

Stinging Behaviour of Solitary Wasps

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I. INTRODUCTION

In contrast to social wasps, which sting basically for defence, in solitary wasps stinging evolved mainly in relation to capture of an insect or spider prey which was used to feed their progeny and/or themselves. Solitary wasps

will sting occasionally for defence if forced to do so, however, and some, like Mutillidae (velvet ants) and Bethyridae, can inflict rather painful stings. The present chapter will deal exclusively with stinging of a host or a prey and with the observable behavioural effects of the stings on the prey.

A. Early Observations on the State of the Prey Stored by Solitary Wasps

As has been pointed out in the historical introduction (Chapter 1) early information on solitary wasps is very scanty, in contrast to that on social wasps, which are of more direct interest to humans. Most of the early reports describe the state of the prey found in the nests of solitary wasps. Some questions asked were: is the prey killed and preserved with an antiseptic; is it only disabled or paralysed and was it done by stinging or by biting? Early information on stinging methods themselves is even more incomplete and essentially reduced to a few chance observations.

B. Early Observations on Stinging and Paralyzing Behaviour

As early as 1802, Latreille had reported that the bee-wolf wasp (*Philanthus triangulum*) stings honey-bees at the juncture between head and thorax (see Chapter 1). Later, Walckenaer (1817) described how a *Cerceris* wasp stung a halictid bee 'under the head'. Darwin, during his voyage (1831–1836), observed, near Rio de Janeiro, a giant spider wasp, the tarantula hawk or *Pepsis*, which attacked a *Lycosa* spider and sting it twice under the cephalothorax (in Engel, 1962, p. 35). This list of initial observations is probably far from complete.

Fabre, from 1855 on, began to publish detailed observations on stinging and paralysis in a number of wasp-prey systems. He first (1855, 1879) challenged Dufour, who had concluded that prey were dead and preserved with an antiseptic. Fabre vividly described how he offered a cricket to a prey-laden 'Yellow-winged Spheg', improperly labelled *Sphex flavipennis* (probably *S. rufocinctus* or *Chlorion maxillosum*). After an initial scuffle, the cricket was laid down and stretched on its back. The wasp, belly to belly with the prey and in the opposite direction, neutralised the motions of the cricket with her fore and middle legs, pushed wide open with her hind legs the joint of the neck and delivered a first sting there. The wasp then stung a second time, between two anterior thoracic segments, ventrally, and then apparently made an attempt to deliver a third sting in the direction of the juncture of the abdomen and thorax, but finally did not sting (Fabre admitted, however, that he might have overlooked it). Fabre also compared stinging methods among wasp species, particularly the number of stings, as apparently related

to the number of separate nerve centres (see Chapter 1, and Fabre, 1879, Vol. 1, pp. 108–112). Such rather deeply paralysed prey were kept alive in glass vials for a month and a half.

Fabre found also cases in which stinging was apparently indiscriminate and resulted in the death of the prey (e.g. flies stung by *Bembix* wasps) (Vol. 1, p. 272, etc.). He also thought that the stinging of honey-bees in the neck by the bee wolf (*Philanthus triangulum*) killed the prey (Vol. 4, pp. 211–240). In most other wasp-prey systems he was impressed by the remarkable overall precision of the stings.

However, Fabre was also well aware of the possibility of considerable variability of stinging within species. Thus he listed numerous deviations from the ‘general rule’ in the caterpillar-hunting wasp *Podalonia hirsuta* (Scopoli) (his ‘Hairy Ammophila’). He stated that the insect is not a machine, unvarying in its mechanism (Vol. 4, pp. 250–251). Critics of his conclusions seem to have overemphasised his claims of precise and rigid behaviour, largely taken out of context, since his main purpose was to make a contrast between ‘blind’ instinctive behaviour of insects and ‘intelligent’, plastic behaviour of humans and many other mammals.

At any rate his observations and conclusions did not remain unchallenged for very long, as we shall see now.

C. Early Controversies

1. *Paralysis or Death of the Prey?*

Dufour was not alone in his claim that prey of solitary wasps were killed (at least of *Cerceris* and *Palarus*); he was joined by many authors (e.g. the Peckhams). These authors wondered whether paralysis was necessary, or even useful, when so often the larvae were found to eat dead or decaying prey without ill effects (see, for instance, Rabaud, 1919, pp. 61–63 and more recently Molitor, 1937, p. 300). In contrast, Roubaud (1916, 1917), who criticised Fabre on several other accounts, felt that life of the prey was indeed of crucial importance, since some eumenid wasps carefully inspect their caterpillar prey and discard the ones that are damaged or dead (1916, p. 72).

2. *Fixity and Variability of Stinging in General*

Roubaud (1916, 1917) (in Eumenidae), Rabaud (1909–1919) (in *Mellinus arvensis*), Ferton (1890–1912) (in spider wasps), the Peckhams (1905) and the Raus (1918), among several other early observers, found much evidence of intraspecific variability of stinging, particularly in hunters of caterpillars

(eumenid wasps or sphecid wasps such as *Ammophila*, *Podalonia*). Ferton (1897), on the basis of his early work on spider wasps (Pompilidae), had concluded that some species did and others did not possess 'paralysing skills'. He later recognised his error and occasionally observed precise stinging in the supposedly 'unskilled' species, presumably when circumstances were more favourable. The same author (1897, p. 14) also observed that *Tachysphex julliani* (a sphecid wasp) stung small versus large specimens of its mantid prey once or several times, respectively. This suggests that the number of stings might depend in part on the size of the prey.

3. *Variability of the Effects on the Prey*

There is little doubt that variability of stinging is reflected in a corresponding variability of the state of the stung prey (see, for instance, Ferton, 1891, from p. 5 on; 1894, p. 219; 1897, pp. 11–13; 1910, pp. 163–171; Rau and Rau, 1918, pp. 62, 119). Sometimes, within the same cell, some prey are found dead, others deeply paralysed and a few can even show various degrees of recovery and/or imperfect paralysis.

4. *Stinging and the Nerve Centres of the Prey*

Critics also questioned the claims that Fabre had made that the nerve centres of the prey were the main or exclusive targets of stinging. Variability of stinging, postulated extensive diffusion of the venom and existence of a limited number of 'soft spots' on the prey were used as alternative hypotheses (see, for instance, Ferton, 1902; Roubaud, 1917).

Such controversies raise a number of very complex problems that are best discussed later (Section III), after reviewing more recent studies and observations made on a broader range of species. Results of recent studies of venoms, not available to the early authors, will also be taken into consideration.

II. OBSERVATIONS ON STINGING IN SELECTED GROUPS OF WASPS

This section deals primarily with observational, descriptive studies of stinging and its behavioural effects on the prey. Experimental studies, controversies and detailed analysis will be considered in Sections III and IV.

For general accounts and reviews of the biology of solitary wasps, the reader is referred to Evans (1963: *Wasp Farm*); Evans and Eberhard (1970:

The Wasps, etc.). Olberg's book (1959) is a treasure house of outstanding photographs of many species and behaviours. Malyshev (1968), Iwata (1942, 1972) and others also review the biology of wasps.

A. Some Terebrantia (Parasitica)

A number of these nonaculeate wasps use their ovipositor (not yet separated from the stinging apparatus, see Chapter 1) for stinging. They inoculate various toxic substances or poisons into their hosts. This can result in temporary or permanent paralysis or even death of the hosts. Generally speaking, ectoparasitic forms have a more potent venom (Iwata, 1972). Clausen (1940), Iwata (1942, 1972), Malyshev (1968), Askew (1971) and others discuss extensively the biology of these wasps, so only a few examples of stinging will be used here (additional information is summarised in Table I). General classification follows that used by Marsh, Carlson *et al.*, in Krombein *et al.* (1979), but no attempt has been made to update scientific names found in the references.

1. *Ichneumonoidea*

Some of these wasps, which use varied hosts, have an enormously developed, thread-like ovipositor.

a. Braconidae. Some primitive ectoparasitic forms use cryptic larvae as hosts and paralyse them permanently (e.g. in Krombein *et al.*, 1979, p. 144). Apparently, some endoparasitic forms also do this (in Clausen, 1940, pp. 28–29). Feeding on the body fluids of the host is sometimes associated with stinging (*Microbracon*) (Krombein *et al.*, 1979, p. 122). *Cedria paradoxa* Wlkn. stays with its paralysed caterpillar host until her progeny has pupated, a rare case of 'maternal' behaviour in the Terebrantia (in Malyshev, 1968, p. 206). Temporary paralysis is found in some forms (about 1 hr in *Microbracon pini* Mues. and 1–2 min in *Alysia manducator*) (Clausen, 1940, pp. 28–29). Complete recovery has been reported for larvae of *Ephestia figulilella* Greg. stung by *M. hebetor* Say. Death can also follow, however, particularly in the case of repeated attacks and resulting poison overdose, as was found in dipterous larvae parasitised by *Alysia manducator* (Clausen, 1940, p. 29) or hymenopterous larvae stung by *Apanteles* or *Meteorus* (Clausen, 1940, p. 200). Oviposition within the host does not always involve piercing with the ovipositor. For instance, *Microctonus melanopus* Ruthe often inserts the ovipositor through the anal opening of its host (Clausen, 1940, p. 28). Some

Table 1
Terebrantia (Parasitica)^{a,b}

Wasp	Prey	Information and source
Ichneumonidea		
Braconidae		
<i>Alysia manducator</i>	[D (I)]	Clausen [1940, 29: E (R, usually 1-2 min, K, RS)]
<i>Apanteles</i>	Hy (I)	Clausen [1940, 200: Muesebeck, 1931: E (usually K)]
<i>Cedria paradoxa</i>	Pyralids [L (I)]	Malyshev [1968, 206: S (/)]
<i>Coeloides dendroctoni</i>	Bark beetles [C (I)]	Clausen [1940, 29: E (P usually 2-3 days; then K)]
<i>Coeloides pissodis</i>	(I)	Clausen [1940, 29: E (Pa, smt K)]
<i>Cosmophorus henschelei</i>	Scolytids (C)	Clausen [1940, 29: E (Rc usually 1 hr)]
<i>Meteorus</i>	Hy (I)	Clausen [1940, 200: Muesebeck 1931: E (usually K)]
<i>Microbracon</i>	—	Clausen [1940, 122: feed on prey]
<i>hebetor</i>	<i>Ephesia figulifella</i> (I)	Clausen [1940, 29: E (Rc)]
<i>pini</i>	<i>Pissodes strobi</i> [C (I)]	Clausen [1940, 28: E (T usually 1 hr)]
<i>Microtonus</i>	—	Clausen [1940, 28: Speyer, 1925 in Ruthe: O (BS: anus)]
<i>melanopus</i>	—	Clausen [1940, 28: O (BS: anus)]
Aphidiidae		
<i>Monoctonus paludum</i>	Aphis (Ho)	Askew [1971, 152: O (BS: in compound thoracic ganglion)]
Ichneumonidae		
<i>Exeristes</i>	(I)	Clausen [1940, 73: E (usually K, or Pa)]
<i>Sericotimpia sagrae sauteri</i>	Bagworms [L (I)]	Iwata [1972, 46-47: E (Pa)]
<i>Zaglyptus varipes</i>	A	Clausen [1940, 69, E (K: Nielsen, 1935)]
<i>Zaglyptus iwatai</i>	<i>Clubiona japonica</i> (A)	Iwata [1972, 41-42: S (/); E (Pa or K)]
Polysphinctini	A	Iwata [1972, 41-42: S (/); O (BS); E (T)]
<i>Polysphincta</i>	A	Clausen [1940, 73: E (T; molt inhibited)]
<i>eximia</i>	A	Clausen [1940, 73: S (H: mouth?); Malyshev [1968, 108: S (H: mouth); E (T)]
<i>Paniscus</i>	L (I)	Clausen [1940, 69: E (A, or C, T)]

<i>(Netelia) ocellaris</i>	<i>Agrotis segetum</i> [L (0)]	Malyshev [1968, 108-109: S (A, end of abdomen; Fig); E (quieter)]
<i>Tryphon incestus</i>	<i>Lophyrus</i> [Hy (0)]	Clausen [1940, 69, 86: O (BS, C: egg pedicel in neck, Fig)]
<i>Exenterus</i>	—	Clausen [1940, 4: O (egg embedded, wound of host)]
<i>Anisoctenion alacer</i>	—	Clausen [1940, 4: O (BS: egg embedded, wound of host)]
<i>Hemiteles hungerefordi</i>	<i>Gyrinus</i> [C (0)]	Clausen [1940, 73: E (stung; no paralysis but development inhibited)]
<i>Aenoplex carpocapsae</i>	Codling moth [L (0)]	Clausen [1940, 72: McClure: E (Pa, X = 26 days, maximum 73 days)]
<i>Spilocryptus extrematis</i>	Cecropia [L (0)]	Clausen [1940, 72-73: E (K, but preserved)]
<i>Amblyteles subfuscus</i>	Cutworms [L (0)]	Iwata [1972, 44: O (BS: salivary glands)]; Askew [1971, 149, 152: O (BS: salivary glands)]
<i>Heteropelma calcarator</i>	Noctuidae [L (0)]	Iwata [1972, 44: O (BS: mouth, anus)]; Askew [1971, 149, 152: O (BS: guts)]
Chalcidoidea		
Torymidae		
<i>Monodontomerus aereus</i>	Gypsy moth [L (0)]	Clausen [1940, 200: Muesebeck, 1931: E (usually K)]
Pteromalidae		
<i>Pirene graminea</i>	<i>Contarinia pisi</i> (0)	Clausen [1940, 125: E (T)]
<i>Cheitropachys colon</i>	Scolytidae [C (0)]	Clausen [1940, 189: E (Pa)]
<i>Habrocytus</i>	L [I]	Clausen [1940, 124: E (Pa)] Askew [1971, 137: S (/)]
<i>cerealellae</i>	Grain moths [L (0)]	Clausen [1940, 124: S (pumps venom, maximum 10 min)]; Askew [1971, 137: S (/)]
<i>cioniciida</i>	<i>Cionus weevils</i> [C (l, p)]	Clausen [1940, 122: Lichtenstein, 1921: feeds on prey through a tube]
<i>Dibrachys</i>	—	Clausen [1940, 124: E (Pa)]
<i>clisocampae</i>	Wax moths [L (0)]	Clausen [1940, 125: E (K)]
<i>Dibrachoides</i>	—	Clausen [1940, 124: E (Pa)]
<i>dynastes</i>	—	Clausen [1940, 124: S (3-100! may require up to 8 hr)]
Eurytomidae		
<i>Eurytoma appendigaster</i>	L (0)	Clausen [1940, 207: S (/), also feeds on prey]
Chalcidoidea		
<i>Lastochalcidia igiliensis</i>	Ant lions [N (0)]	Steffan [1961: S (T)]
Eupelmidae	Usually eggs	Clausen [1940, 193-194: S (often feed only)]
Encyrtidae	—	Clausen [1940, 4: O (some: BS: in brain or ganglion; some: egg stalk inserted in puncture)]
<i>Aphelinus</i>	Aphids (Ho)	Clausen [1940, 159: S (often licks punctures)]

(continued)

Table I (continued)

Terebrantia (Parasitica)^{a,b}

Wasp	Prey	Information and source
<i>Aphelinus jucundus</i>	Aphids (Ho)	Clausen [1940, 166: E (P or K if young host, or T)]
<i>Aphytis chrysomphali</i>	Aphids? (Ho)	Clausen [1940, 159: S (only for feeding); O (not related with stinging)]
<i>Coccophagus saintebeanvei</i>	Aphids? (Ho)	Clausen [1940, 159: Compere: O (BS: anus)]
<i>Coccophagus basalis</i>	Scale insects (Ho)	Askew [1971, 138: O (BS: in subesophageal ganglion)]
<i>Diversinervus elegans</i>	—	Clausen [1940, 4: O (BS: intestine)]
<i>Encyrtus</i>	—	Clausen [1940, 4: O (BS: egg stalk in puncture)]
<i>Microterys</i>	—	Clausen [1940, 4: O (BS: egg stalk in puncture)]
<i>clauseni</i>	—	Clausen [1940, 4: O (BS: egg stalk in puncture)]
<i>Euxanthellus</i>	—	Clausen [1940, 4: O (BS: in intestine)]; Askew [1971, 138: O (BS: in intestine)]
Eulophidae	<i>Ceroplastes</i> (Ho)	Clausen [1940, 4: O (BS: egg stalk in puncture)]
	Leaf miners	Clausen [1940, 139: S (K); O (smt egg stalk in puncture)]
<i>Eulophus viridulus</i>	<i>Pyrausta nubilalis</i> [L (l)]	Clausen [1940, 137, 139: E (Pa); Malyshev [1968, 206: S (prick/ovipositor)]
<i>Microplectron fuscipennis</i>	<i>Diprion sertifer</i> [Hy (p)]	Clausen [1940, 138: E (l)]
<i>Diaulius</i>	Leaf miners (l)	Clausen [1940, 139: E (K)]
<i>Euplectrus</i>	—	Clausen [1940, 4: O (BS: egg stalk o in puncture)]
<i>platyphenae</i>	Noctuidae [L (l)]	Clausen [1940, 150: E (not Pa at oviposition time)]
<i>bicolor</i>	Noctuidae [L (l)]	Malyshev [1968, 204: S (2-3); E (Rq)]
<i>Elachertus</i>	<i>Artona trisignata</i> [L (l)]	Clausen [1940, 152-53: S (pumps venom usually 10 min and feeds); E (T); O (BS: between A1 and A2)]
<i>affinis</i>	<i>Polychrosis ambigua</i>	Clausen [1940, 153: Silvestri, 1910c: E (no Pa)]
<i>Melittobia acasta</i>	Bees [Hy (l)]	Malyshev [1968, 212-13: S (ovipositor pricks, V)]; Askew [1971, 136: E (fresh up to 9 months)]
<i>Elasmus nepantidis</i>	L (p)	Clausen [1940, 118: S (/); O (near host)]
<i>Elasmus hispidarum</i>	<i>Nepantlis</i> [L (l)]	Clausen [1940, 118: S (pierces leaf); E (P)]
<i>Asympiesella</i>	Leaf-mining larvae	Clausen [1940, 139: E (K)]

Proctotrupoidea			
Platygasteridae			
<i>Inostemma boscii</i>	<i>Contarinia</i>	—	Clausen [1940, 241: O (BS: brain)]; Iwata [1972, 45: O (BS: embryo or brain)]
<i>Trichacis remulus</i>	—	—	Clausen [1940, 241: O (BS: posterior portion nerve chain)]
<i>Platygaster zosine</i>	—	—	Clausen [1940, 4, 241: O (BS: mid-intestine; cannot develop elsewhere)]

^aExplanations of symbols and condensed information: Prey (second column): arachnids (A), Orthoptera (O), Hemiptera (He), Homoptera (Ho), Neuroptera (N), Coleoptera (C), Lepidoptera (L), Diptera (D), Hymenoptera (Hy); larvae [l], pupae [p]; Information and source (third column): in parentheses, year of publication, then page number(s). Following the colon, information on stinging(s): O, oviposition; RS, resting; CH, chewing, squeezing with mandibles; +, sting order, when known, otherwise comma separates stings; St, sting(s); numbers that precede and follow symbols indicate number of stings and segment, leg pair, stung (e.g. 3 T1 means 3 stings to first thoracic segment); H, head (neck, throat); M, mouth; T, thorax; A, abdomen; L, leg pair; Seg, body segment; CNS, central nervous system; ggl, ganglionic mass(es); btw, between segments; leg pairs, etc.; wnd, sting wounds studied. Qualifiers: R, random or irregular; pr, preferentially; BS, body site specific. Kind of information: Ph, physiological; ES, experimental; Ve, venom study. Information on effects (E) of stinging: K, killed or dead; C,I,D,L,PT, complete, incomplete, deep, light, permanent and temporary paralysis (Pa), respectively; R, recovery, which can be quick (Rq), slow (Rs), complete (Rc), or incomplete (Ri); LOC, localised effect; NI, not immediate (delayed); MV, movements possible; TW, twitching only; A, very active, NA, normal activity resumed after recovery; SL, sluggish after recovery; durations expressed in minutes (min), hours (hr), days (d) or weeks (wk). General qualifiers: V, variable; C, rather constant; s, several; f, a few; # or o, usually, often; smt, sometimes; m, many; N, number of cases observed, reported; /, no details given or found; dt, detailed reports.

^bTo save space, in the first column, authorities for the scientific names have been omitted after the species' names (which are not updated, except in Table V). In the second column: l.h. and s.h., long- and short-horned (grasshoppers), respectively. The tables (particularly other than Table V) are illustrative, not exhaustive.

constancy of body areas of the prey used by the wasps (body site specificity) is already in evidence. Thus several braconids place their eggs in nerve ganglia (Askew, 1971, p. 152).

b. Aphidiidae. These wasps use mainly Aphids as hosts and provide some additional examples of body site specificity. Thus the eggs of *Monoctonus paludum* are placed precisely in the mass of fused thoracic ganglia. This suggests that aculeate wasps might also be capable of inoculating venom within or near the nervous system of their prey, in spite of widespread belief to the contrary.

c. Ichneumonidae. These wasps are mostly parasites (or parasitoids) of insects with complete metamorphosis or of spiders. Some are ectoparasites and usually paralyse their host (e.g. *Rhyssa*), in most cases temporarily. Sometimes the punctures are used for insertion of the egg pedicel, particularly in some Tryphoninae such as *Anisoctenion alacer* Grav. and *Exenterus* spp. (Askew, 1971, p. 147; Clausen, 1940, p. 4). *Tryphon incestus* Holmg. inserts the egg pedicel in the neck of the host larva (*Lophirus*) (Clausen, 1940, p. 69).

Body site specificity for egg-laying, stinging, or both, is also found in Ichneumonidae. Thus some *Paniscus* sting rather large caterpillars in the thorax prior to inserting the eggs (Clausen, 1940, p. 69), whereas *Polysphincta eximia* Schm. is said to insert its sting in the mouth of spiders (Clausen, 1940, p. 73). Body site specificity of egg laying in the Polysphinctini has been reviewed by Iwata (1972, pp. 52–53). Interestingly, it is rather low when compared with the aculeate Pompilidae, which also prey on spiders, but often on larger and more aggressive, mobile ones. Several species of *Exenterus* lay their eggs on parts of the body of sawfly larvae that are characteristic for each species of wasp. *Heteropelma calcator* lays its eggs in the guts of its host and *Amblyteles subfuscus* in its salivary glands (in Askew, 1971, pp. 149, 152).

Apparently endoparasites seldom, if ever, paralyse their host permanently (in Askew, 1971, p. 149). When stinging occurs, its effects on the host vary greatly from one species to another. For example, stinging of *Gyrinus* larvae by *Hemiteles hungerfordi* Cush. does not result in paralysis at all but inhibits further development (in Clausen, 1940, p. 73). Even within the genus *Paniscus* much variation has been recorded. Eggs can be deposited on active or completely (but temporarily) paralysed caterpillars (Clausen, 1940, p. 69; in Malyshev, 1968, p. 108). *Paniscus (Netelia) ocellaris* stings one of the last body segments of the cutworm *Agrotis segetum* in a spot that is not within or near the nervous system. Therefore, the effects on the host must depend either on diffusion of the venom to the nervous system and/or its action on the neuromuscular system. Stinging results in slower movements of the host. The wasp then oviposits behind the second thoracic segment (Shevyrev, 1912, in

(Clausen, 1940, p. 108). The substance injected by some species such as *Spilocryptus extrematis* is said to have a pronounced preservative effect, even if it kills the host. In permanently paralysed hosts, such as codling moth larvae stung by *Aenoplex carpocapsae* Cush., preservation over as many as 73 days (and an average of 26 days) has been reported (in Clausen, 1940, p. 72). In some species death can only result from repeated attacks (e.g. *Exeristes*) but in others is the normal outcome of stinging (e.g. spiders stung by *Zaglyptus variipes*) (Nielsen, 1935, in (Clausen, 1940, p. 69). The mouth stings of *Polysphincta eximia* Schm., however, paralyse spiders only temporarily but apparently also inhibit moulting (in Clausen, 1940, p. 73).

2. Chalcidoidea

Most are small wasps of very diverse biology, including some phytophagous forms, such as the remarkable 'fig wasps'. In some forms the larva searches for the host, which varies widely in this group.

a. Torymidae. Such wasps as *Monodontomerus aereus* Wlk. sting and kill their hosts, which are larvae of Hymenoptera.

b. Pteromalidae. These wasps (and also Eurytomidae) permanently paralyse larvae of Lepidoptera or Coleoptera and feed upon the fluids exuding from the puncture(s). Some, like *Habrocytus cionicida* and *H. cerealellae* Ashm. use a feeding tube constructed with the ovipositor (Lichtenstein, 1921, and Fulton, 1933, respectively, in Clausen, 1940, pp. 122–124). During stinging, which can take up to 10 min, the latter species pumps several droplets of venom. Stinging can require up to 8 hr for *Dibrachoides dynastes*, which delivers 3–100 stings until its host becomes completely motionless (Clausen, 1940, p. 124). In other species, the host consistently dies (e.g. larvae of the wax moth *Galleria mellonella* L. stung by *Dibrachys clisiocampae*) and even decays, the larvae of the parasite becoming then scavengers (Clausen, 1940, p. 125).

c. Chalcididae. *Lasiochalcidia igiliensis* achieves the remarkable feat of inserting the ovipositor between head and thorax while being seized within the formidable mandibles of the predacious ant-lion larva, a method also used by methocine wasps that attack predacious tiger beetle larvae (described later) (Steffan, 1961) (see Fig. 1).

d. Eupelmidae. Members of this group sting eggs instead of larvae and feed on the fluids that exude from the puncture, with or without subsequent oviposition (in Clausen, 1940, pp. 193–194).

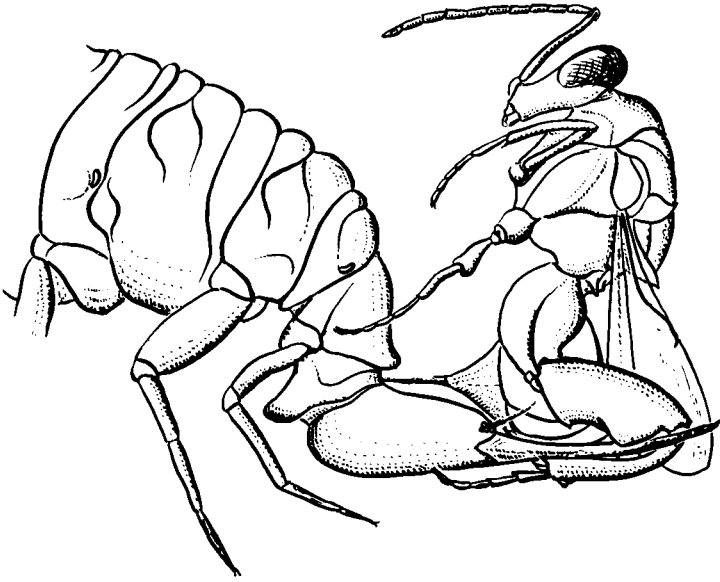


Fig. 1 Stinging of ant-lion larva between head and thorax (oviposition) by the chalcid wasp *Lasiochalcidia igiliensis* (now *pubescens*), while being seized by the predatory larva. From Steffan (1961) with permission of the author.

e. Encyrtidae. Some are of exceptional interest for their extreme body site selectivity of egg-laying. Eggs are laid in the brain or suboesophageal ganglion of scale insects (for example, *Coccophagus basalis*) (Askew, 1971, p. 138). Others, such as *Diversinervus elegans* Silv. and *Microterys clauseni* Comp. oviposit in the intestine of their host, sometimes through the anus (e.g. *Coccophagus saintebeauvi*) (compere, in Clausen, 1940, p. 159). Still other forms insert the egg stalk in the puncture (e.g. *Encyrtus*, *Euxanthellus*) (Clausen, 1940, p. 4). Effects of stings are, again, exceedingly variable, even within a genus. Thus in *Aphelinus* it can vary not only with the species of wasp but also with the stage of development of the aphid host. Many nymphs of *Macrosiphum cornelli* Patch stung by *A. jucundus* Gahan are paralysed permanently, but some are only temporarily paralysed if they are used for the development of the parasite. They are almost always killed if young (in Clausen, 1940, p. 166).

f. Eulophidae. Stinging is also widespread among these wasps. *Euplectrus bicolor* Swed. stings the host, various larvae of noctuid moths, two or three times, after which they become still for a short time (in Malyshev, 1968, p.

