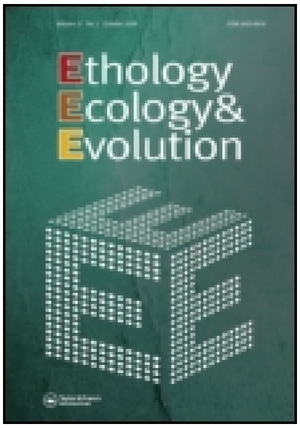

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Nest materials and some chemical characteristics of nests of a New World swarm-founding polistine wasp, *Polybia paulista* (Hymenoptera Vespidae)

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Nest material, nitrogen and amino acid composition of nests were examined in a New World swarm-founding polistine wasp, *Polybia paulista*. This wasp used minute vegetable chips, which were a dominant material, plant hairs, and mud and/or inorganic particles as nest building materials. A SEM observation and nitrogen and amino acid contents indicated that the amount of oral secretion used for construction and maintenance of the nests was quite small, compared with that used in *Polistes* nests. Such a small amount of oral secretion used for nest building is considered to be associated with their social organization (division of labor) and nest material. This study hypothesized that the amounts of oral secretion used for nest building are determined by an interaction among social organization, nest material and environmental factors, such as precipitation.

Twenty-four amino acids were detected from protein in the nests of *P. paulista*, of which serine, glycine, alanine, valine, proline, aspartic acid and glutamic acid were major components. Amino acid composition of the protein in the nests of *P. paulista* differed distinctly from those of other so far known polistine and vespine wasps. The present result supports the view that amino acid composition of the protein in nests reflects phylogenetical relationships among wasps.

KEY WORDS: social wasp, *Polybia paulista*, swarm-founding, nest material, oral secretion, amino acid composition.

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INTRODUCTION

Social wasp nests serve as a place for rearing brood and the centre for their nesting activities (Jeanne 1977, Starr 1991). Wasps collect woody fibres, minute vegetable chips, plant hairs and mud, which they masticate and mix with oral secretion to construct the nest with a variety of architectural design (Jeanne 1975, Wenzel 1991). This salivary secretion is also used to physically maintain their nests. Wasps frequently smear the surface of their nests with the secretion to protect the nest from rain and weathering. It has been reported recently in two Japanese *Polistes* wasps, *P. chinensis* and *P. riparius* that a large amount of the secretion is used for construction and maintenance of pre-emergence nests (Kudô et al. 1998, Yamane et al. 1998, Kudô 2000).

Recently, chemical characteristics of oral secretions have been examined in some genera of the subfamily Polistinae, *Protopolybia*, *Ropalidia* and *Polistes* (Schremmer et al. 1985; McGovern et al. 1988; Maschwitz et al. 1990; Espelie & Himmelsbach 1990; Singer et al. 1992; Kudô et al. 2000a, 2000b; see a review by Jeanne 1996). Most of these studies indicate that the secretion is primarily composed of protein. Maschwitz et al. (1990) and Kudô et al. (1998) estimated in *Ropalidia opifex* and *Polistes chinensis* that the protein content contained in the oral secretion was about 90% and 70%, respectively. On the contrary, Schremmer et al. (1985) detected chitin in the nest of swarm-founding polistine wasp of the New World, *Protopolybia chartergoides* (cited as *Pseudochartergus chartergoides*). Since the oral secretion is composed primarily of protein in most wasp genera so far analyzed (Jeanne 1996), it is presumed that the cost for secretion production is very high (Maschwitz et al. 1990, Kudô et al. 1998, Kudô 2000).

The amino acid composition of protein in the nests has been examined in *Dolichovespula maculata* (McGovern et al. 1988), *R. opifex* (Maschwitz et al. 1990), *Polistes annularis* (Espelie & Himmelsbach 1990), *P. metricus* (Singer et al. 1992), *P. riparius* (Kudô et al. 2000a) and *P. chinensis* (Kudô et al. 2000b). These results showed that alanine, glycine and serine were major components in the nests of these species. Comparing the amino acid composition among the above species, it was found that the composition was closely similar among *Polistes* species, but distinctly differed among different genera (Kudô et al. 2000b). The authors suggested therefore that the amino acid composition of nests may reflect phylogenetical relationships among wasp taxa. In addition, they also suggested that the evolution of the chemical nature of the oral secretion, such as amino acid composition was also important for social evolution in the family Vespidae.

