

COMPARATIVE MORPHOLOGY OF THE STINGER IN THE SOCIAL WASP GENUS *ROPALIDIA* (HYMENOPTERA: VESPIDAE)

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Abstract.—The structure of the venom apparatus is described for *Ropalidia*, the only genus of social wasps with both independent-founding and swarm-founding species. In all qualitative respects it is found to resemble that previously described from other social wasps.

Several parameters of the stinger are measured in 39 species, representing all of O. W. Richards's six subgenera. The data are brought to bear on three predictions arising from the hypothesis that the venom apparatus is more highly developed as an organ of colony defense in swarm-founding species. None of these predictions is upheld, and the structure of the stinger is found to be remarkably uniform across species and social types.

Key Words: Polistinae, *Ropalidia*, social wasp, stinger, venom apparatus

The stinging insects, or Aculeata, are a subgroup of the order Hymenoptera whose outstanding physical peculiarity is the transformation of the female's ovipositor into a venom-injecting device, or stinger. The stinger and associated glands make up the venom apparatus whose form and working are reviewed by Hermann and Blum (1981).

The primitive function of the aculeate venom apparatus is evidently in prey capture. However, it can also serve as a powerful deterrent to large enemies, so that in several lineages it has taken on an important defensive function (Schmidt 1990). As noted by Schmidt (1990), stinging is largely ineffective against arthropod predators, such as ants.

This defensive function is especially prominent in some social insects, and Starr (1985, 1989) and Schmidt (1990) propose that stinging ability was crucial to the evolution of social insects. The view of social

groups, by their concentration of individuals, as inviting the attention of new, larger predators that would disregard scattered individuals. See Kukuk et al. (1989) and Fisher (1993) for dissenting views.

The social wasps, in the formal sense, comprise a clade of three subfamilies of Vespidae (Carpenter 1991). Within the Vespinae the venom apparatus has been studied in *Dolichovespula* (Hermann and Krispyn 1975) and less rigorously in members of *Vespa* (Starr, unpubl.) and *Vespula* (Edwards 1980, Akre et al. 1981). In the Polistinae it has been studied in *Mischocyttarus* (Hermann and Chao 1984), *Polistes* (Crouch and Smith 1958, Saksena 1960, Hunt and Hermann 1970) and *Synoeca* (C. K. Starr and H. R. Hermann, unpubl.). It has not been rigorously studied in any steno-gastrine wasp, but our (unpubl.) dissections of one species each of *Eustenogaster* and *Parischnogaster* indicate no striking