204). *E. plathypernae* How. and *Elachertus affinis* oviposit without paralysing the host (in Clausen, 1940, pp. 150, 153). *Euplectrus* wasps regularly kill the host while feeding on it. Paralysis is permanent in *Eulophus viridulus* (in Malyshev, 1968, p. 206), but only partial in *Microplectron fuscipennis* Zett. (in Clausen, 1940, p. 138). Killing of the host, often followed by rapid decomposition, is not exceptional among Eulophidae such as *Asympiesella* and *Diaulinus* (Clausen, 1940, p. 139). *Melittobia acasta* is a tiny wasp that waits in the cells of bees and wasps until the larva of the host reaches its full development. The larva is then stung into paralysis and can stay fresh for up to 9 months. Stings are highly variable in number and location (in Malyshev, 1968, pp. 211–213; in Askew, 1971, p. 136).

3. Proctotrupeoidea

Within this superfamily the Platygasteridae exhibit, again, a remarkable body site specificity, laying their eggs consistently and with great precision in a particular region of the embryo of the host, again often including the brain (*Inostemma loscii* and *I. piricola*) or the posterior region of the nerve chain (*Trichacis remulus*) (Clausen, 1940, p. 241). The larva of *Platygaster zosine* can develop only in the mid-intestine!

In conclusion, the stings of Terebrantia are often highly variable in number (3–100 in *Dibrachoides dynastes*) and/or location (e.g. *Melittobia acasta*). However, some of these wasps exhibit a remarkable ability to locate, identify and reach precise internal organs or body parts. This foreshadows the remarkable body site specificity consistently found in the aculeate wasps, considered next.

B. Bethyloid and Scolioid Wasps

1. Bethyloidea

a. Bethylidae. The biology of these wasps is considered by some as intermediate between that of the Terebrantia and fossorial wasps (Richards, 1939a,b; Askew, 1971, p. 164), since some still share with the former the habit of laying several eggs on the same host. Stinging, which is painful to humans, is often repeated until all movements of the prey cease, but a single sting can also be sufficient for paralysis to occur (e.g. *Goniozus claripennis* Förster) (see Fig. 2) (Voukassovitch, 1924, in Berland, 1928, pp. 101–102). Paralysis can be temporary (~ 5 min for the prey of *Perisierola emigrata*, stung about three times) (in Malyshev, 1968, p. 208) or permanent and complete (prey of *Epyris extraneus* Bridw., stung in the thorax, and of *Holepyris hawaiiensis*,

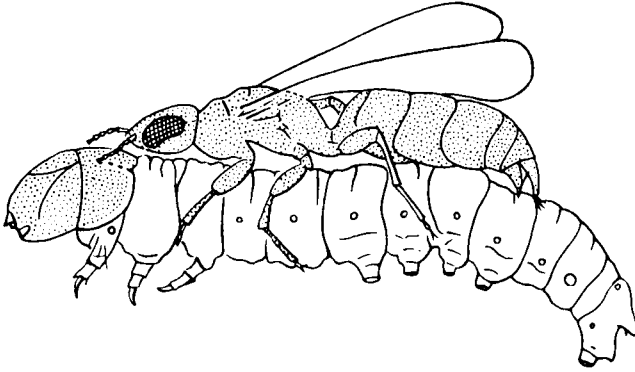


Fig. 2 *Goniozus claripennis* paralyzing the caterpillar *Oenophthera pilleriana*. From Voukassovitch (1924).

stung around the mouth) (Iwata, 1972, pp. 61–62). *Laelius trogodermitis* Ashm. apparently stings the thoracic nerve centres of a beetle larva behind the second and third leg pairs and then rests the egg-laying site several times before ovipositing (in Malyshev, 1968, pp. 209–210). Stinging of the mouth is often done initially by wingless *Sclerodermus* wasps, following which innumerable stings can be added, including abdominal stings, until all movements cease (Berland, 1928, p. 125; Malyshev, 1968, pp. 217–218). It seems that abdominal stings are particularly well suited, generally speaking, for elongate prey such as larvae, since some scolioid, sphecid and eumenid wasps that hunt larvae behave similarly (convergent evolution). Stinging for the sole purpose of feeding on the body fluids of the host is also commonly found. More information is summarised in Table II and in Chapter 5, Table I.

b. Sclerogibbidae. Ectoparasitoids of embiids (Embioptera), these wasps at least sometimes temporarily paralyse their host by stinging, as shown in *Sclerogibba embiidarum* Kieff. and *S. longiceps* Rich. (Ananthasubramanian and Ananthakrishnan, 1959, in Iwata, 1972, p. 54).

c. Chrysididae (and Cleptinae). These brightly coloured cuckoo-wasps do not sting their own prey but exploit the nests of other Hymenoptera, taking advantage of their long, flexible abdominal tube or ovipositor. *Chrysis shanghaiensis* Smith, however, has retained the capacity to sting and inoculate venom into the thorax of the oriental moth, *Monema flavescens* Wlk., after having opened the cocoon with the mandibles. Apparently inhibition of pupation rather than immobilisation of the host results (Piel, 1933; Parker,

Table II
Bethyloidea^a

Wasp	Prey	Information and source
Bethylidae		
<i>Sierola molokaiensis</i>	Leafrollers [L (I)]	Iwata [1972, 61-62: E (C)]
<i>Perisierola gallicola</i>	L (I)	Berland [1928, 103: Kieffer, 1926: S (/); E (Pa)]
<i>Perisierola emigrata</i>	Pink bollworm [L (I)]	Iwata [1972, 61: S (H + T + A); E (C)]
<i>Goniozus</i>	L (I)	Clausen [1940, 310: S (H and/or T + mA); E (s spp.: T: ½-2 hr, R)]
<i>Goniozus claripennis</i>	—	Berland [1928, 102: Voukassovitch, 1923, 24: S (IT); E (R)]; Malyshev [1968, 207: S (/), Fig); E (/)]
<i>Bethylus cephalotes</i>	<i>Tortrix</i> [L (I)]	Iwata [1972, 64: E (C)]
<i>Epyris extraneus</i>	Sand beetles (I)	Iwata [1972, 61: S (T); E (P: Williams, 1919)]
<i>Holepyris hawaiiensis</i>	L (I)	Iwata [1972, 62: S (/); E (C)]; [O (BS: A9: Bridwell, 1920)]
<i>Allepyris microneurus</i>	Dermestidae [C (I)]	Grandi [1961, 625: Yamada: S (/); Malyshev [1968, 127: E (Pa)]
<i>Cephalonomia formiciformis</i>	C (I)	Berland [1928, 134: Hamm, 1922: E (C)]
<i>Cephalonomia tarsalis</i>	<i>Oryzaephilus surinamensis</i>	Iwata [1972, 62: E (C: Powell, 1938)]
<i>Sclerodermus</i>	C (I)	Berland [1928, 125: Bridwell, 1920: S (mR)]; Malyshev [1968, 218: S (usually H or m, elsewhere); E (/)]; Iwata [1972, 63: E (C: inhibits metamorphosis)]; Krombein <i>et al.</i> [1979, 1214: S (humans)]
<i>chilonella</i>	—	Clausen [1940, 310: S (M or T, mA; RS: A)]
<i>Parascleroderma berlandi</i>	Cyladidae [C (I)]	Iwata [1972, 63: S (between appendages; RS); E (R: 8 days: Maneval, 1930)]
<i>Pristocera armifera</i>	Elateridae [C (I)]	Iwata [1972, 61: S (/); E (I)]
Sclerogibbidae		
<i>Sclerogibba embiidarum</i> and <i>Sclerogibba longiceps</i>	Embioptera	Iwata [1972, 54: Ananthasubramanian and Ananthkrishnan, 1959: S (/); E (T)]
Chrysididae		
<i>Chrysis shanghaiensis</i>	L [cocoon]	Buysson (1898, 80-81: V); Clausen [1940, 283: Piel, 1933, Parker, 1936: S (T); E (P)] Malyshev [1968, 116: S (/); E (inhibits metamorphosis)]

(continued)

Table II (continued)
Bethyloidea^a

Wasp	Prey	Information and source
Cleptinae		
<i>Cleptes judzi</i>	<i>Neodiprion japonica</i> Hy (l)	Iwata [1972, 58: S (/)]
Dryinidae	Cicadellidae, Fulgoridae	Clausen [1940, 318: E (Rq or no Pa); 4: O (some spp.: egg partially embedded in puncture)]
<i>Pseudogonatopus hospes</i>	Fulgoridae, Cicadellidae	Clausen [1940, 318: S (T2); O (BS: between 2 seg of anterior A)]
<i>Haplogonatopus japonicus</i>	<i>Delphacodes furcifera</i>	Clausen [1940, 318: Esaki and Hashimoto, 1931: S? O? (midA); E (P or K)]

^aSee footnotes to Table I.

1933, in Clausen, 1940, p. 283). *Cleptes fudzi* Tsuneki behaves similarly towards the cocoons of a sawfly, *Neodiprion japonica* (in Iwata, 1972, p. 58).

d. Dryinidae. These strange small wasps have the tips of their front legs often transformed into small claws with which they seize and hold their leafhopper or related hosts (Cicadellidae, Fulgoridae, exceptionally Membracidae) (Clausen, 1940, p. 316). Stinging in the mesothorax and subsequent oviposition between two of the anterior abdominal segments have been described from *Pseudogonatopus hospes*. Stinging, if used at all, generally results in short-duration, but sometimes permanent, paralysis (and moulting is suppressed; e.g. in *Haplogonatopus japonicus* E. and H.) (Esaki and Hashimoto, 1931, in Clausen, 1940, p. 318).

2. Scolioidea

a. Tiphidae (and Thynnidae). These economically important wasps attack mostly beetle grubs, particularly Scarabeidae, which are often pests. The latter live hidden in the ground or in rotten wood and similar habitats. The stinging behaviour of *Tiphia morio* F., studied in captivity, is remarkably complex, even meticulous, and can involve as many as 130 stings. A single initial sting between the middle legs results in paralysis (Janvier, 1956). The additional stings, which suppress superficial reactions, are given methodically. These are usually three per abdominal segment, near muscle insertions, starting with the sixth. The wasp then proceeds towards the head and back again until the sixth segment is reached a second time. Finally, the wasp lays an egg in the fold between the fourth and fifth abdominal segments. The grubs recover within 40 to 60 min and resume their burrowing activities. *Tiphia popilliavora* Roh. is also said to sting (repeatedly) the thorax, mostly between the first two segments. Extensive abdominal kneading, instead of stinging, follows (in Clausen, 1940, p. 292). According to Ferton (1911) *Myzinus andrei* Ferton paralyzes larvae of the tenebrionid beetle *Tentyria* sp. with a single sting and then buries itself in the sand, still holding the prey (in Malyshev, 1968, p. 134). This foreshadows digging of a burrow where the prey is stored. In contrast to the prey of *Tiphia*, the prey of *Myzinus* (and *Pterombus*) wasps usually remain permanently paralysed (in Clausen, 1940, p. 293). Body site specificity of egg placement, which is high and different among tiphids, has been documented by Clausen *et al.* (1932, in Clausen, 1940, p. 293; see Fig. 138 in Clausen, 1940). Several methocine, ant-like wasps such as *Pterombus* and *Methoca* first sting highly predacious tiger-beetle larvae in the unprotected gular region, while the latter hold the wasp in their mandibles. Then sometimes the thorax is stung. Paralysis is temporary in this species, but

complete and permanent in *M. striatella* and *M. yasumatsui* (Clausen, 1940, p. 72). In the latter case the burrow entrance of the host is then filled with soil particles, a behaviour reminiscent of that of many pompilid and sphecid wasps (see Table III, and Chapter 5, Table I).

b. Mutillidae. Velvet ants deliver very painful stings. Many of them are brood parasites of aculeate Hymenoptera, but *Mutilla europaea* is said to sting before oviposition (Ferton, 1914, in Berland, 1925b, p. 306).

c. Scoliidae. Members of this group have habits rather similar to that of Tiphiidae but are often much larger and attack much larger grubs. Fabre and Malyshev reported a single sting, directed at the concentrated nerve centres of the thorax in *Megascolia flavifrons*, whereas Passerini (1840, 1841, in Grandi, 1961, p. 25, and Piek *et al.*, 1983) observed repetitions of stings on various body parts, but mostly on the thorax. The latter authors also present a very detailed and thorough study of the sting wounds found on the prey and of the venom. The latter produced no paralysis when injected in the haemolymph of some insects, outside the intact ganglia. This suggests that stinging of nerve centres might be more plausible than has generally been assumed. These authors also review stinging and its effects in scolioid wasps. The reader is referred to that paper, Table III, and Chapter 5 in the present volume for further details. Paralysis of the prey of Scoliids is sometimes complete and permanent but is more often temporary or imperfect. The grubs stung by *Scolia formosa* might even continue to feed for some time (Tryon, 1902, in Clausen, 1940, p. 304).

In conclusion, stinging in Scoliids can be precise and localised, as well as irregular and widespread as it is in some eumenid wasps (discussed latter). The latter also paralyse larvae, but of Lepidoptera. Precision of stings, when present, is particularly impressive in these groups, since the whole body of the prey is soft and can be stung anywhere.

C. Pompilidae or Spider Wasps

Since only spiders are attacked, stinging methods are more uniform in this group and consequently only a few selected examples will be considered. No updating of scientific names will be attempted (see Table IV for additional information).

1. *Pepsinae*

The spectacular and huge tarantula hawks (*Pepsis*, *Hemipepsis*) (Fig. 3) are sometimes killed by their formidable opponents (in Iwata, 1972, p. 92). Stinging is apparently not very rigidly fixed. Some authors observed two stings

Table III
Scolioidea*

Wasp	Prey	Information and source
Tiphidae		
<i>Tiphia lucida</i>	<i>Adoretus</i> [C (I)]	Clausen [1940, 289; Thynnidae/grubs: E (P, but exceptions: e.g. <i>Diamma</i> ; <i>Tiphia</i> : T)]; Malyshev [1968, 118-119: S, E]
<i>Tiphia morio</i>	Scarabaeids [C (I)]	Williams [1919, 61-62: E (T)]
<i>Tiphia popillivora</i>	C (I)	Janvier [1956: S (deep anesthesia, then superficial: up to 130 St); E (R)] Clausen [1940, 292: S (T, usually between T1, T2; usually RS)]; Malyshev [1968, 120: S (s: between T1, T2, then kneads ventral region); E (R: 20-40 min)]
<i>Tiphia segregata</i>	C (I)	Williams [1919, 65: S (T, more?); 66: E (R usually 15 min)]
<i>Myzinus andrei</i>	C (I)	Clausen [1940, 293: E (P)]; Malyshev [1968, 134; Ferton, 1911: S (1 St)]
<i>Pterombus</i>	—	Clausen [1940, 293: E (P)]
<i>cicindelitoidus</i>	Cicindelids [C (I)]	Clausen [1940, 293-94; Williams, 1928: S (H: throat, or T); E (C, P)]
<i>piceus</i>	Cicindelids [C (I)]	Palmer [1976, 371: S (sF)]
Methochinae	Cicindelids [C (I)]	Askew [1971, 166: S (T)]; Iwata [1972, 72-73: S (1H: throat or H: thorax and sL2, L3); E (C, P or T, respectively)]
<i>Methoca ichneumonoides</i>	Tiger beetles [C (I)]	Pagden [1925: S (H: below gular region or elsewhere; T, RS: T); E (V, often C)]; Williams [1919, 78: E]; Clausen [1940, 299: S (H: throat, or T); E (C, P)]; Malyshev [1968, 133: S (H: throat)]; Krombein [1982, 84; Adlerz, 1903, 1905: S (H: throat)]
<i>Methoca japonica</i>	Cicindelids [C (I)]	Clausen [1940, 299; Iwata, 1936: S (H: throat, or T, RS); E (Rc; also Pa delayed)]
<i>Methoca punctata</i>	Cicindelids [C (I)]	Williams [1919, 77: S; 77-78: E]
<i>Methoca striatella</i>	Cicindelids [C (I)]	Williams [1919, 72-74: S (H?); E (P)]
<i>Methoca stygia</i>	Cicindelids [C (I)]	Williams [1919, 78-79: E]
Mutillidae		
<i>Mutilla europaea</i>	Hy (I)	Berland [1925b, 306; Ferton, 1914: S (1 St)]

(continued)

Table III (continued)

Scolioidea^a

Wasp	Prey	Information and source
Scoliidae	Usually Grubs [C (0)]	Fabre [1886, Vol. 3, 26, 46-48: cetonid grubs: S (1?); E (C, P)]; Williams [1919, 53: E (often C)]; Clausen [1940, 304: S (sT)]; Askew (1971, 163: E); Piek <i>et al.</i> (1983: reviews: S, E)
<i>Elis (Trielis) sexmaculata</i>	<i>Anoxia</i> [C (0)]	Fabre [1891, Vol. 4, 264-68: S (T1: forelegs); E (C)]
<i>Campsomeris javana</i> and <i>pulchrivestita</i>	Grubs	Clausen [1940, 304: Corbett: S (T and/or H: throat); E (C, P); in Iwata [1972, 67: S (1 H); E (C, P)]
<i>Campsomeris radula</i>	Grubs [C (0)]	Clausen [1940, 304: Illingsworth: S (T: just anterior to L1, H: throat); E (C, P)]
<i>Scolia dorsata</i>	Grubs [C (0)]	Iwata [1972, 67: Nowell, 1915: S (1 T3?)
<i>Scolia formosa</i>	Grubs [C (0)]	Clausen [1940, 304: Tryon, 1902: E (R: continues feeding, some time)]
<i>Scolia hirta</i> (= <i>bifasciata</i>)	Cetonids [C (0)]	Fabre [1981, Vol. 4, 258-63: S (1 T: between T1, T2, always; up to 15 min); E (C)]
<i>Scolia maritiae</i>	Grubs [C (0)]	Williams [1919, 56: S (1 or more H or T); E (C)]
<i>Megascolia flavifrons</i>	Rhinoceros beetles (0)	Grandi [1961, 25: Passerini: S (sT)]; Malyshev [1968, 130: S (T, Fig)]; Piek <i>et al.</i> [1983, N = 11: S (V, but often T1 > T2; also A; Fig); E (T or I; Ve)]

^aSee footnotes to Table I.



Fig. 3 *Hemipepsis ustulata ochroptera* (Pompilidae, Pepsinae) attempting to climb up a leg of a tarantula before stinging. Redrawn from Williams (1956). Reproduced by permission of the Entomological Society of America.

in the cephalothorax (Darwin, in Engel, 1962, p. 35). Others recorded only one sting in the mouth or between the pedipalpi and first legs or else between the first and second legs (in Iwata, 1972, p. 93). Stings are apparently never delivered very far from the large nerve ganglia (Williams, 1956). Stinging is sometimes even repeated until all activity ceases (*P. mildei*, as *formosa*) (Passmore, 1936, in Hurd, 1952, p. 267). The venom of *P. marginata* produces the quickest and deepest effects when inoculated anteriorly (Petrunkevitch, 1926, in Hurd, 1952, pp. 266–267). The huge paralysed spider can remain alive for months if not eaten by the larva of the wasp (e.g. prey of *P. mildei* Stål) (Williams, 1956). Among *Cryptocheilus* (and *Calicurgus*) wasps *C. variegatus* F. stings *Lycosa* spiders between the legs and so does *C. annulatus* F. (Soyer, 1947a, pp. 121–122). When attacked the spider keeps its legs as tight as possible, thus preventing the wasp from inserting the sting for up to 70 min! Stings to the mouth are reported for several species: *C. hyalinatus* (Soyer, 1946), *C. affinis* (Grandi, 1961, p. 72). *C. sexpunctatus* F. (as *scurra*) (Fabre, 1891, Vol. 4). Additional sting(s) can be given, for instance behind the fourth leg, for the prey of the latter species, which, excluding the fangs, slowly recovers to some extent (over a period of 1 month).

Haploneurion (*Priocnemis* subgen. *Sphictostethus*?) are remarkable wasps with atrophied wings. They climb up trees, even of very large size, and drop several meters from one branch to another (Janvier, 1930, p. 247). *H. minus*

Table IV
Pompiloidea^a

Wasp	Prey	Information and source
Pepsinae		
<i>Pepsis</i>	Tarantula	Williams [1956, 452, 464: S (M, T); 460: E]; Malyshev [1968, 136: S (2T or M)]; Iwata [1972, 92-93: S (I, V; M, L1, L2, etc.); E (C)]; Engel [1962, 35: Darwin: S]
<i>chrysothemis</i>	Tarantula	Williams [1956; 456: S (/)]
<i>limbata</i>	Tarantula	Janvier [1930, 264: S (T, middle)]
<i>marginata</i>	<i>Cyrtophilus portoricae</i>	Hurd [1952, 266-67]: Petrunkevitch [1926: S (and RS; V: more efficiently anterior to the sternum); E (usually C, same reference)]
<i>mildei</i>	Tarantula	Williams [1956, 454-56, 460: S (Fig)]; Hurd [1952, 267: Passmore, 1936, as <i>formosa</i> : S (L2)]
<i>thisbe</i>	Tarantula	Williams [1956, 453-456: S (M, legs; Fig)]; Cazier and Mortenson [1964, 539: E (I)]
<i>Hemipepis ustulata ochr.</i>	Tarantula	Williams [1956, 462: S (Fig); 460, 462: E]
<i>Cryptocheilus (and Calicurgus)</i>		
<i>affinis</i>	Clubion., Amaurob.	Grandi [1954, 118: E (C); 1961, 72: S (sM, and RS); E (C)]
<i>annulatus</i>	<i>Lycosa</i> , Tarantula	Fabre [1882? Vol. 2, 221: E (C, kept 7 weeks); 1891, Vol. 4, 280: E]; Soyer [1947a, 123: S (/); E (kept 4 weeks)]
<i>distinctus</i>	<i>Eriophora</i> (Araneid)	Evans <i>et al.</i> [1981, 10: E (C)]
<i>hyalinatus</i>	Argiopidae	Maneval [1939, 93: E (C)]; Soyer [1946: S (M area)]
<i>notatus</i>	Agelenidae	Grandi [1954, 120: E; 1961, 70: E (C)]
<i>octomaculatus</i>	<i>Lycosid</i>	Berland [1925b, 232: Ferton, 1901: S (/)]
<i>scurra</i>	Epeira	Fabre [1891, Vol. 4, 277-82: S (I M: paralyzes fangs, and 1 L4: paralyzes all Ls); E (Rs: 1 week: SL, kept 6-7 weeks)]
<i>sexpunctatus</i>	<i>Hogna radiata</i>	Grandi [1954, 120: E (C)]
<i>variegatus</i>	<i>Lycosa</i> spp.	Soyer [1947a, 121: S (between coxae)]
<i>Salix disperitus</i>	<i>Lycosa aspersa</i>	Janvier [1930, 276: S (A: around spinnerets, N = 1, T: Fig; N = 1)]
<i>dumosus</i>	<i>Lycosa</i>	Janvier [1930, 272, 273: S (1L, T: middle; N = s); E (Ri)]

- flavipes*
scyophanta
Haploneurion apogonum
H. minus
Prionemioioides
unifasciatus
Prionemis
affinis
beltieri
bisdeconatus
cornica
germana
hestia
leucocoelitus
massaliensis
minorata
notha notha
pusillus
Dipogon
brevis brevis
papago anomalus
pulchripennis
sayi
Agenia intermedia
Agenia variegata
Auplopus albifrons
- Clubiona*, *Lycosa*
Galeodes
Araneus adiantus
Drassus, *Dolomedes*
Lycosa spp.
—
Dysdera?
Disderidae
Lycosa narbonensis
Arctosa, errant spp.
—
Amaurobiidae
Clubionids
Nemesia badia
Mygalids
Agelenidae, etc.
Salticidae, etc.
Salticidae
—
Salticidae
Gnaphosids
Salticidae
Thomisidae
Thomisidae
Thomisidae
Thomisidae
- Janvier [1930, 267: S (IL)]
Williams [1919, 82: Bingham, 1900–1901: S (3); E (usually K; or C, P)]
Janvier [1930, 254: S (1 L); 255: E (Rs: NA, if freed)]
Janvier [1930, 249, 251: S (1 L; N = 3; RS if transport hindered); E (1)]
Evans and Yoshimoto [1962, 100: E (oR)]
Ferton [1890, 7: S (R? M to A, 'clumsy'; N = 1)]; Evans and Yoshimoto [1962, 100: S (s); E (usually C, P)]
Ferton [1891, 4–5: S (2; N = 1)]
Soyer [1945, 75: S] (pr between L3, L4); E (C, P)]; Grandi [1961, 74: S (RS: T)]
Ferton [1897, 24: S (M?, from Fabre)]
Evans and Yoshimoto [1962, 96: S (s, V, and T, slowly); E (C, P)]; Kurczewski [1962, 87: S (? T); 1963a, 210, N = 1: S (L1 or L2?); E (1)]
Evans and Yoshimoto [1962, 98: E (C, ?P)]
Evans and Yoshimoto [1962, 98: S (3T; N = 1); E (C, P)]
Ferton [1897, 13: S (M, if undisturbed); 23: E (C, P)]
Soyer [1945, 77: E (C, P, until dies)]
Evans and Yoshimoto [1962, 99: E (C, P: 33 days)]
Evans and Yoshimoto [1962, 98: E (C, ?P)]
Maneval [1939, 91: E (C)]
Evans and Yoshimoto [1962, 105: E (D, P or K)]
Evans and Yoshimoto [1962, 105: E (K?; N = 1)]
Evans and Yoshimoto [1962, 105: E (D, after 4 days)]
Evans and Yoshimoto [1962, 105: E (Pa)]
Evans and Yoshimoto [1962, 102: E (D, P)]; Fye [1965, 735–36: E] Berland [1925b, 226: E (C)]
Ferton [1897, 27–28: S (between M and L1); 28: E (LOC)]
Grandi [1961, 76: E (C)]

(continued)

Table IV (continued)

