Research Article

Poneromorph Ants Associated with Parasitoid Wasps of the Genus *Kapala* Cameron (Hymenoptera: Eucharitidae) in French Guiana

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Eucharitid wasps are specific, specialized parasitoids of ants. The genus *Kapala* Cameron is the most common in the Neotropics but few species are described, and information dealing with their biology, behavior and host associations is scarce. Numerous poneromorph ant colonies were inspected over 4 collection surveys in French Guiana. A diverse fauna of parasites and parasitoids was found, including mermithid nematodes, flies, eucharitids, and another gregarious endoparasitoid wasp. Five new host associations for *Kapala* are reported, all of them involving medium- to large-size poneromorph ant species from 4 genera: *Ectatomma brunneum* Fr. Smith, *Gnamptogenys tortuolosa* (Fr. Smith), *Odontomachus haematodus* (L.), *O. mayi* Mann, and *Pachycondyla verenae* (Forel). Three other associations involving *O. hastatus* (Fabr.), *P. apicalis* (Latreille), and *P. stigma* (Fabr.), already reported for other countries but new for French Guiana, are confirmed. The data extend the number of hosts for *Kapala* to 24 ant species from 7 genera. The high diversity of the ant host genera associated with *Kapala*, combined with the fact that these ant genera are the most widely distributed among Neotropical poneromorph ants, could account for the dominant status of the genus *Kapala* among the eucharitine wasps of Central and South America.

1. Introduction

Within Hymenoptera, the family Eucharitidae (subdivided in three subfamilies: Oraseminae, Eucharitinae, and the Indo-Pacific Gollumiellinae) is the most numerous and diverse group of ant parasitoids [1, 2]. All of the members of this family have a highly modified life cycle [3–6]. Unlike most parasitic wasp species, eucharitid females deposit their eggs away from hosts, in or on plant tissue [2, 7]. The active first-instar larva, termed planidium, is responsible for gaining access to the host ant larvae by using various phoretic behaviors including either attachment to an intermediate host (most often a potential ant prey) or to foraging ant workers, with on occasion the presence of attractive substances in or on the eggs [2, 8]. Within the nest, planidia attach themselves to ant larvae, but development is only completed when the host pupates [6, 7, 9, 10]. In almost

all of the cases, adults emerge among ant brood (but see [11]) and have to leave the host nest to reproduce. Ants show only moderate aggression to newly emerged eucharitids [7, 12–17] and transport them outside as if they were refuse [11, 15, 17], ultimately enhancing wasp dispersal. Parasitism is very variable and localized in time and space [13, 18, 19]. A very high local prevalence may lead to only a very low impact at the regional scale, suggesting that these parasitoids do not have a major influence on the dynamics of their host population [19]. However, they constitute a remarkable example of both host-parasitoid coevolution and host behavior manipulation.

The eucharitine genus *Kapala* Cameron is widespread in the New World, with only one species, *K. ivorensis* Risbec, found in the Old World (Ethiopian region and Malagasy). This is one of the eucharitid genera most commonly collected by traps and aerial nets in the Neotropical region [1].

However, taxonomic and systematic studies of the species belonging to this genus have proved difficult because of the high degree of morphological variability both within and among species [20]. Only 17 species have been described up to now, but more than 60 are estimated to exist [1, 10]. This genus is presently under revision (E. Murray and J. M. Heraty, pers. comm). Information dealing with the biology, ecology, and behavior of *Kapala* wasps is still very scarce (but see [10, 16, 18]), even though the number of known associations with ant hosts significantly increased in the past ten years. To date, all of the ant species which have been recorded as reliable hosts for the genus *Kapala* apply to medium to large poneromorph ant genera belonging to two subfamilies: Ponerinae and Ectatomminae [1, 4, 11, 21–24]. As all of the ant larvae attacked by *Kapala* pupate inside a protective cocoon, immature stages of the parasitoids are not easily spotted unless under close scrutiny. Furthermore, accurate host records can only be obtained by direct rearing of the parasitoids from ant brood and need laborious target sampling and collection. This could explain in part why so few associations have been reported before the late 90s. Here we both summarize the results of several collection surveys in French Guiana aimed to contribute to the knowledge of the diversity and distribution of the *Kapala* species in the Neotropics and provide a comprehensive review of ant-host associations for this highly variable genus.

