THE EVOLUTION OF PREY-CARRYING MECHANISMS IN WASPS[1]

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The elaborate behavior patterns of wasps provide almost unlimited possibilities for comparative ethological studies. That few such studies have actually been made is in large part a consequence of the fact that the behavior of very few species has been described in adequate detail. The available descriptions are widely scattered in the literature and often fragmentary and poorly documented. Observers have often been unaware of the importance of certain components of the behavior, just as taxonomists often overlook structural details that later prove essential in classification. For this reason, there may be justification for studies which focus attention upon one particular facet of behavior and attempt to trace its modifications in various taxa. However preliminary, attempts to discern trends in the evolution of some aspects of behavior may provide direction for further studies. In an early and now classic paper, Ducke (1913) outlined the evolution of nest building in the Vespidae. Wheeler (1928) and others have considered the matter of the origin of sociality among wasps. Leclercq (1954) discussed the probable phylogeny of the Sphecidae as suggested by some aspects of structure and nesting behavior. The present paper is an attempt to outline the different ways in which wasps carry their prey to the nest and to draw certain conclusions regarding the probable phylogeny of prey-carrying mechanisms. Such mechanisms may or may not have obvious morphological components; in some cases, knowledge of the behavior may help explain the significance of structures which might otherwise be difficult to understand.

Such an undertaking does not seem premature at this time for several reasons. The behavior patterns involved are simple, unambiguous, and subject to little intraspecific variation: indeed, they are often constant throughout major taxa. One needs to maintain the usual healthy scepticism of published observations, but in fact so much has been published on this aspect of behavior that one can usually identify reports which are inconsistent with the general picture. Information on this subject is so widely scattered in the literature that it is impractical to cite all original references in this review. Rather, I shall refer mainly to three general sources, each of which provides fuller documentation as well as bibliographic references. I shall make frequent reference to my own papers, since these papers are recent and pay particular attention to prey carriage. I shall also refer many times to two comprehensive studies of the behavior of solitary wasps. These are Iwata's "Comparative Studies on the Habits of Solitary Wasps" (1942) and Olberg's "Das Verhalten der Solitären Wespen Mitteleuropas" (1959). Although Olberg's book deals with a limited fauna, his remarkable photographs provide irrefutable documentation of the method of prey carriage in certain species. Iwata has reviewed the world literature and has presented an outline of types of prey carriage. He recognizes twelve types, arranged under three major headings. Certain of Iwata's types seem to me poorly documented and possibly incorrect, and his three major groupings seem to me in need of re-evaluation. Nevertheless Iwata's paper is an important pioneering work in this field.

THE ANCESTRY OF WASPS

There has been no recent reconsideration of the systematics of the order Hymenoptera as a whole. The classification and

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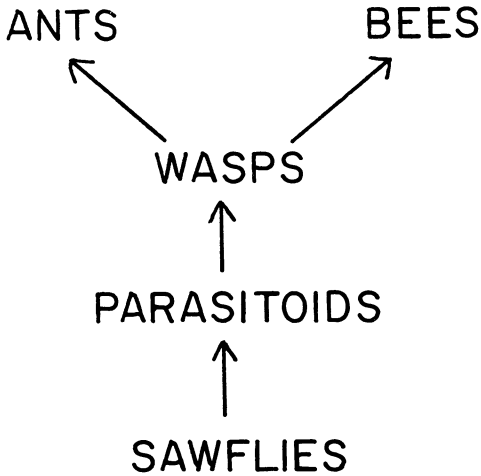

FIG. 1. Diagram showing the most probable relationships of the major groups of Hymenoptera.

arrangement of the families and superfamilies presented in Imms' textbook, as revised by Richards and Davies (1957), is accepted here. Wheeler (1928), although employing an older classification, discussed convincingly some aspects of the evolution of the Hymenoptera. There has evidently been much extinction in the past history of the Hymenoptera, leaving us with a diverse array of forms which may never be classified to everyone's satisfaction. Nevertheless the broad pattern of evolution seems reasonably clear (fig. 1). The wasps occupy a central position in the order, having evolved originally from the sawflies (Symphyta) and later from a common ancestor with an early parasitoid. The ants are generally regarded as having arisen from an unknown stock of early scolioid wasps, the bees from a now extinct stock of sphecoid wasps (see also fig. 6).

The sawflies, parasitoids, and wasps appear in the fossil record in that order. Clearly the wasps cannot have evolved from an extant (or known fossil) group of parasitoids, since all parasitoids exhibit structural simplifications and modifications not found in wasps. Nevertheless, it seems a safe assumption that the ancestral wasps behaved very much as do some of the more generalized Ichneumonoidea today. That is, the female laid her egg directly on the host insect *in situ*, the larva developing upon the host while the latter continued its feeding, being killed only when the parasitoid had nearly completed its development. Quieting of the host by paralyzing substances produced by accessory glands and injected via the ovipositor may have at first functioned to permit deposition of the egg on a more specific part of the body of the host, as well as to permit the female to feed on the body fluids of the host. Temporary paralysis of the host occurs in some Ichneumonoidea and in some primitive, non-nest-building wasps, such as many Tiphiidae. With the development of the first simple nests, paralysis of the prey served to permit safe carriage to the nest and to prevent escape of the prey from the nest. Selection therefore favored more profound and lasting paralysis of the prey. Once set in motion, nest building and prey carriage both tended to become more complex and efficient, but independently of one another. That is, complex nests sometimes evolved in wasps exhibiting simple types of prey carriage—the social Vespidae, for example—and advanced types of prey carriage sometimes evolved in wasps making very simple nests—the solitary wasp *Oxybelus*, for example. These two facets of behavior bear no correlation whatever except that they necessarily had their inception simultaneously. These ideas are summarized in fig. 2.

It is important to remember that primitive wasps, having been derived from parasitoids, utilize a single host specimen per offspring. In the parasitoids there has been an important trend toward what is called "multiple parasitism," which means simply that several offspring develop at the expense of a single host. This trend reaches its ultimate in polyembryonic forms such at *Litomastix* (Encyrtidae), where as many as 3,000 parasitoids may develop in a single *Phytometra* caterpillar. Needless to say, such parasitoids are very much smaller than the host species.

