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## Intra-specific Nest Form Variation in Some Neotropical Swarm-founding Wasps of the Genus *Parachartergus* (Hymenoptera: Vespidae: Epiponini)

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**ABSTRACT:** Previous authors have called attention to nest form variation between and within species of the Neotropical swarm-founding polistine wasp genus *Parachartergus*. One author characterized nests oriented horizontally and having the nest comb petiole central and in-line with nest cells as anomalous, and he suggested that anomalous nests constrain colonies from successful reproduction. We report two distinct nest forms of *Parachartergus amazonensis* (Ducke), one of which was oriented primarily horizontally and one only vertically, from a single locality in Peru. Horizontal and vertical nests, with corresponding difference in orientation of nest comb petioles, have additionally been observed in *P. fulgidipennis* (de Saussure) in Peru and Brazil and *P. griseus* (Fox) in Brazil and French Guiana. Nest orientation and comb petiole placement in these *Parachartergus* species may reflect a labile trait that is variably expressed as a function of availability of suitable nest sites. “Anomalous” nests may not constrain colonies from successful reproduction.

**KEY WORDS:** Nest formation, nest architecture, wasps, Vespidae, Epiponini

“*Comparison of the gross features of the nesting behavior of various wasps teaches us much about the evolution of wasps . . .*” H. E. Evans and M. J. West-Eberhard (1970: 113)

Studies of insect nest architecture have a distinguished history and have contributed significantly to works on taxonomy, phylogenetics, behavior, ecology, and evolution. Starr (1991) highlighted a milestone in the study of social evolution in Hymenoptera: “Since Evans’s landmark paper (1958, expanded in Evans and West-Eberhard (1970)), it is generally regarded as a precondition for the evolution of aculeate sociality that the female have a fixed nest to which she repeatedly returns.” For social wasps of family Vespidae, Wenzel (1991) noted that “the early taxonomy . . . relied on architecture nearly as much as on morphology,” citing the major contributions to classification and description of social wasps’ nests by de Saussure (1853–1858), Ducke (1914), Richards and Richards (1951), and Richards (1978). Ducke (1905) was explicit about the primary importance of nest architecture in phylogenetic interpretation and generic classification. Jeanne (1975) assessed the adaptiveness of social wasp nest architecture. Wenzel (1991) reviewed nest architectural diversity for social wasps in the three subfamilies of social Vespidae: Stenogastrinae, Polistinae, and Vespinae.

Much of the literature just cited reflects a phenomenon well known to vespologists—that nest architecture can be used to identify taxa in the field, often even at the species level. Wenzel (1998) notes that “indigenous people who are alert to insects can identify the majority of local species by nest structure alone.” Experienced vespologists can do the same (pers. obs.). Wenzel (1998) cautions, however, that “not . . . every species has a distinctive nest architecture”, and he continues by noting that “intra-specific variation between habitats or populations can be great.” These caveats do not explicitly encompass

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the kind of observations that we will report here, which include description of nest forms distinct in appearance in a same-habitat population of a single species.

One kind of within-habitat intra-specific difference is ontogenetic. For example, young nests of *Polistes annularis* (L.) are stereotypical and similar in appearance, but older nests may be idiosyncratic and reflect cues from the environment (Wenzel, 1989). Schremmer (1978) reported a different mode of within-habitat intra-specific difference in nest morphology as a function of the inclination angle of the substrate on which nests were founded by the swarm-founding polistine wasps *Parachartergus richardsi* Willink and *P. colobopterus* (Lichtenstein). Schremmer's observations seemed not to be encompassed by Richards' (1978) view that whereas two nest forms are found in the genus *Parachartergus*, each is characteristic only of certain species. Here we briefly review the writings by Richards (1978) and Schremmer (1978), and then we present observations on three additional species of *Parachartergus* in which different nest forms have been found.

### Background

Richards (1978: 203) observed that *Parachartergus* has "a rather surprising diversity in nest-structure." He recognized two species groups, the *P. apicalis* (F.) group, well known throughout the Neotropics for their ferocity, and species related to *P. griseus* Fox. Richards (1978: 204) said, "The nests of *Parachartergus* are of two types but, if the facts are correctly reported, these do not quite coincide with the two groups of species." All species of the *P. apicalis* group were characterized as making flask-shaped or pear-shaped nests, with envelopes that are ridged—whence such appellations as "carachupa" [armadillo] in Peru. Combs are always "laterinidal" (terminology of de Saussure (1853–58), and of Richards and Richards (1951)), that is, the combs have pedicels at right angles to the long axis of the cells. Richards cited Möbius (1856) for showing that "*P. colobopterus* makes nests of the same general type but the envelope is not ridged and a nest of what I am calling *P. lenkoi* is similar." He also mentioned two nests of *P. smithii* (de Saussure) that were similar. These last three species belonged to the *P. griseus* group. He then went on to state, "On the other hand, nests of *P. fulgidipennis* and *P. amazonensis* (according to Ducke, 1910), of *P. griseus* according to R. von Ihering (1904: pl. 5, fig. 2) and Richards & Richards (1951: 84) make flat nests beneath leaves. There is a single comb, parallel to the substrate, suspended from the leaf by one or more central pillars." Richards concluded by remarking "It is an extraordinary instance of nest-structure not agreeing with adult classification. Even without this discrepancy, it is curious that such different nest-types should be made by species which, though superficially very different in colour, are really all very similar structurally." [Note that Richards (1978) misidentified *P. fulgidipennis* (de Saussure) (see Carpenter, 1999). The taxon he referred to by that name is *P. amazonensis* (Ducke), and true *P. fulgidipennis* corresponds to *P. fasciipennis* Ducke, now a junior synonym. Cooper (2000) gives a revised key to key to species.]