Wasp	Prey	Information and source
<i>Auplopus carbonarius</i>	Clubionids, lycosids	Maneval [1939, 87: E (C)]
<i>Auplopus mellipes</i>	Gnaphosidae	Krombein [1952b, 177: E (D; N = 1)]
<i>Auplopus nigrellus</i>	Salticidae	Evans and Yoshimoto [1962, 109: E (D)]
<i>Pseudogena</i>	Drassidae	Janvier [1930, 238: S (s, between, Ls, usually 10: first middle T, and Ls: base; leg amputated; Fig)]
<i>goyi</i>	<i>Araneus cinaberinus</i>	Janvier [1930, 244: S (between Ls)]
<i>Agentiella banoensis</i>	—	Williams [1919, 105: S (1 and 1 M; leg amputated; N = 1)]
<i>Agentiella conflicta</i>	<i>Arctosa</i> , Lycosidae	Evans and Yoshimoto [1962, 106: S (sA, and 1 T; N = 1)]
<i>Agentiella parvita</i>	Gnaphosidae	Kurczewski [1963a, 210: E (L)]
Pompilinae		
<i>Aporus fasciatus</i>	<i>Maevia vittata</i>	Peckham and Peckham [1905, 83: E (V, even R, including c; N = 3)]
<i>Tachyagetes filicornis</i>	Lycosidae, Gnaphosidae	Grandi [1961, 93, 94: E (C: up to 15 days, then R: even feeds; N = 1)]
<i>Agentioideus cinctellus</i>	Salticidae	Evans and Yoshimoto [1962, 88: Richards and Hamm, 1939: E (oR)]
<i>Agentioideus haematopus</i>	<i>Segestria</i>	Grandi [1961, 81: E (R: considerable degree; dead: third day)]
<i>Agentioideus humilis</i>	<i>Araneus</i> , <i>Neoscona</i>	Evans and Yoshimoto [1962, 88: Krombein, 1953a, 113, 115: E (C: 2 days)]; Eberhard [1970, 245-46: S (1 T, sRS if motions)]
<i>Agentioideus nubecula</i>	Salticidae	Grandi [1961, 82: E (I; R: became agile)]
<i>Agentioideus sericeus</i>	Several families	Evans and Yoshimoto [1962, 88: various authors: E (D)]
<i>Sericopompilus apicalis</i>	Salticids, thomis, etc.	Krombein [1952a, 263: E (C; N = 1); 1953b, 115: E (C; N = 1)]; Evans and Yoshimoto [1962, 89: Krombein: S (s; N = 2); 90: E (D or K)]; Kurczewski [1981, 426: S (2-3 T)]
<i>Episyron</i>	—	Evans and Yoshimoto [1962, 92: E (D; exceptionally, Rs)]
<i>begutatus</i> b.	<i>Neoscona</i> (Epeirid)	Krombein [1953b, 115-16: E (C, or K; N = 3)]
<i>posterus</i>	Epeirids	Krombein [1952a, 267-68: E (C; N = 2); 1953b, 116: E (C; N = 1); 1955, 150: E (C; N = 1)]
<i>quinquenotatus</i>	Araneidae	Evans and Yoshimoto [1962, 92: E (D or K; very weak responses; died: 2 weeks; N = 2)]

<i>snowi</i>	<i>Neoscona</i>	Krombein [1952a, 269: E (C; N = 1)]
<i>tripunctatus</i>	—	Malyshev [1968, 136: S (I M)]
<i>Pecilopompilus interruptus cressoni</i>	<i>Argiope</i>	Kurczewski and Kurczewski [1968, 13: E (I; N = 1)]
<i>Pecilopompilus interruptus i.</i>	<i>Argiope, Araneidae</i>	Krombein [1952a, 270-72: E (C; weak reaction; N = 3)]; Evans and Yoshimoto [1962, 94: E (usually P; except Ri, after 8 days)]
<i>Tachypompilus ferrugineus</i>	<i>Lycosa, Pysauridae</i>	Evans and Yoshimoto [1962, 88: E (C; no information on duration)]
<i>Anoplius</i>	—	Soyer [1953, 352: 6 spp.: S (tendency: between L2 and L3); E (T)]; Evans and Yoshimoto [1962, 68-85: (review, subgenera and spp.)]
<i>(Lophopompilus)</i>	<i>Arctosa, Lycosidae</i>	Evans and Yoshimoto [1962, 71: E (usually R: a few hr or days)]
<i>cleora</i>	—	Evans and Yoshimoto [1962, 69: Krombein, 1952: E (Rc: evening, same day)]
<i>carolinus</i>	<i>Wadotes (Agelenid)</i>	Evans and Yoshimoto [1962, 70-71: E (Rc; N = 2)]
<i>(Notiochares)</i>	<i>Arctosa, Lycosa</i>	Evans and Yoshimoto [1962, 72: E (V duration, D: Rau, 1922, or Rs, C in 13 days, feeds; N = 1)]
<i>(N.) amethystinus atr.</i>	<i>Lycosids, Oxyopids</i>	Evans and Yoshimoto [1962, 77: E (R: some in 2 days, c in 1 week; N = 1)]
<i>(Arachnoproctonus) americanus</i>	<i>Arctosa</i>	Evans <i>et al.</i> [1953, 64-65, 73: N = s: 2 complete observations: S (s usually A, and T, if successful, near CNS); E (C, Rc: 1-2 hr)]
<i>apiculatus autumnalis</i>	<i>Arctosa, Lycosidae</i>	Krombein [1952a, 274-75: E (Rc: same day; N = 2)]; Evans [1953, 165: E (T)]; Kurczewski and Kurczewski [1968, 16: E (Rc: about 6 hr; N = 2)]
<i>apiculatus pretiosus</i>	<i>Lycosa</i>	Rau and Rau [1918, 82: E (C, almost dead; N = 1)]
<i>ferrugineus</i>	<i>Lycosids, salticids</i>	Krombein [1952a, 276: E (R, c?; N = 1); 1964a, 12: E (Rq; N = 1)]; Evans and Yoshimoto [1962, 74: E (Rq: a few hr)]; Kurczewski [1962, 88: S (3-4 T?; N = 1)]; Kurczewski and Kurczewski [1973, 68: S (3-4 T?; N = 1)]; Gwynne [1979, 683; S (T; RS A?)]
<i>marginalis</i>	<i>Lycosidae</i>	Krombein [1952a, 278-79: E (Rc: same day; N = 3); 1953b, 117: E (Rc: same day; N = 1); 1958, 103: E (Rc, same day; N = 1)]; Evans [1953, 168: E (Rq: a few hr)]; Evans and Yoshimoto [1962, 76: E (Rc: a few hr)]; Kurczewski and Kurczewski [1968b: E (R: 6 hr; N = 1)]
<i>semirufus</i>		

(continued)

Table IV (continued)

Wasp	Prey	Pompiloidea ^a	Information and source
(<i>Pompilinus</i>) <i>cylindricus</i>	—	Evans and Yoshimoto [1962, 81: E (V, depending on sp.: Rq, Rs or C, P)] Kurczewski [1981, 433: S (T, ventral; RS? A)]	
<i>krombeini</i>	—	Krombein [1953b, 118: E (Rc: same day; N = 1)]; Evans and Yoshimoto [1962, 80: E (No R; N = 2)]	
<i>marginatus</i>	Several families	Krombein [1952a, 280: E (Rc: same day; N = 1)]; Evans and Yoshimoto [1962, 80: E (V duration, even K; D; s; Rc: s days; N = 2)]	
<i>subcylindricus</i>	Thomisidae	Evans and Yoshimoto [1962, 78: S (3 T; N = 1); E (Rs: 10 days; N = 1)]	
<i>tenebrosus</i>	Several families, e.g. lycosids	Kurczewski and Kurczewski [1973, 72: E (R: after 4 hr; N = 1)]	
(<i>Anoplius</i>) <i>depressipes</i>	—	Evans and Yoshimoto [1962, 85: E (R: usually C, sometimes 1)]	
<i>illinoensis</i>	Pisauridae	Evans and Yoshimoto [1962, 84: Guild: S (1; N = 1)]	
<i>ithaca</i>	<i>Lycosa</i>	Evans and Yoshimoto [1962, 83: E (No R; N = 1)]	
	<i>Pardosa, Arctosa</i>	Evans and Yoshimoto [1962, 83: E (Rc: same day; N = 1; Rc: 2 days; N = 1)]	
<i>virginiensis</i>	Agelen., Amaurobiids	Evans and Yoshimoto [1962, 82: E (D; N = 5 of 7; R: 2 days; N = 2 of 7)]	
Miscellaneous <i>Anoplius</i> <i>chalybeatus</i>	Lycosids	Berland (1925b, 251: Ferton, Karsch: E); Soyer [1938b, 219: S (L)];	
<i>concinus</i>	Lycosids	Soyer [1938a, 29: S (1 L, slow, if <i>Lycosa</i> ; 1 M, quick, if <i>Pardosa</i> ; N = ?)]	
<i>dispar</i>	<i>Lycosa</i>	Soyer [1938b, 217: S (1 M)]; Maneval [1939, 93: E (C; N = 1)]	
<i>fuscus paganus</i>	<i>Drassodes, Lycosa</i>	Grandi [1954, 123: E (C; N = 2)]	
<i>viaticus paganus</i>	<i>Drassodes, Pirata</i>	Grandi [1961, 83: E (C; N = 2)]	
<i>Pompilus</i> <i>abnormis</i>	Salticidae	Grandi [1961, 79: E (R?)]	
<i>apicalis</i>	<i>Segestria</i>	Fabre [1879-1910, Vol. 2, 230: S (1 T; N = 1)]	
<i>araucanus</i>	<i>Lycosa</i>	Janvier [1930, 287: E (Rc if freed)]	
<i>arctus</i>	Several families	Evans and Yoshimoto [1962, 86: Evans, E(P)]	

<i>chalybeatus</i>	Lycosid	Ferton [1897, 30: E (R; N = 1)]
<i>cinctellus</i>	<i>Textrix</i>	Ferton [1897, 15: S (1-2, dorsal!, and 1 between M and L1; N = 1); 15-16: E (Rc: next day feeds!)]]; Soyer [1950, 182: <i>nubecular</i> : S (1 T, leg base; N = 1)]
<i>cinctellus nubecula</i>	Salticidae	Bertrand [1925b, 265: E (very L; R)]
<i>cingulatus (= luctuosa)</i>	Lycosidae	Ferton [1910, 159-61: S (M; N = 1); E (R, c?); 1897, 11, 23: E (Rc: 3 hr; N = 1)]; Grandi [1961, 91: E (C; N = 1)]
<i>effodiens</i>	<i>Lycosoides</i>	Ferton [1897, 5: S (no sting?)]
<i>fazii</i>	<i>Lycosa</i>	Janvier [1930, 287: E (Rc if freed)]
<i>fumipennis</i>	Lycosidae	Maneval [1932, 104: E; 1939, 97: E (R; N = 1)]; Grandi [1954, 121: E (R, c?; N = 1); 1961, 80: E on Lycosidae (Rc?)]
<i>gibbus</i>	Thomisidae	Maneval [1939, 96: E (very L; Nicolas, 1888; C, P: Maneval)]
<i>haematopus</i>	<i>Segestria</i>	Grandi [1954, 122: E (L, R, c?; N = 1)]
<i>holomelas</i>	Mygalid	Soyer [1945, 77: E (C, P)]
<i>marginatus</i>	—	Peckham and Peckham [1905, 226: S (V?); 230: E (V: k or l)]
<i>misturatus</i>	<i>Lycosa albata</i>	Janvier [1930, 281-82: S (T: middle; N = 3; RS)]
<i>plumbus</i>	Lycosidae, etc.	Crèvecoeur [1929, 360-361: E; 1945, 158: S (RS; N = 1)] Maneval [1939, 95: E (Rc: 10 min! escaped; N = 1)]
<i>pulcher</i>	Lycosidae, etc.	Ferton [1891, 6: S (many attempts)]; Grandi [1961, 78: E (l)]
<i>quinquenotatus</i>	—	Peckham and Peckham [1905, 204, 216: E (D, P or K; N = 3 of 11; others C, P: 4-10 days, then died)]
<i>republicanus</i>	Agelenids	Soyer [1950, 184: Ferton: E (very l)]
<i>scelustus</i>	Lycosidae, etc.	Rau and Rau [1918, 64, 67: E (R: next day; hopped after 4 days!; N = 1]; Evans and Yoshimoto [1962, 86: Peckhams, Raus: E (C, P: Raus; R: Peckhams, Evans)]; Gwynne [1979, 687, 688: S (/; RS: occasionally; timings)]

(continued)

Table IV (continued)

Wasp	Prey	Information and source
Pompiloidea ^a		
<i>sericeus</i>	Argiopids	Soyer [1950, 183: S (usually 1 M)]
<i>sexmaculatus</i> (= <i>venustus</i>)	Thomisids	Ferton [1897, 16: S (? and M and 3 T, quick; N = 1)]
<i>sobrinus</i>	<i>Lycosa implacida</i>	Janvier [1930, 285: S (T; N = 1)]
<i>spinolae</i>	<i>Lycosa aspersa</i>	Janvier [1930, 278: S (1 T, middle); 279: E (Rc: escapes if freed)]
<i>trivialis</i>	—	Berland [1925a, 40: Nicolas, 1888: E (None at all!)]
<i>vagens</i>	<i>Nemesia</i> , Lycosids	Ferton [1902, 520: S (s; N = 1); E (l; N = 1); 1891, 8: S (gave up; N = 1); 1897, 5-6: S (/); ECT: a few min!]; 1899, 9: S]; Soyer [1945, 80: S (1 L)]
<i>Aporinellus fasciatus</i>	Salticidae	Evans and Yoshimoto [1962, 87: Peckhams: E (T)]
<i>Pompiloides</i>	—	Rau and Rau [1918, 360: E (V; R, D, or K: e.g. Hartman)]
<i>marginatus</i>	—	Rau and Rau [1918, 62: E (Rc; N = 1)]
<i>tropicus</i>	<i>Lycosa frondicola</i>	Rau and Rau [1918, 51, 57: S (/; RS: between L3 and L4 and between L2 and L3)]; 54, 55, 57: E (sometimes R: 15 days; after 3 weeks spun web, jumped; N = 1)
Ceropalinae	—	Evans and Yoshimoto [1962, 102: O (on active or temporarily paralysed spiders?)]
<i>Miragenia</i>	—	Clausen [1940, 280: R (activity and feeding reduced)]
<i>Notocyphus</i>	Aviculariidae	Williams [1919, 106: S (H: fangs)]
Miscellaneous	<i>Polys</i>	Tsuneki [1968, 4, 23, 25: S (T); 15: E (C)]
<i>Batozonus bioculatus</i>	<i>Argiope</i>	Tsuneki [1968, 33: E (C; then Rs: kept 4 weeks)]
<i>Batozonellus annulatus</i>	<i>Neoscona</i>	Evans and Yoshimoto [1962, 95: Iwata, 1939: E (D)]
<i>Batozonellus maculifrons</i>	<i>Araneus ventricosus</i>	
<i>Parabatozonus kakodadi</i>		

^aSee footnotes to Table I.

Kohl and *H. apogonum* Kohl are said to sting the spider once between the legs, but resting (up to seven times) occurred whenever resistance to transport of the incompletely paralysed prey was felt (Janvier, 1930, pp. 249–255). If taken out of the cells, the prey of *H. apogonum* recovered enough to resume normal activities, even after 1 week of confinement.

Complete recovery of the prey of spider wasps is not exceptional. Soyer (1945, p. 75) reported that there is more space between leg pairs three and four of *Nemesia* spiders than between any other two leg pairs. *Priocnemis bellieri* Sichel appears to take advantage of this situation whenever it is given an opportunity and if it can assume the appropriate stinging posture. If not, it will sting near the insertion on the thorax of any leg it can seize in its mandibles. In most cases observed paralysis was complete and permanent.

Such opportunism or even clumsiness in stinging methods is apparently not exceptional in spider wasps. A species close to *Priocnemis opacus* even stings almost anywhere, ineffectively, from mouth to abdomen (Ferton, 1891, p. 7). Correspondingly, the state of the stung prey also varies widely. Later on, however, Ferton (1897, p. 13) discovered with *P. leucocaelius* Costa that the wasps were often prevented from reaching the usual precise body area(s) (often the mouth) by violent struggling of the prey, or by other unfavourable conditions, rather than by an inherent incapacity to do so ('unskilled species'). Evans and Yoshimoto (1962, pp. 96, 98) report that *P. cornica* (Say) stings its prey repeatedly (first apparently anywhere, then in the cephalothorax, ventrally) into deep and permanent paralysis, whereas a *P. hestia* (Banks) also stung its prey (three times) in the cephalothorax, ventrally, into complete, apparently permanent paralysis. One prey of *P. minorata* was kept for 33 days without any recovery (p. 99). In contrast, spiders stung by *Priocnemioides unifasciatus* (Say) often recover (Evans and Yoshimoto, 1962, p. 100). Ferton (1897, pp. 27–28) reports that *Agenia variegata* L. stings thomisid spiders between the mouth and first pair of legs. This observation is among the few that provide evidence of extremely localised effects of spider wasp stings (widespread among sphecids, eumenids). Here they were restricted to the fangs and first leg pair. The other leg pairs still retained some movements.

2. Pompilinae

Again, variability of the state of stung spiders has been reported by the Peckhams (1905, p. 83) for *Aporus fasciatus*, ranging from rather good paralysis to spontaneous movements and even complete recovery (after 17 days) following release. Movements of the prey are suppressed by tight packing within the cell (and presumably lack of stimulation by light, heat, etc.) (personal observation). Recovery can sometimes go very far, including feeding (prey of *Tachyagetes filicornis*) (Grandi, 1961): the fangs, however,

were still paralysed on the forty-third day, whereas the first signs of recovery appeared on the fifteenth day. The mouth sting and resting in response to movements or changes in position have also been reported in *Episyron tripunctatus* (Malyshev, 1968, p. 136) and *Agenioideus humilis* (Cresson) (Eberhard, 1970, pp. 245–246), respectively. Long-lasting, deep paralysis is also found rather consistently in some forms, such as *Episyron* spp. (see Table IV). A review of stinging methods and effects in *Anoplius* wasps, summarised in Table IV, can be found in Evans and Yoshimoto (1962, pp. 68–85) (see also Chapter 5, Table I, for some aspects of host paralysis).

Evans *et al.* (1953, pp. 64–65) observed stinging twice in *Arachnoproctonus apiculatus autumnalis* (Banks). On first contact the prey, *Arctosa littoralis*, was somewhat quieted by stinging quickly and repeatedly anywhere, but especially in the abdomen. Then the wasp carefully inspected the underside of the cephalothorax with the tip of the abdomen and stung a suitable spot in the vicinity of the central nervous system slowly during several seconds. Recovery of the completely paralysed spiders started within 1 to 2 hr and became complete within 24 hr.

According to Soyer (1938a, p. 29), *Anoplius concinnus* appears to adapt stinging methods to the kind of prey attacked. *Lycosa* spiders, which live in shelters, are stung once and slowly, near the base of a leg, whereas running spiders like *Pardosa* are stung quickly, near the mouth. The same author (1953, p. 352) also noticed among six species of *Anoplius* a certain tendency to use the wider space between leg pairs two and three of the prey preferentially for stinging. In five of the six species, recovery somewhat short of the normal state was observed. The prey of *A. viaticus* was found to be completely and permanently paralysed, but not so by other authors (see Piek, 1978, and Chapter 5).

3. *Ceropalinae*

These wasps mostly exploit the prey of other spider wasps, but *Notocyphus* is said to paralyse aviculariid spiders temporarily in the open. The activity of such spiders is much reduced, however, and feeding is particularly affected (in Clausen, 1940, p. 280).

4. *Conclusion*

Pompilidae provide further evidence that special attention is often given to the major weapons, here the fangs, of the prey, which are paralysed first and deeply. Perhaps the high incidence of resting in spider wasps is related to the high frequency of imperfect paralysis of the prey or premature recovery. The Raus (1918, p. 57) wondered whether the primary sting was sufficient

to paralyse the spider stung by *Pompiloides tropicus*. One prey could even jump out of its box and spin a web 3 weeks after stinging (other examples in Grandi, 1961, etc.). Particularly intractable prey such as spiders (or larvae?) might require some measure of saturation by frequent repetition of stings. In many cases, however, the recovered spider remains sluggish, cannot fully resume normal activities, or oviposition is inhibited (Iwata, 1932, in Malyshev, 1968, p. 127).

Could the venom have very selective, differential effects on activities? *Nemesia* spiders stung by *Pedinaspis crassitarsis* Costa can apparently move and catch prey but not spin a web to cover their shelter (Soyer, 1945, pp. 82–83). Effects of age or season on the wasps cannot be ruled out since Ferton (1897, pp. 11–12) reported that *Pompilus vagans* paralysed its prey more lightly earlier than later in the season. The remarkable fact is that nesting behaviour of the wasps is robust enough to accommodate such shortcomings. This weakens the argument that paralysing behaviour could not have originally evolved from imperfect stinging (Fabre).

D. Sphecid Wasp Diversity

Diversification of these wasp–prey systems makes them particularly favourable for ethological, comparative and evolutionary studies and defies all-encompassing explanations of stinging methods, found so often in the literature. Stinging methods will be studied here according to affinities among prey rather than among wasps since they are more likely to have been shaped by the former than the latter. This includes wide differences in sizes, defences, nervous systems and ecologies. In Table V, however, the wasps have been arranged in phylogenetic order, following Bohart and Menke (1976). Their scientific names have been updated, but this is not the case in Table I of Chapter 5.

1. *Hunters of Large, Often Powerful, Orthopteroids*

A large number of rather primitive sphecid wasps (e.g. Ampulicinae, Sphecinae), but also more advanced forms (e.g. Larrinae), attack Orthopteroids, often of a large or very large size, which are used singly or in small numbers in each cell. Some have diverged and become specialised on prey such as spiders (*Sceliphron*) or caterpillars (*Podalonia*, *Ammophila*). It is not easy to overcome the resistance of formidable opponents that can often attack or retaliate with painful bites (even to humans!), strikes or kicks with strong, often spiny, hindlegs. They can also regurgitate or spray a repelling or toxic substance or escape with a single powerful leap. In addition, their widely separated nerve centres often must be neutralised one by one

Table V
Sphecoidea*

Wasp	Prey	Information and source
Ampulicinae		
<i>Dolichurus stantoni</i>	Roaches Cockroaches	Malyshev [1968, 146-147: E (L, T)] Williams [1919, 113-114: S (L or seg? T); 113, 116: E (I, T, R, not C: feeds); 1927, 450: E (L)]
<i>corniculatus</i>	Cockroaches	Nielsen [1933, 313-14; E (very I: resistant; T: rarely C?: Nielsen, 1903)]; Grandi [1954, 142-53: E (very I; R: includes running, but asthma); Soyer [1947, 118-19: also Adlerz: S (I L, and 1 H; RS: left anterior L2); E: (R)]; Benoist [1927: E (R: runs; N = 3)]; Maneval [1932, 92: E (very I); 1939, 53: E]
<i>haemorrhous</i>	Cockroaches	Berland [1925a, 40: Ferton: E (Rc)]; Ferton (1894, 216: E (very I))
<i>Ampulex</i>	Roaches	Iwata [1972, 81-82: S (I, 2 H: throat, or Ls); E (C or I: Ri)]; Williams [1929, 325: S (RS if resists); 316, 324, etc.: E (I; R: considerably)]
<i>assiniilis</i>	Roaches (<i>Sheffordella</i>)	Malyshev [1968, 138: Hingston: S (I T: anterior); E (I)]; Clausen [1940, 328: Hingston, 1925: E (C; Ri)]
<i>(Rhinopsis) canaliculatus</i>	Cockroaches	Williams (1929, 325: S (RS if resists))
Sphecinae		
<i>Stangeella cyaniventris</i>	Praying mantis	Janvier [1928, 198-200: S (I H and 1 L1); 197, 201: E (slight MV: legs, 50 days); 1926: E]
<i>Chlorion aerarium</i>	— Crickets (O)	Bohart and Menke [1976, 2: E (T: some spp.)] Peckham and Kurczewski [1978, 759: S (T, etc., N = 1; 1 H and 1 L3; RS: H; N = 1); 760: E (R: very reactive; N = 20)]; Bohart and Menke [1976, 89: E (L)]
<i>aurul. ferrugin.</i>	Gryllacrididae	Williams [1919, 125: N = 1: S (I); E (I)]
<i>caeruleum</i>	Crickets	Peckham and Peckham [1905, 259: S (I H; N = 1); 260: E (alive)]
<i>lobatum</i>	Crickets (<i>Brachytripes</i>)	Hingston [1925: N > 6: S (2-3 T and 1 H, V); E (C; R much); 1926, 149, 157: S (H: inside ganglion); E (R: c?)]; Baerends (1941, 214: Hingston, 1931)

<i>maxillosum</i> (= <i>xanthocerus</i>)	Gryllids (<i>Brachytripes</i>)	Valdeyron-Fabre [1952: S (1 L3 and H and 1 random? N = ?); E (Rq: 2-3 min, active); 1955, 154: S (id 1952); 154: E (Rc; digs new burrow!)]
<i>Penepodium</i>	Cockroaches	Williams (1928: E)
<i>Podium</i>	Cockroaches	Bohart and Menke [1976, 96: E (C)]; Krombein [1967, 256: E (C; N = m)]
<i>luctuosum</i>	Cockroaches	Krombein [1970, 19: E (C: only weak MV; N = m); 1967, 253: E]
<i>rufipes</i>	Cockroaches or crickets	Bohart and Menke [1976, 98: E (1 to C)]; in Iwata [1972, 222: E (C)]
<i>Trigonopsis</i>	Cockroaches	Richards [1937, 109: E (MV; legs, antennae; N = 1)]
<i>abdominalis</i>	Cockroaches	Richards [1937, 108: E (MV; legs, antennae; N = 1)]
<i>moraballi</i>	Spiders (small)	Fabre [1891, Vol. 4, 27: S (in flight?); 27-28: E (K?); Peckham and Peckham [1905, 268-269: S (1, R?; N = s); 269, 273: E (¾ K)]
<i>Sceliphron</i>	Spiders	Janvier [1928, 165: S (1 L; N = 1; 1 between L2 and L3; N = 1); 164: E (C, P)]
<i>asiaticum</i>	Spiders	Eberhard [1970, 248-49: S (/: N = s)]; Rau and Rau [1918, 119: E (C, some MV; V longevity)]
<i>caementarium</i>	Spiders	Grandi [1961, 154: S (/ or RS; N = 1)]
<i>spirifex</i>	Spiders	Frisch [1937, 1050-51: S (dt: see text); 1052: E (C or D); Peckham and Peckham [1905, 67-68: E (1: rather lively)]; Reinhard [1929, 159-63: S (1 H and 2 T; N = 4); 64: E (C, P; MV slight)]; Rau and Rau [1918, 194: E (MV; slight; N = 4)]; Krombein and Evans [1954, 233: E (C; alive 12 days)]; Steiner [1981a, 334: S (3 T, and 1 H; N = s)]
<i>Sphex ichneumononeus</i>	L. h. grasshoppers	
<i>Sphex latreillei</i>	Conocephal.	Janvier [1928, 183-88: S (about 6 T: each L and 2 wings; N = s); 190: E (C; MV, slight; N = s)]
<i>Sphex flavipennis</i>	<i>Decticus</i> (O)	Berland and Bernard [1947, 14: Zanon, 1924: S (H)]
Yellow-winged <i>Sphex</i> (= <i>S. maxillosus</i> ?)	Crickets	Fabre [1856a, 154-57: S (1 H and between L1 and L2 and 3rd? N = 1); 154, 158: E (C; some MV); 1879, Vol. 1, 108-12, 123: S (1 H and 1 between L1 and L2 and 1 near A); 111-12: E (C, P; MV; kept 6 weeks)]

(continued)

Table V (continued)

