Phylogenetic Relationships Among Yellowjackets and the Evolution of Social Parasitism (Hymenoptera: Vespidae, Vespinae)

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ABSTRACT

Cladistic analysis of 25 species of *Dolichovespula* and *Vespula* (yellowjackets) is used to investigate the evolution of social parasitism in these genera. Three species of yellowjackets are social parasites, or inquilines; that is, lacking a worker caste, and dependent on usurping the colony of a host species to obtain a worker force. Emery's Rule states that social parasites are more closely related to their hosts than to any other species. By investigating the phylogenetic relationships among the parasites and their hosts using cladistic analysis, we attempted to determine if Emery's Rule applies to yellowjackets, as is thought to be the case for the ants on which the theory was based. Sixty-eight morphological and behavioral characters are presented to resolve the phylogenetic relationships among these species. Cladistic analysis does not support Emery's Rule, because social parasites are not more closely related to their hosts than to any other species.

INTRODUCTION

Partly due to their eusocial behavior, vespine wasps of the genera *Vespula* and *Dolichovespula*, or yellowjackets, have been the focus of numerous behavioral studies. Several species are known to exhibit socially parasitic behavior, one of the most interesting offshoots of the evolution of social behavior. In social parasitism among insects, a female enters a colony and usurps the reproductive role of the resident queen, yet retains the worker force of the resident. In its extreme form, workers are not produced by the parasitic species. Such species, called inqui-lines, have no worker caste and do not build nests, rather they invade the colony of a host species and supplant the queen in order to obtain workers to rear their own brood. The peculiar inquiline behavior has sparked interest in various aspects of social parasitism, particularly in the mechanism by which such species have evolved (e.g., Emery, 1909; Wheeler, 1928; Taylor, 1939; de Beaumont, 1958; Buschinger, 1970, 1986, 1990; Wilson, 1971; Richards, 1971; West-Eberhard, 1986, 1996; Matsuura and Yamane, 1990; Hölldobler and Wilson, 1990; Bourke and Franks, 1991; Heinze, 1991).

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Yellowjacket Inquilines

Three species[3] of yellowjackets are inquilines: *Vespula austriaca* (hosts: *V. rufa* and *V. acadica*; Robson, 1898; Reed et al., 1979), *Dolichovespula omissa* (host: *D. sylvestris*; Weyrauch, 1937), and *D. adulterina* (hosts: *D. arenaria*, *D. saxonica*, and *D. alpicola*[4]; Wheeler and Taylor, 1921, de Beaumont, 1944; Wagner, 1978). Forty-three species are presently recognized in the genera *Vespula* and *Dolichovespula* (Carpenter and Kojima, 1997; Eck, 1998; Archer, 1999; Dong et al., 2002, 2005), and thus the inquiline behavior is uncommon (about 7% of the species). The inquiline species have long been recognized as taxonomically distinct. Schmiedeknecht (1881) placed *V. austriaca* in the new subgenus *Pseudovespa* because it lacks a worker caste, and Bischoff (1931) treated *Pseudovespa* as a genus. Bischoff diagnosed the genus on morphological grounds and added to it a new subgenus, *Pseudovespula*, to accommodate *D. omissa* and *D. adulterina*. He stated (Bischoff, 1931: 336–337) that each inquiline is most closely related to its host, as shown by (unspecified) similarity of male genitalia. Bequaert (1932) instead divided the yellowjackets into species groups and placed each inquiline in the same species group as its host. The concept of a polyphyletic genus for inquilines was followed by Blüthgen (1938), but he later (Blüthgen, 1943) broke up the taxon, recognizing two genera of vespine inquilines. Other taxonomists did not generally regard the diagnostic traits as sufficient to warrant high categorical rank for the inquilines, instead preferring to treat these taxa as subgenera (e.g., de Beaumont, 1944) or dispensing with separate categories altogether (e.g., Guiglia, 1948, 1972).

[3] The species taxonomy of Vespinae is historically quite complicated, with most recent literature recognizing a fourth inquiline species, the Nearctic *D. arctica*. We follow here the taxonomy used by Carpenter and Kojima (1997), which treats *D. arctica* as a synonym of the Palearctic *D. adulterina*.

[4] *D. norwegica* is cited as a host as well in some reviews (e.g., Akre, 1982; Matsuura and Yamane, 1990), but this is based partly on treatment of *D. saxonica* as a synonym of *D. norwegica*. The positive host records in Europe are limited to *D. saxonica*, with indirect evidence suggesting *D. norwegica* (Guiglia, 1972: 136).

De Beaumont (1944, 1958) first depicted his views on relationships among the species of European vespines in the form of a branching diagram, although he did not specify the characters. *Vespula austriaca* was shown as most closely related to its host *V. rufa*, but *D. adulterina* was shown as less closely related to its host *D. saxonica* than the latter was to *D. norwegica*, and the position of *D. omissa* was doubtful with respect to its host *D. sylvestris*. Guiglia (1948, 1972) placed *D. omissa* in the same subgenus as *D. adulterina*, *D. saxonica*, and *D. norwegica*; the host *D. sylvestris* was placed in another subgenus. Later treatments of *Vespula* on a world basis left the relationship of *V. austriaca* and *V. rufa* unspecified (Yamane et al., 1980; Archer, 1981a, 1997), while Guiglia's arrangement has usually been followed in the species groups recognized in *Dolichovespula* (e.g., Archer, 1981b, 1999).

Evolution of Social Parasitism: Emery's Rule

Apparent close morphological resemblance between parasite and host led to the classical explanation of the origin of socially parasitic species, known as Emery's Rule. Emery's (1909) Rule states that parasites are more closely related to their host species than to any other species. Acceptance of Emery's Rule subsequently inspired the hypothesis that social parasites originate from their hosts by sympatric speciation (Buschinger, 1970, 1990; Bourke and Franks, 1991). However, the assumption that Emery's Rule is generally true has only recently been evaluated through cladistic tests (Ward; 1989, 1996; Agosti, 1994; Carpenter et al., 1993; Choudhary et al., 1994; Carpenter 1997; Danforth, 1999).

In Vespidae, the inquiline species in the paper wasp genus *Polistes* of the subfamily Polistinae have been shown to be a monophyletic group (Carpenter, 1997; see also Carpenter et al., 1993, and Choudhary et al., 1994). Within the subfamily Vespinae, cladistic treatment of supraspecific taxa (Carpenter, 1987b) has shown that the yellowjackets, the genera *Vespula* and *Dolichovespula*, are sistergroups, and several well-supported species groups can be recognized within these genera. But relationships among the species have not

yet been comprehensively investigated, and the phylogenetic relationships among the inquilines and their hosts are thus unclear.

There has however been one previous noncladistic, ''phylogenetic'' analysis that discussed whether Emery's Rule applies to yellowjackets. Varvio-Aho et al. (1984) analyzed allozymes for eight species of European yellowjackets using distance methods, and concluded that the inquilines were most closely related to their hosts. Carpenter (1987a) showed that the analysis by these authors was flawed and that their data are in fact largely uninformative regarding the relationships of these yellowjacket species. Reanalysis of the data (Carpenter, 1987a) indicated that parasites in *Dolichovespula* were separated from their hosts. In this reanalysis, 50 trees of lower percent standard deviation than those that Varvio-Aho et al. found showed *D. omissa* more closely related to *D. saxonica* than to its host *D. sylvestris*.

EVOLUTION OF SOCIAL PARASITISM: USURPATION IN YELLOWJACKETS

Another species of yellowjacket, *V. squamosa*, displays a different kind of social parasitism. It is evidently capable of founding its own colonies and has a worker caste, but in parts of its range it may usurp nests of other species. It ranges from New York to Guatemala, and in the eastern United States it has been reported to usurp *V. vidua* (Taylor, 1939), *V. maculifrons* (MacDonald and Matthews, 1975), and *V. flavopilosa* (MacDonald et al., 1980); additionally, Greene (1991) mentioned unpublished observations showing usurpation of *V. germanica* and *Vespa crabro*. *Vespula squamosa* has even been characterized as an obligate usurper of the nests of other species (Matthews, 1982), but this can evidently only be true in the northern part of its range (MacDonald and Matthews, 1984), because all of its host species are less widespread, and no other vespine species reaches as far south (Guatemala; see Carpenter and Kojima, 1997).

Usurpation of conspecific nests is common in yellowjacket queens, and may be a manifestation of competition for a nest site (Greene, 1991). Any brood, or even workers, present at the time of such usurpation may be ''adopted'' by the invading queen. Interspecific usurpation also occurs, but much less frequently. It has been reported in *V. germanica* (on *V. vulgaris*; Nixon, 1935), *V. pensylvanica* (on *V. vulgaris*; Akre et al., 1977), *V. flavopilosa* (on *V. maculifrons* and *V. vulgaris*; MacDonald et al., 1980), *D. norwegica* (on *D. sylvestris*; Edwards *in* Bunn, 1982: 172), and *D. arenaria* (on *V. vulgaris*; O'Rourke and Kurczewski, 1984).

Whether intra- or interspecific, such usurpation is considered a temporary form of social parasitism, in that the worker force produced by the usurping queen eventually replaces that of the host. Inquiline behavior may thus be considered an extreme form of usurpation, being permanent, with loss of the worker caste. This was the reasoning underlying the scenario for the evolution of social parasitism in wasps proposed by Taylor (1939). He suggested a progression through four stages: (1) intraspecific, facultative, temporary parasitism; (2) interspecific, facultative, temporary parasitism; (3) interspecific, obligate, temporary parasitism; (4) interspecific, obligate, permanent parasitism.

