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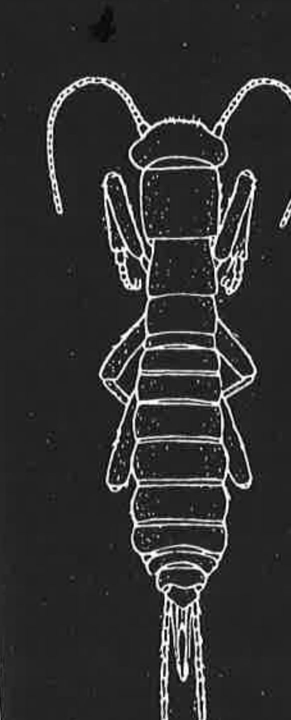

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The Evolution of Social Life in Wasps

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ABSTRACT

The term wasp embraces a great array of hymenopterous insects, most of which are "solitary", while a few are "subsocial" or "social". It is useful to distinguish thirteen steps leading from the simple behavior of the Scolioidea to the complex behavior of the social Vespidæ. Examples can be cited of genera which represent each level of social evolution, and it seems possible that forms now at step thirteen (such as Vespinæ) may have passed through each of the other steps in sequence.

Briefly, these steps are as follows: (1) prey is paralyzed and egg laid upon it; (2) prey is stung, dragged into a hole, and egg laid; (3) prey is stung, a nest is dug, and prey is placed in nest and egg laid, the nest then being closed; (4) nest is made first, prey obtained, placed in nest, egg laid; (5) same, but several more prey added after egg is laid; (6) same, but provisioning is progressive; (7) egg is laid in empty cell before provisioning begins; (8) food is macerated and fed directly to larva; (9) life of female is prolonged to overlap that of some of offspring; (10) trophallaxis; females feed offspring other than their own; (11) egg laying done by one female; original offspring all female; (12) worker caste well defined, intermediates common; differential feeding of larvæ; (13) worker caste differs morphologically from queen; intermediates uncommon or absent.

The term wasp embraces a great array of hymenopterous insects which exhibit much variation both in structure and in biology. Even the most conservative classification must recognize at least five superfamilies for the wasps. The possible relationships of these five superfamilies are indicated in fig. 1. While some may disagree with certain points in the phylogenetic tree, I think that most will agree that the Scolioidea are the most primitive, that the Bethyloidea, Vespoidea, and the ants are all derived independently from the Scolioidea, and that the pompiloid-sphecoid-apoid stock represents a single phyletic line also arising from the Scolioidea.

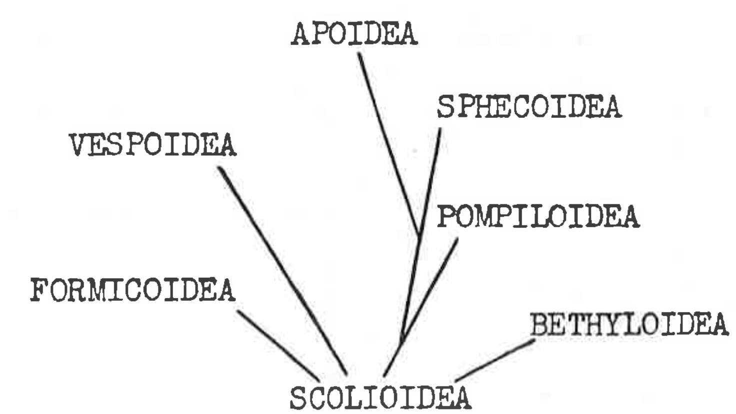

Figure 1

If we scan the wasps as a whole, we find that the vast majority are strictly solitary. A few might be termed "subsocial", and a few Vespidæ may be justly termed "social". But neither the term subsocial nor the term social is capable of precise definition, and different authors use these terms with different shades of meaning. Actually we may define, with much greater precision, a series of steps—or rungs of the social ladder, if you wish—leading from strictly solitary forms to those which, by any standards, are social. More attention has been paid to the higher rungs of the ladder, but the lower rungs seem to me worthy of equal consideration.

Since the Scolioidea are at the base of our phylogenetic scheme, it is logical that we begin with them. The females of most Scolioidea search for beetle grubs in the ground, sting them into temporary or permanent paralysis, lay their egg upon the grub, and leave the grub where it happens to be. This behavior hardly differs from that of many of the lower, parasitoid Hymenoptera from which the wasps are presumed to be derived. Some

Scoliidæ, however, move the grub into a more favorable situation in the soil, even into a prepared cell, before oviposition. This movement of the prey into a more suitable niche is, I submit, the very first step in the direction of the family association which we speak of as an insect society. There is, of course, no contact at all between mother and offspring, but at least the offspring is provided with temperature and moisture conditions which enable it to survive with greater certainty. The selective value of this new element in the behavior is, I think, obvious.