Schremmer (1978) described nests of one species from each of the species groups of *Parachartergus* recognized by Richards: *P. colobopterus* (Lichtenstein) from the *P. griseus* group, and *P. richardsi* Willink from the *P. apicalis* group. Most of these nests were of what he referred to as normal construction ("normale Aufbau"), built on vertical substrates, with laterinidal combs. But he also described two nests, one for each species, that he characterized as anomalous, situated on buildings on surfaces of about 70° inclination, with the pedicels of the combs oriented in the same direction as the long axis of the cells ("rectinidal" form of de Saussure, 1853–58, and of Richards and Richards, 1951). From the small adult populations in each nest he concluded that neither could

produce a reproductive swarm, and that the reason for this was that population growth was limited by small comb size. He thought that the combs could not be expanded, because the wasps always maintained an interval between comb pedicels, and on nearly horizontal substrates only two combs could be built at a "normal" interval. Schremmer (1978: 366) characterized these nests as building disasters ("Katastrophenbauten").

#### Materials and Methods

Colonies of *Parachartergus amazonensis* were observed, photographed, and collected in Peru, Departamento Loreto, Yanamono (3°26'S 72°51'W), in December 1990 by JMC and in June 1997 by JHH. A nest of *Parachartergus fulgidipennis* was collected in Peru, Departamento Loreto, San Pedro (5°50'S 74°02'W), in March 1999 by JMC. Nests of *Parachartergus griseus* were collected in Brazil, Amazonas, 75 km NE of Manaus (2°26'S 59°46'W), in April 1997 by JMC, and in French Guiana, Petit Saut, Valley "PK19" in July 1998 by Alain Dejean.

#### Results

All nests that we observed fulfill the basic diagnostic criteria for *Parachartergus* as illustrated in Richards (1978) and Wenzel (1991, 1998). In terms introduced by de Saussure (1853–1858) and used by Richards and Richards (1951), the nests were *stelocytтарous* (i.e., the multiple nest combs were each attached to the substrate by a stalk, also called a petiole, pedicel, or peduncle) and *calyptodomous* (i.e., the combs were collectively surrounded by an envelope that was not attached to the combs).

#### *Parachartergus amazonensis* (Ducke)

Nests at Yanamono, Peru, vary in shape, size, location, and orientation. One colony (JHH's field number PE97-24) had an envelope that was ovate in shape but with cornered opening and apex (Fig. 1). Approximately 7 cm in maximum width and 14 cm in length, the nest had been placed on the underside of a leaf of a *Heliconia* species (Heliconiaceae) and was ca. 1 m above the ground. The nest was inclined at an angle of approximately 70° beneath the large, nearly horizontal but slightly drooping leaf. The number of nest combs and position of the stalk attachment were not recorded. Three nests of the same form from that locality (JMC's field numbers 901221-4, 901222-4, 901222-5), each similarly located beneath a nearly horizontal *Heliconia* leaf, had respectively two combs, four combs and three combs, all with the stalk at the margin of the comb at a right angle to the long axis of the cells (laterinidal form). Another nest from that locality (JMC's field number 901224-6), had two combs, in one of which the stalk was laterinidal, while in the other the stalk was intermediate between rectinidal and laterinidal (Fig. 2).

A second colony of *P. amazonensis* (JHH's field number PE97-30), located ca. 100 m from colony PE97-24, had an elongate and narrow envelope with a cornered opening and rounded apex (Fig. 3). Approximately 5 cm in maximum width and 48.5 cm in length, the nest was about 2.5 m above the ground on the vertical surface of an unidentified tree that had smooth, green bark. The tree trunk had elongate shallow depressions that resembled fluting on a classic Greek column, although the depressions were irregular in length and placement. The nest envelope neatly covered one of these depressions and contained 18 nest combs, each with the stalk laterinidal (Fig. 4).