Taylor knew of the inquiline species and that intraspecific usurpation occurred, and he observed nest usurpation of *V. vidua* by *V. squamosa*. He considered that usurpation to be facultative, and thus three stages in his progression were observed in nature. Stage 3 was considered to be a theoretically necessary transition, with the usurping queen losing its ability to found a new colony but still retaining a worker caste. As mentioned before, this has been argued in fact to be the case for *V. squamosa* in part of its range.

Emery's Rule was a part of Taylor's arguments, as he stated (Taylor, 1939: 312), ''*Vespula squamosa* and *V. rufa* var. *vidua* are closely related, both belonging to the subgroup of *V. rufa* (Bequaert, 1932). The two known social parasites are also closely related to their hosts.'' The *rufa* group as construed by Bequaert (1932) comprised five species, a polytypic *V. rufa* consisting of no fewer than eight named forms. These forms later came to be treated as distinct species (Miller, 1958, 1961), and subsequent cladistic analysis (Carpenter, 1987b) showed that *V. squamosa*

TABLE 1
Characters for Species of Yellowjackets and Hornet Outgroup[a]

	10	20	30	40	50	60	
Vespa crabro	0000000000	0000000000	0000000000	0000000000	00*0000000	1111000000	0-001000
D. adulterina	1101112120	1111011100	01?0001000	2001100001	00000*00??	?---------	----?--?
D. alpicola	0101011110	1111011100	00?0001000	2001100000	00000*00??	?*00200???	???0????
D. arenaria	0101011100	1111011100	00?0001000	2001100000	00000*0011	1*00200???	?1?*??01
D. maculata	0101011100	1111111100	0010121000	1011100001	00000*1011	1**$2*0100	111*?*01
D. media	0101011100	1111111100	00?0121000	1011100000	*000000011	1000200100	11101101
D. norvegicoides	0101011100	1111011100	00?0001000	2001100000	0*000*0011	1*00200???	???0????
D. norvegica	0101011110	1111011100	0010001000	200110000*	00000*0*11	1*00200100	1??0??0?
D. omissa	1101102120	1111011100	01?0001000	2001100000	00000*00??	?---------	----?--?
D. saxonica	0101011100	1111011100	00?0001000	2001100000	00000*0011	1*00200100	11100101
D. sylvestris	0101001120	1111011100	0010001000	2002100000	00000*0011	1*00200100	1*10??0?
V. acadica	0111011021	0121011011	0010001111	0004110110	0*000100??	?*00111???	???0??0?
V. atropilosa	0111011021	0121011011	0010001111	0004110110	0*00010000	0*00111111	1000??0$
V. austriaca	1111111021	0121011001	01?0001201	0004110110	00*0010??	?---------	----?--?
V. consobrina	0111011021	0121011011	0010001111	0004110111	0010010000	0*00111???	???0??0?
V. flaviceps	0111011021	1121021010	10?1112002	010310100*	00*0000000	0112001111	10010112
V. flavopilosa	0111010021	*121021010	10?1112002	0103101000	00*0100000	0112000???	???1??1?
V. germanica	0111010021	0121021010	10*1112001	0003101000	0010000000	010200011*	10010112
V. maculifrons	0111011021	1121021010	1012112002	0103101000	00*0000000	0*12000111	10?1??1?
V. pensylvanica	0111010021	0121021010	1011112001	0003101000	1000000000	0102000111	2001??1$
V. rufa	0111011021	0121011011	0010001111	0004110110	00*0010100	*100111111	10000?02
V. shidai	0111011021	1121021010	10?1112002	0103101001	0010000000	0112001???	???10?12
V. squamosa	0111011021	0121011011	0000001001	0000110100	0001010??	?100001??	1?0*??1?
V. sulphurea	0111011021	0121011011	0000001001	0000110100	10010*00??	?10000????	???*??1?
V. vidua	0111011021	0121011011	0010001111	0004110110	0000010??	?100111??	1?00??0?
V. vulgaris	0111010021	1121021010	1011112002	0103101000	0*10000000	**12000*1*	10010112

[a]Multistate characters 26, 34, 54, 55, 61, and 68 are treated as nonadditive; multistate characters are otherwise treated as additive. An asterisk denotes a polymorphism showing all applicable states; a dollar sign denotes a subset polymorphism (states 0 and 1 in character 54; states 1 and 2 in character 68), a question mark is an unknown state, and a dash indicates inapplicable character.

and *V. sulphurea* together formed the sister-group of the remaining species placed by Bequaert in the *rufa* group. The other hosts of *V. squamosa*, *V. maculifrons* and *V. flavopilosa*, are placed in the *vulgaris* species group (Bequaert, 1932; Jacobson et al., 1978), to which *V. squamosa* is even less closely related (Carpenter, 1987b). Although still considered to represent a key step in the evolution of social parasites, whether facultative or obligate, *V. squamosa* came to be characterized as an exception to Emery's Rule (e.g., MacDonald and Matthews, 1975; Edwards, 1980; Matsuura and Yamane, 1990; Greene, 1991).

Further elucidation of phylogenetic relationships among yellowjacket species is necessary to assess the applicability of Emery's Rule to yellowjackets. Cladistic analysis of morphological and behavioral characters is presented below, which attempts to resolve the relationships between parasitic and host species.

MATERIALS AND METHODS

Table 1 presents a character matrix for the North American, European and Japanese species of *Vespula* and *Dolichovespula*; the character list is detailed below. Specimens examined are deposited in the American Museum of Natural History. Morphological characters examined were drawn primarily from the previous study of supraspecific groups by Carpenter (1987b) and the keys to species by Bequaert (1932), Guiglia (1972), Jacobson et al. (1978), Wagner (1978), Yamane et al. (1980), Akre et al. (1981) and Archer (1989). A number of characters establishing the monophyly of yellowjackets are retained in table 1. These characters do not pertain to relationships among species but are included to show that yellowjackets indeed constitute a monophyletic group, as demonstrated by Carpenter (1987b). Several prior studies had argued that *Dolichovespula* is more closely related to *Vespa* than to *Vespula*

(Greene, 1979; Archer, 1987), as did one subsequent paper (Schmitz and Moritz, 1990; see Carpenter, 1992). Morphometric differences were excluded: Archer's (1989) key used a few characters such as ocelloccipital length and relative length of the malar space among species of *Dolichovespula*, but we did not find the states to be well delimited (note that the inquilines differ from their host species in a number of such features; see Bischoff, 1931; Weyrauch, 1937; Eck, 1979; Reed and Akre, 1982). The matrix includes nine color characters, which are among the features most commonly used in keys to distinguish species. A few new characters from male genitalia are also included. Male genitalia were dissected, cleared slightly in lactophenol, and examined in glycerin. Morphological terminology is as in Carpenter (1987b). Behavioral characters were also taken from Carpenter (1987b), with specific scores taken from the reviews by Spradbery (1973), Edwards (1980), Akre et al. (1981), Akre and MacDonald (1986), Matsuura and Yamane (1990), Greene (1991), and according to the citations for certain characters detailed below. The outgroup is the hornet *Vespa crabro*, which is not closely related to yellowjackets (Carpenter, 1987b). Multistate characters were treated as additive where similarity among character states was observed to be nested; otherwise, such characters were treated as nonadditive. Cladistic analysis (Hennig, 1966) was implemented with the program NONA (Goloboff, 1999a). Character optimization and diagnoses were accomplished with the WINCLADA program (Nixon, 2002). Illustrations are provided for selected characters.
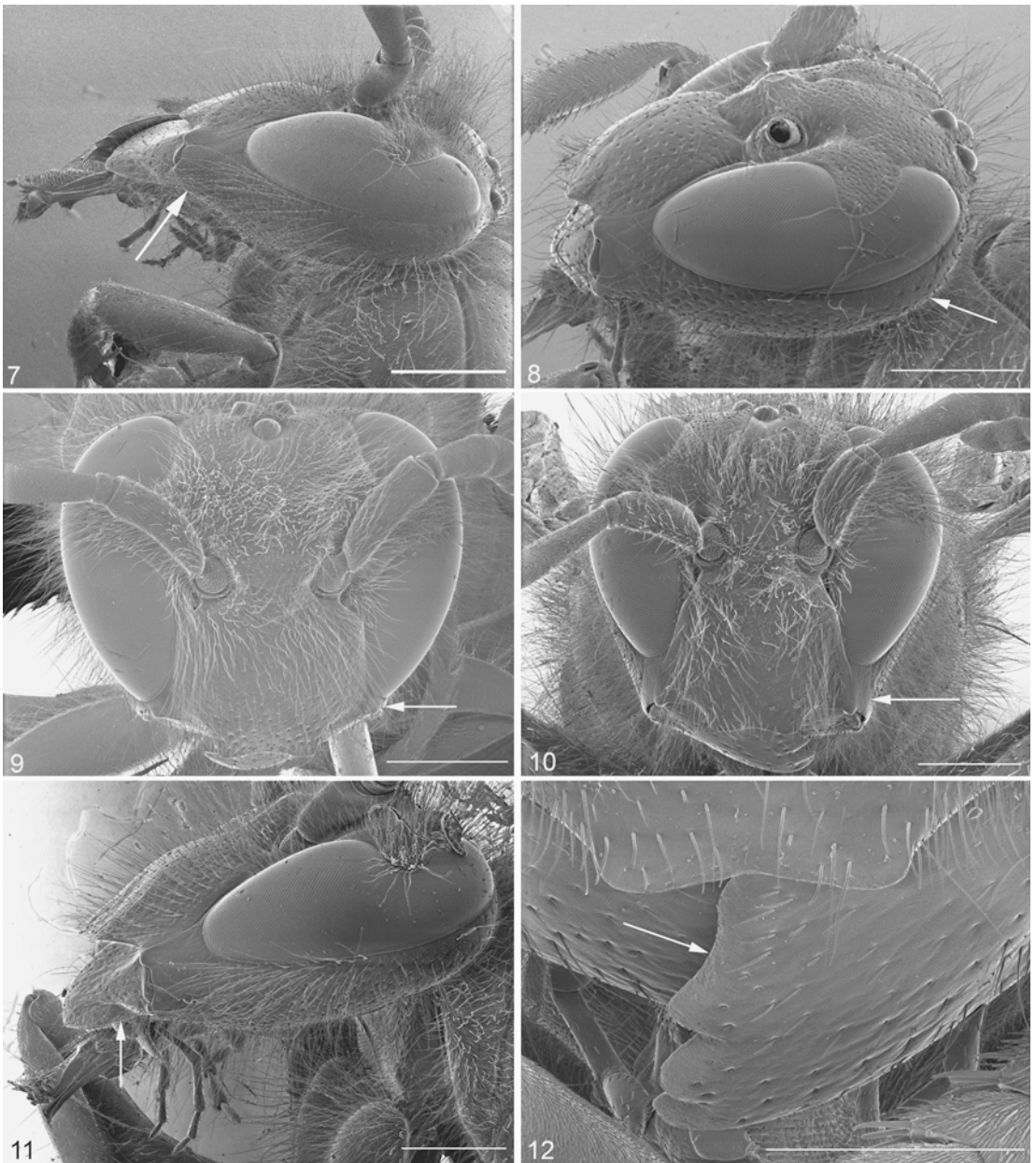
Character List