The New World polistine wasps have developed greatly diverse societies, but the kinds of nest material and their chemical nature have not yet been well studied. In particular, no findings has been reported for the amino acid composition of the nest protein of these wasps. In the present paper, we report the kind of nest material, nitrogen content and amino acid composition of the nests in a New World swarm-founding polistine wasp, *Polybia paulista*.

MATERIALS AND METHODS

The wasps

Polybia paulista is one of the common swarm-founding social wasps in São Paulo state (RICHARDS 1978). Colony size varies greatly (KUDÔ unpubl.), and is sometimes more than ten thousand individuals (NOLL & ZUCCHI 2000). *P. paulista* colonies build ovoid nests that are enclosed in a covering envelope with a single entrance hole. ITÔ et al. (1997) reported the early developmental process of nests in this species, and NOLL & ZUCCHI (2000) have recently made morphological analyses of this species.

Nest collection

Five colonies of *Polybia* (*Myrapetra*) *paulista* were collected on February 12-19, 1999 in Ribeirão Preto (21°11'S, 47°48'W), southeastern Brazil. Three pre-emergence nests (nest 2, 3, 4) and two post-emergence nests (nest 1, 5) were used for analyses.

Observation of fine surface structure

Small fragments cut from the envelope and cell walls of nest 1 and 2 were observed with a SEM (Nihon-denshi, JSN-T20), after coating with gold by an ion sputter (Nihon-denshi, JFC-1100).

Elemental analysis

The nitrogen content of the upper part of envelope and cell walls at the first comb of nest 1 were analyzed by a CHN-corder (Yanagimoto Seisakusho, Co. Ltd, Type MT-5) at the Center for Instrumental Analysis, Ibaraki University.

Amino acid analysis

Small nest fragments, which were cut from envelopes of three nests (nest 3, 4, 5) and cell walls of two nests (nest 3, 4), were weighed to 0.1 mg and hydrolyzed in 6N HCl at 110 °C for 24 hr in sealed, evacuated tubes. Amino acids were then analyzed with an amino acid analyzer, JEOL-300, which outputs an amount (in nmol) of each kind of amino acid. We divided the total amount (nmol) of amino acids by the total sample weight (mg) in order to estimate amount (nmol) of amino acids/mg of nest sample.

RESULTS

Fine surface structure

Nest materials

We first describe the nest materials used in nest 1. A SEM observation revealed that minute vegetable chips (ca 1500 × 300 µm) were used as a major nest material in all parts of the surface of both envelope and cell walls (Fig. 1). On the surface of this plant material, there were several grooves (30-50 µm in width) that were regularly oriented parallel to each other. From this appearance, such materials are considered to be sieve tubes and/or vessels of plant tissues (Fig. 1A, D). Numerous pits (ca 70 × 35 µm in major and minor diameters) (Fig. 1A) were also seen on the surface of minute vegetable chips.

Fig. 1B shows that, in addition to the above plant tissues, *Polybia paulista* also used plant hairs (ca 40 µm in width). Plant hairs are generally characterized in the paper wasp nests, e.g., the nest material of *Apoica*, as thin and curled tissues (YAMANE et al. in prep.).

Minor nest materials other than minute vegetable chips and plant hairs were mud and/or inorganic particles (below to left margin in Fig. 1B). The appearance of this minor nest material was very similar to that of eumenine and some stenogastrine wasps (KUDÔ et al. 1996), whose nests were completely composed of mud (COWAN 1991, TURILLAZZI 1991).

The above description was also applicable to the other nest (nest 2), that is, minute vegetable chips were a major component of the nest materials.

Oral secretion

Oral secretion was mainly used for binding plant tissues and other nest materials (Fig. 1C). It was found by a SEM observation that very small amounts of oral secretion were used for nest construction, compared with that used in *Polistes* nests (KUDÔ et al. 1998, YAMANE et al. 1998). In fact, the coating was only seen on the upper surface of the envelope in nest 1 (Fig. 1D). Fig. 1E is a SEM micrograph taken at a high magnification on the surface of the nest entrance in the envelope in nest 2, showing the occurrence of the secretion coating.