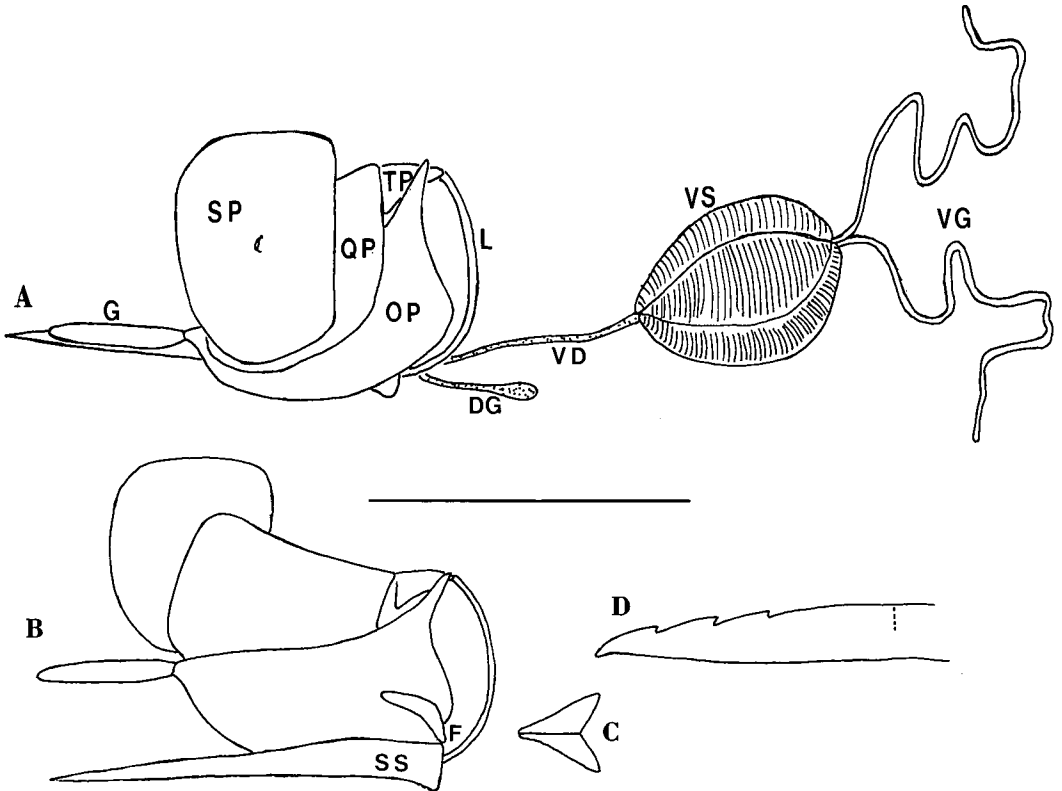


Fig. 1. Venom apparatus of *Ropalidia horni*, to illustrate the main features and condition for the genus as a whole. DG = Dufour's gland. F = furcula. L = lancet. OP = oblong plate. QP = quadrate plate. SP = spiracular plate. SS = sting shaft. TP = triangular plate. VD = venom duct. VG = venom gland. VS = venom sac. Right = anterior in all cases. Scale bar = 1 mm for A-C, approx. 0.1 mm for D. A. Side view of the venom apparatus at rest, with muscles removed except those surrounding the venom sac. B. Side view of the stinger, the plates spread but not detached, right-hand plates removed. C. Furcula in dorsal view. D. Terminal part of a sting lancet in side view. The short vertical dashed line illustrates the serration index; it represents the summed anterior lengths of the three barbs, here equal to 0.5 of the dorsoventral height of the lancet.

Present evidence is of an overall uniformity in the structure of the venom apparatus of social wasps, and perhaps of vespids as a whole. The outstanding shared derived feature is in the way venom is pumped from the venom reservoir down the sting shaft and into the wound. The general method within the Aculeata is by way of valves on the sting lancets, which push the venom along as they slide back and forth within the curl of the shaft. In social wasps, on the other hand, the lancets are without valves, and venom is pumped out by the contraction of large muscles enclosing the venom reservoir (Fig. 1A).

Ropalidia is a genus of about 136 known species (refs. in Gadagkar 1991) restricted

to the Old World. Richards (1978) divided the genus into six subgenera (Table 1). The naturalness of this classification is in some doubt, and in particular there is reason to consider the subgenus *Icariola* paraphyletic (J. M. Carpenter, pers. comm.). However, in the absence of a better arrangement it is convenient here to follow Richards, whose subgeneric classification appears to be a good predictor of gross social habit. Gadagkar (1991) has recently reviewed the nesting biology of the genus.

Jeanne (1980) drew a fundamental distinction between two patterns of social organization in social wasps, the *independent-founding* and *swarm-founding* behavioral complexes. Swarm-founding species are

Table 1. Specimens (adult females) dissected for this study. Subgenera are in parentheses and follow Richards (1978). The use of subspecific names is for present convenience and does not imply a general endorsement of their use.