1. **Worker caste**: present = 0; absent = 1.
2. **Base of forewing 1RS cell**: M oblique with respect to m-cu1 at base of second submarginal (1RS) cell = 0; M vertical (apex of discal cell truncate) = 1.
3. **Placement of forewing m-cu$_2$**: far from r-m$_2$ = 0; close to r-m2 = 1. This was character 4 in Carpenter (1987b), where it was expressed as the second submarginal cell with section of M vein distal to m-cu$_2$ crossvein shorter vs. longer than section

of RS vein basal to r$_2$ crossvein. The sections of M along the posterior edge of the second submarginal cell are subequal in the derived state, while the distal section is much longer than the basal section in the plesiomorphic state.

4. **Hamuli placement**: basad of hindwing R1 and RS = 0; at fork of R1 and RS = 1.
5. **Apical angles of clypeus**: bluntly produced = 0 (fig. 1); sharply produced = 1 (fig. 2). This is usually cited as a key character of females in the inquiline species, but the males also have the apical angles more sharply produced than males of the other species.
6. **Clypeal punctation**: close ventrally (interspaces less than diameter of punctures) = 0 (fig. 3); sparse (interpspaces greater than diameter of punctures) = 1 (fig. 4).
7. **Occipital carina**: running to base of mandible = 0 (fig. 5); effaced near mandible = 1 (figs. 6, 7); obliterated dorsally = 2 (fig. 8).
8. **Malar space**: short (length less than that of last flagellomere) = 0 (fig. 9); long (length greater than or equal to that of last flagellomere) = 1 (fig. 10).
9. **Tyloides**: two per flagellomere = 0; one, only on apical flagellomeres = 1; absent = 2.
10. **Female mandibular flange**: absent = 0 (fig. 11); present basally on outer posterior edge of mandible = 1 (fig. 5).
11. **Margin behind the third mandibular tooth**: distinctly concave = 0 (fig. 12); straight or at most slightly concave = 1 (figs. 13, 14).
12. **Labial palpus**: third segment with a strong seta = 0; without this seta, but with hairs = 1.
13. **Pronotal carina**: present = 0; dorsally reduced = 1 (figs. 15, 16); laterally effaced = 2 (figs. 17, 18).
14. **Pretegular carina**: present = 0; absent = 1.
15. **Pronotal striae**: absent = 0 (fig. 15); present = 1 (fig. 16).
16. **Anterolateral scutal depression**: not developed = 0; present = 1 (fig. 17); with posterolateral extension = 2 (fig. 18). Although Vespinae do not possess notauli, these depressions follow the course of
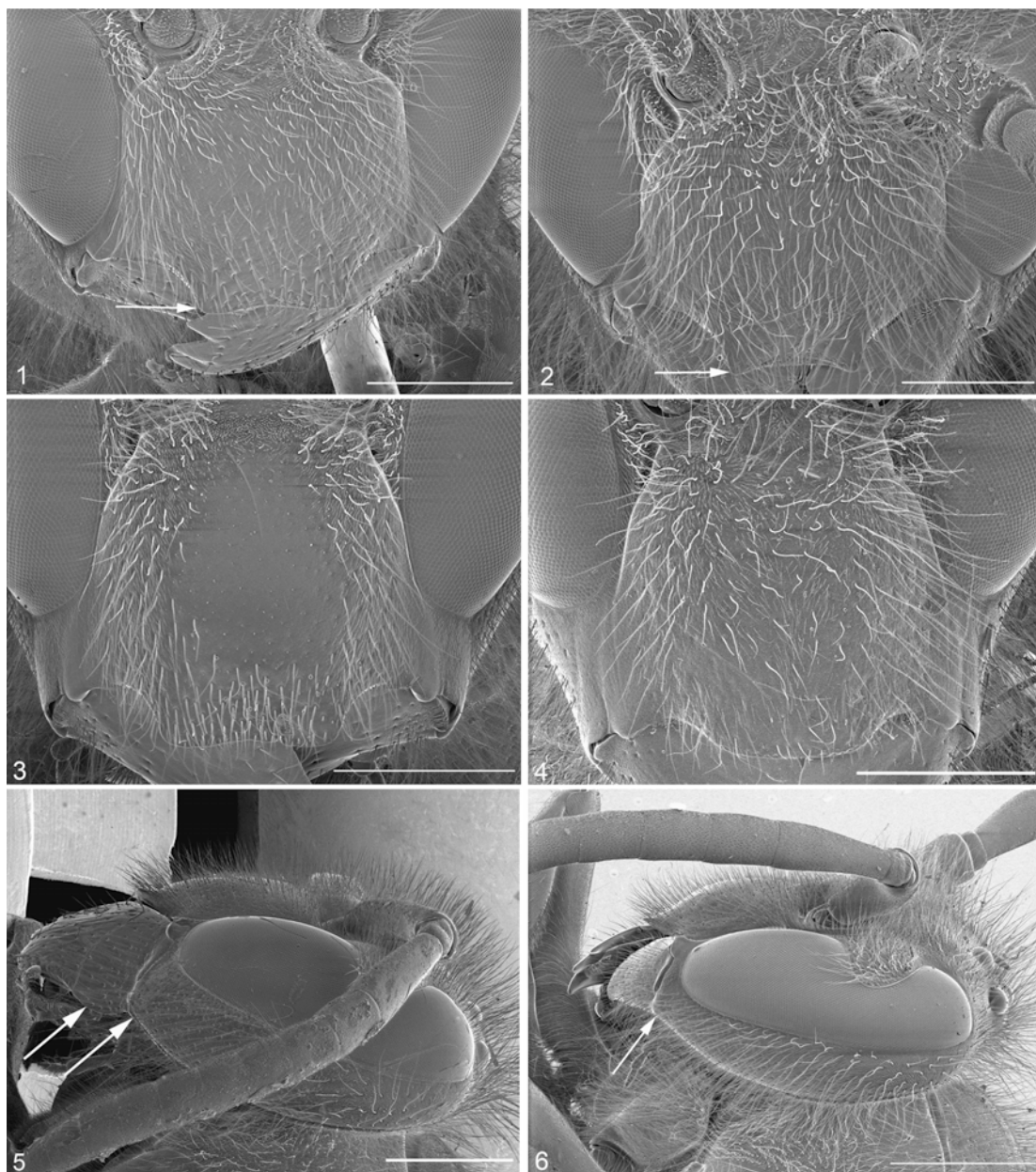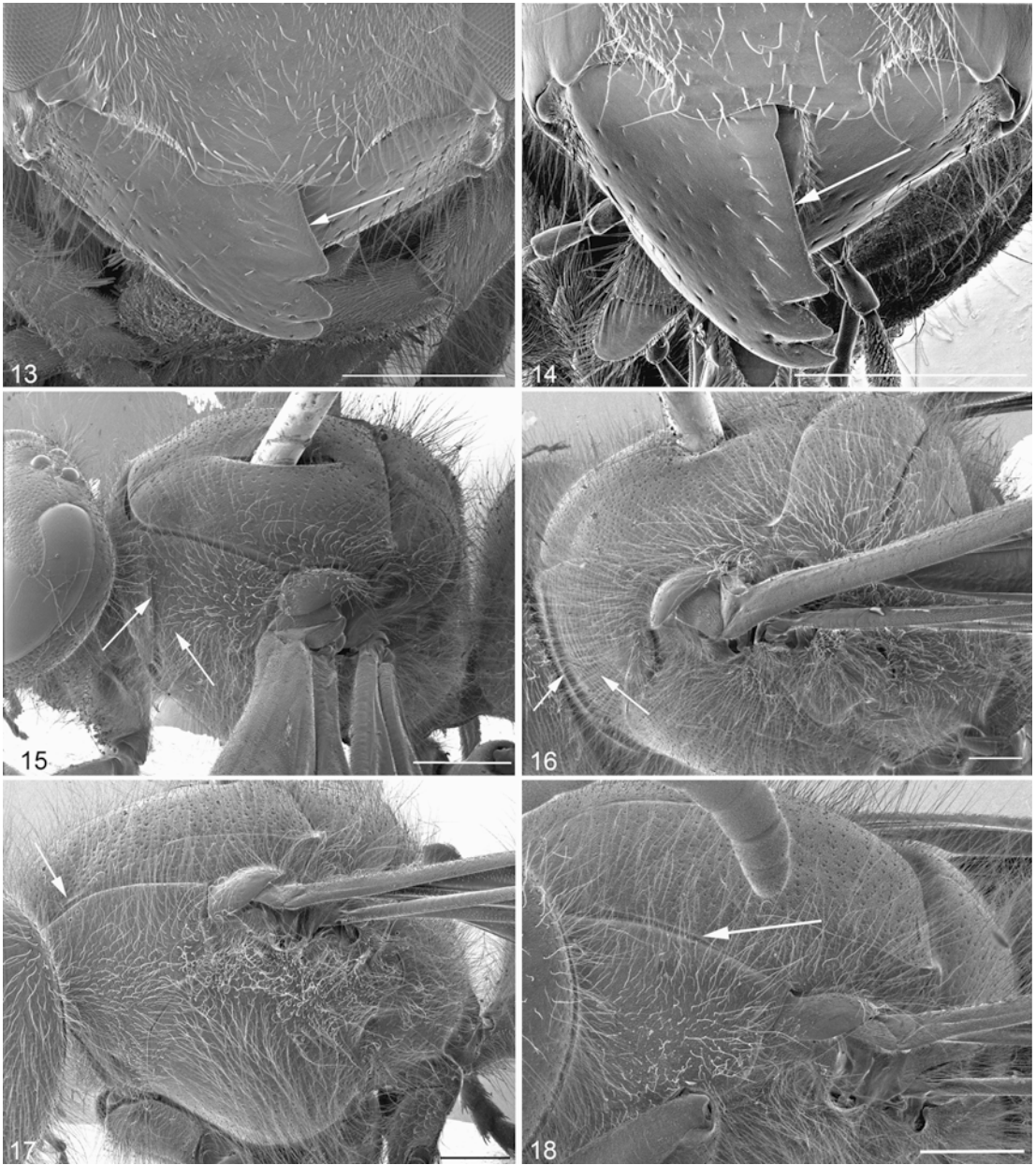
Figs. 1–6. Characters of yellowjackets. **1–2**, clypeus. **1**, *V. rufa* (Linnaeus). **2**, *Vespula austriaca* (Panzer). **3–4**, head in frontal view. **3**, *Dolichovespula sylvestris* (Scopoli). **4**, *D. norvegicoides* (Sladen). **5–6**, head in lateral view. **5**, *V. pensylvanica* (de Saussure). **6**, *V. vidua* (de Saussure). All scale bars equal 1 mm.