Nitrogen content

An elemental analysis indicates that nitrogen (N) was contained in samples from all the nests (n = 20). N content is a good index to indicate the amount of oral secretion contained in the nests. In nest 1, mean (± SE) N content in the upper parts of envelope, close to the first comb, was 2.01 ± 0.04% (n = 10, range: 1.91-2.14%), and that in the cell walls of the first comb was 1.71 ± 0.04% (n = 10, range: 1.59-1.82%). There was a significant difference in N content between these nest parts (Mann-Whitney U-test, $P < 0.005$). This supports the SEM observation that the amount of oral secretion contained in the upper part of envelope was more than that in the cell walls of nest 1. Further, it suggests that *P. paulista* applied different amounts of the secretion to different parts of the nest.

Amino acid composition of protein in the envelope and cell walls

The amino acid composition of protein in the envelope of three nests (nests 3, 4, 5) and the cell walls of two nests (nests 3, 4) was analyzed. Twenty-four amino acids were detected from the five samples, of which the 15 dominant amino acids are shown in Table 1. Twenty-two amino acids except for urea and L-α-aminoadipic

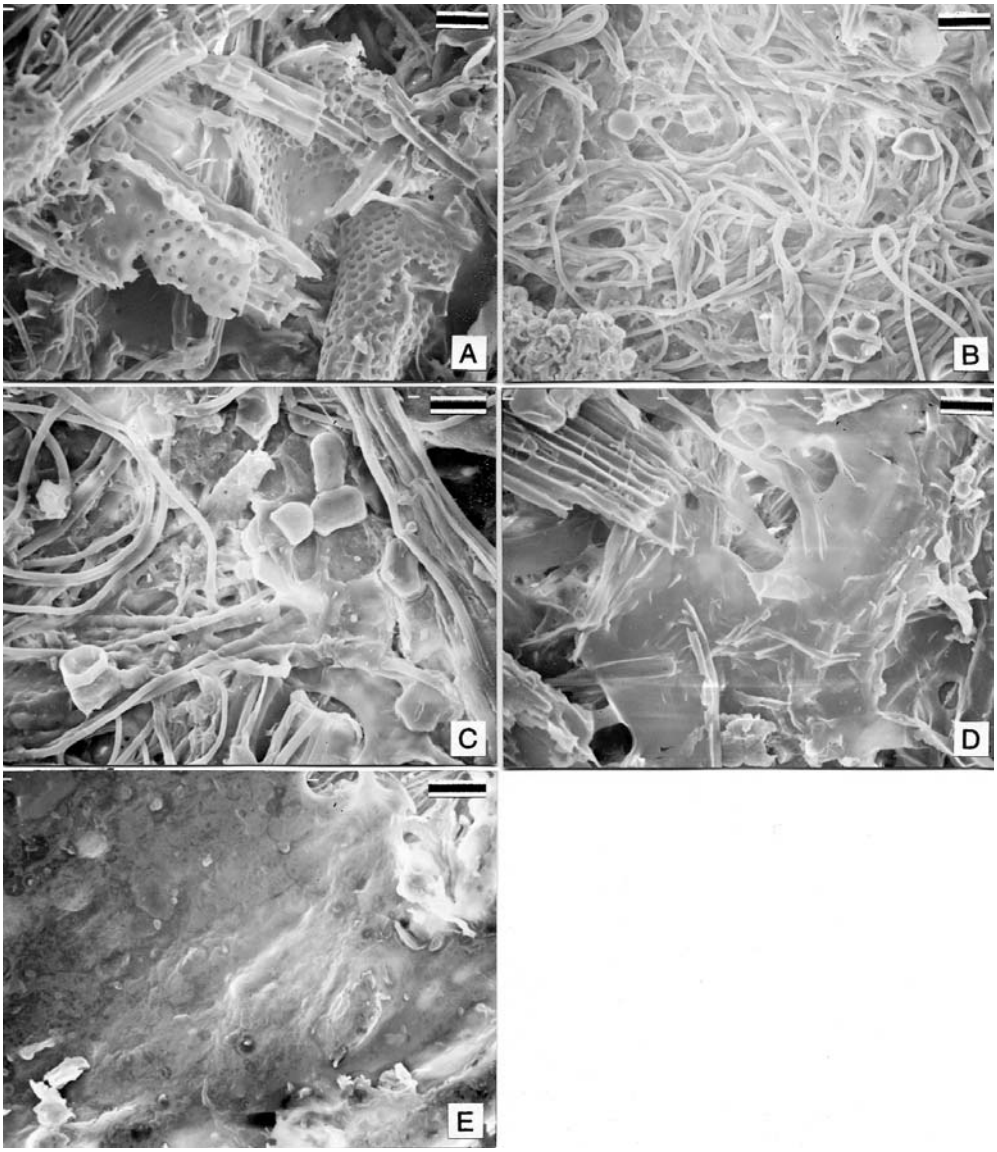

Fig. 1. — Scanning electron micrographs of: (A) the outer surface of the upper part of the envelope; (B) the cell wall; (C) the cell wall; (D) the outer surface of the upper part of the envelope in nest 1; and (E) the nest entrance on the envelope in nest 2. Scale bars = 50 µm in (A), (B) and (D), 30 µm in (C), 25 µm in (E).

Table 1.

Amino acid composition (%) of protein from the envelope and the cell walls in three nests of *Polybia paulista*.

Aminoacids	Nest 3		Nest 4		Nest 5
	envelope	cell wall	envelope	cell wall	envelope
Ser	12.9	13.7	17.9	16.0	14.7
Gly	11.6	11.8	13.6	13.1	12.4
Ala	10.2	10.2	12.1	12.4	11.2
Val	10.2	10.0	12.2	11.4	10.5
