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THE SOCIAL WASPS (HYMENOPTERA: VESPIDAE) OF INDIANA¹J.F. MacDonald² and M.A. Deyrup³

ABSTRACT

An updated taxonomic treatment of the social wasps (Hymenoptera: Vespidae) of Indiana is made. Illustrated identification keys are provided for species of *Polistes*, *Vespa*, *Vespula*, and *Dolichovespula*. New distributional records and biological notes are provided for each species.

Eusocial wasps, including paper wasps, hornets, and yellowjackets, occur in colonies associated with elaborate paper nests and show: (1) cooperative brood care; (2) reproductive division of labor; and (3) an overlap of generations (Wilson, 1971). The eusocial wasps of Indiana were last treated taxonomically by Chandler (1965). The present paper, which updates Chandler's work, presents current taxonomy, identification keys, new distributional and biological data, and selected recent references.

Introduction to the Family Vespidae. Chandler (1965) included in the family Vespidae two subfamilies with eusocial species, Polistinae and Vespinae, together with solitary species in the subfamilies Eumeninae and Zethinae; subsequent taxonomic treatment of these groups has changed. The most recent catalog of Hymenoptera (Krombein 1979) restricted the family Vespidae to eusocial species in the subfamilies Polistinae and Vespinae. However, a recent phylogenetic analysis of the world social wasps and their relatives (Carpenter 1982) has led to a new classification of the family Vespidae in which the subfamilies Polistinae and Vespinae are united with four other subfamilies that include mostly solitary species.

Temperate eusocial wasp colonies are normally annual, being initiated in spring, reaching their peak in mid to late summer, and declining by late summer to fall. The paper nest, used only during the year in which it is constructed, consists of masticated wood fibers mixed with salivary secretions; nest architecture varies among species and may be of systematic importance. Larvae are fed a meat diet consisting primarily of pieces of arthropod prey captured by worker wasps. Adults imbibe a variety of liquid carbohydrates, larval secretions, and fluids from captured prey. The sting of female eusocial wasps appears never to be used in prey capture (as it is in solitary wasps); instead, prey capture is accomplished by grasping with the legs and use of powerful mandibles.

This paper is not intended to cover the importance of social wasps, a topic reviewed by Akre et al. (1981) and Akre and MacDonald (1986). However, a couple of items will be mentioned briefly. Foraging vespids almost never sting unless captured and mishandled; almost all stinging episodes are associated with purposeful or inadvertent disturbance of the nest. Secondly, all social wasp stings are very painful, potentially dangerous if

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delivered in the neck region where rapid swelling can block breathing passages, and may induce dangerous systemic reactions in hypersensitive individuals. Recent research suggests that reactions to social wasp and social bee venoms appear to be at least group specific; for example, people allergic to honey bee venom are not necessarily allergic to social wasp venom. Accordingly, accurate identification of stinging Hymenoptera, including all social wasps, is very important and may even provide the basis for successful diagnosis and eventual desensitization with pure venom extracts obtained from the offending species. Lastly, destruction of most social wasp colonies can be difficult and potentially dangerous, and is best left to experienced people with the proper protective gear and effective insecticidal products.

Identification of the Social Vespidae. The intent of this paper is to facilitate identification of Indiana social wasps without resorting to characters that require special preparation of specimens, such as dissecting and clearing of male genitalia. Structural characters are used whenever possible, but most species can be separated only through variations in color patterns. Nearly all specimens of Vespinae may be determined by the maculation patterns of the gaster, but some *Polistes* species are not easily identified by coloration. Collection of a series of adults and the nest itself is strongly recommended to facilitate identification of *Polistes* species.

Although prepared for Indiana, the information and keys cover the social wasp fauna existing in surrounding states as well. The key to *Polistes*, however, was developed to handle Indiana specimens and may not suffice to accurately identify all specimens from neighboring states.

Social wasp researchers employ a number of morphological terms in identification keys that may not be found in general references. Common terms adopted for use in this paper are listed below and the structures are illustrated in Figure 1 and in figures cited in the keys:

Carina: a slightly raised ridge on the integument (referred to as the "keel" in some *Polistes* keys).

Corona: a more or less rectangular yellow area just above and between the antennal bases.

Gaster: the main portion of the abdomen posterior to the pedicel.

Genal band: a narrow area immediately posterior to each compound eye.

Jugal lobe: the basal, posterior lobe of the hind wing of *Polistes* (often referred to as the anal lobe).

Maculation: a pattern of colors; in *Vespula*, the pattern of yellow or white against a black background on the gaster or clypeus.

Ocular sinus: a small yellow area lying within the medial indentation of each compound eye.

Oculomalar space: a narrow area immediately beneath each compound eye and just above each mandible base.

Pedicel: the "waist" between the gaster and the propodeum; also, the second antennal segment.

Propodeum: the posterior plate of the thorax continuous with the pedicel (actually, the propodeum is the first true abdominal segment united with the last thoracic segment).

Key to the Subfamilies of Eusocial Vespidae

1. Gastral tergum I narrowed anteriorly and convex in lateral view (fig. 2); clypeus rounded or narrowly truncate ventrally (fig. 4); hindwing with a jugal lobe; slender wasps; nest a single, exposed comb Polistinae
- 1'. Gastral tergum I strongly truncate anteriorly and arising nearly vertically from the pedicel in lateral view (fig. 3); clypeus broadly truncate and concave ventrally (fig. 5); hindwing lacking a jugal lobe; robust wasps; nest consists of multiple combs enclosed in a paper envelope Vespinae

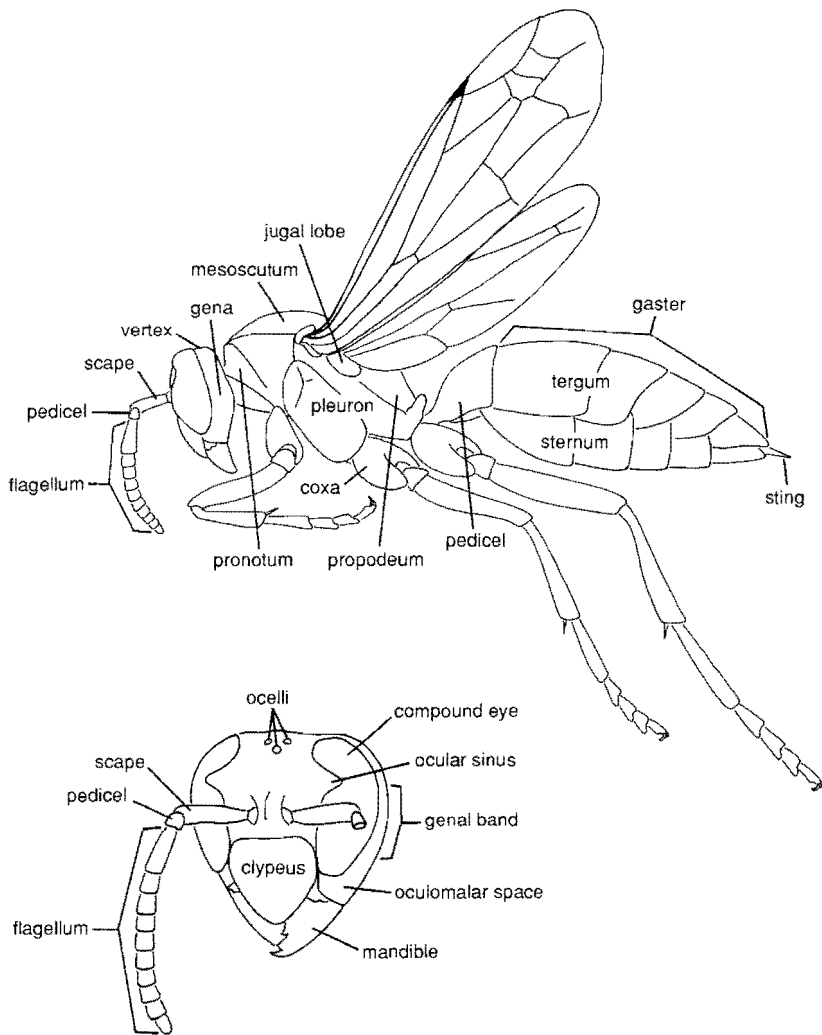


Figure 1. Reference figures for Vespidae.

