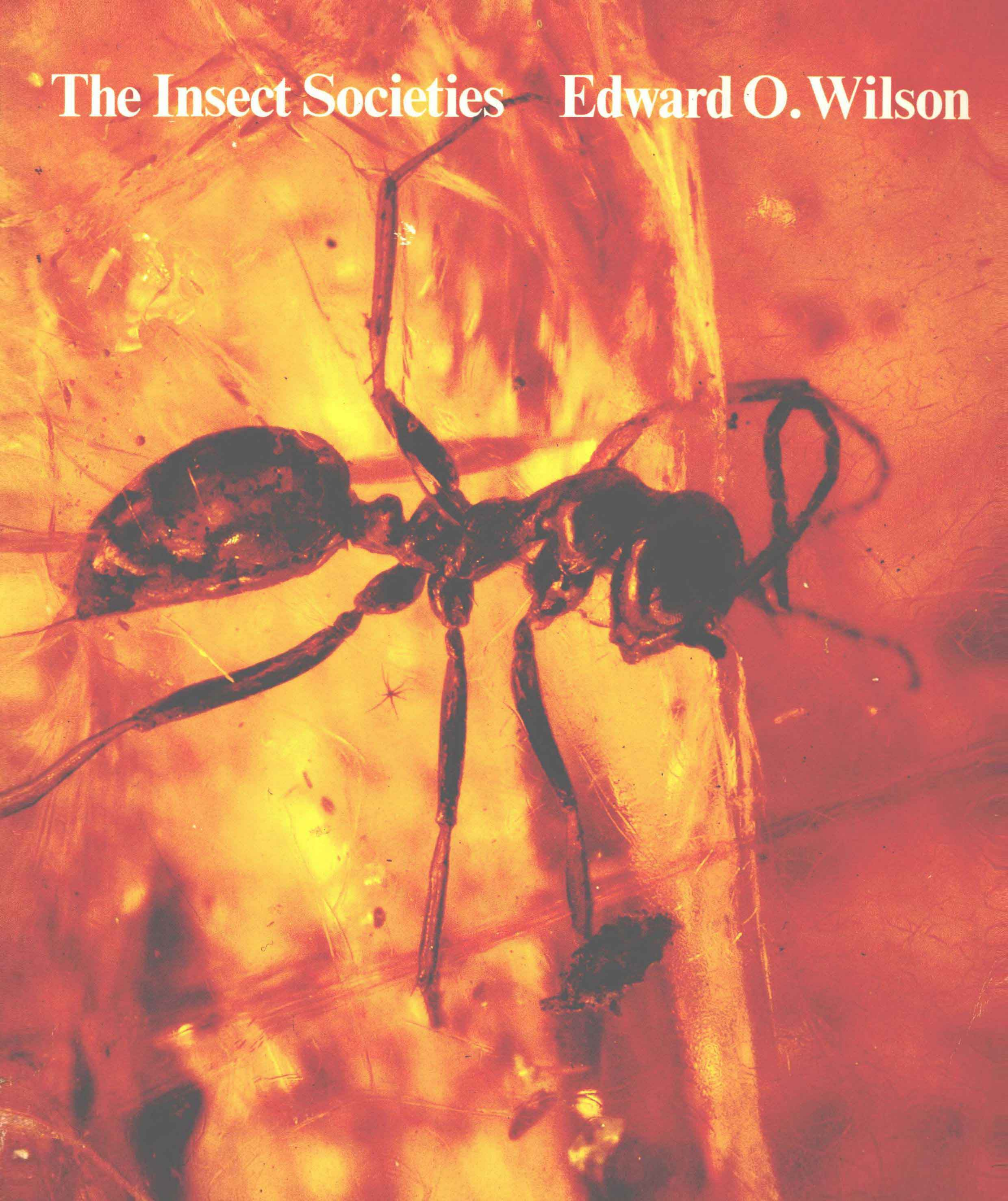
The Insect Societies

Edward O. Wilson



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Cover Illustration: A worker of *Sphecomyrma freyi*, the most primitive known ant species. Two specimens, including this one, were found in amber in a New Jersey deposit of mid-Cretaceous age. They provide a link between the tiphiid wasps and the most primitive known living ants (photograph courtesy of Frank M. Carpenter).