In wasps (other than Bethyloidea), the trend has been in the opposite direction,

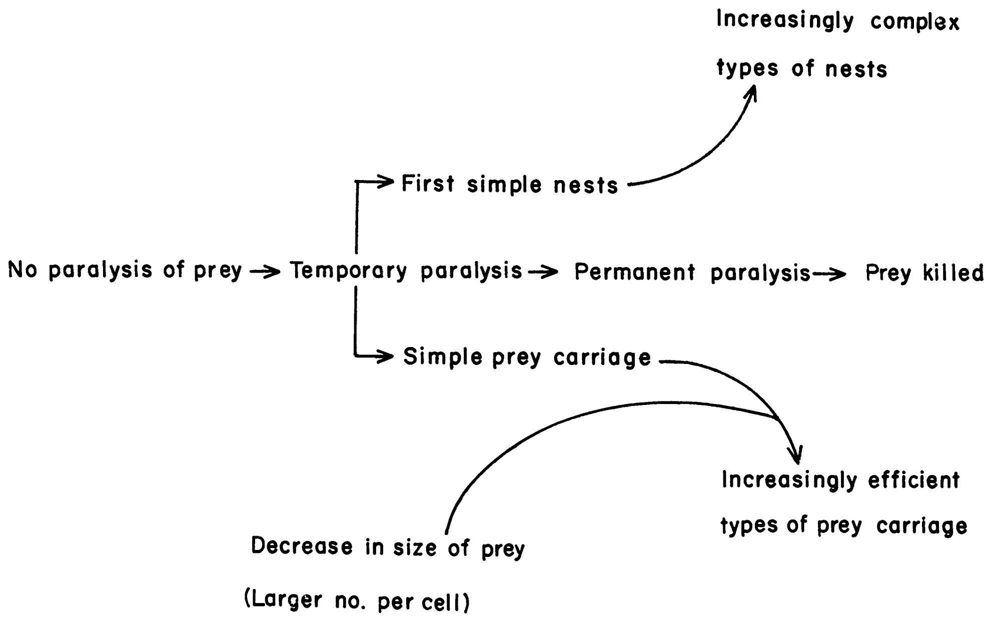

FIG. 2. Schematic representation of some of the factors involved in the evolution of prey-carrying mechanisms.

toward the utilization of several or many host specimens to feed a single larva (fig. 3). Thus the majority of wasps (except in primitive families such as the Tiphiidae, Bethylidae, and Pompilidae) are larger than the arthropods they prey upon. The highest number of prey recorded for a single nest-cell of a wasp is 104, for an aphid-storing species of *Passaloecus* (Sphecidae) (Iwata, 1942). Obviously, the smaller the prey the less of a burden it provides for the wasp carrying it, and it is not surprising that more advanced methods of prey carriage occur in wasps utilizing several prey per nest-cell. To say that in primitive wasps and parasitoids the hymenopteron and its host are equal in size is, of course, not quite correct, even as an approximation. Since the host inevitably contains certain parts which are not eaten or not digested, it follows that it has to be, on the average, larger than the predator. In other words, it is not quite correct to say that $P = H$ in fig. 3; using actual figures compiled by Iwata, H may weigh 0.9 to $8.0 \times P$. To a wasp dragging a paralyzed arthropod several times its own weight, the mere struggle with the force of gravity may preclude the attainment of any appreciable speed or any noteworthy protection against factors which may injure or destroy the prey during transport.

Thus there is an important correlation between prey size and type of prey transport. There is, however, no particular correlation between the taxon of the prey and the type of prey transport, as will be discussed further in a later section. It is true that primitive wasps tend to prey upon phylogenetically earlier types of arthropods (e.g., Tiphiidae on beetle larvae, Pompilidae on spiders, Ampulicidae and Sphecini on Orthoptera). Predatism on such things as adult flies and bees is confined to more advanced groups of Sphecidae, which may also have evolved more advanced types of prey carriage. However, one finds little to support the contention that evolutionary changes in the kind of prey utilized have been closely accompanied by or dependent upon changes in type of prey carriage.

The most important factor to be considered with reference to prey carriage is the

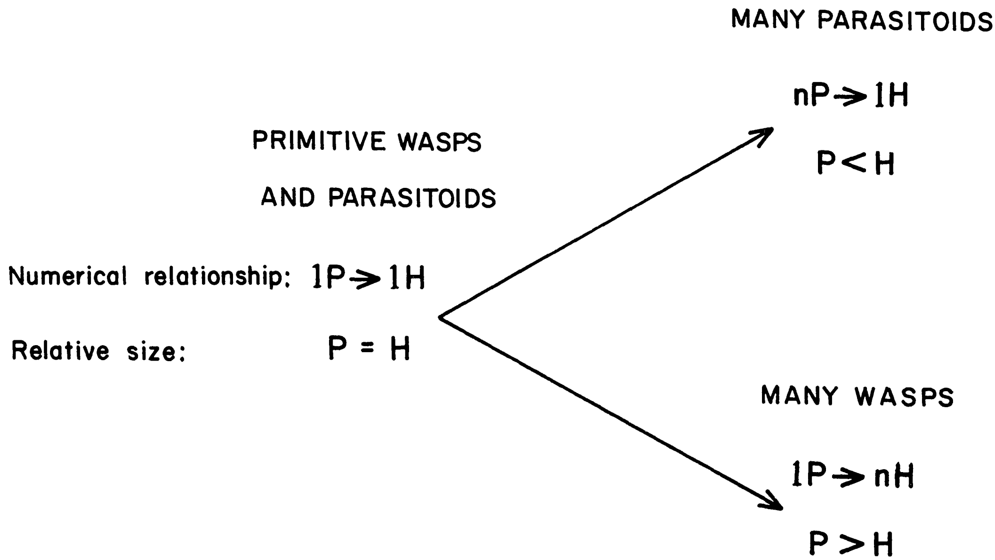

FIG. 3. Trends in the evolution of host size and number. P, predator or parasitoid; H, host.

manner in which the prey is grasped by the wasp. In general terms, the primitive condition is for the wasp to hold the prey in its mandibles; at a more advanced level it is held well back beneath the body by the legs, and finally it is held at and by the posterior extremity of the body, leaving the mandibles and legs free for other functions. The many different methods of prey carriage may be grouped under these three progressively more advanced types, which may be termed respectively mandibular, pedal, and abdominal mechanisms. In the following paragraphs I shall consider the various types and subtypes in turn.

MANDIBULAR MECHANISMS: TYPE ONE (M1)

Certain members of the Scolioidea, finding the subterranean grubs on which they prey lying on top of the ground or in other unsuitable places, simply grasp the grub with their mandibles on any convenient part of the body and drag it backwards into a hole. Behavior of this type can be observed, for example, in the tiphiid genus *Methocha*. The female *Methocha* attacks the larvae of tiger beetles in their vertical burrows in the soil, stings them, oviposits, then leaves the paralyzed grub in its own burrow. When the wasp encounters a tiger beetle outside its burrow, as sometimes occurs, she stings it, grasps it with her mandibles, and proceeds backwards until a suitable hole is located. The prey is generally much heavier than the wasp, and transport is slow and fraught with difficulties. I have observed this behavior twice in the North American *M. stygia*. Iwata records a *Methocha* dragging a larva twenty times its own weight. In most Scolioidea prey transport is facultative, if it occurs at all.

Wasps in which prey carriage is a fixed part of the behavior, that is, those in which there is a definite nest, however crude it may be, typically grasp the prey on some specific part of its body. The vast majority of spider wasps (Pompilidae) grasp the spider by the base of the hind legs and proceed backward; in a few cases the mouthparts or spinnerets are grasped (for specific examples, see Evans, 1953, and Evans and Yoshimoto, 1962). Similar prey transport is exhibited by members of the small, primitive sphecoid family Ampulicidae. As reported by Williams (1919a) and others, these wasps move the cockroaches on which they prey by simply grasping one of the antennae and proceeding backward. The practice of dragging the prey backward over the substrate also occurs in the family Bethylidae, but I am not aware that it occurs in the higher families of wasps, the Sphecidae and Vespidae.