Subfamily POLISTINAE

This subfamily is represented in Indiana and surrounding states by species of *Polistes*, which are fairly large, slender wasps known variously as paper wasps, single-comb paper wasps, and umbrella wasps. Greene and Caron (1980) recommend use of "paper wasp" for all species of *Polistes*, exclusively.

The polistine fauna is richer in species and more diverse biologically in warmer

climates, and even within Indiana there are more species in the southern part of the state. To date, there are no introduced *Polistes* in Indiana. However, *Polistes dominulus* (Christ) (= *P. gallicus* [L.]), a common European and Asian species, is well established in Massachusetts (Hathaway 1981, 1986). This species, which resembles many species of yellowjackets in coloration and size, is expected to spread in North America, based on its ability to survive in a broad range of climates in Europe and Asia.

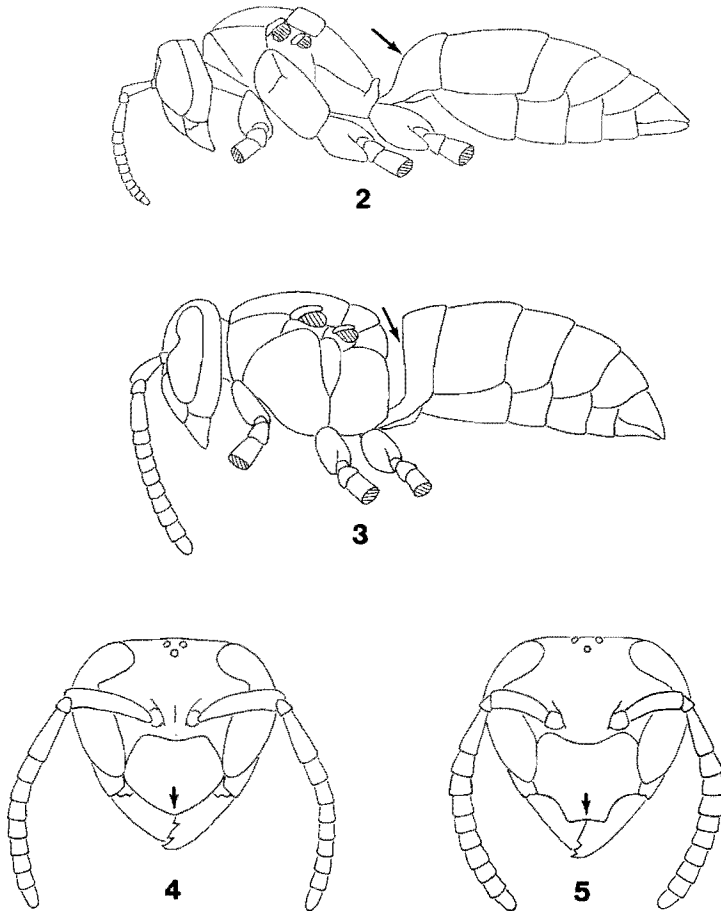
Colonies of *Polistes* are initiated in early to mid-spring, either by one or a small group of overwintered foundresses. Most species initiate colonies in sheltered, above ground sites, with human structures affording the most common nesting substrate; other nesting sites include hollow pipes, fallen trees, and occasionally tree branches and shrubs. Nests consist of a single comb of cells, not enclosed in a paper envelope. Recent research pertaining to the chemical ecology of *Polistes* wasps (Post and Jeanne 1981; Post et. al. 1984) has revealed effective defenses of the exposed brood comb, for example, by application of glandular secretions to the nest pedicel.

Colonies attain their largest size by mid- to late summer and typically decline before fall. Most colonies contain from 25 to 75 workers at their peak, and most mature nests possess 50 to 100 cells, although larger colony and nest size occurs. Nest architecture varies somewhat among species, and may be influenced by constraints of the nest site. In contrast to nests of the Vespinae, *Polistes* nests do not contain special, much larger cells in which queen larvae are reared. Accordingly, except early in the seasonal cycle when *Polistes* workers may be tiny, conspecific queens and workers are similar in size.

Polistes are noted for predation on caterpillars, but additional insect prey are captured. Workers do not collect flesh from carcasses and do not scavenge human foods; therefore, they rarely are pests at outdoor gatherings. Large concentrations of *Polistes* sometimes occur around tall trees or tall structures, but the vast majority are males gathering at these prominent points to which females also are attracted, a behavior that facilitates mating.

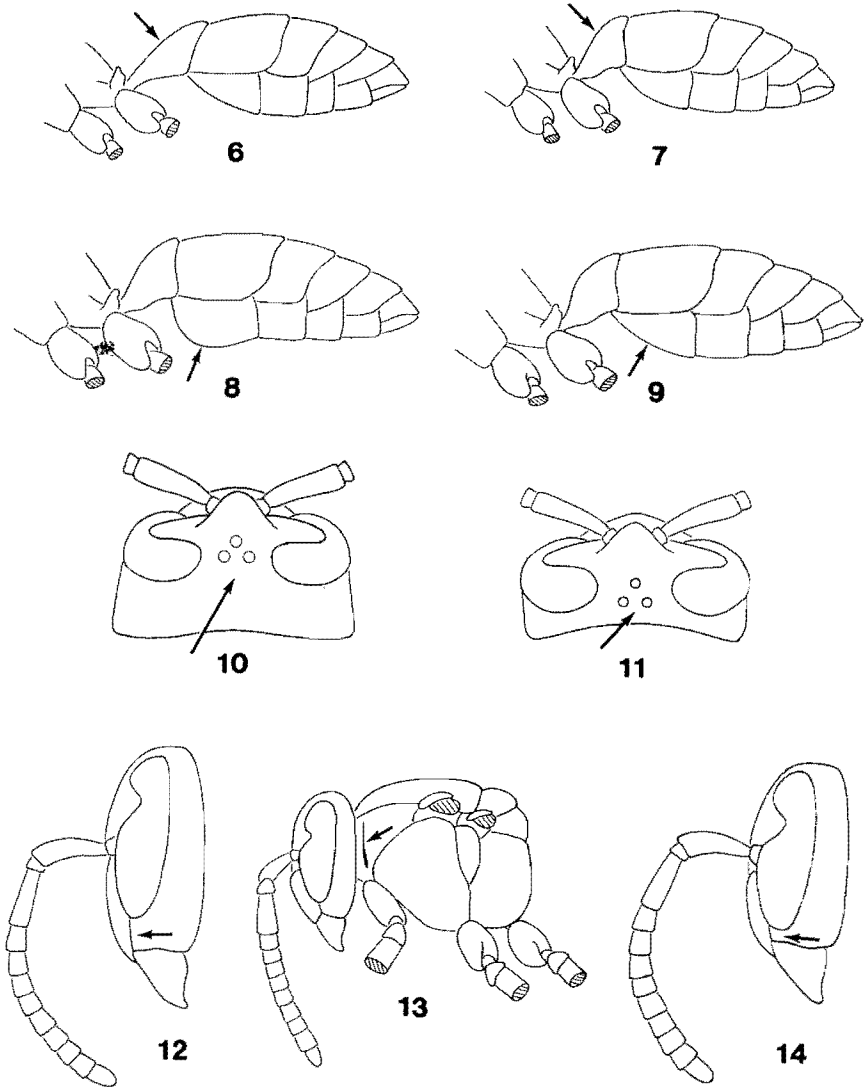
Key to *Polistes* females (unless stated otherwise, species are widely distributed in Indiana)

1. Gastral tergum 1 longer than broad posteriorly, sloping upward gradually behind the propodeum (fig. 6) (subgenus *Aphanilopterus* Muenier) 2
- 1'. Gastral tergum 1 broader posteriorly than long, sloping steeply upward behind the propodeum (fig. 7) (subgenus *Fuscopolistes* Richards) 3
2. Large, dark wasps (female forewing length 20-25mm); gastral tergum 1 mahogany to nearly black with a yellow band distally, remainder of gaster nearly black or with brown patches on tergum 2; thorax mahogany to nearly black with sutural lines; propodeum without yellow longitudinal stripes; central and southern Indiana *P. annularis* (L.)
- 2'. Small, light colored wasps (female forewing length 12-15mm); background color light reddish-brown with extensive yellow and some black; propodeum with 4 yellow, longitudinal stripes; southern and southwestern Indiana *P. exclamans* (Viereck)
3. Head, thorax, propodeum, and gaster concolorous orange to brownish-orange (mesonotum may possess some black); wings purple-black, occasionally lighter; large wasps (female forewing length 20-22mm) 4
- 3'. Head, thorax propodeum, and gaster typically with areas of brown, black, and yellow; if nearly concolorous, body is black, dark brownish, or mahogany, not orange or brownish-orange; wing pigmentation and body size variable 5
4. Oculomalar space and gena mat (not shiny), both areas densely covered with minute punctures within a field of larger pits; central and southern Indiana *P. perplexus* Cresson
- 4'. Oculomalar space appearing shiny against a background of larger pits (due to absence of minute punctures), and contrasting with the mat gena (due to possession



Figures 2-5. (2) Lateral view of a polistine wasp. (3) lateral view of a vespine wasp, (4) frontal view of a polistine head, (5) frontal view of a vespine head.