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For my wife Irene, who understands

Acknowledgments

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The Insect Societies

Contents

1 Introduction: The Importance of Social Insects

Why do we study these insects? Because, together with man, hummingbirds, and the bristlecone pine, they are among the great achievements of organic evolution. Their social organization—far less than man's because of the feeble intellect and absence of culture, of course, but far greater in respect to cohesion, caste specialization, and individual altruism—is nonpareil. The biologist is invited to consider insect societies because they best exemplify the full sweep of ascending levels of organization, from molecule to society. Among the tens of thousands of species of wasps, ants, bees, and termites, we witness the employment of social design to solve ecological problems ordinarily dealt with by single organisms. The insect colony is often called a superorganism because it displays so many social phenomena that are analogous to the physiological properties of organs and tissues. Yet the holistic properties of the superorganism stem in a straightforward behavioral way from the relatively crude repertories of individual colony members, and they can be dissected and understood much more easily than the molecular basis of physiology.

A second reason for singling out social insects is their ecological dominance on the land. In most parts of the earth ants in particular are among the principal predators of other invertebrates. Their colonies, rooted and perennial like woody plants, send out foragers which comb the terrain day and night. Their biomass and energy consumption exceed those of vertebrates in most terrestrial habitats. Social insects are especially prominent in the tropics. In the seventeenth century Portuguese settlers called ants the "king of Brazil," and later travelers referred to them with such phrases as "the actual owners of the Amazon Valley" and "the real conquerors of Brazil." Brazil, it was claimed, is "one great ants' nest." Similar impressions are invariably gained from other tropical countries. Ants in fact are so abundant that they replace earthworms as the chief earth movers in the tropics (Branner, 1910). Recent research has shown they are nearly as important as earthworms in cold temperate forests as well; in one locality in Massachusetts they bring 50 grams of soil to the surface per square yard each year and add one inch to the topsoil every 250 years (Lyford, 1963). Termites are among the chief decomposers of dead wood and such cellulose detritus as leaf litter and humus in the tropics, and they, too, contribute significantly to the turning of the soil.

When considering ecology, it is useful to think of an insect colony as a diffuse organism, weighing anywhere from less than a gram to as much as a kilogram and possessing from about a hundred to a million or more tiny mouths. It is an animal that forages ameba-like over fixed territories a few square meters in extent. A colony of the common European ant *Tetramorium caespitum,* for example, contains an average of about 10,000 workers who weigh 6.5 g in the aggregate and control 40 m^2 of ground (Brian *et al.,* 1967). The average colony of the American harvester ant *Pogonomyrmex badius* contains 5,000 workers who together weigh 40 g and patrol tens of square meters. The giant of all such "superorganisms" is a colony of the African driver ant *Anomma wilverthi,* which may contain as many as 22 million workers weighing a total of over 20 kg. During the statary phase of their cycle, columns of this species regularly patrol an area of between 40,000 and 50,000 m^2 in extent (Raignier and van Boven, 1955). When all of the resident ant populations are counted, the statistics are even more impressive. In Mary-land, a single population of the mound-building ant *Formica exsectoides* comprised 73 nests covering an area of 10 acres and containing approximately 12 million workers (Cory and Haviland, 1938). Since individual workers of this rather large species weigh 11.6 ± 0.13 mg (Dreyer, 1942), the total population weighed about 100 kg, and this was only one of many ant species inhabiting the same area, albeit the most abundant one. Termites have colonies of similar magnitudes, and in tropical habitats their populations approach densities comparable to those of ants. The savannas of Africa are dotted with great mounds of the fungus-growing macrotermitines, some 5 to 20 feet or more in height and containing 2 million workers. The mother of each colony is a grotesquely fattened queen weighing in excess of 10 g.