This type of prey transport is essentially "blind," for the important sense organs of the wasp are on the end of the wasp which is headed away from the direction of travel. Many wasps deposit their prey on the ground for varying lengths of time while they either rest, groom, or explore ahead. When the prey is left alone, even for short periods, it is subject to attack by ants, tiger beetles, or wasps of the same or related species (I have observed, among Pompilidae, attacks on the prey from all these sources; see also examples in Evans and Yoshimoto, 1962). In describing this type of prey transport, one finds various authors using such adjectives as "awkward" and "inefficient." It is hard to think of such wasps as having a "prey-carrying mechanism"; rather they are characterized by the lack of any real "mechanism," by the lack of any structural or behavioral specializations which would shorten the time required to get the prey to the nest or reduce the hazards *en route*.

Some Pompilidae exhibit certain variations on this general theme; some of these variations appear to represent transitions to more advanced types of prey transport. In the genus *Dipogon*, the wasps typically walk sideways when dragging a spider, in this way perhaps making better use of their eyes and antennae than they would if walking backward (which they do when ascending a branch or tree trunk). There are also certain spider wasps that normally proceed backward but that now and then—especially when handling a spider of small size—turn around and walk forward (for example, *Anoplius apiculatus*, as reported by Evans, Lin, and Yoshimoto, 1953). Clearly such wasps may be thought of as representing a transition to the next type of prey transport to be discussed, which is forward transport. There are also some spider wasps which, although normally proceeding backward over the ground, are able in some circumstances to take flight with the spider dangling from the mandibles. Although they of course fly forward, when they land they immediately turn and proceed backward. Particularly good examples of this are to be found in the related genera *Sericopompilus*, *Episyron*, and *Poecilopompilus*. It is not uncommon for wasps of these genera to climb backward up an herb or tree and then take flight, gradually losing altitude but gaining much distance by the procedure. That few or no Pompilidae have made the full transition to aerial transport is a consequence of the fact that all Pompilidae use a single spider per cell; therefore they must take large spiders, which can rarely be lifted from the substrate or flown great distances.

Mandibular Mechanisms: Type Two (M2)

Carriage of the prey forward is an obvious improvement over dragging it backward, and the step to forward transport was made by several stocks of wasps independently. The difficulties in forward transport are several: the prey may be difficult to lift for extended periods of time, it may block the view of the wasp, or it may impede walking, especially if the appendages of the prey are long. Consequently most wasps falling in this category exhibit structural or behavioral modifications, usually of a rather simple sort. One notes particularly the long legs and high stance of many wasps which carry their prey forward over the ground.[2] Spider wasps which drag the prey backward characteristically assume a very low stance, the

[2] An apparently unique method of prey transport has been described for the bethylid wasp, *Epyris extraneus* Bridwell. This wasp is depressed and relatively short-legged, but carries a beetle larva larger than itself forward over the ground by grasping a palpus with the mandibles and "slinging it over her back." The prey hides the wasp from view and makes it appear as if the paralyzed beetle larva were "making headway under its own steam" (Williams, 1919b).

body close to the ground and the legs spread widely. Species in which forward transport is fixed, such as the Palaearctic *Pompilus plumbeus*, hold the body far above the ground, walking on the extremities of their legs, so that they can partially straddle the spider (this is shown very well in the photographs in Olberg, 1959, pp. 198, 229). *P. plumbeus* holds the spider by the base of the hind legs, its anterior end forward; apparently the legs of the spider do not provide a serious impediment to the wasp. The North American spider wasp *Priocnessus nebulosus* also proceeds forward, straddling its spider, but in this case the spider is held by the spinnerets.

One major stock of Pompilidae, the Auplopodini, is characterized by forward prey carriage in which the spider is grasped by the spinnerets (less commonly the mouthparts), the wasp straddling the spider. These wasps amputate the legs of the spider shortly after it is captured. This remarkable behavior may have evolved from a simple malaxation of the prey for feeding purposes, as occurs in many wasps; removal of the legs may have been selected for because it improved the efficiency of prey transport. The Auplopodini may have evolved from a wasp not unlike *Priocnessus*, which exhibits essentially the same type of prey carriage but does not amputate the spider's legs.

Some Auplopodini fly with the prey to a considerable extent, but generally as a series of short flights, often starting from some high perch. Certain other Pompilidae fly with their prey with the aid of a "prop": they fly close to the substrate, dragging the prey over the substrate, which bears much of the weight of the spider. The best known of these is *Anoplius depressipes*, a wasp that has attained a considerable notoriety for its practice of towing large *Dolomedes* spiders over the surface of quiet waters (Evans and Yoshimoto, 1962).

With these examples we may leave the family Pompilidae, few if any members of which exhibit sustained flight with the prey or grasp the prey other than with the mandibles. Some of the more primitive genera of true digger wasps (Sphecidae) carry their prey forward over the ground in a manner similar to that of some Pompilidae. The genus *Priononyx* provides an excellent example (Evans, 1958a). These wasps prey on short-horned grasshoppers and use only one hopper per cell. The grasshoppers are often much larger than the wasp, but the wasp carries them rapidly over the ground to the nest, straddling them and holding their antennae with the mandibles. The wasps often vibrate their wings rapidly and thereby gain additional momentum, but they do not ordinarily lift the prey off the ground. These wasps hold their elongate bodies far above the ground, the femora extending out laterally, the tibiae almost perpendicular to them, thus forming a large space beneath the body to accommodate the prey. One of the diagnostic features of the genus *Priononyx* is the notch on the apical margin of the clypeus of the female. The thick antennae of the grasshopper fit into this notch and are supported beneath by the mandibles. An exceedingly tight grasp is doubtless a necessity for moving large grasshoppers effectively.

The related genus *Palmodes* is very similar in its behavior, but wasps of this genus prey upon long-horned grasshoppers, the antennae of which are much more slender and flexible. The clypeus of the female *Palmodes* lacks a notch. Most species of *Palmodes* use a single hopper per cell and therefore use very large hoppers which, however, are propelled over the ground very rapidly with much buzzing of the wings. LaRivers (1945) found that *P. laeviventris*, a predator on the Mormon cricket, used two somewhat smaller hoppers per cell in over half the nests he dug. He also noted some use of the forelegs in supporting the prey during transport. The related genus *Sphex* characteristically uses two or more long-horned grasshoppers per cell; these are carried in flight, held with the mandibles in the usual way but also supported by all the legs. Thus in this one complex of genera (the tribe Sphecini) one observes a change in prey carriage closely correlated with decreasing relative size of the prey.