Since the Scolioidea show little advance beyond this very simple manipulation of the prey, it is necessary to turn to another group, the Pompilidæ or spider wasps (Fig. 2), which seem to be related on the one hand to the Scolioidea, and on the other hand to the Sphecoidea. All Pompilidæ prey upon spiders. Some of them show hardly any advance in behavior over the Scolioidea. Wasps of the genus *Notocyphus*, for example, are said to sting certain spiders in their webs, lay their egg, and depart, the spider recovers from paralysis and goes about its business with the wasp larva developing like a parasitoid on its abdomen (Williams, 1928). In *Haploneurion apogonum*, Claude-Joseph (1930) reports that the spider is dragged into a beetle burrow in a bank, the egg laid upon it, and the cavity sealed off with debris. The vast majority of spider wasps have advanced one step further, and actually dig

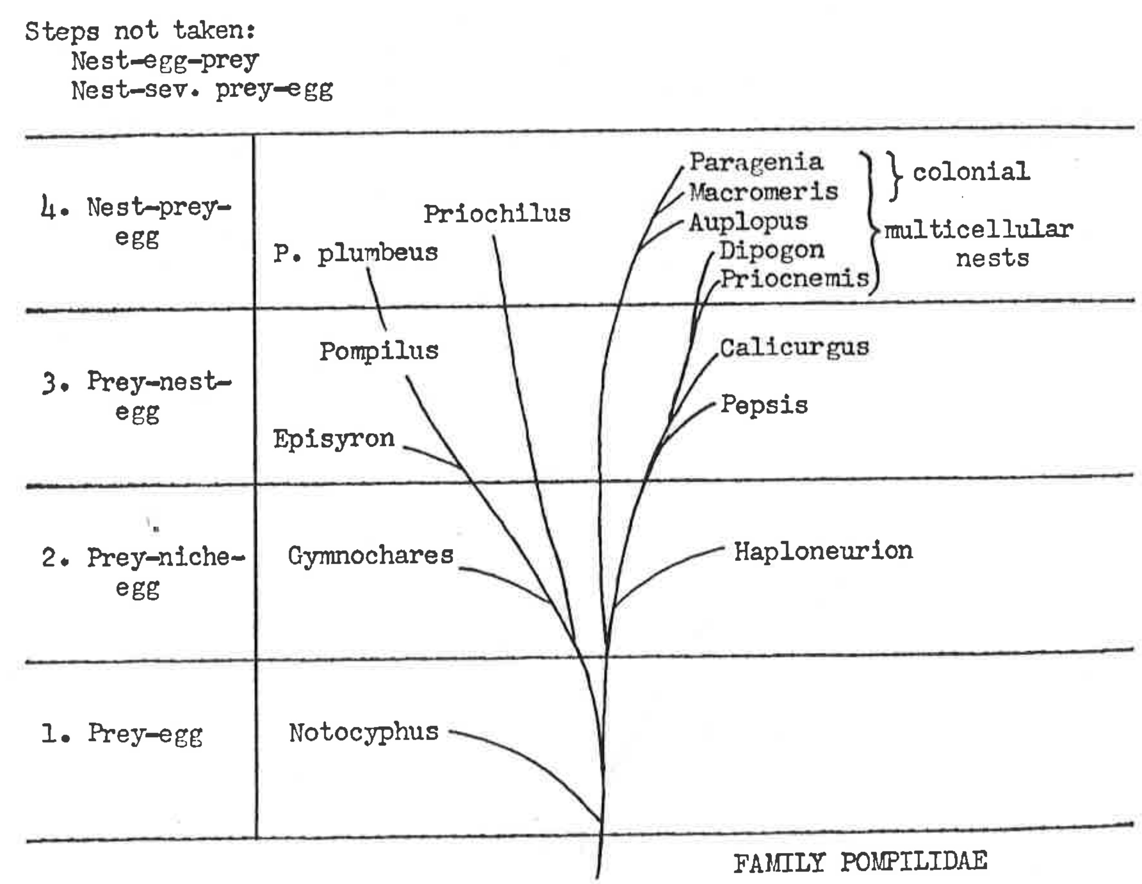

Figure 2

a simple nest in the ground in which the paralyzed spider is placed. I think it is appropriate to use the term *nest* for such a structure, even though the attachment of the wasp to the nest is very temporary. Certainly the possession of a nest is another important prerequisite for becoming social. The majority of genera of Pompilidæ in both major subfamilies belong here—*Episyron*, *Pompilus*, *Pepsis*, *Calicurgus*, and many others—this is merely a selection of representative genera. A relatively few Pompilidæ have attained, in step four, an important rearrangement in the sequence of behavior. These wasps prepare the nest first—either in the soil or of mud or plant fragments—then obtain their prey and lay their egg upon it. Many of these wasps make multicellular nests, and a single nest becomes the focal point of the activity of a female for her entire life. In two genera, *Macromeris* and *Paragenia*, several females tend to nest together—they may be sisters or mother and daughters

(Williams, 1919). Some of the cells are said to be used a second time. The females are said to act as individuals, exhibiting no notable co-operation or aggression. Williams' studies were made many years ago, and these wasps deserve much further study.