These superlatives can be made because of an adaptive radiation that took place for the most part between 50 and 100 million years ago in each of the major groups of social insects. In the social wasps, the ants, the social bees, and the termites, evolutionary convergence has resulted in the repeated appearance of the same basic design features: the systems of castes and labor roles changing according to age; the elaborate systems of chemical communication that typically include signals for alarm, recruitment, and recognition; the elaboration of nest structure to enhance temperature and humidity control; and others. One criterion of adaptive radiation that I use half seriously when thinking about evolution is: a group of species sharing common descent can be said to have truly radiated if one or more species is a specialized predator on the others. Ants have achieved this level with some distinction. Many of the army ants (subfamily Dorylinae) feed primarily on ants and other social insects, while all of the Cerapachyinae so far investigated feed entirely on ants. Among the bees, the meliponine *Lestrimelitta limao* specializes in robbing other meliponine species, while the large wasp *Vespa deusta* preys largely on colonies of the wasp genera *Ropalidia* and *Stenogaster.* Social parasitism, in which one species lives inside the nests of another and in some cases receives food and care unilaterally, occurs in all four of the major groups of social insects. It is tempting to speculate (and perhaps impossible to prove) that the social insects as a whole have employed all, or nearly all, of the social strategies permissible within the limits imposed by the arthropod brain and the peculiarities of their colonial system.

This book is an attempt to provide a modern synthesis of insect sociology. The last attempts at a comprehensive treatment, not counting popular reviews, were W. M. Wheeler's classic *The Social Insects* (1928) and Franz Maidl's excellent but nearly forgotten *Die Lebensgewohnheiten und Instinkte der staatenbildenden Insekten* (1934). Not only has the literature on the subject increased enormously (to about 7,000 articles on termites alone, for example, and 12,000 on ants), but a whole new way of studying insect societies has also been created. I refer to the experimental and statistical analysis of insect colonies as populations. We are at last beginning to understand the physiological basis of caste determination, the nature of communication among workers, the principle of a queen's control over the rest of the colony, the means by which social parasites penetrate the heart of the colony communication system, the factors that limit colony growth, and the stimuli that pace the life cycle. Furthermore, we are molding the rudiments of true evolutionary theories of sociality through which explanations can be supplied for the presence of the underlying physiological phenomena in terms of maximal efficiency and fitness at the colony level. The present status of insect sociology can be made clearer by recognizing three stages in its historical development.

The natural history phase. The discovery and description of the social insects and the cataloging and evolutionary interpretation of their behavior and ecology were the unavoidable first steps. This phase, a necessary precursor to succeeding developments, is far from completed. The natural history of the Halictidae, the group containing most of the species of social bees, to take one of many examples, is still in an early period of exploration.

The physiological phase. The experimental analysis of the social systems and their physiological bases constituted the logical next step. This approach to the subject gained its first solid impetus with the work of von Frisch on honeybees in the 1920's. It is currently being applied vigorously to such diverse topics as caste determination, food exchange, communication, circadian activity, nest micrometeorology, and many others.

The population-biology phase. With the first two approaches now yielding much solid information, it has become possible to commence the construction of a new and more rigorous theory of social evolution. This theory does not consist solely of phylogenetic reconstructions in the nineteenth-century manner. It also attempts to account for social phenomena in terms of the first principles of population genetics and population ecology. Relying on the use of mathematical models in the fashion of the hypothetico-deductive method of any mature science, it predicts the existence of still undiscovered phenomena and relations among phenomena, it establishes quantitative laws to describe the underlying processes, and it suggests the best ways to measure and describe complex systems. This approach has only begun to be applied to a few subjects such as the origin of sociality and the determination of caste ratios, and I have tried to exemplify it in Chapters 17, 18, and 21.

