of *sylvestris* (*Metavespula*). Finally, the autapomorphic state for *Boreovespula* is not true of all the included species, and this taxon is paraphyletic.

Greene (1979) presented a discussion of behavioural characters which he considered to show a 'phyletic sequence' with *Dolichovespula* as the most primitive yellowjacket genus and the *vulgaris* group the most recently derived group. This sequence, he argued, was the opposite of that proposed by Yamane (1976). In fact, Greene's discussion conflated character state change and branching sequence. Although Greene (1979: 614) stated that *Dolichovespula* 'probably has a relatively closer ancestral relationship with *Vespa*', he later stated (p. 618): 'I have assumed the yellowjackets constitute a monophyletic group in which the genus *Vespula* evolved from *Dolichovespula* stock, which in turn arose from the *Vespa* lineage'. This is the same sequence as Yamane proposed. Thus, whereas Greene is probably correct in the polarities inferred for the behaviours discussed, they are irrelevant to the question of phylogenetic relationships among yellowjackets, as either polarity is in accord with the same scheme.

Yamane *et al.* (1980) argued that the division of *Vespula s.l.* into the *rufa* and *vulgaris* groups was inappropriate, and subdivided *Vespula s.l.* into seven groups. Their character states were a mixture of primitive and derived, and they stated (p. 34): 'These groups are, however, rather phenetic'. They did not investigate the interrelationships of these groups (nor establish their monophyly), but did adopt Guiglia's (1972) division of *Vespula* into the subgenera *Vespula* and *Paravespula*! They considered the assignment of the *koreensis* group to *Paravespula* and the *squamosa* group to *Vespula* to throw doubt on this division. They stated (p. 34): 'They have characters both peculiar to them and transitional between the two subgenera'. The interrelationships of these groups are discussed below, and it is shown that the peculiar characters are autapomorphies, whereas the 'transitional' are symplesiomorphies.

Archer (1982) described the subgenus *Rugovespula* for the *koreensis* group, primarily because the male genitalia of this group 'are very different from those of other species of *Para-*

vespula'. It is shown below that the differences discussed all show the primitive state in *Rugovespula*, and this taxon is the sister-group of *Paravespula*.

Varvio-Aho *et al.* (1984) presented an allozyme data set for the eight species of European yellowjackets, and analyses which they suggested showed that *Dolichovespula* was not a monophyletic group, and that *Paravespula* + *Vespula* was not monophyletic. Carpenter (1987) showed that these authors incorrectly analysed their data, and that their data are in fact largely uninformative on the relationships of these yellowjacket species.

Finally, Matsuura & Yamane (1984) published two matrices totalling forty-two characters for the Vespinae (including *Vespula*, *Paravespula, Rugovespula* and the *squamosa* group as terminal taxa). The matrix is reproduced here as Table 2, with correction of some of the inferred polarities as explained below. Matsuura and Yamane could not resolve the placement of *Provespa*, although they recognized *Provespa* + *Vespula* + *Dolichovespula* as a monophyletic group, with *Vespa* as the sister-group of this. Reanalysis of their data is presented below, which resolves the relationships as: *Provespa* + (*Vespula* + *Dolichovespula*).

Materials and Methods

The monophyly of the subfamily is established in Carpenter (1981); its sister-group is the Polistinae. Characters have been polarized with reference to Polistinae. In the tables which follow the state of '0' indicates the primitive state. Where the taxon shows both the primitive and derived states, the parsimonious inference of the groundplan is coded. Usually this is the primitive state, except as noted. The vespine species examined are listed in the appendix.

Cladistic analyses (Hennig, 1966) were performed using the PHYSYS system by J. S. Farris and M. F. Mickevich, State University of New York at Stony Brook and Maryland Center for Systematic Entomology, as implemented on the VAX 11/780 computer running VMS at Harvard.

The tree lengths and consistency indices reported do *not* include autapomorphies or invariant characters. The invariant characters are listed in the character matrix because they are vespine autapomorphies not mentioned by Carpenter (1981). The autapomorphies are included in the matrix to establish the monophyly of each terminal taxon in the 'Cladistic Diagnoses' section.

Character matrix (Table 1)

1 Prestigma length. Prestigma shorter than pterostigma, 0. Prestigma ≥ pterostigma, 1. Prestigma 3× pterostigma, 2.

2 $1R_1$ cell length. Length of first submarginal ($1R_1$) cell ≤ distance from apex of cell to apex of wing, 0. Length of cell > this distance, 1.

3 Base of 1RS cell. M vein obliquely oriented with respect to m–cu_1 at base of second submarginal (1RS) cell, 0. M vein vertically oriented (apex of discal cell truncate), 1.

4 1RS cell M : RS. Second submarginal cell with section of M vein distal to m–cu_2 crossvein shorter than section of RS vein basal to r_2 crossvein, 0. M section equal to or longer than RS section, 1. This is a way of characterizing the autapomorphic distal elongation of the second submarginal cell found in most vespines. It is not found in the *Vespula flaviceps* group (Yamane *et al.*, 1980: Fig. 21), which is here considered an apomorphic reversal.

5 Hamuli placement. Beginning basad of fork of R_1 and RS, 0. Beginning at this fork, 1.

6 Occipital carina. Running to base of mandible, 0. Effaced near base of mandible, 1. The derived state is also found in the *flaviceps* group of *Paravespula*, which is another apomorphy of the group.

7 Occipital carina. Present dorsolaterally, 0. Absent dorsolaterally, 1.

8 Malar space. Length less than that of last antennal segment, 0. Length greater than or equal to that of last antennal segment, 1. *Vespa* has a range of variation in this character which includes the derived state (e.g. *mandarinia*), but this is clearly convergent, as most species show the primitive state.

9 Vertex length. Ocelloccipital distance shorter than or equal to distance between posterior ocellus and eye, 0. Ocelloccipital distance greater than distance between posterior ocellus and eye, 1.

10 Ocelli. Ocellar diameter less than distance between posterior ocellus and eye, 0. Ocellar diameter greater than this distance, 1. An adaptation to nocturnal habits, this state is also found in *Vespa binghami*, which is apparently also nocturnal (van der Vecht, 1959). However, the ocelli in this species are not as large as those in *Provespa*.

11 Labial palpus. Third segment with a strong seta, 0. Third segment without this seta, but with hairs, 1. Duncan (1939) stated that there was 'no striking difference' between the two states,

TABLE 1. Character matrix for Vespinae.

Character	*Vespa*	*Provespa*	*Dolichovespula*	*Vespula*			
				V.	sq.	P.	R.
1. Prestigma length	2	1	1	1	1	1	1
2. R1 cell length	0	1	0	0	0	0	0
3. Base of 1RS cell	0	1	1	1	1	1	1
4. 1RS cell M : RS	1	1	1	1	1	1	1
5. Hamuli placement	0	1	1	1	1	1	1
6. Occipital carina	0	0	1	1	1	0	0
7. Occipital carina	0	1	0	0	0	0	0
8. Malar space	0	0	1	0	0	0	0
9. Vertex length	1	0	0	0	0	0	0
10. Ocelli	0	1	0	0	0	0	0
11. Labial palpus	0	0	1	1	1	1	1
12. Tyloides	0	0	0	1	1	1	1
13. Pronotal carina	0	1	1	2	2	2	2
14. Pretegular carina	0	1	1	1	1	1	1
15. Mesepisternum	1	1	1	1	1	1	1
16. Scutal lamella	0	0	1	1	1	1	1
17. Propodeal striae	0	0	0	0	0	0	1
18. Coxal carina	0	1	1	0	0	0	0
19. ♀ SVI process	0	0	0	0	0	1	1
20. ♂ TVII	0	0	0	0	0	1	1
21. ♂ SVII	0	0	0	0	0	1	1
22. Aedeagus apex	1	0	0	0	0	0	0
23. Aedeagus apex	0	0	0	0	0	1	0
24. Aedeagus apex	0	0	0	1	1	1	1
25. Aedeagus width	0	0	1	0	0	0	0
26. Paramere process	0	1	0	1	0	0	0
27. Paramere process	0	0	0	0	0	1	0
28. Volsella	0	0	0	1	1	0	0
29. Digitus	0	0	0	1	1	0	0
30. Larval mandible	0	0	1	0	0	0	?
31. Larval clypeus	0	0	1	0	0	0	?
32. Spiracle	1	0	1	0	0	0	?
33. Nest aerial	0	0	0	1	1	1	?
34. Paper type	1	0	0	0	0	0	?
35. Scallopping	1	0	0	0	0	1	?
36. Queen cells	1	1	1	1	1	1	?
37. Suspensoria	0	0	2	1	0	0	?
38. Worker-cell comb	0	0	0	1	0	0	?
39. Mixed cell combs	0	0	0	1	0	0	?
40. Colony size	0	0	0	0	1	1	?
41. First pedicel	0	?	0	1	1	1	?
42. First attachment	0	0	1	1	1	1	?
43. Swarming	0	1	0	0	0	0	?
44. Royal court	1	1	0	0	0	0	?
45. Prey	0	0	0	0	0	1	?
46. Nocturnal	0	1	0	0	0	0	0