- of minute punctures within a field of larger pits); extreme southern Indiana *P. carolinus* (L.)
- 5. Thorax and gaster primarily black, without mahogany patches; if present, yellow markings restricted to faint band distally on gastral tergum 2 and/or faint longitudinal stripes on propodeum. *P. fuscatus* (Fab.), in part
- 5'. Thorax and gaster with conspicuous areas of mahogany and/or yellow 6
- 6. Yellow markings prominent, at least as distal bands on gastral terga; gastral tergum 2 may possess lateral yellow spots; broad, yellow, longitudinal stripes on propodeum 7
- 6'. Yellow markings lacking or, if present, much less extensive than above; gastral tergum 2 without lateral yellow spots, but may possess yellow transverse band distally; propodeum without yellow or, at most, with faint longitudinal stripes 8



Figures 6-14. (6) Lateral view of *Polistes (Aphanilopterus)* gaster, (7) lateral view of *Polistes (Fuscopolistes)* gaster, (8) lateral view of *P. metricus* gaster, (9) lateral view of *P. fuscatus* gaster, (10) dorsal view of *Vespa crabro* head, (11) dorsal view of *Dolichovespula* and *Vespula* head. (12) lateral view of *Dolichovespula* head, (13) lateral view of *Dolichovespula* thorax. (14) lateral view of *Vespula* head.

7. Relatively large wasps (female forewing length 13-18mm); coxae with prominent patches of yellow*P. fuscatus* (Fab.), in part

- 7'. Small wasps (female forewing length 10-14mm); coxae without yellow (typically concolorous black, but may possess mahogany); extreme southern Indiana *P. dorsalis* (Fab.)
8. Gastral sternum 2 with prominent bulge in lateral view (fig. 8); thorax extensively mahogany; mesoscutum completely mahogany, or black with 2 broad mahogany stripes; gaster largely black, but terga 1 and/or 2 may have lateral mahogany patches; yellow markings lacking, or restricted to faint, narrow distal band on gastral tergum 1; propodeum mostly mahogany and lacking yellow stripes. *P. metricus* Say
- 8'. Gastral sternum 2 lacking a prominent bulge in lateral view (fig. 9); thorax largely black, with some mahogany on pronotum and scutellum; mesoscutum black, but may possess 2 mahogany stripes; gaster largely black with large mahogany patches laterally on tergum 2; yellow, if present, limited to narrow band distally on gastral terga; propodeum at most with faint yellow stripes . . . *P. fuscatus* (Fab.), in part

***Polistes annularis* (L.).** This species is readily recognized by its large size, mahogany and black color with yellow band on the 1st gastral tergum, and the contrasting lighter tips of the antennae. Chandler (1965) reported this species to be distributed throughout Indiana, but, if so, it is not common. For example, *P. annularis* almost never appears in student collections at Purdue University, and we have seen specimens only from extreme southern, southwestern, and westcentral Indiana.

Colonies of *P. annularis* have been found in association with trees and cliffs along rivers (see Richards, 1978; Scott Davis, pers. comm.). Other nesting sites include in shrubs and in artificial shelters associated with human structures. Colonies may attain much larger size than is true of other Indiana *Polistes*. Nests may reach 15-20 cm in diameter and contain nearly a thousand cells, attended by a few hundred workers (Krispyn and Hermann 1977; Richards 1978).

***Polistes exclamans* Viereck.** Relatively small, slender, and brightly colored with yellow and light reddish-brown, this species is easily recognized. It is known colloquially in the southeastern United States as the "guinea wasp." This species was reported by Chandler (1965) to be restricted to southern Indiana and along the Wabash River north to Vincennes, but two females were collected in Lafayette in June 1988.

Nests are small, about 200 cells or less, and on rare occasions may be situated such that the cells open more or less horizontally instead of downward (Richards 1978). Typical nesting sites include on eaves and support beams, and in artificial nest boxes.

***Polistes dorsalis* (Fab.).** Known previously as *P. fuscatus hunteri*, this species was previously unknown in Indiana (Chandler 1965), and we have seen only a few specimens from along the Ohio River. Except for smaller size of most individuals, females are difficult to distinguish from the more yellow-marked specimens of *P. fuscatus* (the color form previously called *P. fuscatus variatus*). The most reliable character for distinguishing larger specimens of *P. dorsalis* from smaller specimens of xanthic *P. fuscatus* is the absence of yellow on the coxae of the *P. dorsalis*.

Few data are available, but Krispyn and Hermann (1977) report that *P. dorsalis* shuns human structures, using instead nest sites associated with the ground. Colonies in Florida (Mark Deyrup, unpubl. obs.) and Texas (Scott Davis, pers. comm.) are hidden in shrubs, while other authors report colonies suspended on eaves of structures (see Richards, 1978).

***Polistes carolinus* (L.) and *P. perplexus* Cresson.** Known colloquially as "red wasps", these two species are discussed together because of past confusion regarding identification. Both species are large, orange to brownish-orange, typically with purplish-black wings, and thus are easily distinguished from other Indiana *Polistes*. Snelling (1974) proposed morphological characters (see couplet 4) to separate adult *P. carolinus* (= *carolina*) and *P. perplexus*, and Nelson (1982) pointed out traits that separate larvae of these two species. Both species key to *P. rubiginosus* Lepeletier (a junior synonym of *P. carolinus*) in Chandler (1965). Most Indiana specimens are *P. perplexus*, which is distributed throughout all but the northern third of the state; *P. carolinus* may be present in extreme southwestern counties but we have seen no specimens.

Wade and Nelson (1978) provide some natural history data for both species and describe the somewhat confusing taxonomic history of each, which precludes assignment of older biological observations to either species. Most observations on *P. rubiginosus* refer to *P. perplexus*, but some undoubtedly apply to both *P. perplexus* and *P. carolinus*. Both species nest inside protected sites such as hollow logs and inside structures, but only *P. carolinus* also nests in open, exposed sites (Reed and Nelson 1985).

***Polistes fuscatus* (Fab.) complex.** The taxonomic status of the several named entities in the *P. fuscatus* complex is confusing and still undetermined (see Bequaert 1940, Krombein 1979, Richards 1978). Somewhat definable color patterns, occasionally associated with geographical distribution, constitute the primary basis for distinguishing the following named midwestern entities: *fuscatus*, *laurentianus*, *nestor*, *pallipes*, and *variatus*. Taxonomic treatment of these named entities, depending upon author, has ranged from valid species, to subspecies, to varieties, to color forms. However, most recent researchers consider *P. fuscatus* to be a polymorphic species, with several color forms that intergrade throughout its broad geographical range. Complicating identification further is the existence, in some parts of Indiana and southern Michigan, of darker specimens of *P. fuscatus* that are difficult to distinguish from *P. metricus*, as well as the previously mentioned problem, in southern Indiana, of separating some xanthic specimens of *P. fuscatus* from *P. dorsalis*.