Wasp	Prey	Information and source
<i>Sphex maxillosus</i>	Locusts	Molitor [1939a, 69-70: S (1 H and s T, incl. L3; RS, incompl.; N = 2-3?); 1936, 528: S (RS); 1934, 465: E (not C; some MV; N = 1)]
<i>Sphex pennsylvanicus</i>	Katyids (O)	Bartram [1749, E (not K)]; Frisch [1938: dt, see text]; Reinhard [1929, 172, 184: Bartram: S (sing or bite?); 169-90: Bartram: E (some MV, but agility lost)]
<i>Sphex umbrosus</i> (= <i>argentatus</i> ?)	Tettigon. (O)	Piel [1935, 281-82: N = s: S (RS: 1 H and 1-2T?); E (rather D; slight MV)]
<i>Isodontia auripes</i>	Grasshoppers, crickets	Steiner [1981a, 334: Longair and Steiner: S (3 T, 1 H; N = m)]
<i>mexicana</i>	Crickets, katyids (O)	Krombein [1970, 5, 8: E (all: D, P; a few MV; N = m)]
<i>nigella</i>	Crickets	Lin [1966, 240: E (usually I; N = m)]; Medler [1965, 139: E]
<i>Palmodes carbo</i>	Grasshoppers	Piel [1933, 119, 122-27: S (1 H; 0-2 or 3 T, or more, V, see text; N = 8); 128-29: E (C; MV: few, 2-3 days; no R; N = 8)]
<i>Palmodes dimidiatus</i>	L. h. grasshoppers	Steiner [1981a, 334: S (3 T and 1 H; N = 1)]
<i>Palmodes laeiventris</i>	Tettig., e.g. <i>Atlanticus</i>	Krombein [1952a, as <i>daggyi</i> , 282: E (weak MV; N = 1); 1955, 151: E (jerky reflexes; N = 2)]
<i>Palmodes occitanicus</i>	Mormon crickets	Parker and Mabee [1928, 8-10: E (not K)]
	<i>Ephippiger</i> (O)	Fabre [1879, Vol. 1, 175-89: S (s T? and H; N = 3); 164, 173-80, 185-89: E (I; some R; kept 17 days, even 40 with artificial feeding)]; Berland [1926, 174: E (C; no feeding; kept 20 days)]; Berland and Bernard [1947, 9: E (kept 21 days)]; in Malyshev (1968, 140: Fabre)
<i>Chilosiphex argyrius</i>	Phasgonurids (O)	Berland [1958, 67: E (rather C, but some MV: L3, antennae)]
<i>Prionyx atratus</i>	S. h. grasshoppers	Evans [1958b, 179, 184, 185: S (1 or s; R?); 180, 182, 184: E (L)]
	Grasshoppers	Strandtmann [1945, 308: E (C; N = 1)]; Rau and Rau (1918, 165-71: E (MV: kick, wings))

<i>kirbyi</i> (= <i>albisectus</i>)	<i>Oedipoda</i> (s. h. grasshopper)	Grandi [1954, 157: E (D; N = 2)]; Roth [1925, 398: S (1 H; N = 1); E (D)]; Benz [1959, 309: S (sf; N = 1)]; Berland [1925a, 51: E (No preservative effect, venom; N = 2)]
<i>parkeri</i>	S. h. grasshoppers	Steiner [1981a, N > 70, dt: see text: S (1 H, and 1 T1 and 1 T3: ggl); E (L, but P)]
<i>spinolae</i>	Acrimid grasshoppers	Janvier [1928, as <i>Sphex chilensis</i> , 205: S (L3; N = 1)]
<i>niveatus</i>	Grasshoppers	Roth [1925, 380: Morice, Eaton: S (in flight)]
<i>subfuscatus</i>	S. h. grasshoppers	Tsuneki (1963b, 53: S); Ferton [1902, 504-505: S (1 L1 and L2 or L3; not V); 506: E (R: more or less, in 3 to 4 months; venom exhausted?); Piel [1935, 298: S (end: L3?); E (I)]
<i>thomae</i>	Acridae	Rau and Rau [1918, 178-79: S (T, L1); 179-80: E (I: some MV, no walking)]; Grissell [1981, 18: E (weak; N = 1)]
<i>Hoplammophila aemulans</i>	Ceruridae (L)	Tsuneki [1963b, 46-48: E (D; even K)]
<i>Podalonia</i>	Caterpillars	Olberg [1959, 296: S (ventral midline = softer, near ggl)]
<i>hirsuta</i>	Cutworms [L (1)]	Fulcrand [1966: S (dt; N = m)]; Truc and Gervet [1974, N = m, S (dt, exp; see text); 1969: S (dt: see text)]; Molitor [1939a, 68: S (same as Fabre); 64-65: E]; Fabre [1882, Vol. 2, 25-27: S (H and 3 T and 6 A = 10; N = 1); 1891, Vol. 4, 248-52: S (T3 and T2 and T1; then sA, except last 3; some V)]; Truc [1971, 1972a,b,c: S (dt; exp: see text; N = m)]; Molitor [1933a, 162: S (same as Fabre)]; Bougy [1935, 20-21: S (2-3 T, then sA, except last 3-4; V; RS: up to 5 times; N > 50)]; Gervet and Fulcrand [1970: see text]
<i>luctuosa</i>	Cutworms	O'Brien and Kurczewski [1982b, 264, 273: S (2-6 T; 1-4 A; 1-2 anal; RS)]; Steiner [1983b: S (T3, T2, T1 and H; then A1 to A6; V; N = m); E (C, P)]
<i>robusta</i>	Cutworms	Krombein (1936, 98: E)
<i>tydei</i>	Cutworms	Roth [1928, 214: S (very V); E (1 pupa)]; Deleurance [1941, 289: S (5; N = 1)]
<i>violaceipennis</i>	Caterpillars	Parker, J. B. [1915, 71: S (RS: 5 stings; N = 1)]
<i>Eremochares dives</i>	Acridids	Roth [1928, 216: Smirnov: S (1T? = RS; N = 1)]

(continued)

Table V (continued)

Wasp	Prey	Information and source
<i>Eremnophila aureonotata</i>	Caterpillars (Notodontids)	Evans [1959, 464: S (s St; N = 1)]
<i>Ammophila</i>	Caterpillars	Peckham and Peckham [1905, 51-52: E (wiggled)]; Berland [1925b, 26: S (V; some relation with gg)]; Linne (1767, 94): E; Molitor [1937, 302: S; 1939a, 60-65: E (MV)]; Tsuneki [1968a: S (V; exp: see text; Fig: N = s)]; Fabre [1856a, 157: S (I: A5 or A6); 157, 159: E (MV; LOC anesthetic effect)]
<i>aberti</i>	Caterpillars	Parker <i>et al.</i> [1980, 254: S (s St; N = 1; Fig)]; Hicks [1932a, 150: E (2 kept for 34 days)]
<i>breviceps</i>	Caterpillar (looper)	Hicks [1933, 50: S (1 anterior A and 3A more; N = 1); 53: E (MV if stimulated; N = 1)]
<i>campestris</i>	—	Grandi [1961, 130: E (sawfly larva: D; no R; MV: last segs)]; Baerends [1941, 86: S (Figs); 119: E (MV: particularly last segs)]; Malyshev [1968, 130: Nielsen: E (gg)]
<i>dysmica</i>	Caterpillars	Evans [1970, 485: S (RS: s St; N = 1)]
<i>haimatosoma</i>	Caterpillars	Roth [1928, 219-20: S (sH? etc.; N = 1); 221: E (V)]
<i>heydeni</i>	Caterpillars	Roth [1928, 226: Cros: E (MV: particularly posterior end; N = 1)]; Ferton [1899, 12: S (s; N = 1)]; Molitor [1931: S (V; RS); 414: E (some MV); 1932: S (V, incl. order; or no sting); 1933b, 504-11: S (Exp: during closure, etc.); 1934, 455: S (Exp: own larva); E (own larva: none); 1936, 525: S (Exp: after closure); 1937, 303: S (own larva); 1939a, 61-66: S (Exp: see text); 1939b, 349: S (whole length; N = 1)]
<i>holosericea</i>	Caterpillars	Roth [1928, 228: Cros 1911: E (some MV)]
<i>nigricans</i>	Caterpillars	Strandmann [1945, 310: E (violent wriggling; N = 1)]
<i>parkeri</i>	—	Powell (1964, 244: E)
<i>pictipennis</i>	Caterpillars	Rau and Rau [1918, 217, 228, 229: S (RS: 1 A, near prolegs; N = 1; RS: 1 last prolegs; N = 1)]

<i>procera</i>	Caterpillars	Rau and Rau [1918, 240: E (no MV, except last seg; N = 1)]; Krombein [1952a, 285: E (MV)]
<i>pubescens</i>	—	Olberg [1959, 303: S (Fig)]
<i>rufipes</i>	Caterpillars	Janvier [1928, 176-78: S (1 T1, T2, T3; A1, A2, A3 and A4; N = 1; RS: 5 St; N = 1)]
<i>subulosa</i>	Caterpillars (e.g. Notodontids)	Fabre [1891, Vol. 4, 253: S (all segs except last 3; N = 1)]; Grandi [1954, 156: E (I; MV; N = 2); 1961, 141: E (I; N = 1)]; Kopp [1904, 345: S (I; N = 1)]; Olberg [1959: S (s; Figs.)]
<i>subulosa nipponica</i>	Noctuidae (L)	Tsuneki [1968a, 4: E (D; N = 1)]
<i>urnaria</i>	Caterpillars	Peckham and Peckham [1905, 25-27: S (between seg 3 and 4, 3 and 2, 2 and 1; +4, starting between seg 9 and 10; N = 1; first 3 segs, then segs 4, 5, 6, 7; N = 1; RS: 1 between seg 3 and 4; N = 1; (Fig); 29-30, 44: E (very V; some lived 3 days, others 2 weeks; often MV)]
<i>wrightii</i>	Caterpillars	Hicks [1934, 151-52: S (RS: obstacle, 2A; N = 1); 153: E (kicks if stimulated; N = 1)]
<i>zanthoptera (placida?)</i>	Caterpillars	Hicks [1932b, 194: S (at least 5-6 St; N = s)]
Pemphredoninae		
<i>Mimesa bicolor</i>	Leafhoppers	Janvier [1956, 206: E (MV: shivers)]
<i>Mimesa equestris</i>	Jassidae	Spooner [1948, 148: Adlerz, 1903: E (No MV)]
<i>Psen ater</i>	Leafhoppers	Janvier [1956, as <i>Dalibornia atra</i> , 198: E (MV: shivers only)]
<i>Psen barthi</i>	Leafhoppers	Clausen [1940, 339: Barth, 1907: E (K?)]
<i>Nesomimesa antennata</i>	Leafhoppers	Williams [1927, 436: E (D, C)]
<i>Diodontus</i>	Aphids	Powell [1963, 161: Peckhams: S (no St?; CH, neck); 161-62: also Raus: E (K; all)]; Krombein [1967, 34: E (No MV)]
<i>americanus</i>	Aphids	Rau and Rau [1918, 108: Peckhams: S (CH: neck)]
<i>metathoracicus</i>	Aphids	Rau and Rau [1918, 107: E (all dead)]
<i>Pemphredon</i>	Aphids	Bohart and Menke [1976, 180: S (St or CH)]
<i>diervillae</i>	Aphids	Tsuneki [1952a, 72: S (underside); E (C)]
<i>inornatus (= shuckardi)</i>	Aphids	Tsuneki [1952a, 71: S (ventral side)]

(continued)

Table V (continued)

Sphecoidea*

Wasp	Prey	Information and source
<i>Passaloecus</i>	Aphids	Bohart and Menke [1976, 184: S (St or CH)]; Krombein [1967, 34: E (No MV)]
<i>annulatus</i>	Aphids	Peckham and Peckham [1905, 87: E (dead)]
<i>eremita</i>	Aphids	Lomholt [1973, 29, 35: S (St or CH; often only CH)]
<i>montilicornis</i> (= <i>insignis</i> ?)	Aphids	Tsuneki [1955, 7: S (K by CH)]
<i>Stigmus</i>	Aphids	Bohart and Menke [1976, 188: Krombein, 1961: S (St)]; Krombein [1973: S (CH?); E (C)]
<i>pendulus</i>	Aphids	Maneval [1939, 76: S (CH)]
<i>Ammoplanus perrisi</i>	Aphids	Maneval [1939, 78: S (probably CH); E (No MV)]
Astatinae		
<i>Diploplectron peglowi</i>	Lygaeids (He)	Kurczewski [1972a, 389: E (I: MV)]
<i>Astata</i>	Stinkbugs (He)	Evans [1957a, 177-78: Peckhams: S (mostly K?); E (D)]; Iwata [1972, 122: E (C, P or K)]
<i>bicolor</i>	Pentatomids (He)	Evans [1957, 177: Peckhams, 1898: S (usually K)]; Evans [1962b: E (K? N = m)]
<i>boops</i>	He	Tsuneki [1947, 111: E (usually K); 1969c, 10-11: E (No MV: K?)]; Evans [1957, 179: E (usually K)]
<i>boops picea</i>	He	Ferton [1901, 103: S (I H: N = 2)]
<i>occidentalis</i>	Pentatomids (He)	Evans [1957a, 174: E (D or K; some = stiff)]
<i>unicolor</i>	Pentatomids (He)	Evans [1957a, 165: E (D or K)]
<i>Dryudella</i>	Lygaeids (He)	Iwata [1972, 122: E (C, P)]
<i>immigrans</i>	Bugs (He)	Williams [1946, as <i>Astata immigrans</i> , 646: S (/); E (faint MV: toe TW)]
<i>picta</i>	Bugs (He)	Parker, F. D. [1969, 965: S (sternum, between L)]
<i>Dinetus pictus</i>	Nabidae (He)	Grandi [1961, 185: E (I: MV)]

Larrinae
Larva

	Molecrickets	Clausen [1940, 335: E (deeper in spp. with larger eggs)]; Gwynne and Evans [1975, 281: E (T: Rc: s. m)]; Bohart and Menke [1976, 237: S (/); 2, 237: E (T: s. m)]; Iwata [1972, 84: S (/); E (T: Rc: s. m)]; Steiner (1984: review S and E)
<i>amplipennis</i>	Molecrickets	Iwata and Tanihata [1963, 103-104: S (s between L1 and L2; sometimes +H; gula); E (C, T: Rc: sm)]
<i>analis</i>	Molecrickets	Smith, C. E. [1935, 69; N = s; S (between A and T, +H; RS: 1-2 St = incompl.); E (Rc: 5 min, NA: 10 min)]
<i>anathema</i>	Molecrickets	Malyshev [1968, 124-25: Malyshev, 1941: S (T2, +T3, +H; no T3); E (Rc: 5-6 min, NA)]
<i>carbonaria erebus</i>	Molecrickets	Tsunekei [1969b, 15-16: S (between L1 and L2, +H: throat); 16: E (Rc: <1m)]
<i>femorata</i>	Molecrickets	Williams [1928, 46-49: S (between L3 and L2, between L2 and L1, +H)]
<i>polita luzonensis</i>	Molecrickets	Williams [1919, 133; N = 1; S (1 or sT); E (Rc: NA); 1927, 439, 441: E (Rq: walks, sluggish)]
<i>Liris</i>	Crickets	Iwata [1972, 133: E (I)]
<i>aequalis</i>	Crickets	Krombein and Evans [1955, 232: E (I: vigorous MV; N = 2)]; Steiner [1976: N = s; S(T3, +T1, +T2, +H: throat); E (C, T: Rq: s. m, but deactivated)]
<i>argentata</i>	Crickets	Rau and Rau [1918, 153-156: E (lively; jump; N = 7)]; Reinhard [1929, 71: E (I; N = 4)]; Steiner [1976: N = s; S (T3, +T1, +T2, +H: throat); E (C, T: Rq: Ri, s. m, but deactiv.)]; O'Brien and Kurczewski [1982a, 60-61: Rau, 1922, Raus, 1918; N = 3: E (I)]
<i>festinans</i>	Crickets	Williams [1919, as <i>Notogonidea williamsi</i> , 135: E (I; active but tame; N = 12)]
<i>haemorrh. magnifica</i>	Crickets	Clausen [1940, 335: Williams: E (T)]
<i>japonica</i>	Crickets	Tsunekei [1969b, 14: S (between L1 and L2; RS too)]
<i>muesebecki</i>	Crickets	Kurczewski [1976, 330: E (L: jumped; N = 4)]

(continued)

Table V (continued)

Sphecoidea^a

Wasp	Prey	Information and source
<i>nigra</i>	Crickets	Berland [1925a, 43: E (agile; stand, N = 1)]; Fertton [1901, 99: E (I, R: very active, try escape; N = 7)]; in Nielsen [1933, 295: E (I); Grandi [1961, 19]: E (reactive)]; Steiner [1958, 1962, 1963a, 1976: S (T3, +T1, +T2, +H: throat: dt, exp: see text; N = m)] Bonelli [1976a, 229-30: E (very mobile; N = 3)]
<i>Motes abyssinica</i>	Crickets	Iwata [1972, 134: E (I: MV but no escape, no coordination)]
<i>Larropsis chilopsidis</i>	Crickets	Gwynne and Evans [1975, 277, 281: E (Rc; N = 1)]
<i>Ancistromma distincta</i>	Crickets	Evans [1958a, 199: E (L, but no coordinated locomotion; N = m)]
<i>Tachytes</i>	Crickets	Bohart and Menke [1976, 263: E (# C, except <i>mergus</i> and <i>intermedius</i>)]
<i>aurulentus</i>	L. h. grasshoppers	Strandtmann [1945, 307: E (MV: palpi, antennae)]
<i>crassus</i>		Evans and Kurczewski [1966, 326: E (No R, but MV)]
<i>intermedius</i> (= <i>minutus</i>)	Pygmy molecrickets	Kurczewski (1966, 149: same as Krombein and Kurczewski, 1963)
"manticide"	Praying mantis	Fabre [1886, Vol. 3, 255-58: S (I L1, +1 L2, +1 L3; N = 1?)]
<i>mergus</i>	Pygmy molecrickets	Krombein and Kurczewski [1963, 147: Yoshimoto: S (I in flight; then 1 T after alighting); E: Williams, 1928 (L: jump 15-20cm; cannot use forelegs)]; Kurczewski [1976, 332: E (L)]
<i>validus</i>	Katydid (O)	Kurczewski and Ginsburg [1971, 124: E (rather C; some MV)]
<i>Tachysphex</i>		Kurczewski [1964, 142-46: S (2-8 T: 1-2 often sufficient for small prey; N = 16; Figs); 146-47: E (P or I; MV; rarely Rc)]; Fertton [1894, 216, roach, <i>T. mocsargi</i> : E (C)]
<i>apicalis</i>	Grasshoppers (<i>Melanoplus</i>)	Krombein [1964a, 15: E (MV: leg; N = 1)]
<i>bengalensis japonicus</i>	S. h. grasshoppers	Tsuneki [1969b, 7: E (I: some R: rather vigorous, walk; N = s)]
<i>boharti</i>	S. h. grasshoppers	Krombein [1963, 179-80: E (MV)]
<i>costae</i>	Praying mantis	Deleurance [1945, 29; N = s: S (I L1, then L2 and L3?); E (LOC if first St only)]; Grandi [1961, 197: E (I; MV important)]
<i>filicornis</i> (= <i>fugax</i>)	Acridids (O)	Grandi [1954, 180: E (I; MV)]; 1961, 201: E (I; active MV)]

<i>fluctuatus (erythropus? sericeus?)</i>	Praying mantis	Ferton [1911, 404; Cros: S (RS: 1 T1; N = 5-6); 400, 404; Cros: E (MV: antennae, mouthparts: for 12 days)]
<i>julliani</i>	Praying mantis (small)	Ferton [1897, 14; S (number St depends on size? 1 St if small); E (V)]
<i>lativalvis (obscuripenn.)</i>	Roaches	Grandi [1961, 192; E (C, more or less; N = 3)]
<i>mantiraptor (albocinctus)</i>	Praying mantis	Ferton [1911, 362; E (not K; N = s)]
<i>mediterraneus</i>	Tree crickets	Ferton [1901, 99; E (I; N = 2)]; Grandi [1961, 201; E (I; MV: important)]
<i>mundus</i>	Tertig. (O)	Kurczewski [1979, 646; E (MV: antennae, mouthparts)]
<i>nitidus</i>	S. h. grasshopper	Grandi [1961, 203, 205; E (MV: legs, antennae, palpi)]
<i>panzeri</i>	S. h. grasshoppers	Ferton [1899, 11; S (T, +H: near mouth)]; Grandi [1961, 206; E (I, MV)]
<i>parvulus</i>	S. h. grasshoppers	Alcock [1973; S (at least 1 L1: anterior; N = 1)]
<i>pechumani</i>	S. h. grasshoppers	Kurczewski and Elliott [1978, 770; S (/); 776; E (some MV; N = s)]
<i>pisomoides??</i>	??Hemiptera nymphs	Janvier [1928, 96; S (1 L)]
<i>pompiliformis</i>	S. h. grasshoppers	Grandi [1961, 208; E (I: energetic MV, even jump)]
<i>quebecensis</i>	S. h. grasshoppers	Peckhams [1905, as <i>Larra quebecensis</i> , 263; E (lived for 5, 6, 7 days; N = 3)]
<i>rufipes (ashmeadi?)</i>	Locustids (<i>Platycléts</i>)	Ferton [1899, 10; S (H; N = 1); 1901, 100; E (can still jump; N = 7)]
<i>rufitarsis</i>	Acridid grasshoppers	Janvier [1928, 93; S (1 H: under jaws, +1 T, between L; N = 1)]
<i>similis</i>	S. h. grasshoppers	Kurczewski [1967, 280; E (P or T)]; Krombein [1964a, 17; E (not D; MV; N = s)]
<i>tarsatus</i>	S. h. grasshoppers	Peckhams [1905, 262; E (dead; N = 1)]; Steiner [1981; S (1 T3, +1 T1, +1 H: throat; N = s); E (C, but some MV)]
<i>terminatus</i>	S. h. grasshoppers	Rau and Rau [1918, 149; E (many killed)]
<i>Holotachysphex turneri</i>	Grasshoppers	Gess [1978, 211; E (C; MV: slight TW)]
<i>Prosopigastra creon</i>	Lygaeid bugs (He)	Ferton (1912; E)
<i>Prosopigastra creon cimicivora</i>	Lygaeids (He)	Ferton (1912; E)
<i>Kohliella alaris</i>	Tree crickets	Gess [1980, 52; E (I: some MV)]
<i>Palarus</i>	Hymenoptera	Iwata [1972, 160; S (H: neck); E (C, P)]
<i>flavipes (= rufipes?)</i>	Hymenoptera (varied)	Berland [1925b, 106; Dufour: S (CH: twists neck; no St)]

(continued)

Table V (continued)

Wasp	Prey	Information and source
Sphecoidea		
<i>variegatus</i>	Hymenoptera (bees, wasps)	Grandi [1954, 169-74: S (St: twists head only after, contrary to Móczár, 1952); 1961, 186-90: (St)]; Móczár [1952, 123: S (CH: neck; no St); 122: E (K)]
<i>Lyroda japonica</i>	Grouse crickets	Tsuneki and Iida [1969, 14-15: E (MV: can jump: R considerably)]; Iwata [1972, 131: E (I; MV: active, but weak)]
<i>Lyroda subita</i>	Crickets	Kurczewski and Peckham [1982, 150: S (sH: throat, +L3; N = 2); 152: E (I; MV)]; Peckham and Peckham (1905, 255: E)
<i>Sericophorus</i>	Muscoid flies	Bohart and Menke [1976, 302: Rayment: E (D or K)]; Rayment (1955, 58: E)
<i>viridis roddi</i>	Flies	Rayment [1955, 69: S; 68-69: E]
<i>Plenocultus davisi</i>	Bugs (Mirids = He)	Kurczewski [1968, 190: E (I; MV, but no walking)]
<i>Solierella striatipes</i>	Grasshoppers (<i>Melanoplus</i>)	Williams [1950, 391: E (antenna TW only)]
<i>Miscophus</i>	Spiders (small)	Kurczewski [1969, 471: E (usually D)]; Nielsen [1933, 291: E (D)]
<i>americanus</i>	Spiders	Kurczewski [1982, 69: E (MV: legs; N = m)]
<i>bicolor</i>	Spiders	Maneval [1939, 72: E (MV: if stimulated, but not coordinated)]
<i>slossonae</i> subsp. / <i>barberi</i>	Spiders	Powell [1967, 342: E]; Krombein and Kurczewski [1963, 141: E (D; N = s)]; Kurczewski [1969, 485: S (near front end); E (usually D; some MV)]; 1982, 73: E (I; MV: legs; N = m)]
<i>Niela spinolae</i>	Psocids	Valkela [1955a, 55: E]
<i>Pisonopsis areolata</i>	Spiders	Janvier [1928, 90: E (D; no MV)]
<i>Pison strandi</i>	Spiders (Thomisidae)	Tsuneki [1970a, 2-4: E (D; but some MV: legs; N = m)]
<i>Trypoxylon</i>	Spiders	Peckham and Peckham [1905: 184-88: E (D or K; some MV; very V; N = s)]; Krombein [1967, 34: E (usually D; only tremors)]
<i>attenuatum</i>	Spiders	Nielsen [1933, 277: E (C)]; Grandi [1954, 168: E (I; N = m); 1961, 181: E (I; N = m)]
<i>bicolor</i>		Yoshimoto [1964, 520: E (P; N = m)]

<i>bidentatum</i>	Spiders	Peckham and Peckham [1905, 194: S (ventral cephalothorax)]
<i>collinum rubro-cinctum</i>	Epeirid spiders	Krombein [1954; 5: E (a few: MV, legs; N = 10)]
<i>elongatum</i>	Attid spiders	Richards [1934, 343: Williams, 1919, 143: E]
<i>figulus</i>	Spiders	Nielsen [1933, 282: E (L)]
<i>palliditarse (= albitarse)</i>	Argiopid spiders	Richards [1934, 351: Bruch, 1932: S (1 St, dorsal region); E (K)]
<i>pollitum</i>	Spiders	Lin [1969, 130: E (C; N = m)]
<i>responsum hatogayuum</i>	Spiders	Tsuneki [1970a, 10: E (MV: palpi; N = s)]
<i>rugiceps</i>	Argiopid spiders (<i>Epeira</i>)	Richards [1934, 346: Rau, 1933, 151-56: E (Not K: D)]
<i>spinosum</i>	Spiders	Lin [1969, 126: E (usually C; N = m)]
<i>texense</i>	Spiders (Attids, Thomisidae, Epeirid)	Kurzewski [1963b, 244: E (L; MV: considerable; N = m)]; Richards [1934, 350: Hartmann (1905), 57: E (not K; St)] Hamm and Richards [1926, 299: E (usually quick death)]
Crabroninae	Dasytidae (C)	Valkeila [1963, 233: S (between L2 and L3?)]
<i>Belomicrus borealis</i>	Diptera	Ferton [1899, 14: E (die soon; max 72 hr; N = s); 1901, 110-12: E (D: 5 of 8; others dead); 1902, 517: E (D; N = s)]; Peckhams [1905, 79: Verhoeff: E (dead; thorax crushed)];
<i>Oxybelus</i>	Diptera	Ferton [1902, 517: E (D; no MV; N = s)]
<i>ambiguus (= mucronatus)</i>	Diptera	Grandi [1954, 190: E (faint MV; N = s); 1961, 256: E (very D, but faint MV)]
<i>argentatus</i>	Diptera	Tsuneki [1969a, 14: S (center T; N = 1); E (some MV)]; Peckham <i>et al.</i> [1973, 649: E]
<i>bipunctatus</i>	Diptera	Krombein and Kurzewski [1963, 151: E (slight MV; N = 4)]; Snoddy [1968: S (St and CH)]
<i>emarginatus</i>	Diptera	Kurzewski [1972b, 401: E (slight MV: proboscis; N = 5)]
<i>exclamans</i>	Sarcoph.: <i>Senotainia</i> (D)	Ferton [1901, 111: S (between T1 and H; also RS); E (D)]; Grandi [1954, 187: E (D; no MV; N = s); 1961, 262: E (D; faint MV; N = m)]
<i>melancholicus (= victor)</i>	Diptera	
<i>pilosus</i>	Diptera	Bonelli [1976a, 232: E (D; N = 10)]
<i>platenis</i>	Diptera	Ferton [1901, 111: Brethes: S (s L1)]

