THE SOCIAL WASPS (HYMENOPTERA: VESPIDAE) OF TAIWAN

CHRISTOPHER K. STARR*

National Museum of Natural Science, Taichung, Taiwan 40419, R.O.C.

ABSTRACT—The social wasps of Taiwan are reviewed, with biological notes on some species. A total of 28 species are recognized. Of these, 10 are in the subfamily Vespinae (genera *Vespa* and *Vespula*) and 18 in the Polistinae (genera *Parapolybia, Polistes* and *Ropalidia*). Two of the *Polistes* species appear to be undescribed.

Four nominal species are placed in synonymy: *Parapolybia nodosa* Vecht = *P. takasagona* Sonan, *Polistes hengchunensis* Kuo = *Polistes japonicus* Saussure, *Polistes shekouensis* Kuo = *P. japonicus* Saussure, and *Ropalidia formosana* Kuo = *R. taiwana* Sonan.

KEY WORDS: Vespinae, Polistinae, Vespidae, Taiwan, Taxonomy.

INTRODUCTION

The social wasps (in the formal sense) form a natural group of three subfamilies within the family Vespidae. The Stenogastrinae extend from Ceylon and eastern India to New Guinea and north to Luzon. They do not occur in Taiwan, although a very few species are found as near as Guangdong and Hainan (Lee, 1985; pers. obs.). The other two subfamilies -- Polistinae and Vespinae -- are well represented in Taiwan.

The groundwork for present systematic knowledge of Taiwan social wasps was laid by Jinhaku Sonan. In a paper on various vespids and sphecids, Sonan (1927) treated two species of *Vespa* and two of *Polistes*. In a review of the vespines of Taiwan, he treated and keyed 12 forms (Sonan, 1929). With nomenclatural changes taken into account, his species list is not very different from the present one. In revising *Ropalidia* for Taiwan, he recognized the same two species as are recognized here, including the new *R. taiwana* (Sonan, 1935). In revising *Parapolybia,* he likewise recognized the same two as are recognized here, describing one as now. Sonan (1943) also provided the only revision to date of the *Polistes* of Taiwan. Taking into account nomenclatural changes, his list of species differs from mine only in the difficult subgenus *Polistella*.

In a monograph on the vespids of China, Lee (1985) recorded nine species from Taiwan. However, he had access to relatively little Taiwan material, so that the incompleteness of his list is not surprising.

Yamane and Tano (1985) revised the vespine genus *Vespula* in Taiwan. The present treatment of that genus is largely based on their work and adds little except a few new locality records.

In the present faunistic study I review the social wasps of Taiwan, discuss the geographic distribution of each, and present such new habitat and other ecological information as is available. Microtaxonomy is for the most part disregarded. The Polistinae include two apparent undescribed species. These are diagnosed here, but description of new taxa in a regional review would be inappropriate. In nomenclatural matters I likewise restrict myself to such minor problems as can be solved within the confines of Taiwan. Sô. Yamane and Sk. Yamane are preparing a full revision of the

* Present address: Dep't of Zoology, University of the West Indies, St. Augustine, Trinidad.

Bulletin of National Museum of Natural Science, No. 3, PP. 93-138, 1992

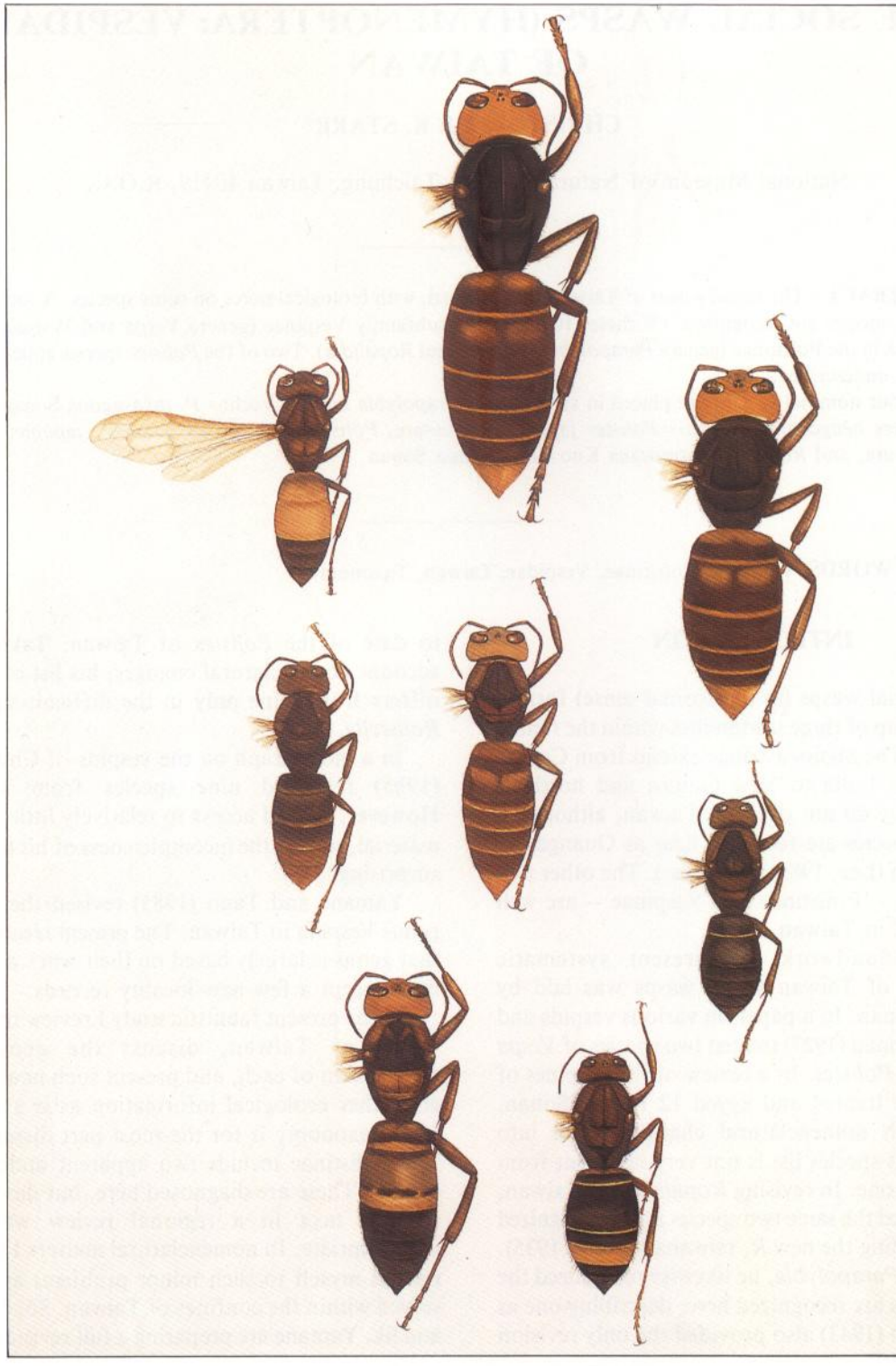

Figure 1. Hornets of Taiwan. Center: ***Vespa analis*** worker. Clockwise from top: ***V. mandarinia*** queen, ***V. mandarinia*** worker, ***V. basalis*** worker, ***V. wilemani*** worker, ***V. ducalis*** worker, ***V. velutina*** worker, ***V. affinis*** worker. Painting by H.C. Yu.

polistines of Taiwan.

MATERIALS AND METHODS

This study is based on about 8300 specimens (Table 1) from nine institutional and private collections. Collections are listed here, each preceded by the acronym used in the text. Where I borrowed material, the person arranging the loan is identified in brackets.

BSC Personal collection of Mr. Chang Baw-sing, Yangmei, Taoyuan (Chang Baw-sing)
CKS Author's personal collection, University of Georgia, Athens, Georgia, USA
CNC Canadian National Collection, Biosystematics Research Centre, Ottawa, Canada
NCHU National Chunghsing University, Taichung (Yang Jeng-tze)
NCIA National Chiayi Institute of Agriculture, Chiayi (Kuo Muh-chwan)
NMNS National Museum of Natural Science, Taichung
NTU National Taiwan University, Taipei (Hsu Tung-ching)
TARI Taiwan Agricultural Research Institute, Wufeng, Taichung (Chou Liang-yih)
TPM Taiwan Provincial Museum, Taipei (An Kwei)

Place names in Taiwan are romanized according to the simplified form of the Wade-Giles system in general use here. Place names in mainland China follow the Pinyin system. Japanese names of Taiwan localities (on specimens collected during the colonial period, 1896-1945) are interpreted according to Chiu (1948), Chu and Yamanaka (1973-1975) and Price (1982).

Table 2 shows the proportional provenance by county of material from different parts of Taiwan. This indicates large geographic biases in collecting effort, with most attention until now focused along the western side of the island and in Nantou County (see Figure 2). I suggest that future collecting in the eastern counties of Hualien and Taitung should be especially fruitful.

Figure 2 shows the positions of 13 especially well collected localities. Except in the case of rare species, the lack of a collecting record from any of these localities is good evidence that the species does not occur there. This is taken into account in estimating distribution limits.

Table 1. Checklist of social wasp species of Taiwan and numbers of specimens examined.

Species	Females	Males	Total
VESPINAE			
Vespa affinis (Linnaeus)	633	24	657
Vespa analis Fabricius	53	3	56
Vespa basalis F. Smith	143	5	148
Vespa ducalis F. Smith	349	13	362
Vespa mandarinia F. Smith	240	4	244
Vespa velutina Lepeletier	747	37	784
Vespa wilemani Meade-Waldo	25	2	27
Vespula arisana Sonan	50	0	50
Vespula flaviceps (F. Smith)	68	11	79
Vespula schrenckii (Radoszkowsky)	4	0	4
POLISTINAE			
Parapolybia takasagona Sonan	162	40	202
Parapolybia varia Fabricius	735	141	876
Polistes species A	24	1	25
Polistes species B	39	1	40
Polistes chinensis Fabricius	214	28	242
Polistes eboshinus Sonan	209	94	303
Polistes gigas Kirby	356	17	373
Polistes huisunensis Kuo	29	2	31
Polistes jadwigae DallaTorre	228	21	249
Polistes japonicus Saussure	727	157	884
Polistes rothneyi Cameron	513	78	591
Polistes shirakii Sonan	252	96	348
Polistes stigma (Fabricius)	10	7	17
Polistes strigosus Bequaert	9	0	9
Polistes sulcatus F. Smith	172	17	189
Polistes takasagonus Sonan	483	61	544
Ropalidia fasciata (Fabricius)	877	24	901
Ropalidia taiwana Sonan	52	9	61
Total	7403	893	8296

KEY TO GENERA OF SOCIAL WASPS OF TAIWAN (ADULTS)

The genera present in Taiwan can be distinguished from other aculeate hymenoptera by the following characters: both sexes winged, wings folded longitudinally at rest; no part of the body clothed in dense, long pubescence; mandibles short,

Figure 2. Counties and city administrative districts of Taiwan. Shown also are the positions of 13 especially well-collected localities. A species not recorded from one of these localities is presumed not to occur there.

Table 2. Provenance by county of material examined for this study, proportional to land area. Changhua County is taken as the point of reference. For example, there were twice as many specimens overall (2.3 times as many polistines and 1.5 times as many vespines) from Yunlin County as from Changhua County, which is 0.83 times as large as Yunlin County; the resulting figures for Yunlin County of 1.66, 1.91 and 1.25 are rounded off below to 2, 2 and 1, respectively. See Figure 2 for positions of counties. The Taipei, Keelung, Taichung, Tainan and Kaohsiung city administrative districts and the smaller islands are not included in the computation.

County	Relative number of specimens		
	overall	Polistinae	Vespinae
Changhua	1	1	1
Yunlin	2	2	1
Tainan	2	2	2
Hualien	4	3	5
Miaoli	6	9	1
Taitung	7	11	0
Kaohsiung	7	8	4
Chiayi	9	7	11
Taoyuan	9	11	6
Yilan	12	17	5
Hsinchu	19	29	5
Taipei	55	77	23
Taichung	81	70	97
Nantou	88	99	73
Pintung	93	140	23

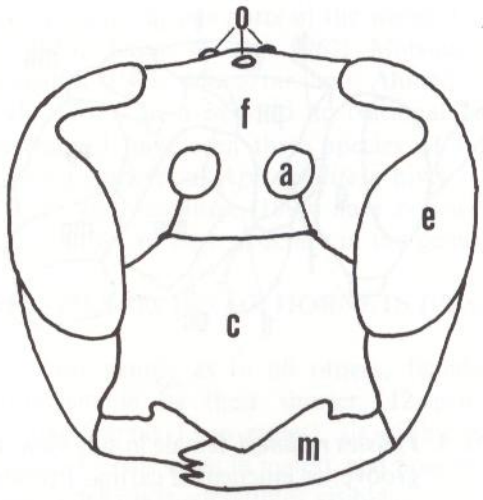

Figure 4. Face of ***Polistes rothneyi*** female, to show general characters. a: antennal socket. c: clypeus. e: eye. f: frons. m: mandible. o: ocelli.

mostly fitting below the labrum when folded; pronotum extending back to the tegula; mesopleuron without a distinct, oblique suture; in the female, stinger well developed.

1. Gaster sessile, expanding abruptly near base (Figure 5a). Hindwing without an anal lobe. Neither dorsal episternal groove nor epicnemial carina (see Figure 3) present. Very stout wasps ..... (Vespinae) 2

- Gaster sessile (Figure 5b) or petiolate (Figure 5c-d), expanding gradually from base. Hindwing with an anal lobe (Figure 6). Dorsal episternal groove and/or epicnemial carina present or absent. Slender to moderately stout wasps ..... (Polistinae) 3

2. Vertex short, posterior ocelli about as far from each other as from back of head (Figure 7a) .. .. *Vespula*

- Vertex long, posterior ocelli more than twice as far from back of head as from each other (Figure 7b) ..... *Vespa*

3. Gaster sessile (Figure 5b); medium-sized to very large, moderately stout wasps ..... *Polistes*

- Gaster petiolate, i.e. with a slender, approximately parallel-sided basal section (Figure 5c-d) 4

4. 2nd gastral tergum and sternum not overlapping, mostly or completely fused (Figure 8). Pronotum without a fovea (see Figure 3). Dorsal episternal groove absent, epicnemial carina present (see Figure 3). Small, medium-stout wasps .... *Ropalidia*

- 2nd gastral tergum and sternum overlapping, as in Figure 3. Pronotum with or without a fovea. Dorsal episternal groove present, epicnemial groove absent. Medium-sized, very slender wasp ..... *Parapolybia*

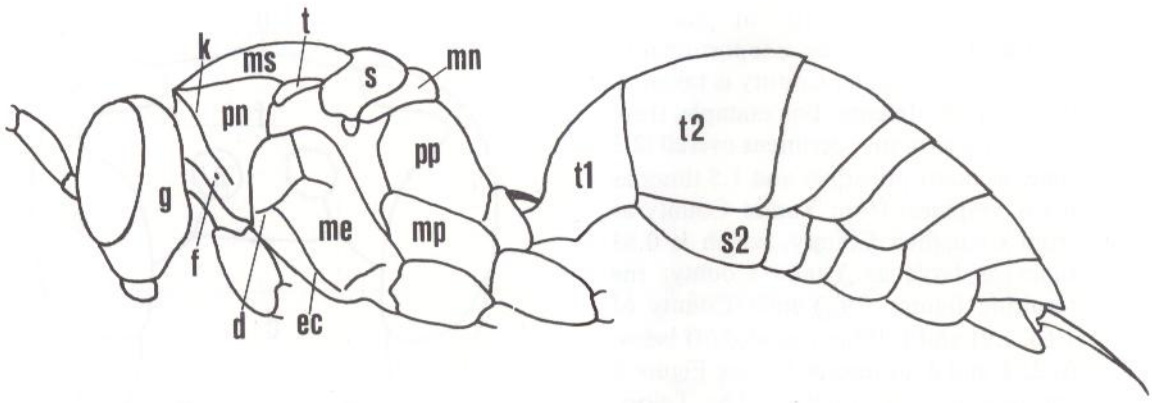

Figure 3. ***Polistes rothneyi*** female in side view, to show general characters of social wasps. d dorsal episternal groove. ec epicnemial carina. f pronotal fovea. g gena. k pronotal keel. me mesepisternum. mn metanotum. mp metapleuron. ms mesoscutum. pn pronotum. pp propodeum. s scutellum. s2 gastral sternum 2. t tegula. t1 gastral tergum 1. t2 gastral tergum 2.

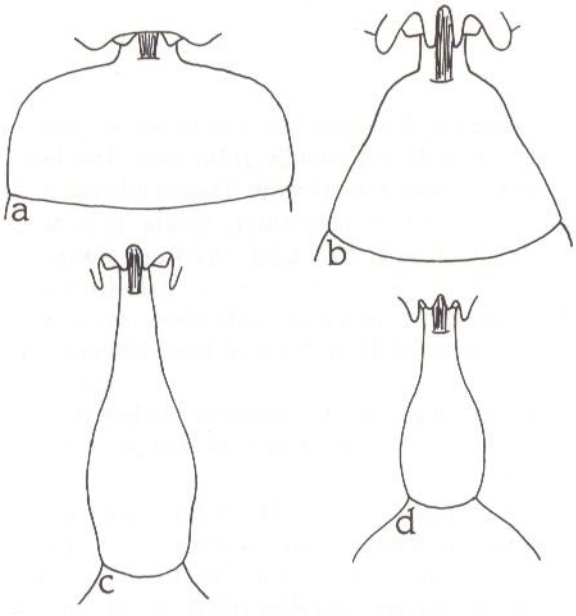

Figure 5. Base of gaster in top view. a. ***Vespa basalis.*** b. ***Polistes japonicus.*** c. ***Parapolybia varia.*** d. ***Ropalidia fasciata.***

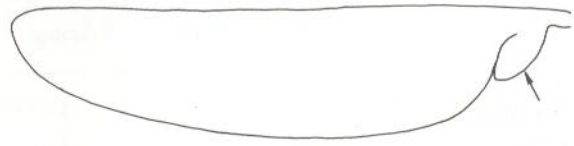

Figure 6. ***Polistes japonicus*** hindwing, to show anal lobe.

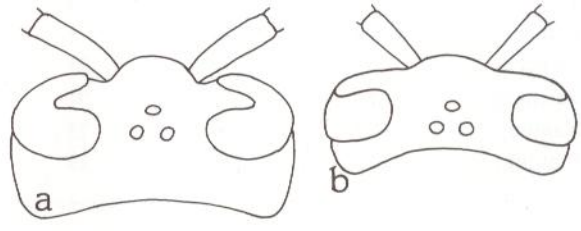

Figure 7. Head in top view. a. ***Vespa affinis.*** b. ***Vespula flaviceps.***

Subfamily ***Vespinae*** -- hornets and yellowjackets.

The biology of this group has been reviewed by Spradbery (1973), Edwards (1980) and Matsuura and Yamane (1990). The latter reference is the most relevant to east Asian species. Vespine wasps distinguish themselves from the polistines occuring in Taiwan by their usually much larger colonies, enclosed, multi-comb nests and greater differentiation between queens and workers. Carpenter (1987) has analyzed phylogenetic relationships among the genera.

Distribution ranges outside of Taiwan in this

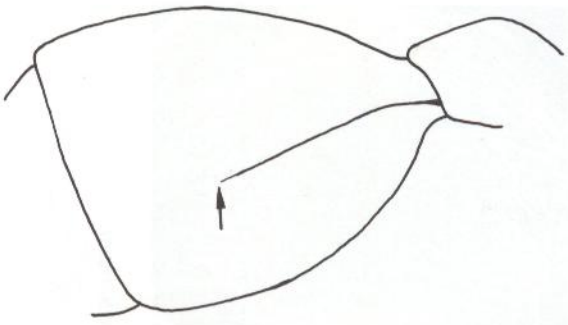

Figure 8. ***Ropalidia fasciata*** second gastral segment in side view, to show fusion of tergum and sternum.

subfamily are taken from Archer (1989) and Matsuura and Yamane (1990).

Genus ***Vespa*** Linnaeus -- hornets.

This genus of 23 known species (Archer, 1989; Matsuura and Yamane, 1990) is widespread in Eurasia, with its center of diversity in east Asia. It is represented in Taiwan by seven species, known collectively as 虎頭蜂 . Aside from references given above for the subfamily as a whole, the biology of hornets is reviewed by Matsuura (1991). These are the largest social wasps in the world and are often pugnacious in defense of the colony, so that they are generally feared by humans. However, not all species are equally aggressive, and colonies of some can be safely approached even to within one or two meters if this is done with care.

As even a quick glance at Figures 15-21 will show, there is considerable geographic overlap among the different species in Taiwan. It might be supposed that the species show micro-geographic separation, with some nesting and foraging mainly in forests and others in open areas, for example, but there is no indication that this is so. The ecological differentiation that allows several species of such similar insects to coexist in Taiwan is an interesting problem. Matsuura and Yamane (1990) have addressed this question as it applies to five species found together on Honshu island, Japan. They emphasize food as the principal factor, each species having a characteristic array of preferred prey which differs from that of other hornets.