Hypotheses to explain color variation among the color forms of *P. fuscatus* include environmental factors at the nest site (MacLean et al. 1978) and clinal variation, with more melanistic forms in the north and more xanthic forms in the south and west. The latter holds somewhat, but dark *P. fuscatus* are collected both in the southern states and in the upper Midwest, and xanthic specimens not uncommonly are found in northern Indiana. We possess data obtained from rearings that appear to negate the hypothesis of environmental control of coloration proposed by MacLean et al. (1978). In August 1981, we removed 211 (previously empty) beer and pop cans that had been partially filled with blood meal and attached to apple seedlings to serve as deer repellent. All cans were in a 20 h orchard, 5 km west of Purdue University, W. Lafayette, Indiana. Each can appeared to receive nearly identical sunlight and exposure to climatic elements. An active *Polistes* colony was found in 77 of these cans, and each nest was placed in a separate plastic rearing container or plastic bag; all emerged adults were collected and preserved in 70% ethyl alcohol for future study. Based on a cursory examination of the original adult population at time of collection, most colonies initially were designated "*P. fuscatus*", several as "*P. variatus*", and a few as "*P. pallipes*" or "*P. nestor*."

A given colony collected by us usually produced adults assignable to the originally designated color form. However, numerous colonies produced adults assignable to one or more other color forms and individuals fitting descriptions of nearly all color forms associated with *P. fuscatus* were produced by several colonies. These observations, of multiple *P. fuscatus* color forms produced from colonies developing under nearly identical environmental parameters, suggest that microclimate is not the critical factor contributing to *P. fuscatus* color variation. We conclude that *P. fuscatus*, in the upper Midwest at least, is a single, highly variable species with several recognizable color forms, none of which are valid species or even fit the subspecies concept. A likely explanation is that the appearance of man-made structures throughout the Midwest allowed isolated populations of *P. fuscatus* to expand, by taking advantage of the increase in permanent, sheltered nest sites, resulting in a situation that facilitated intergrading. In support of this hypothesis, at the northern, western and southern extremes of its range, *P. fuscatus* is more uniformly dark, xanthic, and reddish, respectively. An alternative hypothesis is that in the Midwest, but not elsewhere, natural selection strongly favors diversity in color pattern; this explanation, while not impossible, seems to us less likely.

Distributed throughout Indiana, *P. fuscatus* is our most abundant species of paper wasp. Nests commonly are associated with structures, with the most typical nesting site being eaves; however, nests are also found in open attics, in crawl spaces, behind fence panels and shutters, and occasionally in shrubs. Nests are not large, less than 10 cm in diameter,

and usually possess several pedicels serving as attachment to the substrate. The comb is rather symmetrical in form and in cell depth.

***Polistes metricus* Say.** This rather large, dark species is found throughout the state, but is more common from central Indiana southward. Coloration varies from nearly uniform mahogany with black gaster, to a more melanistic thorax with two well developed mahogany stripes on the mesonotum. Females of the latter coloration are difficult to separate from similar appearing *P. fuscatus*, as suggested above and in the key to *Polistes*. The prominent bulge on the second gastral sternum of *P. metricus* often helps to distinguish questionable females from similarly colored *P. fuscatus* females, but it is not totally reliable. Collection of nests and nest series of females and males is strongly recommended for accurate identifications.

Nests of *P. metricus* are reported from shrubs and from the interior of dark sheds and other out-buildings (see Richards 1978); rather unusual among Indiana *Polistes*, nests also may be attached to metallic surfaces. Nests are not large, usually less than 9 cm in diameter, and are suspended by a single, central pedicel. The comb appears somewhat asymmetrical, with some cells disproportionately deeper than others; thus, *P. metricus* nests, at least in Indiana, are usually distinct from nests of *P. fuscatus*.

Subfamily VESPINAE

Wasps in this subfamily include the familiar hornets and yellowjackets. Common names assigned within this subfamily often are misapplied, resulting in confusion (Greene and Caron 1980). Technically, only one species, *Vespa crabro* Christ (the European hornet), is a true hornet. All other vespines are yellowjackets, although one familiar species, *Dolichovespula maculata* (L.), is black and white, and known as the baldfaced or the whitefaced hornet.

In contrast to polistines, the vespine fauna is richer in species and more diverse biologically in cold climates. A number of species that may occur in extreme northern Indiana are absent in the central and southern parts of the state. Two species accidentally introduced from Europe onto the east coast are now well established in Indiana. The European hornet, *Vespa crabro*, occurs throughout the state, while the German yellowjacket, *Vespula germanica* (Fab.), often exists in high densities in urbanized areas in all but the southern third of Indiana.

Vespine wasps construct nests of multiple combs enclosed within a paper envelope. *Vespa crabro* and all *Vespula* species nest inside well protected sites, whereas *Dolichovespula* species typically nest in exposed sites, suspending their nests in trees, in shrubs, or on structures.

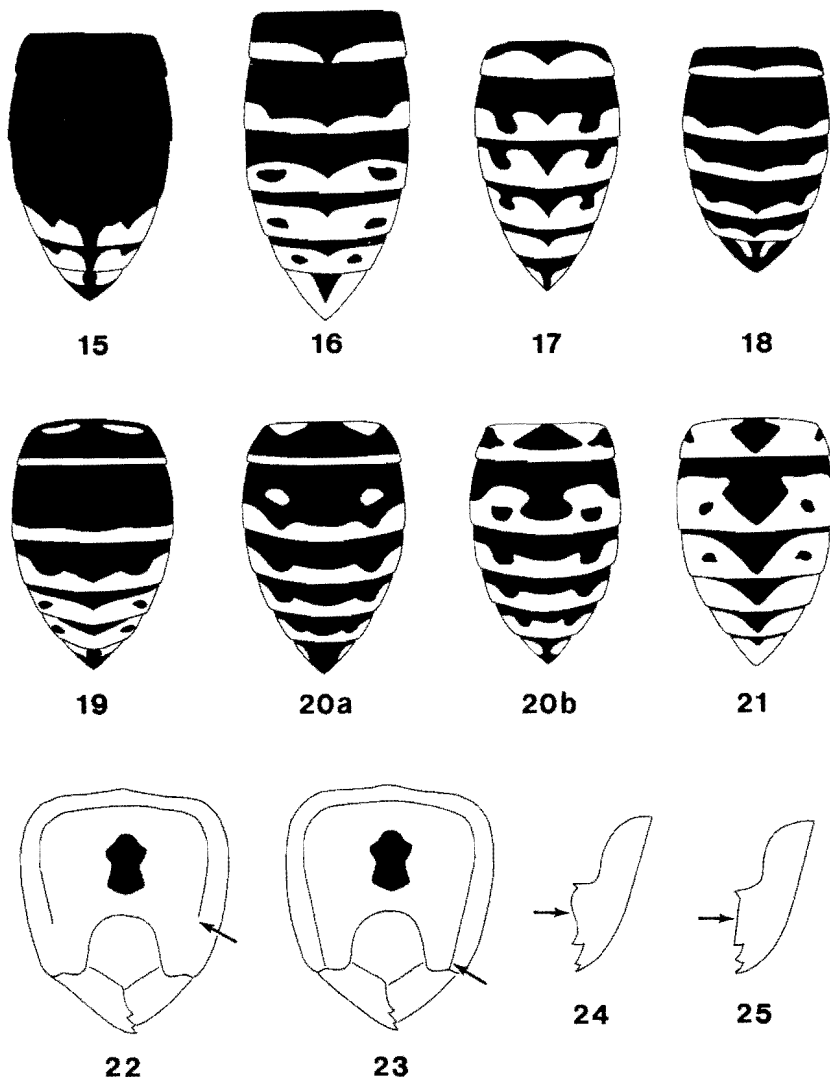
A vespine colony is initiated by a lone, overwintered queen, usually around the first of May. Seasonal duration and size of colonies vary depending on species, but colonies persist much later and attain much greater size than those of *Polistes*. In addition, vespines construct two sizes of cells, relatively small cells in which workers and eventually males are reared, and much larger cells in which queens and some males are reared. Accordingly, substantial size difference exists between conspecific queens and workers, especially among *Vespula* species.

Vespines capture a variety of arthropod prey, most of which consists of insects and, to a lesser extent, spiders. In addition to capturing live prey, workers of some species of *Vespula* scavenge for flesh from carcasses and from meats eaten by humans. Carbohydrate sources include nectar, sap honeydew, and various sweets eaten by humans. Synthetic lures such as heptyl butyrate are attractive in varying degrees to *Vespula* species, but not to *Vespa crabro* and *Dolichovespula* species (see Akre et al. 1981).