Pro	7.3	7.0	8.5	7.9	7.9
Asp	7.5	6.5	6.0	7.1	7.0
Glu	7.2	6.5	5.9	7.1	6.9
Leu	5.7	4.8	4.8	5.5	5.4
Thr	4.9	4.3	4.1	4.9	5.0
H-Pro	5.2	4.5	1.7	5.1	1.4
Ile	3.3	2.8	3.0	3.6	3.2
Lys	3.1	2.6	2.2	3.0	2.5
Phe	2.5	2.0	1.7	2.2	2.2
Cit	2.3	2.2	1.0	1.5	3.2
Arg	2.1	1.6	1.7	2.6	2.0

acid were seen in all the samples analyzed. Seven amino acids, such as serine (15.0 ± 0.9%, mean ± SE), glycine (12.5 ± 0.4%), alanine (11.2 ± 0.5%), valine (10.9 ± 0.4%), proline (7.7 ± 0.3%), aspartic acid (6.8 ± 0.3%) and glutamic acid (6.7 ± 0.2%), were major components, and these seven amino acids occupied approximately 70% of the protein. The proportions of these amino acids were similar for the envelope and cell walls, suggesting that *P. paulista* use oral secretion with similar chemical components and composition in these two areas of the nest.

The mean amount of amino acids per mg in the above five samples was estimated at 591.2 ± 38.4 nmol. This value will be used for a comparison with those of other known *Polistes* species in the discussion.

DISCUSSION

Nest materials

Polybia paulista uses three kinds of nest material, i.e., minute vegetable chips, plant hairs and a small amount of mud and/or inorganic particles. According to Wenzel (1991), wasps of genus *Polybia* utilize a great variety of nest materials. In addition to the above nest materials, some *Polybia* species use long woody fibres like *Polistes* (Wenzel 1991), but in the case of *P. paulista*, woody fibers were never found in the nests.

We cannot conclude that *P. paulista* regularly collects mud and/or inorganic particles in the field, because a possibility that such a material contaminated the plant materials is not excluded. However, contamination with inorganic particles has never been detected during SEM observations of nest material, which consists only of long woody fibres, in two Japanese *Polistes* wasps, *P. chinensis* (Kudô et al.