Many hornets are known to take honey bees as prey, and some have become serious pests of beekeeping in various parts of the world (Chao et al., 1989; Ishay et al., 1967; Matsuura and Sakagami, 1973; Muzaffar and Ahmad, 1986; Singh, 1962). In a beeyard at National Taiwan University I have seen three species of hornets attacking workers at *Apis mellifera* hives.

Starr and Jacobson (1990) have reviewed the main features of nest structure in the genus.

KEY TO SPECIES OF HORNETS *(VESPA)*

In this genus, as in all others, females are distinguishable by their shorter, 12-segmented antennae (versus 13 in males), six visible gastral segments (versus seven in males), and possession of a stinger which is sometimes visible.

I. Females

1. Apical margin of clypeus with a median tooth, surface of clypeus densely coarsely punctate (Figure 9b)·····*analis* F.
- Apical margin of clypeus without a median tooth·····2
2. Head strongly produced behind eyes (Figure 10a), which thus appear relatively small·····*mandarinia* F. Smith
- Head not strongly produced behind eyes (see Figure 10b, c), which appear relatively larger·····3
3. Clypeus strongly punctured (Figure 9a, d). Pretegular carina complete (Figure 11a)·····4
- Clypeus more finely punctured, with a smoother surface (Figure 9c, f, g). Pretegular carina incomplete (Figure 11b)·····5
4. First gastral tergum relatively long, about half as long as wide (Figure 13a). Gastral terga 1 and 2 entirely orange, remaining terga entirely or almost entirely black (Figure 1). Lateral apical margins of clypeus rounded (Figure 9a)·····*affinis* (L.)
- First gastral tergum shorter (Figure 13b). Gastral terga with numerous, mostly indistinct orange and brown markings (Figure 1). Lateral apical margins of clypeus ending in a pair of triangular projections (Figure 9b)·····*ducalis* F. Smith
5. Gastral terga 2-6 entirely black (Figure 1). Clypeus (Figure 9c) and mesoscutum very finely punctured. Clypeus reddish. Pronotal keel little displaced by fovea (Figure 12a)·····*basalis* F. Smith

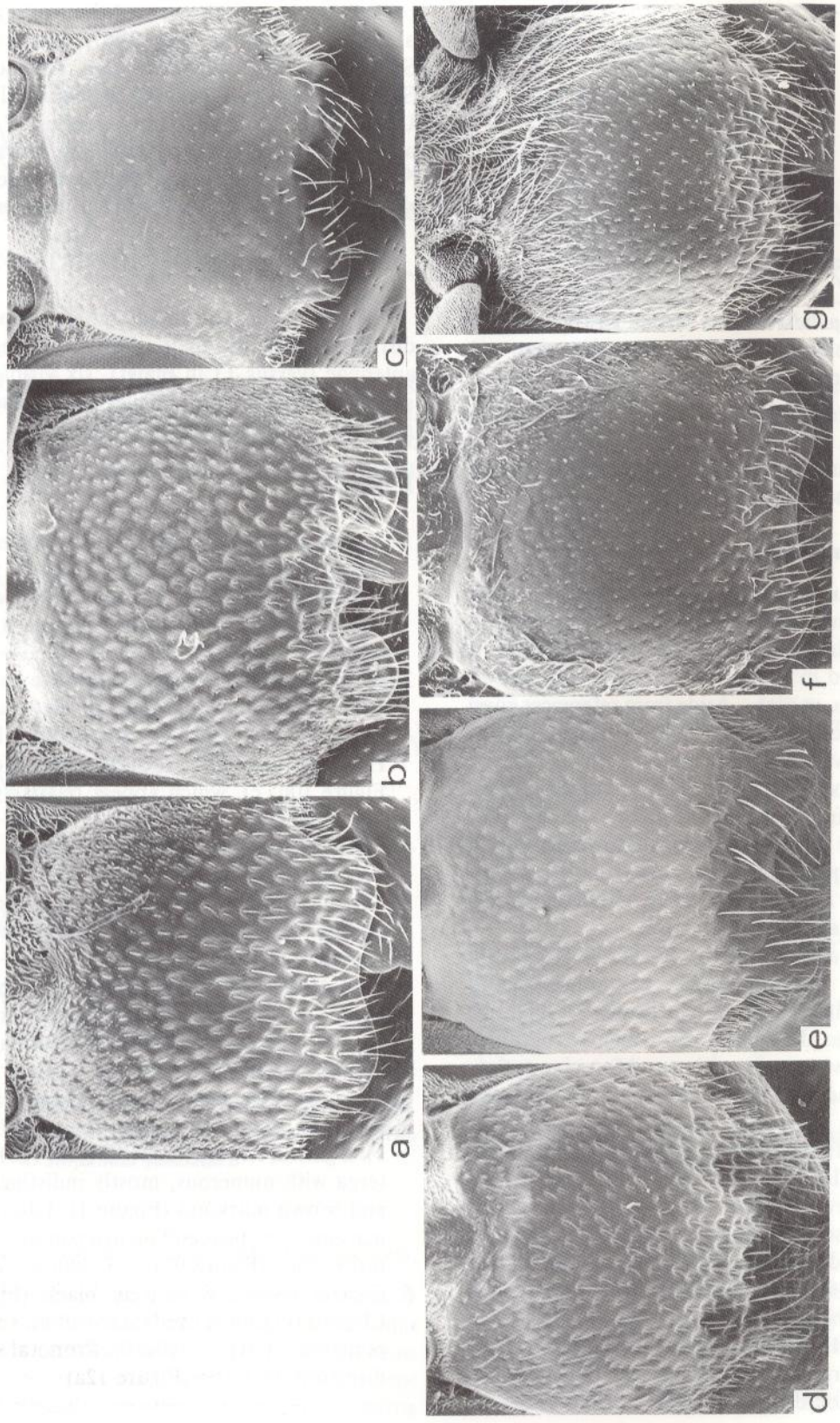

Figure 9. Female clypeus. a. ***Vespa affinis.*** b. ***V. analis.*** c. ***V. basalis.*** d. ***V. ducalis.*** e. ***V. mandarinia.*** f. ***V. velutina.*** g. ***V. wilemani.***

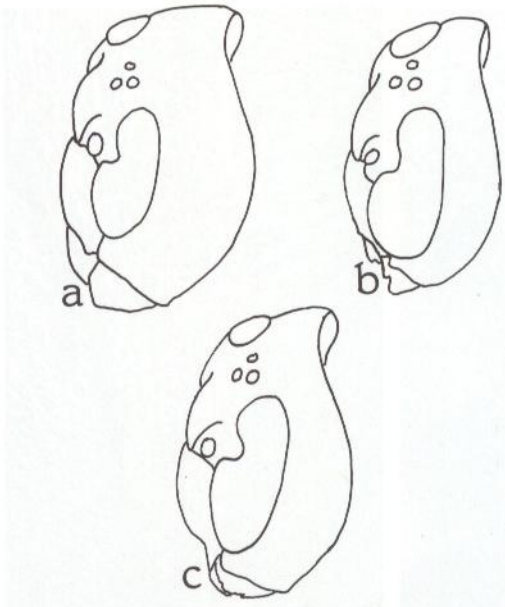

Figure 10. Head in dorsolateral view. a. ***Vespa mandarinia.*** b. ***V. affinis.*** c. ***V. ducalis.***

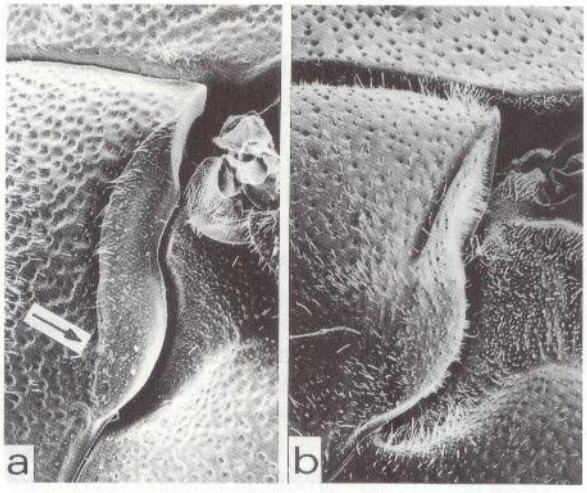

Figure 11. Tegular area (tegula removed), to show condition of the pretegular carina. a. ***Vespa affinis.*** b. ***V. velutina.***

- Gastral terga 2-6 not entirely black. Clypeus and mesoscutum not especially finely punctured. Clypeus orange. Pronotal keel much displaced by fovea (Figure 12b, c)·····6

6. Lower lateral surface of pronotum rugose (Figure 12b) (may be indistinct in workers). Thorax (except pronotum) and propodeum mainly black. Apical bands of gastral terga 1-3 and visible parts of terga 4-6 dull orange (Figure 1)·····*velutina* Lep.
- Lower lateral surface of pronotum not rugose (Figure 12c). Thorax and propodeum uniformly reddish-brown. Gastral terga 1-3 each with a narrow yellow apical band, tergum 4 with a conspicuous, broad yellow band (Figure 1)·····*wilemani* Meade-Waldo

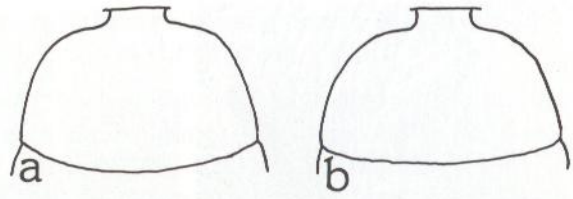

Figure 13. First gastral tergum in top view. a. ***Vespa affinis.*** b. ***V. ducalis.***

II. Males

1. Apical margin of gastral sternum 7 produced and convex (Figure 14c). Punctation of clypeus and mesoscutum extremely fine····*basalis* F. Smith
- Apical margin of gastral sternum 7 more or less straight or concave·····2
2. Apical margin of gastral sternum 6 with a deep emargination, semicircular or deeper (Figure 14a, b, f, g)·····3
- Apical margin of gastral sternum 6 with a more or less evenly curving emargination, shallower than semi-circular (Figure 14d, e). Pretegula carina complete, as in Figure 11a. Pronotal keel little displaced by fovea, as in Figure 12a)···6
3. Pretegular carina complete (Figure 11a)·····4
- Pretegular carina incomplete (Figure 11b). Pronotal keel much displaced by fovea (Figure 12b, c)·····5
4. Pronotal keel much displaced by fovea, as in Figure 12b, c. First gastral tergum relatively long, about half as long as wide (Figure 13a). Gastral terga 1 and 2 entirely orange, remaining terga entirely or almost entirely black (Figure 1)·····*affinis* (L.)
- Pronotal keel little displaced by fovea, as in Figure 12a. First gastral tergum shorter·····

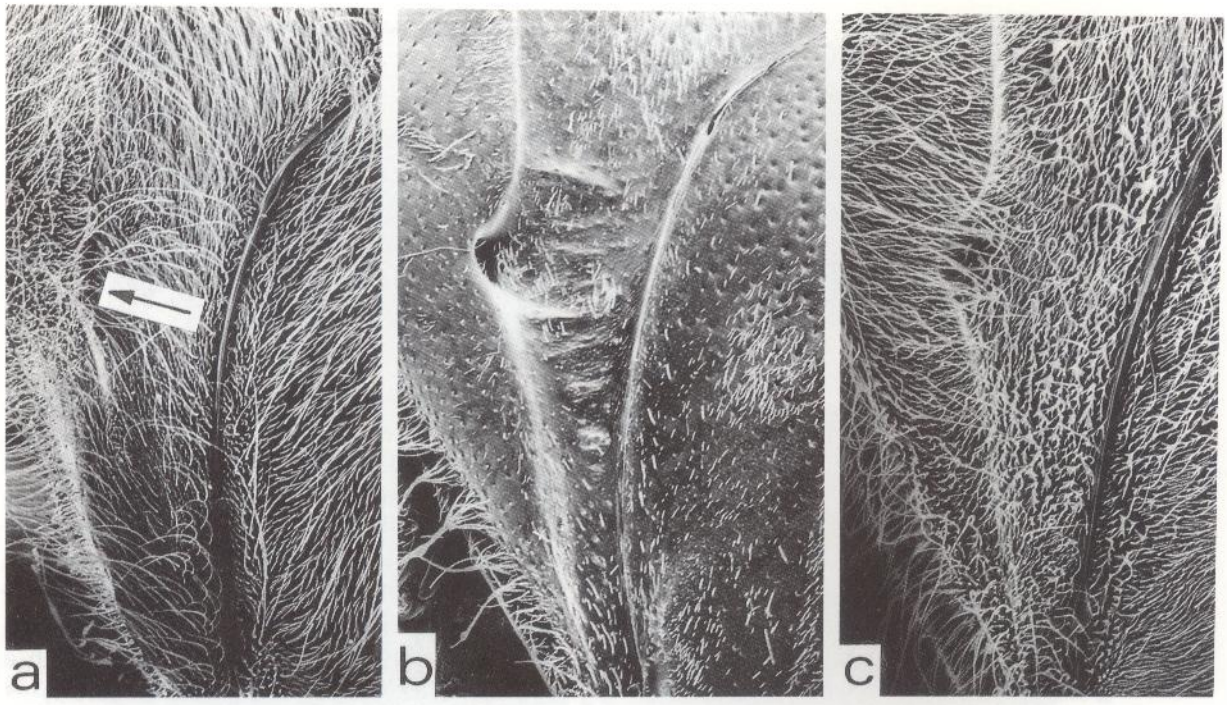

Figure 12. Lower part of pronotum in side view. a. ***Vespa basalis.*** b. ***V. velutina.*** c. ***V. wilemani.*** The relative bareness in ***V. velutina*** is an artefact of preparation.

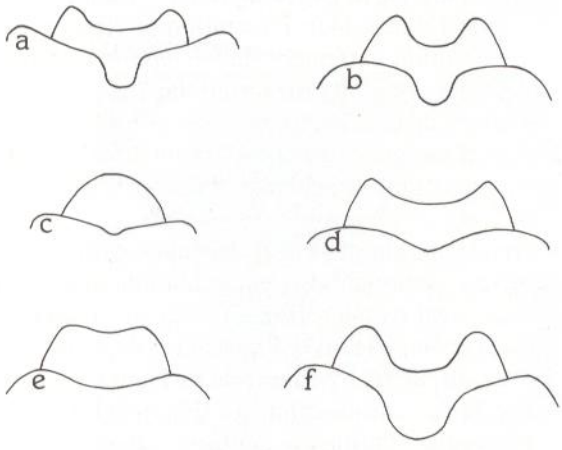

Figure 14. Gastral sternum 7 and apical margin sternum 7 in ***Vespa*** males. a. ***V. affinis.*** b. ***V. analis.*** c. ***V. basalis.*** d. ***V. ducalis.*** e. ***V. mandarinia.*** f. ***V. velutina.*** g. ***V. wilemani.***

..... *analis* F.

5. Lower lateral surface of pronotum rugose (Figure 12b). Thorax (except pronotum) and propodeum mainly black. Apical bands of gastral terga 1-3 and visible parts of terga 4-6 dull orange (Figure 1) ..... *velutina* Lep.
- Lower lateral surface of pronotum punctate, not rugose (Figure 12c). Thorax and propodeum uniformly reddish-brown. Gastral terga 1-3 each with a narrow yellow apical band, tergum 4 with a conspicuous, broad yellow band (Figure 1) ..... *wilemani* Meade-Waldo

6. Head strongly produced behind eyes, which therefore seem relatively small (Figure 10a). Gastral tergum 1 less than half as long as wide ..... *mandarinia* F. Smith
- Head not strongly produced behind eyes (Figure 10b), eyes appearing relatively larger. Gastral tergum 1 more than half as long as wide..... ..... *ducalis* F. Smith

Vespa affinis (Linnaeus)

Vespa formosana Sonan, 1927:125-128 [types examined: 1 queen, 1 worker, 1♂] -- Sonan, 1929:145-146 (key, distribution, description) -- Kuo, 1984

Vespa affinis Linnaeus -- Edwards 1980:360 (listed)

Figure 15. Distribution of ***Vespa affinis*** in Taiwan. Contour lines are at 100,1000 and 2000 m. Dashed line delimits estimated range.

-- Archer 1989:32 (listed, key) -- Matsuura and Yamane, 1990:233-234 (listed)

Distribution: India to southeastern China and the Ryukyus, Indochina to Sumatra, Borneo to Palawan and New Guinea. This species is found throughout Taiwan island at altitudes up to about 1000 m and is one of two hornets found on Orchid Island (Figure 15). In my experience it is by far the most aboundant hornet in lowland areas throughout Taiwan.

Biology: At more tropical latitudes this species is noted for the frequent presence of multiple queens in the colony and for colony reproduction by swarming (Matsuura, 1983; Spradbery, 1986), traits not known in other *Vespa*. It is not known whether it also exhibits these traits here in the northern part of its range. As reported by beekeepers, this is a more serious beekeeping pest in Taiwan than any other hornet (Chao et al., 1989).

Nest: Nesting is usually above ground, in trees and often on buildings (Matsuura, 1973; Starr and Jacobson, 1990; Yamane, 1977). However, M.C. Kuo showed me a colony near Chiayi nesting on the soil surface among tall grass, a habit which he has occasionally encountered, and Sô. Yamane (pers. comm.) reports seeing others among pineapple plants. Nests can grow exceptionally large. often including several thousand cells at maturity. There appears to be some significant variation in nest features in different parts of the species's large range. For example, old, abandoned cells in the upper combs are often papered over in the Philippines (Starr and Jacobson, 1990), while this is not found in the Ryukyus (S. J. Martin, pers. comm.). Nests from Taiwan have not yet been analyzed with such intraspecific variation in mind.

Vespa analis Fabricius

Vespa nigrans Buysson -- Sonan, 1929:141-142 (key, distribution, description)

Vespa analis Fabricius -- Matsuura and Yamane, 1990:234 (listed) -- Edwards, 1980:360 (listed) -- Archer, 1989:32 (listed, key)

Distribution: Northern India and Himalayas to eastern China, north to Japan, Korea and Siberia, south to Sumatra and Java. Although this species cannot be called rare in Taiwan, it is known only from a few medium-elevation localities in the central part of the island (Figure 16).

Biology: V. analis in Japan has relatively small colonies at maturity (Matsuura, 1984; Matsuura and Yamane, 1990), and the one Taiwan colony examined to date followed this same pattern (Matsuura, 1973). Vecht (1957) and Matsuura (1973) characterized this as an exceptionally docile species which almost never attacks humans.

Nest: Like *V. affinis,* this species nests above ground (Matsuura, 1973; Starr and Jacobson, 1990). Nest structure has not been thoroughly analyzed, so that careful description of additional nests from Taiwan would be worthwhile.

Vespa basalis F. Smith

Vespa basalis Smith -- Sonan, 1929:144-145 (key, distribution) -- Matsuura and Yamane, 1990:234

Figure 16. Distribution of ***Vespa analis*** in Taiwan. Contour lines are at 100, 1000, and 2000 m. Dashed line delimits estimated range.

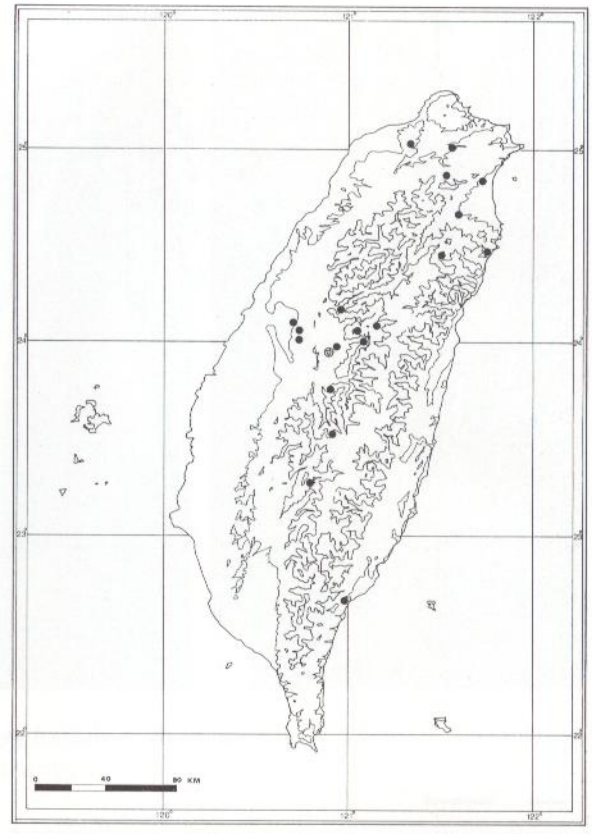

Figure 17. Distribution of ***Vespa basalis*** in Taiwan. Stippled dot represents a record from Matsuura (1973). Contour lines are at 100, 1000 and 2000 m.