2. Materials and Methods

Several dozen colonies (or portions of colonies) of poneromorph ants were collected in French Guiana, during 4 extensive surveys between 2002 and 2010. Collecting surveys were performed during both dry and rainy seasons and at several biotopes, mainly lowland rainforest fragments but also second growth vegetation. Ants were collected from several forest fragments along the road leading to the Hydroelectric complex at Petit Saut, Sinnamary (5°03'39"N; 53°02'36"W). Samples were obtained by systematically breaking up all of the fallen rotten logs found on the ground or were visually detected in the case of tree-inhabiting ants. Colonies of *Ectatomma brunneum* Fr. Smith were common in a ruderal area running along Route No. 1 from Kourou to Sinnamary (kilometric point 101) and were collected from the soil by excavation. Complete colonies or significant parts of colonies containing cocoons and larvae were taken to the laboratory. Most ants were identified to species level with available keys. Nest composition (presence and number of dealate females, alate females, males, workers, cocoons, and larvae), including the presence of adult eucharitids, was determined, and all of the pupae (cocoons) were dissected under a stereomicroscope and checked for the presence of eucharitids or for evidence of their attack. In particular, we looked both for wasp remains (exuvia) within empty ant cocoons denoting previous eucharitid emergence and for the presence of any abnormal pupa (phthisergate, phthisogyne, or phthisaner, according to the caste) indicating an unsuccessful eucharitid attack [12]. Larvae were also checked for the presence of planidia attached to their cuticle or for

the presence of round melanized scars, an evidence of the previous attachment of a planidium [19]. Voucher specimens of ants were deposited in the Arthropod Collection at El Colegio de la Frontera Sur-Chetumal. Eucharitid specimens were sent to the specialist of this group, Dr. John M. Heraty (UCR).

3. Results

A total of 161 complete colonies of poneromorph ants or colony fragments with pupae, representing 26 species from 3 subfamilies, were collected and their contents examined (Table 1). No evidence of eucharitid attack to larvae was found for any of the poneromorph ant species examined, but several species of *Kapala* were found parasitizing the pupae of 8 different ant species. Of these, 5 represent new host associations (Table 1): one for the genus *Ectatomma* Fr. Smith (*E. brunneum* Fr. Smith), one for the genus *Gnamptogenys* Roger (*G. tortuolosa* (Fr. Smith)), and two for the genus *Odontomachus* Latreille (*O. haematodus* (L.), *O. mayi* Mann). The fifth new host record involves the genus *Pachycondyla* Fr. Smith and concerns a *P. verenae* (Forel) colony which was collected by Ronara de Souza Ferreira in the Southwestern part of French Guiana, at Camp Patawa, about 40 km from Roura in the direction of Raw. In addition, the host status of *O. hastatus* (Fabr.)—already reported for Ecuador [1]—and of *P. stigma* (Fabr.) and *P. apicalis* (Latreille)—already reported for Mexico [10, 22, 24]—were confirmed, and this constitutes the first report for French Guiana.

Due to the very reduced number of sampled nests for *O. mayi* and *P. apicalis*, percent parasitism figures (number of infested nests/number of revised nests) for these species are given only as indicative of eucharitid attack. For those species where a significant number of nests could be revised, prevalence of parasitism was generally low to medium (from 14.3% for *P. stigma* to 27.3% for *G. tortuolosa*) but reached up to 50% in the case of *O. hastatus*. However, parasitism rate within parasitized colonies was very low for all of the species, and only few eucharitid specimens were retrieved (Table 1).

Apart from eucharitids, some other parasites were found attacking ant colonies. Pupae of *P. goeldii* (Forel) were parasitized by a gregarious endoparasitoid wasp, and those of *P. commutata* (Roger) and *Paraponera clavata* (Fabr.) were parasitized by two gregarious dipteran species. Finally, a mermithized worker was found in a *P. stigma* colony, and this constitutes the first report of mermithid nematode parasitization for this species. In the absence of any post-parasitic juvenile, the mermithid species identification was not possible. Voucher specimens of both the ants and the mermithid nematode were deposited in the authors' collection.