Excellent transitions are also exhibited within the large genus *Ammophila* (tribe Ammophilini, subfamily Sphecinae). *A. procera* uses a single large caterpillar per cell; the caterpillar is carried over the ground venter-up, head-forward, the wasp grasping it with her mandibles a short distance behind the thoracic legs and also grasping it somewhat farther back with the front legs. This species, when handling a very large caterpillar, moves its long abdomen up and down rhythmically as it moves along, presumably gaining some mechanical advantage thereby. Some species of *Ammophila* use two or three caterpillars per cell, and these wasps take smaller caterpillars which can be carried over the ground more rapidly and without the up-and-down movements of the abdomen. Some species carry the prey short distances in flight, and species such as *harti*, which use many small caterpillars per cell, carry the prey considerable distances in flight. (For further discussion of *Ammophila*, see Evans, 1959a; also Olberg, 1959, the latter with excellent photographs of prey carriage in two species.)

In the sphecid subfamily Larrinae many forms carry their orthopterous prey forward over the ground: for example, *Larropsis*, *Motes*, *Lyroda*, *Dinetus*, *Tachysphex*, and other genera (Iwata, 1942); Evans, 1958c; Olberg, 1959). In each case one or both antennae of the hopper are held in the wasp's mandibles, and in many cases the front legs of the wasp also embrace the thorax of the prey. The use of the front legs is shown clearly in Olberg's photographs of *Dinetus pictus* (p. 271) and *Tachysphex helveticus* (p. 259). Most of these wasps are capable of carrying the prey short distances in flight (all use more than one hopper per cell).

Mandibular Mechanisms: Type Three (M3)

This type includes species which exhibit full aerial transport. Clearly there is no sharp distinction between this type and those members of the preceding type which fly with the prey in a series of short hops. In several genera one finds species which prey upon large insects and fly not at all, others which prey upon slightly smaller insects and fly for short stretches, and still others which take still smaller prey and fly all or most of the way to the nest: *Ammophila* and *Tachysphex* provide good examples. There are also many genera of Sphecidae which fall entirely within this category; most of these either prey on very small insects (for example, *Pemphredon* and *Xylocelia* and their aphids) or are unusually powerful fliers (for example, *Tachytes* and *Sphex* and their grasshoppers).

In the simplest situation, the prey is held with the mandibles alone. This occurs in *Pemphredon* and a number of related genera, also in the spider-hunting genera *Trypoxylon* and *Sceliphron*. Even in these genera, there is evidence that the front legs sometimes help support the prey during flight. Wasps which prey on larger insects generally support the prey in flight with all the legs. This is true of *Sphex*, *Tachytes*, *Astata*, *Mellinus*, and several other genera. When these wasps land at the nest entrance or elsewhere they hold the prey with the mandibles alone, standing on all three pairs of legs (see, for example, photographs in Evans, 1958b, and Olberg, 1959, p. 335).

An interesting and important variation on this theme is provided by certain species of *Aphilanthops* (Evans, 1962) and *Cerceris* (Olberg, 1959, p. 365) (both genera belong to the Philanthinae). These wasps hold their prey with the mandibles and support it in flight with the legs, but it is the middle legs that provide the major support. When *Cerceris arenaria* lands, she stands on all her legs and holds the prey only with the mandibles. *Aphilanthops frigidus* normally continues to hold the prey with the middle legs as well as with the mandibles unless the wasp has some occasion to walk about, in which case the middle legs release the prey. Olberg reports that *Philanthus triangulum* occasionally grasps the antenna of the prey with its mandibles, although the species of *Philanthus* normally use only the middle legs. Thus the Philanthinae show several transitional stages from mandibular to pedal prey carriage.

Another major family of wasps, the Vespidae, apparently had their beginnings as solitary digger wasps but have undergone a remarkable evolution in nesting behavior and in social behavior. Yet prey-carrying behavior is monotonously uniform throughout the Vespidae; all species fly with the prey and carry it in the mandibles (the social forms macerate the prey first and carry it as a ball in the mandibles). In many Vespidae the front legs assist the mandibles, and in Eumeninae such as *Odynerus* and *Eumenes*, which carry whole caterpillars, all the legs support the prey in flight (Olberg, 1959, fig. on pp. 132, 146). Iwata (1942) lists many vespids as using only the mandibles and many as using the mandibles assisted by the legs, but he lists no vespids under any other type of prey carriage. Cooper (1953), in his intensive studies of *Ancistrocerus antilope*, reports that when these wasps walk with their caterpillars, the prey is held by the mandibles alone, although some support is provided by the legs when the wasp is in flight. Cooper found that *antilope* occasionally takes caterpillars too large to lift from the ground, in which case the burden is carried in short hops, the wasp ascending vertical surfaces on foot. Presumably the Vespidae were derived from a stock which carried the prey over the ground, later achieved partial transport in flight (like some of the Pompilidae), and finally full aerial carriage. Doubtless a good many vespids return to the ground to some extent when handling large prey, as also occurs in Sphecidae such as the cicada killer, *Sphecius*.

In general, few structural modifications are associated with this type of prey carriage. There is a general trend toward more compact body form and shorter legs in the higher Sphecidae (also the Vespidae) as compared to the Sphecinae, the Ampulicidae, and the Pompilidae. The spheroidal thorax suggests a stronger flight mechanism, and the shorter legs may be better adapted for holding the prey tightly beneath the body in flight. However, the correlation of body form and type of prey carriage is at most a vague one. Doubtless some of the modifications of the mandibles and clypeus in various stocks of Sphecidae represent devices for better grasping the prey, but I can cite no well-documented specific examples of this.

Pedal Mechanisms: Type One (P1)

Pedal mechanisms involve the use of the legs, unassisted by the mandibles. All wasps employing pedal mechanisms carry the prey in flight. Iwata (1942) lists one wasp, the Australian *Exeirus lateritus*, as carrying the prey over the ground holding it only with the hind legs, but I believe this record to be erroneous. McCulloch (1923) and Musgrave (1925) both state that the middle legs are employed, not the hind legs, and McCulloch mentions that there is much use of the wings and cites one author who states that the wasp "rides the cicada to the nest." I suspect that prey carriage in *Exeirus* is no different from that in the American cicada killer, *Sphecius speciosus*. These wasps are gorytines, and like other members of that tribe they typically carry the prey in flight by the middle legs. But because of the great weight of their prey, the cicada killers have secondarily returned to partial ground transport. *Sphecius* typically takes flight only from some high object and often can be found carrying its prey considerable distances over the ground.

Pedal prey carriage releases the mandibles for other functions, for example, removing impediments from the nest entrance or driving away potential predators. But the major advantage is more subtle than this. True pedal prey carriage involves only the middle or hind legs or both; there are no wasps that carry their prey by the front legs alone (the two examples cited by Iwata require confirmation). When these wasps land at the nest entrance not only are the mandibles free but also the front legs, the major digging devices of wasps. The vast majority of these wasps close the nest entrance with soil when they leave to hunt prey; when they return they scrape it open with the front legs, the soil being thrown beneath the body and behind. They then enter quickly with the prey still clutched beneath them. Closure of the nest surely prevents various parasites and predators (such as hole-searching miltogrammine flies) from finding and entering the nest. The vast majority of wasps employing mandibular prey transport leave the nest open. In certain genera which employ the mandibles (*Ammophila* is a good example) the nest entrance is closed, but in this case the wasp has to put the prey down while the entrance is cleared. It is mechanically impossible to dig open a nest entrance while holding prey with the mandibles, for the front legs are unable to perform their digging movements.