Figs. 7–12. Characters of yellowjackets. **7–8**, head in lateral view. **7**, *Dolichovespula norvegicoides* (Sladen). **8**, *D. adulterina* (du Buysson). **9–10**, head in frontal view. **9**, *Vespula rufa* (Linnaeus). **10**, *D. alpicola* Eck. **11**, head in lateral view, *D. arenaria* (Fabricius). **12**, mandibular teeth, *V. germanica* (Fabricius). All scale bars equal 1 mm.

Figs. 13–18. Characters of yellowjackets. **13–14**, mandibular teeth. **13**, *Vespula shidai* Ishikawa, Yamane and Wagner. **14**, *Dolichovespula saxonica* (Fabricius). **15–18**, mesosoma in lateral view. **15**, *D. adulterina* (du Buysson). **16**, *Dolichovespula maculata* (Linnaeus). **17**, *V. rufa* (Linnaeus). **18**, *V. germanica* (Fabricius). All scale bars equal 1 mm.

notauli in other vespids that possess them (Duncan, 1939).

17. **Scutal lamella**: rim of scutum raised into lamella beside tegula = 0; absent = 1.

18. **Hindcoxal carina**: absent = 0; present = 1.

19. **Hindtibia**: with long erect hairs = 0; without long erect hairs = 1.

20. **Dorsum of metasomal tergum I**: flat in lateral view = 0; with slight depression behind anterior edge = 1.

21. **Female metasomal sternum VI process**: without dorsolateral process = 0; with dorsolateral process = 1.

22. **Queen sting**: straight = 0; recurved = 1. It has long been known that inquiline females have the sting recurved in comparison to their hosts (Weyrauch, 1937). Reed and Akre (1982: fig. 2E) noted a sharp distal bend in the sting of *V. squamosa*; however, this is evidently not found in all queens of this species.

23. **Ovariole number**: 7 = 0; 6 = 1. See Kugler et al. (1976).

24. **Male metasomal tergum VII**: disc evenly convex in profile = 0; disc depressed = 1; disc depressed steplike = 2.

25. **Male metasomal tergum VII apex**: rounded = 0; emarginate = 1.

26. **Male metasomal sternum VII apex**: rounded = 0; transverse = 1; emarginate = 2 [nonadditive].

27. **Apex of aedeagus**: transverse, projecting laterally = 0; not projecting laterally = 1; subcircular = 2.

28. **Subapical expansion of aedeagus**: absent = 0; present, about as broad as shaft of aedeagus = 1; present, broader than shaft of aedeagus = 2.

29. **Thickened margins of aedeagus**: not projecting apicad = 0; projecting apicad = 1.

30. **Aedeagal apical indentation**: deep = 0; shallow = 1; absent = 2.

31. **Width of aedeagus**: broad (aedeagus as wide or wider apically as medially) = 0; narrower apically than medially = 1; attenuate, much narrower apically than basally = 2.

32. **Aedeagal apical lobes**: absent = 0; present = 1.

33. **Aedeagal medial lobes**: absent = 0; present = 1.

34. **Paramere process**: paramere with broad inflection near spine = 0; broad pointed process = 1; process distally prolonged = 2; narrowed distally = 3; absent = 4 [nonadditive].

35. **Paramere base**: not emarginate dorsally = 0; emarginate dorsally = 1.

36. **Volsella**: long (extending at least to apex of parameral spine and aedeagus)= 0; short (not extending as far as apex of parameral spine or aedeagus) = 1.

37. **Volsella dorsal lobe**: absent = 0; present = 1.

38. **Digitus**: large, pincer-shaped lobe = 0; very slender, fingerlike lobe = 1.

39. **Hairs on parameral spine and digitus**: present dorsally = 0; absent dorsally = 1.

40. **Pale markings**: yellow = 0; white = 1.

41. **Yellow eye loop**: absent = 0; present = 1.

42. **Genal band**: continuous = 0; interrupted = 1.

43. **Scape ventrally**: pale = 0; dark = 1.

44. **Two longitudinal yellow stripes on scutum**: absent = 0; present = 1.

45. **Lateral surface of the thorax**: without yellow hairs = 0; with yellow hairs = 1.

46. **Metasomal tergum I hairs**: pale = 0; dark = 1.

47. **Metasomal terga I and II maculations**: present = 0; terga entirely black = 1.

48. **Reddish markings on metasomal tergum I or II**: absent = 0; present = 1.

49. **Larval mandible**: tridentate = 0; single apical tooth, ill-defined dorsal tooth = 1.

50. **Larval clypeus**: frontoclypeal suture present = 0; absent = 1.

51. **Larval spiracle**: collar processes simple = 0; branched = 1.

52. **Nest**: nesting site aerial = 0; nesting site in cavity or underground = 1. See Akre et al. (1981, 1982) on variation in nesting site.

53. **Paper type**: gray, pliable = 0; tan, fragile = 1. See Greene (1979) on variation in *D. maculata*.

54. **Scalloping**: absent, envelope laminar = 0; elongate = 1; imbricate = 2 [nonadditive]. See Greene (1979).

55. **Suspensoria**: comb suspensoria pillarlike = 0; ribbonlike supporting first comb = 1; interconnected and ribbonlike throughout = 2 [nonadditive].

56. **Worker-cell comb**: multiple combs of worker cells = 0; one comb of worker cells = 1.

57. **Mixed cell combs**: present = 0; worker and queen cells on different combs = 1. The scoring for *V. flaviceps* and *V. shidai* is based on Kojima (personal commun.).

58. **Attachment of embryo nest**: pedicel of embryo nest with simple cylindrical shape = 0; thin and twisted, with hanging sheet = 1. See Yamane and Makino (1977), Yamane et al. (1981) and Matthews et al. (1982) on architecture of embryo nests. Yamane and Makino (1977: 26) and Yamane et al. (1981: 496, footnote) allude to some confusion in the literature about the state in *V. vulgaris*, but Matthews et al. (1982) do not describe it as different from other species of *Vespula*.

59. **Pedicel of embryo nest**: coated with glossy oral secretion = 0; uncoated = 1.

60. **Embryo nest disc**: absent = 0; present = 1.

61. **First sheet of embryo nest**: bonded to substrate = 0; bonded to hanging sheet = 1; bonded to pedicel = 2 [nonadditive].

62. **Expansion of envelope of embryo nest**: later sheets beginning on previous sheet = 0; later sheets independent = 1. Yamane et al. (1981) considered this character to be an important difference between *Vespula* and *Dolichovespula*, although it has not been studied for many species. In addition to the species they listed, figures in Duncan (1939) show the states in a few species. On the other hand, the figures in Brian and Brian (1948), cited by Yamane et al. (1981) as showing later sheets beginning on the previous sheet in *D. sylvestris*, actually appear to show variation in this character (cf. Brian and Brian, 1948: figs. A and B).