It is interesting to speculate why the Pompilidæ have never progressed further up the social ladder, and which rungs in particular they have been unable to span. For one thing, they all use but a single spider in a cell, a distinctly primitive trait and one which makes progressive provisioning impossible. Further, the sequence nest-egg-prey, that is, the laying of the egg in the empty cell, which is characteristic of the social wasps, has never been attained.

Let us turn now to the superfamily Sphecoidea, a very large complex containing two families, the Ampulicidæ and the Sphecidæ (Fig. 3). The Ampulicidæ are on a level with

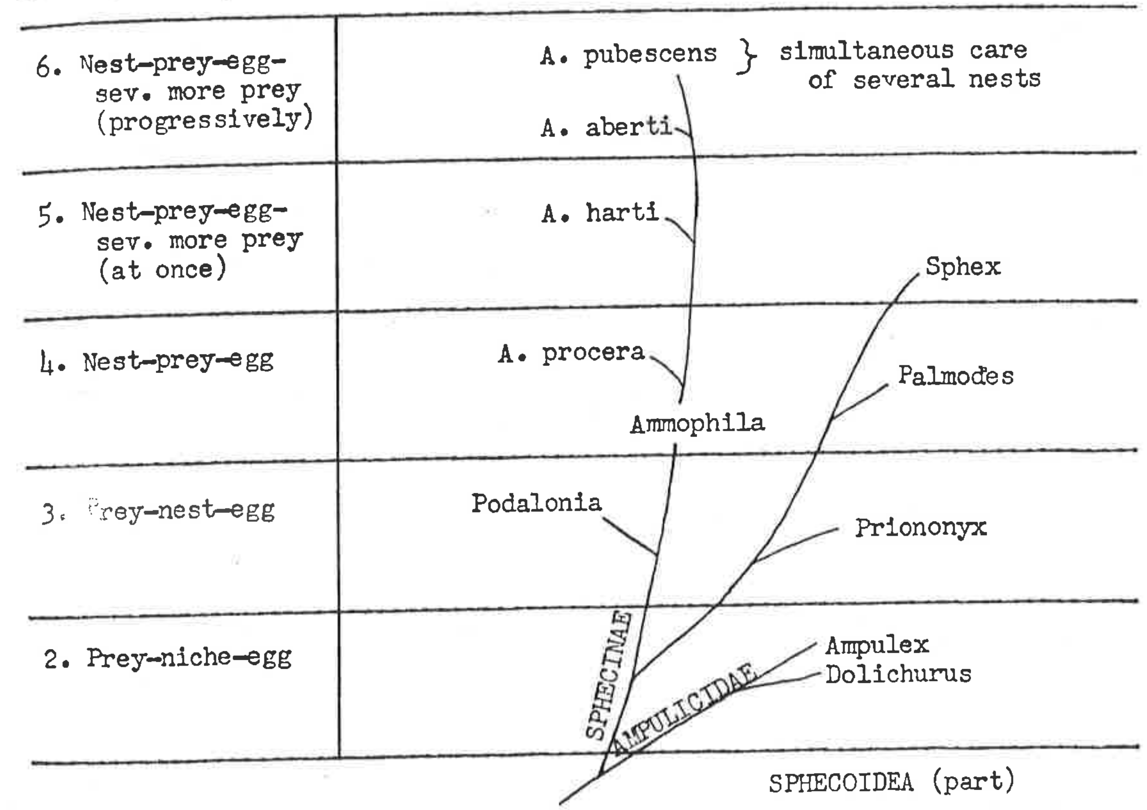

Figure 3

some of the Scoliidæ and the primitive Pompilidæ. They sting a cockroach, drag it to a suitable niche, lay an egg upon it, and seal up the niche. The most primitive Sphecidæ are on a level with the majority of Pompilidæ; *Prionony x*, for example, captures a grasshopper, then digs a nest, places the prey in it, lays the egg, and closes the nest. *Podalonia* does essentially the same with its cutworms. But nearly all Sphecidæ prepare the nest first, as in *Palmodes*, and many, such as *Sphex*, add a number of additional prey to the cell after the first has been put in place and the egg laid upon it. The genus *Ammophila* is one of those very interesting genera which exhibit several different levels of specialization. Some species, such as *procera*, place a single caterpillar in the previously prepared cell and lay an egg upon it. Others add several additional caterpillars to the cell, usually on the same day, but occasionally, if unfavorable weather intervenes, over several days. Thus, in *Ammophila harti*, there may occasionally be some accidental contact between mother and offspring. In some other species, typified by *Ammophila aberti*, the female lays her egg on the first caterpillar and then actually delays provisioning until just before hatching, after this bringing in caterpillars as required by the larva. This progressive provisioning, as it is called, involves considerable contact between mother and offspring; the mother inspects the nest each morning and receives stimuli emanating from the egg or larva which determine the course of her activity for the day. The European species *pubescens*, which has been studied by a number of workers, including particularly G. P. Baerends (1941), is known to care for several nests simultaneously, inspecting each active nest in the morning and provisioning in accordance with the needs of each larva as made known to her at the time of inspection.