(listed) -- Edwards, 1980:360 (listed) -- Archer, 1989:32 (listed, key)

Distribution: Pakistan to southern China and Indochina. In Taiwan it is widespread at medium elevations north of the Hengchung Peninsula (Figure 17). In the Nepal Himalaya it appears to rarely nest above 1500 m (Yamane, 1974).

Biology: This species has been biologically very little studied. Sô. Yamane (1977) reported that it develops large colonies, comparable to those of *V. affinis* and has recently (Sô. Yamane, unpubl.) described a *V. basalis* colony from Taiwan which appears to be the largest on record for this genus.

Nest: Matsuura (1973) and Starr and Jacobson (1990) reported *V. basalis* nesting only in trees and shrubs. However, Kuo and Yeh (1985) stated that this species and *V. velutina* initially nest in cavities or low vegetation but that in the late spring or summer they re-nest high in trees. It is not clear whether this is based on few or many observations, and confirmation would be valuable. A very similar habit is known from *V. crabro* and *V. simillima* in Japan (Matsuura, 1984; Matsuura and Yamane, 1990). Very few *V. basalis* nests have been structurally described (Matsuura, 1973, Starr and Jacobson, 1990), and there is certainly room for more data on this subject.

Vespa ducalis F. Smith

Vespa ducalis Smith -- Sonan, 1927:128-129 -- Sonan, 1929:138-140 (key, distribution, description) -- Archer, 1989:33 (listed, key)
Vespa tropica ducalis Smith -- Edwards, 1980:361

(listed)

Vespa tropica pseudosoror Vecht -- Kuo and Yeh, 1985 -- Matsuura and Yamane, 1990:235 (listed)

Until very recently this species was treated as a variant of *V. tropica* (Linnaeus), so that many observations attributed to *V. tropica* in fact refer to *V. ducalis,* including all from Japan and Taiwan. As presently understood, the two species have very little geographic overlap.

Distribution: Central and southeastern China north to Japan, Korea and Siberia. Distribution of *V. tropica:* Ceylon and India, Himalayas east to southern China, Indochina, Greater and Lesser Sunda Islands, Philippines east to New Guinea. *V. ducalis* is very widespread in Taiwan at low and medium elevations, and it is found on Orchid Island, so that its range closely resembles that of *V. affinis* (Figure 18). However, my field impression is that *V. ducalis* is not so much a lowland species as is *V. affinis* and instead has its greatest abundance at about 500-1500 m.

Biology: Behavioral-ecological information on *V. ducalis* is almost entirely based on studies done in Japan (Sakagami and Fukushima, 1957; Matsuura, 1984; Matsuura and Yamane, 1990). Colonies are exceptionally small, although it is not certain that they will be found to be similarly small in Taiwan and other more southerly areas. The outstanding feature of this species is its specialized predation of independent-founding polistine wasps, which in Japan appear to be its sole prey. The closely related *V. tropica* is also a major predator of these wasps (Vecht, 1957; pers. obs.; R. Gadagkar, pers. comm.). However, in the Philippines *V. tropica* is also a frequent predator of honey bees (pers. obs.), and I have likewise seen *V. ducalis* hunting honey bees here. My brief observations suggest that it is in fact quite specialized to do so. Unlike *V. affinis,* which lands at the hive entrance and attacks worker bees on foot, in my experience *V. ducalis* hovers in front of the entrance and dashes at bees in flight. I suspect that it thus takes longer for *V. ducalis* to grapple with a bee but that it is much less vulnerable to attack by guard bees. Both of these hypotheses are open to testing, as is the question of whether the native honey bee, *Apis cerana,* and the introduced *A. mellifera* differ in their defensive responses to *V. ducalis.*

Nest: It seems well established *V. ducalis* nests in cavities, mostly commonly under ground (Matsuura, 1984). However, few nests have been examined in detail, so that there is still much to be learned about their structure.

Figure 18. Distribution of ***Vespa ducalis*** in Taiwan. Contour lines are at 100, 1000 and 2000 m.

Vespa mandarinia F. Smith

Vespa magnifica Smith var. *nobilis* Sonan, 1929:140-141 (key, distribution, description)

Vespa mandarinia Smith -- Matsuura and Yamane, 1990:234 (listed) -- Edwards, 1980:361 (listed) -- Archer, 1989:33 (listed, key)

Distribution: Northern India and Nepal to Indochina and southeastern China, north to Japan, Korea and Siberia. The known distribution of this species in Taiwan is rather spotty and is largely restricted to medium-elevation localities in the northern half of the island (Figure 19). I have not found it abundant anywhere. One possible reason is that its colonies

Figure 19. Distribution of ***Vespa mandarinia*** in Taiwan. Contour lines are at 100, 1000 and 2000 m. Dashed line delimits estimated range.

are heavily hunted in order to add its larvae and pupae into distilled liquor. This lucrative business is based on the popular idea that, as the largest social wasp in Taiwan and in fact in the world, it imbues the liquor and thence the drinker with its strength and supposed fierceness (J.T. Chao, pers. comm). Attractive as this nonsensical idea may be, it appears to lead to a marked decrease in hornet populations throughout populated parts of the island.

Biology: This species develops fairly large colonies in Japan, but this aspect has not been studied in Taiwan. Given the large activity in hunting this and other hornet species, it should be feasible for an entomologist to make contacts to examine newly collected colonies and record their social composition. *V. mandarinia* takes a broad range of prey, but with emphasis on other hymenoptera (Matsuura, 1984). In Japan its outstanding feature is coordinated attacks on honey bee hives, often resulting in destruction of the colony (Matsuura and Sakagami, 1973; Matsuura, 1984). I have not heard reports of similar behavior in Taiwan, and Chao et al. (1989) do not cite it as an exceptional pest of beekeeping here. The cause for this geographic difference, if real, is unknown, but it may have to do with the apparent role of *V. affinis* as the foremost bee-predatory hornet in Taiwan.

Nest: This species nests in cavities, almost exclusively under ground (Matsuura, 1984; Starr and Jacobson, 1990; J.T. Chao, pers. coom.). Its nests may comprise several thousand cells at maturity.

Vespa velutina Lepeletier

Vespa flavitarsus Sonan, 1929:142-143 [holotype worker examined]

Vespa velutina nigrithorax Buysson -- Vecht, 1957:37

Vespa velutina Lepeletier -- Matsuura and Yamane, 1990:235 (listed) -- Edwards, 1980:361 (listed) -- Archer, 1989:34 (listed, key)

Distribution: Northeastern Pakistan to central and southern China, south to Greater and Lesser Sunda Islands, Celebes. It is found throughout Taiwan at elevations up to about 2500 m, but it appears to be most common at about 1000-2000 m (Figure 20). This is consistent with Sonan's (1929) remark that *V. velutina* is common in mountain areas. Yamane (1974) found the closely related *V. auraria* (as *V. velutina auraria*) to be the commonest species in the Nepal Himalaya, nesting mostly at 1000-1500 m. Vecht (1957) reported that in Malaysia and Indonesia this is characteristically a mountain species, but that on some of the Lesser Sunda Islands where *V. affinis* and *V. analis* are absent it is also common in the lowlands. The implication of this is that *V. velutina* is competitively displaced from lowland areas by the other two species.

Biology: Despite its abundance in parts of its range, this species has received very little biological study. Yamane (1977) reported that it develops large colonies, as do *V. affinis* and *V. basalis*. Vecht (1957) and Matsuura (1973) regarded species as exceptionally aggressive, which may in part account for the little attention it has received.

Figure 20. Distribution of ***Vespa velutina*** in Taiwan. Contour lines are at 100, 1000, 2000 and 3000 m. Area above 3000 m is shaded.

Figure 21. Distribution of ***Vespa wilemani.*** Contour lines are at 1000, 2000 and 3000 m. Area above 3000 m is shaded. Dashed line delimits estimated range.

Nest: As presently recorded, the species nests almost exclusively in trees and shrubs (Vecht, 1957; Matsuura, 1973; Starr and Jacobson, 1990). Matsuura (1973) described an apparently immature nest from Puli, Nantou, and Vecht (1957: Plate 6) figured two nests from Java, but to date no mature nest has been structurally described. See also remarks on *V. basalis* above.

Vespa wilemani Meade-Waldo

Vespa wilemani Meade-Waldo -- Sonan, 1929:146-147 (key, distribution, description) -- Edwards, 1980:361 (listed) -- Matsuura and Yamane, 1990:236 (listed)

Vespa vivax wilemani Meade Waldo -- Archer, 1989:34 (listed, key)

It is still not certain that this form is specifically distinct from *V. vivax* F. Smith. If it is not, then the combined *V. vivax* has a disjunct distribution comprising northeastern Pakistan to northern Burma and Sichuan, and Taiwan. Without having compared Taiwan specimens with those from the Himalayas, I regard it as likely on geographic grounds that *V. wilemani* is a separate species.

Distribution: Taiwan endemic. There are still few data on the habitat of this species, but it appears to be uncommon below about 2000 m (Figure 21; J.T Chao, pers. comm.). M.C. Kuo (unpubl.) similarly states that it occurs at 1500-2500 m.

Biology and Nest: As far as I know, the published literature contains not one single biological fact about either *V. wilemani* or *V. vivax*. This

represents an outstanding opportunity for any researcher working where *V. wilemani* is abundant. The few nests observed have all been in trees and have resembled those of *V. affinis* (J.T. Chao, pers. comm.; M.C. Kuo, unpubl.). The detailed structural description of even one mature nest would be of significance.

Genus ***Vespula*** Thomson -- yellowjackets.

This genus of 20-22 known species (Archer, 1989; Matsuura and Yamane, 1990) is largely confined to temperate parts of Eurasia and North America. Three species are known in Taiwan, each representing one of the three subgenera into which the genus is commonly classified. In Taiwan yellowjackets are largely confined to higher-elevation areas, and none appears to be common in any part of the island.

Aside from references given above for the subfamily as a whole, the biology of hornets is reviewed by Greene (1991). They characteristically nest underground and may develop very large colonies. There is usually a clear size disparity between queens and workers, commonly more marked than that found in most hornets. Species vary in their diet, but none is known to be highly specialized. The workers tend to be small, about the size of the smaller *Polistes* species of Taiwan.

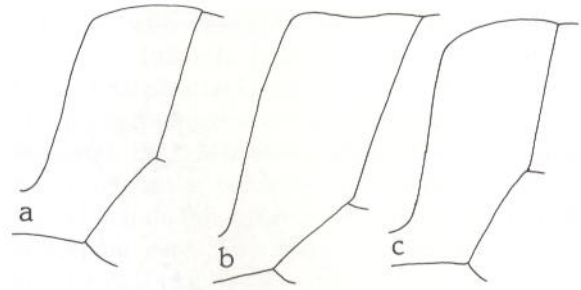

Figure 22. Gastral tergum 1 of ***Vespula*** workers in side view. a. ***V. schrenckii.*** b. ***V. arisana.*** c. ***V. flaviceps.***

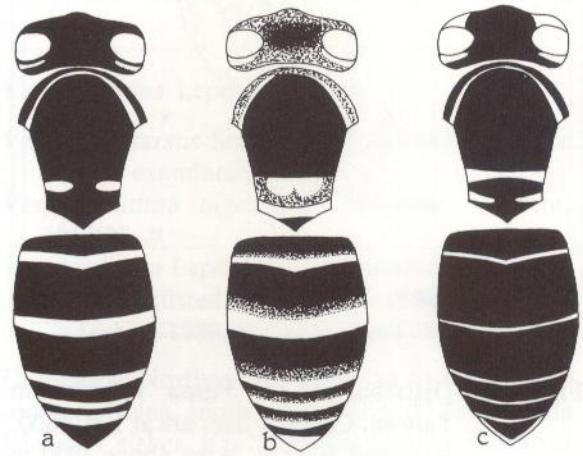

Figure 23. Color pattern (semi-diagrammatic) of color pattern in ***Vespula*** workers. a. ***V. schrenckii.*** b. ***V. arisana.*** c. ***V. flaviceps.***

KEY TO SPECIES OF YELLOWJACKETS *(VESPULA)*

1. First gastral tergum with long black hairs. Occipital carina ending well above base of mandibles (cf. Figure 39a). Tergum 1 as in Figure 22a. Color pattern as in Figure 23a····· ····· *schrenckii* (Radoszkowsky)
   - First gastral tergum with long pale hairs. Occipital carina approaching or reaching base of mandibles (cf. Figure 39b)·····2
2. Occipital carina reaching base of mandibles. Gastral tergum 1 longer, with a slight depression in side view (Figure 22b). Color pattern as in Figure 23b (queen unknown)···· *arisana* Sonan
   - Occipital carina ending a short distance above base of mandibles. Gastral tergum 1 shorter, straight or slightly convex in side view (Figure 22c). Color pattern as in Figure 23c····· ····· *flaviceps* (F. Smith)

Vespula arisana Sonan

Vespa arisana Sonan, 1929:147-148 [holotype worker examined]

Vespula minuta arisana Sonan -- Yamane et al. 1980:32 -- Edwards 1980:363 (listed)

Vespula orbata arisana (Sonan) -- Archer, 1982:268 -- Matsuura and Yamane, 1990:236 (listed)

Vespula arisana (Sonan) -- Yamane and Tano, 1985:421-424 (key)

Paravespula orbata arisana Sonan -- Archer, 1989:37 (listed, key)

Present indications are that this is the sister species of *V. orbata* (Buysson), which is found in the Himalayas and northern Burma. In that case,

Figure 24. Distribution of ***Vespula arisana*** in Taiwan. Stipled dots represent records from Yamane & Tano (1985). Contour lines are at 100, 1000 and 2000 m.

Figure 25. Known localities of ***Vespula flaviceps*** (dots) and ***V. schrenckii*** (triangles) in Taiwan. Stippled dots and triangles represent records from Sonan (1929) and Yamane & Tano (1985). Contour lines are at 100, 1000 and 2000 m. Dashed line delimits estimated range of ***V. flaviceps.***

the combined clade shows a disjunct Himalayan-Taiwan distribution similar to that of *Vespa vivax + wilemani.*

Distribution: Taiwan endemic. The few known localities suggest that it is distributed at low and (mostly) medium elevations in the northern half of the island (Figure 24).

Biology and Nest: No biological information of any kind is on record about this species. The careful collection of a few or even one colony could thus yield data of significance. It should also be noted that the queen is not yet described.

Vespula flaviceps (F. Smith)

Vespa flaviceps Smith, 1872:174 -- Matsuura and Yamane, 1990:236 (listed)

Vespa karenkona Sonan, 1929:148 [types examined: holotype worker, 2 paratype workers]

Vespa 4-maculata, Sonan 1929:148-149 [holotype queen examined]

Vespula flaviceps karenkona Sonan -- Yamane et al., 1980:16-18 -- Edwards, 1980:362 (listed)

Vespula flaviceps karenkona (Sonan) -- Yamane and Tano, 1985:421

Paravespula flaviceps (Smith) -- Archer, 1989:37 (listed)

Distribution: Northern India and Nepal to southeastern China, north to Japan, Korea and Siberia. In Taiwan the species is known from only a few localities, mostly at high elevation (Figure 25). Yamane and Tano (1985) characterize it as the

commonest yellowjacket in Taiwan, but it might be better to say that the others are even less common.

Biology: In Japan this species develops large colonies and nests, with up to 17,000 cells (Matsuura and Yamane, 1990). Yamane and Yamane (1975) reported some colonies in Taiwan persisting for two years. The species appears to be a foraging generalist, taking a broad range of both prey and scavenged material (Shida, 1963; Matsuura and Yamane, 1990).

Nest: V. flaviceps in Japan usually nests in underground cavities, although it has occasionally been found in more exposed situations (Matsuura and Yamane, 1990). Present indications are that it has a similar habit in Taiwan (Yamane and Yamane, 1975).

Vespula schrenckii (Radoszkowski)

Vespula schrenckii (Radoszkowski) -- Edwards, 1980:363 (listed) -- Yamane and Tano, 1985:424 -- Matsuura and Yamane, 1990:237 (listed)
Vespula rufa schrenchii (Radoszkowski) -- Archer, 1989:32 (listed, key)

Distribution: Eastern Siberia and Mongolia to Japan, Taiwan. Known in Taiwan from only a very few localities (Figure 25).

The apparent disjunct range of this species is noteworthy. Yamane (1987) did not include it or any closely related species among the vespines of the Ryukyus, and Yamane and Tano (1985) added it to the Taiwan fauna on the basis of a single worker from near Wushe, Nantou. The little that I have been able to add seems adequate to confirm that the species is in fact established in Taiwan.

Biology: Unlike *V. flaviceps,* this species appears to be strictly predatory (Matsuura and Yamane, 1990).

Nest: V. schrenckii nests under ground in Japan and presumably here as well. In Japan its colonies and nests are much smaller than those of *V. flaviceps,* usually below 1,000 cells at maturity (Matsuura and Yamane, 1990).

Subfamily ***Polistinae***

This very diverse, worldwide group comprises the bulk of social wasp species. A majority of the genera are endemic to the New World. Carpenter (1991) has recently analyzed phylogenetic relationships within the subfamily. Among his results is corroboration of the naturalness of the group of four Old World genera that includes *Parapholybia* and *Ropalidia.*

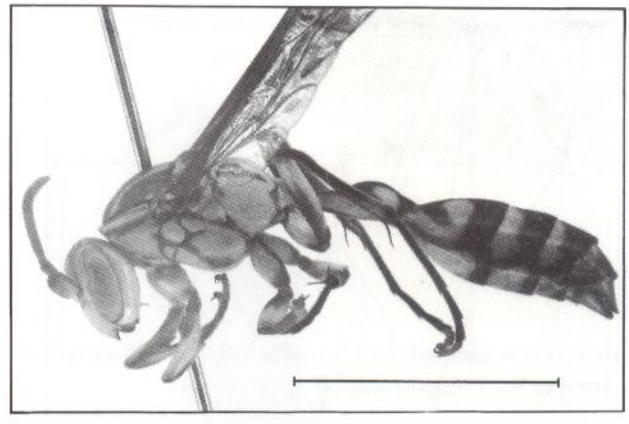

Figure 26. ***Parapolybia varia*** female in dorsolateral view, to show overall body form in the genus. Scale bar=5 mm.

The subfamily includes both independent-founding (i.e. colonies initiated by one or more queens without workers) and swarm-founding (i.e. with the participation of workers) groups. However, all Taiwan species appear to be independent founders. One general difficulty in studying the social organization of these wasps is that queens and workers are rarely readily distinguishable on the basis of external structure.

Genus ***Parapolybia*** Saussure

This genus of three known species ranges from Iran to New Guinea and as far north as Japan (Vecht, 1966). Two species are definitely known in Taiwan. These medium-sized, very slim wasps (Figure 26) are easily distinguishable from other genera found in Taiwan.

Biology: The species of *Parapolybia* appear relatively uniform in behavioral and ecological features (reviewed by Gadagkar, 1991). Recent studies include those of Kojima (1983a), Sekijima et al. (1980), Sugiura et al. (1983a-1984), and Yamane and Maeta (1985) on *P. indica,* Yamane (1984) on *P. takasagona* (as *P. nodosa*), and Yamane (1976, 1984, 1985) on *P. varia.*

In *P. varia* in southern Taiwan, colony founding is usually by a group of several queens. The one

single-foundress colony that I have seen failed at an early stage. Colonies may come to comprise several hundred individuals.

Strassmann and Hughes (1986) have recently emphasized that the relative timing of production of males and new queens in independent-founding social wasps is a question of theoretical significance. Until now, little attention has been paid in field studies to this factor, so that data are sparse. Results from two colonies of *Parapolybia varia* and one of *P. takasagona* support the hypothesis that males are produced ahead of new queens, at least in Taiwan. The presence of males in each colony showed that it was in the reproductive stage, and the marked paucity of brood (especially eggs and small larvae) showed that the stage was well advanced. In social wasps the compound eyes are black at emergence, lightening over the next few days to the species-characteristic color. I divided specimens from each colony into a group of younger and a group of older individuals, based on a convenient, arbitrary designating as immature those with black to dark gray and as mature those with light gray to yellow eyes. Table 3 shows the sex ratios of immature and mature adults. Each colony showed a significant female bias among the immatures (Chi-square test, $p<0.05$). From this we can conclude that the reproductive stage began with the production of males, and the immature females present at this time were queens. It should be noted that, because it is difficult to distinguish new queens from workers, a contrary result would not necessarily have been conclusive. If the immature adults had been mostly males it could mean either that a) the reproductive had only just begun, and new queen production had not yet started, or b) production of new queens came ahead of male production and was now well advanced. However, we can safely assume that workers are not produced after the reproductive stage is well advanced, so that in these three colonies the immature females were queens.

Mating behavior has not yet been studied in this genus. At Wushe, Nantou in the late afternoon I saw a great many *P. varia* flying about within a few meters of two reproductive-stage colonies. They were inspecting leaves of broadleaf plants and pouncing on other wasps. All of the 26 individuals that I netted were males. This behavior closely resembles that of *Ropalidia flavobrunnea* males that I have seen in the Philippines. My interpretation in each case is that the males were hunting for mates and that they may have been inspecting leaves for scent marks left by new queens.