(continued)

Table V (continued)

Sphecoidea

Wasp	Prey	Information and source
<i>uniglumis</i>	Diptera	Hamm and Richards [1930, 114-15; Sickmann, 1883, Chevalier, 1926, Adlerz, 1903: S (H: neck)]; Nielsen [1933, 274: E (die: several days)]; Steiner [1979, N > 150: S (1 L1); E (C, P; death in a few days)]
<i>victor</i>	Diptera	Grandi [1961, 260: E (no MV)]
<i>Anacrabro ocellatus</i>	Bugs (Miridae = He)	Bohart and Menke [1976, 377: Barth, 1909: E (dead?)]
<i>Entomognathus brevis</i>	Chrysomelid beetles	Grandi [1961, 242: E (D, but MV if stimulated)]; Miller and Kurczewski [1972, 62: Benoist, 1915, Grandi, 1927, 1931, Maneval, 1928, Abrahamsen, 1951: E (not K)]; Janvier [1977, Vol. 2, 4, 5: E (MV, but no walking; N = m)]
<i>Entomognathus memorialis</i>	Chrysomelid beetles	Miller and Kurczewski [1972, 67: E (I; MV: antennae, legs; N = m)]
<i>Lindeni</i>	Diptera	Miller and Kurczewski [1975, 105: S (St; N = 1); 86, 88, 90, 105: E (not K; some MV, V)]
<i>albilabris</i>	Miridae (He)	Janvier [1977, Vol. 1, 78: E (MV, but no walking)]
<i>meliponus</i>	Chloropidae (D)	Janvier [1977, Vol. 1, 70: E (faint MV; N = m)]
<i>mesopleuralis</i>	Chironomidae	Janvier [1977, Vol. 1, 104: E (some MV; N = m)]
<i>panzeri</i>	Chloropidae (D)	Janvier [1977, Vol. 1, 124: E (faint MV, several days; N = m)]
<i>pygmaeus</i>	Hymenoptera	Janvier [1977, Vol. 1, 112: E (faint MV; N = m)]
<i>pygmaeus armatus</i>	<i>Apanteles</i> wasps	Ferton [1901, 114; N = 1: S (/); E (D)]
<i>subaeneus</i>	Empididae (D)	Janvier [1977, Vol. 1, 61: S (an ant!: 1 L2; N = 1); 60: E (slight MV; N = m)]
<i>Rhopalum brevinodum</i>	Aphids	Janvier [1928, 78: S (first between Ls); E (I; MV: whole body, no coordination)]
<i>Rhopalum claudii</i>	Aphids	Janvier [1928, 84: S (1 T); E (D)]
<i>Rhopalum clavipes</i>	Psocoptera	Janvier [1977, Vol. 1, 14: E (MV, if stimulated)]
<i>Rhopalum latronum</i>	Diptera	Tsuneki [1952b, 115: S; 1960, 48: S (T)]
<i>Rhopalum longinodum</i>	Diptera	Janvier [1928, 76: E (I)]

<i>Rhopalum nipponicum</i>	Diptera: daddy-long-legs	Tsuneki [1960, 49: E (D; not K; N = m)]
<i>Podagritys gayi</i>	Diptera	Janvier [1928, 70-71: S (I between Ls; N = s); E (D, but MV if large: shivers)]
<i>Podagritys rufotaeniatus</i>	—	Janvier [1928, 74: S (I between Ls); E (no MV)]
<i>Crossocerus ambiguus</i> (= <i>annulipes</i>)	Leafhoppers	Janvier [1977, Vol. 1, 221: S (use of St not seen; N = s); 218-20: E (MV, no walking; N = m)]
<i>Crossocerus carbonarius</i>	Diptera	Hamm and Richards [1926, 313: E (TW)]
<i>Crossocerus elongatulus</i>	Diptera (small)	Janvier [1977, Vol. 1, 143: E (rather faint MV; N = m)]
<i>Crossocerus nigrinus</i> (= <i>pubescens</i>)	Diptera	Tsuneki [1960, 45: S (H: throat; N = 1)]; Janvier [1977, Vol. 1, 261: E (MV, no walking; N = m)]
<i>Crossocerus quadrimaculatus</i>	Diptera	Maneval [1939, 84: E (most: faint MV; N = s)]; Grandi [1954, 185: E (D; N = s); 1961, 245: idem]
<i>Crossocerus sexmaculatus</i>	Gnats	Peckham and Peckham (1905, 101: E)
<i>Crossocerus vagabundus</i>	Diptera	Hamm and Richards [1926, 316: E (Sickmann: some MV: antennae)]; Tsuneki [1960, 39: E (not K; faint MV; N = m)]
<i>Tracheliodes quinquenotatus</i>	Ants	Pate [1942, Emery, 1893, Fertton, 1892, 1896, Grandi, 1928-1935: E (very I)]; Grandi [1961, 249: E (MV: quite active; N = s)]; Janvier [1977, Vol. 2, 20: E (MV)]
<i>Crabro</i>		Evans [1960, 133: E (K?)]; Bohart and Menke [1976, 407: E (D or K)]
<i>argusinus</i>	Diptera	Mathews <i>et al.</i> [1979, 157: E (alive; N = m)]
<i>cingulatus</i>	Diptera	Rau and Rau [1918, 99: E (as <i>Paranothreus cingulatus</i> : all dead; N = m)]
<i>cribrarius</i>	Syrphids, muscids (D)	Hamm and Richards [1926, 299: Adlerz: S (T; not CH?); Nielsen [1933, 270: S (/)]; Janvier [1977, Vol. 2, 36: E (faint MV; N = m)]
<i>peltarius</i>	Rhagionids, etc. (D)	Hamm and Richards [1926, 308: Adlerz: S (sternum)]; SimonThomas and Veenendaal [1974, 60: S (I T; N = m)]; Janvier [1977, Vol. 2, 47: E (faint MV; N = m)]
<i>Ectemnius cavifrons</i>		Janvier [1977, Vol. 2, 202-203: S (apparently no St; N = s)]
? <i>Ectemnius cephalotes</i>	Lepidoptera (adults)	Peckham and Peckham [1905, 105, as <i>Crabro interruptus</i> : E (some alive, some dead)]
<i>Ectemnius continuus</i>	Diptera	Tsuneki [1960, 25: E (R: even wing beats; N = m)]

(continued)

Table V (continued)

Wasp	Prey	Information and source
<i>Ectemnius crassicornis</i>	Syrphids (D)	Janvier [1977, Vol. 2, 113: S (no St? CH?; N = s)]
<i>Ectemnius discrepans</i>	Diptera	Williams [1927, as <i>Melanocrabro discrepans</i> , 446: S (caught in mid-air; N = 1)]
<i>Ectemnius laevigatus</i>	Diptera	Grandi [1961, 251: E (D; some dead; N = m)]
<i>Ectemnius lapidarius</i>	Diptera	Berland [1925b, as <i>Crabro chrysostratus</i> , 200: Nielsen: S (K)]; Leclercq (1949: E)
<i>Ectemnius nigrifrons</i> (= <i>ruficornis</i>)	Syrphids (D)	Janvier [1977, Vol. 2, 182: E (MV; N = m)]
<i>Ectemnius pauchimaculatus</i>	Diptera	Krombein [1964b, 86: E (L; MV: legs, antennae; N = m)]
<i>Ectemnius rubicola</i>	Syrphids (D)	Janvier [1977, Vol. 2, 65: S (T); 66: E (slight MV; N = m)]
<i>Ectemnius stirpicola</i>	Diptera	Rau and Rau [1918, 94, as <i>Hypocrabro stirpicola</i> : E (all dead)]; Krombein [1960a, 65: E (no MV)]
<i>Lestica alata</i>	Butterflies	Tsuneki [1960, 30: S (T; N = 1)]
<i>Lestica clypeata</i>	Diptera	Hamm and Richards [1926, 302: Perris, as <i>Thyreus clypeata</i> : E (K)]
<i>Lestica heros</i>	Butterflies (Geometridae)	Tsuneki [1960, 28: E (not K; still alive after 3 days; N = 1)]
<i>Lestica subterranea</i>	Lepidoptera	Janvier [1977, Vol. 2, 223: E (MV, even wing beats at times; N = s)]
Nyssoninae		
<i>Mellinus arvensis</i>	Diptera	Ferton [1899, 14: E (die < 4 days)]
	Diptera	Rabaud [1917: S (ES, V: see text)]; Hamm and Richards [1930, 96-99: S (Chevalier, 1924, ES, H: neck); E (die soon)]; Molitor (1939a, 73: Rabaud, Chevalier, Hamm: S); Olberg [1959, 329-33: S (V, 1 L? Figs)]; Huber [1961, 70-71, 81, also Bristowe, 1948: (S†; RS; N = m); 71: E (MV or not, if large or small)]; Grandi [1961, 110: S (T)]; Piek <i>et al.</i> [1982, 159: van Marle: Ph (labeled venom in ggl only)]
<i>obscurus tristis</i>	Diptera	Maruyama [1948, 9: E (C; no MV; N = m)]
<i>sabulosus</i> (= <i>crabroneus</i>)	Diptera	Hamm and Richards [1930, 101: Adlerz, 1903: S (T or A); E (kept alive 6 weeks!)]

<i>Alysson conicus</i>	Leafhoppers	Evans [1966a, 29: E (no R; usually die in several days)] O'Brien and Kurczewski [1979: E (D, or dead; N = s); 1982c, 230: E (C or K)]
<i>melleus</i>	Leafhoppers	Rau and Rau [1918, 141: E (dead?; N = 12)]; Evans [1966a, 26; E (often appear dead)]
<i>Cliternestra chilensis</i>	Homoptera	Janvier [1928, 136, N = s: S (1 between L2); E (D; no MV)]; Evans [1966a, 73: same]
<i>Cliternestra goyi</i>	Homoptera	Janvier [1928, 142: S (1 between L); E (C, in small prey, but MV in large ones)]
<i>Exeirus lateritius</i>	Cicadas	Evans [1966a, 114: Musgrave: S (in ggl)]
<i>Argogorytes mystaceus</i>	Spittle bugs (Ho)	Hamm and Richards [1930, as <i>campestris</i> , 102: S (St into the foam)]
<i>Gorytes canaliculatus</i>	Leafhoppers	Evans [1966a, 62: E (smt MV, but soon die)]; Powell [1974, 6: E (no R; die soon)]
<i>Gorytes laticinctus</i> (= <i>provancheri</i>)	Cercopids (Ho)	Hamm and Richards [1930, 103: Maillard, 1847: E (D?)]; Maillard [1847, 94: E]
<i>Gorytes planifrons</i>	Leafhoppers	Maneval [1939, 59: E (very faint MV only)]
<i>Spheticus speciosus</i>	Cicadas	Reinhard [1929, 50-52: S (always 1 L1, near ggl; N = s); 1929, 52-53: E (fresh usually 1 week or more)]; Clausen [1940, 339: Riley, 1892, Harzell, 1935 (CNS lesions): E]; Evans [1966a, 104-105: S (Dambach and Good, 1943: between A seg; also Reinhard obs)]
<i>Hoplisoides costalis</i>	Membracids, Cercopids (Ho)	Reinhard [1929, 246-47: E (no MV; rarely some)]; Clausen [1940, 337: E (die, 1 week)]
<i>Hoplisoides nebulosus</i>	Membracids (Ho)	Evans [1966a, 40: E (no R; fresh several days; N = m)]
<i>Hoplisoides tricolor</i>	Leafhoppers	Evans [1966a, 54: E (C; N = m)]
<i>Stizus fasciatus</i>	Acridids	Evans [1966a, 124: Fertton: S (T; N = s)]; Fertton [1899, 13: E (not K; N = 7)]
<i>Stizus pulcherrimus</i>	Acridids	Tsuneki [1965a, 4: S (2 T; N = 1); 11: E (D; some MV; N = m); 1976, 6-7: S (H: neck?, +sf; RS)]
<i>Stizus ruficornis?</i>	Praying mantis	Deleurance [1941, as <i>distinguendus</i> , 287-88: S (1 L1: LOC, +1 L3 N = 1); E (D; fresh 13 days)]

(continued)

Table V (continued)

Wasp	Prey	Information and source
<i>Bembecinus</i>	Leafhoppers	Evans [1966a, 140: E (very D, or K?)]
<i>cingulatus</i> (= <i>agilis</i>)	Jassidae (Ho)	Richards [1937, 116: S (T; N = 1)]
<i>neglectus</i>	Leafhoppers	Evans [1955, 293: E (very D, or dead; N = m)]
<i>tridens</i>	Cicadellids (Ho)	Ferton [1902, 514: E (not K; react; N = s)]; Grandi [1961, 114: E (D; no MV; N = m)]
<i>tridens errans</i>	Cicadellids (Ho)	Ferton [1911, 357: (some MV; N = s)]
<i>Bicyrtes</i>	Hemiptera	Evans [1966a, 174: E (C; die in several days)]
<i>fodiens</i>	Hemiptera	Evans [1966a, 169: E (D; smt MV, several days)]
<i>quadrifasciata</i>	Coreids, Pentatomids (He)	Evans [1966a, 157: E (die soon)]; Krombein [1955, 155-56: E (D, P; faint MV: 2.5 weeks)]
<i>variegata</i>	Hemiptera	Janvier [1928, 120: E (usually no MV, except a few)]
<i>Microbembex</i>	—	Nielsen [1933, 299: E (dead and dry)]; Malyshev [1968, 174, 269-70: S (no St?); Iwata [1972, 184: S (no St?); Matthews and Evans [1974, 79, 84: S (St at all?)]
<i>californica</i>	—	Goodman [1970, 208: S (no St)]
<i>ciliata</i>	Insects: wide variety	Janvier [1928, 117: S (St in flight); E (C if small, I if large)]
<i>monodonta</i>	Insects, mostly dead	Rau and Rau [1918, 39: E (dead and dry: N = 6)]; Evans [1966a, 375-76: S (no St?); E (dead)]
<i>uruguayensis</i>	Small carabid beetles	Alcock [1975, 195, 196: S (vestigial St?); Evans [1966a, 390: Llano: S (St)]
<i>Rubrica gravida</i>	Diptera	Evans [1966a, 264: Llano: S (St in the air)]
<i>Rubrica surinamensis</i> (= <i>nasuta</i>)	Diptera	Evans [1966a, 260: Callan: E (dead)]; Evans <i>et al.</i> [1974, 340: S (K)]
<i>Stictia</i>	Diptera	Malyshev [1968, 173: E (dead?)]
<i>carolina</i>	Diptera	Evans [1966a, 238: E (Hartman: usually K; often MV, however)]
<i>maculata</i>	Diptera	Matthews <i>et al.</i> [1981, 252: capture in mid-air]
<i>punctata</i> (= <i>Monedula p.</i>)	Diptera	Roubaud [1910, 17: E (K)]
<i>signata</i>	Diptera	Elliott <i>et al.</i> [1979, 359: S (in flight; N = 1)]

<i>Bembix</i>	Diptera	Fabre [1856b, 186: S (St?); E (usually some MV); 1879, Vol. 1, 274-75: E (apparently dead; dry fast)]; Fertton [1899, 1: S (not seen); 1899, 1-4, 6, 8, 14: S (H: near mouth; often mid-air); E (also Lepelletier, 1841: MV, fresh several days)]; Roth [1922: S (stung, not killed); E (also Lepelletier, 1841: MV; some still alive after 10 days)]; Evans (1957b, 13: die)
<i>americana comata</i>	Diptera	Evans [1957b, 45: E (D; N = m)]
<i>americana spinolae</i>	Diptera	Evans [1957b, 28-29: S (/); E (apparently dead; N = 1)]
<i>belfragei</i>	Diptera	Evans [1957b, 73: S (T); E (V: C to I, even escape; N = s)]
<i>brullei</i>	Diptera	Janvier [1928, 104, 106: S (s St? in flight, or CH if own feed.); E (V, depending on size)]
<i>cinerea</i>	Diptera	Evans [1957b, 91: E (D or dead; N = m)]
<i>handlirschi</i>	Diptera	Ferton [1911, 397: E (slight MV)]
<i>'integra'</i>	Diptera	Grandi [1961, 124: S (Sb); E (die quickly? N = m)]
<i>multipicta</i>	Tabanid flies	Cane and Miyamoto [1979, 671: S (St, often mid-air)]
<i>niponica</i>	Diptera	Tsuneki [1957, 14, N = m: E (all: MV, one even wing beats); 1958, 24, 30: S (anterior T)]
<i>nubilipennis</i>	Diptera	Rau and Rau [1918, 32: E (all dead; N = m)]
<i>oculata</i>	Diptera	Grandi [1961, 120: S (repeated RS: no effect; N = 1)]
<i>olivacea</i>	Diptera	Grandi [1961, 117: E (D; MV: antennae, legs, at least 36 hr; N = m)]
<i>rostrata</i>	Diptera	Roth [1922, 47: E (MV, not dead)]; Berland [1925b, 70: E (not dead; survives several days)]; Nielsen (1945, S, E); Olberg [1959, 348: S (St; Fig)]
<i>trogloidytes</i>	—	Evans [1957b, 130: E (D or dead; occasionally R; N = m)]
<i>vidua</i> (= <i>rostrata</i>)	Diptera	Fabre [1856b, 186: S (CH? no St?); E (dead)]
<i>Zyzyx chilensis</i>	Diptera	Janvier [1928, 124, 126: S (CH if own feeding; St otherwise, or not?); E (fresh; N = m)]; Evans [1966a, 257; Janvier: E (K if small? often I if large)]
<i>Stictiella formosa</i>	Lepidoptera: adults	Evans [1966a, 183: E (D or K?)]
	Lepidoptera: Adults	Gillaspay <i>et al.</i> [1962, 561: E (a few I)]

(continued)

Table V (continued)

Sphecoidea^a

Wasp	Prey	Information and source
<i>Glenostictia scitula</i>	Solitary bees	Evans [1966a, 199: S (St in mid-air; N = 1); E (often MV, but dead after storage)]
<i>Steniolia obliqua</i>	Diptera	Evans and Gillaspay [1964, 270: E (K)]; Evans [1966a, 218–20: E (dead? no MV)]
Philanthinae		
<i>Philanthus</i>		Evans and Lin [1959, 116: E (killed)]; Bohart and Menke (1976, 563: S)
<i>bicinctus</i>	Bees	Armitage [1965, 94: S (T; N = 1)]
<i>crabroniformis</i>	Bees	Alcock [1974a, 237: S (T; N = 1)]
<i>flavifrons</i> (crabroniform)	Bees	Bohart, G. E. [1954, 26: S (H: throat; N = 4)]
<i>gibbosus</i>	Bees	Reinhard [1924, 367, 374: S (K); E (no MV)]; 1929, 95, 111, 120: S (H); 113–14: E (reflexes)]
<i>punctatus</i> (= <i>gibbosus</i>)	Halictid bees	Peckham and Peckham [1905, 161: S (H: throat; N = s); 162: E (dead)]; Rau and Rau [1918, 115: E (always dead; N = m)]
<i>triangulum</i>	Honey-bees	Latreille (1802: S); Fabre [1891, Vol. 4, 213–27: S (H: throat; N = s); 216–17: E (dead)]; Hamm and Richards [1930, 106: S (Fabre: H, neck); E (D); some survive 15 days: Lepeletier, 1841, p. 563)]; Molitor [1933b, 497: S; E (no MV)]; 1937, 298: S (H: neck); 299: E (not always C immediately); 1939a, 72: S (between H and T?); Petzer [1936: S]; Tinbergen [1958, 74–75, 78–80: S (H: chin; dt, exp)]; Grandi [1961, 166: E (no MV; D?; N = m)]; Rathmayer [1962, dt: S, Ph, E; (see also Chapter 5)]
<i>triangulum diadema</i>	Bees	Bonelli [1976a, 228: E (C; no MV; N = s)]
<i>venustus</i>	Halictid bees	Grandi [1961, 167: E (D; some MV; N = m)]
<i>Trachypus denticollis</i>	Bees	Janvier [1928, 149: S (1 H: throat, +1 between L1 and L2); E (faint MV; shivers)]
<i>Aphilanthops frigidus</i>	Ants	Evans [1962a, 244: E (P, D)]

<i>Chypeadon</i>		
<i>evansi</i>		
<i>Cerceris</i>	<i>Pogonomyrmex</i> ants	Iwata [1972, 158: E (C, P)] Alcock and Gamboa [1975, 163: S (T; Figs; N = s)] Fabre [1979, Vol. 1, 79-92: E (D; some MV; fresh several weeks)]; Walckenaer (1817: S); Byers [1962, 319: S (some spp. St. only after storage)]; Scullen [1965, 338: E (K? or not? V, even same wasp)]; Tsuneki [1965b, 5-6: E (Coleopteran prey: usually D, P; Hymenoptera: often I)]
<i>angularis</i>	Long-horned beetles	Williams [1919, 147: E (no MV)]
<i>arenaria</i>	Weevils	Molitor [1937, 299: S (ES); E; 1939a, 71: S (between H and T1, T1 and T2; Fig; N = s); 1939b, 362: S)]; Hamm and Richards [1930, 111: S (Chevalier, 1927: between T and A); E (Adlerz, 1903: MV: even vigorous; died in 4 days; Richards: no MV, 2 of 7)]; Grandi [1961, 168: E (I; vivacious MV; N = s)]; Tsuneki [1965b, 27: S (between T1 and T2; N = 1); E (no MV)]; Eck [1971, 347-49: S (s T; Figs; N = m); E (no MV)]
<i>bicornuta</i>	Weevils	Strandtmann [1945, 311: E (C or dead; N = 15)]
<i>californica</i>	Buprestid beetles	Linsley and MacSwain (1956: S, E); Iwata [1972, 154: Linsley and MacSwain: E (I; C in cells)]
<i>chilensis</i>	Weevils	Janvier [1928, 153: S (H: neck); E (no MV; N = s)]
<i>emarginata</i> (= <i>sabulosa</i>)	Haliictid bees	Ferton [1910, 153: S (RS: near H, throat; N = 1); 154: E (not K; one even tried escape; N = s)]; Hamm and Richards [1930, 109: Ferton, 1905: S (H; N = 1); E (C; rarely MV)]
<i>fidelis</i> (= <i>bicornuta</i>)	Weevils	Krombein [1960b, 75-76: E (weak MV; N = 1)]
<i>finitima</i>	Chrysomelid beetles	Strandtmann [1945, 312: E (some quite active: leap)]
<i>flavofasciata</i>	Chrysomelid beetles	Krombein [1959, 197-98: E (L after capture; D in cells; N = m)]
<i>frontata</i> f.	Weevils	Krombein [1960b, 77: E (C; no MV)]
<i>fumipennis</i>	Beetles	Rau and Rau [1918, 129: E (no signs of life: D? or K?)]
<i>gayi</i>	Chrysomelid beetles	Janvier [1928, 156: S (H or L1); 157: E (smt faint MV; N = s)]
<i>hortivaga</i>	Hymenoptera	Tsuneki [1965b, 10, 16: S (T); 11: E (MV; rather active: legs, wings; N = s)]

(continued)

Table V (continued)
Sphecoidea^a

Wasp	Prey	Information and source
<i>quinquefasciata</i>	Weevils	Hamm and Richards [1930, 113: Adlerz, 1903: E (slight MV)]; Grandi [1961, 169-170: E (D; N = m)]
<i>robertsonii</i>	Weevils	Krombein [1952a, 290, 292: E (I; MV: one walked); 1953b, 120: E (MV, but no walk)]
<i>rubida</i>	Various Coleoptera	Grandi [1961, 175: E (I; N = m)]
<i>rufimoda</i>	Weevils	Strandtmann [1945, 312: E (some MV; N = 36)]
<i>rybyensis</i>	Bees	Berland [1925b, 54: Marchal, 1887: S (I-s T); E (delayed)]; Hamm and Richards [1930, 107: S (Marchal, 1887: 2-3 T; N = m; others between T1 and T2 mostly; also H; V)] Molitor [1933a, 164: E (not K); 1937, 299: E (C or dead); 1939a, 70: E (I; MV, walk)]; Tsuneki [1965b, 24: S (center T; N = 1)]
<i>simplex</i> (= <i>intrica</i>)	Tenebrionid beetles	Alcock [1974b, 647: E (I; MV)]
<i>tuberculata</i>	Weevils	Fabre [1879, Vol. 1, 61-78: S (2-3 St: between L1 and L2; N = 3); kept alive 4 weeks]
<i>Eucerceris ruficeps</i>	Weevils	Linsley and MacSwain [1954, 77: E (very active, but not in cells: Rs? N = m)]
<i>Eucerceris tricliliata</i> (<i>bitruncata</i> ?)	Weevils	Krombein [1960b, 77: E (some MV; N = 2)]

^aSee footnotes to Table I.

to fully abolish locomotion defences. Not surprisingly, some of the more sophisticated and efficient stinging methods are found among these hunters.

When a single but large prey is sufficient for the larva, return to the nest with more prey, as in many more advanced wasps, is not needed. If equipped with efficient stinging methods, even very primitive wasps devoid of homing (and/or prey-carrying) ability could paralyse such large prey and leave or bury them on the spot. At the other extreme of the spectrum, a weak aphid can be merely plucked from a plant and summarily squeezed between the mandibles, instead of being stung (many pemphredonine wasps).

Paralysis of large orthopteroids, which is often predominantly local, for each sting, can vary with wasp-prey systems from very light and temporary (including complete recovery) to deeper and more permanent. Generally speaking, however, paralysis of cockroaches, molecrickets and crickets is often much lighter and more reversible than that of 'surface' prey such as katydids, locusts, grasshoppers or mantids.

a. The Larra-Molecricket System (Temporary Paralysis with Complete Recovery). Not very long ago, larrine wasps were considered among the most primitive sphecoid wasps, very close to the Ampulicinae. In some forms such as *Larra*, brood care is reduced to stinging a molecricket into very light, temporary paralysis, laying an egg on it and leaving the prey to recover, go back to its tunnels and apparently resume fully normal activities. The latter possibility is very exceptional among sphecoid wasps. Such a rudimentary nesting behaviour calls to mind the more primitive bethyloid or scolioid wasps but it could be a derived character instead, a secondary simplification, adapted to the special ecology of the prey (see Gwynne and Evans, 1975, for instance). Storage in a nest could have become unnecessary or impossible owing to the burrowing habits of an only lightly paralysed prey. Perhaps 'surface' or nonfossorial prey such as grasshoppers would be more likely to stay put if stored in the ground, away from the light and/or heat that activates them.