1998) and *P. riparius* (YAMANE et al. 1998). In the absence of the accidental mixture of the inorganic substance in these *Polistes* nests, it is possible that *P. paulista* collected mud and/or inorganic particles as one of its nest materials. Two subgenera of *Polybia*, *Pedothoeca* and *Furnariana*, rely solely on mud for their nest building (RICHARDS 1978, WENZEL 1991). *P. paulista* belongs to another subgenus, *Myrapetra*, but there is still a possibility that this species partially depends on some inorganic materials for its nest building.

Factors determining the amount of oral secretion used for nest building

We found from a SEM observation that *P. paulista* uses only a small amount of oral secretion for the construction and maintenance of their nests. This was supported by the low nitrogen contents (1.59-2.14%) of the envelopes and cell walls. These values were much smaller than those for other known polistine species (*Polistes fuscatus*: 6.6%, MCGOVERN et al. 1988; *P. annularis*: 2.8%, ESPELIE & HIMMELSBACH 1990; *P. metricus*: 1.4-8.0%, SINGER et al. 1992; *P. chinensis*: 1.3-4.2%, KUDÔ unpubl.; *Parapolybia indica*: 6.4%, KUDÔ unpubl.; *Ropalidia romandi*: 2.7-7.6%, KUDÔ unpubl.; *R. montana*: 2.9-5.0%, KUDÔ unpubl.), but nearly comparable to those of *Vespa* species (KUDÔ unpubl.) (*V. analis*: 1.1-2.0%, *V. simillima*: 0.9-2.0%, *V. crabro*: 2.5%). In general, the nitrogen content in most *Polistes* nests varies considerably (ESPELIE & HIMMELSBACH 1990, SINGER et al. 1992), but the variation is not very high in the nests of *P. paulista* and *Vespa* species. Large variances in nitrogen content between different parts of the nest in most polistine wasps may be due to differences in the frequency of licking different areas with oral secretion. In other words, these wasps would smear different nest parts with different amounts of the secretion.

In *P. paulista*, the mean amount of amino acids/mg was estimated at 591.2 ± 38.4 nmol, and this value was much smaller than those of two Japanese consubgeneric *Polistes* species, *P. chinensis* (1159.5 ± 184.7 nmol, n = 9, KUDÔ unpubl. data, Mann-Whitney U-test, $P < 0.05$) and *P. riparius* (1295.5 ± 127.0 nmol, n = 5, KUDÔ et al. 2000a, U-test, $P < 0.01$). This also supports that the amount of oral secretion contained in *P. paulista* nests was much smaller.

P. paulista builds an envelope to cover their nest combs, of which the first one is directly attached to the substrate (e.g., under a leaf of a palm tree) without making pedicels (ITÔ et al. 1997). As stated above, although *P. paulista* uses a very small amount of oral secretion, it builds large nests covered by an envelope. How can this species build large nests using only a small amount of the secretion that functions as an adhesive? WENZEL (1991) suggested that a notable feature of the nests of *Polybia* and its nearest relatives, such as *Brachygastra* and *Epipona* is the lack of a conspicuous matrix of secretion binding together the vegetable chip material of the carton (*Charterginus* is exceptional). He considered that the reduced role of secretion in the genera allied to *Polybia* may be due in part to the division of labour in nest construction (see JEANNE 1986 for *Polybia occidentalis*). In addition to his interpretation, there is a possibility that wasps do not need to use ample secretion to bind minute vegetable chips. Interestingly, there are several facts that support this interpretation. One of the facts is that *Vespa* species, which primarily collect minute vegetable chips for nest building (WENZEL 1991, 1998; KUDÔ pers. obs.), use a small amount of oral secretion for building and maintaining the nests (see nitrogen content; WENZEL 1991). In contrast, some New World swarm-founding polistine wasps, such as *Protonectarina* and *Brachygastra mellifica* that use woody fibres, use more secretion than their near relatives, such as *Polybia*, *Brachygastra* and *Epipona* (Wenzel 1991).