Table 3. Sex ratio of immature and mature adults in three *Parapolybia* nest series from the vicinity of Wushe Nantou County. The sample from nest series 1500 comprises 200 randomly chosen specimens, while in the other two the sample is the entire colony.

Nest series no. (species)	Immature		Mature		Total
	females	males	females	males	
1500 (*P. varia*)	32	0	120	48	200
1502 (*P. varia*)	47	0	94	31	172
1506 (*P. takasagona*)	39	1	42	27	109

Inasmuch as they are most likely sister species, the very broad sympatry of *P. takasagona* and *P. varia* (see *Distribution*) is noteworthy. The large range of the first appears to be entirely contained within that of the second or almost so. In contrast, much of *P. indica's* range lies outside of that of *P. varia*. It is puzzling how speciation between the two putative sister species might have taken place. Furthermore, ecological separation between the two species is far from evident. As far as is known, *P. takasagona* is the less common of the two throughout the area of overlap, yet it seems to nest in much the same habitats and sites. Both species in my experience are mainly found in secondary forest and advanced second-growth in Taiwan, rarely in primary forest or large open areas. There are noteworthy differences in nest structure (see below), but it is hard to see how these could be a causal factor in niche differentiation. I suggest the ecological separation of these species as a very worthwhile problem which could be pursued in many places in Taiwan where the two occur in reasonable abundance.

Species identification: *P. takasagona* and *P. varia* are remarkably similar. *P. takasagona* is on average larger and darker, but neither of these differences

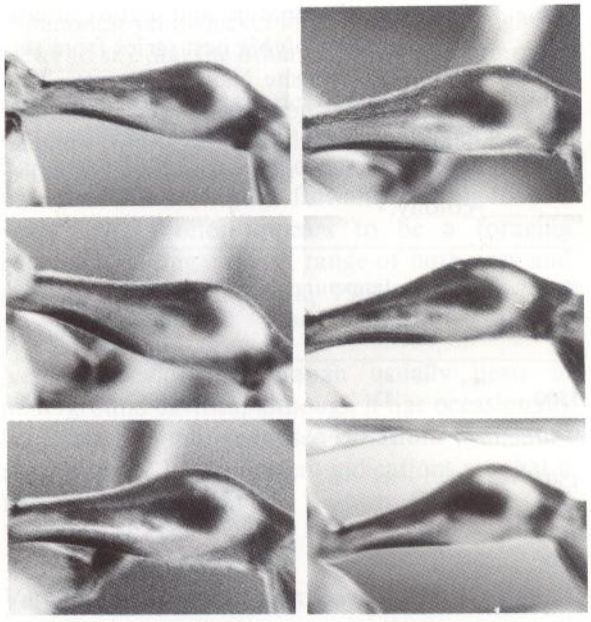

Figure 27. First gastral segment in side view, from selected females of a ***Parapolybia varia*** nest series, to show variation in the dorsal profile.

is nearly consistent enough to serve as a key character. Vecht (1966) gave as the diagnostic character the dorsal curvature of the first gastral tergum in the female (the male was unknown to him), and in his illustrations this is indeed a usable, although subtle, character. In my experience, however, this feature also much too variable (Figure 27). I have been unable to use it for consistent separation of the species, let alone as a key character for others. Das and Gupta (1989) cited differences in the depth and width of the propodeal groove in these species in India, but I have also not found this useful. Tano (1976) relied mainly on color differences in the female clypeus, and this is the only character that I have been able to use with confidence. In *P. varia* the yellow clypeus almost always has a narrow, contrastingly dark median band, while in *P. takasagona* a much broader yet lighter and less distinct patch occupies the upper central part of the clypeus (Figure 28). Virtually all fresh or well preserved specimens from Taiwan unequivocally show one state or the other, and only one state is found within a nest series. On the other hand, I have found no character that will separate

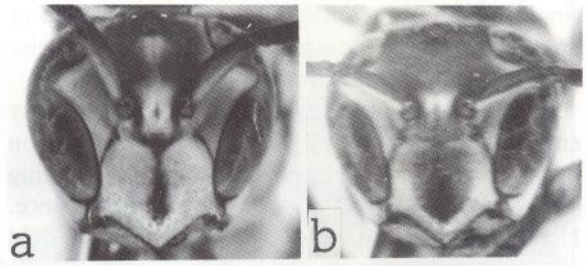

Figure 28. Female face. a. ***Parapolybia varia.*** b. ***P. takasagona.***

males without dissection of genitalia. Except where nest-series correlation was possible, I have identified males probabilistically on the basis of color.

Parapolybia varia (Fabricius)

Parapolybia varia (Fabricius) -- Sonan, 1944:343-44 (description, key) -- Vecht, 1966:30-39 (description, key) -- Tano, 1976 (key, distribution) -- Das and Gupta 1989:180-183 (description, key)

Distribution: Northeastern India to southeastern China, north to Japan and Korea, south to the Greater and Lesser Sunda Islands, Philippines, Celebes, New Guinea. In Taiwan this species appears to occur throughout the island at low and medium elevations, and it is one of the few social wasps known from Hsiau Liouchiou Island (Figure 29). However, there appears to be a great deal of variation in local abundance within this range. It appears to be the commonest social wasp in the low-elevation Kenting National Park, Pintung, and among the commonest around Wushe, Nantou at about 1000 m, but at most localities it seems to be much less in evidence.

Nest: Nests of this species have been figured by Iwata (1969b) and Tano (1976) and structurally analyzed by Yamane (1984). In brief, they are usually found nesting in scrubby vegetation, usually within about 1-3 m of the ground. The nest begins as an elongate, buff-colored comb, hanging from a single petiole such that the cells are only slightly inclined from the horizontal. As the colony grows the comb may develop distinct lobes from near the base, and additional combs may be built approximately in parallel with the first.

P. varia nests closely resemble dead, hanging

leaves or clusters leaves, which may serve to camouflage the colony from visually-hunting predators. I have on several occasions nearly bumped into colonies that I failed to notice at a distance. It is possibly inconsistent with this crypsis hypothesis that most cells are utilized just once (Yamane, 1984), so that nests become larger than they would with cell reutilization.

Parapolybia takasagona Sonan

Parapolybia takasagona Sonan, 1944:344-45 (key) [types examined: holotype ♀, 6 paratype ♀♀, 5 paratype 12 ♂♂] -- Kuo and Yeh, 1987:82 (listed, adults and nest figured)

Parapolybia nodosa Vecht, 1966:39-40 -- Tano 1976:8, 10 (key, distribution) -- Yamane 1984 (biology) -- Das and Gupta, 1989:183-184 (description, key) -- NEW SYNONYMY

I have examined the type series of this species in TARI. The holotype female (Tamuru [Rutu], 30.VII.1923, Col. J. Sonan) is discolored, but in fair condition and with the color pattern discernible. Her clypeus shows no trace of a central dark stripe, but the main central part of the clypeus is a somewhat darker orange than the yellow sides. I interpret this as the discolored remnant of a brown patch, consistent with the diagnostic character given above. The gastral petiole is relatively humped, as described by Vecht (1966) for *P. nodosa*. Five of the paratype females fit my diagnosis of *P. takasagona*, some obviously so. However, the profile of the gastral petiole is variable, so that not all specimens match *P. nodosa* in this character. The other paratype female is equivocal. Her clypeus is all yellow, so that there is neither a stripe nor a patch, but the overall color pattern is more like that of *P. varia* than of most *P. takasagona* females I have seen. The gastral petiole, is not humped in profile. The paratype males are much discolored. It is not evident to me how Sonan matched them with the type females, except that they were collected at the same localities.

Sonan's (1944) and Vecht's (1966) descriptions left room for doubt that *P. takasagona* is in fact specifically distinct from *P. varia*. However, since that time the nest (see below) and male of *P. takasagona* have become known. I have found no external features to consistently distinguish males of the two species, and their color differences are, if anything, less reliable than those of the females.

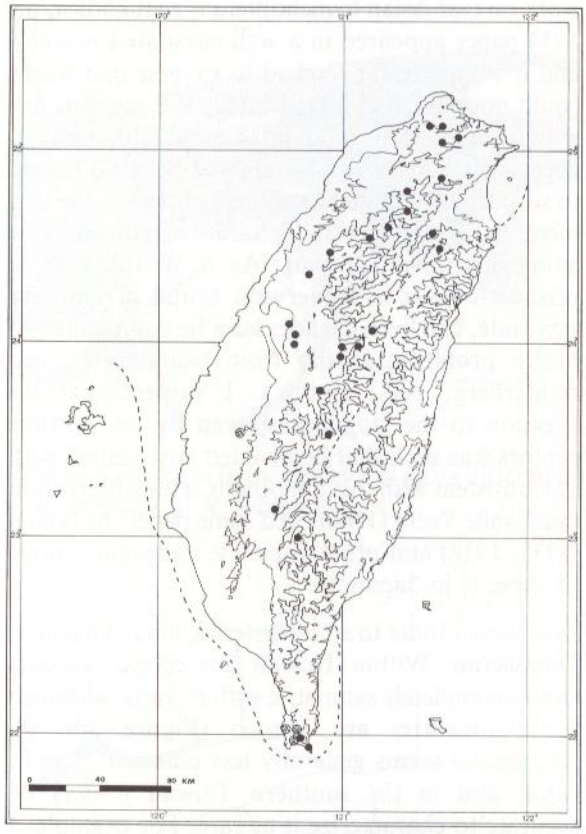

Figure 29. Distribution of ***Parapolybia varia*** in Taiwan. Stippled dots represent records from Vecht (1966) and Yamane (1984). Contour lines are at 100, 1000 and 2000 m. Dashed line delimits estimated range.

Dissection of six *P. varia* (nest series no. 1500 and 1502) and five *P. takasagona* (nest series no. 1506) males, all from near Wushe, Nantou, show slight but consistent differences in the genitalia. The parameres (including spines) are about 11% shorter in *P. takasagona* and have a flattening along part of the posterior-dorsal curve toward the outside. In addition, the apical bulge of the aedeagus in top view is disklike in *P. varia*, while that of in *P. takasagona* is somewhat lanceolate.

Vecht's (1966) failure to recognize *P. takasagona* as a senior synonym of *P. nodosa* calls for some comment. That he did not cite Sonan's (1944) paper at all seems highly peculiar in so thorough a worker as J. van der Vecht. Ordinary carelessness was certainly not the cause, yet it seems very unlikely to be due to simple ignorance. Sonan's

work on east Asian hymenoptera is well known, his 1944 paper appeared in a well circulated journal, and it would be far-fetched to suggest that Vecht could not have had it translated. We are thus left with the hypothesis of an intentional (although not necessarily conscious) oversight. I have no reason to suspect any personal animosity between the two men, but Vecht certainly harbored considerable animosity toward Japan. As a World War II prisoner-of-war he underwent brutal involuntary servitude, and even decades later he complained of health problems arising from beatings (C. van Achterberg, pers. comm.). I suspect that his aversion to the language spoken by his wartime captors was such that he avoided any contact with it. Consistent with this hypothesis is the observation that, while Vecht (1966) cited some papers by Sonan (1935, 1938) and other Japanese colleagues, none of these is in Japanese.

Distribution: India to southeastern China, Thailand, Tenasserim. Within Taiwan this species appears almost completely sympatric with *P. varia,* although fewer localities are known (Figure 30). *P. takasagona* seems generally less common than *P. varia,* and in the southern Taiwan it may be accurate to characterize it as rare. For example, I have never seen it in the Kenting National Park, Pintung, where *P. varia* is extremely common. I have double-checked the one record of this species on the Hengchun Peninsula, which is based on a series of nine *Parapolybia* females and three males collected by Sonan in 1926 and 1938 at Kuraru (=Gueichihchiueh). The females separate unequivocally into two *P. varia* and seven *P. takasagona,* and the males are very probably *P. takasagona.*

Nest: Yamane (1984) described one mature nest of this species, and I have seen one other, both from northern Nantou County. A third nest is figured by Kuo and Yeh (1987: Figure 42), although obscurely. All three differ from mature-form *P. varia* nests in consisting of a single, compact comb without side-lobes. Each is also a great deal smaller than many *P. varia* nests.

Figure 30. Distribution of ***Parapolybia takasagona*** in Taiwan. Stippled dots represent records from Vecht (1966). Contour lines are at 100, 1000 and 2000 m.

Genus ***Ropalidia*** Guérin

This genus of about 136 known species (Richards, 1978) is widespread in Africa, Australia and south Asia. These are usually small, moderately robust wasps, often with contrasting red and yellow marks. The genus manifests a greater diversity in social organization and nest structure than any other in social wasps, although the two Taiwan species are both independent founders with exposed, single-comb nests. The biology of the independent-founding *Ropalidia* is reviewed by Gadagkar (1991).

Species distribution ranges in this genus are taken from Vecht (1962) and Das & Gupta (1989).

Species identification: The two species found in Taiwan are readily distinguished by the following combinations of characters:

1. *R. fasciata* (Figure 31a) -- very small, medium-stout wasps, forewing length (not including tegula) 7-8 mm; body red with abundant yellow marks, including scutellum, metanotum,

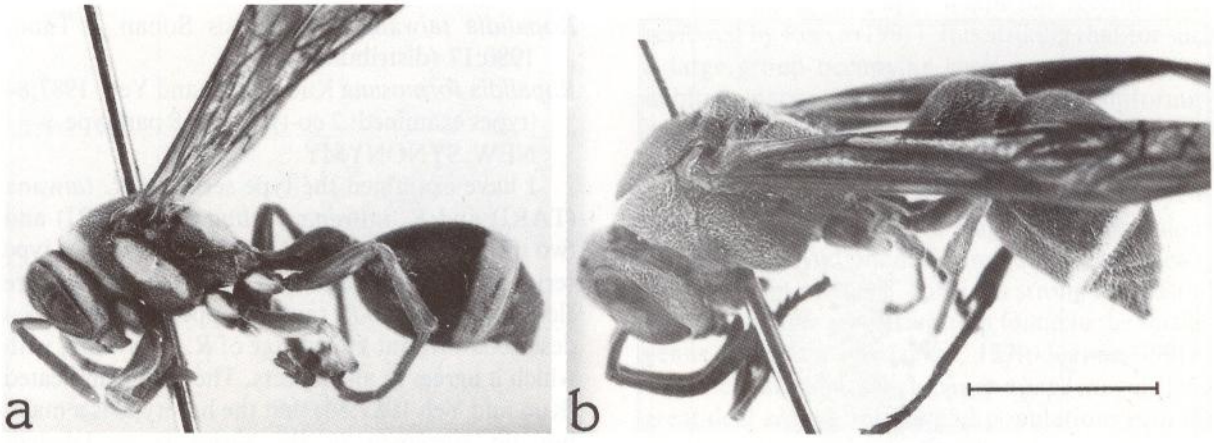

Figure 31. ***Ropalidia*** females in dorsolateral view, to show overall body form in the genus and gross differences between Taiwan species. Scale bar = 2 mm. a. ***R. fasciata*** b. ***R. taiwana.***

posterior face of propodeum, and most or all of clypeus. Tip of male antenna as in Figure 32a.

2. *R. taiwana* (Figure 31b) -- small, stout wasps, forewing length 9-11 mm; body red with only slight yellow marks but abundant dark brown or black marks, including mesoscutum and propodeum; scutellum and clypeus mainly red. Tip of male antenna as in Figure 32b.

Ropalidia fasciata (Fabricius)

Icaria variegata Smith -- Sonan, 1927:122
Ropalidia veriegata Smith -- Sonan, 1935:199-200 (description, key) -- Kuo and Yeh, 1987:82
Ropalidia picta (Saussure) -- Vecht, 1941:145-149 (description, key)
Ropalidia fasciata (Fabricius) -- Vecht, 1962:23-27 -- Tano, 1980:16 (distribution)

Distribution: India to eastern China, Ryukyus, south to the Greater and Lesser Sunda Islands, Palawan (Vecht, 1941, 1962). In Taiwan it is probably found throughout the island at low and medium elevation (or it may be absent along much of the east coast), and it is one of the few social wasps recorded from Hsiau Liouchiou Island (Figure 33).

Of interest is the apparent vicariance between *R. fasciata* and its sister species, *R. gregaria* (Saussure), which is found from the Philippines Proper (i.e. excluding Palawan) and Celebes to northern Australia.

Biology: The nesting biology of this species has received a great deal of attention on Okinawa (Itô, 1983a-1986; Itô et al., 1985; Itô and Iwahashi, 1987; Itô and Yamane, 1985; Iwata, 1969b; Kojima, 1983b-1989; Suzuki and Murai, 1980) and Java (Turillazzi and Marucelli-Turillazzi, 1985). Its sister species, *R. gregaria,* has so far been much less studied (Kojima, 1982). In Okinawa most *R. fasciata* colonies are founded by single queens, and my casual observations suggest that this is also true for both species in the Philippines. Exact data on colony size are unavailable for Taiwan, but mature colonies of more than 1000 adults appear not to be uncommon.

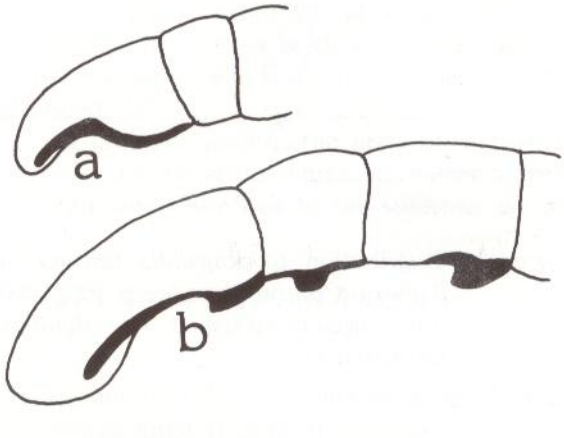

Figure 32. Tip of the male antenna in side view. a. ***Ropalidia fasciata*** b. ***R. taiwana.***

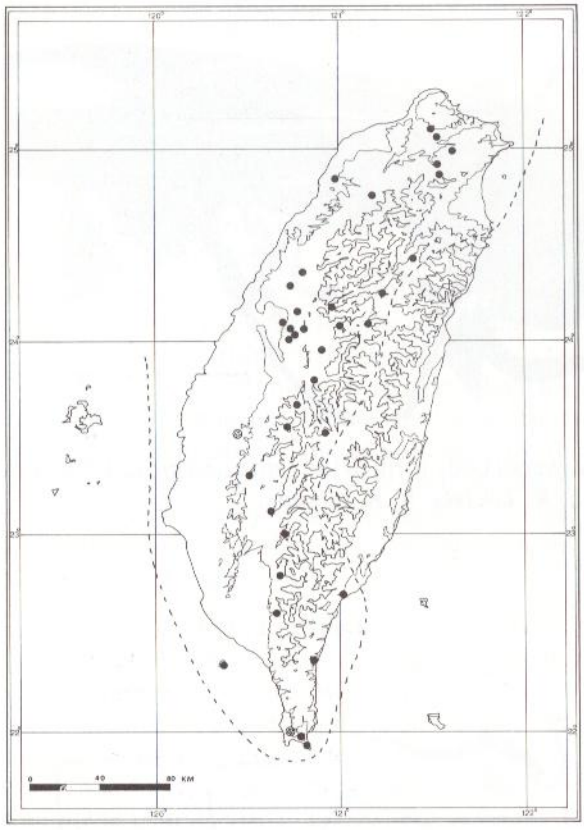

Figure 33. Distribution of ***Ropalidia fasciata*** in Taiwan. Contour lines are at 100, 1000 and 2000 m. Dashed line delimits estimated range.

Nest: On Palawan I have found considerable variation in nest structure in this species, including nests of several combs, but all nests I have seen from Taiwan consisted of a single compact comb, hanging nearly perpendicular from a single petiole usually attached to the underside of a broad leaf. Kuo and Yeh (1927: Figure 43) also show a nest of this form.

Ropalidia taiwana Sonan

Ropalidia taiwana, Sonan 1935:201-202 (key) [types examined: holotype ♀ , 5 paratype ♀♀ , 1 paratype ♂] -- Vecht, 1941:143-145 (description, key) -- Tano, 1980:17 (distribution)

Ropalidia taiwana var. *koshunensis* Sonan, 1935:202 (key) [types examined: holotype ♀ , 9 paratype ♀♀ , 6 paratype ♂♂]

Ropalidia taiwana koshunensis Sonan -- Tano, 1980:17 (distribution)

Rapalidia formosana Kuo *in* Kuo and Yeh, 1987:84 [types examined: 2 co-type ♂♂ , 8 paratype ♀♀] NEW SYNONYMY

I have examined the type series of *R. taiwana* (TARI) and *R. taiwana koshunensis* (TARI) and two of five males and eight of 12 females of the type series of *R. formosana* (NCIA, NMNS). All are clearly conspecific. *R. taiwana* appears to have been described without knowledge of *R. t. taiwana,* with which it agrees in all respects. The author indicated (Kuo and Yeh 1987:84) that the holotype is a male, but no specimen in the series is so labeled. Accordingly, I have labeled as co-types the two males that I have seen (NCIA).