Reports on stinging methods of *Larra* wasps (reviewed in Steiner, 1984) often show important differences. These could be observer, interspecific, individual, differences or be related to different internal or external conditions. It seems clear, however, that *Larra* wasps deliver several rather precise stings in succession to their prey. According to Smith (1935), the North American species *L. analis* F. first stings *Gryllotalpa hexadactyla* Perty near the juncture between thorax and abdomen, thereby paralysing the hind legs and stopping locomotion. The wasp applies a few more stings laterally in the suture between head and thorax, apparently in the vicinity of the nervous system. However, the middle legs remain unparalysed and the rest of the body becomes active again after about 5 min. Incomplete sequences of resting [one or two sting(s)] occur when previously paralysed

molecrickets are found. Williams studied several species, even in captivity, and reported that stinging of *G. coarctata* Walker by the Australian *L. femorata* Sauss. did not vary much. The wasps stung the area between the third and second pairs of legs one or several times, then the second and first, not far from the median ventral line, and finally stung the side of the mouthparts or cheeks (1928, pp. 46–49). The latter sting was also described from *L. luzonensis* Roh. by the same author. In Japan, Iwata and Tanihata (1963) reported that *L. amplipennis* (Smith) stung between the coxae of the legs repeatedly and . . . ‘sometimes she stings also the gular region of the prey’. *L. carbonaria erebus* started between the first and second pairs of legs, the last sting being delivered in front of the forelegs in the throat (Tsuneki, 1969b, p. 15). Apparently this last sting did not fully abolish movements of the buccal palpi, suggesting that the suboesophageal ganglion had not been hit or the venom was weak. Malyshev (1941, in Malyshev, 1968, pp. 124–125) also made a detailed study of the Palearctic species *L. anathema* Rossi and gave in his book detailed figures that show stinging. After flushing the molecricket from its galleries, the wasp delivered three successive stings in the following constant order: mesothorax, prothorax, then beneath the pharynx. Again, clear evidence of local action of the venom is apparent: the last thoracic segment was apparently not stung and the last pair of legs remained capable of active movements. Interestingly, paralysis of prey is apparently less complete in *Larra* species that lay comparatively smaller eggs (in Clausen, 1940, p. 335), which are presumably less likely to be damaged or destroyed, actively or by accident. Thus the egg of *L. scelestus* is extremely small (only 1.7 mm!). Why can molecrickets resume normal activities, whereas recovered crickets, stung essentially in the same way by *Liris* wasps (Steiner, 1962, 1976), cannot do so, even after their release from the cells in which they had been confined (Steiner, 1984)? It is the throat sting near the suboesophageal ganglion which ‘deactivates’ crickets (Steiner, 1963a) (also cockroaches stung by *Ampulex compressa*) (Piek *et al.*, 1984a) but apparently not molecrickets. In the latter case several options come to mind:

1. The venom is weaker.
2. It is inoculated in smaller doses.
3. It is chemically different.
4. The prey are comparatively larger or otherwise less sensitive than the crickets attacked by *Liris*.
5. They are affected differently by a venom which is not fundamentally different (in the unlikely event that the molecrickets could be physiologically so different from the closely related crickets).

b. *Ampulicine Cockroach Hunters (Primacy of Deactivation over Paralysis?)*. Among these primitive wasps, *Dolichurus stantoni* (Ashm.), studied in captivity, is said to sting *Blatella bisignata* somewhere in the breast once or several times. This does not result in complete paralysis, only in subdued activity and passive, but ineffective, resistance (Williams, 1919, pp. 113–114). Recovery is not complete, and the prey remains unable to make a long-sustained or rapid run. Interestingly, feeding is resumed, in contrast to crickets stung by *Liris*. This seems to indicate that the state is somewhat intermediate between that of the molecrickets and crickets. In other reports, a sting in or near the throat is also consistently mentioned, even in the same species as above (in Clausen, 1940, p. 327) and in some *Ampulex* wasps (in Iwata, 1972, p. 82) such as *A. assimilis* (Hingston, 1925, in Malyshev, 1968, p. 138) *A. compressa* (Piek *et al.*, 1984a) and *D. corniculatus* (Spinola) (Adlerz, in Soyer, 1947b, pp. 118–119). See also Chapter 5, pp. 236–241.

Therefore molecrickets, cockroaches and crickets are all stung in the throat and recover from temporary paralysis, but the general effect is somewhat different each time: no deactivation at all, partial deactivation (but feeding), complete deactivation (no feeding). As in spider wasps, resting frequently occurs in response to growing or residual resistance (*Ampulex canaliculatus*) (Williams, 1929, p. 325). Uncertainties remain as to how many and/or which thoracic stings are given. Since control of the legs is not fully abolished at any time, one might wonder whether thoracic stinging is rather related to protecting the future egg by weakening the legs(s) that will bear it. Compared with the legs of grasshoppers, mantids or molecrickets, those of cockroaches are rather weak for defence or escape. Priority might then be given to deactivating over paralysing effects (Steiner, 1984). For further details on the state of cockroaches stung by ampulicine wasps the reader is referred to Chapter 5, Piek *et al.* (1984a) and Grandi (1954, pp. 152–153; 1961, pp. 128–129).

c. *Cockroach Hunting in Sphecine and Larrine Wasps*. Among the Sphecinae, which are more advanced than the Ampulicinae, *Penepodium*, *Podium* and *Trigonopsis* also attack cockroaches. Unfortunately, the details of stinging are apparently not well known. This is especially regrettable in view of the more advanced phylogenetic position of these wasps, which could make comparisons with the Ampulicinae very instructive. The state of the roaches stung by *Podium* wasps varies from extensive recovery, but usually lasting docility (Williams, 1928, p. 126) (*P. haematogastrum*), to complete paralysis, but these roaches are often smaller and more numerous than in the cells of Ampulicinae (Krombein, 1967, p. 256; 1970, p. 19) (*P. rufipes*)

(various authors in Bohart and Menke, 1976, p. 96). Imperfect paralysis, when present, is therefore not related to an invulnerability of cockroaches to venom.

Paralysis of roaches stung by *Trigonopsis* wasps is said to vary from partial to complete (in Bohart and Menke, 1976, p. 98), whereas Iwata (1972, p. 222) speaks only of complete paralysis and also stresses the differences in egg-laying behaviour when compared with that of Ampulicinae. Among the Larrinae, a few *Tachysphex* species also hunt roaches (*obscuripennis* group) (Bohart and Menke, 1976, p. 271). Thus Grandi (1961, p. 192) took well-paralysed *Ectobius lividus* F., one from a prey-laden *Tachysphex lativalvis* Thoms. and two others from a nest of this species. No recovery is mentioned even though development of the young larva was followed.

d. Hunters of Long-horned Grasshoppers of Rather Large Size. In contrast to hunters of harmless roaches, a number of Sphecinae, particularly within the genus *Sphex*, but also *Palmodes*, *Isodontia* and *Chilosphex* prey on rather fierce predacious Orthoptera of the suborder Ensifera, such as Tettigoniidae, particularly Phaneropterinae (bush and round-headed katydids), Pseudophyllinae (true katydids), Decticinae (shield-backed grasshoppers), Conocephalinae (meadow grasshoppers) and Tittigoniinae (pine tree katydids). This places particularly heavy demands on the wasps.

Efficient and elaborate stinging methods are especially well represented here. Usually these wasps sting most or all thoracic segments, leg pairs or ganglia at least once in addition to the neck sting. Each sting has a very clear local paralysing effect that appears immediately and is essentially restricted to one leg pair (or the mouthparts for the throat stings). Stinging sequences, although not immutable, tend now to become more predictable, at least in their most complete form, the CSP (complete stinging pattern), emphasised from now on. Abortive sequences (ASP, abortive stinging pattern) and variations within species will be discussed more fully in the analysis (Sections III and IV).

Again, discrepancies can be found in the literature. A few reports will now be examined, starting with that of Fabre (1897, Vol. 1, pp. 164, 175–189) on the 'Languedocian *Sphex*' (in fact a member of the genus *Palmodes*: *P. occitanicus* Lep. and Serv.). This solitary species hunts the 'Ephippiger of the vine', a shield-backed grasshopper which is (Berland, 1926, p. 174) or is not completely paralysed. It can progressively exhibit many rather incoherent movements of appendages, including the powerful jaws. Some of these prey were kept alive by Fabre for 17 days without food, or for 40 days when fed with sugar water. Stinging obtained by substitution of prey involved, according to Fabre, several thoracic stings, followed by a throat sting interpreted as a thoracic, not a cephalic, sting (this was complemented by cranial compression with the jaws). Fabre doubted that the suboesophageal

ganglion could have been affected by the throat sting, since persisting movements of the jaws were observed. His doubts were probably reinforced by his belief that head stings were lethal, as exemplified by the bee-wolf wasp, which stings honey-bees in the head (into deep paralysis, not death, however). In retrospect it seems almost certain that this was indeed a cephalic sting, in the vicinity or inside the suboesophageal ganglion, as in many other Sphecids. Perhaps Fabre had observed an aborted throat sting that had failed to produce any effect.

This often occurs at very early stages of or after the hunting period (discussed in Sections III and IV). Stinging of one mormon cricket by a *P. carbo* wasp involved four stings: one to each leg pair and then one in the throat (Steiner, 1981a, p. 334). Precise location of the stings near the ganglia was later confirmed by a study of sting wounds, using a dissection microscope. This complete sequence of four stings (C4SP, complete four-sting pattern) is probably much more common among hunters of Orthopteroids than had been realised (list in Steiner, 1981a, p. 334). Turning to the more gregarious *Sphex sensu stricto* we have, of course, Bartram's very early (1749) report on the 'Great Black Wasp from Pensilvania' (*S. pensylvanicus* Linn.) (see Chapter 1) thoroughly reinvestigated by Frisch (1938) along with *S. ichneumoneus* (1937). He also used the substitution method and is one of the earliest and few authors who studied the sting wounds. He even tried to stain them by using a 5% aqueous solution of acid fuchsin through which SO₂ had been bubbled.

A study of sting wounds is much more precise and reliable than mere naked-eye observation of such elusive behaviour and even more so if complemented by a graphical representation (e.g. Roubaud, 1916, for caterpillars stung by eumenid wasps) (see Fig. 9). Frisch reported considerable variability, including three cases of incomplete paralysis, but it is not clear whether this was associated with different stinging conditions. The throat sting was apparently delivered first, along with at least two successive thoracic stings between the first and second, then second and third legs. Reinhard (1929, pp. 159-164) observed four similar cases. Sting wounds were also studied on conocephaline grasshoppers (with unparalysed abdomen and ovipositor) brought back by *Sphex ichneumoneus* and corresponded very closely, in number (C4SP) and location, to those of *Palmodes carbo* (Steiner, 1981a). Paralysis of the thorax and mandibles is clearly much deeper and long-lasting than in the Ampulicinae (and cricket hunters).

Turning to some other species, we find a report by Janvier (1928, pp. 183-190) that *Sphex latreillei* Lep. can sting its conocephaline prey, as many as six times or more, into deep paralysis. The first sting, at the base of one foreleg, appears to affect the whole body and could well be a neck sting. The other stings were given while the *Sphex* carried the prey from branch to branch. The second sting was delivered at the base of the other foreleg;

a third at the base of one middle leg; a fourth at the base of the other middle leg and finally two additional stings, one at the base of each jumping hind leg. Janvier even observed stings directed at the bases of the wings, on one side. He does not mention any throat sting, however. Such a rather unusual eight-sting sequence, perhaps resulted from the acrobatic conditions of capture, since the wasp continued to sting while hopping from branch to branch. Restinging often occurs in response to any disturbance (personal observation).

Piel (1935, pp. 281–282) used the prey-substitution method to study stinging by *S. umbrosus* Christ (*argentatus* Fabricius?). First a throat sting was delivered, then the wasp stung between the forelegs and finally in the vicinity of the abdomen. Considering the nonoptimal situation (restinging of a previously paralysed prey) one can doubt whether this was the complete (four-sting?) sequence. In another instance, Piel observed a sting between the middle legs, not seen before, which was given after the throat sting. This makes then four kinds of stings: throat, forelegs, middle legs and near the abdomen (hind legs?) as in previous cases. *Isodontia* wasps also use long-horned but smaller grasshoppers (and/or tree crickets).

A C4SP was found again in some species, on the basis of a study of sting wounds on many prey kindly provided by R. Longair (in Steiner, 1981a, p. 334). Stinging was not observed and consequently sting order is unknown.

Piel (1933) also studied *Isodontia nigella*, which first stings the throat (Fig. 4) in an antiparallel posture, then the leg pairs three or four times or less, starting with the forelegs. Paralysis was thorough, and incomplete stinging sequences were viewed as reflecting venom shortages. A detailed inventory of sting wounds shows that this species of *Isodontia* uses the same body sites as *Palmodes carbo*, *Sphex ichneumoneus* and the above *Isodontia*, suggesting a certain unity of methods among these sphecine (and also some larrine) wasps.

e. Sphecine Cricket Hunters. *Isodontia* provide an excellent transition, since they also take bush and tree crickets along with long-horned grasshoppers and sting them in essentially the same way (Longair and Steiner, in Steiner, 1981a, p. 334). Interestingly, such crickets have a much more elongate shape than ground crickets and are more reminiscent of arboreal long-horned grasshoppers, with which they also share common habits. This probably promoted interchangeability of prey. Lin (1966, p. 240) reports that the snowy tree crickets (*Oecanthus niveus*) (De Geer) brought back by *I. mexicana* (Sauss.) were usually partially paralysed. Cricket-stinging has also been described by Fabre in the ‘Yellow-winged *Sphex*’ (see Section I) and

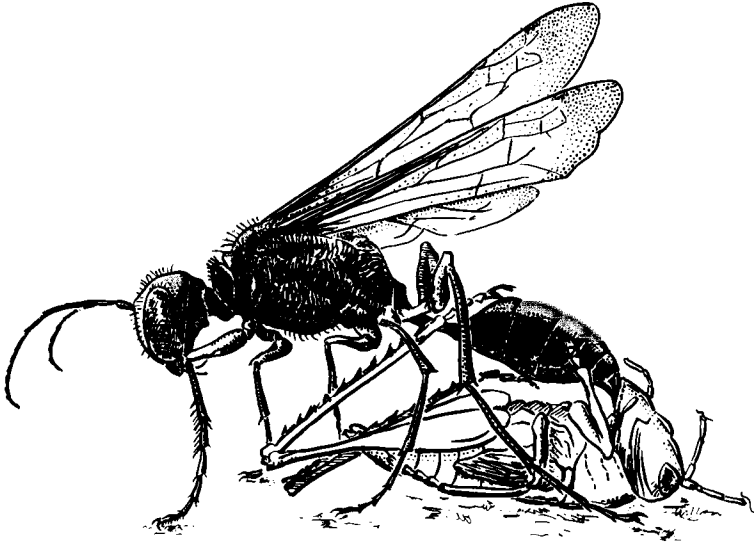


Fig. 4 The sphecine wasp *Isodontia nigella* giving the first sting in the throat of a male *Conocephalus* grasshopper. Redrawn from Piel (1933), with permission of Société Entomologique de France.

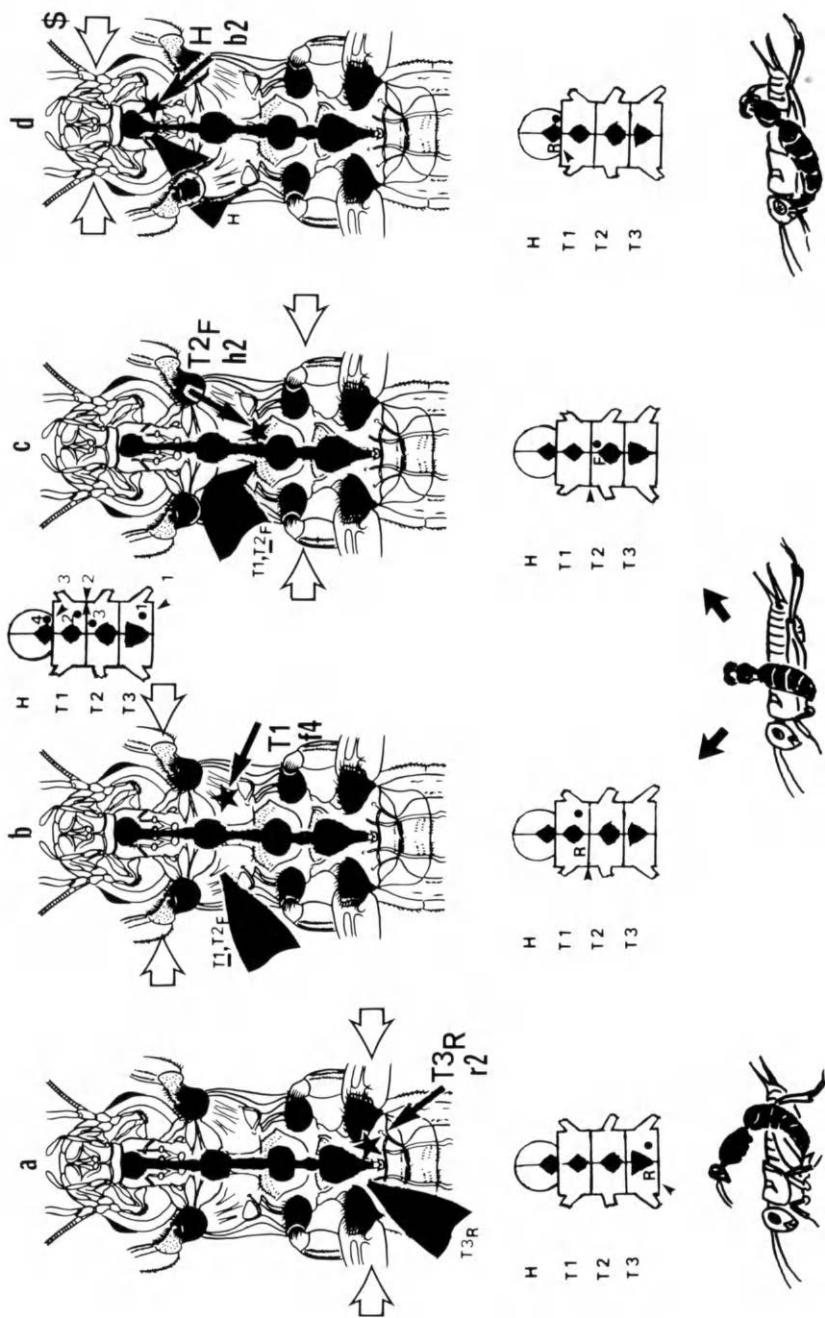
by Molitor (1934, p. 465; 1939a, pp. 69–70) as starting with the throat sting.

Among the Sphecinae the real (ground) cricket specialists are found in the genus *Chlorion* (same tribe as the *Podium* roach hunters, the Sceliphronini). According to Hingston (1925–1926) *C. lobatum* (Fabr.) stings the thorax two to five times, irregularly and perhaps without inoculation of venom, then the neck of its prey. This is a good approximation of the C4SP but with the sting order reversed, since the neck sting is given last and with great insistence and precision. This final ‘deadly blow never fails’, using Hingston’s own words, and has a dramatic effect on the *Brachytripes* cricket, which becomes totally motionless, ‘as though it were struck dead’. Hingston considered it certain that the nerve centre had been struck. A few abdominal stings were reported. The wasp would burst into a frenzy if the prey was especially large and/or capable of some movements after stinging. Finally the cricket was stored back in its own burrow, from which it had been driven away, and the entrance was plugged with dirt. A similar increasing precision from first to last sting was recorded in *Liris* wasps (Steiner, 1962, 1976), but this was

correlated with progressive weakening of the prey after each additional sting. To his surprise, Hingston discovered a 'resurrected' but somewhat weakened cricket in the burrow, 3 min later. It became progressively capable of running, leaping, biting him, or even burrowing its way into the sand and was about to escape.

This comes much closer to the molecrickets stung by *Larra* than to the crickets 'deactivated' by *Liris*. But what prevents them from burrowing their way out of confinement and resuming normal activities? Do they feel safe in their own burrow or below ground? Would they try to escape from a foreign burrow, dug by the wasp or another cricket? Would they fully resume normal activities if released, as the *Brachytripes* stung by *Chlorion maxillosum* do, in spite of the throat sting (Valdeyron-Fabre, 1952, 1955) (as *xanthocerus*)? The latter crickets, apparently abandoned like the molecrickets stung by *Larra*, can even dig a new burrow if attacked and paralysed outside their own ones. Finally, *C. aerarium* digs its own tunnel for the cricket (*Gryllus pennsylvanicus*) but only from burrows previously constructed, by other wasps for instance (Peckham and Kurczewski, 1978). The throat sting (also found in '*C. caeruleum*') (Peckham and Peckham, 1905, pp. 259–260) is apparently given first and/or during resting. Perhaps these suggested gradations in the state of the prey among *Chlorion* species reflect gradations from lack of prey storage to storage in the burrow of the prey and ultimately in the one dug by the wasp.

f. Larrine Cricket Hunters. A detailed 10-year study, in captivity, involving more than 150 house crickets and dozens of *Liris nigra* wasps, showed that the complete stinging sequence was again a very precise and predictable C4SP. First the jumping legs were instantly paralysed with one sting, usually behind (sometimes before) the jumping hind legs. Next the forelegs were stung from behind and paralysed. The middle legs were then stung anteriorly and paralysed in turn. Finally, the wasps delivered a throat sting that cut down the frantic snapping of the jaws (Steiner, 1962) (see Fig. 5). This last sting is also responsible for permanent deactivation of the crickets, which becomes apparent after recovery from paralysis, within a few minutes. The crickets have been transformed into passive 'reflex machines'; they can stand on their feet and jump or walk if prodded but do not try to escape, feed or groom. The latter capacities (and 'volition') are retained if this last sting had been eliminated experimentally, until the long-term deleterious effects of the venom rob the crickets again of their locomotion (Steiner, 1963a). All other stings had clear local, instant, paralysing effects. Stings were clearly aimed at the nerve centres and varied little in location.



1 **2** **3**
Fig. 5 Typical unfolding (a to d) of complete stinging sequence (C4SP) by *Liris nigra*, *L. argentata* and *L. aequalis*. Abdominal tip of the wasp and ganglia in solid black; average stinging direction (—); stinging location (★); body segments of cricket prey indicated by symbols (H, head; T, thorax) and serial number. Diagrammatical representation in second row and corresponding postures in last row. The slashed s on d = suppression of prey “spontaneity”. From Steiner (1976), with permission of Paul Parey, Berlin.

In contrast, stinging sequences varied in completeness (one to four stings or more) and structure, depending on circumstances (analysed in Sections III and IV). Several rather small crickets are usually stored in each cell, preferably in preexisting burrows or cavities in the soil which the wasp had summarily remodelled. *Liris* wasps have retained the capacity to dig their own burrow if necessary. A study of two other related species, *L. argentata* and *L. aequalis*, gave extremely similar results (Steiner, 1976). This shows how conservative stinging methods can be among related wasps which use the same prey.

g. Hunters of Short-horned Grasshoppers. Among the Sphecinae, some of the more advanced and/or specialized forms, such as *Prionyx*, have apparently switched from long- to short-horned grasshoppers. The latter have escape-defence systems that are similar to those of the former but a more concentrated thoracic nervous system, which has visibly affected stinging methods (discussed in Section IV).

An intensive study, in captivity, of *Prionyx parkeri* Bohart and Menke (Steiner, 1981a) (see Fig. 10c,d) showed that the four stings (C4SP) were aimed at the nerve centres, starting with the throat (in an antiparallel position), then in front of the forelegs and finally in front of and behind one middle leg. This remarkable duplication of stings for the middle legs has apparently been promoted by the presence there of two ganglia (instead of one in long-horned grasshoppers and crickets): the meso- and metathoracic ganglia, which are located in front and behind the middle legs, respectively (analysed later). The first (throat) sting massively reduces resistance of the prey but does not completely overshadow the usual local effects of the thoracic stings. Sporadic or even violent movements can still be exhibited by the grasshopper, including kicking, but usually no walking or standing on the feet is possible. This C4SP has apparently not been reported in the literature, only some of the stings described here. Observations made by Ferton on *P. subfuscatus* will be discussed in Section III.

Among the Larrinae, many *Tachysphex* wasps also prey on short-horned grasshoppers but their movements are so swift (*tachy* means fast in Greek!), that stinging is almost impossible to analyse adequately without a subsequent study of the sting wounds. This was done for *T. tarsatus*, which uses a method very similar to that of *Liris* wasps (Steiner, 1981a).

h. Hunters of Other, More Specialised, Orthopteroids. A few wasps apparently radiated into less heavily exploited prey 'niches', in which they became highly specialised, like their prey. Mantid hunters offer interesting examples of both convergent evolution (using the same prey) and striking divergence in stinging priorities. Some of them, predictably enough, sting the raptorial legs first, for instance, *Tachysphex costai* (De Stefani), a larrine wasp, and *Stizus ruficornis*, a much more advanced unrelated nyssonine wasp

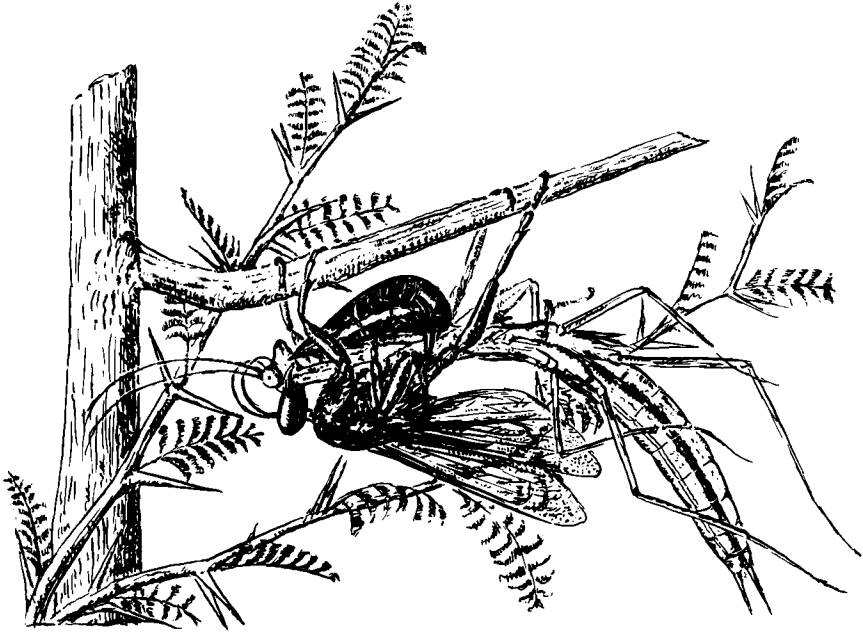


Fig. 6 *Stangeella cyaniventris* (Sphecinae) delivering the first sting in the throat of a *Mantis crenaticollis*. Redrawn from Janvier (1928), with permission of the author.

(Deleurance, 1945 and 1941, respectively; see also Fabre, 1886, pp. 255–258, for the ‘Manticidal Tachytes’, which uses the same method). Deleurance reported that mantids so stung had dangling paralysed forelegs but could still stand on the other unparalysed legs for days, as long as no additional stings were given, a clear confirmation of restricted local effect of a single sting and nondiffusion of the venom to other nerve centres. Other wasps, such as the sphecine *Stangeella cyaniventris* (Guérin-Méneville), sting the neck first, after neutralising the opponent by a powerful embrace (Janvier, 1928, pp. 198–199) (Fig. 6) as another sphecine wasp, *Prionyx parkeri*, does with its grasshopper.

A few specialists on pygmy mole crickets (Tridactylidae) are found among the Larrinae: *Tachytes mergus* and *T. intermedius*, for instance. Williams (1928) found the stung prey so reactive that they could jump 15–20 cm into the air, but apparently (like the crickets stung by *Chlorion lobatum*) they did not attempt to dig their way out of the cell. Perhaps their digging legs were more deeply paralysed (see also Krombein and Kurczewski, 1963, p. 149; Kurczewski, 1966). In sharp contrast, most other *Tachytes* species attack ‘surface’ prey such as grasshoppers and typically paralyse them very thoroughly (in Bohart and Menke, 1976, p. 263)! The contrast between burrowing and surface prey is found once more, even within the same genus of wasps.