Under pedal mechanisms of type one, I include the many Sphecidae in which the middle legs provide the major support. During flight, the prey may also be supported by the front and hind legs (if the prey is large; see Olberg's photographs of *Philanthus triangulum* carrying a honeybee, p. 354); or only the hind legs may assist the middle legs (if the prey is small; see Olberg's photographs of *Mimesa equestris,* p. 274, and *Lindenius pygmaeus*, p. 375). Although both Iwata and Olberg make a distinction between these two types, the difference seems to me unimportant. In either case the prey is held only by the middle legs when the wasp lands at the nest entrance, the wasp standing on the hind legs and opening the nest entrance with the front legs. Then, as the wasp enters the burrow, the prey is slipped backward and grasped by the hind legs, so that the prey follows the wasp down the small bore of the burrow. This type of prey transport seems characteristic of all Gorytini, Stizini, and Bembicini, also of most Psenini, Crabronini, and Philanthini. Some Crabronini are reported to hold the prey with only one middle leg rather than both (Hamm and Richards, 1926), but others clearly use both middle legs.

One would expect various modifications of the legs which would enable the wasp to obtain a firmer grasp on the prey. Actually there seem to be no modifications in the legs of the females as striking as those which occur in some males and serve to hold the female during copulation. A careful survey of differences in leg structures of female Sphecidae would doubtless reveal that certain of these are associated with differences in type of prey or type of prey carriage. For example, those Bembicini which prey upon adult Lepidoptera exhibit marked reduction in the pretarsal arolia. In this instance there is no proof that the reduction in the arolia is of positive value in carrying moths or butterflies to the nest. In the case of the cicada killer, *Sphecius speciosus*, it has been shown that the very large, hooked tibial spurs actually play an important role in supporting the cicada in flight. When Howes (1919) removed the hind tibial spurs from a female cicada killer, the wasp continued to bring in cicadas, but they were held "suspended, tail down, in a line perpendicular to the wasp's body, the two insects forming the letter T while in the air." In normal prey carriage, the cicada is held parallel to the wasp's body, and it may be surmised that the hind tibial spurs hook onto some part of the cicada's body.

Pedal Mechanisms: Type Two (P2)

A few wasps hold their prey only with the hind legs. In this case the prey is held far back, actually behind the wasp, so that the wasp and its prey are in tandem. The only wasps which without question exhibit this type of prey transport are certain members of the crabronine genus *Oxybelus*. As mentioned above, wasps which carry the prey with the middle legs generally shift it to the hind legs as they enter the burrow. By using the hind legs from the beginning, *Oxybelus* is able to avoid this shifting of its load; this behavior may in fact have evolved by a simple shifting forward in time of this behavioral component. Most other Crabroninae carry the prey with the middle legs.

There has been some dispute as to whether the species of *Oxybelus* actually hold the prey with the hind legs or impaled on the sting. These are among the smallest of digger wasps, and it is not easy to be sure of this point except by very close and repeated observation. There is now no question that some species of *Oxybelus* do impale the fly on the sting (also embracing it loosely with the hind legs when in flight). On the other hand, several reputable observers report that the hind legs alone are used in certain species (for example, Bohart and Marsh, 1960, have recently reported this for *O. sericeum*).

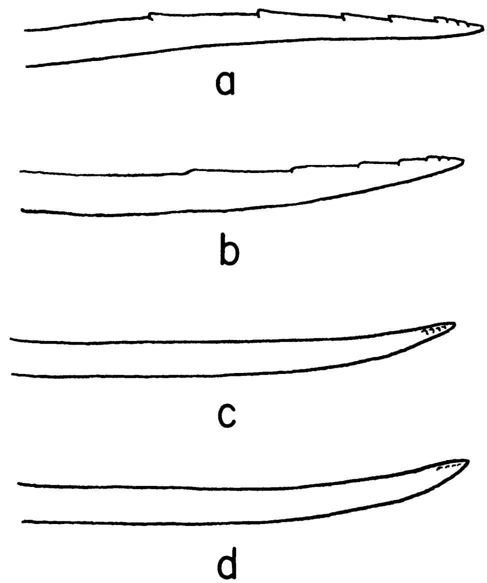

FIG. 4. Stings of several Crabroninae, greatly enlarged. a, *Oxybelus quadrinotatum*. b, *O. sericeum*. c, *Crossocerus elongatulus*. d, *Crabro argus*.

ABDOMINAL MECHANISMS: TYPE ONE (A1)

By holding the prey on the sting, some species of *Oxybelus* have effectively released all three pairs of legs for other purposes. Skeptics of this type of carriage should study Olberg's fine photographs of *O. uniglumis* carrying its fly (1959, pp. 379–381). During flight the hind tarsi of the wasp are also pressed against the thorax of the fly to give it additional support, but when the wasp lands the fly is held only by the sting. The tip of the wasp's abdomen turns down sharply, with the sting being inserted through the side of the anterior part of the thorax; the fly is upside down or more or less on its side during transport, extending straight out or somewhat obliquely behind the body of the wasp (see also Hamm and Richards, 1930, and the references cited therein).

I have observed *O. uniglumis quadrinotatum* and *O. bipunctatum* in some detail, and my observations agree closely with those of Olberg. Close study of the sting of *quadrinotatum* reveals that it possesses minute barbs (fig. 4a). So far as I know these barbs have not previously been described. In all probability they represent an adaptation for holding the prey more securely. Barbs are also present on the sting of *O. sericeum*, a species that carries the prey with the hind legs (fig. 4b). However, while the barbs of *quadrinotatum* are clearly visible under a magnification of 40×, those of *sericeum* are barely discernible under twice that magnification. Whether the barbs of *sericeum* should be considered rudimentary or vestigial is a moot question. Clearly it would be worth studying the stings of other species of *Oxybelus* and attempting to correlate the strength of the barbs with the type of prey carriage.

Nielsen (1933) has reported that another crabronine wasp, *Crossocerus elongatulus*, carries its prey on the sting, and has provided a sketch of prey transport in this wasp. I have studied the sting of this species and found that it is not barbed (fig. 4c). Iwata also records *Crabro cingulatus* and *Aphilanthops quadrinotatus* as carrying the prey on the sting, but I believe these records to be erroneous. The latter species will be considered below, under abdominal mechanisms of type two. The record for *Crabro cingulatus* is based on observations by the Raus (1918), but these authors were not certain on this point. They remark merely that the prey is carried beneath the abdomen, with the tip of the abdomen curving forward beneath the prey, the "sting holding the prey like a hook." I have observed prey carriage in several species of *Crabro* and found that they often do, in fact, embrace the posterior end of the fly with the deflected tip of the abdomen; however, the fly is held principally with the middle legs and the sting does not pierce the fly. This deflection of the tip of the abdomen may, however, represent a precursor of carriage on the sting.