4. Discussion

A diverse fauna of parasites and parasitoids attacked the different poneromorph ant species present in French Guiana near Petit Saut, including nematodes, flies, a gregarious

TABLE 1: Poneromorph ants of French Guiana and parasitism by *Kapala*. Ant species revised (n = number of nests containing pupae), presence of eucharitid wasps, parasitism rate by eucharitids (in %), and number and developmental stage of specimens of Eucharitidae retrieved (F: female; M: male; A: adult, damaged specimen; Lif: first-instar larva feeding on host; Lf: last-instar larva; Pht.: phthysergate; Ex.: presence of eucharitid exuvia within an empty cocoon).

Ant species	Parasites and parasitoids
Ectatomminae	
<i>Ectatomma brunneum</i> ($n = 46$)	<i>Kapala</i> sp. (21.7%): 7 F, 1 M, 1 A, 2 Lif, 1 Pht., 1 Ex.
<i>Gnamptogenys pleurodon</i> ($n = 5$)	—
<i>Gnamptogenys tortuolosa</i> ($n = 11$)	<i>Kapala</i> sp. (27.3%): 1 F, 1 Lf, 1 Lif, 1 Pht.
<i>Gnamptogenys</i> sp. ($n = 1$)	—
Ponerinae	
<i>Anochetus</i> sp. 1 ($n = 1$)	—
<i>Anochetus</i> sp. 2 ($n = 3$)	—
<i>Centromyrmex</i> sp. ($n = 1$)	—
<i>Hypoponera</i> sp. 1 ($n = 4$)	—
<i>Hypoponera</i> sp. 2 ($n = 1$)	—
<i>Leptogenys</i> sp. 1 ($n = 2$)	—
<i>Leptogenys</i> sp. 2 ($n = 1$)	—
<i>Odontomachus haematodus</i> ($n = 20$)	<i>Kapala</i> sp. (15.0%): 1 F, 3 M, 1 Pht.
<i>Odontomachus hastatus</i> ($n = 6$)	<i>Kapala</i> sp. (50.0%): 2 F, 1 M, 2 Lf, 1 Lif
<i>Odontomachus mayi</i> ($n = 2$)	<i>Kapala</i> sp. (50.0%): 1 F
<i>Odontomachus</i> sp. 1 ($n = 1$)	—
<i>Pachycondyla apicalis</i> ($n = 2$)	<i>Kapala</i> sp. (50.0%): 1 F, 2 M, 1 Ex.
<i>Pachycondyla commutata</i> ($n = 2$)	— ^(a)
<i>Pachycondyla constricta</i> ($n = 6$)	—
<i>Pachycondyla crenata</i> ($n = 1$)	—
<i>Pachycondyla goeldii</i> ($n = 2$)	— ^(b)
<i>Pachycondyla harpax</i> ($n = 6$)	—
<i>Pachycondyla obscuricornis</i> ($n = 3$)	—
<i>Pachycondyla stigma</i> ($n = 21$)	<i>Kapala</i> sp. (14.3%) ^(c) : 1 F, 1 M, 1 Lif
<i>Pachycondyla verena</i> ($n = 6$)	<i>Kapala</i> sp. (16.7%): 1 M
<i>Platythyrea sinuata</i> ($n = 6$)	—
Paraponerinae	
<i>Paraponera clavata</i> ($n = 1$)	— ^(a)

(a) Presence of dipteran parasitoids;

(b) Presence of unidentified, gregarious parasitoid wasps;

(c) Presence of a mermithid nematode.

endoparasitoid wasp, and, above all, eucharitids. Several authors have recorded the presence of eucharitids in ant nests, but the information is scattered in the literature and concerns only few ant species. Neotropical eucharitine wasps are represented by approximately 160 species from 16 genera [1], but information on the host plant(s) used for oviposition is extremely scarce, and the identity of the ant host has been clearly established for only a few species belonging to 5 genera (*Dilocantha* Shipp, *Isomerula* Cameron, *Kapala* Cameron, *Obeza* Heraty, and *Pseudochalcura* Ashmead). These ant hosts concern exclusively formicine, ponerine, and ectatommine ants, whose larvae pupate inside a protective cocoon.