R. taiwana koshunensis was described from the Hengchung Peninsula on the basis of minor color differences. The description includes two apparent lapses. First, the type series is labeled *"Ropalidia taiwana formosensis".* It seems likely that Sonan intended formosensis as the subspecific epithet, as the type series of *R. taiwana* includes a female from Koshun (i.e. Hengchun), so that *Koshunensis* makes little sense as an epithet for the alternative form. Second, he stated that the non-allotype paratypes comprised 11 females and three males, when in fact there are nine females and five males. However, mention of these details should not suggest that a serious problem is at hand. The color differences separating the two forms are quite insignificant, and their apparent range overlap shows that these are probably not true geographic variants.

Distribution: Northern Burma, southern China, Taiwan (Vecht, 1941, 1962). This species is known from so few localities and does not appear to be common anywhere, so that its range can be only roughly indicated. Within Taiwan its range resembles that of *R. fasciata* (Figure 34).

Biology: Iwata (1969a) recorded observations on the composition of six colonies. Colony founding appears to be haplometrotic.

Nest: R. taiwana builds a distinctive nest, consisting of a single, hanging row of cells, each descended about 1/3 of its length from the previous cell (Sonan, 1935: Figure 9; Iwata, 1969a: Figure 1-6, 1969b, 1976: Figure 39-1; Kuo and Yeh, 1987: Figure 44, 45; pers. obs.). This structure presumably serves to disguise the nest as a twig or section of

Figure 34. Known localities of ***Ropalidia taiwana*** in Taiwan. Contour lines are at 100, 1000 and 2000 m.

a hanging vine. The largest nest seen by Iwata (1969a) comprised 21 cells. The sequence of cell use is of interest in such a linear arrangement; Iwata's data are consistent with the idea that use generally proceeds along with construction, but with significant variation.

Genus ***Polistes*** Latreille -- paper wasps

This genus has by far the broadest distribution among social wasps, encompassing virtually all of the habitable world. It has not been revised since the 18th century, so that the number of known species can be only roughly estimated at 200. Richards's (1973) subgeneric classification remains the standard, although the monophyly of some of his subgenera is in doubt (J.M. Carpenter and Sô. Yamane, pers. comms.). I recognize 13 Taiwan species in five subgenera.

The biology of paper wasps has recently been reviewed by Reeve (1991). It is striking that for such a large group occupying such a great variety of habitats, paper wasps show substantial uniformity in their social organization. Except as a secondary tactic, none is known to be a swarm founder. As far as is known, all have a definite colony cycle, with a single reproductive stage preceding colony breakdown. And in none are queens physically distinct from workers. This is in strong contrast to the considerable social variation found in the smaller genus *Ropalidia* (Gadagkar, 1991; Jeanne, 1991).

One feature in which paper wasps may differ a great deal among species and populations is in the number of queens cooperating to found new colonies. As a rough rule, in cool-temperate populations (almost invariably in Japanese species) founding is by a single queen, a habit known as "haplometrosis", while in the tropics group founding -- known as "pleometrosis" -- is much more prevalent. There are also suggestions of substantial differences in the social behavior of males (e.g. Starr, 1990), a question that remains little explored.

As far as is known, the nests of all Taiwan species follow the genus-characteristic plan: a single, exposed comb attached to the substrate by one petiole.

KEY TO SPECIES OF PARER WASPS *(POLISTES)*

1. Pronotum with a small pit (the fovea) above its ventral angle (Figure 3) 2
- Pronotum without a fovea. Dorsal mesepisternal groove and epicnemial carina (see Figure 3) absent. Small to medium-sized species ..... (subgenus *Polistella*) 6
2. Dorsal mesepisternal groove and epicnemial carina both present (Figure 3). Male: Clypeus distinctly flattened. Medium-sized species with abundant yellow markings, including clypeus 3
- Lacking either a dorsal mesepisternal groove or an epicnemial carina. Large to very large, robust species. Body uniformly red-brown without yellow markings 5
3. Mesepisternum rounded at its base, as in Figure 35a. Propodeal striae at most moderately strong. Male clypeus with a pair of low lateral ridges that converge below (Figure 36). Male gastral

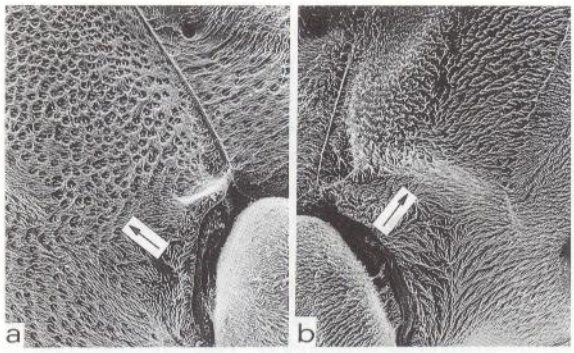

Figure 35. Base of mesepisternum in ventrolateral view. a. ***Polistes japonicus*** b. ***P. rothneyi.***

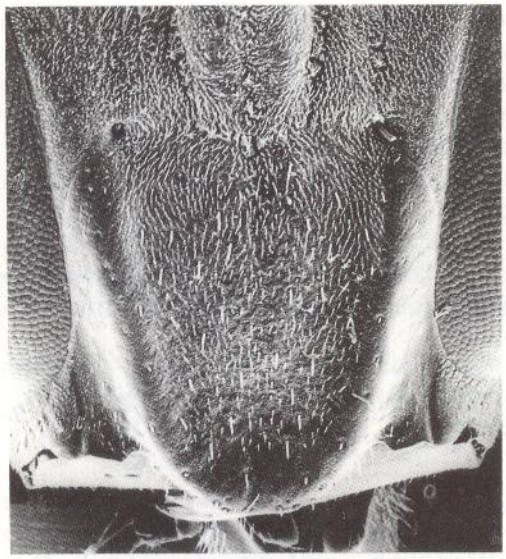

Figure 36. ***Polistes chinensis*** male clypeus.

sternum 7 without terminal apophyses (cf. Figure 39)·····*chinensis* Fabricius

- Mesepisternum distinctly angled at its base (Figure 35b). Propodeal striae strong. Male clypeus entirely flat or slightly concave, without lateral ridges. Male gastral sternum 7 with distinct terminal apophyses (Figure 39)·····4

4. Yellow genal band continuous with yellow area behind ocelli (Figure 37a). Female occipital carina becoming indistinct well above mandibles (Figure 38a). Male clypeus clearly separated from eye. Male terminal sternal apophyses shorter and broader (Figure 39a). Male terminal

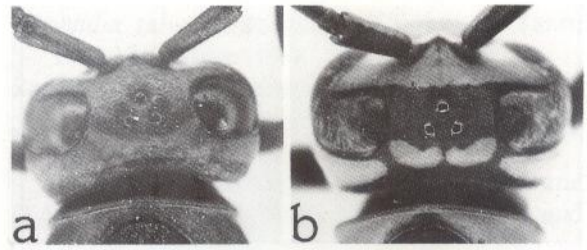

Figure 37. Head in top view. a. ***Polistes jadwigae*** b. ***P. rothneyi.***

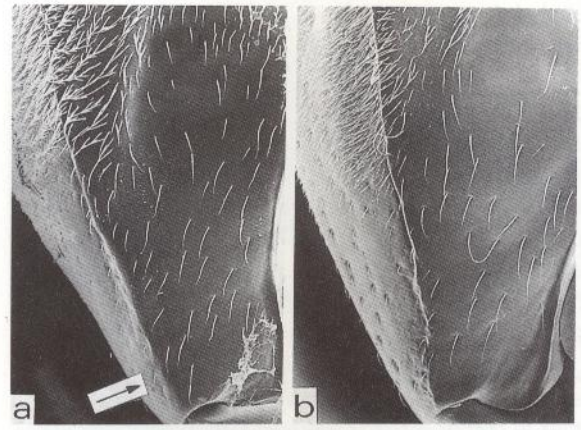

Figure 38. Female occipital carina. a. ***Polistes jadwigae*** b. ***P. rothneyi.***

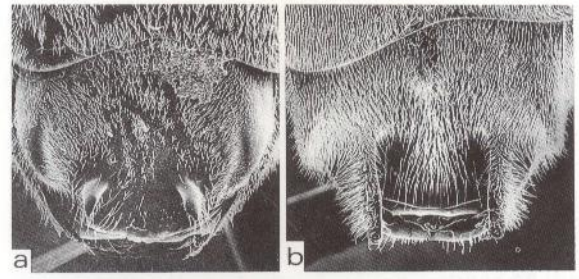

Figure 39. Male gastral sternum 7 to show apophyses. a. ***Polistes jadwigae*** b. ***Polistes rothneyi.***

antennal segment nearly conical (Figure 40a, b) ·····*jadwigae* DallaTorre

- Yellow genal band separated from pair of yellow patches behind ocelli (Figure 37b). Female

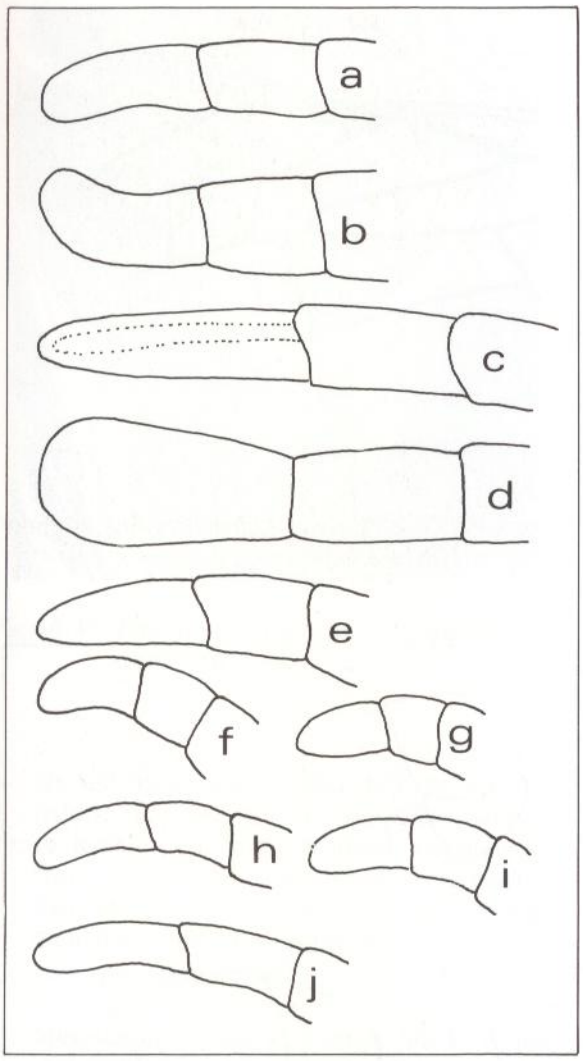

Figure 40. Tip of male antenna (in side view except where indicated). a. ***Polistes jadwigae*** b. ***P. jadwigae*** (top view). c. ***P. rothneyi*** d. ***P. rothneyi*** (top view). e. ***P. japonicus*** f. ***P. stigma*** g. ***P. stigma*** h. ***P. takasagonus*** i. ***P. eboshinus*** j. ***P. huisunensis***.

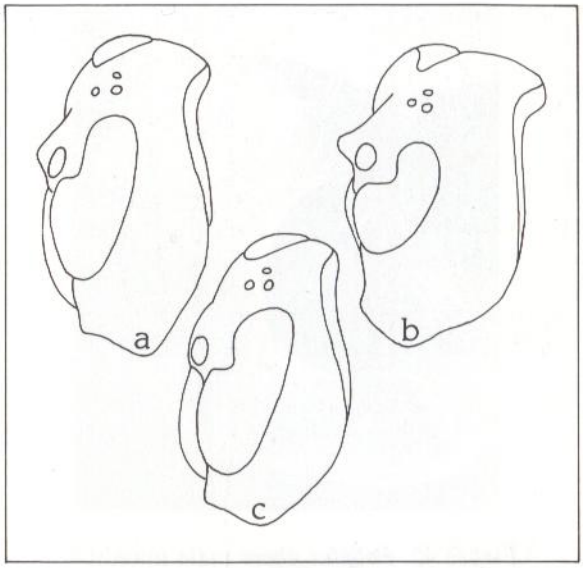

Figure 41. Head in dorsolateral view. a. ***Polistes gigas*** female. b. ***P. gigas*** male. c. ***P. sulcatus*** female.

occipital carina strong to base of mandibles (Figure 38b). Male clypeus in contact with eye. Male terminal sternal apophyses longer and narrower (Figure 39b). Male terminal antennal segment somewhat spatulate (Figure 40c, d)·· ·····*rothneyi* Cameron

5. Dorsal mesepisternal groove absent, epicnemial carina present. Genae extraordinarily broad (Figure 41a, b). Male mandibles of a uniquely bizarre form (Figure 42). Very large species·· ·····*gigas* Kirby
- Dorsal mesepisternal groove present, epicnemial carina absent. Genae not extraordinarily broad (Figure 41c). Male mandibles not as in Figure 42. Large species ·····*sulcatus* F. Smith
6. Gastral sternum 2 in side view with a low, even curve (Figure 43a, b)·····7
- Gastral sternum 2 with 2 distinct basal bulge (Figure 43c-h)·····9
7. Small wasps. Forewing with a distinct, diffuse dark spot near the tip (Figure 44). Mesoscutum black, often with a central red area. Propodeal furrow very narrow and shallow, hardly more than a trace, propodeal striae extremely weak. Gastral terga 1-3 with contrasting yellow apical bands·····*stigma* (Fabricius)
- Medium-sized wasps, not fitting the above description·····8
8. Pronotum distinctly striate, dorsal and lateral surfaces separated by a distinct angle that runs back toward the tegula (Figure 45). Body almost entirely dark reddish·····*strigosus* Bequaert
- Pronotum densely punctate, without distinct striae, the dorsal and lateral surfaces connected by a smooth curve. Body abundantly yellow-marked, including a prominent pair of stripes

Figure 42. ***Polistes gigas*** male mandible.

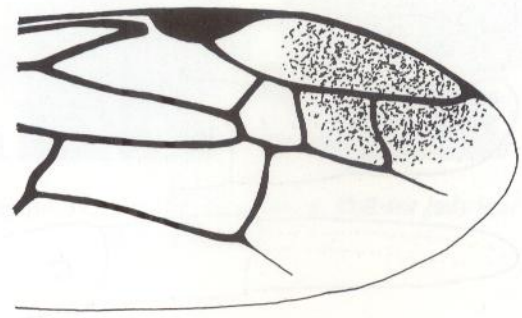

Figure 44. Tip of ***Polistes stigma*** forewing, to show diffuse dark spot.

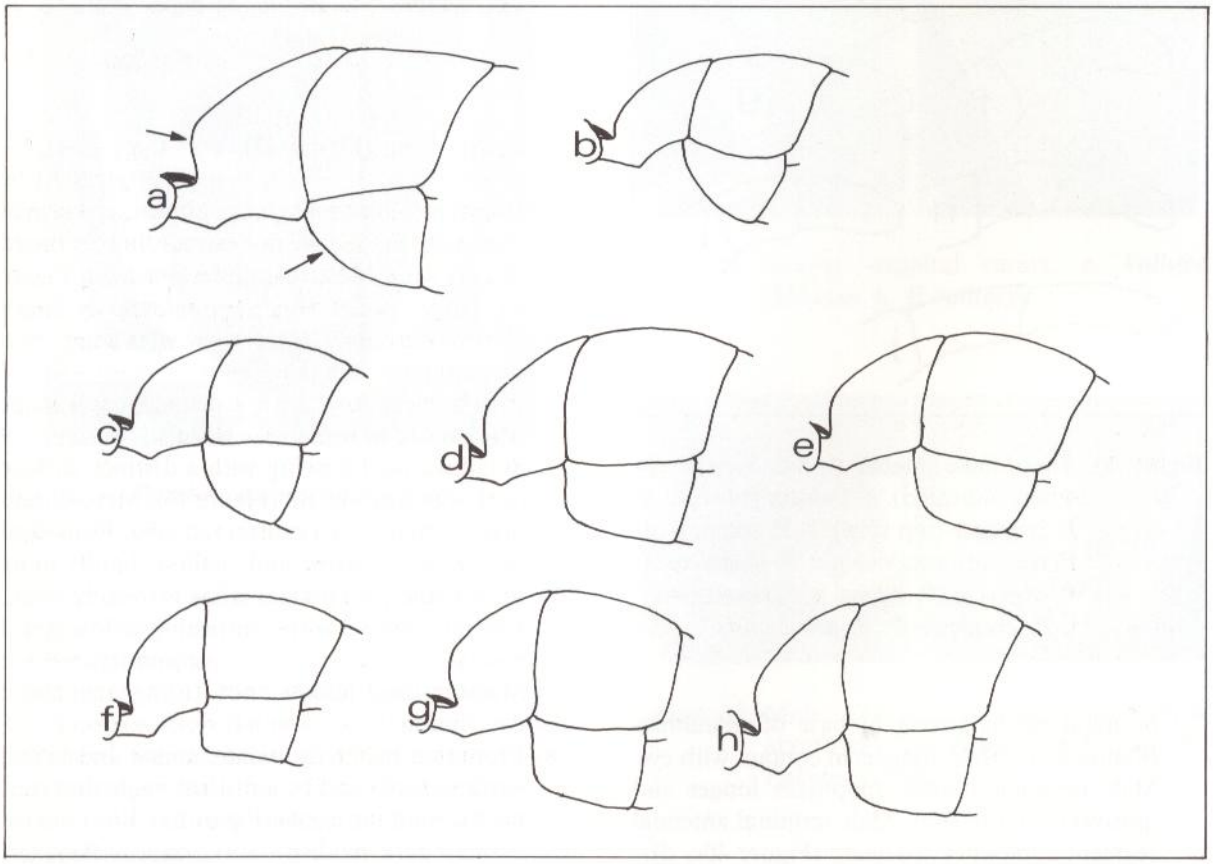

Figure 43. Base of gaster in side view, to show rise in tergum 1 behind muscle insertion and basal bulge in sternum 2. a. ***Polistes japonicus*** b. ***P. stigma*** c. ***P. shirakii*** d. ***P. takasagonus*** e. ***P. eboshinus*** f. ***P.*** sp. A g. ***P. huisunensis*** h. ***P.*** sp. B.

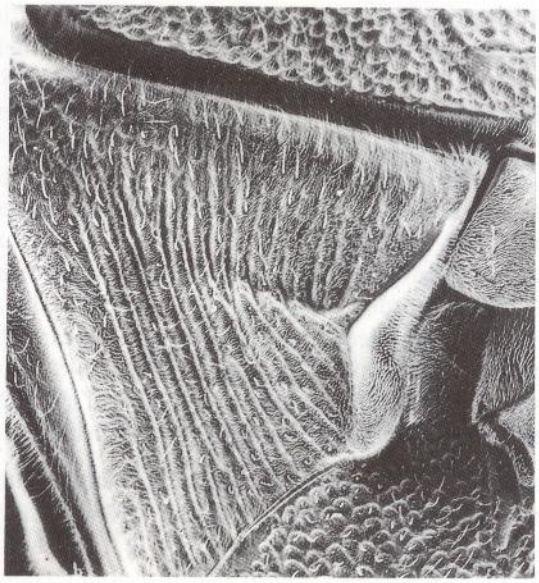

Figure 45. ***Polistes strigosus*** pronotum in dorsolateral view.

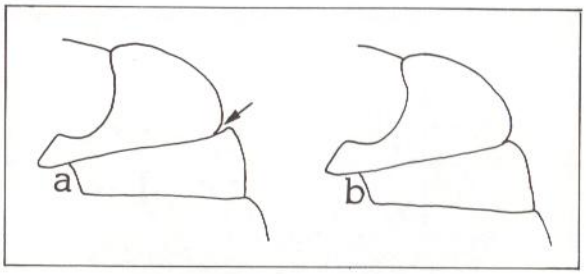

Figure 46. Scutellum (s) and metanotum (mn) in side view. a. ***Polistes huisunensis*** b. ***P.*** sp. B.