attributing the size of the seta in *Vespa* to the relatively large size of the species in this genus. Duncan did not examine any *Provespa* or members of other vespid subfamilies with the seta present. The presence of the seta in these other groups shows that it has nothing to do with size of the individual, and the distinction of these two states is thus well supported.

12 Tyloides. Present, 0. Absent, 1. Tyloides are present in the groundplan of Polistinae, and the Vespinae as well, *contra* Yamane (1976). They are absent in a few species in *Provespa* and *Dolichovespula* (*sylvestris*, social parasites). Yamane *et al.* (1980) stated that they were present in *Vespula vulgaris*, but whereas there are shiny areas ventrally on the antennal segments, there are no raised ridges.

13 Pronotal carina. Present, 0. Dorsally reduced, 1. Laterally effaced, 2. The state in *Dolichovespula* is problematic. Although some species, e.g. *maculata*, have the carina developed dorsolaterally close to the scutal margin, as in *Vespa*,

it is not as strong dorsolaterally, is weaker in workers, and most other species have it effaced well laterad of the scutum. Coding this genus with the plesiomorphic state does not affect the resulting tree shape, and when the data are analysed using this scoring, the state in *Dolichovespula* is inferred to be a reversal on Fig. 1 (due to median state optimization; Farris, 1970). Therefore I am treating the state in *Dolichovespula* as the first reduction state, although it is not as reduced as the state in *Provespa.*

14 Pretegular carina. Present, 0. Absent, 1.

15 Mesepisternum. Epicnemial carina and dorsal groove present, 0. Epicnemial carina and dorsal groove absent, 1.

16 Scutal lamella. Rim of scutum raised into lamella beside tegula, 0. Scutal lamella effaced beside tegula, 1.

17 Propodeal striae. Propodeum not striate, 0. Propodeum striate in queens, 1.

18 Coxal carina. Carina present on posterior surface of hind coxa, 0. Carina absent ventrally on posterior surface of hind coxa, 1.

19 ♀ SVI process. Female without dorsolateral process on metasomal sternum VI (SVI), 0. Female with dorsolateral process on Sternum VI, 1 (see Archer, 1982: Fig. 1).

20 ♂ TVII. Male with disc of metasomal tergum VII (TVII) evenly convex, 0. Male with disc of TVII depressed, 1 (see Bequaert, 1932: Fig. 2).

21 ♂ SVII. Male with metasomal sternum VII (SVII) triangular, 0. Male with SVII transverse, 1 (see Archer, 1982: fig. 3).

22 Aedeagus apex. Apex of aedeagus not projecting laterally, 0. Apex of aedeagus projecting laterally, apex transverse, 1 (see Buysson, 1905: Plate 7). A state approaching this is found in *Provespa anomala* (Buysson, 1905: Plate 5, Fig. 1). The genitalia in this genus are very diverse in form, but a state similar to *Vespa* does not seem to be the groundplan state.

23 Aedeagus apex. Apex of aedeagus not subcircular on spoon-shaped, 0. Apex of aedeagus subcircular, spoon-shaped, 1 (see Bequaert, 1932: Figs. 2, 3).

24 Aedeagus apex. Rods forming aedeagus separated apically, 0. Rods forming aedeagus fused by membrane apically, 1. Although in general the Vespidae have the rods forming the aedeagus fused apically (Carpenter, 1981), the parsimonious interpretation is that they are separated apically in the vespine groundplan.

25 Aedeagus width. Aedeagus as wide or wider apically as medially, 0. Aedeagus tapering towards apex, narrower there than medially, 1 (see Bequaert, 1932: Figs. 1, 6).

26 Paramere process. Paramere with dorsal process near spine, 0. Paramere without process, margin smooth, 1. Although not found in the outgroup, a process of some sort is rather generally found throughout vespines, in groups that 'otherwise have little in common' (Kluge & Farris, 1969). The parsimonious inference is therefore that it is part of the groundplan of Vespinae (Farris, 1982).

27 Paramere process. Parameral process not projecting fingerlike, 0. Parameral process strongly projecting, fingerlike, 1 (see Bequaert, 1932: Figs. 2, 3).

28 Volsella. Volsella long, extending to apex of parameral spine and aedeagus or further, 0. Volsella short, not extending as far as apex of parameral spine or aedeagus, 1 (see Bequaert, 1932: Figs. 4, 5).

29 Digitus. Digitus a large, pincer-shaped lobe, 0. Digitus a very slender, fingerlike lobe, 1 (see Bequaert, 1932: Figs. 4, 5).

30 Larval mandible. Larval mandible tridentate, 0. Bindentate, 1. Yamane (1976) listed *D.sylvestris* (*Metavespula*) as tridentate. He did not see this species, but followed Short (1952). Wagner (1978) examined the larva of *sylvestris*, and stated that it does not differ in its mandible from other *Dolichovespula*. I have examined the larva of this species and confirm this. The mandible is more or less bidentate, with serration between the teeth, as figured for other species by Yamane (1976).

31 Larval clypeus. Larval frontoclypeal suture developed, 0. Larval frontoclypeal suture effaced dorsally, 1.

32 Spiracle. Larval spiracular collar processes simple, 0. Collar processes branched, 1.

33 Nest aerial. Nesting site aerial, 0. Nesting site in cavity or underground, 1. This character occasionally varies in *Vespa* and *Dolichovespula*, but the polarity is clear.

34 Paper type. Grey, pliable, 0. Brittle brown, 1. The difference in colour and strength is attributed to collection of sound wood fibres versus rotten wood fibres (Spradbery, 1973). Yamane (1976) inferred the opposite polarity, but this is not supported by outgroup comparison. This character apparently varies in *Vespa* (van der Vecht, 1957), *Dolichovespula* (Greene, 1979) and *Paravespula* (MacDonald, 1977). The species of *Paravespula* which have the plesiomorphic state (*germanica* and *pensylvanica*; group 3 of Yamane *et al.*, 1980) are apparently relatively basal in the group, therefore the apomorphic state cannot even be a groundplan characteristic of the group. This character is not very informative.

35 Scallopping. Envelope laminar, 0. Envelope scallopped, 1. The situation is complicated by variation within *Vespa* (e.g. Matsuura, 1984) and *Dolichovespula* (Greene, 1979), as well as a mixed type of construction in *Provespa* (Matsuura, 1985). This character cannot be regarded as very informative.

36 Queen cells. No special cells constructed for rearing queens, 0. Special queen cells constructed, 1.

37 Suspensoria. Comb suspensoria pillarlike, 0. Ribbonlike supporting first comb, 1. Ribbonlike

throughout nest, 2. MacDonald (1977), citing Spradbery (1973), suggested that pillarlike suspensoria were secondary, but these are like the suspensoria built in polistines.

38 Worker-cell comb. Multiple combs of worker cells, 0. One comb of worker cells, 1. Although there is some variation (e.g. Greene, 1979, mentions the derived state as occurring in *D.maculata*), it is confined as a groundplan trait to the *rufa* group (Akre *et al.*, 1981). Thus, it is apomorphic within Vespinae, contrary to Greene (1984).

39 'Mixed cell combs' (MacDonald & Matthews, 1984) present, 0. Worker and queen cells on different combs, 1. This is probably related to character 38, and similarly, the derived state is an autapomorphy of the *rufa* group (*Vespula s.str.*).