In this book an attempt is made not only to review, in an objective and straightforward manner, the substance of insect sociology but also to create a theme in which the relationships of the three historical phases are made clear. Exploration along all three approaches will continue indefinitely to yield exciting discoveries. In time all of this information will be assembled within the framework of population biology and form an important branch of that larger science. A principal theme of this book is, therefore, the expression of insect sociology as population biology.

Now what delight can greater be
Then secrets for to knowe,
Of Sacred Bees, the Muses Birds,
All of which this booke doth shew.
And if commodity thou crave,
Learne here no little gaine
Of their most sweet and sov'raigne fruits,
With no great cost or paine.
If pleasure then, or profit may
To read induce thy minde;
In this smale treatise choice of both,
Good Reader, thou shalt finde.

Charles Butler,
The Feminine Monarchie (1609)

2 The Degrees of Social Behavior

The "truly" social insects, or eusocial insects as they are sometimes more technically labeled, include ants, all termites, and the more highly organized bees and wasps. These insects can be distinguished as a group by their common possession of three traits: individuals of the same species cooperate in caring for the young; there is a reproductive division of labor, with more or less sterile individuals working on behalf of fecund individuals; and there is an overlap of at least two generations in life stages capable of contributing to colony labor, so that offspring assist parents during some period of their life. These are the three qualities by which the majority of entomologists intuitively define eusociality. If we bear in mind that it is possible for the traits to occur independently of one another, we can proceed with a minimum of ambiguity to define *presocial* levels on the basis of combinations of two or less of the three traits. Presocial refers to the expression of any degree of social behavior beyond sexual behavior yet short of eusociality.* Within this broad category there can be recognized a series of lower social stages, for which Michener (1969a) has provided the most recent and sound classification:

Solitary—showing none of the three traits listed immediately above;
Subsocial—the adults care for their own nymphs or larvae for some period of time;
Communal—members of the same generation use the same composite nest without cooperating in brood care;
Quasisocial—members of the same generation use the same composite nest and also cooperate in brood care;
Semisocial—as in quasisocial, but there is also reproductive division of labor, that is, a worker caste cares for the young of the reproductive caste;
Eusocial—as in semisocial, but there is also an overlap in generations so that offspring assist parents.

In this arrangement, presocial applies to all the intermediate stages between solitary and eusocial. Michener (1969a) has introduced yet another term, *parasocial,* to embrace those presocial states in which members of the same generation interact—namely, communal, quasisocial, and semisocial. An agreeable feature of this classification is its explicit recognition that the subsocial and communal states, while undoubtedly serving as early evolutionary steps, contain none of the three intuitive criteria of eusociality. The same can be said of aggregations, including even those of aphids, lepidopteran larvae, and locusts, in which relatively elaborate physiological group effects and coordinated swarming occur (Chauvin and Noirot, 1968). The system also provides a means of making a graphic contrast between the two alternate routes to eusociality, the parasocial and the subsocial, which most students of the subject believe to have been followed in evolution. The logical possibilities framed by the terminology are presented in Tables 2-1 and 2-2. Later in this book virtually all of these states are demonstrated in various groups of insects. In fact, wasps alone exhibit most conceivable degrees of both subsocial and parasocial behavior, as well as both the extreme solitary and eusocial

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*Bequaert (1935) invented the term "presocial" for the narrow category of behavior in which one or both of the parents merely guard the offspring temporarily, without providing it with food. This usage has not caught on, and Wilson (1966) suggested that the word, which has the advantage of being mnemonically superior, is best used in the broad sense employed in this book.

TABLE 2-1. Degrees of sociality, showing intermediate parasocial states.

	Qualities of sociality		
Degrees of sociality	Cooperative brood care	Reproductive castes	Overlap between generations
Solitary, subsocial, and communal	−	−	−
Quasisocial	+	−	−
Semisocial	+	+	−
Eusocial	+	+	+

states. In later chapters on the social wasps and presocial insects (Chapters 3 and 7), the successive stages of parental care defined in Table 2-2 will be exemplified in detail.