63. **Vestibule**: absent = 0; present = 1.

64. **Colony size**: "small" (<2500 cells and 400 workers at peak) = 0; "large" (3500 cells and 500 workers or more) = 1. Ranges overlap in many species (see Akre et al., 1981).

65. **Hibernaculum**: in pre-existing cavities = 0; partly dug by queen = 1. See Matsuura and Yamane (1990).

66. **Royal court**: "royal court" of workers present, surrounding queen = 0; no distinct royal court of workers surrounding queen = 1. See Matsuura and Yamane (1990).

67. **Prey**: live arthropods = 0; also vertebrate carrion = 1. This behavior varies more than indicated in the matrix; see Akre et al. (1981).

68. **Larval hunger signal**: consistent, audible cell wall scraping = 0; low frequency scraping = 1; inaudible = 2 [nonadditive]. See Matsuura and Yamane (1990).

RESULTS

Analysis of the combined morphological and behavioral characters using the *mult** (random addition of terminals during tree construction, with up to 100 replications, each of which hit minimum length) and *max** (branch swapping by tree-bisection-reconnection) commands of NONA resulted in one cladogram (fig. 19; 106 steps, consistency index = 0.79, retention index = 0.93), which is stable to either successive weighting using the rescaled consistency index and NONA or implied weighting as implemented in the program PIWE (Goloboff, 1999b).

The morphological and behavioral characters are not significantly incongruent, according to the incongruence length difference test (Farris et al., 1994) as implemented in WINCLADA (1000 replicates, $p = 0.4016$ with autapomorphies not deleted and the default "amb- poly=" setting; $p = 0.3876$ with "amb= poly-"). Analysis of the 51 morphological characters resulted in the same cladogram as in figure 19 (81 steps, consistency index =0.77, retention index = 0.93), which is stable to either successive or implied weighting. By contrast, analysis of the 17 behavioral characters produced 1705 cladograms (24 steps, consistency index = 0.87, retention index = 0.95), only 343 of which are strictly supported (see Nixon and Carpenter, 1996), but the consensus of either set of cladograms is entirely unresolved. This is due to the fact that the inquiline species are scored as missing or inapplicable for all the behavioral characters. When those three species are deleted and the behavioral characters reanalyzed, one cladogram resulted (fig. 20, 24 steps), differing from the topology supported
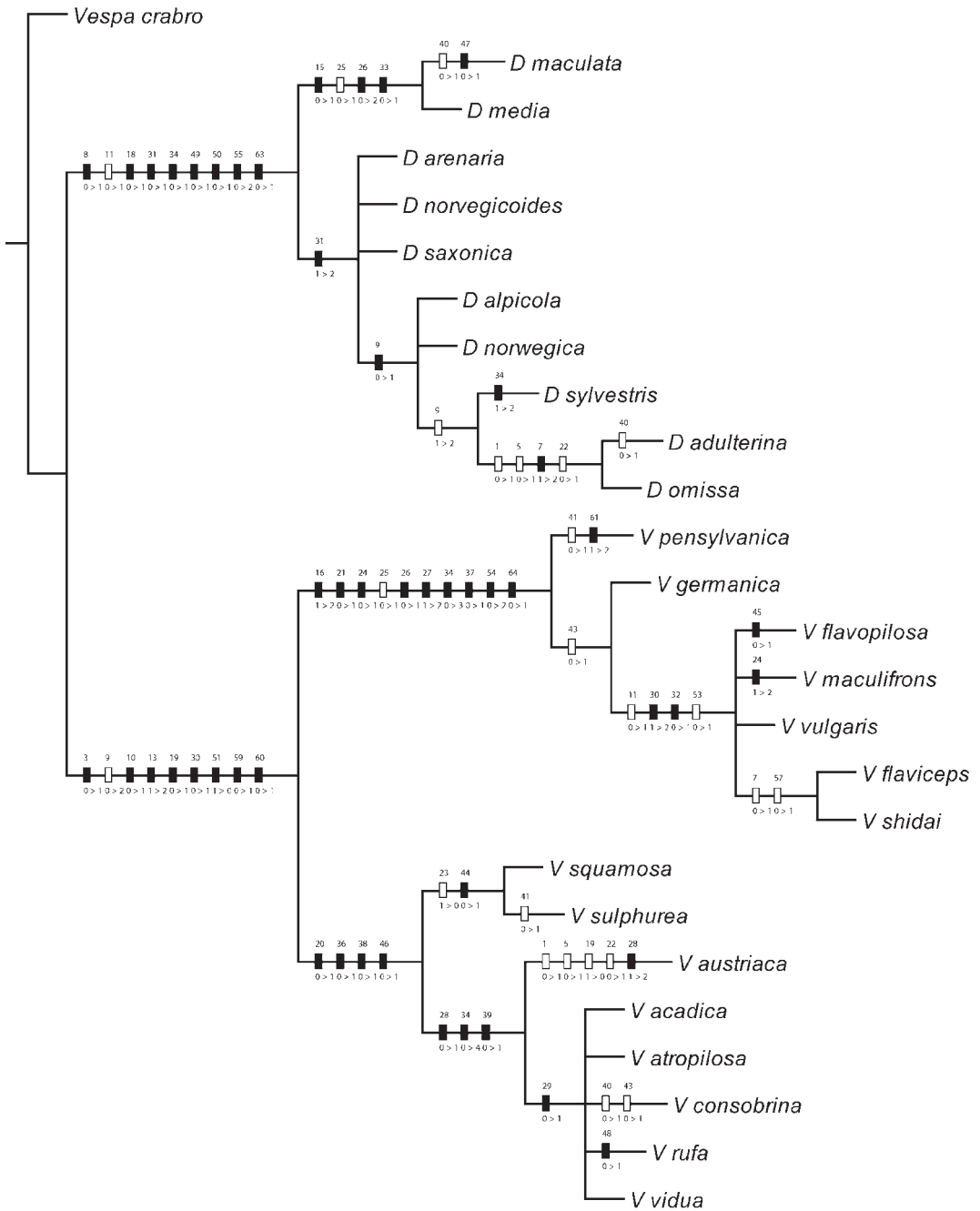
Fig. 19. Cladogram resulting from analysis of all the characters in table 1. Characters have been optimized with only unambiguous changes plotted. Character numbers are above the hashmarks; state changes are shown below, with the respective primitive and derived conditions separated by a ">". Filled hashmarks denote uncontroverted changes, whereas open hashmarks indicate homoplasy in the character. Characters supporting the monophyly of yellowjackets as a whole are not plotted. This cladogram also results from analysis of only the morphological characters in table 1.
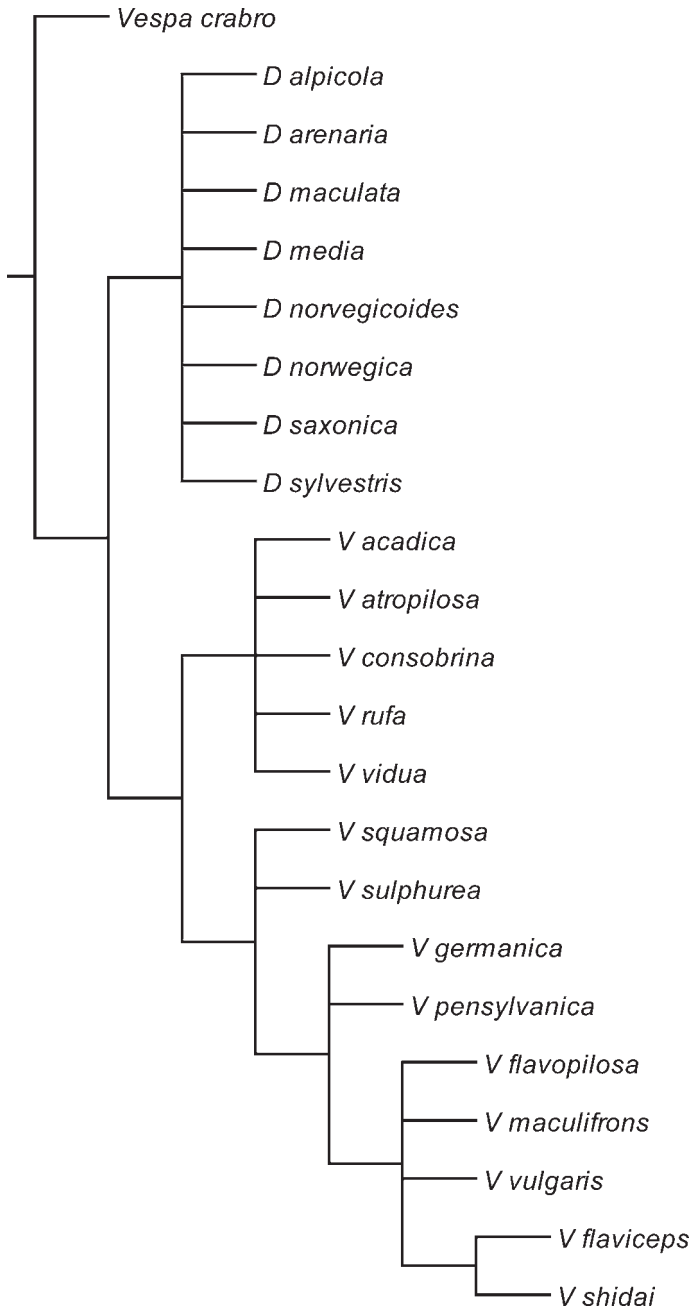
Fig. 20. Cladogram resulting from analysis of the behavioral characters in table 1, with the three inquiline species deleted.

by either the combined or morphological characters primarily in being less resolved. *Dolichovespula* and *Vespula* are both supported, but the former is not otherwise

resolved, while within *Vespula* the *rufa* and *vulgaris* groups are supported, but *V. squamosa* and *V. sulphurea* are grouped with the *vulgaris* group, not the *rufa* group. This is the

only point in which the morphological and behavioral characters disagree, and the combination of characters gives the result supported by morphology. The placement of *V. squamosa* and *V. sulphurea* in the behavioral result is supported only by character 66 (collection of carrion in addition to live prey), and, as noted above, reports of this behavior vary more than indicated in the matrix. In general the behavioral characters suffer more ambiguity, due primarily to lack of observations: the behavioral characters comprise 442 cells in the matrix of table 1, 24.2% of which are scored with missing values, 10.4% of which are inapplicable, and 5.88% of which are polymorphic. Thus, "real" values are observed in only 59.5% of the cells. The morphological characters have only 2.63% missing values and 2.11% polymorphisms, and thus 95.24% of the 1326 cells are "real" values.