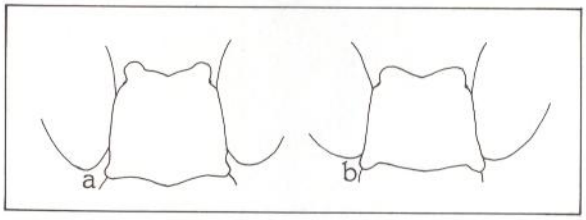

Figure 47. Male clypeus. a. ***Polistes huisunensis*** b. ***P.*** sp. B.

on the mesoscutum, with little or no dark reddish marking ..... *japonicus* Saussure

9. In female (and often in male), mesoscutum, frons and vertex substantially red-marked. Propodeum strongly yellow-marked. Female mandibles yellow. Last segment of male antenna very short (Figure 40f) ..... *shirakii* Sonan
- Mesoscutum, frons and vertex black. Female mandibles orange to reddish. Last segment of male antenna longer (Figure 40 h-j) 10

10. Propodeum with a pair of substantial yellow stripes. Pronotum behind keel red with narrow yellow borders in front and behind. Female clypeus yellow to yellow-orange, with a narrow dark band at each side. Tip of male antenna as in Figure 40h ..... *takasagonus* Sonan
- Propodeum (except valves) all black or with at most a pair of very short, slight yellow stripes. Female clypeus red. Pronotum behind keel not yellow-marked 11

11. Small, medium-robust wasps, forewing length (not including tegula) 8-10 mm. Female genae mainly red only in lower 1/3 to 1/2, without a continuous red band. Bulge in gastral sternum 2 rounded (Figure 45e, f) Last segment of male antenna shorter (Figure 40i) 12
- Medium-sized, robust wasps, forewing length 10-14 mm. Female genae mainly red, with a continuous red band next to the eye. Bulge in gastral sternum 2 angular (Figure 45g, h). Last segment of male antenna very long (Figure 40j) 13

12. Gastral tergum 1 longer relative to height, bulge in sternum 2 less acute (Figure 45e). Gastral terga 2-6 finely, indistinctly punctured ..... *eboshinus* Sonan
- Gastral tergum 1 shorter relative to height, bulge in sternum 2 more acute (Figure 45f). Gastral terga 2-6 distinctly punctured ..... species A

13. Metanotum at its front edge projecting up, not in a continuous line with scutellum (Figure 46a). Female clypeus with the upper third to half covered in a layer of appressed pubescence, the punctures in this area smaller than in the lower half. Male clypeus longer (Figure 47a) ..... *huisunensis* Kuo
- Metanotum lying in a continuous line with scutellum (Figure 46b). Female clypeus without a layer of appressed pubescence on its upper part, punctures about equally coarse below and

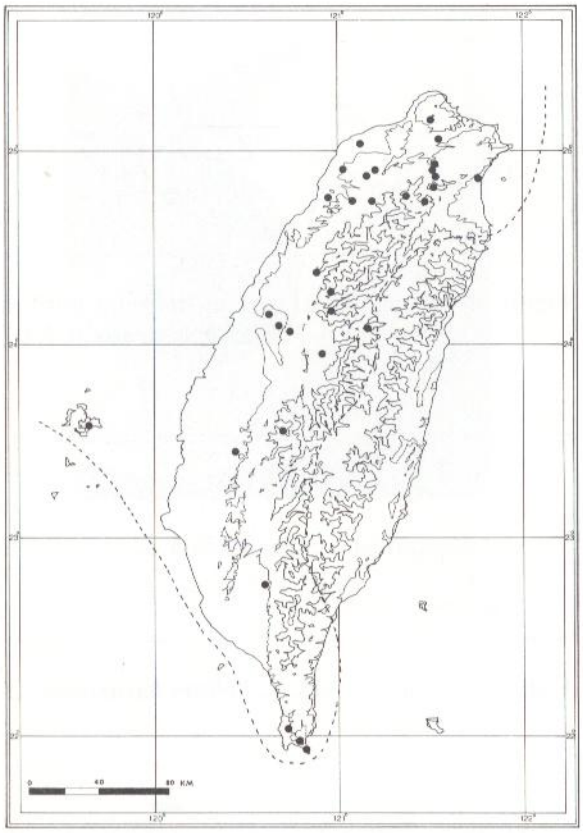

Figure 48. Distribution of ***Polistes jadwigae*** in Taiwan. Contour lines are at 100, 1000 and 2000 m. Dashed line delimits estimated range.

above. Male clypeus shorter (Figure 47b)·····
·····species B

Subgenus ***Megapolistes*** Vecht

The two *Megapolistes* species found in Taiwan are physically very similar to each other, and it is tempting to think that they may also be very similar ecologically. The observation that only one of them, *P. jadwigae,* is found on Penghu Island, while the other, *P. rothneyi,* is found on Orchid Island is consistent with the idea that whichever species becomes established on a small island will competitively exclude the other from immigrating.

Polistes jadwigae DallaTorre

Polistes olivaceus DeGeer -- Sonan, 1943:477-79

Distribution: Widespread in east Asia. At least on the western side of Taiwan, this species is occurs widely at elevations up to about 2000 m (Figure 48), although it is my impression that it is generally less common than the very similar *P. rothneyi.* I tentatively accept as real its implied absence to the east of the central mountain range, although there has been so little collecting in that area that confirmation is needed. Early in this study I or an assistant recorded a specimen from Orchid Island. I have since tried without success to locate the specimen for confirmation, and in Figure 48 I have not included Orchid Island in its range. This is the only social wasp known from Penghu Island.

Biology: This species has received considerable study in Japan (Hirose and Yamasaki, 1984a, 1984b; Kasuya, 1981a, 1981d; Lu et al., 1989; Yamasaki et al., 1978; Yoshikawa, 1957). The occasional records of pleometrosis (Kasuya, 1981a; Yoshikawa, 1957) illustrate that this habit is very rare in this species in Japan. In a large-scale census at a locality on Kyushu, Hirose and Yamasaki (1984b) found an incidence of pleometrosis of less than 1%. It is not yet known whether Taiwan populations are similar in this respect.

Polistes rothneyi Cameron

Polistes jokohamae Radoszkowski -- Sonan, 1943:475-77

Polistes jokohamae Radoszkowski var. *yaeyamae* Matsumura -- Sonan, 1943:477-79

Distribution: Very widespread in south and east Asia (Vecht, 1968; Das and Gupta, 1989). It is found throughout Taiwan at low and medium elevations and is one of two *Polistes* definitely known from Orchid Island (Figure 49).

Biology: Unknown. Despite its wide distribution and abundance in some places, I am not aware of any behavioral-ecological study of this species.

Nest: The two supposedly mature nests I have seen were each had a rather thick, centric petiole, with the comb top quite flat away from the petiolar area. The larger of these had about 700 cells, remarkably large for a *Polistes* nest in Taiwan.

Subgenus ***Nygmopolistes*** Richards

Polistes sulcatus F. Smith

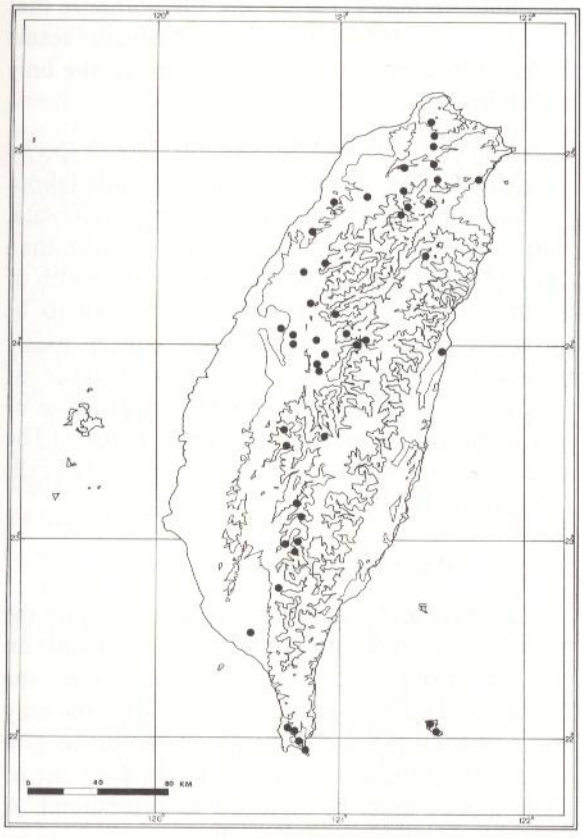

Figure 49. Distribution of ***Polisted rothneyi*** in Taiwan. Contour lines are at 100, 1000 and 2000 m.

Figure 50. Distribution of ***Polistes sulcatus*** in Taiwan. Contour lines are at 100, 1000 and 2000 m. Dashed line delimits estimated range.

Polistes tenebricosus Lepeletier -- Sonan, 1943:471-72

The subgenus *Nygmopolistes* is in need of revision. Das and Gupta (1989) have treated all forms as belonging to a single species, *P. tenebricosus.* However, there are distinct differences in the abdomen and nest between specimens from Java and Taiwan which make it seem unlikely that they are conspecific (Sô. Yamane, pers. comm.). Following Dr. Yamane's advice, I tentatively treat the species found in Taiwan as *P. sulcatus.*

Distribution: Uncertain, possible restricted to southern and eastern China. At least on the western side of Taiwan, this species is widespread at elevations up to about 2000 m (Figure 50), although I am not aware that it is common anywhere. I tentatively accept as real its implied absence east of the central mountain range, although there has been so little collecting in that area that confirmation is needed.

Biology: Unknown.

Subgenus ***Gyrostoma*** Kirby and Spence

Polistes gigas Kirby

Polistes (Gyrostoma) confusus Smith -- Sonan, 1927:121

Polistes gigas Kirby -- Sonan, 1943:469-71

This very distinctive species, the only known member of its subgenus, is the largest *Polistes* in the world.

Distribution: Northern India to southern China and Taiwan (Das and Gupta, 1989). This is a widespread lowland species in Taiwan, found throughout the island up to about 1000 m (Figure 51).

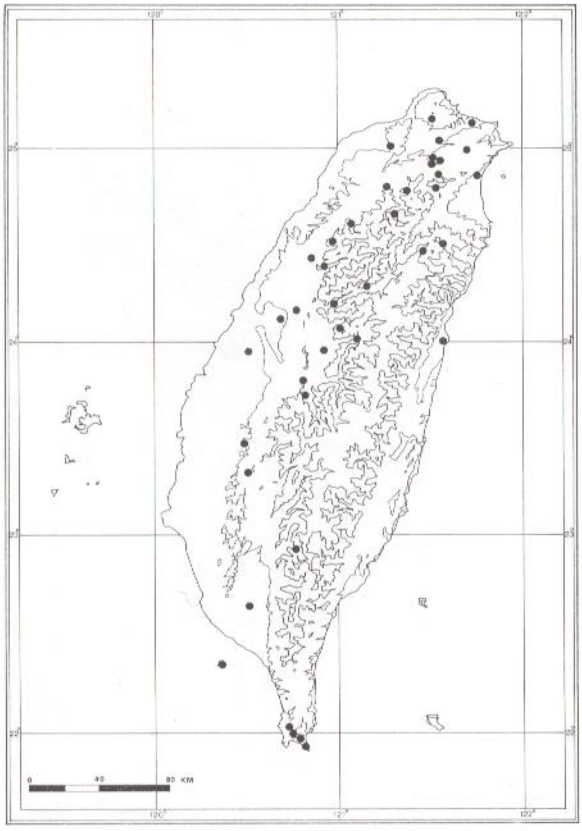

Figure 51. Distribution of ***Polistes gigas*** in Taiwan. Contour lines are at 100, 1000 and 2000 m.

Biology: As far as I know, only two short papers have been devoted to this peculiar species (Iwata, 1965; Matsuura, 1970). Matsuura's data indicate that colonies are typically small, and the several nests (not colonies) that I have seen are consistent with this conclusion. The species appears to be fairly common in Kenting National Park, and I suggest that a study of its nesting biology there would be very worthwhile. In particular, close observation of male behavior promises to yield very interesting results. *P. gigas* males are sometimes about the size of females, but most specimens that I have seen are outstandingly large, about the size of *Vespa mandarinia* workers. They also resemble *V. mandarinia* in having the head greatly thickened behind the eyes (Figure 41b). This deepening most likely serves to accomodate very large mandibular muscles and/or glands, which may have something to do with the uniquely bizarre form of the mandibles in males (Figure 42). I hypothesize that this has to do with agonistic competition for access to females, although this is by no means the only possibility.

Nest: The nests are distinctive among Taiwan species for their narrow, varnished, centric petiole (about 5-8 mm long), domed top, and very long cells (Iwata, 1965; pers. obs.). The cells are also broader than those of other species, with a side-to-side width of about 7-9 mm. Male-producing cells tend to be extremely large, with pupal caps conspicuously protruding. There is some indirect evidence of removal of material from cells for construction of new ones, a very unusual practice in *Polistes*. The largest nest recorded appears to be one of 126 cells (Matsuura, 1970).

Subgenus ***Polistella*** Ashmead

This large and problematic group consists for the most part of small, colorful species. It is mainly an Oriental group, but with extensions into the Australian and Palearctic Regions. This is the only group among the social wasps of Taiwan to give substantial difficulty in this review, and my list of eight species must be regarded as provisional. A forthcoming revision of the polistines of Taiwan by Sô. Yamane and Sk. Yamane may introduce changes.

Polistes japonicus Saussure

Polistes formosanus Sonan, 1927:122-125 [types examined: holotype ♀, 8 paratype ♀♀]

Polistes japonicus var. *formosana* Sonan, 1938:67-69

Polistes japonicus Saussure var. *formosanus* Sonan -- Sonan, 1943:479-81

Polistes hengchunensis Kuo *in* Kuo and Yeh, 1987:80-81 [types examined: 2 co-type ♂♂, 13 paratype ♀♀] NEW SYNONYMY

Polistes shekouensis Kuo *in* Kuo and Yeh, 1987:81-82 [types examined: 1 co-type ♂, 5 paratype ♀♀] NEW SYNONYMY

The number of published names relating to this species in Taiwan attests to its local variability. I have not rigorously considered whether the Taiwan form is a distinct species, as originally indicated by Sonan (1927), but the few *P. japonicus* specimens I have seen from Japan do not differ substantially from those from northern Taiwan. I therefore accept Sonan's (1938, 1943) synonymy of *P. formosanus*

with *P. japonicus.*

I have seen two of five males and 13 of 20 females of the type series of *P. hengchunensis,* and one of three males and five of six females of the type series of *P. shekouensis.* It was stated in the original descriptions that the holotype of each of these species was a male, but in each case the specimens were without any indication of which male was selected. Accordingly, I have labeled the males that I have seen as co-types of their respective nominal species. Both are relatively light-colored (for Taiwan) forms of *P. japonicus.*

The considerable color variation in this species within Taiwan can be reduced to three main characters: a) black band connecting the eyes strongly continuous (dark state) vs interrupted or only weakly continuous (light state), b) mesopleuron substantially black, a strong band extending from the base to below the wings (dark state) vs black band at most very weakly continuous (light state), and c) gastral sternum 2 mainly or entirely black (dark state) vs with a substantial yellow area on each side (light state). The fraction of specimens that cannot in each character be readily assigned to one or the other state is acceptably small. To obtain an indication of geographic variation in average darkness, I tabulated the frequency of the dark state in each of these characters at localities from which samples of 10 or more specimens were on hand; in the few cases where a specimen was intermediate between states it was treated as half dark and half light. The results (Table 4) suggest a south-north

Table 4. Distribution of color variants of *Polistes japonicus* within Taiwan. In each column are the fractions of individuals showing the dark state for that character. Explanation in text. Below the name of each locality are its latitude and mean annual temperature. Temperature data from the National Weather Service (unpubl.); approximate figures are averaged from the closest weather stations in cases where no station is very near.

	n	Ocellar band	Mesopleuron	Sternum 1
		FEMALES		
Taipei City 25°03′N, 22.9°C	100	0.89	0.83	0.86
Wulai, Taipei 24°51′N, about 22°C	33	0.88	0.76	0.83
Taichung City 24°09′N, about 23°C	34	0.97	0.97	1.00
Wushe, Nantou 24°02′N, 18.5°C	14	1.00	1.00	1.00
Puli, Nantou 23°58′N, about 19°C	35	0.94	0.90	0.87
Gueichihchuei, Pintung 22°00′N, 24.8°C	10	0.50	0.10	0.10
Kenting, Pintung 21°57′N, about 25°C	60	0.38	0.05	0.17
Ouluanpi, Pintung 21°52′N, about 25°C	10	0.40	0.20	0.20
		MALES		
Taipei City 25°03′N, 22.9°C	13	1.00	0.31	0.65
Kenting, Pintung 21°57′N, about 25°C	50	1.00	0.00	0.08

Figure 52. Distribution of ***Polistes japonicus*** in Taiwan. Contour lines are at 100, 1000 and 2000 m.

tendency toward increased darkness, and are consistent with the idea of a distinct lighter variant occupying the Hengchun Peninsula (Sonan 1943:481). In the absence of good data for the large area between Gueichihchuei and Puli it is uncertain whether there is any abrupt transition. The overall pattern suggests that darker adults are produced under cooler rearing conditions, such as Entemann (1904) showed in a widely distributed and variably colored North American paper wasp. However, the present data do not show a significant correlation of overall darkness with either latitude or mean annual temperature among the five localities north of the Hengchun Peninsula (Kendall's rho, $P \approx 0.08$).

Distribution: Uncertain, partly due to taxonomic difficulties. The species as conceived here is present at least in the Ryukyus and southern Japan, as well as throughout Taiwan at low and medium elevations (Figure 52). At many localities it appears to be the commonest *Polistes,* and it is one of only two paper wasps definitely found on Orchid Island.

Biology: Little known. The two founding-stage colonies I have seen each had just one queen.

Nest: Kuo and Yeh (1987: Figure 36) show a nest of this species with bright yellow pupal caps.

Polistes strigosus Bequaert

Polistes strigosus Bequaert -- Sonan, 1943:472-73

The key characters separate this distinctive species unambigiously from all others. However, I suspect that it is in fact a group of at least two species. The very large color variation described by Bequaert (1940) and very broad range are enough to cause suspicion in this regard, and within the Philippines I have seen two extremely different color forms.

Distribution: Within the broad concept of the species, widespread in south Asia, from eastern India to southern China. As far as I know, the species is not abundant anywhere, although M.C. Kuo (pers. comm.) characterizes it as common around Lukuei, Kaohsiung. In Taiwan it is known only from scattered localities which give little indication of its local distribution (Figure 53).

Biology and Nest: No information on record.

Polistes shirakii Sonan

Polistes shirakii Sonan, 1943:481-82 [types examined: holotype ♀, 2 paratype ♀♀, 4 paratype ♂♂]

I provisionally include in this species a series of 15 females and six males in CNC labeled "FORMOSA, 1965-1966, Coll. Chin-kin-yu". Most of these are markedly darker than typical *P. shirakii,* especially the females. Among the distinctive color characters of a majority of CNC females are: Clypeus with broader dark line at sides, mandible with yellow mark reduced or absent, mesoscutum mainly or entirely black, and propodeum with posterior yellow stripes reduced or absent.

Distribution: Taiwan endemic. The known localities of this wasp suggest that it is mainly a lowland species with some presence at medium elevations (Figure 53).

Figure 53. Known localities of ***Polistes strigosus*** (triangles) and ***P. shirakii*** (dots) in Taiwan. Stippled triangles and dots represent records from Sonan (1943). Contour lines are at 100, 1000 and 2000 m.

Biology: No information on record.

Nest: The nests that I have seen were all of light brown carton, with an excentric petiole, the cells narrower than those of *P. takasagona,* and with white pupal caps. At the Chiayi Institute of Agriculture this species commonly nests high on the outsides of buildings, and Sô. Yamane (pers. comm.) reports similar observations from Taichung and Puli. One mature colony in an *Araucaria* tree near Chiayi had the nest much elongated (Figure 54), in the manner of *Parapolybia varia.* This nest has three features of note: a) where two shoots of the tree touched the nest the wasps had affixed the shoot to the nest carton with a varnish-like substance which is evidently that used to make the petiole, b)

Figure 54. Nest of mature ***Polistes shirakii*** colony.

about 3/4 of the way down the comb was sharply flexed, so that the distal part lay more or less horizontal, and c) approximately the terminal third of the nest was in very active brood-rearing use, but none of the oder cells above the well-defined pupal zone was in use. In this feature, as in its physical makeup, the species closely resembles *P. snelleni* in Japan (Sô. Yamane, pers. comm.).

Polistes stigma (Fabricius)

Polistes stigmus (Fabricius) -- Sonan, 1943:473-74

Inclusion of this species here is based on a series of 11 females and six males from Hsinhua, Tainan (NCIA, CKS).