Species	No. of Specimens	Origin(s)
(<i>Anthreneida</i>) <i>latebalteata</i> Cameron	2	Malay Peninsula
(<i>A.</i>) <i>opulenta</i> (Smith)	2	Borneo
(<i>A.</i>) <i>sumatrae</i> (Weber)	2	Malay Peninsula
(<i>Icarielia</i>) <i>bensoi</i> Richards	2	New Guinea
(<i>Ie.</i>) <i>conservator</i> (Smith)	2	New Guinea
(<i>Ie.</i>) <i>extrema</i> Vecht	8	Philippines
(<i>Ie.</i>) <i>flavobrunnea</i> Fecht	4	Philippines
(<i>Ie.</i>) <i>flavopicta</i> (Smith)	2	Malay Peninsula
(<i>Ie.</i>) <i>nigrescens</i> Vecht	8	Philippines
(<i>Ie.</i>) <i>romandi cabeti</i> (Saussure)	2	Australia
(<i>Icariola</i>) <i>aristocratica</i> (Saussure)	2	Malay Peninsula
(<i>Io.</i>) <i>capensis</i> (Saussure)	2	South Africa
(<i>Io.</i>) <i>cincta</i> (Lepeletier)	2	Ghana, Uganda
(<i>Io.</i>) <i>cyathiformis</i> (Fabricius)	6	Philippines
(<i>Io.</i>) <i>distigma</i> (Gerstaecker)	4	South Africa, Mozambique
(<i>Io.</i>) <i>fasciata</i> (Fabricius)	5	Philippines
(<i>Io.</i>) <i>formosa</i> (Saussure)	2	Madagascar
(<i>Io.</i>) <i>granulata borneensis</i> Vecht	2	Malay Peninsula
(<i>Io.</i>) <i>gregaria</i> (Saussure)	8	Philippines
(<i>Io.</i>) <i>horni</i> Sonan	8	Philippines
(<i>Io.</i>) <i>kurandae</i> Richards	2	Australia
(<i>Io.</i>) <i>malayana</i> (Cameron)	2	Malay Peninsula
(<i>Io.</i>) <i>marginata sundaica</i> Vecht	3	Philippines
(<i>Io.</i>) <i>nobilis</i> (Gerstaecker)	2	Zambia, Zanzibar
(<i>Io.</i>) <i>spatulata</i> Vecht	2	Pakistan, unknown
(<i>Io.</i>) <i>stigma</i> (Smith)	2	Malay Peninsula
(<i>Io.</i>) <i>timida</i> Vecht	2	Malay Peninsula
(<i>Io.</i>) <i>tomentosa</i> (Gerstaecker)	2	Kenya, Zaïre
(<i>Io.</i>) <i>trichophthalma</i> Richards	2	Australia
(<i>Io.</i>) <i>turneri</i> Richards	2	Australia
(<i>Io.</i>) <i>variegata</i> (Smith)	3	India, Malay Peninsula
(<i>Paraicaria</i>) <i>bicolorata</i> Vecht	2	Burma (?), Malay Peninsula
(<i>Pa.</i>) <i>nigerrima</i> Vecht	2	Malay Peninsula
(<i>Polistratus</i>) <i>bambusae</i> Richards	2	New Guinea
(<i>Po.</i>) <i>domestica</i> Cheesman	2	New Guinea
(<i>Po.</i>) <i>melania</i> Richards	2	New Guinea
(<i>Ropalidia</i>) <i>humboldti</i> Cheesman	2	New Guinea
(<i>R.</i>) <i>maculiventris</i> Guérin	2	New Guinea
(<i>R.</i>) <i>pratti</i> Cheesman	2	New Guinea

characterized by larger, more complex colonies and usually more complex, enclosed nests. Independent founding is evidently the primitive condition, with swarm founding appearing in an estimated four extant lineages of social wasps (Jeanne 1991, Matsuura 1991). Each habit is well represented

in the Polistinae, and *Ropalidia* is the one genus in which both are known (Gadagkar 1991, Jeanne 1991).

Where members of the two largest subgenera, *Icariola* and *Icarielia*, have been studied, the first are seen as independent-founding and the second as swarm-found-

ing (Richards 1978, Gadagkar 1991). Nest structure in species whose behaviour has not been directly studied corroborates this rule. In all but one polistine genus, exposed nest-combs are associated with independent founding and enclosed combs with swarm founding. Richards (1978) has given evidence that swarm founding also prevails in the subgenus *Paraicaria*. The habits of the remaining subgenera—*Anthreneida*, *Polistratus* and *Ropalidia*—are less certain. Gadagkar (1991) treats them as independent-founding, but we tentatively follow Richards (1978) in treating their social organization as intermediate between those of the independent-founding and swarm-founding groups.

The sting lancets are the most active part of the venom apparatus. Their primary function is evidently to cut a wound which the shaft can penetrate for more effective venom delivery (illustrated by Akre et al. 1981). In many aculeates the lancets are armed with barbs, which project anteriorly away from the tip (Fig. 1D) and apparently serve in anchoring the stinger in the wound (Hermann and Blum 1981). In some species the barbs are so well developed that they cannot normally be withdrawn from vertebrate skin, so that the insect's struggles to free herself result in a rupture of the venom apparatus from the body, a phenomenon known as *sting autotomy* (Hermann 1971, Hermann and Blum 1981). Sting autotomy is presumably always fatal, and autotomous stinging in defense of the colony is a standard example of biological altruism (e.g. Starr 1979).