The combined characters do not completely resolve the interrelationships among the species (fig. 19). According to the cladogram, however, the social parasites of both *Dolichovespula* and *Vespula* have evolved separately from their hosts: *D. omissa* and *D. adulterina* are more closely related to each other than they are to their hosts, *D. sylvestris* for *D. omissa*, and *D. arenaria*, *D. saxonica* and *D. alpicola* for *D. adulterina*. *Vespula austriaca* is the sister-group to a clade comprising the remaining species of the *V. rufa* species group, which includes the host species *V. rufa* and *V. acadica*. Even a looser formulation of Emery's Rule, to allow for subsequent speciation (Ward, 1996), in which a clade of social parasites has as nearest non-parasitic outgroup a clade that includes the host species, is not applicable to *Dolichovespula*. *Dolichovespula sylvestris* is the sister-group to *D. omissa* (its parasite) + *D. adulterina*, but the hosts of the latter are scattered in a paraphyletic grade of other *Dolichovespula* species.

Of course, an even looser formulation (Danforth, 1999), in which a social parasite clade renders the host group paraphyletic, does apply to the yellowjacket inquilines—but such a statement has very little empirical content, because it could apply to a myriad of possible paraphyletic "groups".

It is worth commenting that the monophyly of *D. adulterina* + *D. omissa* is established by four synapomorphies, three of which (i.e., character 1, absence of a worker caste;, character 5, produced apical angles of the clypeus;, and character 22, recurved sting) are also found in the other inquiline species, *V. austriaca*. These features might thus be considered "morphological accoutrements of parasitism" (West-Eberhard, 1996: 316), and thereby be dismissed as convergent adaptations. Whereas such an argument may be advanced for characters 1 (which is an expression of inquiline behavior) and 22 (which is used in combat during usurpation), the argument is less defensible for character 5, because the apical angles of the clypeus are produced in males, less so than in females but more than in nonparasitic species. A character expressed in males seems less obvious as a candidate for an adaptation related to host domination, unlike features not included in the matrix of table 1 such as enlarged mandibles and femora (see Weyrauch, 1937; Reed and Akre, 1982). But that aside, the fourth synapomorphy for *D. adulterina* + *D. omissa* (i.e., character 7, occipital carina effaced dorsally) does not appear to be at all related to parasitism—and is not found in *V. austriaca*. The monophyly of *D. adulterina* + *D. omissa* thus is established not just by characters that are possible parasitic convergences—and moreover it is not rejected by the other characters analyzed here.

DISCUSSION

As shown by this study, social parasites are not more closely related to their host than to any other species, and hence Emery's Rule is not applicable in yellowjackets. Other studies have rejected the applicability of Emery's Rule to paper wasps (see Carpenter, 1997). The utility of Emery's Rule in wasps is thus diminished altogether.

To the extent that this and other studies fail to support Emery's Rule in wasps, the theory that social parasites evolve sympatrically from their hosts is likewise undermined. But although Emery's Rule is not supported in wasps, nor in ants (Agosti, 1994; Ward, 1989, 1996) or bees (Williams, 1994; Danforth,
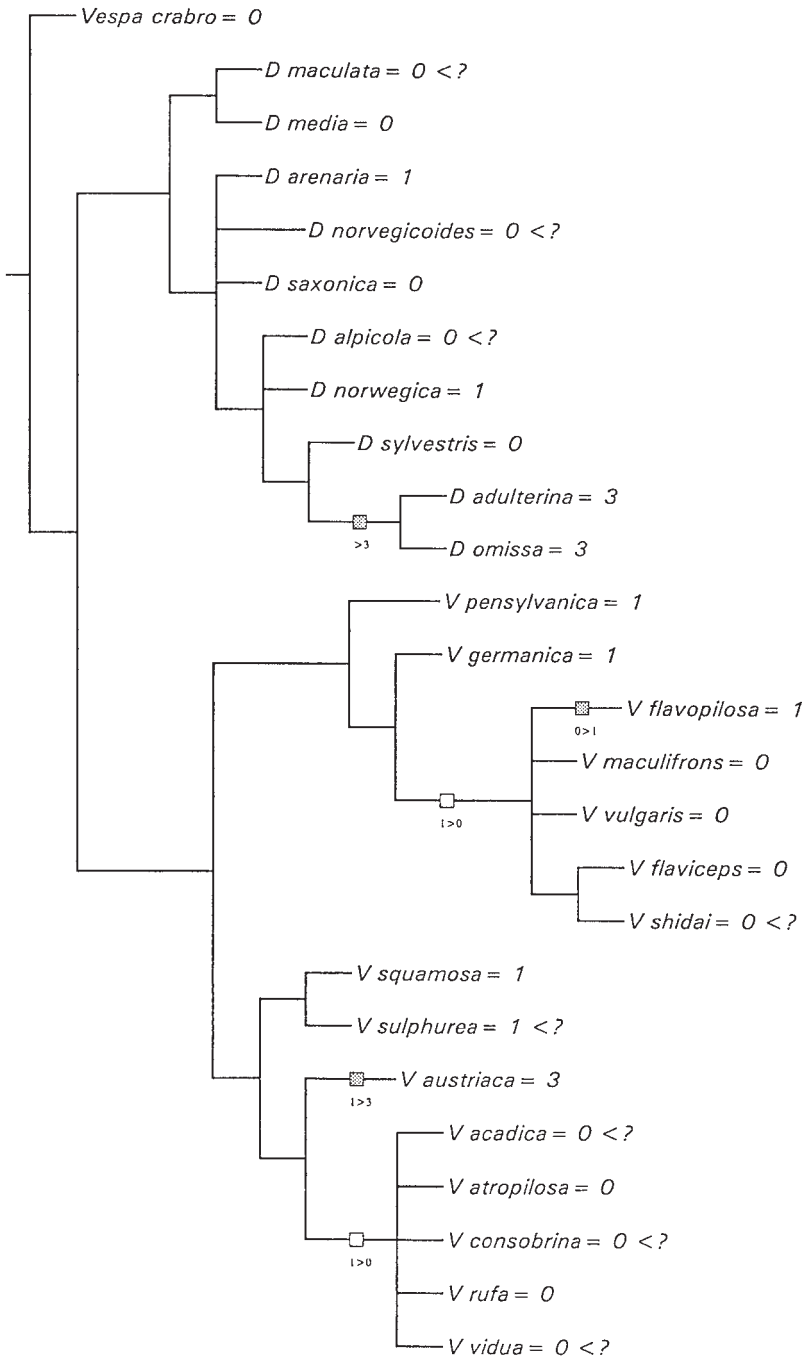
Fig. 21. Cladogram for yellowjacket species, with usurpation behavior optimized. State changes are shown below squares, with the respective primitive and derived conditions separated by a ">". Grayscaled squares denote convergent changes whereas open squares indicate reversal.

1999) where it has been tested, it has not been tested in most ant and bee social parasites. Social parasitism has arisen numerous times in ants, bees and wasps, and so sympatric speciation cannot be rejected out of hand. However, it should be clear that the basic tenets of the principle that have become generally known as Emery's Rule need to be reanalyzed and assessed carefully. Any rule that generalizes the way species evolve without regard to specific conditions is bound to be suspect and clearly needs to be tested before any further assumptions are made. If it seems plausible that in some cases the parasites evolve sympatrically from their hosts, in other cases the parasites just as plausibly evolved allopatrically, for example in relation to climatic factors (Richards, 1971; Matsuura and Yamane, 1990).

What then of Taylor's scenario for the evolution of inquiline behavior as a progression from conspecific queen competition? The extension of such usurpation into inquilinism may still seem a compelling explanation, despite the inapplicability of Emery's Rule (Carpenter et al., 1993). However, there is no clear phylogenetic progression. Grandcolas et al. (1994) have outlined how correspondences between types of phylogenetic patterns and theoretical evolutionary processes may function as tests of the theories. For evolutionary scenarios, the "time lag" or order of appearance of features may support or reject a suggested evolutionary progression based on the association of those features. This approach was applied to the origin of inquiline behavior in *Polistes* by Carpenter (1997), by cladistic optimization of behavioral traits on a cladogram for the inquiline species and their hosts. The optimizations accorded with part of Taylor's scenario, specifically that (obligate and permanent) interspecific usurpation evolved from (facultative and temporary) intraspecific usurpation. Stage 1 in Taylor's scenario thus preceded stage 4. But other parts of the scenario were not supported; specifically, it is unclear whether (facultative and temporary) interspecific usurpation preceded inquiline behavior. Inquiline behavior could have evolved directly from intraspecific usurpation (stage 1) or via an intervening stage of temporary interspecific usurpation (stage 2).