Before going on to the documentation of social evolution, however, let us quickly review the rather confused history of definitions of the expression "social insect." Most authors have used the phrase interchangeably with "true social insect," or eusocial insect as it has just been defined. There have been semantic problems, stemming almost exclusively from differences in opinion concerning the multiple qualities that go into the definition. This basic aspect of the problem largely escaped the disputants themselves. In essence, one group of writers, starting with W. M. Wheeler, incorporated all three of the traits I have listed; another, smaller group incorporated only two of the traits, omitting the criterion of overlap of generations.

In his last attempt at a major synthesis, Wheeler (1928) defined social insects *sensu stricto* as those in which "progeny are not only protected and fed by the mother, but eventually cooperate with her in rearing additional broods of young, so that parent and offspring live together in an annual or perennial society." Among the many recent authors retaining this usage is Michener (1953b, 1969a), who uses the definition as the terminological cornerstone in his productive writings on the evolution of social bees.

O. W. and Maud J. Richards (1951) evidently tried to apply a more flexible definition to the social wasps when they stated that "Real social life appears when the mother and her offspring (or, less probably, a number of sisters) co-operate in making a nest and feeding their young. The best criterion is that a wasp should feed a larva laid by another individual or help construct its cell." Later O. W. Richards (1965) eliminated the criterion of overlap of generations altogether and made the criterion of reproductive castes optional: "The term 'social' is reserved for communities in which there is more than one female, one or more usually being sterile, unfertilized and nursing the young derived from one or a few of them. The mother that actually lays the eggs usually does no other work in the mature colony." Emerson (1959) also omitted the criterion of overlap of generations: "True social insects are those that live in populations exhibiting division of labor for various functions among mature individuals separated into reproductive and sterile castes." In my opinion nothing is to be gained by broadening the category of true social insects. The stricter Wheeler-Michener usage has the great advantage of permitting the more finely structured classification of presocial states needed to cope with the immense amount of new information on social evolution now finding its way into the literature.

Finally, to complete this circle of nomenclature, what is a "society"? It is a group of individuals that belong to the same species and are organized in a cooperative manner. I believe that the terms society and social must be defined quite broadly in order to prevent the arbitrary exclusion of many interesting phenomena. Such exclusion would cause confusion in all comparative discussions of sociobiology. Not only eusocial insect colonies but also most parasocial and subsocial groups should be designated as societies and their members as social in the most general sense. The same is true of aggregations of locusts and other insects in which organization transcends mere re-

TABLE 2-2. Degrees of sociality, showing intermediate subsocial states.

	Qualities of sociality		
Degrees of sociality	Cooperative brood care	Reproductive castes	Overlap between generations
Primitively subsocial	−	−	−
Intermediate subsocial I	−	−	+
Intermediate subsocial II	+	−	+
Eusocial	+	+	+

productive activity. Reciprocal communication of a cooperative nature is the essential intuitive criterion of a society. Thus it is difficult to think of an egg, a pupa, or even a bee larva sealed into a brood cell as a member of the society that produced it, even though it functions as a true member at other stages of its development. It is also not very satisfying to view the simplest aggregations of organisms, such as swarms of courting males, as true societies. They may be held together initially by mutually attractive stimuli, but if they interact in no other way it seems excessive to refer to them by a term stronger than aggregation. By the same token a pair of animals in courtship can be called a society in the broadest sense but only at the price of diluting the expression to the point of uselessness. Bird flocks, wolf packs, locust swarms, and groups of communally nesting bees are good examples of elementary societies. So are parents and young if they communicate reciprocally. This last, extreme example will seem to approach the trivial and may be questioned by other students of the subject. In my view, however, it is appropriately included and is of special interest because it calls attention to the important topic of the relation of kinship to the evolution of true, organized societies, a relation that can be shown to be of the greatest importance to the study of social insects and will be examined in some depth in later chapters of this book.