40 Colony size. 'Small' (<2500 cells and 400 workers at peak), 0. 'Large' (higher numbers), 1. This is another variable feature, the ranges in *Vespa, Provespa* and *Dolichovespula* overlapping that in *Paravespula* (cf. Matsuura, 1983, 1984, 1985; Greene *et al.*, 1976; with Akre *et al.*, 1981) – as does the range, exceptionally, in the *rufa* group (MacDonald *et al.*, 1974). It is about the only derived character linking the *squamosa* and *vulgaris* groups that I have been able to adduce, so I have coded it to reflect similarity between these groups. It is weak evidence indeed, as shown by the results below.

41 First pedicel. Pedicel of embryo nest coated with glossy oral secretion, 0. Uncoated, 1. See Greene *et al.* (1976).

42 First attachment. Pedicel of embryo nest with simple cylindrical shape, 0. Pedicel thin and twisted, 1. Yamane & Makino (1977) note that the plesiomorphic state occurs in *Vespula vulgaris*.

43 Swarming. Colony founded by queen only, 0. Swarming, 1. See Matsuura (1985).

44 Royal court. No distinct royal court of workers surrounding queen, 0. Royal court of workers present, surrounding queen, 1. This varies in *Vespa* (Matsuura, 1984, 1985).

45 Prey. Live insects, 0. Vertebrate carrion in addition, 1. This varies in the *squamosa* group (MacDonald & Matthews, 1984) and *Dolichovespula* (Greene *et al.*, 1976).

46 Nocturnal. Diurnal, 0. Nocturnal, 1. *Vespa binghami* is apparently also nocturnal (van der Vecht, 1959). Enlarged ocelli (character 10) is presumably an adaptation to nocturnal habits, as enlarged ocelli are a feature of virtually all other nocturnal Hymenoptera.

Matsuura & Yamane (1984) matrix (Table 2)

Matsuura & Yamane presented their data as two matrices (1984: Tables 10.1a and 10.1b). The first consisted of characters 1–24, and the second of the remaining eighteen. These latter were characterized as 'difficult to determine the ancestral or derived condition'. I have determined the polarities for these features using the Polistinae as an outgroup.

1 Vertex length. OOD ≥ 2POD (exceptionally OOD=POD), 0. Distance between ocellus and posterior of head (POD) > distance between ocellus and eye (OOD), 1. Matsuura & Yamane originally coded these states in reverse. Thus, they considered the elongate vertex of *Vespa* to be primitive, which is clearly erroneous; it is not approached in any primitive polistine.

2 Ocelli size. Ocellus diameter < OOD, 0. Ocellus diameter > OOD, 1.

3 Clypeal apex. Narrow, 0. Broad, 1.

4 Clypeal teeth. Rounded or truncate, 0. Sharp and pointed, 1. The derived state characterizes the social parasites only. Although autapomorphic in these species, the subgenera from which these species are removed if placed in their own subgenera are then characterized only by the absence of this feature (and others associated with parasitism, cf. Bischoff, 1931a, b), and are thus paraphyletic. This character is not used in the following analyses.

5 Pronotal carina. Present, 0. Dorsally effaced, 1. Matsuura & Yamane scored *Dolichovespula* as ancestral for this, an interpretation I doubt (see above). Nevertheless, I have used Matsuura & Yamane's scoring, since a blunt carina is present dorsolaterally at least primitively in the genus.

6 Coxal carina. Present, 0. Absent, 1. This is the interpretation of Carpenter (1981). Matsuura & Yamane originally scored this in reverse, but dorsal remnants of the carina are present in *Provespa*. Using their coding does not affect the resulting tree shapes, although it of course lowers the consistency of the trees. Matsuura & Yamane also scored *Dolichovespula* as having the carina, although it is reduced to at most traces in the group (*maculata*).

7 Prestigma length. Pterostigma longer than prestigma, 0. Prestigma longer than pterostigma, 1.

8 Prestigma length. Length of prestigma < 2× r_1 vein, 0. Prestigma > 2× r_1 vein (pterostigma extremely short), 1. A way of characterizing the extremely elongate prestigma of *Vespa*.

9 Base of 1RS cell. M oblique, 0. Vertical, 1.

10 Jugal lobe. Present, 0. Absent, 1.

11 Hamuli placement. Beginning distad of fork of R_1 and RS, 0. Beginning at this fork, 1.

12 Ovariole number. 3 pairs, 0. ≥ 6 pairs, 1.

13 Ovariole number. 6 pairs, 0. 7–10 pairs, 1. Iwata (1955) reported that the number varied within four species of *Vespa*, and even from ovary to ovary in individuals. He also reported six pairs or fewer in three of the species (*xanthoptera, crabro flavofasciata* and *tropica pulchra*). Kugler *et al.*

TABLE 2. Data matrix from Matsuura & Yamane (1984).

Character	*Vespa*	*Provespa*	*Dolichovespula*	*Vespula*			
				V.	sq.	P.	R.
1. Vertex length	1	0	0	0	0	0	0
2. Ocelli size	0	1	0	0	0	0	0
3. Clypeal apex	1	1	1	1	1	1	1
4. Clypeal teeth	0	0	[0]	[0]	0	0	0
5. Pronotal carina	0	1	0	1	1	1	1
6. Coxal carina	0	1	0	0	0	0	0
7. Prestigma length	1	1	1	1	1	1	1
8. Prestigma length	1	0	0	0	0	0	0
9. Base of 1RS cell	0	1	1	1	1	1	1
10. Jugal lobe	1	1	1	1	1	1	1
11. Hamuli placement	0	1	1	1	1	1	1
12. Ovariole number	1	?	1	1	1	1	1
13. Ovariole number	1	?	0	0	1	0	0
14. Larval clypeus	0	0	1	0	0	0	0
15. Mandible shape	0	0	0	0	0	0	0
16. Mandible teeth	0	0	1	0	0	0	0
17. Inner processes	0	0	1	0	0	0	0
18. Spiracle	1	1	1	1	1	1	1
19. Prey	0	0	0	0	0	1	?
20. Swarming	0	1	0	0	0	0	?
21. Cocoon cover	0	?	0	0	0	1	?
22. First attachment	0	0	1	1	1	1	?
23. First pedicel	0	?	1b	1a	?	1a	?
24. Embryo nest disc	0	?	0	1	?	1	?
25. Occipital carina	0	0	1	1	1	0	0
26. Malar space	0	0	1	0	0	0	0
27. Labial palpus	0	0	1	1	1	1	1
28. Pretegular car.	0	1	1	1	1	1	1
29. TI	0	1	0	0	0	0	0
30. Aedeagus apex	0	1	0	0	0	0	0
31. Larval labrum	0	0	1	0	0	0	0
32. Collar processes	2	1	2	1	1	0	?
33. Nest site	0	0	0	1	1	1	?
34. Colony duration	0	?	0	0	1	1	?
35. Hunger signal	0	?	0	1	?	1	?
36. First sheet	0	0	1	1	1	1	?
37. Expansion	0	?	1	0	0	0	?
38. Paper type	?	?	1	1	1	0	?
39. Suspensoria	0	0	1	1	0	0	?
40. Suspensoria	0	0	1	0	0	0	?
41. Scallopping	0	0	1	1	1	0	?
42. Hibernaculum	1	?	1	?	?	0	?

(1976) reported intraspecific and intraindividual variation in ovariole number in *Vespa crabro, mandarinia* and *tropica trimeres*; and in *Vespula germanica*. Therefore, the homology implied by Matsuura and Yamane's scoring seems quite dubious, and I have not used this character in any analyses.

14 Larval clypeus. Larval frontoclypeal suture developed, 0. Larval frontoclypeal suture effaced dorsally, 1.

15 Mandible shape. Larval mandible thick and strong, 0. Larval mandible thin and weak, 1.

16 Mandible teeth. Larval mandible tridentate, 0. Bidentate, 1. Matsuura & Yamane actually used 'monodentate' to describe the derived state, following Yamane (1976), but bidentate seems to describe the state better.