Altogether *Ammophila* is a remarkable genus deserving much further study. But for further advance toward social life in the family we must turn to another group, the Bembicini (Fig. 4). We find even the most primitive of the Bembicini already ensconced on the fifth rung of the social ladder, with behavior essentially comparable to the genus *Sphex* and to such species of *Ammophila* as *harti*. The species of *Bicyrtes*, which prey upon stink bugs, occasionally, during unfavorable weather, do not complete their provisioning until after the egg has hatched. In some species of *Stictiella*, and in all species of *Bembix*, *Stictia*,

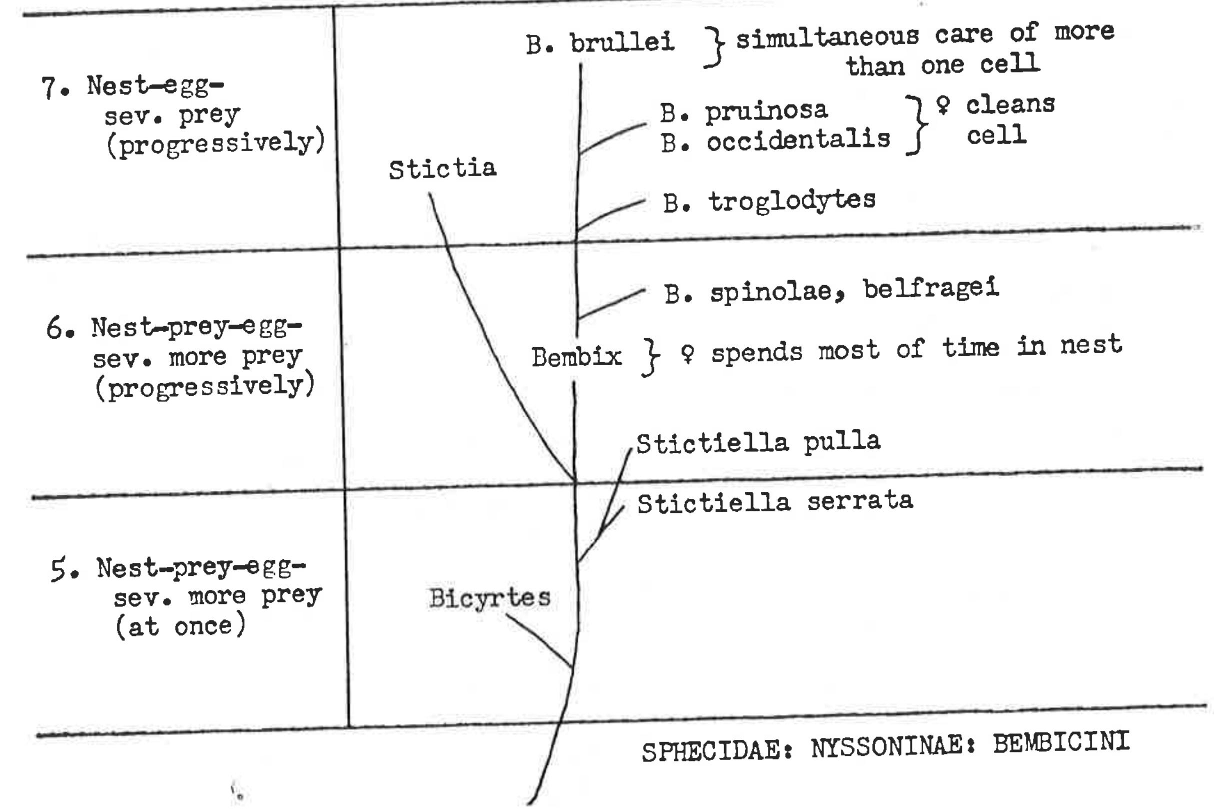

Figure 4

and certain other genera omitted here, progressive provisioning is the rule. But note that some of these insects have achieved another important rearrangement in the sequence of behavior. They omit the first prey and lay the egg directly in the empty cell. This is an important economy in the life of the wasp, and presages the universal condition in the social wasps. These wasps of the genus *Bembix* have other very interesting traits. The females remain within the nest at all times when not actually feeding or provisioning; thus the nest is very definitely the focal point of the life of the females, and the female to some extent protects the larva from predation. Contacts between mother and offspring have been studied by Tsuneki (1951), using glass burrow and cells; he finds that the female places paralyzed flies close to the larva as needed, but that there is no trophallaxis, that is, no exchange of secretions between larva and adult. A few species of *Bembix* are known to clean out the cells of the remains of flies which have been consumed, thus reducing infestation by various inquilinous maggots and again presaging the condition in the social insects. Several species make nests of several cells, and one of these, the Chilean *brullei*, exhibits simultaneous care of more than one cell (Claude-Joseph, 1928). The egg is laid in the cell before provisioning of the previous cell is complete. Conceivably, the offspring may begin emerging before the mother dies, although whether or not this actually occurs is unknown.