Among the large number of social wasps in TARI identified by Sonan I do not find any identified as this species, and I wonder if he personally examined any from Taiwan. His key mistakenly gave the presence of a dorsal mesepisternal groove and epicnemical carina as a diagnostic character of *P. stigma* (Sonan, 1943). If this was not just a lapse, Sonan may have partially confused *P. stigma* with *P. chinensis.*

Distribution: Ceylon and India to Australia, north to Taiwan. (Petersen, 1987) This is evidently among the species which maintains only a marginal presence in Taiwan, at the northern limit of its range. It is known with certainty in Taiwan only from Hsinhua, Tainan (23°02′N 120°18′E). Sonan's (1943) records from near Chungli, Taoyuan (24°57′N 121°13′E), Huwei, Yunlin (23°43′N 120° 25′E), Pintung (22°41′N 120°29′E) and Kaohsiung

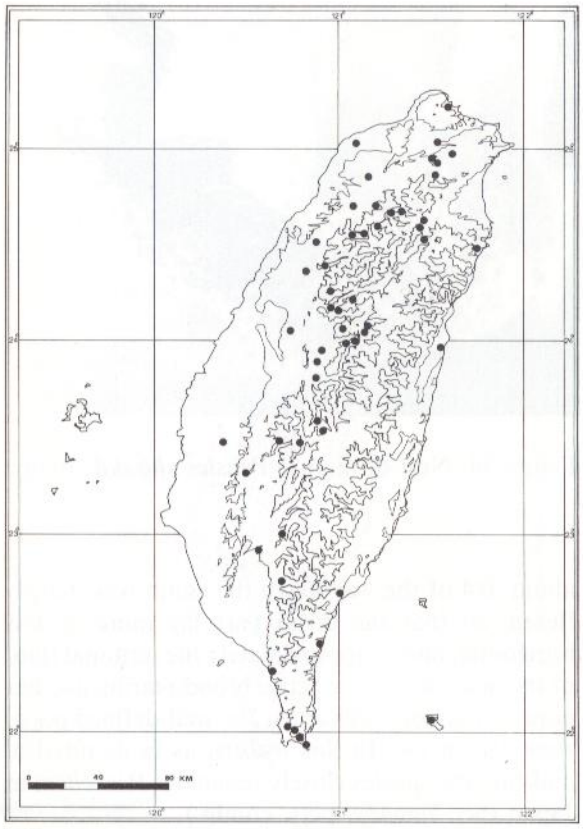

Figure 55. Distribution of ***Polistes takasagonus.*** Contour lines are at 100, 1000 and 2000 m.

City (22°35′N 120°18′E) may correctly refer to this species.

Biology: Little known. In the Philippines, where *P. stigma* is evidently the commonest paper wasp, it appears usually to nest haplometrotically (pers. obs.).

Nest: The nests I have seen in the Philippines resembled those of *P. shirakii* and were never very large.

Polistes takasagonus Sonan

Polistes takasagonus Sonan, 1943:482-83 [types examined: holotype ♀, 4 paratype ♀♀, 4 paratype ♂♂]

Distribution: Taiwan endemic, found at low- and medium-elevation localities throughout the island (Figure 55). Early in this study I or an assistant recorded a specimen from Orchid Island, which I have subsequently failed to locate for confirmation. However, there is no a-priori reason to think that it should not occur there, so that the record is tentatively accepted.

Biology: The three mature colonies I have seen were all quite small, each with just 14-20 adult females and 4-11 males. They were collected during the day, so that the true number of females was probably a little higher. Two of the nests were heavily infested with parasitoids, in my experience an uncommon occurrence in Taiwan polistines.

Nest: The several nests I have seen of this species were all compact combs with excentric petioles, like those of *P. shirakii.* They differed from *P. shirakii's* nests in having broader cells and bright yellow pupal caps.

Polistes eboshinus Sonan n.stat.

Polistes mandarinus Saussure var. *eboshinus* Sonan, 1943:483-84 [types examined: holotype ♀, 7, paratype ♀♀, 2 paratype ♂♂]

This and the next three form a complex of moderately stout to stout species similar in structure and especially in color pattern. The status change of this form from subspecies to species is tentative and is not based on examination of the type or mainland specimens of *P. mandarinus.* It is rather a probabilistic assessment, based on the observation that Sonan identified as *P. mandarinus* specimens of all four of these closely related species (TARI). They cannot all be P. mandarinus, and it may well be that none of them is. Furthermore, Sonan treated *P. eboshinus* and *P.* sp. A as *P. mandarinius eboshinus,* evidently considering them different from the typical form.

Distribution: As presently understood, endemic to Taiwan. This seems mainly to be a medium- to high-elevation species, occurring throughout Taiwan at about 1000-2500 m, rarely at lower elevations (Figure 56).

Biology: No information on record.

Nest: I have seen nests identified by J. Sonan as belonging to *P. mandarinius eboshinus.* They are thus probably from *P. eboshinus* and/or *P.* sp. A. The nests have white pupal caps and in other respects resemble nests of *P. shirakii.*

Figure 56. Distribution of ***Polistes eboshinus.*** Contour lines are at 100, 1000 and 2000 m.

Figure 57. Distribution of ***Polistes*** sp. A. Contour lines are at 100, 1000 and 2000 m. Dashed line delimits estimated range.

Polistes sp. A

Polistes mandarinus Saussure var. *eboshinus* Sonan, 1943:483-84

This designation is given to a species of very similar size and overall form to *P. eboshinus.* Most of the material is in TARI, but the sole male I have seen is in BSC. This latter is in very good condition and bears the locality information "Jul. 10, 1969, 巴陵, B.S. Chang). Among the material that I have directly compared are two females of each species from Wushe, Nantou. In both sexes *P.* sp. A differs from *P. eboshinus* in having the bulge in gastral sternum 2 distinctly more angular (Figure 43f; cf. Figure 43e) and the gastral terga more strongly punctured. The flagellum of the male antenna seems thicker and the propodeal striae stronger in *P.* sp. A than *P. eboshinus,* although I have not quantified these characters. The male specimen of *P.* sp. A is also more extensively black marked, including: a large sub-triangular patch occupying most of the upper part of the clypeus, entire supraclypeal area, yellow in eye orbits less extensive, entire gena except a narrow yellow line along the upper part of the eye, mesopleuron and coxae entirely.

Distribution: Possibly a Taiwan endemic. The few known localities of this species suggest that it occurs mainly or exclusively above 1000 m (Figure 57).

Biology and Nest: No information on record.

Polistes huisunensis Kuo

Polistes huisunensis Kuo *in* Kuo and Yeh, 1987:80 [types examined: holotype ♂, 8 paratype ♀♀]

I have examined the type series of this species (all NCIA, except paratype female in CKS). It comprises a single nest series (M.C. Kuo, pers.

comm.) collected together with the nest.

Aside from length measurements, the original description of this species is based entirely on color. The following are among its diagnostic structural characters:

Female: Medium-size, very stout wasps. Clypeus without a layer of appressed pubescence, with large, scattered punctures, about the same size in the upper and lower parts. Pronotum, mesoscutum and mesopleuron strongly, densely punctate-rugose. Metanotum upraised anteriorly, including in the middle (Figure 46a). Propodeum with a distinct horizontal ledge just below the metanotum. Propodeal furrow moderately deep and very broad, roughly rounded at the angles, striae almost as strong centrally as at the angles. Gastral tergum 1 exceptionally stout. Tergum 2 distinctly broader than tergum 1. Gastral sternum 2 with a pronounced bulge, although not sharply angular (Figure 43g).

Male: Similar to female in overall body form. Clypeus relatively elongate (Figure 47a), not strongly punctured. Terminal antennal segment elongate (Figure 40j).

This species fits into in the *P. adustus*-group, in which Das and Gupta (1989) recognize six species. These authors give the following as the diagnostic characters of the group: body black with abundant red markings, propodeal furrow deep and wide, wings dark brown hyaline, stigma brownish, forewing without apical fuscous cloud, gastral sternum basally distinctly margined, gastral sternum 2 angled or rounded at base. *P. huisunensis* does not appear to match any of Das and Gupta's six species. It closely resembles *P. adustus* Bingham -- known from northern India and Nepal -- except in the shape of gastral sternum 2. In *P. huisunensis* the basal bulge (Figure 43g) is not nearly as acute as in *P. adustus* (Das and Gupta, 1989: (Figure 2G, 9E).

Distribution: Possibly a Taiwan endemic. Known only from scattered, mainly medium-elevation localities in the central part of the island (Figure 58).

Biology: No information on record.

Nest: The nest of the type series is a compact comb with an excentric petiole and yellow pupal caps.

***Polistes* sp. B**

This species evidently belongs in the *P. adustus*-group along with *P. huisunensis*. The material examined is mostly in TARI and NCHU. Among the six *adustus*-group species recognized by Das and Gupta (1989), the present species resembles *P. dawnae* Dover and Rao in lacking an uplifted front margin of the metanotum. However, I have not been able to match *P.* sp. B with confidence against Das and Gupta's (1989:68-69) description of *P. dawnae*, which is based on just a single specimen. In the absence of good evidence to the contrary, I prefer to treat this species as undescribed.

P. sp. B is remarkably similar to *P. huisunensis* in size, overall shape, and color. It differs in the following characters: Female clypeus covered in its upper third to half with a layer of appressed pubescence, under which the punctures are finer than in the lower part of the clypeus; male clypeus shorter (Figure 47b); metanotum hardly upraised anteriorly in the middle (Figure 46b); horizontal

Figure 58. Known localities of ***Polistes huisunensis*** (stippled dots) and ***P.*** sp. B (solid dots). Contour lines are at 100, 1000 and 2000 m.

propodeal ledge just below metanotum narrower. Propodeal striae finer and denser in the furrow than at the angles.

Distribution: Possibly a Taiwan endemic. Known from scattered, mostly medium-elevation localities in about the northern half of the island (Figure 58).

Biology and Nest: No information on record.

Subgenus ***Polistes*** Latreille

This is mainly a palearctic group, with very little presence in Taiwan.

Polistes chinensis Fabricius

Polistes chinensis Fabricius -- Sonan, 1943:474-75

Distribution: Widespread in temperate east Asia. The scattered known localities of this species in Taiwan indicate a lowland distribution throughout the island (Figure 59). I have seen only one specimen ostensibly from a locality above 1000 m. The species seems to be rarely collected in Taiwan, and I have never seen it in the field. The majority of specimens seen are in CNC.

Biology: This species has been extensively studied in Japan (Hoshikawa, 1979; Kasuya, 1980-1981c, 1982-1983c; Kasuya et al., 1980; Miyano, 1980-1990; Morimoto, 1953-1960; Suzuki, 1978-1983). As with all paper wasps in Japan, *P. chinensis* is almost exclusively haplometrotic (Hoshikawa, 1979b; Yamane, 1973). In other respects, it can be characterized as generalized for its genus within the north temperate zone.

Figure 59. Known localities of ***Polistes chinensis*** in Taiwan. Stippled dot represents a record from Sonan (1943). Contour lines are at 100, 1000 and 2000 m.

EXCLUDED SPECIES

Vespa soror Buysson

Vespa ducalis Smith ab. *soror* Buysson -- Sonan, 1929:140 (recorded)

Vespa mandarinia soror du Buysson -- Matsuura and Yamane, 1990:235

Vespa soror du Buysson -- Archer, 1989:34

According to Archer (1989) and Matsuura and Yamane (1990), this species is found in Burma, Indochina and the southernmost part of China (Yunnan and Hainan). Lee (1982, 1985) did not record it from China under any combination of the name *soror*. Sonan's record consists of seven females collected in the Taipei area. It seems out of the question that a large lowland species could have passed unnoticed by anyone else. I have not seen any of the specimens and assume that they represent *V. mandarinia*, rather than *V. ducalis*.

Provespa anomala (Saussure)

Vespa (Provespa) doryloides Saussure -- Sonan, 1929:137-138 (recorded)

Sonan included this species without comment on the basis of a single female collected by T. Kato in 1923 at "Kagi (Taikozan)". However, the known range of the species is from the Greater Sunda Islands to Thailand and west into India (Archer, 1989; Matsuura and Yamane, 1990). Only one of its congeners comes any closer to Taiwan: *P. barthelemyi* Buysson is known from the mainland provinces of Sichuan and Guangxi (Lee, 1985;

Archer, 1989; Matsuura and Yamane, 1990). *Provespa* are not small or inconspicuous, and they are very often found at electric lights, so that if there was a population in Taiwan it would almost certainly be known.

Parapolybia indica (Saussure)

Sô. Yamane (pers. comm.) has positively identified as this species a specimen collected by K. Ohara, ostensibly at about 1000 m near Hsitsun Taoyuan (24°38′N 121°27′E). *P. indica* is known from Fujian, the mainland province nearst to Taiwan (Vecht, 1966; Lee, 1982, 1985), so that its presence here is certainly not out of the question. However, I know of no other records from Taiwan and prefer to leave this species aside pending confirmation. *P. indica* can be recognized by the occipital carina extending down to the base of the mandibles (cf. Figure 39b), while in the othe two *Polybia* species it ends well above the mandibles (cf. Figure 39a).

DISCUSSION

In seeking a general pattern of social wasp species distributions within Taiwan, we might expect historical factors to have only a minor role in delimiting ranges of such vagile animals within a single land mass, compared with present-day ecological factors. The evidence favors this expectation. The primary candidate for a barrier to movement of land organisms within Taiwan is the north-south-tending Central Mountain Range. The various watershed ridges which can be expected to serve as secondary barriers radiate mainly to the east or west from this range. Overlaying the distributions of the better known social wasps over a map of these putative barriers, one finds little correlation. A few species (e.g. *Vespa affinis, Parapolybia varia, Polistes jadwigae*) seem conspicuously absent from the area to the east of the Central Mountain Range, although we cannot yet be sure that this is not an artefact of collecting biases (Table 2). And there is no indication that any of the secondary watersheds is a barrier to gene flow in social wasps.

Inasmuch as Taiwan spans 3.5 degrees of latitude, it is surprising that virtually all of the well collected species extend from Yangmingshan in the north to the southern end of the Hengchun Peninsula. A finer analysis at the level of relative species abundance would most likely show latitudinal effects (suggested above in the case of *Parapolybia takasagona* and *P. varia*), but at the grosser level of presence/absence none is evident. And in only one species, *Polistes japonicus,* do I detect a north-south trend in within-species variation. It thus appears that any ecological constraints on species distributions are unlikely to correlate strongly with latitude.

On the other hand, they can be expected to correlate with altitude. This is an especially pronounced factor in Taiwan, with approximately 1/3 the land area above 1000 m and a significant fragments above 3000 m. While no social wasp appears to occupy a narrow altitudinal zone, few have been collected above 2000 m (as is also true in India; see Gupta & Das 1977), and many (e.g. *Polistes gigas, P. rothneyi)* appear to have little presence above about 1000 m, while *Polistes eboshinus* is little represented below 1000 m. If we had complete distribution maps of each species, then, it is expected that most would occupy a certain (usually broad) altitudinal band around the entire island. Much the same is expected in bumble bees, with the difference that the Central Mountain Range may play a larger role in inhibiting east-west gene flow than in social wasps (Starr, 1992).

The social wasp fauna of Taiwan is rather peculiarly species-rich. This is illustrated by a comparison with the nearby Philippines. Taiwan, a warm-temperate to subtropical island of about 36,000 km^2, has 28 known species of social wasps. The Philippines are a tropical archipelago of some 230,000 km^2, from which 49 species are known (Starr, unpubl.). Applying the biogeographer's rule-or-thumb of a doubling in number of species with a tenfold increase in land area, we find that Taiwan has exactly the number of species predicted from the same land area within the Philippines. This is inconsistent with the well known global tendency toward increased species richness at lower latitudes (Pianka, 1966). As a beginning hypothesis toward accounting for this unexpected result, let me suggest the island's rugged topography as the primary factor. Although topography seems not to constitute a set of barriers to dispersal by social wasps, it may increase habitat diversity through local climatic heterogeneity. If this hypothesis is correct, then colonies of the rarer species (about half of the total) should not be randomly distributed throughout the island. Rather, they are predicted

to be highly habitat-specific and locally abundant at scattered localities.

ACKNOWLEDGEMENTS

Thanks to Chang Lien-hau, Huang You-liang and Yang Wan-tzung for help in recording data, Hu Shao-kang for the SEMgraphs, Seiki Yamane for bibliographic assists, Yang Chung-tu for advice on taxonomic practice, Sôichi Yamane for comments on an earlier version, and Lin Cheng-shing for frequent advice. Sincere thanks also go to anonymous reviewers who provided valuable comments on this manuscript. Financial support for this study came from the National Science Council (project no. NSC79-0211-B187-03).

REFERENCES

Akre, R.D., Greene, A., MacDonald, J.F., Landolt, P.J., and Davis, H.G., 1980. The yellowjackets of American north of Mexico. USDA Agriculture Handbook no. 552, 102 pp.

Archer, M.E., 1981. The Euro-Asia species of the *Vespula rufa* group (Hymenoptera, Vespidae), with descriptions of two new species and one new subspecies. Kontyû 49:54-64.

Archer, M.E., 1982. A revision of the subgenus *Rugovespula* nov. of the genus *Vespula* (Hymenoptera, Vespidae). Kontyû 50:261-269.

Archer, M.E., 1989. A key to the world species of the Vespinae (Hymenoptera). Res. Monogr. Coll. Ripon & York St John (2):1-41 + figures.

Bequaert, J., 1940. Notes on Oriental *Polistes* wasps. Trans. Amer. Entomol. Soc. 66:265-273.

Brian, M.V., 1983. Social Insects: Ecology and Behavioural Biology. London: Chapman & Hall 388 pp.

Carpenter, J.M., 1982. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). Syst. Entomol. 7:11-38.

Carpenter, J.M., 1987. Phylogenetic relationships and classification of the Vespinae (Hymenoptera: Vespidae). Syst. Entomol. 12:413-431.

Carpenter, J.M., 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. pp.7-32 in: Ross, K.G., and Matthews, R.W. (eds.), *op. cit.*

Chao, J.T., Ho, S.L. and Chang, S.Y., 1989. A preliminary analysis of the influence of hornets in apiaries in Taiwan. Chinese J. Entomol. 9:304-305. (In Chinese)

Chiu, S.C., 1948. Revisional notes on the Formosan bombid-fauna. Notes Entomol. Chin., Shanghai 12:57-81.

Chu, Y.I., and Yamanaka, T., 1973-1975. A checklist of the present and old names of insect-collected localities in Taiwan. Trans. Nat. Hist. Soc. Formosa 16:31-72, 17:51-75, 18:121-150. (In Chinese)

Das, B.P., and Gupta, V.K., 1989. The social wasps of India and adjacent countries (Hymenoptera: Vespidae). Orient. Ins. Monogr. (11):1-292.

Edwards, R., 1980. Social wasps: Their biology and control. Rentokil, East Grinstead 398 pp.

Entemann, M.M., 1904. Coloration in *Polistes*. Carnegie Inst. Washington Publ. no. 19:1-88.

Evans, H.E., and West-Eberhard, M.J., 1970. The Wasps. Ann Arbor: Univ. Michigan Press,265 pp.

Gadagkar, R., 1991. *Belonogaster, Mischocyttarus, Parapolybia,* and independent-founding *Ropalidia*. pp. 149-190 in: Ross, K.G., and Matthews, R.W. (eds.), *op. cit.*

Greene, A., 1991. *Dolichovespula* and *Vespula*. pp. 263-308 in: Ross, K.G., and Matthews, R.W. (eds.) *op. cit.*

Gupta, V.K., and Das, B.P., 1977. Distributional patterns of Indian Vespidae (Hymenoptera) with special reference to altitude. Entomon 2:209-213.

Hirose, Y., and Yamasaki, M., 1984a. Dispersal of females for colony founding in *Polistes jadwigae* Dalla Torre (Hymenoptera, Vespidae). Kontyû 52:65-71.

Hirose, Y., and Yamasaki, M., 1984b. Foundress association in *Polistes jadwigae* Dalla Torre (Hymenoptera, Vespidae): relatedness among co-foundresses and colony productivity. Kontyû 52:172-174.

Hoshikawa, T., 1979a. Colony development and foraging activity of *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae). Proc. Assoc. Plant Prot. Kyushu 25:162-164.

Hoshikawa, T., 1979b. Observations on the polygynous nests of *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae) in Japan. Kontyû 47:239-243.

Itô, Y., 1983a. Social behavior of a subtropical paper wasp, *Ropalidia fascitata* (F.): Field

observations during the founding stage. J. Ethol. 1:1-14.

Itô, Y., 1983b. A note on the social behaviour of a subtropical paper wasp, *Ropalidia fasciata* (F.), on a reconstructed nest. Kontyû 51:269-275.

Itô, Y., 1985. Colony development and social structure in a subtropical paper wasp, *Ropalidia fasciata* (F.) (Hymenoptera: Vespidae). Res. Popul. Ecol. 27:333-349.

Itô, Y., 1986. Social behaviour of *Ropalidia fasciata* (Hymenoptera: Vespidae) females on satellite nests and on a nest of multiple combs. J. Ethol. 4:73-80.

Itô, Y., Iwahashi, O., Yamane, S., and Yamane, Sk., 1985. Overwintering and nest reutilization in *Ropalidia fasciata* (Hymenoptera, Vespidae). Kontyû 53:486-490.

Itô, Y., and Iwahashi, O., 1987. An analysis of foundress group size in *Ropalidia fasciata* (Hymenoptera: Vespidae), with zero-truncated distributions. Res. Popul. Ecol. 29:189-194.

Itô, Y., and Yamane, Sk., 1985. Early male production in a subtropical paper wasp, *Ropalidia fasciata* (Hymenoptera: Vespidae). Ins. Soc. 32:403-410.

Iwata, K., 1965. Description of the nest of the giant paper-wasp, *Polistes gigas* Kirby, from Formosa, with some ethological considerations (Hym.: Vespidae). Kontyû 33:284-290.

Iwata, K., 1969a. On the nidification of *Ropalidia (Anthreneida) taiwana koshunensis* Sonan in Formosa (Hym., Vesp.). Kontyû 37:367-372.