Colony PE97-24, collected in the daytime, had 109 adult females. Colony PE97-30, collected at dusk, had 135 females. Colony number 901221-4 had 90 females, 901222-4 had 49 females, 901222-5 had 76 females and 8 males, but colony 901224-6 had just 18



Fig. 1. *Parachartergus amazonensis* nest PE97-24, situated on the underside of a *Heliconia* leaf, as seen from beneath. Photo by K. E. Espelie.

females collected, because most of the wasps escaped at the time of collection (all colonies collected in daytime). At the time of collection, wasps from colony PE97-30 appeared to be slightly larger in body size than those of PE97-24, but 50 workers from each colony did not differ in two common measures of body size defined by Jeanne et al. (1995), thorax length ( $\bar{X}_{\text{PE97-24}} = 3.36 \pm 0.17$  mm;  $\bar{X}_{\text{PE97-30}} = 3.41 \pm 0.11$  mm;  $t = -1.765$ ,  $P = 0.08$ ) and wing (radial cell) length ( $\bar{X}_{\text{PE97-24}} = 4.58 \pm 0.11$  mm;  $\bar{X}_{\text{PE97-30}} = 4.56 \pm 0.12$  mm;  $t = 0.758$ ,  $P = 0.45$ ).

#### *Parachartergus fulgidipennis* (de Saussure)

A nest of this species from San Pedro (JMC's number 990317-1), located in a tree on the midrib of a leaf, less than 2 m from the ground, had one comb with the petiole rectinidal (Fig. 5); there were 29 females collected. Another nest of this species was found in the APEG forest, Belém, Pará, Brazil, in October 1991 by Orlando Tobias Silveira. It was under a palm leaf, about 1.5 m from the ground; at least 14 females were collected according to correspondence. A photograph sent to JMC clearly shows the nine combs to have laterinidal petioles.

#### *Parachartergus griseus* (Fox)

A nest of this species at an INPA field station northeast of Manaus (JMC's number 970425-1) was located on a vertical pipe more than 4 m from the ground. It had three

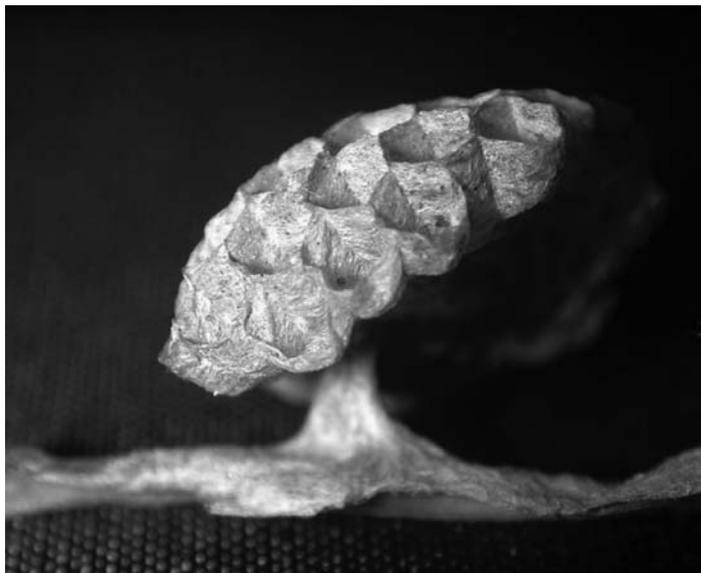


Fig. 2. A comb of *P. amazonensis* nest 901224-6 with the petiole intermediate between laterinidal and rectinidal.

combs, all with laterinidal petioles (Fig. 6); 39 females were collected. Another nest of this species from French Guiana sent by Alain Dejean (Dejean sample 98A) was under a bromeliad. There was a single comb, with a rectinidal petiole (Fig. 8); 4 females and 3 males were sent with the nest.

#### Discussion

Nest shape did not differ between the two *P. amazonensis* nests collected in 1997 due to colony size, which differed by only 26 wasps (and the smaller colony, collected in daytime, presumably had foragers that were away at the time). One might also hypothesize that the two forms of *P. amazonensis* nests differ due to the differences in orientation, one being vertical and the other being close to horizontal. We believe that this is not the case, because we also observed but did not collect a third nest that was strongly similar to PE97-24 in size and shape yet it was situated on the vertical wall of a house. Because it was out of reach we did not collect it and cannot confirm its specific identity. Extra effort was not made to collect it because it was confidently believed (based on architecture of the nest!) to be the same taxon as PE97-24. Another possibility for the two different forms of *P. amazonensis* nests is that shape and size of the elongate nest were determined by the wasps' responses, during construction, to the contours of the depression on the tree trunk that the envelope covered over. Yet another possibility, which cannot be separated from the previous one, is that the wasps of colony PE97-30 would have constructed an elongate nest even on a flat surface such as the wall of a house. With only a single example seen of the elongate nest, it is impossible to eliminate either of these possibilities.