Vespine workers aggressively defend their nests, and some species possess venom that induces serious systemic reactions in hypersensitive people. The most dangerous stingers appear to be certain species of yellowjackets, more precisely those in the *V. vulgaris* (L.) species group (= *Paravespula* of some authors).

Key to Vespinae (unless noted otherwise, species are widely distributed in Indiana)

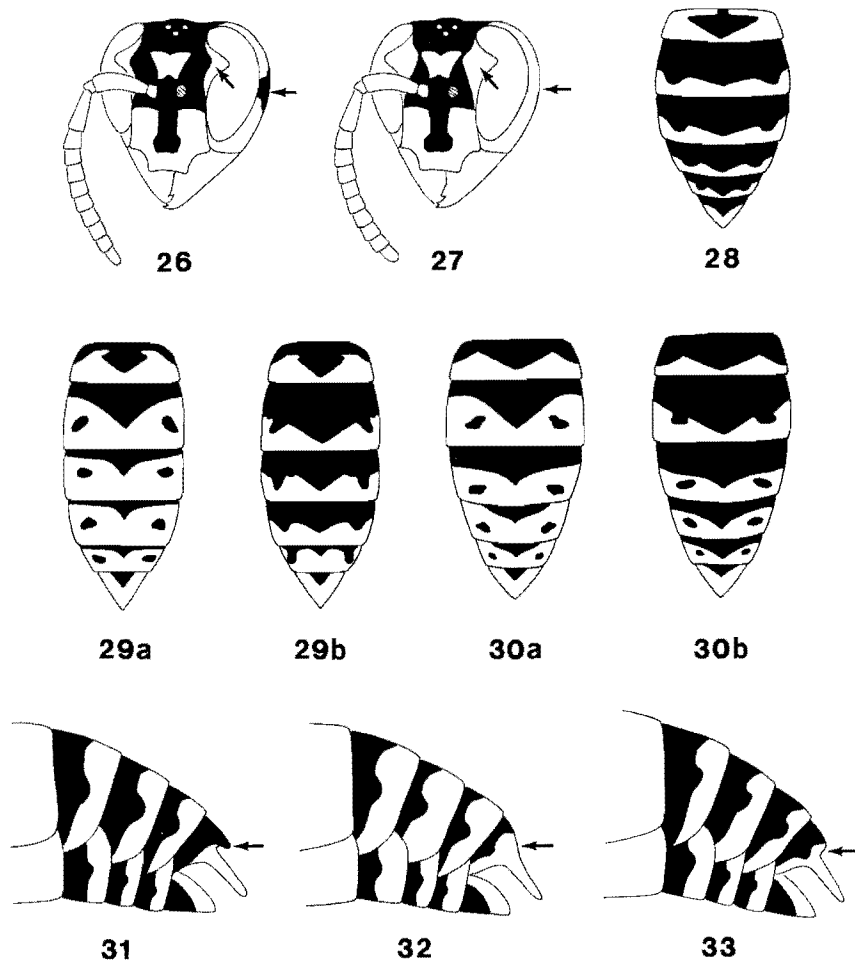
1. Very large (worker forewing length 20-22mm), brown and yellow wasps; vertex expanded behind the compound eyes, with distance between lateral ocelli and occipital carina greater than distance between the lateral ocelli (fig. 10) (European hornet) *Vespa crabro* Christ
- 1'. Smaller wasps with either yellow or whitish markings on a black background; vertex only slightly expanded behind the compound eyes, with distance between the lateral ocelli and occipital carina about equal to distance between lateral ocelli (fig. 11) 2
2. Oculomalar space long (fig. 12), distance between base of mandible and bottom of compound eye greater than diameter of an antenna; vertical carina on pronotum well developed (fig. 13); nest typically in vegetation or on structures *Dolichovespula* Rohwer 3
- 2'. Oculomalar space short (fig. 14), distance between base of mandible and bottom of compound eye less than diameter of an antenna; vertical carina on pronotum lacking or only faintly developed; nest underground or in an enclosed site *Vespula* Thomson 6
3. Pale markings white or (rarely) yellowish-white 4
- 3'. Pale markings distinctly yellow 5
4. Gastral terga 1, 2, and usually 3, entirely black; terminal gastral terga largely white or ivory (fig. 15); moderately large wasps (worker forewing length 12-16 mm) (baldfaced hornet) *D. maculata* (L.)
- 4'. All gastral terga with white or yellowish-white distal bands (fig. 16); smaller wasps (queen forewing length 12-13 mm); if present in Indiana, this social parasite species will be associated with nests of its host, *D. arenaria* (Fab.) *D. arctica* Rohwer
5. Distal yellow bands on at least gastral terga 1 and 2 deeply incised medially by black (fig. 17); gena with continuous yellow band, uninterrupted by black; clypeus with small black spot medially (aerial yellowjacket) *D. arenaria* (Fab.)
- 5'. Distal yellow bands on gastral terga 1 and 2 continuous, not deeply incised medially by black (fig. 18); gena largely black with yellow dorsally and ventrally; clypeus with elongate, black maculation medially; if present, in extreme northern Indiana *D. norvegicoides* (Sladen)
6. Mesoscutum with 2 complete longitudinal stripes; queen orange and black, in contrast to yellow and black workers and males (southern yellowjacket) *V. squamosa* (Drury)
- 6'. Mesoscutum entirely black, occasionally with 2 incomplete, longitudinal stripes arising from the posterior margin; queens, workers, and males similar in coloration 7
7. Pale markings whitish or ivory (similar to the baldfaced hornet); if present, in extreme northern Indiana (blackjacket) *V. consobrina* (Saussure)
- 7'. Pale markings distinctly yellow 8
8. Scape (basal antennal segment) yellow on ventral surface; occipital carina incomplete ventrally (fig. 22) (*V. rufa* (L.) species group, in part) 9
- 8'. Scape entirely black; occipital carina complete, typically reaching base of mandible (fig. 23), but may be incomplete ventrally in some males (*V. vulgaris* species group) 10
9. Gastral tergum 2 black with narrow, yellow band distally, gastral terga 4 and 5 with "free" black spots laterally (fig. 19); gena largely yellow with small to prominent black interruption medially; clypeus usually with 3 black spots medially; gaster relatively hairless *V. vidua* (Saussure)
- 9'. Gastral tergum 2 typically with 2 lateral yellow spots enclosed within the black basal band, gastral terga 4 and 5 lacking "free" black spots laterally (fig. 20a);



Figures 15–25. Dorsal views of the gaster are shown for figs. 15–21:(15)*D. maculata*, (16)*D. arctica*, (17)*D. arenaria*, (18)*D. norvegicoides*, (19)*V. vidua*, (20a)*V. acadica*, (20b)*V. acadica* (xanthic form), (21)*V. germanica*, (22) posterior view of *Vespula rufa* group head, (23) posterior view of *Vespula vulgaris* group head, (24) anterior view of left mandible of *V. germanica* female, (25) anterior view of left mandible of *V. maculifrons* female.

occasionally, gastral tergum 2 resembles that of *V. vidua* (fig. 19), or the 2 lateral yellow spots are not fully enclosed in the black basal band (fig. 20b); gena largely black with ventral and dorsal yellow patches; clypeus usually with one prominent