Sting autotomy is best known from honey bees, but it appears also to be widespread among swarm-founding polistine wasps. To our knowledge, it is reliably recorded from 15 species in six genera: *Brachygastra augusti* (C. R. Hughes, in litt.), *B. bilineolata* (pers. obs. of CKS), *B. lecheguana* (Overal et al. 1981; C. R. Hughes, in litt.), *Epipona guerini* (C. R. Hughes, in litt.), *E. tatusa* (Rau 1933), *Polybia ignobilis* (C. R. Hughes, in litt.),

occidentalis (C. R. Hughes, in litt.), *P. rejecta* (Overal et al. 1981), *P. sericea* (C. R. Hughes, in litt.), *P. simillima* (Rau 1933; J. O. Schmidt, in litt.; pers. obs. of CKS), *P. striata* (C. R. Hughes, in litt.), *Protopolybia sedula* (Overal et al. 1981), *Ropalidia nigrescens* (pers. obs. of CKS), *R. romandi* (R. L. Jeanne, in litt.) and *Synoeca septentrionalis* (Rau 1933).

However, sting autotomy is evidently not a constant, species-characteristic feature. One of us (CKS) has on several occasions been stung by *Polybia occidentalis* and *R. nigrescens*, yet has never noticed sting autotomy in the first species and only sometimes in the second.

Special mention should be made of the furcula, a small, wishbone-shaped sclerite at the base of the sting shaft (Fig. 1C). This is the pivotal structure in rotation of the shaft and thus central to the precision of stinging (Hermann and Chao 1983). The length of the arms is an important variable in furcula structure, with relatively longer arms allowing finer control of shaft movement.

How do colony-defensive tactics differ between related taxa of differing colony size and social complexity? Surprisingly, the diffuse literature on defense in social insects contains little, if any, comment on this question. Nonetheless, it is our perception that as a general rule species with larger, more complex colonies have more powerful, sophisticated, means at their disposal. Furthermore, our reading of the literature suggests that this perception is widely shared, at least on an implicit level. This is consistent with the view, expressed above, that social groups of increasing size attract novel and more menacing kinds of enemies and so must have more effective defense, although one need not accept this view in order to observe the general rule.

If there are differences between the venom apparatus in independent-founding and swarm-founding *Ropalidia*, this general rule predicts that any adaptations allowing

a more effective venom-delivery system will be found among the swarm founders.

In this paper we: a) examine the venom apparatus of *Ropalidia* for any striking differences from those of other polistines, and b) test the above-mentioned prediction. This test is based on three predicted adaptations for more effective stinging by swarm-founding species, relative to independent-founding species:

1. A larger stinger, relative to the body as a whole.
2. A longer furcula, relative to the stinger as a whole.
3. More highly developed barbs on the sting lancets. The third prediction is consistent with that of Alexander et al. (1991) that sting autotomy will be found only among swarm-founding social wasps and bees, not among independent-founding species.

MATERIALS AND METHODS

The specimens examined are listed in Table 1. Those from the Philippines were in liquid preservative, identified by C. K. Starr according to Kojima (1982, 1984). All others were dry, pinned specimens identified by O. W. Richards. Specimens in the British Museum (Natural History) identified by Starr or Richards will serve as vouchers. All permanent microscope slides from this study are deposited in the BM(NH).

Soft parts are described from specimens in Dietrich's solution. To facilitate examination of sclerites, we cleared the stinger of soft tissue in dilute KOH for about a day. The sclerites were then wet-mounted on a slide and later permanent-mounted.