The short life of the female in all Sphecidæ seems to be one reason why none of them have become truly social. A second reason is that none of them macerate the prey before presenting it to the larva. Here are at least two rungs of the social ladder which the Sphecidæ, for some reason, have been unable to climb.

Finally, let us turn to the Vespidæ (Fig. 5). Wheeler (1928) lists four subfamilies of Vespidæ as being solitary or subsocial, and five as being social. The curious thing is that even the most primitive forms are already well advanced beyond all Pompilidæ and most Sphecidæ. All build their nest and lay an egg in it before beginning to hunt prey; nearly all build several cells in close proximity; and nearly all use some building material in making their nest, in the lower forms mud and in the higher forms paper which they make from decaying wood. Everyone is familiar with *Eumenes*, the potter wasp, which, although it

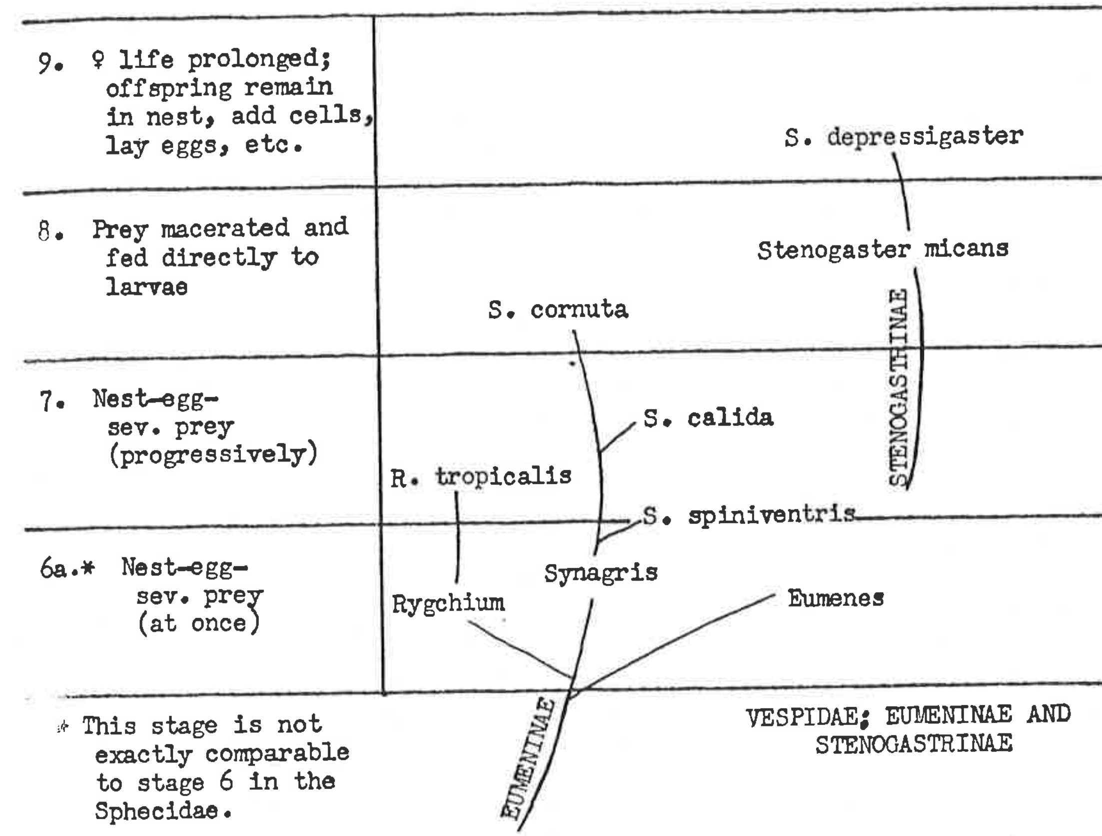

Figure 5

practices mass provisioning, lays its egg in the empty cell before capturing several caterpillars, placing them in the cell, and sealing off the top. This sequence of nest-egg-several prey, which is the starting point in the Vespidæ, is only achieved by a few of the higher Sphecidæ. Presumably the ancestors of the Vespidæ went through a series of steps similar but not necessarily identical to those described for the Sphecidæ.

Even within the most primitive subfamily, the Eumeninæ, there are forms which advance to still higher rungs on the social ladder. Roubaud (1916) found that an African species of the genus *Rygchium* practices progressive provisioning. The mother wasp waits until the egg is ready to hatch and then brings in the first caterpillar; she inspects the cell periodically and brings in provisions slowly and as needed by the larva, finally closing the cell when the larva is ready to pupate. There is also a tendency in this species for the mother to care for two or more cells simultaneously. All of this is reminiscent of *Bembix brullei*.