- black maculation medially; gaster hairy; if present, in extreme northern Indiana *V. acadica* (Sladen)
- 9''. Coloration similar to *V. acadica*, but posterior surface of hind tibia with a row of long hairs, which all other *Vespula* lack; if present, in extreme northern Indiana *V. austriaca* (Panzer)
10. Antennal flagellum (that portion distal to the scape and pedicel) with 10 articles; 6 visible abdominal sterna; abdomen ending in a sting (may be retracted and not visible) (females) 11
- 10'. Antennal flagellum with 11 articles; 7 visible abdominal sterna; abdomen elongate and ending in a large genital capsule with paired claspers (may be retracted and not visible) (males) 14
11. Basal tooth (3rd from tip) of mandible distinctly concave along medial (cutting) surface (fig. 24); medial black maculation on gastral tergum 2 usually longer than wide and arising from a black, basal band that is nearly parallel-sided (fig. 21); gastral color pattern occasionally like that of *V. flavopilosa* Jacobson (fig. 29a) (*German yellowjacket*) *V. germanica* (Fab.)
- 11'. Basal tooth (3rd from tip) of mandible straight or, at most, slightly concave along medial (cutting) surface (fig. 25) (the latter trait seen in some *V. flavopilosa* workers); gastral maculations variable, but not as in fig. 21 12
12. Yellow genal band with black interruption medially, varying from a small spot to a broad patch of black; yellow of ocular sinus concave medially (penetrated by black), separated from corona by a distance greater than diameter of an ocellus (fig. 26); worker maculation on gastral tergum 1 variable, but usually resembling that of *V. flavopilosa* (fig. 29b); queen gastral maculation nearly identical to *V. flavopilosa* queens (figs. 30a,b); extreme northern Indiana *V. vulgaris* (L.)
- 12'. Yellow genal band continuous, uninterrupted by black; yellow of ocular sinus not penetrated by black, separated from corona by a distance less than diameter of an ocellus (fig. 27) 13
13. Medial, black maculation on gastral tergum 1 arising as a narrow stalk, and typically resembling a broad arrowhead (fig. 28) (*eastern yellowjacket*) *V. maculifrons* (Buysson)
- 13'. Medial, black maculation on gastral tergum 1 broadly attached to anterior margin, not arising as a narrow stalk (figs. 29a,b); gastral tergum 1 of queen similar in maculation to that of most *V. vulgaris* queens (figs. 30a,b) *V. flavopilosa* Jacobson
14. Gastral tergum 7 with a strongly concave union of basal portion and flat apical portion (fig. 31); gastral maculations usually like that of conspecific workers (fig. 28), but melanistic specimens resemble *V. flavopilosa* (fig. 29b) (*eastern yellowjacket*) *V. maculifrons*
- 14'. Gastral tergum 7 with a gradual union of basal portion and flat apical portion, producing a "duck bill" appearance in lateral view (figs. 32, 33) 15
15. Yellow of ocular sinus concave medially (penetrated by black), separated from corona by distance greater than diameter of an ocellus (fig. 26); yellow genal band usually narrowed medially by encroachment of black; gastral maculations resemble those of *V. flavopilosa* (fig. 29b); extreme northern Indiana *V. vulgaris* (L.)
- 15'. Yellow of ocular sinus not penetrated by black, separated from corona by distance less than diameter of an ocellus (fig. 27); yellow genal band uninterrupted by black 16
16. Gastral tergum 7 with very smooth union of basal and flat apical portions (fig. 32); gastral maculation either like conspecific females (fig. 21), or resembling that of some *V. flavopilosa* specimens (fig. 29b); gaster with dark hair *V. germanica* (Fab.)
- 16'. Gastral tergum 7 with abrupt union of basal and flat apical portions (fig. 33); gastral maculation resembling that of most conspecific workers (fig. 29b); gaster with rather long, yellowish hair *V. flavopilosa* Jacobson



Figures 26–33. (26)Anterior-lateral view of *V. vulgaris* head, (27) anterior-lateral view of *V. flavopilosa* head; dorsal views of the gaster are shown for Figs. 28–30b: (28)*V. maculifrons* (29a)*V. flavopilosa* (worker), (29b)*V. flavopilosa* (melanistic worker), (30a)*V. flavopilosa* (queen), (30b)*V. flavopilosa* (melanistic queen); Figs. 31–33 are lateral views of male gasters, terminalia are deleted: (31)*V. maculifrons*, (32)*V. germanica*, (33)*V. flavopilosa*.

***Vespa crabro* Christ.** Our largest social wasp, this brown and yellow species has the official common name of European hornet, but is also known as the “giant hornet.” Introduced into the New York city area around 1850, this species has spread over much of eastern North America (Akre et al. 1981). Chandler (1965) reported *V. crabro* to be restricted to southern Indiana, but within the past several years numerous specimens and several colonies have been discovered in central Indiana, including colonies reported by citizens from Marion, Tippecanoe and Carroll counties.

The large, variegated brownish nest usually is situated inside hollow trees or logs, but

nests are also found inside attics, hay lofts, and abandoned bee hives. A large colony at its peak in late summer may contain 500-700 workers associated with a nest of 2000-3000 cells arranged in 6-9 combs.

Although well studied in Europe (Spradbery 1973), little is known about *V. crabro* biology in this country (Akre et al. 1981). Workers capture a variety of insects, including prey much larger than is taken by other vespines; for example, large horse flies and other social wasps are included in prey records. An apiary pest in Europe, hive depredation by *V. crabro* is unreported in North America. Interestingly, unlike nearly all temperate social wasps, *V. crabro* workers may be active on moonlit nights and specimens have been taken at lighted windows.

Previously considered an uncommon inhabitant of undisturbed eastern hardwood forests, the European hornet apparently is becoming more common in areas of human activity. For example, workers have become significant pests in southern Indiana apple orchards, not only by intimidating pickers but also by severely damaging ripening fruit. Workers may also become pests when imbibing juices from piles of fruit and at cider presses, and by girdling twigs as they collect fibers for nest construction.

Dolichovespula Rohwer

Formerly treated as a subgenus of *Vespula*, Carpenter (1987), based on phylogenetic analysis, and Greene et al. (1976), based on morphology, physiology, and behavior, provide ample evidence to support elevation of *Dolichovespula* to generic status. Diverging from treatment in the Hymenoptera catalog (Krombein 1979), we follow Carpenter (1987) and Greene et al. (1976) and treat *Dolichovespula* as a separate genus, not a subgenus of *Vespula*. Akre et al. (1981) reviews the biology of Nearctic species.

Dolichovespula nests usually are situated in exposed sites, being suspended in trees or shrubs, or from sides and eaves of structures. However, one species (*D. arenaria*) tends to nest in tall grass just above ground in western North Carolina (unpubl. obs.) and occasional subterranean nesting has been reported for two species in the Pacific northwest (Greene et al. 1976). The variegated grey envelope is arranged in laminar sheets, but scalloping patterns may occur on top of some nests. Quite resistant to wind and rain, the structure may persist over winter if sheltered, but will not be reused the following season.

Dolichovespula colonies are founded by a lone queen around the first of May and the seasonal cycle normally is completed by late August to mid-September. Peak worker populations of less than a hundred to several hundred occur by mid-summer, associated with a nest of several hundred to a few thousand cells arranged in 3-6 combs.

Predacious on a variety of insects, especially flies, *Dolichovespula* workers only rarely scavenge flesh from carcasses. They do not forage on meats eaten by humans and are not part of the complex of yellowjacket species that become pestiferous scavengers in late summer and fall. However, workers do imbibe fruit juices and may become pests at cider presses.

***Dolichovespula arctica* Rohwer.** Unreported from Indiana, this species is found across Canada, extreme northern United States and southward at higher elevations of the Appalachians, the Rockies and mountain ranges of the west coast. It is included here because one of its primary hosts, *D. arenaria*, is found in Indiana. One of only a few known obligate socially parasitic wasps, *D. arctica* lacks a worker caste and relies on host workers to rear its young. Excellent biological accounts are given by Evans (1975), Greene et al. (1978), and Jeanne (1977). People discovering a parasitized *D. arenaria* colony will recognize the social parasite by its whitish markings, in contrast to the bright yellow markings of its host.

***Dolichovespula arenaria* (Fab.).** Known officially as the aerial yellowjacket, this species closely resembles most ground-nesting yellowjackets in coloration. However, the long oculomalar space and well developed pronotal carina distinguishes *D. arenaria* from yellowjackets in the genus *Vespula*. Considered rare and restricted to extreme northern Indiana (Chandler 1965), *D. arenaria* appears to be expanding its range. For example, we

collected numerous *D. arenaria* workers in Clark State Forest in southcentral Indiana in 1981 and five colonies were found in 1985, three in Indianapolis, one in Bloomington and one in Lafayette.

Based on an excellent study in Washington state (Greene et al. 1976) and our data from colonies studied in western North Carolina, *D. arenaria* nests are suspended in trees, shrubs, or just above ground in clumps of tall grass. Structural nests are found on eaves and hanging from roofs of picnic sheds and open barns. Subterranean colonies are not uncommon in the mountains of Oregon and Washington (Green et al. 1976), but are unreported elsewhere. The three colonies in Indianapolis were built on houses and the one in Lafayette suspended just above ground in a spruce tree.