Furthermore, the third stage of the scenario is not observed in *Polistes*.

A similar optimization of usurpation behavior in yellowjackets is shown in figure 21. State 0 is intraspecific usurpation; state 1 is facultative, temporary usurpation; state 2 is obligate, temporary usurpation (for which *V. squamosa* is scored as polymorphic); and state 3 is obligate, permanent usurpation (inquiline behavior). The variable is treated as additive. Species with a question mark are those for which we have not been able to find reports of usurpation. The optimization that is shown plots only unambiguous changes, with the state preceding the "<" symbol being the state inferred by the optimization for taxa with missing values. As with *Polistes*, the behavior of the inquilines may have evolved directly from intraspecific usurpation (possible with *D. adulterina* + *D. omissa*, where the optimization is ambiguous) or from facultative interspecific usurpation (*V. austriaca*). Obligate temporary usurpation evolved from facultative interspecific usurpation only within *V. squamosa* (not plotted). It is not part of a progression to inquiline behavior, and the conclusion remains the same even if *V. squamosa* is scored as monomorphic for state 2. Not all of the stages of Taylor's scenario may thus be necessary in the evolution of social parasitism. The tactics used by the inquilines during usurpation are known to differ among the species: *D. adulterina* is passive when invading the nest of *D. arenaria*, assuming a submissive posture during attacks and coexisting with the *D. arenaria* queen for a time (Evans, 1975; Jeanne, 1977; Greene et al., 1978), while *V. austriaca* immediately attempts to kill the *V. acadica* queen of an invaded nest (Reed and Akre, 1983). The usual timing of invasion is also different, whether before emergence of the first workers (*D. adulterina*) or after (*V. austriaca*). Inquiline behavior, which originated more than once in yellowjackets, has thus undergone more than one evolutionary pathway. A single, simple scenario may therefore not be universally applicable.

ACKNOWLEDGMENTS

REFERENCES

Agosti, D. 1994. A new inquiline ant (Hymenoptera: Formicidae) in *Cataglyphis* and its phylogenetic relationship. Journal of Natural History 28: 913–919.

Akre, R.D. 1982. Social wasps. *In* H.R. Hermann (editor), Social insects 4: 1–105. New York: Academic Press.

Akre, R.D., A. Greene, J.F. MacDonald, P.J. Landolt, and H.G. Davis. 1981. The yellowjackets of America North of Mexico. Agriculture Handbook 552: 1–102. Washington, DC: United States Department of Agriculture.

Akre, R.D., and J.F. MacDonald. 1986. Biology, economic importance and control of yellowjackets. *In* S.B. Vinson (editor), Economic impact and control of social insects: 353–412. New York: Praeger.

Akre, R.D., H.C. Reed, and P.J. Landolt. 1982. Nesting biology and behavior of the blackjacket, *Vespula consobrina* (Hymenoptera: Vespidae). Journal of the Kansas Entomological Society 55: 373–405.

Akre, R.D., C.F. Roush, and P.J. Landolt. 1977. A *Vespula pensylvanica/Vespula vulgaris* nest (Hymenoptera: Vespidae). Environmental Entomology 6: 525–526.

Archer, M.E. 1981a. The Euro-Asian species of the *Vespula rufa* group (Hymenoptera, Vespidae), with descriptions of two new species and one new subspecies. Kontyû 49: 54–64.

Archer, M.E. 1981b. Taxonomy of the *sylvestris* group (Hymenoptera: Vespidae, *Dolichovespula*) with the introduction of a new name and notes on distribution. Entomologica Scandinavica 12: 187–193.

Archer, M.E. 1987. A working cladogram for the *Vespinae*. *In* J. Eder and H. Rembold (editors), Chemistry and biology of social insects: 74. Munich: Verlag J. Peperny.

Archer, M.E. 1989. A key to the world species of the Vespinae (Hymenoptera). Research Monographs of the College of Ripon and York 2.

Archer, M.E. 1997. Taxonomy, distribution, and nesting biology of the species of the Euro-Asian *Vespula rufa* group (Hym., Vespinae). Entomologist's Monthly Magazine 133: 107–114.

Archer, M.E. 1999. Taxonomy and world distribution of the Euro-Asian species of *Dolichovespula* (Hym., Vespinae). Entomologist's Monthly Magazine 135: 153–160.

Beaumont, J. de. 1944. Les guêpes (*Vespa* L. s.l.) de la Suisse. Bulletin de la Société Vaudoise des Sciences Naturelles 57(261): 329–362.

Beaumont, J.de. 1958. Le parasitisme social chez les Guêpes et les Bourdons. Mitteilungen der Schweizerischen Entomologischen Gesellschaft 31(2): 168–176.

Bequaert, J. 1932. A tentative synopsis of the hornets and yellow-jackets (Vespinae; Hymenoptera) of America. Entomologica Americana (new series) 12(2): 71–138.

Bischoff, H. "1930" [1931]. Zur Kenntnis der Gattung *Pseudovespa*. Sitzungsberichte der Gesellschaft naturforschender Freunde 1930: 329–346.

Blüthgen, P. "1937" [1938]. Systematisches Verzeichnis der Faltenwespen Mitteleuropas, Skandanaviens und Englands. Konowia 16: 270–295.

Blüthgen, P. 1943. Taxonomische und biologische Notizen über palaarktische Faltenwespen (Hym. Vespidae). Stettiner Entomolgische Zeitung 104: 149–158.

Bourke, A., and N. Franks. 1991. Alternative adaptations, sympatric speciation and the evolution of parasitic inquiline ants. Biological Journal of the Linnean Society 43: 157–178.

Brian, M.V., and A.D. Brian. 1948. Nest construction by queens of *Vespula sylvestris* Scop. (Hym., Vespidae). Entomologist's Monthly Magazine 84: 193–198.

Bunn, D.S. 1982. Usurpation in wasps (Hym., Vespidae). Entomologist's Monthly Magazine 118: 171–173.

Buschinger, A. 1970. Neue Vorstellungen zur Evolution des Sozialparasitismus und der Dulosis bei Ameisen (Hym. Formicidae). Biologisches Zentralblatt 89: 273–299.

Buschinger, A. 1986. Evolution of social parasitism in ants. Trends in Ecology and Evolution 1: 155–160.

Buschinger, A. 1990. Sympatric speciation and radiative evolution of socially parasitic ants—heretic hypotheses and their factual background. Zeitschrift für Zoologische Systematik und Evolutionsforschung 28: 241–260.

Carpenter, J.M. 1987a. On "The evolutionary genetics of social wasps" and the phylogeny of the Vespinae (Hymenoptera, Vespidae). Insectes Sociaux 34: 58–64.

Carpenter, J.M. 1987b. Phylogenetic relationships and classification of the Vespinae (Hymenoptera: Vespidae). Systematic Entomology 12: 413–431.

Carpenter, J.M. 1992. Distances, assumptions and social wasps. Cladistics 8: 155–160.

Carpenter, J.M. 1997. Phylogenetic relationships among European *Polistes* and the evolution of social parasitism (Hymenoptera: Vespidae, Polistinae). Mémoires du Muséum National d'Histoire Naturelle 173: 135–161.

Carpenter, J.M., and J. Kojima. 1997. Checklist of the species in the subfamily Vespinae (Insecta: Hymenoptera: Vespidae). Natural History Bulletin of Ibaraki University 1: 51–92.

Carpenter, J.M., J.E. Strassmann, S. Turillazzi, C.R. Hughes, C.R. Solis, and R. Cervo. 1993. Phylogenetic relationships among paper wasp social parasites and their hosts (Hymenoptera: Vespidae; Polistinae). Cladistics 9: 129–146.

Choudhary, M., J.E. Strassmann, D.C. Queller, S. Turillazzi, and R. Cervo. 1994. Social parasites in polistine wasps are monophyletic: implications for sympatric speciation. Proceedings of the Royal Society of London (series B) 257: 31–35.

Danforth, B.N. 1999. Phylogeny of the bee genus *Lasioglossum* (Hymenoptera: Halictidae) based on mitochondrial COI sequence data. Systematic Entomology 24: 377–393.

Dong, D., X. Liang, Y. Wang, and Y. He. 2005. A new species of the genus *Vespula* (Hymenoptera: Vespidae) from Gongshan Yunnan, China. Entomotaxonomia 27(1): 65–68.

Dong, D., Y. Wang, Y. He, and R. Wang. 2002. A new species of *Vespula* (Hymenoptera: Vespidae) from Yunnan China. Journal of the Southwestern Agricultural University 24(5): 396–397.

Duncan, C.D. 1939. A contribution to the biology of North American vespine wasps. Stanford University Publications in the Biological Sciences 8: 1–272.

Eck, R. 1979. Biometrische Untersuchung zur Klärung der Artunterschiede bei sozialen Faltenwespen (Hymenoptera, Vespinae). Entomologische Abhandlungen der Staatliches Museum für Tierkunde in Dresden 42: 315–344.

Eck, R. 1998. Eine neue Art der *Vespula vulgaris*—Gruppe aus Asien (Insecta: Hymenoptera: Vespidae). Reichenbachia 32(43): 299–302.

Edwards, R. 1980. Social wasps: their biology and control. East Grinstead: Rentokil.