17 Inner processes. Small processes not present on inner surface of larval mandible, 0. Processes present, 1.

18 Spiracle. Larval spiracular collar processes absent, 0. Collar processes present, 1.

19 Prey. Live insects, 0. Vertebrate carrion in addition, 1.

20 Swarming. Colony founded by queen only, 0. Swarming, 1.

21 Cocoon cover. Cap consisting of two layers, simple in structure, no sex or caste differences, 0. Cap

consisting of two layers in the ☿ and ♂, and three in the ♀, with complex structure, 1.

22 First attachment. Pedicel of embryo nest with simple cylindrical shape, 0. Pedicel thin and twisted, 1. Matsuura & Yamane did not code this or the following two characters for *Provespa*, as this genus is supposed to found nests by swarming and so does not have a strictly comparable 'embryo' nest. However, Matsuura (1985) indicates that the pedicel of the nest in *Provespa* is the same as the primitive state for an embryo nest, and so it is coded as 0 here.

23 First pedicel. Final coating on pedicel of embryo nest dry, 0. Final coating either adhesive (1a) or lacking (1b). As state 1b is an autapomorphy of *Dolichovespula*, I have simply scored it as 0 for state 1a in the analyses.

24 Embryo nest disc. Lacking, 0. Present, 1.

25 Occipital carina. Present close to mandible, 0. Effaced within one third of that distance, 1. Matsuura & Yamane originally scored *Provespa* as having the apomorphic condition. Indeed, the carina is absent dorsally in all species of this genus, but is present ventrally in females. Therefore it is clear that the carina reduction in *Provespa* is not homologous with that in other vespines, and I have treated it as having the primitive condition in analyses of Matsuura & Yamane's matrix.

26 Malar space. Length less than half the length of the eleventh antennal segment, 0. Length $\geq$ the length of the eleventh antennal segment, 1.

27 Labial palpus. Third segment with 1 or 2 strong setae, 0. Third segment with weak hairs, 1.

28 Pretegular carina. Present, 0. Absent, 1.

29 TI. Sharply angled between dorsal and anterior faces, 0. Angle indistinct, 1. Considering polistines, this could be coded in reverse, but doing this simply produces an interpretation of reversal in *Provespa* on the cladograms. Therefore I have used the original scoring for this character.

30 Aedeagus apex. Rounded, 0. Bifurcate, 1. Actually, an aedeagus with a divided tip is plesiomorphic in Vespinae (see above) so *Vespa* and *Delichovespula* are not coded as derived here. However, the very deeply divided tip in *Provespa* appears autapomorphic.

31 Larval labrum. Widest basally and emargination somewhat deep, 0. Greatest width more apical, emargination shallow, 1. Yamane (1976), following Short (1952), listed *D.sylvestris* as having the primitive condition. I have seen the larva of this species and it has the derived condition.

32 Collar processes. Short, simple, 0. Long and simple (1) or long and branched (2). The 'primitive' state, occurring only in *Paravespula*, is most parsimoniously inferred to be derived, but I have followed Matsuura & Yamane's coding here, as it simply appears as a reversal.

33 Nest site. Open space, 0. Covered space, 1.

34 Colony duration. Early decline, 0. Decline in late fall, 1. I have maintained Matsuura & Yamane's scoring for this feature. However, it actually varies not only within genera in a single locality (e.g. Matsuura, 1984), but within species latitudinally (cf. Akre *et al.*, 1981) and also seasonally (Roush & Akre, 1978; cf. Greene, 1984, with Spradbery, 1973, and Edwards, 1980) – and, of course, does not apply to tropical species. It is thus poorly defined, and apparently simply dependent on climate in many species. Members of the *vulgaris* group (*Paravespula*) may exhibit a tendency for later colony decline (Spradbery, 1973; MacDonald *et al.*, 1974), but Matsuura & Yamane's scoring of the derived state also in the *squamosa* group is questionable. Whereas the southern North American *squamosa* has relatively late colony decline, its sister species *sulphurea* has early decline (Wagner, in Akre *et al.*, 1981).

35 Hunger signal. Larvae use consistent cell wall scraping, 0. Larvae use low frequency wall scraping, 1. As this type of signalling does not occur in Polistinae (Yamane, 1976), the polarity could be coded in reverse. I have followed Matsuura & Yamane's coding, as this is the parsimonious interpretation of the character for any of the resulting cladograms.

36 First sheet. Bonding point of first envelope sheet of embryo nest directly to the nesting foundation, 0. Bonded to pedicel, 1. Matsuura & Yamane did not score *Provespa* for this character, because its nests are built by swarms and hence are not true embryo (built by the queen) nests. But the nests are homologous as initial nests, and according to Matsuura (1985), *anomala* exhibits the plesiomorphic condition in the bonding point. R. W. Matthews (personal communication) has discovered that *squamosa* has the apomorphic state of this character, and so I have scored the *squamosa* group as 1.

37 Expansion. Expansion of envelope of embryo nest with sheet after the second or third beginning on previous sheet, 0. Independent sheet begins from the pedicel and nesting foundation, 1. R. W. Matthews (personal communication) has found that *squamosa* has the pleisomorphic condition of this feature, and so I have scored the *squamosa* group as 0.

38 Paper type. Brittle brown, 0. Grey, pliable, 1. As discussed above, this polarity is not supported by outgroup comparison. Matsurra & Yamane in addition originally had *Vespa* and *Provespa* not coded for this character, and *Paravespula* with both states. I coded paper type both ways, and as the coding does not affect the results, I used Matsuura & Yamane's original coding.

39 Suspensoria. Suspensoria between first comb and envelope pillarlike, 0. Ribbonlike, 1.

40 Suspensoria. All other suspensoria pillarlike, 0. Ribbonlike, 1.

41 Scallopping. Envelope scallopped, 0. Envelope laminar, 1. This polarity is incorrect considering polistines. I have coded it both ways; it does not affect the resulting tree shapes. I have followed Matsuura & Yamane's original scoring here.

42 Hibernaculum. Using pre-existing cavities, 0. The queens hibernate singly, in a hibernaculum which is at least partly dug by the queen herself, 1.

Results

I first analysed the seventeen informative morphological characters from Table 1. A branch-and-bound routine (XWAGNER) was used to perform an exact solution for parsimony. The tree of Fig. 1 resulted; it has a length of 22. The consistency index (the sum of the *states* of all the characters, divided by the length of the tree; Kluge & Farris, 1969) is 0.82 as calculated with the LFIT command. *Vespa* is the sister-group of the remaining Vespinae; *Dolichovespula* and *Vespula* are sister-groups, and *Vespula s.l.* is monophyletic. The *squamosa* group is the sister-group of *Vespula s.s.*, and *Rugovespula* is the sister-group of *Paravespula*.

When the seven informative behavioural characters listed in Table 1 were included and the analysis performed again, the same tree resulted. The length is 34, with consistency of 0.76. The behavioural data are ambiguous relative to the morphological data. This was explored further. When the seven behavioural characters were analysed alone, five trees resulted, all of length 10 and consistency 0.8. The strict consensus tree – the tree that has only the groups found on all five of the cladograms (Nelson, 1979; calculated with the NELSON command) – was completely unresolved. The trees do not agree, but this is due to the fact that *Rugovespula* is scored as missing for all of the characters. The Adams consensus tree, which takes the intersection of groups (Adams, 1972; calculated with the ADAMS command), showed that the trees differed only in where *Rugovespula* was placed. *Provespa* grouped with *Vespa* (on the basis of character 44, royal court), and *Dolichovespula* with *Vespula* + (the *squamosa* group + *Paravespula*). The latter two taxa were grouped by character 40, 'large' colonies. When the five behavioural trees were diagnosed with the morphological data (meaning that the morphological data were fit to the behavioural trees, using the DIAGNOSE com-

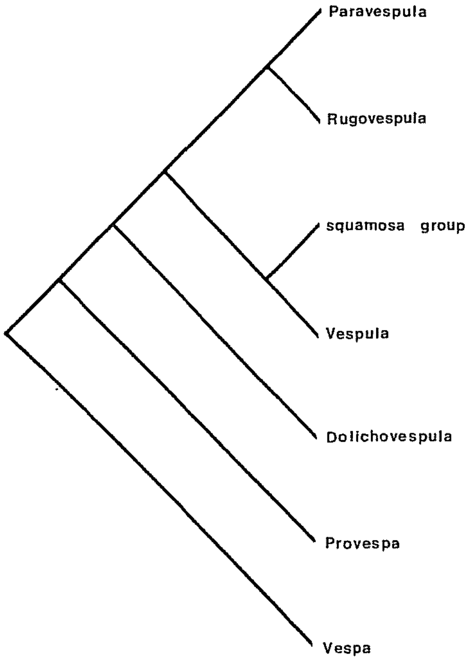

FIG. 1. Cladogram for the subgenera of the Vespinae.