In conclusion, in spite of such important 'tactical' variations around the 'central theme' (C4SP), there is a basic unity of 'strategy' among most or all hunters of Orthopteroids: the neck sting is consistently present, and several thoracic stings are usually given, ideally at least one for each leg pair, but sometimes less. Very different stinging methods are found in the wasp-prey systems to be considered now, but some of the same rules are still valid.

2. Hunters of Caterpillars

One other stock of the specialised Sphecinae (*Podalonia*, *Ammophila*) apparently sharply diverged from the more common orthopteroid-hunting forms and switched to a most unusual prey for a sphecid wasp: insect larvae (caterpillars) instead of the usual adults or nymphs. Almost everything in such prey is radically different from the more orthodox prey (details in Section IV). Not surprisingly, stinging methods are also drastically different. Interestingly, the C4SP, or basic prototype, is still found here. It is represented in a separate sequence of four cephalothoracic stings which has perhaps been handed down from their orthopteroid-hunting ancestors (Steiner, 1983b). A second sequence of about six abdominal stings (C6SP) has been added to the original sequence. The complete stinging pattern can therefore be represented ideally by the formula C4SP plus C6SP equals C10SP (Fig. 7a).

Repetition of individual stings and stinging sequences, whether complete or incomplete, is extremely common, however, even apparently the rule. This was shown by Fulcrand, Gervet and Truc in their extensive and very thorough study of the Palearctic *Podalonia hirsuta* (see publications of each of these authors from 1966 to 1972). This species stings large cutworms (caterpillars of agrotid moths). They called the C4SP and C6SP type I and II, respectively. The former sequence generally starts on the last thoracic segment and ends on the head (throat), whereas the second one proceeds from the first abdominal segment (sometimes the last thoracic one) to the sixth in its most complete form but often stops even before. The last three or four visible segments, which contain no nerve centres, are usually not stung. Both sequences are generally separated by a rather long pause, during which the wasp vigorously rubs its body on the ground, apparently rubbing off the repelling mouth fluid used by the cutworm for defence (numerous variations will be discussed in Sections III and IV).

The second sequence, the C6SP, is unique and found in no other sphecid wasp. It must therefore have evolved secondarily as a more recent adaptation and has been added to the 'ancestral' sequence, the C4SP (Steiner, 1983b). Not too surprising, some advocates of a fundamental intrinsic variability of stinging had studied caterpillar hunters mostly or exclusively (e.g. Roubaud)

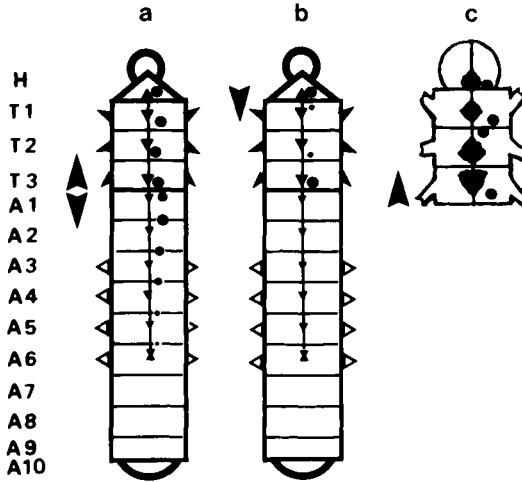


Fig. 7 Diagrammatic and idealised representation of the typical, complete, stinging sequence of three wasps (excluding abortive and repetitive stinging): two caterpillar hunters, *Podalonia luctuosa* (a), which attacks large cutworms, and *Euodynerus foraminatus* (b), which preys on small caterpillars, and the cricket hunters *Liris nigra*, *L. argentata* and *L. aequalis* (c). The nerve centers are represented by solid triangles (or diamonds). Arrowheads indicate the direction of progression of the wasps during stinging. Large dots mark frequently stung sites; smaller dots show stings which are less likely to be given (and/or repeated) in a and b. Further explanations in text. From Steiner (1983a), with permission of Masson, Editeur, Paris.

(eumenid wasps) (the Peckhams, the Raus, Molitor, etc.) (*Podalonia*, *Ammophila*). Clearly, such general all-encompassing conclusions cannot be based on a limit case. This kind of variability is of a different magnitude and nature than that found in other sphecid wasps. Fabre had already stressed this very special kind of variability, also found in another genus of caterpillar hunters: *Ammophila*, many of which apparently use similar, if not identical, stinging methods. Species that take many small caterpillars might use a method closer to that of eumenid wasps, however. Stinging methods become much more uniformly convergent and less sophisticated in the next catchall category, which will be reviewed rather superficially.

3. Hunters of Smaller and/or Weaker Prey (Prevalence of Single- or Dual-sting Patterns)

In this very heterogeneous group of more phylogenetically advanced wasps, one or two stings, often summarily delivered, are often sufficient to incapacitate these weaker prey. They often survive only for a short period

of time. This is of little consequence for progressive provisioners, which bring prey to their larva on a day-to-day basis. The range of prey selection is often wide, apparently less constrained by complicated, nontransferrable stinging methods. Extreme generalists and even scavengers that do not sting their dead prey (*Microbembex*) appear on the scene. Especially weak prey (aphids) are often squeezed with the mandibles and not stung. For this section the reader is referred mainly to Table V. Forms such as the mud-daubers *Sceliphron*, from the Sphecinae, and *Trypoxylon*, *Miscophus*, etc., among the Larrinae, hunt small spiders, Stinging methods seems quite unrefined. A whole subfamily, the Pemphredoninae, preys exclusively on Homoptera such as leafhoppers or aphids, the latter being often merely squeezed. A single (thoracic?) sting is apparently given to leafhoppers or related prey. The Astatinae specialise on Hemiptera, often common stinkbugs (Pentatomidae), which are perhaps killed by stinging. The vast majority of the Crabroninae prey on a great variety of flies. At least some of them aim their one sting at the single mass of fused thoracic nerve centres with great precision (e.g. *Oxybelus uniglumis*) (Steiner, 1979). Among sand wasps or Nyssoninae, some prey on flies (*Mellinus*, *Bembix*, *Stictia*, *Rubrica*, etc.), others on bugs (*Bicyrtes*) and still others on various Homoptera (*Alysson*, *Gorytes*, *Hoplisoides*, *Bembecinus*, etc.). A few have become highly specialised, for instance on large cicadas (*Sphecius*, *Exeirus*) or adult Lepidoptera (*Stictiella*). The Philanthinae attack Hymenoptera, mostly various bees and/or wasps (*Philanthus*, *Trachypus*, etc.), but a few take ants (*Aphilanthops*, *Clypeadon*, *Listropygia*) and use remarkable ant-carrying devices located at the tips of their abdomens, as was discovered by H. E. Evans. Other genera prey on various beetles, particularly weevils or buprestids (*Cerceris*, *Eucerceris*). Mainly single or dual stings are found and prey usually become deeply paralysed or die. Hunters of weevils have virtually no choice in the very few soft spots they can sting: between the head and thorax and/or between the pro- and mesothorax. The bee wolf, *Philanthus triangulum* F., has been intensively studied, including the important peripheral and central effects of the venom (Rathmayer, 1962; Piek, 1982; Piek *et al.*, 1984b) (see Table V and Chapter 5).

E. Eumenid Wasps

Wasps in this group have rather uniform preying habits. In sharp contrast to the Sphecidae, they attack larvae almost exclusively, mostly of caterpillars, but also of weevils and chrysomelids (e.g. *Symmorphus*, etc.) (Fig. 8). Interestingly, their stinging methods are very different from the sphecid caterpillar hunters (compare *a* and *b* in Fig. 7), but just as variable. Variability is very apparent in the sketches of sting wounds made by Roubaud (1916, 1917) (see Fig. 9) or in the extensive work on sting wounds by Bonelli (1976a,b,

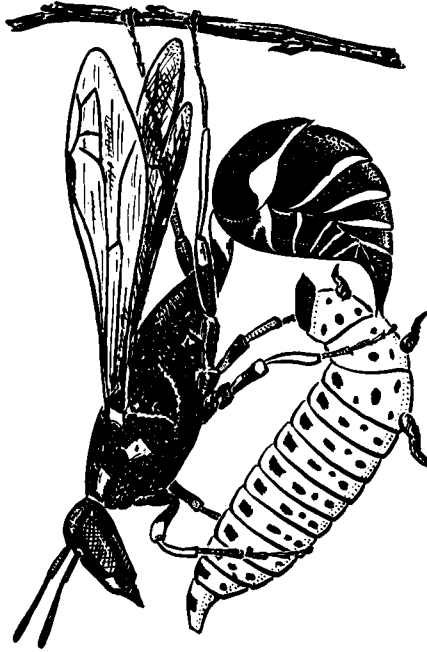


Fig. 8 The eumenine wasp '*Odynerus gracilis*' stinging a chrysomelid larva, *Melasoma populi*. Redrawn from Maneval (1932), with permission of Société Entomologique de France.

Bonelli *et al.* (1980), Gess and Gess (1976), etc. This recognised variability made Roubaud an eloquent champion of the view that there is basic imprecision in stinging methods of solitary wasps, in disagreement with Fabre's claims to the contrary. Only a few case histories will be considered here (see also Table VI).

Using once more the prototypal C4SP as a standard of comparison (Fig. 7c), we find it again in the Eumenidae, but often in weakened form, reduced to the first and last sting of the usual sequence, namely in the throat and third thoracic ganglion. [e.g. *Euodynerus foraminatus* (Sauss.)] (Steiner, 1983a) (see Fig. 7b). In all likelihood, reduction of the number of stings is again related to the weakness of the prey (often leaf-rollers), as in the sphecids wasps previously studied, rather than to the different phylogenetic position of these wasps. Instead of the well-defined C6SP of *Podalonia* we often find a few irregularly scattered sting wounds (called irregular stings), mostly on the abdomen. In contrast to the regular thoracic stings, they are not consistently located near the median ventral line and ganglia, as in *Podalonia* (Fig. 9).

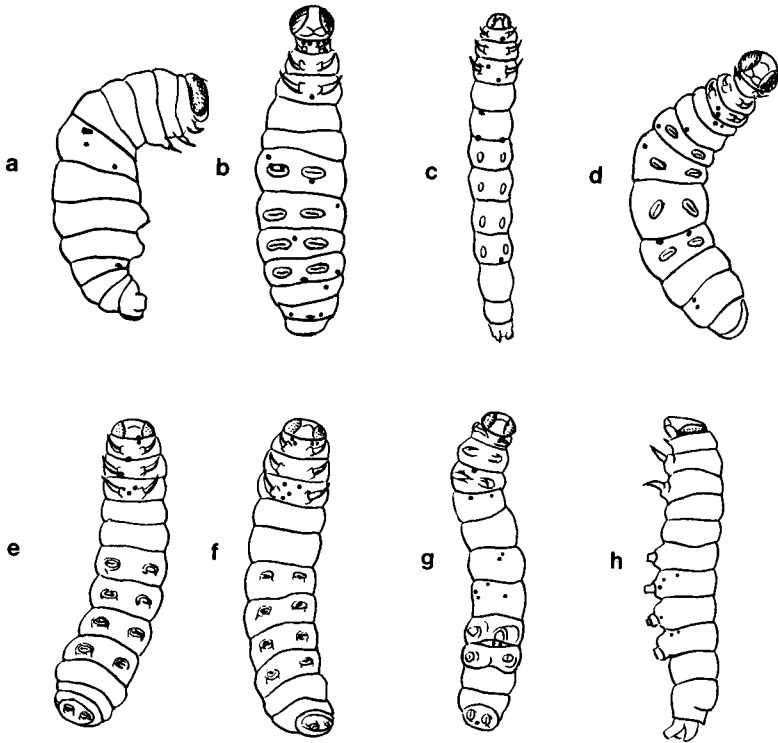


Fig. 9 Inventory of sting wounds (dots) found on caterpillars paralysed by several eumenid wasps (kind of caterpillar indicated in parenthesis): *Synagris calida* (a: *Thalpocharis*; b: Hesperid), *S. sicheliana* (c: Pyraline; d: Hesperid), '*Rhynchium anceps*' (e, f: *Phycitina*), and *Eumenes tinctor* (g: *Plusia*; h: *Pieris*). Note irregular distribution of stings, particularly on the abdominal region (and no concentration near the median ventral line, in contrast to the thorax). Further explanations in text. From Roubaud (1916), with permission of Masson, Editeur, Paris.

What could this clear dichotomy between regular (thoracic) and irregular (mostly abdominal) stings mean? Cooper had earlier made similar observations (1953, p. 25) on *Ancistrocerus antilope* and found three times more stings on each of the two previously described regular thoracic stinging sites than in all other areas combined (17 cases studied). In 70% of all cases, only these two regular stings were found. The majority of stings in these two species are therefore of the classical precise type. In the *Euodynerus foraminatus* study, irregular abdominal stings were found only in three cases out of 23, or only 13%. In two of these cases only one abdominal sting was found (first versus second segment, respectively) and in the remaining case two abdominal sting wounds were found on segments four and five (Steiner, 1983a, Fig. 3, p. 20).

Table VI
Eumenidae^a

Wasp	Prey	Information and source
<i>Odynerus ambigua</i>	Lepidoptera (l)	Janvier [1930, 325: S (1 L1, +1 L2, +1 L3); E (I; MV)]
<i>Odynerus anomis</i>	Lepidoptera (l)	Peckham and Peckham [1905, 91: E (very active; N = s)]
<i>Odynerus bianchardianus</i>	Lepidoptera (l)	Berland [1928, 45: E (I; N = m)]
<i>Odynerus capra</i>	Lepidoptera (l)	Peckham and Peckham [1905, 93-94: E (wriggle; N = s)]
<i>Odynerus consobrinus</i>	Tenthredinidae (l): Hymenoptera	Bernard [1934, 248: E (C; N = 2)]
<i>Odynerus dorsalis</i>	Lepidoptera (l)	Rau and Rau [1918, 320: S (2-3 T)]
<i>Odynerus egregius</i>	Lepidoptera (l): Noctuids	Bernard [1934, 248: E (I; N = 18)]
<i>Odynerus fastidiosissimus</i>	Lepidoptera (l)	Ferton [1901, 135: E (vivacious)]
<i>Odynerus gallicus</i>	Small yellow larvae	Ferton [1901, 129: E (some still alive after 68 days)]
<i>Odynerus gayi</i>	Lepidoptera (l)	Janvier [1930, 331: S (T1, T2, T3); E (C; N = s)]
<i>Odynerus geminus</i>	Lepidoptera (l)	Rau and Rau [1918, 309-12, 326: E (writhing briskly; alive up to 54 days, mostly 10-25 days)]
<i>Odynerus gracilis</i>	Chrysomehid larvae [C]	Maneval [1932, 105: S (T seg; Fig)]
<i>Odynerus humeralis and labiatus</i>	Lepidoptera (l)	Janvier [1930, 296-308: S (1 T1, +1 T2, +1 T3; Fig); E (I: former; C, P: latter)]
<i>Odynerus molinae</i>	Microlepidoptera (l)	Janvier [1930, 337-38: S (between L1, +L2, +L3); E: (C if small; some MV if large)]
<i>Odynerus paludicola</i>	Lepidoptera (l)	Williams [1927, 458: E (I: N = s)]
<i>Odynerus perennis</i>	Lepidoptera (l)	Peckham and Peckham [1905, 89: S (anterior? N = s); E (MV, but one-third dead)]
<i>Odynerus reniformis</i>	Lepidoptera (l)	Ferton [1901, 136: E (vivacious)]; Peckham and Peckham [1905, 90: E (very I; N = s)]
<i>Odynerus spinipes</i>	Weevil grubs	Réaumur [1742, Vol. 6: E: see text]
<i>Odynerus spiricornis</i>	Tenthredinidae (l): Hymenoptera	Móczár [1962, 346: E (kept alive up to 9 months)]
<i>Odynerus subpetiolaris and vespiformis</i>	Geometridae [L (l)]	Janvier [1930, 327, 315: S (T1, T2, T3); 329: E (subparalysis: important: MV)]

(continued)

Table VI (continued)

Wasp	Prey	Information and source
<i>Odynerus tuberculiventris</i>	Lepidoptera (l)	Janvier [1930, 340: S (T1, +T2, +T3; hesitation between both ends)]
<i>Pterochilus 5-fasciatus</i>	Lepidoptera (l)	Evans [1977, 331: E (somewhat active; N = s)]
<i>Stenodynerus fulvipes</i> f.	Lepidoptera (l)	Krombein [1967, 155: Rau and Rau, 1918: E (some: L, even pupation; N = s)]
<i>Stenodynerus lineatifrons</i>	Tortricids [L (l)]	Krombein [1953b, 115: E (faint MV; N = 1)]
<i>Euodynerus foraminatus</i>	Lepidoptera (l)	Rau and Rau [1918, 336: E (MV)]; Steiner [1983a; N = 23; S (usually 1 H, +1 T3; other); E (l: abdomen)]
<i>Ancistrocerus antilope</i>	Lepidoptera (l) (leafrollers)	Cooper [1953, 22-25: S (dt: wnd; N = m); see text; usually 1 anterior L1, +1, T3]; E (violent spasms)]
<i>Ancistrocerus capra</i>	Lepidoptera (l)	Buckle [1929, 265: S (one of the front seg)]
<i>Ancistrocerus fulvipes</i>	Lepidoptera (l)	Rau and Rau [1918, 342-43: E (alive; some very active; some dead; N = m)]
<i>Monobia quadridentis</i>	Lepidoptera (l)	Rau and Rau [1918, 350: E (alive; N = s)]
<i>Symmorphus canadensis</i>	Chrysomelid beetle (l)	Krombein [1967, 116: E (MV; abdomen; N = m)]
<i>Symmorphus cristatus</i> c.	Chrysomelid beetle (l)	Fye [1965, 734: E (C, but perhaps short-lived; N = m)]
<i>Symmorphus murarius nidulator</i>	Chrysomelid beetle (l)	Fabre [1891, Vol. 4, 204-209: S (3 T, ggl; smt A; N = s); 195-97, 206, 208: E (C, kept 60 days)]
<i>Symmorphus sinuatissimus</i>	Chrysomelid beetle (l)	Grandi [1954, 108: E (no MV; N = s)]
<i>Rhynchium anceps</i>	Lepidoptera (l)	Roubaud [1916, 24: S (s T: e.g. 4, 8; wnd, Figs: N = 2); E (strong paralysis; N = m)]
<i>Rhynchium marginellum</i>	Lepidoptera (l)	Bonelli [1976b, 40: S (dt: wnd; average 2.96; mostly T1, T2; some A; N = 30); 37, 38: E (MV)]
<i>Rhynchium oculatum</i>	Lepidoptera (l)	Bonelli <i>et al.</i> [1980, 95-96: S (dt: wnd; 1-15 St; very V in number and location; N = 800)]; Grandi [1961, 52: S (St); 49: E (f: active MV; N = s)]
<i>Delta bonellii</i>	Lepidoptera (l)	Bonelli [1976b, 47: S (dt: wnd; V: 5-10 T and A; more T1; N = 4)]

<i>Delta emarginatum</i>	Noctuids [L (I)]	Bonelli [1976b, 44–45: S (dt: wnd; very V; 5–15 T and A; predominantly TI; N = 42)]
<i>Delta fenestrata</i>	Noctuids [L (I)]	Bonelli [1976b, 43: S (dt: wnd; sT and A; V; predominantly TI; N = 14)]
<i>Hemipterochilus bembecif.</i>	Lepidoptera (I)	Grandi [1961, 65: E (V: C to I; N = s)]
<i>Parachilus insignis</i>	Psychids (bagworms) [L (I)]	Gess and Gess [1976, 94: S (dt: wnd; anterior: L1, L2, L3; occasionally no L2, L3; no A; RS; N = 144); 94: E (I; kept alive up to 120 days)]
<i>Orancistrocerus</i>	Pyralids [L (I)]	Iwata [1972, 267: E (no reaction to stimuli; N = s)]
<i>Discoelius japonicus</i>	Lepidoptera (I)	Tsuneki [1970b, 14: E (quite active; one even pupated)]
<i>Alastor atropos</i>	Weevils [C (I)]	Grandi [1954, 100: E (vivacious MV; N = s)]
<i>Hoplomerus reniformis</i>	Weevil grubs	Grandi [1961, 62: E (I; N = s)]
<i>Eumenes</i>	Lepidoptera (I)	Fabre [1882?, Vol. 2, 76: E (important MV)]; Grandi [1961, 33: Deleurance: E (I)]
<i>curvatus</i>	Lepidoptera (I)	Williams [1919, 154: E (I; N = s)]
<i>pomiformis</i>	Microlepidoptera (I)	Ferton [1902, 525: E (vivacious MV)]; Grandi [1961, 37: E (I; N = s)]
<i>tinctor</i>	Lepidoptera (I)	Roubaud [1916, 57: S (s T, A; wnd; Figs; N = 2)]
<i>Zethus cyanopterus</i>	Lepidoptera (I)	Williams [1919, 161: S (no St? CH; N = 1)]
<i>Zethus discomboda</i>	Geometridae [L (I)]	Janvier [1930, 343–45, 347: S (all seg. in 2 series); 347: E (I; MV)]
<i>Synagris calida and sicheliana</i>	Lepidoptera (I)	Roubaud [1910, 3, 6: S (CH and/or St); E (C); 1916, 10–11: S (s T and A; wnd; Figs; N = 4)]
<i>Synagris cornuta</i>	Lepidoptera (I)	Roubaud [1910, 12: S (CH, no St); 1917, 407: S CH)]

^aSee footnotes to Table I.

Most authors, Roubaud included, had not made such a crucial distinction between regular and irregular stings, thus giving the impression that all stings of eumenids are imprecise. From personal observations, it seems that irregular stings could have been given during the laborious extraction of leaf-rollers, the wasp often poking its abdomen in the shelter of the resisting caterpillar. Once extraction is accomplished, however, these caterpillars were invariably (re?)stung, presumably then in the regular way. Variability of thoracic stings was largely restricted to the optional, uncommon, addition of one or two or more stings in the prothorax and/or mesothorax, as Cooper had also observed.

One observation by Bougy (1935, p. 21) on *Podalonia hirsuta* lends some additional credence to the above explanation: a cutworm was hidden among shell pieces of a mollusk with only its posterior end accessible. The first stings were delivered there, instead of the thorax, but after extraction, the prey was resting in the usual way. Such opportunistic modifications of stinging have already been mentioned for spider wasps and are perhaps at work in the Eumenids too.

In conclusion, the bases for the claims about the fundamental imprecision and inconstancy of stinging should be carefully reevaluated. Studies of sting wounds must be complemented by direct observations of stinging. In this way possible effects of stinging conditions can be evaluated, as will be done next, using studies of variations in natural and experimental conditions.

III. ANALYSIS OF STINGING CHARACTERISTICS, EFFECTS AND CONTEXTS: PROXIMATE FACTORS

Reviews and discussions of stinging and of its effects can be found in Bouvier (1919), Berland (1925b, p. 364), Janvier (1930, pp. 287–290), Molitor (1934, 1937, etc.), Leclercq (1954), Grandi (1961, pp. 625–627), Malyshev (1968), Iwata (1942, 1972), Evans (1963, 1966a), Evans and Eberhard (1970), etc., in addition to the early references given in Section I. Stinging is also frequently discussed in reviews of wasp venoms (see corresponding chapters of this book).

A. Limitations and Uncertainties of Observations

Some of the differences in reports derive from inherent difficulties of observation or limitations of the data. Modern recording techniques such as high speed movie cameras and films, photomacrography and electronic flash were not readily available, if at all, to the early authors. Separation of successive stings is often difficult and unreliable by naked-eye observation alone, particularly with swift wasps and/or when the nerve centres of the

prey are very close together. This often results in an underestimation of the number of successive stings.

In an effort to reduce such difficulties, many authors have used the now classical method of prey substitution. However, resting of a handicapped, nonescaping prey, often after the normal hunting period is over, is generally less complete than, or otherwise different from, initial stinging (discussed later). Furthermore, single observations prevail in the literature (see Tables). Repeated observations, large sample sizes and long-term studies, best conducted in controlled conditions and in captivity, are essential. Only in this way can the full range of variations be properly assessed and analysed.

Unwritten and/or unwarranted assumptions are often made. Thus the prey-substitution method rests on the assumption that stinging is the same during and after hunting and with intact as well as previously immobilised or disabled prey. It has also been widely assumed (by this reviewer among others) that the number of successive stings correspond to the number of successive postures assumed by the wasp. In fact, a single posture can correspond to *two* successive stings (e.g. to the fore- and middle legs of the cricket by *Liris* wasps: see posture 2, bottom of Fig. 5) Such double stings can easily be mistaken for accidental repetitions of the same sting because of their close proximity (and because the very different stinging directions are usually not noticed or recorded). A number of overgeneralisations are apparently based on the unwarranted assumption that conclusions based on the study of one or a few wasp-prey system(s) can automatically be extended to others, in spite of the great diversity of selection pressures which have shaped stinging methods.

Description of stinging conditions (contexts) is often incomplete and vague, if not lacking altogether. Sting wounds are seldom studied [except Roubaud, 1916; Reinhard, 1929; Frisch, 1937, 1938; Piel, 1933; Cooper, 1953, and more recently Gess and Gess, 1976 (144 cases studied); Bonelli *et al.*, 1980 (more than 800 cases!); Piek *et al.*, 1983, etc.] and almost never mapped graphically for comparisons. In the absence of such crucial information it is difficult to make a proper evaluation of probably internal target organs (if any), quantifications and comparisons. Interpretation of wounds found on easily bruised soft prey (e.g. caterpillars) is not always easy or reliable, since various traumas, malaxation or rough manipulation with the sharp mandibles are often involved, rather than stinging (Cooper, personal observation, and Cooper, 1953, p. 24). Thus irregular wounds of small caterpillar prey taken by eumenid wasps are often found precisely on the body regions firmly seized and squeezed laterally between the mandibles during stinging (see Fig. in Steiner, 1983a, p. 18). This perhaps also applies to Fig. 9(a,h) in this chapter. Prey-stealing and fights over prey, common in populous wasp colonies, also can result in frenzies of resting and rough manipulation (A. L. Steiner, personal observation). Such antecedents, stinging postures, directions and

order remain unknown in studies of wounds recorded on prey taken from nests.

Finally, diverging reports can also reflect diverging philosophies, approaches and emphases. Thus Rabaud discussed stinging from a rather reflexological, stimulus–response standpoint. Fabre and ethologists interpret such behaviour from a more holistic standpoint. They see stinging as a fixed action pattern, an instinctive activity, not reducible to a chain of reflexes, since internal conditions are considered to be at least as important as external stimuli. Some authors emphasise inherent fixity and stereotypy. To others variability is inherent or else situation-dependent (e.g. Ferton). In some studies only proximate or only ultimate factors are considered or emphasised, making the results one-sided. In conclusion, sources of divergence among reports are very diverse and this makes interpretation and comparison of differences difficult.

B. Quantifications and Permanent Data Records: Sources of Variation

Variability is always relative and often conditional and therefore best expressed in quantitative, comparative terms, or by graphical methods. This requires accumulation of large samples (in various conditions), permanent data records and manipulation, measurement of intervening variables. Only then can an attempt be made to partition the total variance into distinct main and interaction effects.