We measured forewing length with an ordinary ruler to the nearest half millimeter. We measured maximum sting-shaft and furcula length in wet-mounted specimens with an eyepiece micrometer to the nearest 0.01 mm. Following Haggard and Gamboa (1980), Reed and Akre (1982) and others, forewing length is taken as an index of overall body size. We utilize sting-shaft length as a convenient index of the overall

size of the stinger. The length ratio of shaft/forewing thus serves as an index of the stinger's physical prominence within the body. The length of the furcula is measured as the distance from the tip of the dorsal (posterior) arm to the midpoint between the tips of the ventral (anterior) arms. The furcula/shaft length ratio is taken as an index of the furcula's prominence within the stinger, and by implication of the relative precision of stinging motions.

Lancet barbs are not all equally sharp, but the frequency of exceptionally sharp or blunt ones seems insignificant. For convenience, we have disregarded those few that meet the lancet in an obtuse angle anteriorly. As a more realistic way of comparing the expected anchoring capacity of different lancets than just counting barbs, we use a *serration index* $\sum b_i/h$, in which b_i is the length of the i th barb along its anterior edge and h is the dorsoventral height of the lancet along the middle part of its length (see Fig. 1D). This index unites the number and length of barbs in a single measure of overall barbedness that is undisturbed by differences in stinger size. Serration figures reported here are all to the nearest 10%.

RESULTS

Fig. 1 illustrates the venom apparatus of *R. horni*, an independent-founding species. This and other *Ropalidia* closely resemble other studied polistines in the structures shown. We found no qualitative differences of note between the stingers of 39 *Ropalidia* spp. or in the soft parts of the independent-founding *R. horni* and *R. fasciata* and the swarm-founding *R. nigrescens*.

Table 2 shows the quantitative data for within-genus comparisons according to three social groups. Although the three primary length measurements (forewing, sting shaft and furcula) vary considerably, the length ratios of shaft/forewing and furcula/shaft are each quite uniform across the genus. Neither ratio differs significantly (one-way anova; $P = 0.43$ and 0.66 , respective-

Table 2. Structural parameters of the stinger in *Ropalidia* spp. Subgenus abbreviations follow Table 1. Fw = forewing length, SS = sting-shaft length, Fu = furcula length, NB = number of barbs/lancet, Sr = serration. Average values per species of Fw, SS and Fu are means if based on two specimens, but medians if based on three or more (see Table 1). Group means are of species averages. Further explanation in text.

Species	Fw (mm)	SS (mm)	Fu (mm)	SS/Fw	Fu/SS	NB	Sr
Independent-founding species							
<i>Io. aristocratica</i>	7.00	1.35	0.35	0.18	0.26	5	0.7
<i>Io. capensis</i>	6.00	1.32		0.22		4	0.5
<i>Io. cincta</i>	8.50	1.64	0.40	0.19	0.24	4	0.5
<i>Io. distigma</i>	9.75	2.01	0.54	0.20	0.26	4	0.5
<i>Io. formosa</i>	11.25	2.39	0.65	0.21	0.27		
<i>Io. granulata</i>	6.00	1.35	0.37	0.22	0.27	4	0.7
<i>Io. gregaria</i>	7.50	1.14	0.31	0.15	0.27	3	0.3
<i>Io. kurandae</i>	7.00	1.21	0.34	0.17	0.28	4	0.5
<i>Io. malayana</i>	5.00	1.21	0.32	0.24	0.26		
<i>Io. nobilis</i>	11.50	2.28	0.62	0.19	0.27	3	0.5
<i>Io. spatulata</i>	10.00	2.07	0.51	0.20	0.24	5	0.6
<i>Io. stigma</i>	8.25	1.39	0.41	0.19	0.25	4	0.5
<i>Io. timida</i>	5.00	1.03	0.26	0.20	0.25	4	0.4
<i>Io. tomentosa</i>	10.25	2.42	0.63	0.24	0.25	4	0.5
<i>Io. trichophthalma</i>	8.00	1.53	0.37	0.19	0.24	4	0.7
<i>Io. turneri</i>	8.50	1.71	0.41	0.20	0.23	3	0.5
<i>Io. variegata</i>	6.00	1.30	0.31	0.21	0.24	3	0.3
Group mean	7.97	1.61	0.38	0.20	0.26	3.9	0.51
Socially intermediate species							
<i>Po. bambusae</i>	7.00	1.32	0.42	0.18	0.32	3	0.5
<i>Po. domestica</i>	7.50	1.64	0.60	0.21	0.37	3	0.4
<i>R. humboldti</i>	11.25	2.42	0.55	0.21	0.22	4	0.5
<i>A. latebalteata</i>	8.00	1.42	0.37	0.17	0.26	4	0.6
<i>R. maculiventris</i>	11.00	1.92	0.32	0.18	0.16	4	0.7
<i>Po. melania</i>	7.00	1.42	0.39	0.20	0.27	3	0.4
<i>A. opulenta</i>	9.00	1.71	0.40	0.19	0.23	4	0.6
<i>R. pratti</i>	11.25	2.05		0.18		4	0.4
<i>A. sumatrae</i>	8.00					4	0.6
Group mean	8.89	1.74	0.36	0.19	0.26	3.7	0.52
Swarm-founding species							
<i>Ie. bensoni</i>	7.75	1.03	0.31	0.14	0.30	5	0.6
<i>Pa. bicolorata</i>	5.50	0.96	0.25	0.17	0.26	3	0.5
<i>Ie. conservator</i>	9.75	1.53	0.42	0.15	0.27	5	0.7
<i>Ie. extrema</i>	6.00	0.99	0.25	0.16	0.25	3	0.4
<i>Ie. flavobrunnea</i>	6.50	1.39	0.32	0.21	0.23	3	0.4
<i>Ie. flavopicta</i>	5.75	1.08	0.29	0.18	0.26	3	0.5
<i>Pa. nigerrima</i>	5.50	1.07	0.38	0.22	0.35	3	0.4
<i>Ie. nigrescens</i>	7.00	2.30	0.31	0.33	0.13	3	0.5
<i>Ie. romandi</i>						5	0.7
Group mean	6.72	1.29	0.32	0.20	0.26	3.7	0.52