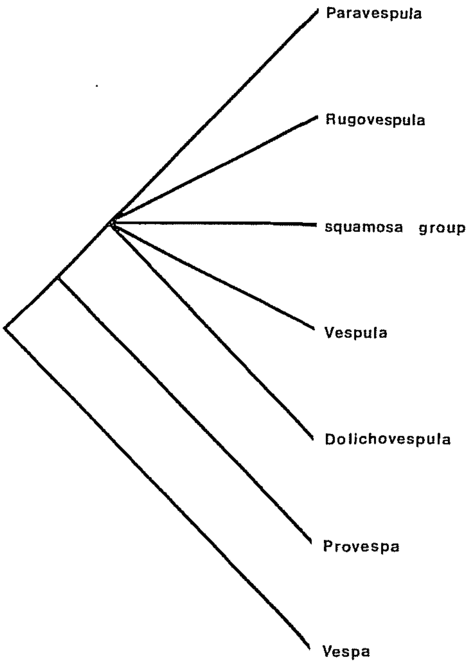

FIG. 2. Strict consensus tree for the six most parsimonious trees for the data of Table 2.

mand), their lengths ranged from 32 to 36 with consistencies of 0.56 – 0.5. Conversely, diagnosing the tree of Fig. 1 with only the behavioural characters produced a length of 12, consistency 0.67. The morphological data better account for the behavioural data than the reverse. Even disregarding the problems in scoring the behavioural characters (see above), they are less informative than the morphological characters.

In Matsuura & Yamane's matrix (Table 2), six characters are invariant in the subfamily, sixteen are autapomorphies, one (no. 4, clypeal teeth) applies only to parasitic species, and one (no. 13, ovarioles per ovary) in my view questionably homologizes all numbers >6, as discussed above. I have analysed the remaining eighteen characters. Note that I have corrected the polarity for characters 1, 6 and 30 (ocelloccipital distance, hind coxal carina and aedegus), coded 22 and 36 (pedicel of embryo nest and bonding point of first envelope sheet) for *Provespa*, scored 36 and 37 (pedicel of embryo nest and expansion of first sheet) for the *squamosa* group, and corrected the error in no. 25 (occipital carina). These are the only changes in informative characters I have made.

The matrix is ambiguous; there are six distinct equally parsimonious cladograms when it is analysed using the XWAGNER routine. The length is 29; the consistency is 0.69. However, the trees only disagree on the interrelationships of the *Vespula* subgenera/*squamosa* group/ *Dolichovespula*. The strict consensus tree is given in Fig. 2. *Vespula* in the broadest sense (i.e. including *Dolichovespula*) is unresolved. The Adams consensus tree differs in having *Vespula* and the *squamosa* group as sister-groups. Thus, *Vespula* in the broadest sense if monophyletic on every tree. *Provespa* is always its sister-group, and *Vespa* is always the sister-group to this.

The tree of Fig. 1 accounts for the data of Table 2 equally well. When the cladogram is diagnosed with the informative characters from Table 2, a length of 29 also results. When the converse diagnosis is made, the six trees range in length from 35 to 42. The tree among the six which does best has *Vespula s.l.* as a group, but resolves it as: *Vespula* + (*squamosa* group + (*Rugovespula* + *Paravespula*)). Agreement between different data sets on one tree many be used to choose among trees even if one or both data sets are ambiguous (Schuh & Farris, 1981). Thus although Matsuura & Yamane's matrix admits of multiple trees, both data sets support the cladogram of Fig. 1. But Fig. 1 is also the best choice as the general cladogram for these wasps when the partly overlapping data sets are combined. When the characters from Matsuura & Yamane's matrix not also listed in Table 1 are added to that latter character matrix (as coded in Table 2), the cladogram of Fig. 1 again results. The converse analysis (that is, simply adding characters to Matsuura & Yamane's matrix, while leaving the codings intact) also produces this result. The cladogram of Fig. 1 is thus quite robust. The ambiguity in Matsuura & Yamane's matrix is partly due to arguable characters and codings among their behavioural traits, as discussed above. This is exacerbated by the paucity of morphological relative to behavioural data in their informative characters. But the additional data adduced here obviate this. Fig. 1 is the best present hypothesis of the phylogenetic relationships among vespine taxa.

The diagnosis of the cladogram (Farris, 1979, 1980) follows: the apomorphies of each terminal taxon and ancestral node are discussed. The previously proposed subdivisions of each genus are also discussed in terms of the evidence for their naturalness.

Cladistic diagnoses

Vespa

The monophyly of *Vespa* is shown by seven characters in Table 1: 1, elongate prestigma in the forewing; 9, elongate ocelloccipital distance; 22, aedeagus apex transversely projecting; 32, larval spiracular collar processes branched (convergent in *Dolichovespula*); 34, nest paper brittle and brown (convergent in some species of *Paravespula*); 35, nest envelope scallopped (variable within *Vespa*, convergent in *Paravespula*); 44, royal court (convergent in *Provespa*).

Bequaert (1930) divided *Vespa* into four species groups. Group 1 (*analis, parallela* and *nigrans*) was defined with a character interpretable as apomorphic: female clypeus toothed medially. However, Bequaert later (1939) reduced the latter two names as colour forms of *analis*. Group 2 (*binghami*) also had an apomorphy: enlarged ocelli. Group 3 (*tropica, affinis, basalis* and *mandarinia* are considered valid now) had the apomorphy of an elongate malar space, but Bequaert observed that the genus showed a gradual range of variation, and that the character varied within species. Van der Vecht (1957) rejected this character as a basis for division of the genus. Group 4, the remaining species, was defined only by the absence of the features of the other three groups. Obviously, it is paraphyletic, and this system must be abandoned. Van der Vecht (1957) also stated that the system was unworkable.

Van der Vecht (1959) described the subgenus *Nyctovespa* for *binghami*, citing its 'isolated position' within *Vespa*. Two of the characters mentioned in the diagnosis, enlarged ocelli and absence of tyloides, are autapomorphies. But the other, male metasomal sterna not emarginate, appears to be primitive within Vespinae. Consequently, *binghami* may be the sister-group of the rest of the Vespinae. I have not verified that the apomorphic state characterizes all of the remaining *Vespa*, and van der Vecht (1959: 212) only stated that the apomorphic condition was present 'as a rule'. It thus is presently uncertain whether the division is natural, but in any event, recognition of a formal category for one species which expresses this division scarcely seems justified. I am therefore synonymizing this subgenus with *Vespa* (new synonymy).

Provespa + (*Dolichovespula* + *Vespula*)

The grouping of *Provespa* with *Vespula* and *Dolichovespula* is supported by four characters in Table 1: 3, vertical orientation of M with respect to m–cu$_1$ in the forewing; 5, clustering of the hamuli of the hindwing apically of the fork of R and RS; 13, reduction of the pronotal carina dorsally; 14, loss of the pretegular carina.

Provespa

Provespa is shown to be monophyletic by eight characters in Table 1: 2, elongate first submarginal cell; 7, dorsal reduction of the occipital carina; 10, enlarged ocelli (and dorsal approximation of the compound eyes); 18, loss of the hind coxal carina (convergent in *Dolichovespula*); 26, loss of the parameral process (convergent in *Vespula s.s.*); 43, swarming; 44, royal court (convergent in *Vespa*); 46, nocturnal habits. In addition, characters 29 (TI not sharply angled) and 30 (aedeagus apex deeply divided) from Table 2 are autapomorphies of this genus. *Vespa binghami* also has enlarged ocelli, and is presumably nocturnal, but the ocelli are not nearly as enlarged as *Provespa*, nor is the rest of the head similar.