Abdominal Mechanisms: Type Two (A2)

Under this heading are included those wasps that have structural modifications of the apical abdominal segment for holding the prey. This type was not discussed by Iwata, since it has only recently been described (Evans, 1962). It has been established only in *Clypeadon*, a subgenus of *Aphilanthops* (Philanthinae), but probably occurs also in the related subgenus *Listropygia*. *Aphilanthops quadrinotatus*, mentioned above, is a member of the subgenus *Clypeadon* (*laticinctus* is an earlier name for the species). Although this species has been reported as carrying its prey on its sting, the sting of these wasps is very small, and it is doubtful that it pierces the body during transport. The species of *Clypeadon* and *Listropygia* prey upon worker ants of the genus *Pogonomyrmex*. My observations indicate that females of at least three species, after they sting the ant, plunge the tip of their abdomen between two pairs of coxae of the ant and fly off to the nest. The ant is venter-up, its head beneath the abdomen of the wasp, its abdomen extending out behind. Originally I believed that the tip of the wasp's abdomen was inserted between the middle and hind coxae of the ant, but a careful study of motion pictures taken in the summer of 1961 reveals that in *Clypeadon laticinctus*, at least, the insertion is between the front and middle coxae.

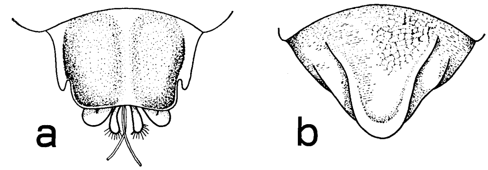

FIG. 5. Apical abdominal tergites of two species of *Aphilanthops* (Philanthinae). a, *A. Clypeadon) haigi*, showing the biconcave tergite, and protruding beyond it the bilobed sternite and the sting and sting-sheaths. b, *A.* (*Aphilanthops*) *frigidus*, showing a pygidial plate typical of many fossorial wasps.

The apical abdominal segment of these wasps is uniquely modified. The apical tergite is expanded and biconcave (fig. 5a), the apical sternite bilobed and deeply concave or biconcave. This double set of concavities appears to embrace the coxae or possibly portions of the mesothorax grooved for reception of the coxae. Probably the wasp exerts pressure on the coxae by forcing apart the tergite and sternite slightly by muscular action. The result is a highly efficient "ant-clamp," by means of which the wasp carries the ant so far behind that it is no impediment whatever to the activities of the wasp. Prey transport in these wasps is very rapid, and I have never seen a wasp drop its prey. There is little doubt that the modifications of the apical tergite evolved from the flattened pygidial plate present in many digger wasps and used for packing soil in the burrow (fig. 5b). Indeed, the related subgenus *Listropygia* was so named by Bohart on the assumption that the elaborate apical segment served as some sort of a scoop for soil (*listron*, shovel, plus *pyge*, rump). I have not observed prey transport in the one known species of *Listropygia*, but I have little doubt that the apical segment functions as it does in *Clypeadon*.

Discussion

The original method of prey carriage in wasps was apparently simply to seize the prey with the mandibles and drag it back-

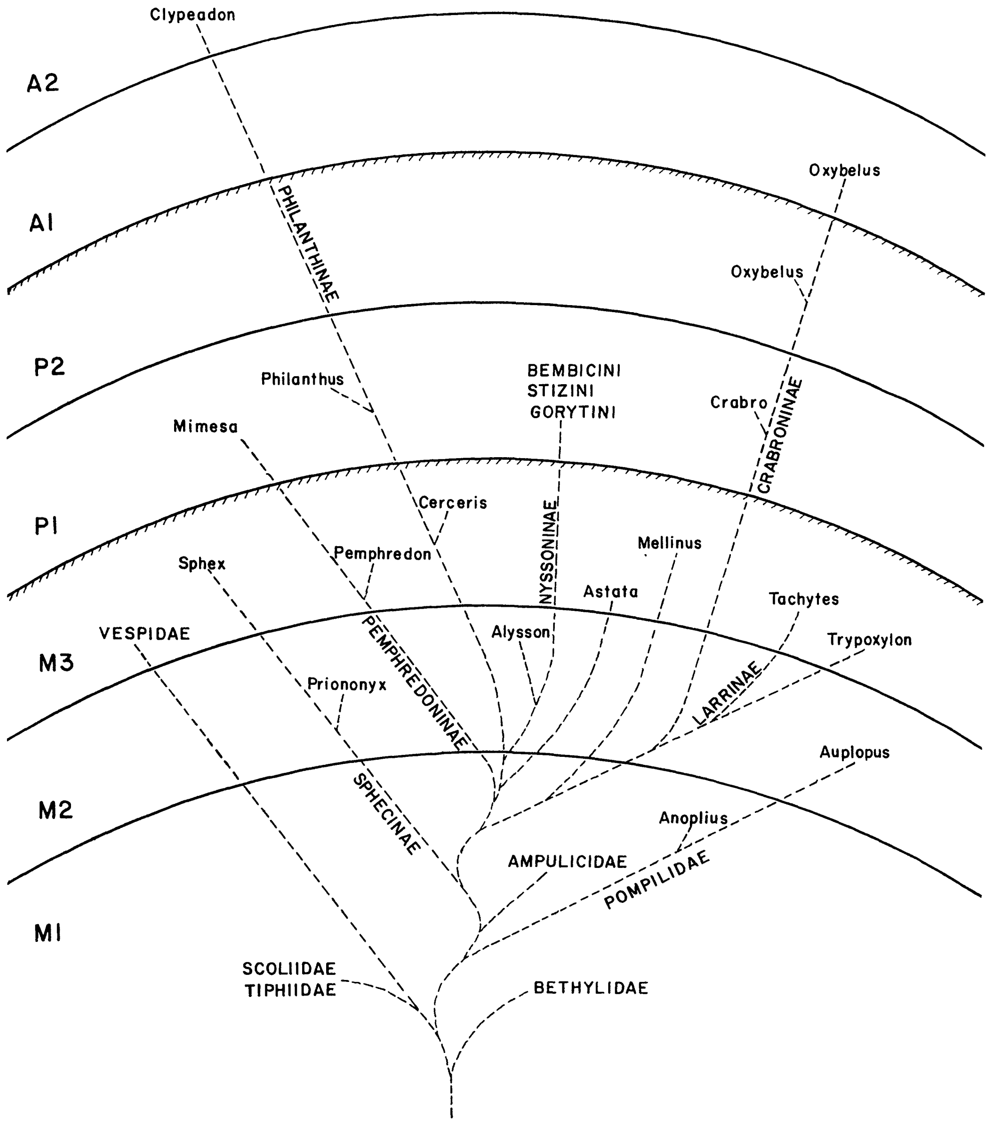

FIG. 6. Phylogenetic arrangement of major stocks and selected genera of wasps, emphasizing type of prey carriage achieved by each stock. M, mandibular mechanisms, P, pedal mechanisms, A, abdominal mechanisms; see text for significance of numbers. (Phylogenetic tree of Sphecidae based on Evans, 1959b).

ward over the ground, a method which is characteristic of the Bethylidae, Ampulicidae, many Pompilidae, and those Scolioidea which move their prey. Forward transport, still employing the mandibles, developed in several stocks of wasps independently. Use of several paralyzed arthropods per nest-cell in certain of these stocks involved the use of smaller prey and permitted the carriage of the prey in flight. Thereafter the tendency was for the prey to be displaced progressively backward in the course of evolution. From its position in front of or beneath the wasp's head, the prey was moved to a position beneath the thorax and abdomen, finally to a position behind the body of the wasp. As one proceeds down the list to progressively more advanced types of carriage, fewer examples can be adduced for each type. Only four stocks of Sphecidae (and none of any other family) have developed pedal prey carriage, and only two of these stocks have progressed further to abdominal carriage (fig. 6).