Another related genus, *Synagris*, is even more interesting. This is an African genus and several species have been studied by Roubaud (1911, 1916). *Synagris spiniventris* is said to build mud cells in an irregular mass and to practice mass provisioning, much like *Eumenes* and most species of *Rygchium*. However, if food is scarce, due to weather conditions or other factors, the female may bring in caterpillars more slowly, completing provisioning when the larva is about three-fourths grown. Thus progressive provisioning is optional in this species. In another species, *calida*, progressive provisioning apparently is the rule. Still another species, *cornuta*, not only feeds the larva progressively, but actually chews up the caterpillar into a paste which it feeds directly into the mouth of the larva. Maceration of the prey is characteristic of all the truly social wasps and certainly deserves to be regarded as a new and very important step. It is the highest behavior achieved by any of the Eumeninæ.

The Stenogastrinæ are a poorly known group, consisting of a single genus occurring in the Oriental and Australian regions. So far as known, these insects all feed their larvæ with what is described as a "gelatinous paste", presumably consisting of macerated prey and the secretions of the wasp. According to F. X. Williams (1919), some species are solitary, although the female attends several young simultaneously. Others, such as *depressigaster*, live in small colonies apparently consisting of a mother and several daughters. These daughters differ neither in structure or in function from the mother; they merely remain on the nest, adding cells, laying eggs, and caring for their own larvæ. All of the Stenogastrinæ make nests of paper; the nests are small, delicate, and often very odd in form.

In the Stenogastrinæ we find for the first time that the life of the female is prolonged so as to overlap that of several of her offspring. Richards and Richards (1951) have suggested that in species which practice progressive provisioning and feed the larva directly, and where the demands of the larva at least partially determine how much food they receive, conditions are particularly favorable for the production of "over-fed" individuals which may be capable of living longer than they would otherwise.

I should like now to turn to the subfamily Polybiinæ, one of the largest groups of Vespidæ and mainly tropical in distribution (Fig. 6). The simplest type of behavior is exhibited by the African genus *Belonogaster* (Roubaud, 1916). These wasps have a number of structural specializations, and whether their behavior is truly primitive or specialized by reduction is difficult to say. At any rate they suggest a stage of evolution through which the bulk of the Polybiinæ may have passed. The nests are small, simple, and suggestive of those of *Polistes;* the cells are lengthened and broadened as the larva grows, giving the nest a somewhat splayed-out appearance. These nests are inhabited by a small number of adults, both male and female, and the number of cells is usually around 50 or 60. The females are all identical structurally and physiologically; all of them mate and lay eggs, and none can be called workers. The nest is said to be founded by a single female which may be joined by other females at an early period of construction. As the offspring emerge, the females first remain on the nest for a few days and assist in the feeding of the larvæ and in cleaning cells; later they hunt prey and bring in paper for the cells. Egg laying, in advanced colonies, is done mostly by the more mature females, although all the females are normally fecundated. Any given female does not restrict her nursing to her own offspring, but feeds any larva which needs food. The larvæ produce a salivary secretion which is lapped up by the adults. Roubaud believed the feeding of the larvæ by the adults was in response to this secretion by the larva. He called this phenomenon "ecotrophobiosis", although Wheeler later used the more familiar term "trophallaxis". Both Roubaud and Wheeler considered trophallaxis extremely important in the evolution of social life in insects.

Recently the trophallaxis concept has been modified by some workers and even rejected altogether by others. One recent writer terms it a "combination of anthropomorphic thinking and Lamarkianism" (Schmieder, 1956). It is impossible to review the concept of trophallaxis here, but I believe I am safe in saying that in all Vespidæ above this point, some interchange of fluids does occur between larva and adult.

I believe that we are fully justified in calling *Belonogaster* a "social" wasp. Whatever may be said about trophallaxis, the fact remains that in *Belonogaster* mother and daughters do co-operate in nest-building and brood-rearing, and individual wasps often feed larvæ derived from eggs laid by other individuals. Richards considers the latter phenomenon the best criterion for considering a wasp as truly social.

The more familiar wasps of the genus *Polistes* actually represent only a slight advance over *Belonogaster*. Although *Polistes* is traditionally placed in a separate subfamily, some contemporary workers, including myself, feel that its characters are of only generic value, and that it really belongs with the Polybiine wasps. There are many species of *Polistes*, mostly in the tropics and subtropics, but a few have invaded the temporate regions. There seems to be much variation in biology in the different species, and it is impossible to review all the work of various authors on different species of *Polistes*. I would, however, like to review briefly some of Pardi's (1948) work on *Polistes gallica*.