Dolichovespula + *Vespula*

The grouping of *Vespula* and *Dolichovespula* is supported by three characters in Table 1: 11, loss of the strong seta on the third segment of the labial palpus; 16, reduction of the scutal lamella; 42, presence of a twisted pedicel in embryo nests. In addition, character 36 of Matsuura and Yamane (bonding point of first sheet of embryo nest); although not coded for *Rugovespula*, is parsimoniously interpreted as supporting this clade.

Dolichovespula

Dolichovespula is also monophyletic, as established by eight characters in Table 1: 6, occipital carina ventrally effaced (convergent in *Vespula* + *squamosa* group); 8, elongate malar space; 18, coxal carina reduced (convergent in *Provespa*); 25, apical attenuation of the aedeagus; 30, larval mandible bidentate; 31, larval frontoclypeal suture dorsally effaced; 32, larval spiracular collar processes branched (convergent in *Vespa*); 37, comb suspensoria ribbonlike throughout nest. In addition, four characters from Matsuura and Yamane's matrix are unique derived features in this genus: 17, development of small processes on the inner surface of the larval mandible; 23, final coating of embryo nest pedicel lacking (an unclear character which remains to be reconciled with character 41 from Table 1, pedicel not coated with glossy oral secretion, also scored for *Vespula*); 31, shape of larval labrum; 37, mode of expansion of the embryo nest. The monophyly of *Dolichovespula* in the present sense has been recognized since Bequaert (1930), but was questioned recently by Varvio-Aho *et al.* (1984). However, Carpenter (1987) showed that the data used by these authors were so ambiguous as to be phylogenetically uninformative at this level. The present results further support that conclusion.

The subdivision of *Dolichovespula* is a matter of confusion. This is due primarily to Blüthgen

(1938, 1943). He followed Bischoff (1931b) in recognition of a polyphyletic taxon *Vespula* for the social parasites *Vespula austriaca, Dolichovespula omissa* and *D.adulterina* (Bischoff incorrectly used the objective junior synonym *Pseudovespa* for this genus). Blüthgen (1938) raised *Dolichovespula* to genus, with the subgenus *Paravespula* described for *Vespula germanica, rufa* and *vulgaris*. Both *Dolichovespula* and *Paravespula* were thus paraphyletic in terms of *Vespula sensu* Blüthgen. Blüthgen (1943) described the subgenera *Metavespula* (for *sylvestris*) and *Boreovespula* (for *norwegica* and *saxonica*) in *Dolichovespula*, and raised *Pseudovespula* (following Weyrauch, 1937) and *Paravespula* to generic rank (with the new subgenus *Allovespula* in the latter for *rufa*). Thus, all but four European Vespinae were in a separate genus or subgenus, and Blüthgen had created an instability in vespine classification similar to that which he created in the Eumeninae (cf. Carpenter & Cumming, 1985). His system was eventually widely adopted, even in North America (Wagner, 1978), except that generally the parasitic species have been placed in the same subgenus as their hosts (Guiglia, 1948). Although this step removed some obvious paraphyly, this has itself resulted in some nomenclatural errors (viz the use of the name *Boreovespula* Blüthgen, 1943 for a subgenus of *Dolichovespula* including the species *D.adulterina*, type species of *Pseudovespula* Bischoff, 1931b; cf. Guiglia, 1948, 1971; Edwards, 1980; Matsuura & Yamane, 1984).

So the question arises: are the subgenera in *Dolichovespula* natural groups? If they are, then the question of their formal recognition is a subjective matter, but if not, some or all must be sunk. Of the four subgenera, *Dolichovespula* including *maculata* and *media*, is clearly monophyletic. It has several autapomorphies, including the striate pronotum and propodeum, and the male genitalia. The aedeagus has a pair of medial lobes which are unique in the Vespinae (cf. Bequaert, 1932: Fig. 1). Further, the remainder of the genus may form a monophyletic group in relation to this subgenus. The aedeagus is far more attenuate, and the apical division between the rods not as pronounced in the remaining species (see figures in Bequaert, 1932). These features appear to be apomorphic. *Metavespula*, including *sylvestris* and *asiatica* (Archer, 1981c; not *omissa*), is apparently also monophyletic, with the distal prolongation of the parameral process and basally narrow aedeagus (cf. Archer, 1981c: Fig. 3) as autapomorphies. But the other two subgenera are not monophyletic. *Boreovespula* is minimally paraphyletic in terms of *Pseudovespula*, and the latter may be polyphyletic. *Boreovespula* is definable only in terms of the absence of defining features of both *Pseudovespula* and *Metavespula*. Yamane (1976) treated an 'indistinct' parameral process as an autapomorphy of this subgenus, but in fact it is well developed in nearctic species. Thus *Boreovespula* may be paraphyletic in terms of both *Pseudovespula* and *Metavespula*. *Pseudovespula*, including *omissa* and *adulterina*, has several apomorphic traits common to its two species, but also shared with *arctica*. These are the sharply pointed apical teeth, loss of tyloides, dorsal reduction of the occipital carina, and of course the parasitic habits. However, all of these traits are apparently uninformative at this level: the sharp clypeal teeth also occur in *Vespula austriaca* and so this is correlated with the parasitic habits. Loss of tyloides occurs in other *Dolichovespula* (*sylvestris*), and the development of the occipital carina varies in the genus. The parasitic species have the apomorphic, attenuate aedeagus typical of *Boreovespula* and *Metavespula*, and so regardless of the relationships among the parasites, they are a component of this clade. I have not investigated the relationships of the individual parasitic species further, but note that *omissa* is apparently not closely related to its host, *sylvestris*. In addition to not sharing the apomorphies of *Metavespula* noted here, the allozyme data of Varvio-Aho *et al.* (1984) consistently indicated closer relationship of *omissa* to *saxonica* and *norwegica* despite multiple trees (Carpenter, 1987).

In summary, the monophyly of no more than two subgeneric groups can be shown, *Dolichovespula* and a group composed of the remaining species, for which *Pseudovespula* is the senior synonym. I do not consider the recognition of these subgenera to serve any other purpose than to further overburden vespid nomenclature, and synonymize them below.

Vespula

Vespula is shown to be monophyletic by five characters in Table 1: 12, loss of tyloides in the male antennae; 13, complete loss of the pronotal carina; 24, rods forming aedeagus fused apically; 33, nesting site in cavity or underground; 41, pedicel of embryo nest not coated with glossy oral secretion. In addition, two characters from Table 2 are autapomorphies of the genus: 24, embryo nest with disc (not scored in *Rugovespula* and the *squamosa* group); 35, larval hunger signal low frequency scraping (also not scored in *Rugovespula* and the *squamosa* group). Matsuura and Yamane's character 23, final coating on pedicel of embryo nest adhesive (not scored in *Rugovespula* and the *squamosa* group) is an apomorphy of this clade when Fig. 1 is diagnosed with the data from Table 2, but as pointed out previously under *Dolichovespula*, its relation to character 41 from Table 1 (pedicel not coated with glossy oral secretion) is unclear.

Within *Vespula*, *Vespula s.s.* and the *squamosa* group are sister-groups, sharing three characters: 6, occipital carina ventrally effaced (convergent in *Dolichovespula*); 28, volsella short; 29, digitus slender and fingerlike. Archer (1981b) also considered the *squamosa* group to be close to *Vespula s.s.*, but confused plesiomorphic and apomorphic character states. Consequently, nearly all of the characters he cited to support this are plesiomorphic in the two groups. Archer did include the short volsella, which is a synapomorphy.

Vespula s.s. is monophyletic, as shown by four characters in Table 1: 26, loss of the parameral process (convergent in *Provespa*); 37, suspensoria of first comb ribbonlike; 38, one worker cell comb; 39, worker and queen cells on different combs.

The *squamosa* group is also monophyletic, and thus *squamosa* and *sulphurea* are sister-groups. The only character establishing this in Table 1 is 40, large colonies; and from Table 2: 34, colony decline in late fall. Both are convergent in *Paravespula*. In the *squamosa* group's case they are presumably correlated with the southerly nearctic distribution of the group. Other characters not considered in this analysis show that these two species are sister-groups, such as the mesoscutal stripes.