3 The Social Wasps

In spite of the relatively small number of wasp species that are truly social, the study of their behavior has repeatedly yielded results of major interest. Four of the basic discoveries of insect sociology—nutritional control of caste (Marchal), the use of behavioral characters in studies of taxonomy and phylogeny (Ducke), trophallaxis (Roubaud), and dominance behavior (Heldmann, Pardi)—either originated in wasp studies or were based primarily on them. Even more importantly, the living species of wasps exhibit in clearest detail the finely divided steps that lead from solitary life to advanced eusocial states.

Eusocial behavior in wasps is limited almost entirely to the family Vespidae. The only known exception is a primitive eusocial organization recently discovered in the sphecid *Microstigmus comes* (Matthews, 1968). In order to put these and other social hymenopterans in perspective, consider the phylogenetic arrangement given in Figure 3-1 of the seven superfamilies of the aculeate Hymenoptera. The aculeates, as they are familiarly labeled by entomologists, include the insects referred to as "wasps" in the strict sense. Also included in this phylogenetic category are ants (Formicoidea), which are considered to have been derived from the scolioid wasp family Tiphiidae, and bees (Apoidea), which are considered to have originated from the wasp superfamily Sphecoidea. The Vespoidea is comprised of three families, the Masaridae, Eumenidae, and Vespidae. These wasps are often called the Diploptera because of the extraordinary ability of the adults to fold their fore wings longitudinally. The trait does not occur in the stenogastrine vespids or in the great majority of Masaridae, but its absence there may be a derived rather than a primitive characteristic. Vespoids are further distinguished from other wasps by the manner in which the combined median vein and radial sector slant obliquely upward and outward from the basal portion of the fore wing. Most can also be recognized by the emarginate (notched) condition of the inner margin of each compound eye.

Most references to the biology of the Vespidae employ the classification of Bequaert (1918, 1928), who recognized 11 subfamilies: Euparagiinae, Gayellinae, Masarinae, Raphiglossinae, Zethinae, Eumeninae, Stenogastrinae, Polybiinae, Ropalidiinae, Polistinae, and Vespinae. Recently Richards (1962), on the basis of new morphological evidence, reduced the number of subfamilies to 9 and split them into 3 families. His arrangement follows the phylogeny shown in Figure 3-2 and the checklist of Table 3-1.

Of approximately 15,000 living species of aculeate wasps believed to occur in the entire world (Hurd, 1955), probably less than 1,000 belong to the Vespidae. The

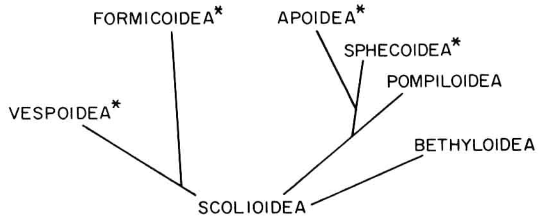

FIGURE 3-1. A simple branching diagram of phylogeny in the aculeate Hymenoptera, or "wasps" in the strict sense. An asterisk indicates the superfamilies in which eusocial behavior has been evolved, probably as at least one independent event in each case (modified from Evans, 1958).

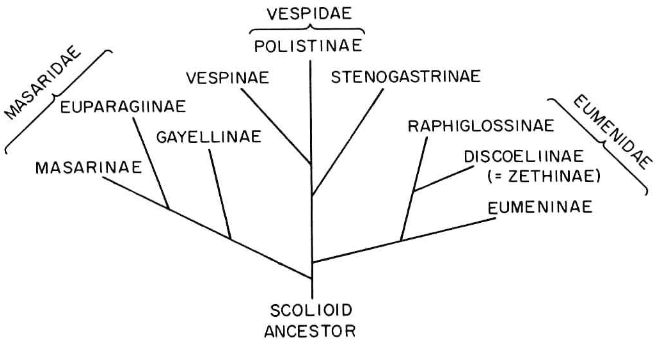

FIGURE 3-2. Phylogeny of the families and subfamilies of the "Diploptera," or wasp superfamily Vespoidea (modified from Richards, 1962).