Seasonal duration and size of colonies appears to vary geographically and annually in the Pacific northwest. Initiated in late April or early May, colonies normally complete their seasonal cycle by late August. Mature colonies in North Carolina were quite small in late August, with fewer than a hundred workers associated with a nest of several hundred cells. Greene et al. (1976) reported large size variation in the Pacific Northwest, but most nests were relatively small with 300-1500 cells, with the largest colonies containing about 700 workers with nests of 4000 or more cells.

Workers do not forage at picnic tables, but may be nuisances since they tend to fly about the heads of people. Quite responsive to nest disturbance, *D. arenaria* colonies constitute a serious stinging threat when located on or around human dwellings (Akre et al. 1981).

***Dolichovespula maculata* (L.).** Perhaps the most familiar of North America social wasps, this relatively large, black and white species is known officially as the baldfaced hornet. It is widely distributed over North America, being found throughout the eastern United States, most of Alaska and Canada, and the mountains of the western United States. See Akre et al. (1981) for a review of the natural history of this species.

Occurring throughout Indiana, *D. maculata* is among the most common wasps in many areas. Around Lafayette, Indiana in 1977 for example, *D. maculata* comprised nearly 34% (29/85) of vespine colonies collected, and 17% (109/637) of vespines captured in Malaise traps from 1977-1980.

The large, grey nest of the baldfaced hornet is one of the best known insect structures, and representatives adorn most nature exhibits and many cabins and rustic restaurants. Around Lafayette, nearly 2/3 of the nests are arboreal and often situated high in trees; the remainder are suspended from eaves, against windows or walls, and from power pole transformers. Nests seem large, up to 40 cm in circumference and 670 cm long, but much of the structure is insulating envelope paper. Mature colonies in late summer typically consist of 200-500 workers associated with a nest of 1000-2000 cells, with the largest colony, collected 8 Sept 1978, containing 771 workers and 3300 cells. Colonies are initiated in early May, but usually are not noticed until mid-summer or later. Most complete their cycle by late September, but some remain active well into October.

Baldfaced hornet workers capture a variety of insect prey, including workers of other yellowjacket species, but seem particularly adept at capturing adult flies. Workers commonly may be seen taking blow flies (Calliphoridae) at garbage cans. We observed marked workers returning to dog feces over a period of several days and capturing various "filth" flies (Calliphoridae, Muscidae, Sarcophagidae, etc.); one worker took up to 17 flies per hour.

Although known to occasionally scavenge flesh from carcasses, *D. maculata* workers typically do not forage on meats eaten by humans. However, workers do imbibe fruit juices and can be pests at cider presses.

***Dolichovespula norvegicoides* (Sladen).** Closely resembling *D. arenaria*, this species has not been reported in Indiana and most likely is not found south of the Great Lakes. It appears to possess a similar but somewhat more restricted distribution than the social parasite *D. arctica*. Little is known of its natural history, but it serves as a host for *D. arctica*, forms relatively small colonies, and nests low in vegetation or partially underground (Akre et al. 1981, Akre and Bleicher 1985).

Vespula Thomson

Six species represent this genus in Indiana, and 3 additional species might occur in extreme northern Indiana. As originally proposed by Bequaert (1932) and recently shown by Carpenter (1987), *Vespula* species may be treated as belonging to two species groups, the *V. rufa* group or the *V. vulgaris* group. Except for *V. squamosa*, colonies of the *V. rufa* group are much smaller, possess a substantially shorter seasonal cycle, and their nest structure differs from that of *V. vulgaris* group nests in a number of parameters (see Akre et al. 1981). Unlike species of the *V. rufa* group (*V. squamosa* is an exception), workers of the *V. vulgaris* group, in addition to taking live prey, scavenge readily for flesh from carcasses and forage on meats eaten by humans.

Vespula nests typically are situated in well protected sites, usually underground but occasionally inside fallen trees and tree stumps (see Akre et al., 1981). However, increasing numbers of colonies are being found inside structures, and the introduced German yellowjacket, *V. germanica*, is primarily a structural nester in North America (MacDonald et al. 1980a). An occasional *Vespula* nest is found in completely exposed sites such as on the eaves of a house, or other unusual locations.

Except for *V. squamosa*, nests of the *V. rufa* group contain only one comb of small cells in which workers and some males are reared; subsequent combs consist of much larger cells in which queens and some males are reared. Nest envelope consists of a pliable, variegated grey paper arranged in a laminar structure. Except for many *V. squamosa* colonies that may persist later and attain much larger size, *V. rufa* group colonies reach their peak by mid-summer and complete their cycle by early September. At their peak, colonies contain from 75-400 workers associated with nests of several hundred to 2500 cells arranged in 2-5 combs (see Akre et al. 1981).

Nests of the *V. vulgaris* group contain multiple combs of small cells, initially rearing workers and later males. Nest envelope paper is either brittle and variegated grey or fragile and variegated tannish-orange; both types of envelope paper assume a scalloped appearance. Colonies reach their peak in late summer-early fall and may remain viable well into November. At their peak, colonies contain from 1000-3500 workers associated with nests of 3500-10,000 cells arranged in 4-10 combs (see Akre et al., 1981).

Vespula acadica (Sladen), *V. consobrina* (Saussure), and *V. austriaca* (Panzer). All three species are distributed across Canada, extreme northern United States, and southward at higher elevations of western mountains, with *V. consobrina* also found in the Appalachians as far south as northern Georgia. *Vespula acadica* and *V. austriaca* are characteristic appearing yellowjackets, but *V. consobrina*, the black-jacket, could be mistaken at first glance for a small baldfaced hornet. Unreported from Indiana, these species are not likely to be collected even in extreme northern counties.

According to Akre et al. (1981), and Reed and Akre (1983a), *V. acadica* nests in soil or in logs and stumps, with colonies consisting of 75-400 workers and a nest of 400-2500 cells. Based on Akre et al. (1981), Akre et al. (1982), and MacDonald and Matthews (1976), *V. consobrina* colonies usually are subterranean and relatively small, consisting of 300-1400 cells and probably containing about 200 workers at their peak. *Vespula austriaca* is an obligate social parasite of *V. acadica*, whose interesting biology has been worked out by Reed and Akre (1983b, c).

Vespula vidua (Saussure). This species is restricted to the upper Midwest, the Northeast and extreme southeastern Canada, and southward along the Appalachians into northern Georgia. Previously reported only from northern Indiana, where it is quite common in the sandy soils in Christmas tree plantings in La Porte country (Chandler 1965), *V. vidua* workers were collected by us in Clark State Forest in southcentral Indiana and in Yellowwood State Forest just east of Bloomington in central Indiana. An occasional specimen has been collected in Tippecanoe county and several queens have been taken by us in heptyl butyrate traps in W. Lafayette.

Comparatively melanistic, this species might be confused with darker specimens of *V. acadica*, and one usually must employ several key characters to separate them. No

colonies have been reported in Indiana, but *V. vidua* is a subterranean nester in the southeast (MacDonald and Matthews 1976) and in the northeast, where it also nests inside wall voids and fallen trees (Akre et al. 1981). Colonies normally end their seasonal cycle by mid-September, and the largest one contained over 350 workers associated with a nest of nearly 2500 cells.

***Vespula flavopilosa* Jacobson.** Recognized and described as a new species relatively recently (Jacobson et al. 1978), *V. flavopilosa* previously has been identified as either *V. vulgaris* or *V. maculifrons*, or considered a "hybrid" of the latter two species. The North American distribution of *V. flavopilosa* is similar to that of *V. vidua*; *V. flavopilosa* probably occurs throughout Indiana, but has not yet been collected in the southwest. We have collected numerous queens and workers from extreme northeastern Indiana, throughout central Indiana and from southcentral Indiana. Relatively common around Lafayette, *V. flavopilosa* comprised over 18% (117/637) of the vespines collected in Malaise traps from 1977-1980.

Key characters separate nearly all females of *V. flavopilosa* from *V. maculifrons* and *V. vulgaris*, but occasional workers are difficult to distinguish from *V. germanica* (the mandibular tooth trait is the best discriminator). Males of *V. flavopilosa*, *V. maculifrons*, and *V. vulgaris* may closely resemble one another, but characters used in the key facilitate identification of nearly all specimens. Some *V. flavopilosa* and some *V. germanica* males closely resemble one another and the key may seem unsatisfactory for separating certain specimens. Problem specimens can, however, be distinguished by examining male genitalia (see Jacobson et al. 1978).