The structural modifications accompanying these behavior patterns are often of a very generalized type: long legs and high stance in wasps that straddle their prey and carry it on the ground; a trend toward shorter legs and more compact body in wasps carrying their prey in flight. More specific adaptations for holding the prey appear to be uncommon among wasps employing the mandibles or legs, but more careful study will surely reveal more examples. At present one can cite such structures as the notched clypeus of *Prionyx*, apparently a device for holding the antennae of short-horned grasshoppers, and the large, hooked hind tibial spurs of *Sphecius*, which appear to play an important role in holding the cicada in flight. Wasps employing abdominal carriage exhibit structural modifications of the sting or apical abdominal segment, sometimes of unique form, for the abdomen is otherwise devoid of structures capable of holding the prey.

The selection pressures which have molded these behavior patterns have undoubtedly been complex, and different factors may have been of prime importance at different times and in different stocks of wasps. There is no question that wasps exhibiting more advanced types of prey carriage proceed much more rapidly to their nest. Many wasps which fly with their prey (but by no means all!) carry the prey far enough back so that its center of gravity is close to that of the wasp, in this way providing the least disturbance to the normal equilibrium of the wasp. But since these wasps employ several prey per cell, it may actually take a *Crabro*, for example, longer to provision its cell than a *Pompilus*. There is no evidence that any solitary wasp provisions more than about one cell per day; thus greater speed in prey carriage appears to have no effect in increasing the number of progeny of wasps. It does, however, permit the wasps to obtain their prey at some distance from their nests. In *Sphex*, for example, the hunting grounds are often far from the nesting site, but in *Prionyx*, which drags its grasshoppers over the ground, the nests are always within the general area where the prey is captured. The very use of smaller prey, of course, requires greater speed in transport. A *Passaloecus* using 104 aphids per cell cannot afford to bring these in at a rate of one a day, the rate at which most pompilids procure spiders. The development of more advanced types of prey carriage appears to be part of the general picture of adaptive radiation in wasps, enabling them to take diverse types of prey, often at some distance from their nests.

It is also probable that the more advanced types of prey carriage serve to reduce attacks by predators and parasites. Unfortunately there are no quantitative data to support this, and I can only point to the innumerable observations by myself and others indicating that prey in transit may be attacked by miltogrammine flies, by cleptoparasitic wasps such as *Ceropales* (see Olberg, 1959, pp. 231–237), and by ants, tiger beetles, and other roving predators and scavengers. Here speed is unquestionably important, also the protection afforded by holding the prey tightly beneath the body. Still more important may be the avoidance of having to leave the prey on the ground, as pompilid wasps so commonly do. Furthermore, it is only those wasps that employ pedal and abdominal carriage that are able to close the nest entrance when they leave and reopen it without depositing their prey when they return. It is well known that hole-searching miltogrammine flies, which larviposit on the prey, and wasps of the families Chrysididae and Mutillidae, which attack the digger wasp larvae, readily find and enter open holes. That bombyliid flies, which are important parasites of many wasps and bees, deposit eggs indiscriminately in many types of open holes is well established (see, for example, a recent article by Frick, 1962). It is difficult to believe that nest closure is not a device for deterring various natural enemies. That the higher Sphecidae are appreciably more free of parasites than other wasps has not actually been demonstrated. In any event, one might expect some evolution in the behavior patterns of the parasites, adapting them to advances in the behavior of their hosts (e.g., the development of fossorial legs and digging behavior in the miltogrammine fly genus *Phrosinella*).

It is clear that there is no important correlation of type of prey carriage with kind of prey. For example, aphids may be carried in the mandibles (*Pemphredon*) or by the middle legs (*Diodontus*), while flies may be carried with the mandibles (*Mellinus*), the legs (*Bembix*), or the sting (*Oxybelus*). Although the philanthine subgenus *Clypeadon* has a special abdominal device for carrying worker ants, the genus *Tracheliodes* remains true to its subfamily (Crabroninae) and carries worker ants with its legs (Hicks, 1936). From another point of view, one finds that taxa restricted to one type of prey carriage often prey upon a variety of insects. The Bembicini, for example, prey upon stinkbugs, flies, butterflies, and moths, rarely even damselflies, yet they always carry their prey with their middle legs. A striking example is provided by *Microbembex*, a highly evolved genus of Bembicini which "preys" upon dead arthropods of two classes, including insects of at least ten orders. Yet these wasps, whether carrying a spider, a cricket, a caterpillar, or an ant, always employ the middle legs.

Nor is there any correlation with type of nest. The common mud dauber, *Sceliphron*, carries her prey no differently than her ground-nesting relatives. The twig-nesting genus *Ectemnius* exhibits exactly the same type of prey carriage as the related, ground-nesting genus *Crabro*.

Clearly type of prey carriage is "conservative," that is, it is not readily modified even when major reorganizations occur in other, closely integrated aspects of the behavior. Prey carriage often provides excellent generic, tribal, and subfamilial characters. This being the case, one can predict with some confidence how various wasps of unknown ethology will be found to carry their prey. For example, the species of the genus *Bothynostethus* (Larrinae) must surely carry their prey with their mandibles, while the species of *Enoplolindenius* (Crabroninae) surely carry the prey in flight with the middle legs. Also, it seems evident that certain records in Iwata's compilation are in error, for example, the records for *Zyzzyx chilensis* and *Bembix hesione* carrying prey in their front legs. Curiously, in the few groups in which prey carriage is not conservative, the changes in prey carriage seem independent of other aspects of the behavior. The species of *Oxybelus* which employ the sting exhibit no other known behavioral differences from the species which employ the hind legs. Spooner (1948) reports that the nominate subgenus of *Mimesa* carries leafhoppers with its middle legs, while the very similar subgenus *Mimumesa* carries leafhoppers with its mandibles.[3]

Despite many unanswered questions, it is clear that a knowledge of methods of prey carriage is useful to taxonomists and essential to students of the bionomics of wasps. Attention should be focused upon more careful studies of the details of prey carriage, preferably documented with photographs such as those of Olberg. More data on the weight of prey and wasp, on the physics and physiology of carriage, and on the incidence of successful attacks by various parasites and predators, should do much to fill in the details of a picture which can only be sketched in a very preliminary way at this time.