species of this family are distinguished by the possession of short mandibles that do not cross in the resting position. The ranges of most of the principal tribes and genera are shown in Figure 3-3. The Stenogastrinae, containing about 50 species, range from India to New Guinea. The Vespinae also are centered in southeastern Asia, where about 50 species are known; 12 species also occur in Europe and 16 in North America, including our familiar hornets and yellow jackets. The Polistinae is the most diversified of the subfamilies. The paper wasp genus itself, *Polistes,* occurs over most of the world and, in 1962, was known to contain 189 species and 97 subspecies. Among the social insects it is rivaled in the extent of this range and in the degree of speciation only by several of the largest ant genera such as *Camponotus* and *Pheidole.* The rest of the Polistinae belong to the tribe Polybiini, which is centered in South America and contains no less than 300 species classified in about 20 genera. Approximately 200 additional polybiine species in 4 or 5 genera occur in Africa and tropical Asia.

The species-level taxonomy of the social wasps is only moderately well worked out, and some large and inconvenient gaps remain. Few comprehensive studies of modern vintage exist to which the beginning taxonomist can turn: Bequaert (1918) on the Vespidae of central Africa; Blüthgen (1961) and Kemper and Döhring (1967) on the Vespidae of Europe; van der Vecht (1957) on the Vespinae of southeastern Asia and New Guinea; Ducke (1910) on the South American Polybiini; Willinck (1952, 1953) on the Argentine Polistinae; and Bequaert on the Polybiini of North America and the West Indies (1933) and on the Vespidae of northern South America (1944a). The Poly-

TABLE 3-1. Families, subfamilies, and genera of vespoid wasps, with an indication of the degree of sociality and the distribution of the subfamilies.

Division	Degrees of sociality	Distribution
Family Masaridae		
Subfamily Euparagiinae (*Euparagia*)	Solitary	North America
Subfamily Gayellinae (*Gayella, Paramasaris*)	Solitary	Australia, Mexico to South America
Subfamily Masarinae (*Celonites, Ceramiopsis, Ceramius, Jugurtia, Masaris, Metaparagia, Microtrimeria, Paragia, Pseudomasaris, Quartinia, Quartiniella, Quartinioides, Riekia, Rolandia, Trimeria)*	Solitary	World-wide
Family Eumenidae		
Subfamily Raphiglossinae (*Psiloglossa, Raphiglossa)*	Solitary	Africa
Subfamily Discoeliinae (*Ctenochilus, Discoelius, Elimus, Labus, Zethus*)	Solitary	New World tropics, Africa, tropical Asia
Subfamily Eumeninae (*Ancistrocerus, Cephalodynerus, Dolichodynerus, Eumenes, Euodynerus, Hypalastoroides, Leptochiloides, Leptochilus, Maricopodynerus, Microdynerus, Monobia, Montezumia, Odynerus, Pachodynerus, Pachymenes, Pseudepipona, Pseudodynerus, Pterocheilus, Stenodynerus, Symmorphus*)	Solitary to subsocial	World-wide
Family Vespidae		
Subfamily Stenogastrinae (*Eustenogaster, Liostenogaster, Parischnogaster, Stenogaster*)	Subsocial to communal	Tropical Asia and Australia
Subfamily Polistinae (*Apoica, Belonogaster, Brachygastra, Charterginus, Chartergus, Clypearia, Epipona, Leipomeles, Metapolybia, Mischocyttarus, Parachartergus, Parapolybia, Polistes, Polybia, Polybioides, Protonectarina, Protopolybia, Pseudochartergus, Pseudopolybia, Ropalidia, Stelopolybia, Synoeca, Synoecoides*)	Advanced subsocial to eusocial	Primarily Old and New World tropics; *Polistes* ranges to Canada and Sweden
Subfamily Vespinae (*Provespa, Vespa, Vespula*)	Advanced eusocial	North Temperate Zone, tropical Asia