The colonies of *Polistes gallica* are typically annual. The nest may be started in the spring by one fecundated female, but she is ordinarily soon joined by several others. Within this group of co-operating females a hierarchy or "peck-order" is soon established. Pardi has described the various types of contacts between females which result in the psychological

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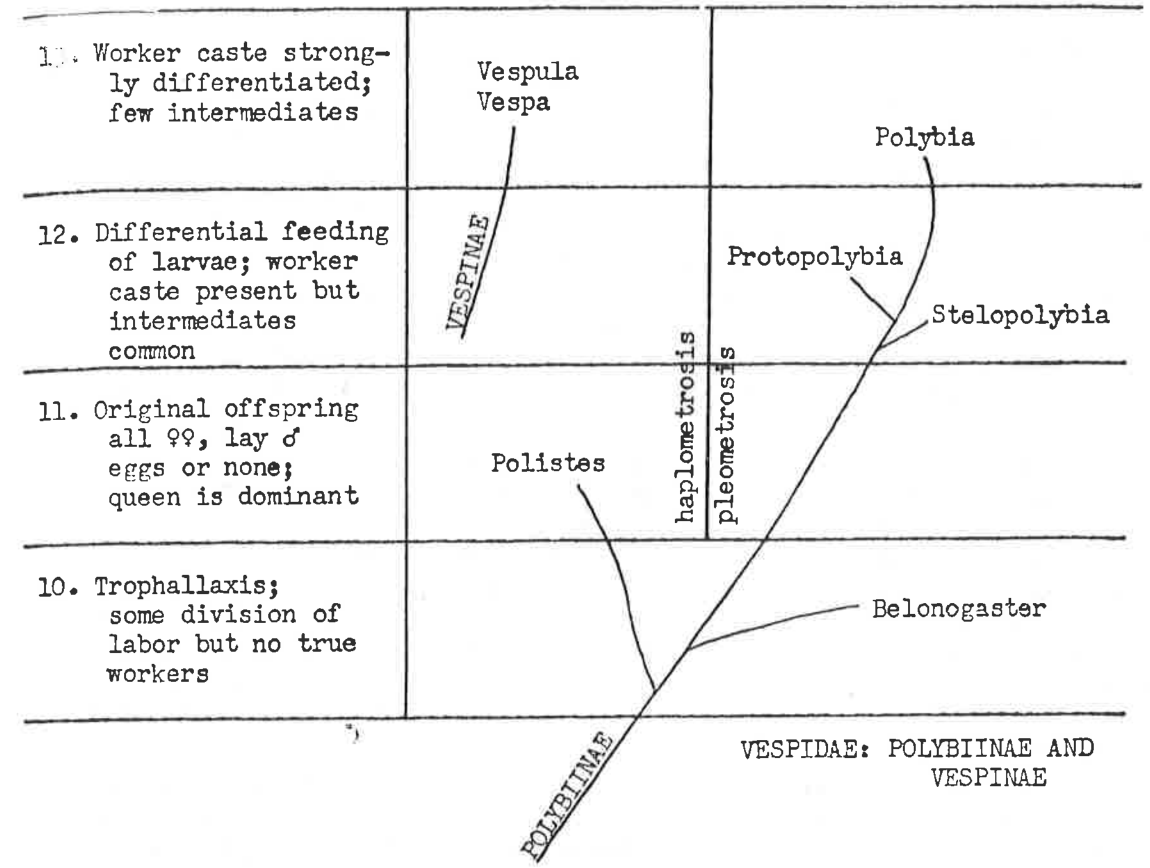

Figure 6

dominance of one of them. Dissection of these individuals reveals a direct correlation between size of the ovaries and degree of dominance. This dominance is associated with a trophic advantage; the higher in the peck-order, the more food an individual is able to obtain from the social stomach. Dominants spend more time on the nest and assume most of the duties on the nest, and the top individual does most of the egg-laying. Due to their trophic advantage, the dominants show increasingly full development of the ovaries, while those of individuals lower in the hierarchy undergo regression. Thus there is but one effective queen. The offspring of this queen are females, similar to the queen but unfecundated and with reduced ovaries. These workers establish a social hierarchy based on age, and if the queen dies the top worker assumes the role of the queen, laying eggs which produce only males, of course. Well along in the active season, males are produced, probably due to cyclical factors in the development of the queen, and some of the females are fecundated and overwinter to start the cycle in the spring. Strictly tropical species usually send out small swarms of females which may start new colonies immediately. It has never been clearly demonstrated that the workers of *Polistes*, such as they are, are the result of differential feeding in the larval stage.

The most important things which have occurred here are physiological matters which are not fully understood. The queen at first produces chiefly if not entirely diploid, fertilized eggs which give rise to females; these females act as workers either because of the psychological dominance of the queen, or because nutritional factors in the larval or adult stage do not permit full development of the ovaries, or because males are not present to effect fertilization (or perhaps all three). Rau (1939) has suggested that the so-called queens of *Polistes* are merely workers which have become inseminated and have survived the winter. *Polistes* seems to be something of a "key genus" in understanding the origins of social life in wasps. Unfortunately there are some contradictions in recent work on the genus. Khalifa (1953) failed to confirm the dominance theory. Deleurance (Richards, 1953) has shown that temperature has a direct relationship to the production of queens. When workers were kept warm at night, the grubs they were feeding turned into queens, suggesting that temperature somehow alters the physiology of the worker so that they give the grubs different food. This, of course, suggests that differential feeding of larvæ does occur in *Polistes*.