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[3] The generalization regarding *Mimumesa* is based solely on Adlerz' observations on *M. dahlbomi*. Although Adlerz is a very reliable authority, further verification of this point is needed.

Summary

1. Wasps evolved from parasitoid Hymenoptera, and primitive wasps, like parasitoids, use a single host insect or spider for each offspring. Thus the prey is generally as large as or larger than the wasp.

2. Primitive wasps seize the prey with their mandibles and drag it backwards to the nest. Good examples of this can be found in the families Tiphiidae, Bethylidae, Ampulicidae, and Pompilidae.

3. At a more advanced stage, wasps acquired various mechanisms for straddling their prey and proceeding forward over the substrate. This occurs in many Pompilidae and in some Sphecidae.

4. Most Sphecidae, and all Vespidae, use more than one paralyzed insect or spider per cell; thus the prey is slightly to considerably smaller than the wasp. The prey is carried in flight, primitively held by the mandibles, often assisted by the legs.

5. Four stocks of Sphecidae have advanced to full pedal prey transport; that is, the prey is held by the middle or hind legs or both, unassisted by the mandibles.

6. Two stocks of Sphecidae have advanced still further to abdominal prey carriage. In one of these stocks (a portion of the subfamily Crabroninae), the prey is carried on the sting, which in some cases is barbed. In the other stock (two subgenera of the genus *Aphilanthops*, subfamily Philanthinae), the apical abdominal segment itself is greatly modified for clamping onto the prey.

7. The more advanced types of prey carriage permit more rapid provisioning of the nest and presumably provide fewer opportunities for predators and parasites to attack the prey in transit; they also enable the wasp to close the nest upon leaving and to reopen it upon returning without depositing the prey. The employment of rapid prey transport in flight also permits wasps to take their prey at a considerable distance from their nesting site.

Literature Cited

Bohart, R. M., and P. M. Marsh. 1960. Observations on the habits of *Oxybelus sericeum* Robertson (Hymenoptera: Sphecidae). Pan-Pac. Ent. **36**: 115–118.

Cooper, K. W. 1953. Biology of eumenine wasps. I. The ecology, predation and competition of *Ancistrocerus antilope* (Panzer). Trans. Amer. Ent. Soc., **79**: 13–35.

Ducke, A. 1913. Ueber Phylogenie und Klassification der sozialen Vespiden. Zool. Jahrbücher, Syst. **36**: 303–330.

Evans, H. E. 1953. Comparative ethology and the systematics of spider wasps. Syst. Zool., **2**: 155–172.

——. 1958a. Studies on the nesting behavior of digger wasps of the tribe Sphecini. Part I: Genus *Prionony*x Dahlbom. Ann. Ent. Soc. Amer., **51**: 177–186.

——. 1958b. Ethological studies on digger wasps of the genus *Astata* (Hymenoptera, Sphecidae). J. N. Y. Ent. Soc., **65**: 159–185.

——. 1958c. Observations on the nesting behavior of *Larropsis distincta* (Smith) (Hymenoptera, Sphecidae). Ent. News, **69**: 197–200.

——. 1959a. Observations on the nesting behavior of digger wasps of the genus *Ammophila*. Amer. Midl. Nat., **62**: 449–473.

——. 1959b. Studies on the larvae of digger wasps (Hymenoptera, Sphecidae). Part V: Conclusion. Trans. Amer. Ent. Soc., **85**: 137–191.

——. 1962. A review of the nesting behavior of digger wasps of the genus *Aphilanthops*, with special attention to the mechanics of prey carriage. Behaviour, **19**: 239–260.

——, C. S. Lin, and C. M. Yoshimoto. 1953. A biological study of *Anoplius apiculatus autumnalis* (Banks) and its parasite, *Evagetes mohave* (Banks) (Hymenoptera, Pompilidae). J. N. Y. Ent. Soc., **61**: 61–78.

—— and C. M. Yoshimoto. 1962. The ecology and nesting behavior of the Pompilidae (Hymenoptera) of the northeastern United States. Misc. Publ. Ent. Soc. Amer., **3**: 67–119.

Frick, K. E. 1962. Ecological studies on the alkali bee, *Nomia melanderi*, and its bombyliid parasite, *Heterostylum robustum*, in Washington. Ann. Ent. Soc. Amer., **55**: 5–15.

Hamm, A. H., and O. W. Richards. 1926. The biology of the British Crabronidae. Trans. Ent. Soc. London, **74**: 297–331.

——. 1930. The biology of the British fossorial wasps of the families Mellinidae, Gorytidae, Philanthidae, Oxybelidae, and Trypoxylonidae. Trans. Ent. Soc. London, **78**: 95–132.

Hicks, C. H. 1936. *Tracheliodes hicksi* Sandhouse hunting ants (Hym. Sphecidae). Ent. News, **47**: 4–7.

Howes, P. G. 1919. Insect Behavior. Gorham Press, Boston. 176 p.

Imms, A. D. 1957. A General Textbook of Entomology. Ninth edition, revised by O. W. Richards and R. G. Davies. Methuen, London. 886 p.

Iwata, K. 1942. Comparative studies on the habits of solitary wasps. Tenthredo, **4**: 1–146.

LaRivers, I. 1945. The wasp *Chlorion laeviventris* (Cresson) as a natural control of the Mormon cricket (*Anabrus simplex* Haldeman). Amer. Midl. Nat., **33**: 743–763.

Leclercq, J. 1954. Monographie systématique, phylogénétique et zoogéographique des hyménoptères crabroniens. Lejeunia, Liege. 371 p.

McCulloch, A. R. 1923. War in the garden. Australian Mus. Mag., **1**: 209.

Musgrave, A. 1925. The sand wasp's burrow. Australian Mus. Mag., **2**: 243.

Nielsen, E. T. 1933. Sur les habitudes des Hyménoptères aculéates solitaires. III (Sphegidae). Ent. Meddel., **18**: 259–348.

Olberg, G. 1959. Das Verhalten der solitären Wespen Mitteleuropas. Deutsch. Verlag Wissenshaften, Berlin. 402 p.

Rau, P., and N. Rau. 1918. Wasp Studies Afield. Princeton Univ. Press. 372 p.

Spooner, G. M. 1948. The British species of Psenine wasps (Hymenoptera: Sphecidae). Trans. R. Ent. Soc., London, **99**: 129–172.

Wheeler, W. M. 1928. The Social Insects: their Origin and Development. Harcourt Brace, New York. 378 p.

Williams, F. X. 1919a. Philippine wasp studies. Bull. Hawaiian Sugar Planters' Assoc., Ent. Ser., no. 14. 186 p.

——. 1919b. *Epyris extraneus* Bridwell (Bethylidae), a fossorial wasp that preys on the larva of the tenebrionid beetle, *Gonocephalum seriatum* (Boisduval). Proc. Hawaiian Ent. Soc., **4**: 55–63.