Iwata, K., 1969b. Nidification habits of *Ropalidia* and *Parapolybia*. Kontyû 37:437-443. (In Japanese)

Iwata, K., 1976. Evolution of instinct: Comparative ethology of Hymenoptera. New Delhi: Amerind 535 pp.

Jeanne, R.L., 1980. Evolution of social behavior in the Vespidae. Annu. Rev. Entomol. 25:371-96.

Kasuya, E., 1980a. Life tables of colonies and workers in a paper wasp, *Polistes chinensis antennalis*, in central Japan. Res. Popul. Ecol. 22:69-88.

Kasuya, E., 1980b. Behavioral ecology of Japanese paper wasps, *Polistes* spp. (Hymenoptera: Vespidae). I. Extranidal activities of *Polistes chinensis antennalis*. Res. Popul. Ecol. 22:242-254.

Kasuya, E., 1981a. Polygyny in the Japanese paper wasp, *Polistes jadwigae* Dalla Torre (Hymenoptera, Vespidae). Kontyû 49:306-313.

Kasuya, E., 1981b. Nest foundation by a single worker of the Japanese paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae). Insectes Soc. 28:341-342.

Kasuya, E., 1981c. Internidal drifting of workers in the Japanese paper wasp, *Polistes chinensis antennalis* (Vespidae: Hymenoptera). Insectes. Soc. 28:343-346.

Kasuya, E., 1981d. Male mating territory in a Japanese paper wasp, *Polistes jadwigae* Dalla Torre (Hymenoptera, Vespidae). Kontyû 49:607-614.

Kasuya, E., 1982. Take-over of nests in a Japanese paper wasp, *Polistes chinensis antennalis* (Vespidae: Hymenoptera). Appl. Entomol. Zool. 17:427-431.

Kasuya, E., 1983a. Social behavior of early emerging males of a Japanese paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae). Res. Popul. Ecol. 25:143-149.

Kasuya, E., 1983b. Behavioral ecology of Japanese paper wasps, *Polistes* spp. (Hymenoptera: Vespidae). II. Ethogram and internidal relationship in *Polistes chinensis antennalis* in the founding stage. Z. Tierpsychol. 63:303-317.

Kasuya, E., 1983c. Behavioral ecology of Japanese paper wasps, *Polistes* spp. IV. Comparison of ethograms between queens and workers of *P. chinensis antennalis* in the ergonomic stage. J. Ethol. 1:34-45.

Kasuya, E., Hibino, Y., and Itô, Y., 1980. On "intercolonial" cannibalism in Japanese paper wasps, *Polistes chinensis antennalis* Pérez and *P. jadwigae* Dalla Torre. Res. Popul. Ecol. 22:255-262.

Kojima, J., 1982. Notes on rubbing behavior in *Ropalidia gregaria* (Hymenoptera, Vespidae). New Entomol. 31:17-19.

Kojima, J., 1983a. Occurrence of the rubbing behavior in a paper wasp, *Parapolybia indica* (Hymenoptera, Vespidae). Kontyû 51:158-159.

Kojima, J., 1983b. Peritrophic sac extraction in *Ropalidia fasciata* (Hymenoptera, Vespidae). Kontyû 51:502-508.

Kojima, J., 1983c. Defense of the pre-emergence colony against ants by means of a chemical barrier in *Ropalidia fasciata* (Hymenoptera, Vespidae). Jap. J. Ecol. 33:213-223.

Kojima, J., 1984a. Construction of multiple independent combs in *Ropalidia fasciata* (Hymenoptera: Vespidae). Jap. J. Ecol. 34:233-234.

Kojima, J., 1984b. Division of labor and dominance interaction among co-foundresses on pre-emergence colonies of *Ropalidia fasciata* (Hymenoptera, Vespidae). Biol. Mag., Okinawa 22:27-35.

Kojima, J., 1988. Nest construction of *Ropalidia fasciata* (Hymenoptera, Vespidae). Kontyû 56:169-179.

Kojima, J., 1989. Growth and survivorship of preemergence colonies of *Ropalidia fasciata* in relation to foundress group size in the subtropics (Hymenoptera: Vespidae). Ins. Soc. 36:197-218.

Kojima, J., and Hagiwara, Y., 1990. Foundress behavior in a bigynic colony of *Polistes chinensis antennalis* (Insecta: Hymenoptera: Vespidae). Publ. Itako Hydrobiol. Stn. 4:1-5.

Kojima, J., and Suzuki, T., 1986. Timing of mating in five Japanese polistine wasps (Hymenoptera: Vespidae): anatomy of fall females. J. Kansas Entomol. Soc. 59:401-404.

Kuo, M.C., 1984. A study of the ecology of *Vespa formosana* Sonan (Studies of Vespidae in Taiwan, Part I). J. Natn. Chiayi Inst. Agric. 10:73-92. (In Chinese)

Kuo, M.C., and Yeh, W.H. 1985. Ecological studies of *Vespa basalis* Smith, *Vespa velutina flavitarsis* Sonan and *Vespa tropica pseudosoror* Vecht (Studies of Vespidae in Taiwan, Part II). J. Natn. Chiayi Inst. Agric. 11:95-106. (In Chinese)

Kuo, M.C., and Yeh, W.H. 1987. Ecological studies of *Vespa, Polistes, Parapolybia* and *Ropalidia* (Studies of Vespidae in Taiwan, Part III). J. Natn. Chiayi Inst. Agric. 16:77-104. (In Chinese)

Kuo, M.C., and Yeh, W.H. 1988. A study of the effects of wasps on the homeostasis of forest insect populations in Taiwan. J. Natn. Chiayi Inst. Agric. 17:79-97. (In Chinese)

Lee, T.S., 1982 Vespoid wasps of agricultural regions of China. 255 pp.

Lee, T. S., 1985. Economic insect fauna of China. Part 30. Hymenoptera: Vespoidea. Beijing: Science Press 159 pp.

Lu, S.S., Chao, J.T., and Lee, L.L., 1989. Preliminary studies on the ecology of the social wasp *Polistes jadwigae*. Chinese J. Entomol. 9:304. (In Chinese)

Lu, S.S., Chao, J.T., and Lee, L.L., 1990. Preliminary studies of the activity pattern of *Polistes jadwigae*. Chinese J. Entomol 10:355-356. (In Chinese)

Matsuura, M., 1970. Data for nests of the giant paper-wasp, *Polistes gigas* Kirby, in Formosa with special consideration of colony size. Life Study (Fukui) 14:35-40.

Matsuura, M., 1973. Nesting habits of several species of the genus *Vespa* in Formosa. Kontyû 41:286-293.

Matsuura, M., 1983. Preliminary report on the polygynous colonies of *Vespa affinis indosinensis* (Hymenoptera, Vespidae) in Sumatra. Kontyû 51:80-82.

Matsuura, M., 1984. Comparative biology of the five Japanese species of the genus *Vespa* (Hymenoptera, Vespidae). Bull. Fac. Agric. Mie Univ. (69):1-131.

Matsuura, M., 1991. *Vespa* and *Provespa*. pp. 232-262 in: Ross, K.G., and Matthews, R.W. (eds.), *op. cit.*

Matsuura, M., and Sakagami, S.F., 1973. A bionomic sketch of the giant hornet, *Vespa mandarinia*, a serious pest for Japanese apiculture. J. Fac. Sci. Hokkaido Univ. (6)19:125-162.

Matsuura, M., and Yamane, Sk., 1990. Biology of the vespine wasps. Springer, Berlin. (Original Japanese edition published by Hokkaido Univ. Press, Sapporo, 1984)

Miyano, S., 1980. Life tables of colonies and workers in a paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae). Res. Popul. Ecol. 22:69-88.

Miyano, S., 1983. Number of offspring and seasonal changes of their body weight in a paper wasp, *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae), with reference to male production by workers. Res. Popul. Ecol. 25:198-209.

Miyano, S., 1986. Colony development, worker behavior and male production in orphan colonies of a Japanese paper wasp, *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae). Res. Popul. Ecol. 28:347-361.

Miyano, S., 1990. Number, larval durations and body weights of queen-reared workers of a Japanese paper wasp, *Polistes chinensis*

antennalis (Hymenoptera, Vespidae). Nat. Hist. Res. (1):93-97.

Morimoto, R., 1953. On the nesting sites of *Polistes chinensis antennalis* Pérez. (Studies on the social Hymenoptera of Japan.) Kyushu Univ. Fac. Agric. Sci. Bull. 14:235-245. (In Japanese)

Morimoto, R., 1954. On the nest development of *Polistes chinensis antennalis* Pérez. I, II, III. (Studies on the social Hymenoptera of Japan. III, IV, V.) Kyushu Univ. Fac. Agric. Sci. Bull. 14:337-353, 511-522, 523-533. (In Japanese)

Morimoto, R., 1959. On the nesting activity of the founding female of *Polistes chinensis antennalis* Pérez. I. (Studies on the social Hymenoptera of Japan. VI.) Kyushu Univ. Fac. Agric. Sci. Bull. 99-133. (In Japanese)

Morimoto, R., 1960. On the social cooperation in *Polistes chinensis antennalis* Pérez.(Studies on the social Hymenoptera of Japan. IX.) Kontyû 28:198-206. (In Japanese)

Muzaffar, N., and Ahmad, R., 1986. Studies on hornets attacking honeybees in Pakistan. Pakistan J. Agric. Res. 7:59-63.

Pardi, L., 1948. Dominance order in *Polistes* wasps. Physiol. Zool. 21:1-13.

Petersen, B., 1987. Subspecies of the Indo-Australian *Polistes stigma* (Fabricius) (Hymenoptera: Vespidae). Entomol. Scand. 18:227-259.

Pianka, E.R., 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100:33-46.

Price, W.R., 1982. Plant collecting in Formosa. Chinese Forestry Assoc., Taipei.

Reeve, H.K., 1991. *Polistes*. pp. 99-148 in: Ross, K.G., and Matthews, R.W., (eds.), *op. cit.*

Richards, O.W., 1973. The subgenera of *Polistes* Latreille (Hymenoptera: Vespidae). Rev. Bras. Entomol. 17:85-104.

Richards, O.W., 1978. The Australian social wasps (Hymenoptera: Vespidae). Aus. J. Zool. (Suppl. Ser.) 61:1-132.

Ross, K.G., and Matthews, R.W. (eds.), 1991. The Social Biology of Wasps. Ithaca: Cornell Univ. Press 678 pp.

Sakagami, S.F., and Fukushima, K., 1957. Some biological observations on a hornet, *Vespa tropica* var. *pulchra* (du Buysson), with special reference to its dependence on *Polistes* wasps (Hymenoptera). Treubia 24:73-82.

Sekijima, M., Sugiura, M., and Matsuura, M., 1980. Nesting habits and brood development of *Parapolybia indica* Saussure (Hymenoptera: Vespidae). Bull. Fac. Agric. Mie Univ. 61:11-23.

Shida, T., 1963. Prey list of *Vespula lewisii* in the suburbs of Tokyo. Kontyû 31:198-199 (In Japanese; cited from Matsuura & Yamane 1990)

Singh, S., 1962. Beekeeping in India. New Delhi: Ind. Counc. agric. Res. 214 pp. (Cited from Matsuura and Yamane 1990)

Skorikov, A.S., 1933. Zur Hummelfauna Japans und seiner Nachbarlander. Mushi 6:53-65.

Sonan, J., 1927. Taxonomic notes and observations on Hymenoptera of Taiwan. Trans. Nat. Hist. Soc. Formosa 17:121-138. (In Japanese)

Sonan, J., 1929. On *Vespa* from Formosa (1). Trans. Nat. Hist. Soc. Formosa 19:136-149. (In Japanese)

Sonan, J., 1935. On the genus *Ropalidia* from Formosa and Okinawa (Hymenoptera, Vespidae). Trans. Nat. Hist. Soc. Formosa 25:199-202.

Sonan, J., 1938. H. Sauter's Formosa-collection: *Polistes, Montezumia* and *Pareumenes* (Hymenoptera: Vespidae and Eumenidae). Arb. Morphol. Taxon. Entomol. Berlin-Dahlem 5:66-70.

Sonan, J., 1943. On the genus *Polistes* Latreille in Taiwan. Trans. Nat. Hist. Soc. Formosa 33:467-484. (In Japanese)

Sonan, J., 1944. On *Parapolybia* Saussure in Taiwan. Trans. Nat. Hist. Soc. Formosa 34:342-345. (In Japanese)

Spradbery, J.P., 1973. Wasps: An account of the biology and natural history of solitary and social wasps. Univ. Washington Press, Seattle 408 pp.

Spradbery, J.P., 1986. Polygyny in the Vespinae with special reference to the hornet *Vespa affinis picea* Buysson (Hymenoptera Vespidae) in New Guinea. Monit. Zool. Ital. (NS) 20:101-118.

Starr, C.K., 1990. Holding the fort: colony defense in some primitively social wasps. pp. 421-61 in: Evans, D.L., and Schmidt. J.O. (eds.), Insect Defenses. Stony Brook: State Univ. New York Press.

Starr, C.K., 1992. The bumble bees (Hymenoptera:

Apidae) of Taiwan. Bull. Nat. Mus. Nat. Sci. 3: 139-157.

Starr, C.K., and Jacobson, R.S., 1990. Nest structure in Philippine hornets (Hymenoptera, Vespidae, *Vespa* spp.). Jap. J. Entomol. 58:125-143.

Strassmann, J.E., & C.R. Hughes, 1986. Latitudinal variation in protandry and protogyny in polistine wasps. Monit. Zool. Ital. (NS) 20:87-100.

Sugiura, M., Sekijima, M., and Matsuura, M., 1983a. Life cycle of *Parapolybia indica* (Hymenoptera, Vespidae), with special reference to the colony development. Bull. Fac. Agric. Mie Univ. 66:11-25.

Sugiura, M., Sekijima, M., and Matsuura, M., 1983b. Intracolonial polyethism in *Parapolybia indica* (Hymenoptera, Vespidae) I. Behaviour and its changes in the foundress and worker wasps in relation to colony development. Bull. Fac. Agric. Mie Univ. 66:27-43. (In Japanese)

Suzuki, T., 1978. Area, efficiency and time of foraging in *Polistes chinensis antennalis* (Hymenoptera, Vespidae). Jap. J. Ecol. 38:179-189.

Suzuki, T., 1980. Flesh intake and production of offspring in colonies of *Polistes chinensis antennalis* (Hymenoptera, Vespidae) I. Flesh intake and worker production by solitary foundresses. Kontyû 48:149-159.

Suzuki, T., 1981a. Flesh intake and production of offspring in colonies of *Polistes chinensis antennalis* (Hymenoptera, Vespidae) II. Flesh intake and production of reproductives. Kontyû 49:283-301.

Suzuki, T., 1981B. Male production by foundresses of *Polistes chinensis antennalis* (Hymenoptera, Vespidae) in the founding stage. Kontyû 49:519-520.

Suzuki, T., 1981c. Effect of photoperiod on male egg production by foundresses of *Polistes chinensis antennalis* (Hymenoptera, Vespidae). Jap. J. Ecol. 31:347-351.

Suzuki, T., 1982. Cessation and resumption of laying of female-producing eggs by foundresses of a polistine wasp, *Polistes chinensis antennalis* (Hymenoptera, Vespidae) under experimental conditions. Kontyû 50:652-655.

Suzuki, T., 1983. Resting posture at night in the lone foundress of *Polistes chinensis antennalis* (Hymenoptera, Vespidae). Kontyû 51:488-489.

Suzuki, H., and Murai, M., 1980. Ecological studies of *Ropalidia fasciata* in Okinawa Island. I. Distribution of single- and multiple-foundress colonies. Res. Popul. Ecol. 22:184-195.

Tano, T., 1976. The *Parapolybia* species of Japan and Taiwan, with a record of a nest. Hymen. Comm. (3):8-11. (In Japanese)

Tano, T., 1980. On the *Ropalidia* species of Japan, Taiwan and the Philippines. Hymen. Comm. (11):16-19. (In Japanese)

Turillazzi, S., and Marucelli-Turillazzi, C., 1985. Notes on the social behaviour of *Ropalidia fasciata* (F.) in West Java (Hymenoptera, Vespidae). Monit. Zool. Ital. (NS) 19:219-230.

Vecht, J. van der, 1941. The Indo-Australian species of the genus *Ropalidia* (= *Icaria*) (Hym., Vespidae). Treubia 18:103-190.

Vecht, J. van der, 1957. The Vespinae of the Indo-Malayan and Papuan areas (Hym., Vespidae). Zool. Verh. (34):1-83.

Vecht, J. van der, 1959. Notes on Oriental Vespinae, including some species from China and Japan (Hymenoptera: Vespidae). Zool. Meded. 36:205-232.

Vecht, J. van der, 1962. The Indo-Australian species of the genus *Ropalidia* (= Icaria) (Hymenoptera: Vespidae) (Second part). Zool. Verh. (57):1-72.

Vecht, J. van der, 1966. The East Asiatic and Indo-Australian species of *Polybioides* Buysson and *Parapolybia* Saussure (Hymenoptera: Vespidae). Zool. Verh. 82:1-42.

Vecht, J. van der, 1968. The geographic variation of *Polistes (Megapolistes* subg. n.) *rothneyi* Cameron. Bijdr. Dierk. 38:97-109.

Yamane, Sk., 1973. Discovery of a pleometrotic association in *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae). Life Study 17:3-4.

Yamane, Sk., 1974. On the genus *Vespa* (Hymenoptera, Vespidae) from Nepal. Kontyû 42:29-39.

Yamane, Sk., and Maeta, Y., 1985. Notes on the hibernation of *Parapolybia indica* (Hymenoptera, Vespidae). Kontyû 53:576-577.

Yamane, Sk., and Makino, S., 1977. Bionomics of *Vespa analis insularis* and *V.mandarinia latilineata* in Hokkaido, northern Japan, with notes on vespine embryo nests (Hymenoptera: Vespidae). Ins. Matsum. (NS) 12:1-33.

Yamane, Sk., and Tano, T., 1985. Supplements to the *Vespula* fauna of Taiwan (Hymenoptera, Vespidae). Kontyû 53:420-425.

Yamane, Sk., Wagner, R.E., and Yamane, S., 1980. A tentative revision of the subgenus *Paravespula* of eastern Asia (Hymenoptera: Vespidae). Ins. Matsum. (NS) 19:1-46.

Yamane, Sô., 1976. Life of a paper wasp, *Parapolybia varia,* in Taiwan. Insectarium 13:206-212. (In Japanese)

Yamane, Sô., 1977. On collection techniques of vespine nests, chiefly based on practices during a survey in Taiwan from 1972 to 1974 (Hymenoptera, Vespidae). Seibutsu Kyôzai (Kikonai) 12:42-59. (In Japanese)

Yamane, Sô., 1984. Nest architecture of two Oriental paper wasps, *Parapolybia varia* and *P. nodosa,* with notes on its adaptive significance (Vespidae, Polistinae). Zool. Jb. Syst. 111:119-41.

Yamane, Sô., 1985. Social relations among females in pre- and post- emergence colonies of a subtropical paper wasp, *Parapolybia varia* (Hymenoptera: Vespidae). J. Ethol. 3:27-38.

Yamane, Sô., and Yamane, Sk., 1975. Investigating methods for dead vespine nests (Hymenoptera: Vespidae). Seibutsu Kyôzai (Kikonai) 10:18-39. (Cited from Matsuura and Yamane 1990)

Yamane, Sô., and Yamane, Sk., 1979. Polistine wasps from Nepal (Hymenoptera, Vespidae). Insecta Matsum. (NS) 15:1-37.

Yamasaki, M., Hirose, Y., and Takagi, M., 1978. Repeated visits of *Polistes jadwigae* Dalla Torre (Hymenoptera: Vespidae) to its hunting site. Jap. J. Appl. Entomol. Zool. 22:51-55. (In Japanese)

Yoshikawa, K., 1957. A brief note on the temporary polygyny in *Polistes fadwigae* Dalla Torre, the first discovery in Japan. (Ecological studies of *Polistes* wasps, III.) Mushi 30:37-39.

Zimmermann, K., 1929. Zur Systematik der palearktischen *Polistes* (Hymenoptera: Vespidae). Mitt. Zool. Mus. Berlin 15:609-621.

台灣的社會性胡蜂（膜翅目：胡蜂科）

石達愷

摘 要

本文綜述２８種台灣的社會性胡蜂，其中１０種屬Vespina亞科（即*Vespa*及*Vespula*屬），另１８種屬於Polistinae亞科（即*Parapolybia*、*Polistes*及*Ropalidia*三屬），其中*Polistes*屬中有２新種。另外，訂正４種胡蜂爲同物異名，分別爲：*Parapolybia nodosa* Becht = *P. takasagona* Sonan、*Polistes hengchunensis* Kuo = *P. japonicus* Saussure、*Polistes shekouensis* Kuo = *P. japonicus* Saussure及*Ropalidia formosana* Kuo = *R. taiwana* Sonan。

關鍵詞：胡蜂亞科，長脚蜂亞科，胡蜂科，臺灣。