Similar to nests of *V. vulgaris* and *V. maculifrons*, the nest of *V. flavopilosa* is constructed of fragile, variegated tannish-orange paper, and is strikingly distinct from the variegated grey nest of *V. germanica*. Predominantly a subterranean nester, *V. flavopilosa* also nests occasionally inside wall voids. At least in the southeast (MacDonald et al. 1980b), colonies reach maturity by late September and contain from 500-2000 workers associated with a nest of 2000-5000 cells.

Little is known about the behavior of *V. flavopilosa*, but workers scavenge flesh from carcasses and from meats eaten by humans, in addition to taking live insects.

***Vespula maculifrons* (Buysson).** Common over most of eastern United States and southeastern Canada, *V. maculifrons* is known officially as the eastern yellowjacket. This species is commonly collected throughout Indiana, but is particularly prevalent in hardwood forests, parks and other recreational areas. Over 56% (48/85) of the vespine colonies studied in the Lafayette, Indiana area in 1977 were *V. maculifrons*, and workers comprised nearly 60% (380/637) of the vespines collected in area Malaise traps from 1977-1980.

Most workers and queens are easily recognized by the characteristic arrowhead-shaped, black maculation on the first gastral tergite, with the narrow black stalk attaching it to the anterior border. Some males share the female maculation, but others closely resemble males of *V. flavopilosa* and/or *V. vulgaris*.

The eastern yellowjacket usually builds its fragile, tannish-orange nest in subterranean sites, but it is not uncommon to find nests in structural sites such as wall voids and attics (MacDonald and Matthews 1981). Of 71 colonies studied in the Lafayette area in 1977, 57 were subterranean, 11 inside wall voids, and 3 in exposed, above ground sites.

In Indiana, colonies reach their peak in late September to early October and may contain 1000-3000 workers associated with a nest of 5000-8000 cells. The nesting biology of *V. maculifrons* in the southeastern states was described in detail by MacDonald and Matthews (1981).

Workers scavenge flesh from carcasses and from meats eaten by humans. This habit, together with widespread distribution and often very high population densities in recreational and residential areas make the eastern yellowjacket one of our most important species.

***Vespula germanica* (Fab.).** Distributed over much of the world, this introduced species is found throughout the upper Midwest, the Northeast, and adjoining areas of southern Canada, with recently discovered pockets in Idaho, Washington, Oregon, and

California (MacDonald and Akre 1984). Apparently reaching eastern Indiana in the mid-1970's, this species was established in the Lafayette area in 1976 (MacDonald et al. 1980a). Our observations and various reports suggest that the German yellowjacket is common in nearly all urban areas of central and northern Indiana, but has not been found in the southern part of the state; the southernmost records are from the cities of Bloomington and Columbus.

Most specimens possess a distinctive color pattern, but more melanistic individuals may be confused with other species in the *V. vulgaris* group. As mentioned above, the "hooked" mandibular tooth of the females is the best discriminating character for workers and queens. Male genitalia (see Jacobson et al. 1978) and the variegated grey nest paper of the German yellowjacket are very distinct from other *V. vulgaris* group species in Indiana.

Previously considered almost exclusively a structural nester (MacDonald et al. 1980a), subterranean nesting has appeared in the German yellowjacket population, at least in central Indiana (MacDonald and Akre 1984). For example, whereas only 3/64 nests were subterranean in the Lafayette area from 1977-1981, nearly 38% (11/29) of the nests were situated in underground sites in 1982. Still, the propensity to build nests in such structural sites as wall voids, attics, and basements characterizes the German yellowjacket.

Seasonal duration and size varies, but *V. germanica* colonies in Indiana tend to persist later and attain greater size than those of other *V. vulgaris* group species. For example, viable colonies have been observed as late as early December in the Lafayette area although most appear to complete their cycle by early November. Typical colonies reach their peak in September-October, with a peak worker population of 2000-3000 associated with a nest of 5000-8500 cells. The largest colony, situated in a Frankfort, Indiana attic, consisted of 6500 workers and a nest of 17,000 cells when collected on 2 November 1979.

On account of its big population densities in urban and recreational areas, its structural nesting habits, and its scavenging workers, the German yellowjacket is our most significant pest species.

***Vespa vulgaris* (L.).** This Holarctic species is distributed across Canada, the upper Midwest, the Northeast, south along the Appalachians, and higher elevations of the west. Apparently restricted to extreme northern Indiana, this species is rarely encountered even there. However, specimens of *V. vulgaris* could easily be mistaken for *V. flavopilosa*, and mistakenly have been identified as *V. maculifrons* in museum collections.

Detailed study of this species in North America is lacking, but *V. vulgaris* is well studied in Europe (see Spradbery 1973 and Edwards 1980). This species is closely related to *V. maculifrons* and appears to be similar to the eastern yellowjacket in all aspects of its biology. According to Akre et al. (1981), *V. vulgaris* typically nests underground, but nests are also built in logs, stumps, and inside structural voids. Few *V. vulgaris* colonies have been studied, but those from the Pacific Northwest appear to be smaller (average nest size = 2100 cells; largest nest 4972 cells) than most colonies of the *V. vulgaris* group. Large colonies with several thousand workers and nests of over 15,000 cells are reported from California (Duncan 1939).

***Vespa squamosa* (Drury).** Distributed over most of the eastern United States, from the southern Great Lakes southward, the southern yellowjacket, as its official common name suggests, is most abundant in the Southeast and westward into Texas (MacDonald and Matthews 1984). This species is distributed statewide, but is much more common in southern Indiana.

One of the easiest eastern social wasps to recognize, *V. squamosa* possesses two complete longitudinal stripes on the mesonotum. Queens are different from other yellowjackets, as well as their conspecific workers and males, in being predominantly orange with black maculations. In fact, *V. squamosa* queens and workers originally were described as different species.

Long suspected of being a social parasite of *V. vidua*, and possibly other *Vespa*, the southern yellowjacket has been shown to be a social parasite of *V. maculifrons* in the southeast (MacDonald and Matthews 1975). Further study revealed that the socially parasitic relationship between these two species exists throughout their broadly overlap-

ping ranges and that *V. flavopilosa* may also serve as a host for *V. squamosa* (MacDonald and Matthews 1981, 1984). The southern yellowjacket is considered a facultative social parasite because at least some queens (approximately 20% in the Southeast) behave like other *Vespula* in starting their own colonies, whereas all queens of obligate social parasite species are incapable of initiating a colony and therefore must usurp an established colony of another species. Furthermore, *V. squamosa* possesses a worker caste, whereas obligate social parasites lack a worker caste and therefore must rely on a host species to rear the parasite's progeny.

In Indiana, *V. squamosa* queens typically usurp a host colony sometime in June, but later usurpations occur. About a month or so after usurpation, the first brood of *V. squamosa* workers emerge, having been reared by the host's workers. Eventually, as the unreplaced host workers die and the numbers of *V. squamosa* workers increase, the colony will assume all appearances of a southern yellowjacket colony. In such colonies excavated late in the season, one can discern the original host nest because its tannish-orange cells contrast strongly with the grey cells build by *V. squamosa* workers. Therefore, even when host workers are no longer present, the heritage of a mature *V. squamosa* colony can be determined.

Nesting biology of *V. squamosa* was described in detail by MacDonald and Matthews (1984). Most colonies are subterranean because most host colonies are, but structural colonies are not uncommon. In the southeast, a few mature colonies are relatively tiny (a few hundred cells), while others approach the size of *V. vulgaris* group colonies (1500-3000 workers associated with a nest of 6000-10,000 cells). Based on 11 colonies studied in Indiana (4 from Lafayette, 7 from Clark State Forest in southcentral Indiana), colony demise occurs by mid-September, and peak populations in late August consist of several hundred to a thousand or so workers associated with nests of 2000-5000 cells.

Southern yellowjacket workers are primarily predators, but workers occasionally scavenge flesh from meats eaten by humans. This species rarely is a pest at outdoor gatherings, but workers are strongly responsive to disturbances near their nest and tend to be aggressive in their defense of it.

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Voucher specimens from this study are deposited in the Purdue University Entomological collection and in our personal collections.

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