Variations in stinging behaviour, studied now, depend on two very different categories of factors. First, *proximate factors* (this section), such as fluctuating external and internal conditions, affect sequences directly on a moment-to-moment basis. Second *ultimate factors* (Section IV), such as selection pressures and ecological conditions, have shaped stinging methods during their evolutionary history. This corresponds roughly to ontogenetic versus phylogenetic contingencies, best studied by different methods: experimental versus comparative, respectively.

C. Effects of Some Proximate Factors on Stinging Sequences

1. Quantitative Effects (Completeness of Stinging Sequences)

Depending on circumstances one might observe a complete or abortive stinging sequence (CSP versus ASP, respectively). Some of the intervening variables must therefore affect stinging quantitatively. First, many authors

have reported that stinging is repeated (or resumed) until the prey ceases to move. Previously immobilised (stung) prey, found by wasps, often receive fewer stings on the whole than intact ones, if any at all (*Liris nigra*, *L. argentata* and *L. aequalis*) (Steiner, 1962, 1976). Thus the proportion of ASPs to C4SPs was significantly higher for previously stung than for intact grasshoppers paralysed by *Prionyx parkeri* (Steiner, 1981a: $\chi^2 = 4.93$, for a critical value of 3.84 at $p = .05$). Fulcrand, Gervet and Truc, in their various publications, also reported that the total number of stings delivered by *Podalonia hirsuta* was significantly lower when previously paralysed instead of intact cutworms were used. The same applies to the Nearctic *P. luctuosa* (Steiner, 1983b), in which the lengthy sequences of 10 or more stings are particularly favourable for a fine-grained analysis of quantitative effects. In the latter species, probability of continuation or repetition of stinging was assessed by the number of stings per segment delivered during each of 58 stinging episodes (totalling more than 1500 stings). This number decreased rather regularly and significantly from the beginning to the end of each of the two stinging sequences, cephalo-thoracic (type I) and abdominal (type II) ($F = 12.48$, for a critical value of 7.88 at $p = .005$). Correlatively, the reactions of the cutworm weakened with each new sting. However, variation within segments (error variance) accounted for over 90% of the total variance, showing just how variable stinging is in these caterpillar hunters. In conclusion, fluctuations of external origin, such as responses of the attacked prey, do affect stinging quantitatively.

Turning to fluctuations in internal conditions it is also evident from continuous observations that readiness of the predator to attack and sting suitable prey (wasp responsiveness for short) varies widely throughout the hunting period. It is low at very early stages and the proportion of ASPs was then significantly higher in *Prionyx parkeri* (Steiner, 1981a: $\chi^2 = 8.59$, for a critical value of 7.88 at $p = .005$). Responsiveness declines or even disappears completely outside the hunting period (refractoriness). In several wasp-prey systems studied (e.g. *Liris nigra*), these ASPs consistently lacked the end of the stinging sequence (type *b* in Steiner, 1962).

The reader will have noticed a switch to a probabilistic approach, which is the only one which adequately describes the uncertainties; the above-mentioned effects are not expressed in every individual case, only statistically speaking. Finally, the data accumulated also provide evidence of a dynamic interaction between external and internal variables. Some other as yet unanalysed or undetected quantitative effects will probably be discovered in the future. Interruptions of stinging sequences are, of course, also produced by any interference with their free unfolding.

2. Qualitative Effects (Organisation of Stinging Sequences)

After the hunting period is over, wasps usually refocus their activities onto body sites of the prey different from stinging sites, as they perform feeding, malaxation, transport, storage and egg-laying. Therefore the wasps have undergone qualitative changes in their responsiveness which are likely to affect stinging if triggered at these stages. In *Liris* wasps, this happened in case of premature recovery of the prey. The wasps often delivered the first or only sting on the future egg-laying site (T2 in Fig. 10a, in front of the middle legs) instead of the hind legs (T3, in Fig. 10a). Stinging often remained very incomplete too (type *c* in Steiner, 1962). This reorganisation of the stinging sequence and corresponding change in stinging priorities (T2 instead of T3) apparently reflects the priority of the egg-laying site at this stage (Steiner, 1971). The prey-substitution method, if done after initial stinging or hunting, could have similar modifying effects. It cannot replace a study of stinging in hunting conditions. Gervet, Fulcrand and Truc (see literature) have also extensively analysed qualitative changes in stinging sequences of *Podalonia hirsuta* in different experimental situations, including changes in proportions of stings and sequences of types I and II, longer-lasting effects of early exposure, etc.

More generally, it is not too surprising that stinging can vary considerably with the stinging situation or context, as Ferton had already reported for spider wasps and Rabaud (1917) for the sphecid wasp *Mellinus arvensis*, studied in glass tubes. In contrast to Rabaud, however, Ferton abandoned the idea that this proved the inherent imprecision of stinging. It shows, however, that solitary wasps can make the best of a bad job. Variability of stinging, when present, also results in correlative variability in the state of the prey, as has been emphasised by so many authors after the Peckhams, the Raus, Molitor, etc. Larvae of wasps are known to develop on dead or rotting prey, occasionally or sometimes as a rule (e.g. in some pimpline or braconid wasps). Molitor (1931–1939), in a series of remarkable field experiments, conducted mostly on the caterpillar hunter *Ammophila heydeni*, also tested a wide range of situations and prey (including the wasps' own larvae!). Correspondingly, the responses of the wasps, including stinging, varied widely. Molitor, a critic of Fabre, recognised, however, that in more orthodox and stable conditions stinging became much more regular and predictable, as Fabre had described. Tsuneki (1968a) also reported important variations in stinging in *Ammophila* caterpillar hunters, according to circumstances. In conclusion, much remains to be learned on variability of

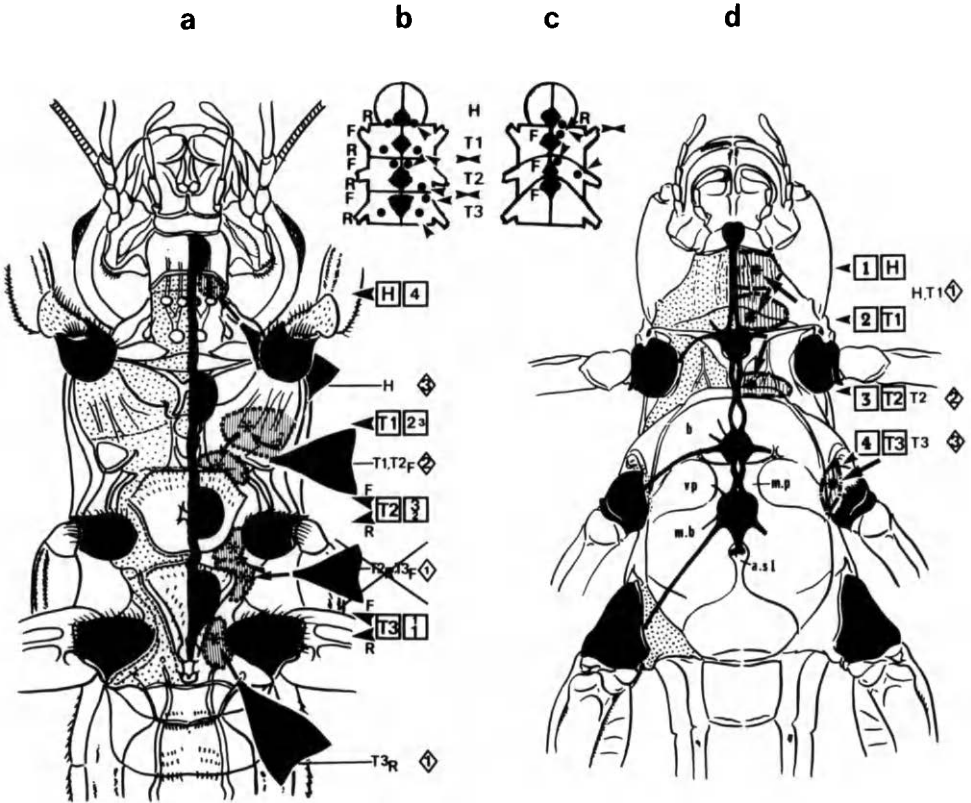


Fig. 10 Idealised and complete stinging sequences of cricket hunters [*Liris nigra*, *L. argentata*, *L. aequalis* (a, b) based on 800 stings] and hunters of short-horned grasshoppers [*Prionyx parkeri* (c, d) based on 300 stings], excluding abortive and repetitive stinging. Nerve centers are shown in solid black, by transparency. Each stinging site is characterised by its location, range of dispersion of stings (.....), points of maximum sting concentration (*), average stinging direction (—), immediate local paralysing effect, essentially restricted to the appendages of one body segment (indicated in square boxes as H for head, T for thorax), typical sequential position within the stinging sequence (numbers in square boxes) and corresponding posture of the wasp (numbers in diamonds). Note that in crickets (a) the ganglion that controls the hind legs can be reached by stinging one hind leg posteriorly (T3R) or anteriorly (T3F), whereas in short-horned grasshoppers (d) it can be more easily reached by stinging the base of one middle leg (T3). Stinging patterns have apparently been shaped by such anatomical differences in the nervous system of the prey. Further explanations in text. From Steiner (1976), with permission of Paul Parey, Berlin.

stinging sequences, which is usually much greater than that of individual stings.

IV. DIVERSITY OF WASP-PREY SYSTEMS, SELECTION PRESSURES: ULTIMATE FACTORS

A. Need for Evolutionary and Comparative Studies

Studies of proximate factors alone do not tell us why Orthoptera are usually stung four times by *Liris*, *Prionyx*, *Palmodes*, *Sphex* and *Isodontia*, flies only once by *Oxybelus uniglumis*, caterpillars at least 10 times by *Podalonia* but only twice by some Eumenidae. Why is stinging relatively variable and unpredictable in *Podalonia* but much more fixed and well defined in many Orthopteroid hunters? It does not tell us either why the prey of various species recover fully versus partially or not at all. Answers must be sought in the past history of the wasp-prey systems, using comparative studies in which wasp and prey factors are assessed independently. Similarities by common descent or by convergent evolution can be evaluated by comparing closely versus distantly related wasps and wasps that use very similar versus very different prey (divergent evolution in the latter case). An evolutionary approach implies that stinging methods are not acquired individually. This could be done by trial and error, but this would be a formidable task for complex multi-sting patterns and wasps that live only a few weeks as adults. Many initial errors would be expected but they were never observed in *Liris nigra* wasps raised in captivity from the egg, on incomplete crickets with one stinging site missing (Steiner, 1963b). These wasps used the right stinging method the very first time they paralysed a cricket, even if the latter was again incomplete. They stubbornly attempted to deliver the fourth (throat) sting to a nonexistent stinging site they had never known! There was no evidence of major subsequent improvement in precision or efficiency of stinging. Cultural transmission can also be safely ruled out since there is no generation overlap in many species and no opportunity for imitation. In sharp contrast, in social wasps stinging for defence is neither body site specific nor organised into a predictable sequence.

B. Testing Some Evolutionary Hypotheses

Contrary to common belief, evolutionary hypotheses are not necessarily non-falsifiable. In favourable cases they can be tested experimentally, on the

basis of precise predictions. Tinbergen (and others) has used this method very successfully, in a series of famous experiments on predator and antipredator behaviour (pike and stickleback; egg-shell removal by some gulls, etc.). For stinging methods, correlations between various stinging and prey characteristics will be analysed in the next section in relation to various evolutionary hypotheses. Also, by isolating experimentally the effects of a single sting of *Liris nigra*, it has been possible to prove that the throat sting in the vicinity (or inside) the suboesophageal ganglion of the cricket was a necessary and sufficient condition for deactivation effects to occur (Steiner, 1983a). Effects of the venom have also been tested by experimental inoculation (e.g. Piek et al; see Chapter 5).

C. Correlates and Predictors of Sting Number, Location and Other Characteristics

Conceivably, the number and location of successive stings could have been affected by (1) "soft spots" of the prey (soft membrane hypothesis or H1); (2) body segmentation (segment hypothesis or H2); (3) leg bases (limb hypothesis or H3); (4) the complete set of ganglia (all ganglia hypothesis or H4); (5) ganglia involved in locomotion and defence (locomotor ganglia hypothesis or H5). Finally, the null hypothesis (H0) would be random stinging (Steiner, 1981a, p. 326). Fabre was the most obvious advocate (and discoverer) of the ganglion hypothesis and Ferton probably the inventor and defender of the membrane hypothesis (without necessarily rejecting all tenets of the ganglion hypothesis). The latter author noticed that many wasps apparently had little choice in the few soft points they could sting on strongly sclerotised prey. This applies well to weevils (Steiner, 1981a), but not at all to soft caterpillars and only moderately well to chitinised prey, such as grasshoppers, studied by Ferton (1902) in relation to stinging by *Prionyx subfuscatus* (Dahlbom). Ferton observed two successive stings, one around the forelegs, the other near the base of one middle or hind leg. This did not match the number of separate thoracic ganglia (three) and even less so those of the cephalothoracic region (four). Complete paralysis must then have been brought about by diffusion of the venom to the other nerve center(s), from the points of inoculation. The latter would then be affected more by the soft spots than by the nerve centers. In *P. parkeri*, however, the number and location of stings, and even stinging directions, clearly match the number (four) and location of cephalo-thoracic nerve centers, not of soft spots (Steiner, 1981a) (see Fig. 10 c,d). Had Ferton overlooked the first sting, in

the throat (and another one in the thorax)? It seems unlikely that *P. subfuscatus* should omit this sting and not *P. parkeri* (observed dozens of times) and *P. albisectus* (Roth, 1925), when stinging methods are usually very conservative among related wasps that use the same prey (Steiner, 1976, 1981a)? Plausibly, Ferton mistook the initial double stings (throat, then forelegs) for a single sting (forelegs) or else observed ASPs rather than C4SPs in these nonoptimal stinging conditions (staged encounters inside his net!). Ironically, Ferton was one of the first to correctly interpret the throat sting as a head, not a thoracic sting, as Fabre had suggested; yet he apparently missed this very sting in *P. subfuscatus*.

The *Prionyx*-grasshopper system provides the strongest evidence in support of the ganglion, not the soft-spot hypothesis! As mentioned in Section II, *P. parkeri* sting the middle legs *twice* (from before and behind) and in fact there are *two* ganglia there (meso- and metathoracic) (see Fig. 10, d). The wasps do not sting the hindleg bases (devoid of ganglia!) at all (Fig. 10d). Neither the soft spot (H1) nor the limb hypotheses (H3) can be used to provide an explanation for this remarkable exception to the usual stinging methods. In sharp contrast, *Palmodes carbo*, *Sphex ichneumoneus*, *Isodontia* and *Liris* spp., which prey on long-horned grasshoppers and/or crickets, sting all leg pairs (once). At the base of each of them there is a pair of ganglia and only one (Fig. 10a,b).

Furthermore the 'all ganglia' hypothesis (H4) should also be rejected, since abdominal ganglia are stung only if involved in locomotion, as they are in caterpillars stung by *Podalonia* (but not in grasshoppers or crickets stung by sphecine and larrine wasps). The membrane hypothesis also fails to explain why pooled sting wounds are round on the prey of *P. parkeri* in about equal numbers on each stinging site, when in fact the size and accessibility of the soft spots vary so widely. Furthermore, the membrane behind the hind legs is very large and accessible, but never stung, whereas the one around the middle legs is extremely small and not very accessible, but consistently stung (Steiner, 1981a).

Finally, no hypothesis other than H5 can explain why stinging directions coincide so consistently with that of the nerve centers (Steiner, 1962, 1976, 1981a). H5 is the most powerful and accurate predictor of stinging characteristics for the following wasp-prey systems: *Prionyx parkeri*, *Palmodes carbo*, *Sphex ichneumoneus*, *Isodontia* sp(p.), *Liris nigra*, *L. argentata*, *L. aequalis* and several *Tachysphex*, which are all hunters of Orthopteroids and use a C4SP as basic stinging method. It also fits the cutworm-*Podalonia hirsuta* and *luctuosa* systems very well, since the C10SP matches the number of clearly separated ganglia (10), not leg pairs (seven), or visible body segments

(13 or 14) (see Fig. 7a), not to mention the presence of an infinite number of soft spots! However, H5 does not apply well to all wasp-prey systems. It should not be used as a single general rule that can explain all stinging characteristics in all wasp-prey systems. Thus some eumenid wasps apparently still aim their stings at ganglia, but only at two out of 10 (Fig. 7b). In this case, small size and weakness of the prey are much better predictors of elimination of stings. Going now back to other ultimate factors, they can be separated into two broad categories:

D. Wasp and Prey Factors

1. *Prey Factors*

These will be treated first because they are more directly and visibly related to the major characteristics of the various stinging methods, as abundantly illustrated in previous sections.

a. Characteristics of the Nervous System. These have just been reviewed and often found to be correlated with major stinging characteristics such as number, location of stings and, especially, stinging directions and local paralysing effects. This strongly suggests, but does not prove in itself, that the venom is probably inoculated very close to the ganglia or even within them. The latter has now been confirmed by more direct, histological, (autoradiographic) methods (e.g. Fig. 11 and Chapter 5). It is also quite clear that *Prionyx parkeri* aim their stings at the displaced ganglia that control the hind legs of the prey and not at the hind legs themselves.

b. Concentrated and Nonconcentrated Nervous Systems. More concentrated stinging patterns usually correspond to more concentrated, even fused, nerve centers of the prey, not to more concentrated or fused soft spots, leg pairs or body segments (e.g. Fig. 12). This is perhaps the most compelling behavioural evidence that stinging methods have been strongly influenced by the nervous system of the prey during their evolutionary history.

c. Offensive and Defensive Systems (and Locomotion). These aspects of the prey are often given special attention and/or priority at initial stages of capture (e.g. poisonous fangs of spiders, raptorial forelegs of mantids, hind legs or jaws or large orthopteroids). This can be done in different ways by different wasps, however (discussed later). Locomotion and resistance of the prey must be overcome, sooner or later, if the wasp is to manipulate its prey

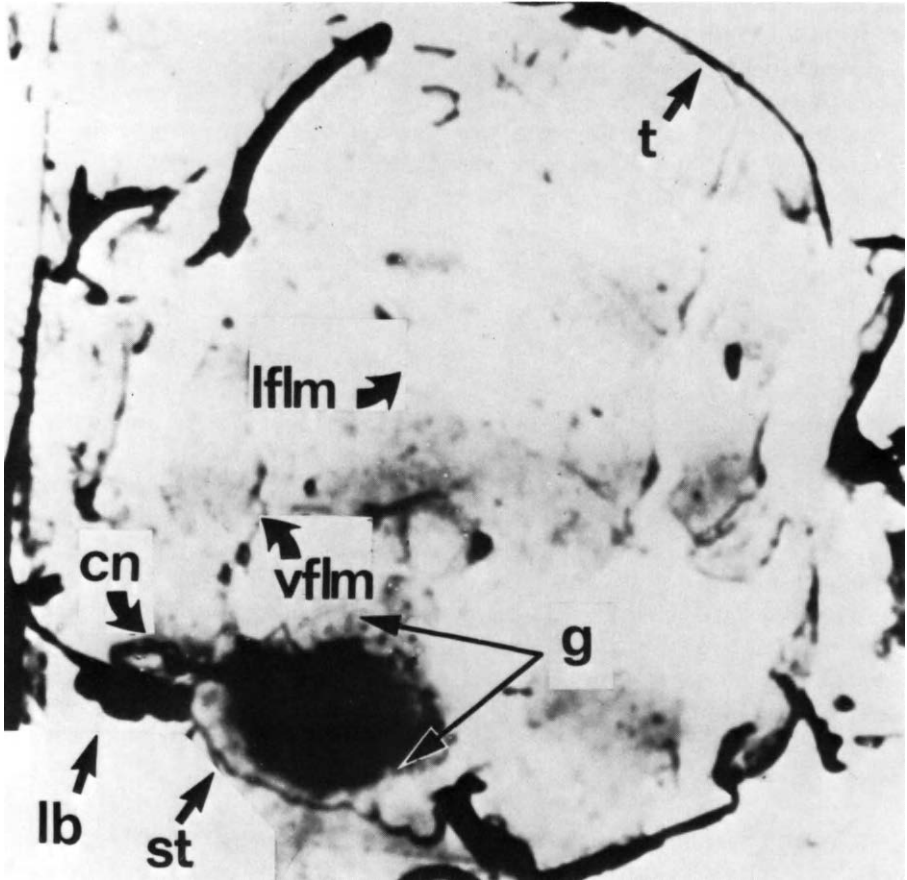


Fig. 11 Microautoradiographic localisation of the radioactivity labelled venom of *Mellinus arvensis* in a cross section of the mesothorax of *Musca domestica*. t, Tergum; st, sternum; lb, leg base; lflm, longitudinal flight muscle; vflm, vertical flight muscle; g, compound thoracic ganglion, nearly all of which is covered by silver grains on the X-ray film (Kodak Industrex D #54); cn, crural nerve (not radioactive). Photograph courtesy of Dr J. van Marle (from Piek, 1978).

freely and safely. This is imperative if the latter is large and powerful or especially intractable as is a large writhing cutworm. It is impossible to store a coiled-up cutworm in a narrow tunnel! This might explain why *Podalonia* wasps are so eager and willing to pursue (or resume) stinging of the prey,

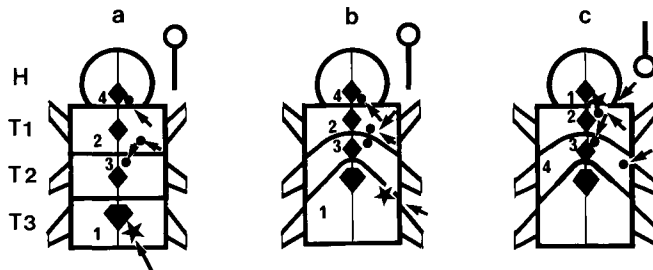


Fig. 12 Increasing concentration and cephalisation of nervous systems and stings (dots) in various wasp-prey systems: (a) *Liris*-cricket; (b) *Tachysphex*-grasshopper; (c) *Prionyx*-grasshopper. (★), First sting; (♀,♂), general body orientation of wasp. From Steiner (1981a), with permission of Paul Parey, Berlin.

including its abdominal region, until all movements cease. In sharp contrast, other sphecid wasps pay no attention to and do not sting the abdomen of their adult or nymphal prey, since it is not involved in locomotion or resistance.

d. Size and Power of the Prey. These factors have affected stinging methods in opposite ways in wasp-caterpillar systems: positively (stings are added) in *Podalonia* and negatively (stings are deleted) in some Eumenidae. Resistance of small and thin caterpillars is so easily overcome by the latter wasps that the abdomen is left unparalysed, even though it is involved in locomotion. Very weak prey (aphids, small flies, etc.) can be mandibulated (e.g. squeezed) instead of stung (reviewed by Janvier, 1977, Vol. 2, pp. 202-203), as social forms and some Eumenidae (*Synagris cornuta*, etc.) do regularly. Of course, disabled or dead prey are neither stung nor squeezed (scavenging *Microbembex* wasps).

e. Sclerotisation of the Prey. Sclerotisation, as found in beetles and especially weevils, can also contain evolution of stinging methods by limiting the number of potential stinging sites. (Ferton's soft spots hypothesis).

f. Ecology and Life-style of the Prey. Molecrickets already live in the ground and return to it if left on the surface. Why then bother to bury them in the soil after stinging? Accordingly, paralysis is only light and has only transient effects, so that the prey can literally store itself in the ground! Many crickets also live, temporarily at least, in the ground, within their own burrows or cracks, etc. (including pigmy molecrickets). It would therefore be economical to reuse such ready-made shelters for prey storage, as some *Chlorion* and most or all *Liris* wasps do. Somehow, these 'subterranean' prey

are often paralysed only lightly and recover in part or completely. Perhaps this is so because they are less likely to escape from ground nests (where they already live!) then 'surface' prey such as grasshoppers and mantids, which could try to regain the surface after storage, if not more thoroughly paralysed. This contrast between subterranean and surface prey is especially impressive among *Tachytes* species, some of which sting grasshoppers thoroughly and others pigmy molecrickets only lightly (in Bohart and Menke, 1976, p. 263). If stinging methods are the same, then different venoms could have evolved in function of the different ecologies of the prey (eco-biochemistry of the venoms, a new discipline?). It is also possible that the same venom affects these two types of prey differently.

g. Unusual Stinging Methods. Such methods are to be expected when sphecid wasps (e.g. *Podalonia*) turn to prey (e.g. larvae, caterpillars) with very unusual characteristics (Steiner, 1981b): (a) writhing, resistance and coiling with the entire body is particularly difficult to eliminate fully in this kind of prey and requires additional (abdominal) stings and some measure of saturation by frequent repetition; (b) monotonous repetition of many rather featureless body segments offers few regional cues for proper differential identification of stinging sites (and perhaps consequently less precise stings); (c) a long stinging sequence of 10 stings or more, divided into two separate bouts (type I and II), has more potential for variability and fractioning than a shorter sequence (C4SP); as a limiting case a one-sting sequence is unbreakable; (d) if many stings are given it makes little difference if a few are added or omitted. This should make the sequence more labile than when a single sting is given (the latter accounts then for 100% of the total effect!); (e) finally, soft larvae are often found in protected situations (soil, humus) or shelters (leaf-rollers, grubs in rotten wood), where they are not easily or directly accessible. Extraction might initially require indiscriminate stinging (as apparently in eumenid wasps).

2. Wasp Factors

Stinging priorities often vary sharply among very different wasps, even if they use the same kind of prey, suggesting alternative evolutionary solutions to similar or identical prey-related problems.

a. Morphological and Behavioural Adaptations: the Evolution of Stinging Priorities. At initial stages of attack, *Prionyx parkeri* and *Stangeella cyaniventris* successfully neutralise defence or attack by their grasshoppers or mantids with their long and strong prehensile legs, in a powerful embrace. Stinging priority then goes to the jaws (neck sting). Larrine wasps, in contrast, do not possess such legs and must quickly eliminate escape of a grasshopper

or cricket by paralysing the hind legs first (Fig. 10a). If the prey is a mantid, the raptorial forelegs are stung first. Attention to the neck sting, if any, is subordinated to this crucial initial sting.

b. Possible Biochemical Adaptations of the Venoms. These are suggested by presence or absence of deactivation, which apparently does not depend on fundamentally different stinging methods. Some (weaker?) venoms appear to paralyse the prey only lightly and/or temporarily, others (more potent?) more deeply and/or permanently. Some authors think, however, that differences in effects are related to different prey, not venoms (see Roubaud, 1917; Molitor, 1939a,b, etc.). Venoms of solitary wasps are analysed in Chapter 5.

c. Differences in Nesting Behaviour. Some wasps store a single or a few large prey per cell that is preserved for several days, sometimes a week or more. Progressive provisioners, on the other hand, often use many smaller prey, brought in on a day-to-day basis. Preservation of the prey is then less important or unimportant. Correspondingly these prey often die quickly and can therefore be treated with less refinements.

V. CONCLUSION

Although such a wide spectrum of stinging methods cannot easily be encapsulated in a single simple formula, the locomotor ganglia hypothesis of stinging is the best-fitting one for a number of aculeate wasps which prey on large and powerful prey. The following empirical rule summarises this trend: give at least one different sting for each clearly separate nerve centre involved in locomotion, attack, defence or resistance of the prey...considering only complete stinging sequences, of course. Reduction of sting numbers evolved in many forms which attack prey that are small, weak, and/or have a very concentrated nervous system. In many Terebrantia (also a number of bethylid, scoliid, pompilid and eumenid wasps) irregular or indiscriminate stinging is widespread, but body site specificity for oviposition and stinging is also found.

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