In any case, it seems clear that Schremmer's (1978) characterization of nests on nearly horizontal surfaces as anomalous is wrong. For each of the two species he studied, he saw one such nest, on a manmade structure. We report horizontal nests on natural substrates for three species. We observed numerous *P. amazonensis* nests on nearly horizontal surfaces at



Fig. 3. *Parachartergus amazonensis* nest PE97-30 in situ. Photo by K. E. Espelie.

Fig. 4. *Parachartergus amazonensis* nest PE97-30 with wasps removed and the envelope partially peeled. The combs are attached to the tree via a laterinidal petiole at each comb's margin. Photo by K. E. Espelie.

Yanamono—many more in 1990 than we collected. We have documented that comb petiole orientation, laterinidal vs. rectinidal, can vary intra-specifically in *P. fulgidipennis* and *P. griseus* as well as in the two species studied by Schremmer. Moreover, in *P. amazonensis* comb petioles with intermediate orientation may occur. Thus comb petiole orientation in *Parachartergus* is a labile trait that is responsive to orientation of the nesting substrate. The frequency in a population of horizontal nest architectures and rectinidal comb petiole orientations may reflect, in part, the availability and abundance of particular nesting sites.



Fig. 5. The comb of *P. fulgidipennis* nest 990317-1 with rectinidal petiole.

We believe that Schremmer was also incorrect in his assertion that colonies in nearly horizontal nests with rectinidal combs are unable to successfully reproduce. Schremmer reported a decline in the adult population from 400 to 19 over the course of three months in his “anomalous” *P. colobopterus* colony with rectinidal combs. Rather than indicating the impossibility of successful reproduction in this colony, however, the population decline might reflect seasonal effects. Colonies of *P. colobopterus* with sizes from 48 to more than 4000 nest cells (Strassmann *et al.*, 1991) and from few to many adults (numerical data not presented) in a final sample of 286 colonies were located “on trees, barns, sheds, classrooms, and laboratories” in Maracay, Venezuela (Strassmann *et al.*, 1997). Nest architectures were not reported, although Strassmann *et al.* (1997: 75) stated that “most” nests were on vertical surfaces. Strassmann *et al.* (1997) do, however, give rainfall data for Maracay that show that Schremmer’s anomalous nest, founded on 22 October in nearby Sucre, was established just at the onset of the severe dry season, and so its (inferred) failure could have been due to the mis-match of colony needs and resource availability. Indeed, Schremmer surmised the anomalous colony might have been founded by an absconding swarm following destruction of a previous nest rather than by a reproductive swarm. JMC collected a nest of *P. colobopterus* at Hato Masaguaral, Guárico, Venezuela in May 1985, just before onset of the rainy season. The nest was horizontal under a roof, with two rectinidal combs; the two combs covered an area much larger than that of the colony studied by Schremmer (more than 500 cells vs. fewer than 300). Of the 74 adults collected, 37 were inseminated and had eggs, a percentage that does not seem to indicate imminent failure, but which might be expected just before the growing season (see also Strassmann *et al.*, 1997). Moreover, both combs contained pupae (78 capped cells total; emergences scattered but not at the edges). Colony sizes in other species in which we observed horizontal orientation with rectinidal combs did not seem anomalously small. JHH saw in October 1993, a nest of *P. colobopterus* at Hato Piñero, Cojedes, Venezuela that was on an

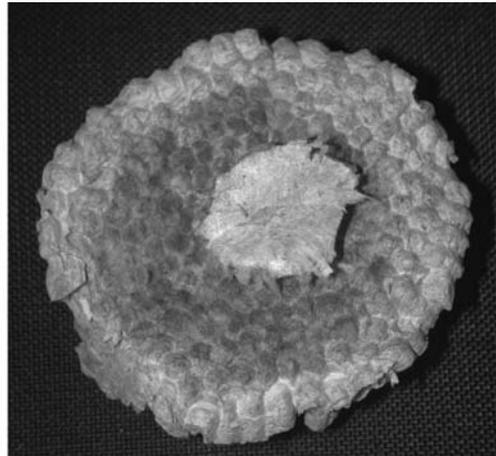


Fig. 6. The uppermost comb of *P. griseus* nest 970425-1 with laterinidal petiole.

Fig. 7. The comb of *P. griseus* nest Dejean 98A with rectinidal petiole, showing the upper side of the comb after detachment from the substrate.

inclined tree branch and enclosed in a flask-shaped envelope that housed an apparently thriving colony. We would anticipate that observation over time of “anomalous” colonies in the field would show that most of those that are founded during seasons favorable for colony establishment are capable of producing reproductive swarms.

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This paper is dedicated to the memory of Howard E. Evans. We will miss him for his facile pen as well as for his contributions to science and his love of wasps.

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