In *Polistes* there is ordinarily only one effective, egg-laying queen, a condition often referred to as monogyny, but more properly termed haplometrosis (single + mother). The vast majority of Polybiine wasps, however, exhibit pleometrosis, that is, there are several to many fecundated, egg-laying females in a single nest. Authors disagree as to whether haplometrosis or pleometrosis is more primitive, but perhaps it is not possible or even necessary to solve this dilemma. In the tropics, a species can afford to be lavish with its queens, and pleometrosis is the rule. In *Polistes*, colonies in the tropics and subtropics are founded by several fecundated females, while in temperate species such as *fuscatus*, colonies are usually founded by a single female. Undoubtedly haplometrosis is more efficient in temperate regions, where the queens must overwinter, since it represents a maximum use of those which succeed in surviving the winter. This may explain why *Polistes*, although essentially a tropical genus, has succeeded in invading many parts of the North Temperate Zone.

Most of the tropical Polybiinæ build more elaborate nests than *Polistes* or *Belonogaster*, surrounded by one or more protective envelopes. The colonies are often large. To give some examples, a colony of *Protopolybia pumila* studied by Richards and Richards (1951) in Guiana contained over 21,000 cells. Over 7000 wasps were taken from this nest, of which 93 were queens, that is, had well-developed ovaries and had sperm in the spermatheca. About 2000 were workers, with more or less filamentous ovaries, and nearly 5000 were intermediates, having moderate-sized eggs in the ovaries, but no sperms. There were also 213 males in the nest. These authors were able to sort out the queens, after some experience, by the more swollen abdomens; later they found that queens had, on the average, longer wings and more hamuli.

This condition of many intermediates and no outstanding external differences between queens, intermediates, and workers, is presumably more primitive than the condition found in many species of *Polybia*. Whether or not differential feeding of larvæ occurs in *Protopolybia* is uncertain; certainly it must occur in *Polybia*, where intermediates are uncommon and the queen often distinguishable by clear-cur morphological differences. One colony of *Polybia occidentalis* studied by Richards and Richards was found to have 596 wasps; 48 were queens and 548 were workers. There were no intermediates, and the queens differed from the workers in having a longer mesonotum, longer and wider first abdominal tergite, and fewer hamuli per millimeter of wing-length. Nothing is known, of course, about caste-determination in these insects, but Richards is probably right in stating that structural differences such as these can scarcely have any other explanation than differential feeding of the larvæ. Queen cells, by the way, do not differ in any way from worker cells.

Richards and Richards have suggested that changes in the larva/worker ratio as the colony progresses may result in larvæ automatically receiving more food and thereby producing queens. They have shown that, in general, the ratio of larvæ to workers increases gradually to a certain point and then undergoes steady decline; it is during this decline in the larva/worker ratio that queens and males are produced. The paper of Richards and Richards on the social wasps of South America is replete with suggestive data of this sort, and I can only suggest that interested persons read their paper in detail.

The final group which deserve consideration are the common hornets and yellow-jackets, which form the subfamily Vespinæ. These insects are more poorly known than might be expected. It is known that colonies ordinarily have only one queen, which is sharply differentiated in size from the workers and often differs in color pattern and in minor structural details. These queens are reared in special, large cells making up the last few combs in the nest. It seems logical to assume that the larvæ in these cells receive a larger amount of food than those in smaller cells. The queens are capable of storing up considerable fat, and they are the only members of the colony which survive the winter. The Vespinæ are basically a Holarctic group adapted for survival even, in some cases, close to the Arctic Circle. They are sharply differentiated from other Vespidæ and probably evolved from some early vespid independently from the other subfamilies. The steps they went through to attain their lofty position on the social ladder are unknown and can only be deduced by analogy with other groups of Vespidæ.

The recent work of Brian and Brian (1952) on *Vespula sylvestris* is particularly interesting. These workers studied several aspects of the social behaviour of this species, including trophallaxis. They found experimentally that the fluid secreted by the larvæ actually was not attractive to adults. Apparently the larvæ secrete excess water via the salivary glands, and the behavior patterns of the workers are such that they collect this fluid when they feed the larvæ, so that it does not dampen the nest. They conclude that the trophallactic stage in the evolution of these insects, if it ever existed, has been superseded.

There is scarcely a group of wasps which could not bear much further study. In fact, speculation on the origin of social life seems to have far outstripped the observational data. While no group of wasps can be said to have attained the high degree of social evolution of certain of the bees and ants, the wasps deserve much further study for that very reason. I think we should not expect the steps in the evolution of bees and ants to be exactly the same as in the wasps. We are dealing with several different phyletic lines in which numerous parallelisms can be noted. Even in the Vespidæ social life must have arisen at least twice; in the bees I believe it is supposed to have arisen more than twice independently. While the problem of the evolution of social life in insects is perennially interesting, I think we should be cautious about trying to find broad generalizations which will apply equally to all groups.

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