Emery, C. 1909. Über den Ursprung der dulotischen, parasitischen und myrmekophilen Ameisen. Biologisches Zentralblatt 29(11): 352–362.

Evans, H.E. 1975. Social parasitism of a common yellowjacket. Insect World Digest 2(1): 6–13.

Farris, J.S., M. Källersjö, A.G. Kluge, and C. Bult. 1994. Testing significance of incongruence. Cladistics 10: 315–319.

Goloboff, P.A. 1999a. NONA, version 2. Program and documentation. Tucumán, Argentina: Fundación e Instituto Miguel Lillo.

Goloboff, P.A. 1999b. PIWE, version 3. Program and documentation. Tucumán, Argentina: Fundación e Instituto Miguel Lillo.

Grandcolas, P., P. Deleporte, and L. Desutter-Grandcolas. 1994. Why to use phylogeny in evolutionary ecology? Acta Oecologica 15: 661–673.

Greene, A. 1979. Behavioral characters as indicators of yellowjacket phylogeny (Hymenoptera: Vespidae). Annals of the Entomological Society of America 72: 614–619.

Greene, A. 1991. *Dolichovespula* and *Vespula*. *In* K.G. Ross and R.W. Matthews (editors), The social biology of wasps: 263–305. Ithaca, NY: Cornell University Press.

Greene, A., R.D. Akre, and P.J. Landolt. 1978. Behavior of the yellowjacket social parasite, *Dolichovespula arctica* (Rohwer) (Hymenoptera: Vespidae). Melanderia 29: 1–28.

Guiglia, D. 1948. Le *Vespa* d'Italia. Memorie della Società Entomologica Italiana 17, Fascicolo Supplementare: 1–84.

Guiglia, D. 1972. Les guêpes sociales (Hymenoptera Vespidae) d'Europe occidentale et septentrionale. Faune de l'Europe et du Bassin Mediterraneen 6, Paris: Masson.

Heinze, J. 1991. Biochemical studies on the relationship between socially parasitic ants and their hosts. Biochemical Systematics and Ecology 19: 195–206.

Hennig, W. 1966. Phylogenetic systematics. Urbana: University of Illinois Press.

Hölldobler, B., and E.O. Wilson. 1990. The ants. Cambridge, MA: Harvard University Press.

Jacobson, R.S., R.W. Matthews, and J.F. MacDonald. 1978. A systematic study of the *Vespula vulgaris* group with a description of a new yellowjacket species in eastern North America (Hymenoptera: Vespidae). Annals of the Entomological Society of America 71: 299–312.

Jeanne, R.L. 1977. Behavior of the obligate social parasite *Vespula arctica* (Hymenoptera: Vespidae). Journal of the Kansas Entomological Society 50: 541–557.

Kugler, J., T. Orion, and J. Ishay. 1976. The number of ovarioles in the Vespinae (Hymenoptera). Insectes Sociaux 23: 525–533.

MacDonald, J.F., and R.D. Matthews. 1975. *Vespula squamosa*: a yellow jacket wasp evolving toward parasitism. Science 190: 1003–1004.

MacDonald, J.F., and R.D. Matthews. 1984. Nesting biology of the southern yellowjacket, *Vespula squamosa* (Hymenoptera: Vespidae): social parasitism and independent founding. Journal of the Kansas Entomological Society 57: 134–151.

MacDonald, J.F., R.W. Matthews, and R.S. Jacobson. 1980. Nesting biology of the yellowjacket, *Vespula flavopilosa*. Journal of the Kansas Entomological Society 53: 448–458.

Matsuura, M., and S. Yamane. 1990. Biology of the vespine wasps. Berlin: Springer-Verlag. [translation of the 1984 book ''Comparative ethology of the vespine wasps,'' published by Hokkaido University Press, Sapporo, in Japanese]

Matthews, R.W. 1982. Social parasitism in yellowjackets (*Vespula*). *In* P. Jaisson (editor), Social insects in the tropics 1: 193–202. Paris: Université Paris–Nord.

Matthews, R.W., K.G. Ross, and R.A. Morse. 1982. Comparative development of queen nests of four species of yellowjackets (Hymenoptera: Vespidae) reared under identical conditions. Annals of the Entomological Society of America 75: 123–129.

Miller, C.D.F. 1958. Distributional and nomenclatorial problems in some forms of *Vespula* in North America (Hymenoptera: Vespidae) Proceedings of the Tenth International Congress of Entomology, Montreal, 1956, 1: 257–264.

Miller, C.D.F. 1961. Taxonomy and distribution of Nearctic *Vespula*. Canadian Entomologist 93(suppl. 22): 1–52.

Nixon, G.E.J. 1935. Notes on wasps. IV. Entomologist's Monthly Magazine 71: 106–111.

Nixon, K.C. 2002. WINCLADA, version 1.00.24. Program and documentation at cladistics.com.

Nixon, K.C., and J.M. Carpenter. 1996. On consensus, collapsibility and clade concordance. Cladistics 12: 305–321.

O'Rourke, M.E., and F.E. Kurczewski. 1984. Nest usurpation of *Vespula vulgaris* by *Dolichovespula arenaria* with successive parasitism of *D. arenaria* by *D. arctica* (Hymenoptera: Vespidae). Entomological News 95: 212–214.

Reed, H.C., and R.D. Akre. 1982. Morphological comparisons between the obligate social parasite, *Vespula austriaca* (Panzer), and its host, *Vespula acadica* (Sladen) (Hymenoptera: Vespidae). Psyche 89: 183–195.

Reed, H.C., and R.D. Akre. 1983. Usurpation behavior of the yellowjacket social parasite, *Vespula austriaca* (Panzer) (Hymenoptera: Vespidae). American Midland Naturalist 110: 419–432.

Reed, H.C., R.D. Akre, and W.B. Garnett. 1979. A North American host of the yellowjacket social parasite *Vespula austriaca* (Panzer) (Hymenoptera: Vespidae). Entomological News 90: 110–113.

Richards, O.W. 1971. The biology of the social wasps (Hymenoptera, Vespidae). Biological Reviews 46: 483–528.

Robson, J.E. 1898. *Vespa austriaca*, a cuckoo-wasp. Science–Gossip 5: 69–73.

Schmiedeknecht, O. 1881. Über einige deutsche *Vespa*–Arten. Entomologische Nachrichten 7: 313–318.

Schmitz, J., and R.F.A. Moritz. 1990. Mitochondrial DNA variation in social wasps (Hymenoptera: Vespidae). Experientia 46: 1068–1072.

Spradbery, J.P. 1973. Wasps: an account of the biology and natural history of solitary and social wasps. Seattle: University of Washington Press.

Taylor, L.H. 1939. Observations on social parasitism in the genus *Vespula* Thomson. Annals of the Entomological Society of America 32: 304–315.

Varvio-Aho, S.L., P. Pamilo, and A. Pekkarinen. 1984. Evolutionary genetics of social wasps (Hymenoptera, Vespidae, *Vespula*). Insectes Sociaux 31: 375–386.

Wagner, R.E. 1978. The genus *Dolichovespula* and an addition to its known species of North America (Hymenoptera: Vespidae). Pan-Pacific Entomologist 54: 131–142.

Ward, P.S. 1989. Genetic and social changes associated with ant speciation. *In*: M.D. Breed and R.E. Page (editors), The genetics of social evolution: 123–148. Boulder, CO: Westview Press.

Ward, P.S. 1996. A new workerless social parasite in the ant genus *Pseudomyrmex* (Hymenoptera: Formicidae), with a discussion of the origin of social parasitism in ants. Systematic Entomology 21: 253–263.

West-Eberhard, M.J. 1986. Alternative adaptations, speciation and phylogeny (a review). Proceedings of the National Academy of Sciences of the United States of America 83: 1388–1392.

West-Eberhard, M.J. 1996. Wasp societies as microcosms for the study of development and evolution. *In* S. Turillazzi and M.J. West-Eberhard (editors), Natural history and evolu-

tion of paper-wasps: 290–317. Oxford: Oxford University Press.

Weyrauch, W. 1937. Zur Systematik und Biologie der Kuckuckswespen *Pseudovespa*, *Pseudovespula* und *Pseudopolistes*. Zoologische Jahrbücher (Abteilung für Systematik, Ökologie und Geographie der Tiere) 70: 243–290.

Wheeler, W.M. 1928. The social insects. New York: Harcourt, Brace.

Wheeler, W.M., and L.H. Taylor. 1921. *Vespa arctica* Rohwer, a parasite of *Vespa diabolica* de Saussure. Psyche 28: 135–144.

Williams, P.H. 1994. Phylogenetic relationships among bumblebees (*Bombus* Latr.): a reappraisal of morphological evidence. Systematic Entomology 19: 327–344.

Wilson, E.O. 1971. The insect societies. Cambridge, MA: Belknap Press.

Yamane, S., and S. Makino. 1977. Bionomics of *Vespa analis insularis* and *V. mandarinia latilineata* in Hokkaido, northern Japan, with notes on vespine embryo nests (Hymenoptera: Vespidae). Insecta Matsumurana (new series) 12: 1–33.

Yamane, S., S. Makino, and R.P. Macfarlane. 1981. Embryo nest architecture in three *Vespula* species (Hymenoptera, Vespidae). Kontyû 49: 491–497.

Yamane, S., R.E. Wagner, and S. Yamane. 1980. A tentative revision of the subgenus *Paravespula* of Eastern Asia (Hymenoptera: Vespidae) Insecta Matsumurana (new series) 19: 1–46.