Paravespula and *Rugovespula* are also sister-groups, sharing three unique characters in Table 1: 19, female SVI with a dorsolateral process; 20, male TVII disc depressed; 21, male SVII transverse. Archer (1982) listed these characters, as well as the long volsella (a symplesiomorphy), as distinguishing these two groups.

Rugovespula. is monophyletic as shown by character 17, propodeum striate in queens. In addition, the distally short second submarginal cell (see above), and medially constricted aedeagus (cf. Yamane & Tano, 1985: Fig. 1c; Archer, 1982: Fig. 4) are apomorphic. The sharply pointed female SVI dorsolateral process may also be apomorphic in relation to *Paravespula* (Archer, 1982: Fig. 1), but the polarity is unclear.

Paravespula is monophyletic as shown by five characters in Table 1: 23, aedeagus apex spoon-shaped; 27, parameral process fingerlike; 35, nest envelope scallopped (convergent in *Vespa*), 40, large colonies (convergent in the *squamosa* group); 44, use of vertebrate carrion. In addition, three characters from Table 2 support this group: 21, cocoon cover complex; 32, larval spiracular collar processes short and simple – inferred to be a reversal; 34, colony decline in late fall (convergent in the *squamosa* group).

In relation to the subdivision of *Vespula* of Yamane *et al.* (1980), first, contrary to the statement of these authors, the recognition of only the *rufa* and *vulgaris* groups is a natural system. The *rufa* group (*Vespula s.s.*) corresponds to their groups 5–7, and within this group, the *squamosa* group (their group 5) and the remainder (groups 6 and 7) are sister-groups. However, group 6 (*Allovespula*) is paraphyletic in terms of *austriaca* (type of *Vespula*). The latter species was separated categorically because of its socially parasitic habits and attendant structural peculiarities (e.g. Blüthgen, 1943). These traits are autapomorphies, and further, occur also in the parasitic species of *Dolichovespula*, so they are not even unique. *Vespula austriaca* shares with the species in *Allovespula* the apomorphies discussed above, but the latter subgenus is definable only in terms of the absence of the derived traits of *austriaca.* Recognition of *Allovespula* must therefore be abandoned, as has been done even by some authors who recognized subgenera in *Vespula* (Guiglia, 1948, 1971, 1972; Edwards, 1980; Matsuura & Yamane, 1984). Blüthgen (1961) defended the categorical separation of social parasites from their hosts in Vespidae, citing similar practice in Apidae (viz *Bombus vs. Psithyrus*). This is unacceptable in a phylogenetic system (Hennig, 1966); it results in paraphyly.

As for *Paravespula* (groups 1–4 of Yamane *et* *al.*, 1980), *Rugovespula* (group 4) and the remainder are sister-groups. Their group 1 (*flaviceps* and *shidai*) is monophyletic, as shown by the ventrally evanescent occipital carina (convergent elsewhere) and a small ventral projection of the paramere (Yamane *et al.*, 1980: Fig. 20). Group 2 (*vulgaris, structor, maculifrons* and *flavopilosa*) may also be monophyletic, having the synapomorphy of the aedeagus with pointed lateral projections basad of the apex (Bequaert, 1932: Fig. 2). However, similar projections are found in the *flaviceps* group, differing only in that they are more basally directed (cf. Yamane *et al.*, 1980: Figs. 7–9). It is not clear which is the primitive condition, but presence of the projections is certainly apomorphic. These groups are thus closely related, which is also shown by the mesally straight third mandibular tooth (generally curved in other *Vespula* and *Dolichovespula*) and brittle brown nest paper. But it is not clear if the last group (group 3, *germanica* and *pensylvanica*) is monophyletic – the traits by which it is defined (complete occipital carina, third mandibular tooth mesally concave, aedeagus without lateral projections, nest paper grey and pliable) are plesiomorphic. Thus the naturalness of this subdivision of *Paravespula* is unclear.

To sum up, aside from *Allovespula*, the subgenera recognized within *Vespula* are natural groups. The *squamosa* group is monophyletic, but contrary to MacDonald & Matthews (1975, 1984), it is closely related to the *rufa* group. And although the *squamosa* group is 'distinct' in relation to its sister-group, that is, it has some derived traits, recognition of a new subgenus for the two species (Edwards, 1980; Archer, 1982) is scarcely justified. It shares outstanding synapomorphies with the *rufa* group, while it is separated from the *rufa* group primarily by plesiomorphies. And while recognition of *Rugovespula* separate from *Paravespula* is consistent with monophyly, that does not mean it is well conceived. Most of the features by which *Rugovespula* was originally distinguished from *Paravespula* (Archer, 1982) are plesiomorphies, and the division separates just two species in *Rugovespula* (or three, Yamane & Tano, 1985) from the other eight species in *Paravespula*. This sort of oversplitting has rendered the classification of the Eumeninae chaotic (cf. Carpenter & Cumming, 1985), and is resisted here. In fact, in my view the subdivision of *Vespula* is better done by the use of species groups (Bequaert, 1932), which do not constitute a nomenclatural burden, and I am therefore synonymizing all of the subgenera of *Vespula*.

Classification

In the phylogenetic system, cladograms are exactly reflected in classification (Hennig, 1966). Not only are cladistic classifications most useful for evolutionary studies, as other types are misleading (Hennig, 1966), but such classifications best reflect anagenetic information, as shown by Farris (1979).

However, the matter of formal ranking retains a subjective element. Namely, which monophyletic groups will be given formal nomina? Recognition of just four genera is most prevelant in current systems; only a few European authors recognize *Paravespula* as a genus. This taxon must include *Rugovespula* in order for *Vespula* to be monophyletic, and as shown in the 'Cladistic diagnoses' these taxa are distinguished by relatively few apomorphies, which moreover may be considered relatively less important that the apomorphies distinguishing *Vespula s.l.* But as shown in the section on cladistic diagnoses, recognition of several subgenera in *Dolichovespula* and *Vespula* is consistent with phylogenetic principles. However, this results in nomenclatural burden with little discernible benefit (cf. Menke & Carpenter, 1984; Menke, 1985). Therefore in the following classification not only am I deleting all unnatural taxa, I am sinking all of the subgenera.

The classification is sequenced (Nelson, 1972; Wiley, 1979); each genus is the sister-group of all of the following genera taken as a group. It thus mirrors the cladogram exactly. The resulting classification is very similar to that of Bequaert (1930), with *Dolichovespula* in Bequaert's sense raised to generic rank (Duncan, 1939). Full synonymies are given with each genus, as the sinking of all the subgenera involves some new changes in status.

Vespa L., 1758: 343. Type species *Vespa crabro* L., 1758. Designated by Lamarck, 1801:271.
  Macrovespa Dalla Torre, 1904: 64. Type species *Vespa crabro* L., 1758. Designated by Bequaert, 1930: 64.
  Nyctovespa van der Vecht, 1959: 210. Type

species *Vespa binghami* Buysson, 1905. Original designation. **syn.n.**

Provespa Ashmead, 1903: 182. Type species *Vespa dorylloides* Saussure, 1853 (= *Vespa anomala* Saussure, 1853). Monotypic.

Dolichovespula Rohwer, 1916: 642. Type species *Vespa maculata* L., 1763. Original designation.

Pseudovespula Bischoff, 1931b: 346. Type species *Vespa norwegica* var. *adulterina* Buysson, 1905. Original designation.

Boreovespula Blüthgen, 1943: 149. Type species *Vespa norwegica* F., 1781. Original designation.

Metavespula Blüthgen, 1943: 149. Type species *Vespa silvestris* [!] Scopoli, 1763. Original designation.

Vespula Thomson, 1869: 79. Type species *Vespa austriaca* Panzer, 1799. Designated by Ashmead, 1902: 164.

Pseudovespa Schmiedeknecht, 1881: 314. Type species *Vespa austriaca* Panzer, 1799. Monotypic.

Paravespula Blüthgen, 1938: 271. Type species *Vespa vulgaris* L., 1758. Original designation.

Allovespula Blüthgen, 1943: 149. Type species *Vespa rufa* L., 1758. Original designation.