ly) among the three groups. The three groups were similarly uniform in number of barbs per sting lancet ($P = 0.62$) and serration of the lancets ($P = 0.50$). Eliminating the intermediate groups to compare just the

independent-founding and swarm-founding groups did not alter the outcome in any of these parameters.

This consistent negative result is the core of our findings.

DISCUSSION

The venom apparatus of *Ropalidia* shows no striking departure from those of other studied polistine wasps. Qualitatively, no particular modification or reduction of any of the eight sclerites, the venom gland, venom reservoir or Dufour's gland is apparent. It is thus generalized for the subfamily and possibly for the family as a whole. Given the overall uniformity of the venom apparatus in previously-studied social wasps, this result was expected.

Nonetheless, quantitative differences from other studied polistines are apparent. In *Ropalidia* the stinger is moderately stouter overall than seems to be the rule in polistines. This is most readily seen in its more elongate elements:

1. The gonostyli are almost always clearly shorter than the oblong plates.
2. The length ratio of shaft/forewing is slightly less than in most other wasps and bees studied (Starr, unpubl.).
3. The furcula is stouter.

We admit to some surprise that none of the predicted quantitative differences between swarm-founding and independent-founding *Ropalidia* was upheld. In particular, in view of widespread sting autotomy among swarm-founding polistines and personal experience with this phenomenon in *R. nigrescens*, we were quite confident of finding more barbed sting lancets in the swarm-founding group.

How can we account for this unequivocal and unexpected negative result? We note two kinds of possible answers.

First, key differences may exist, but not where we have looked for them. Rather, they may be in the soft parts of the venom apparatus, in venom chemistry and/or the behavior of stinging. While we did not rigorously compare the sizes of venom sacs, for example, they seem comparable in the few species in which we examined them. We doubt that individual swarm-founders produce a much greater quantity of venom.

The hypothesis of differences in venom

chemistry is more open, but it does not seem especially promising. In the species studied to date, there does not seem to be any overall difference in venom toxicity between independent-founding and swarm-founding polistines, and the two *Icarielia* species studied are not outstanding (Schmidt 1990). We have likewise seen no evidence that swarm founders tend to have more painful venom.

As far as we know, there have been no studies of the stinging behavior of social wasps that would suggest that different species utilize their similar equipment in divergent ways.

The second answer is that the perceived pattern of more powerful defensive weapons and tactics in species with larger colonies is an illusion, or at least that it does not especially apply to *Ropalidia*. Unattractive as it is, we cannot discount this possibility.

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