There are, however, several cases that are inconsistent with our interpretation. For example, the basic nest material of two Old World swarm-founding polistine species, *Ropalidia romandi* and *R. montana* is minute vegetable chips (Kudô unpubl.), but these species build large nests covered by an envelope with much larger amounts of oral secretion (see nitrogen content for these species; Yamane & Itô 1994). Furthermore, according to Yamane & Itô (1994), *R. romandi* changes the amount of oral secretion used for nest maintenance in response to environmental conditions, such as precipitation. This fact suggests that the amount of oral secretion used is determined by environmental factors, but not by division of labour and nest materials. Flexible behaviours in smearing the nest surface with oral secretion in response to precipitation have also been reported in the field colonies of *P. chinensis* (Kudô et al. 1998, Kudô 2000).

It is very important to know whether the amount of oral secretion used is determined by division of labour, nest materials or environmental factors. Our current information would lead to the following interpretation. *P. paulista* builds their nests using primarily minute vegetable chips, and further this species may have a distinct division of labour in nest construction as measured by other *Polybia* species (Jeanne 1986). Therefore, this species does not use a large amount of the secretion. In addition, since most of their nests were built under the eaves of artificial buildings (sheltered sites) (Simões & Mechi 1983) and palm trees (Itô et al. 1997), the wasps do not need to smear the nest surface frequently with the secretion for maintenance. It may be plausible that the amount of oral secretion used for building itself may be primarily determined by a division of labour in nest construction and nest materials. In addition, wasps may change the amount of secretion used for maintenance in response to given environmental conditions, e.g. precipitation (Yamane & Itô 1994, Kudô et al. 1998, Kudô 2000).

It is important to know how the different amount of the secretion and the different kind and dimension of the construction materials affect the mechanical properties of the nests in social wasps. Cole et al. (2001) recently analyzed the physical properties of nest paper in three species of vespine wasps, and concluded that the physical properties of nest paper could result from the collection of pulp from different sources. In *P. paulista*, also, the physical properties of the nest materials should be analyzed in future work, because the capability for building big and resistant nests is considered to be very important for the evolution of larger and more complex colonies.

Amino acid composition of protein in envelope and cell walls

In *P. paulista* nests, seven dominant amino acids, i.e., serine, glycine, alanine, valine, proline, aspartic acid and glutamic acid, occupied nearly 70% of the protein. The first five amino acids were also dominant in the nests of *Polistes* (*P. annularis*, Espelie & Himmelsbach 1990; *P. metricus*, Singer et al. 1992; *P. riparius*, Kudô et al. 2000a; *P. chinensis*, Kudô et al. 2000b) and *Dolichovespula maculata* (McGovern et al. 1988), although their proportions are considerably different. For example, the proportion of glycine in the nests of *P. chinensis* (Kudô et al. 2000b) and *P. riparius* (Kudô et al. 2000a) is much greater than in that of *P. paulista*. These data are consistent with a view that the amino acid composition of protein in the nests reflects phylogenetical relationships among social wasp taxa (Kudô et al. 2000a, 2000b).

In *P. paulista*, amino acid composition of the protein was similar among nests and nest parts (envelope and cell walls). This suggests *P. paulista* produce oral secretion with similar amino acid components and compositions regardless of the parts of the nests and nesting environments. Kudô et al. (2000b) also found in pre-emergence nests of *P. chinensis* that amino acid composition of protein in nest papers and the secretion membrane covering the petiole surface were very similar among nests built at different localities and nesting environments. They concluded that the foundresses produced a similar kind of the secretion for construction and maintenance of their nests.

Proline is a dominant component of structural proteins (Bursell 1981, Chen 1985). In spite of the small amount of secretion used in *P. paulista* nests, a relatively high proline content (about 7.7%) would increase the mechanical strength of the nest paper (Espelie & Himmelsbach 1990, Singer et al. 1992, Kudô et al. 2000b). The large amounts of aspartic acid and glutamic acid detected are a characteristic feature seen in *D. maculata* nests (McGovern et al. 1988). According to Wenzel (1991), the nest materials in *Polybia* and *Dolichovespula* are very similar. It would be very interesting to know the relationships between the kinds of nest materials and amino acid composition, especially in the New World polistine wasps that have greatly diversified.

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