Rugovespula Archer, 1982: 261, 264. Type species *Vespa koreensis* Radoszkowski, 1887. Original designation. **syn.n.**

As established in the 'Cladistic diagnoses', within *Dolichovespula* two monophyletic sister-groups can be recognized: the *maculata* species group (*maculata* and *media*) and a group comprised of the remaining species, which may be termed the *norwegica* group. Within *Vespula*, the *austriaca* (*rufa*) group and the *vulgaris* group are sister-groups.

Discussion

The data presented here strongly support the relationships depicted in Fig. 1. The expression of those relationships by use of species groups in addition to formal taxa is one similarity to the system of Bequaert (1930, 1932). Another is some of the groups themselves: the *maculata* group in *Dolichovespula*, the *austriaca* (*rufa*) and *vulgaris* groups in *Vespula* are natural. This is not true of all of the groups Bequaert recognized; the system was not phylogenetic in *Vespa* and is ambiguous in *Dolichovespula*. Further study is required in *Dolichovespula*, as the *norwegica* and *sylvestris* groups *sensu* Bequaert may yet prove to be monophyletic. But the morphological grounds for recognizing the three aforementioned species groups remain good characters, and behavioural data gathered since Bequaert's time generally confirm the other groups, as shown above. The oversplit classification produced by Blüthgen merely applies formal nomina to Bequaert's original groups, with the addition of some unnatural taxa. The result has been an inflexible, confusing nomenclature, for contrary to Edwards (1980), the species group and subgenera concepts are not equivalent. One falls under the rules of the International Code of Zoological Nomenclature. Because some of the groups must be dispensed with as being unnatural, formal synonymies are required, and must henceforth accompany taxonomic works on the subfamily. Continued use of Bequaert's system, as has been done in North America, would not have required these actions when the system was modified.

The present arrangement, as a phylogenetic one, is of particular use in behavioural studies, upon which much current interest is focused. This is shown in the character matrices, where many of the behavioural features discussed during the past decade are for the first time separated into primitive and derived states. Some of the doubts expressed by various behaviourists concerning Bequaert's system result from a failure to consider all of the available evidence (viz morphology), but also result from confusion regarding the evolutionary polarity of behavioural features. For example, both the *rufa* group and *vulgaris* group are seen to exhibit a mosaic of primitive and derived behavioural traits, and the nature of each trait must be taken into account when attempting to explain the basis for differences in these traits. Thus, MacDonald (1977) suggested that the single worker cell comb in the *rufa* group was a consequence of reliance on live prey. The first trait is derived but the second is primitive, shared with most other vespines, and so clearly is not a cause of the single worker comb. Consideration of such features in the context of the phylogenetic system is required for critical understanding of the evolutionary basis of behaviour.

The Vespinae seem to be a particularly tract able group for further investigation on species-level relationships. This should be very rewarding especially for the study of the biogeography of these wasps. A Southeast Asian centre of origin has generally been assumed for Vespinae (van der Vecht, 1964), but Carpenter (1981) pointed out that this was based on fallacious grounds. Carpenter (1981) concluded that the distribution of the subfamily as a whole as laurasian (Bequaert, 1932, also inferred a 'northern common origin' for the subfamily), and the present system does not permit any more precise inferences. This is because the connections between Eurasia and North America are within the species groups in both *Vespula* and *Dolichovespula*, and the connections between Eurasia and the Oriental region are completely unclear in the absence of a species level hypothesis in *Vespa*. Inference of patterns in historical biogeography is a problem in character state optimization (Mickevich, 1981), and because the relevant area transformations occur within the groups established here, the state assignments are ambiguous. Elucidation of the phylogenetic relationships among all the species is thus necessary for further progress in understanding of vespine biogeography.

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Appendix

List of taxa examined

The status of some of the names listed here as species is a matter of considerable current disagreement (cf. Archer, 1981a, 1982; Eck, 1981, 1984a, b; Matsuura & Yamane, 1984; Yamane & Tano, 1985; Yamane *et al.*, 1980). I have not followed any of these authors in all respects regarding classification; many of their taxonomic decisions are in my view insufficiently supported. All specimens listed are deposited in the Museum of Comparative Zoology and the U.S. National Museum. Larvae are in the collection of the British Museum.

Vespa affinis (L.) (9 subspecies) ♀☿♂
analis F. (8 subspecies) ♀☿♂
basalis Smith ♀☿♂
bellicosa Saussure ☿
bicolor F. (2 subspecies) ♀☿
crabro L. (8 subspecies) ♀☿♂
dybowskii André ♀
fervida Smith ♀♂
luctuosa Saussure (3 subspecies) ♀☿♂
mandarinia Smith (5 subspecies) ♀☿♂
mocsaryana Buysson ♀☿
multimaculata Pérez (2 subspecies) ♀☿
orientalis L. (3 subspecies) ♀☿♂
philippinensis Saussure ♀♂
simillima Smith (2 subspecies) ♀☿
tropica (L.) (12 subspecies) ♀☿♂
variabilis Buysson (2 subspecies) ♀☿♂
velutina Lepeletier (11 subspecies) ♀☿♂
walkeri Buysson ☿
wilemani Meade-Waldo ♀
(*Nyctovespa*) *binghami* Buysson ☿

Provespa anomala (Saussure) ♀☿♂
barthelemyi (Buysson) ♀☿♂
nocturna Vecht ♀☿♂

Dolichovespula macultata (L.) ♀☿♂
media (Retzius) ♀☿♂
(*Metavespula*) *sylvestris* (Scopoli) ♀☿♂

- (*Pseudovespula*) *adulterina* (Buysson) ♀♂
  - *omissa* (Bischoff) ♀♂*
- (*Boreovespula*) *albida* (Sladen) ♀☿♂
  - *alpicola* Eck ♀☿♂
  - *arctica* (Rohwer) ♀♂
  - *arenaria* (F.) ♀☿♂
  - *loekenae* Eck ♂
  - *norvegicoides* (Sladen) ♀☿♂
  - *norwegica* (F.) ♀☿♂
  - *pacifica* (Birula) ☿
  - *panda* Archer ☿
  - *saxonica* (F.) ♀☿♂
- *Vespula austriaca* (Panzer) ♀♂
- (*Allovespula*) *acadica* (Sladen) ♀☿♂
  - *atropilosa* (Sladen) ♀☿♂
  - *consobrina* (Saussure) ♀☿♂
  - *intermedia* (Buysson) ♀☿♂
  - *kingdonwardi* Archer ☿
  - *rufa* (L.) (2 subspecies) ♀☿♂
  - *schrenckii* (Radoszkowski) ♀
  - *vidua* (Saussure) ♀☿♂
- '*squamosa*-group'
  - *squamosa* (Drury) (2 subspecies) ♀☿♂
  - *sulphurea* (Saussure) ♀☿♂
- (*Paravespula*) *flaviceps* (Smith) (2 subspecies) ♀☿♂
  - *flavopilosa* Jacobson ♀☿♂
  - *germanica* (F.) ♀☿♂
  - *maculifrons* (Buysson) ♀☿♂
  - *pensylvanica* (Saussure) ♀☿♂
  - *shidai* Ishikawa, Yamane and Wagner ♀☿♂
  - *structor* (Smith) ☿
  - *vulgaris* (L.) (2 subspecies) ♀☿♂
- (*Rugovespula*) *arisana* (Sonan) ☿
  - *koreensis* (Radoszkowsi) (2 subspecies) ♀☿
  - *orbata* (Buysson) ☿

*The name *ingrica* was originally proposed as an infrasubspecific name ('*Vespula n.saxonica* morpha *ingrica* nov.'; Art. 45f(iii)) by Birula (1930: 309). It therefore must be considered to have been elevated (Art. 10c), and to compete in priority from the date upon which it was elevated (Art. 23j). The earliest this could be considered to have been done is Bequaert (1932: 89); Bequaert is therefore the author of this species (Art. 50c). *Vespula ingrica* Bequaert, 1932 is thus a junior synonym of *Vespa omissa* Bischoff, 1931a. Edwards (1980) and Matsuura & Yamane (1984) used the name *ingrica* for this species, but Eck (1984b) correctly used *omissa*.