With about 60 estimated species, the genus *Kapala* is by far the most diverse and dominant eucharitine genus of Central and South America [1]. All of the hosts reported until now for this genus belong to 7 genera of ectatommine

and ponerine ants (Table 2). Only *K. floridana* (Ashmead) has been reported associated with a host from another subfamily, the myrmicine ant *Pogonomyrmex badius* (Latreille) (according to Ashmead, in [12]), but, considering that *Pogonomyrmex* larvae do not spin a cocoon, such an association seems very doubtful [1, 10]. Even if the presence of an undetermined species of eucharitid was already signaled for *Gnamptogenys annulata* (Mayr) and also for *G. horni* (Santschi) in Venezuela [26], and, very likely concerned a *Kapala* species, reliable associations between the genus *Kapala* and the ant genera *Ectatomma* and *Gnamptogenys* have previously been reported only for Mexico [10, 22] and for Colombia [25]. The new associations with these two ectatommine genera reported here for French Guiana, as well as the new associations or confirmations of record for the ponerine genera *Odontomachus* and *Pachycondyla*, support the outstanding importance of these four genera

TABLE 2: Known ant host species associated with the eucharitid genus *Kapala*.

Host species	Associated <i>Kapala</i> species
Ectatomminae	
<i>Ectatomma</i> Fr. Smith	
<i>E. brunneum</i> Fr. Smith	<i>Kapala</i> sp. [this work]
<i>E. ruidum</i> Roger	<i>K. iridicolor</i> (Cameron) [10, 18, 25], [16, 22]*, <i>K. izapa</i> Carmichael [10, 18]
<i>E. tuberculatum</i> (Olivier)	<i>Kapala</i> sp. [23]
<i>Gnamptogenys</i> Roger	
<i>G. regularis</i> Mayr	<i>K. iridicolor</i> (Cameron) [10], [22]**
<i>G. striatula</i> Mayr	<i>K. iridicolor</i> (Cameron) [10], [22]**
<i>G. sulcata</i> (Fr. Smith)	<i>K. iridicolor</i> (Cameron) [10], [22]**, <i>Kapala</i> sp. [24]
<i>G. tortuolosa</i> (Fr. Smith)	<i>Kapala</i> sp. [this work]
<i>Typhlomyrmex</i> Mayr	
<i>T. rogenhoferi</i> Mayr	<i>Kapala</i> sp. [24]
Ponerinae	
<i>Dinoponera</i> Roger	
<i>D. lucida</i> Emery	<i>Kapala</i> sp. [11]
<i>Hypoponera</i> Santschi	
<i>H. nitidula</i> (Emery)	<i>Kapala</i> sp. [24]
<i>Odontomachus</i> Latreille	
<i>O. bauri</i> Emery	<i>Kapala</i> sp. [1]
<i>O. brunneus</i> (Patton)	<i>Kapala</i> sp. [10, 22]
<i>O. haematodus</i> (L.)	<i>Kapala</i> sp. [this work]
<i>O. hastatus</i> (Fabr.)	<i>Kapala</i> sp. [1], [this work]
<i>O. insularis</i> Guérin-Méneville	<i>K. terminalis</i> Ashmead [4]
<i>O. laticeps</i> Roger	<i>Kapala</i> sp. [10, 22, 24]
<i>O. mayi</i> Mann	<i>Kapala</i> sp. [this work]
<i>O. meinerti</i> Forel	<i>Kapala</i> sp. [24]
<i>O. opaciventris</i> Forel	<i>Kapala</i> sp. [10, 22]
<i>Pachycondyla</i> Fr. Smith	
<i>P. apicalis</i> (Latreille)	<i>Kapala</i> sp. [22, 24], [this work]
<i>P. crassinoda</i> (Latreille)	<i>K. cuprea</i> Cameron [21]
<i>P. harpax</i> (Fabr.)	<i>K. atrata</i> (Walker) [1]***, <i>Kapala</i> sp. [24]
<i>P. stigma</i> (Fabr.)	<i>K. iridicolor</i> (Cameron) [10], [22]**, <i>Kapala</i> sp. [24], [this work]
<i>P. verenae</i> (Forel)	<i>Kapala</i> sp. [this work]
Myrmicinae	
<i>Pogonomyrmex</i> Mayr	
<i>P. badius</i> (Latreille)	<i>K. floridana</i> (Ashmead) [12] (doubtful record) [1, 10]

* Referred to as *Kapala sulcifacies*;** Referred to as *Kapala* sp.;*** Referred to as *Kapala surgens*.

of medium- to large-size poneromorph ants as potential hosts for *Kapala* wasps, a hypothesis previously formulated on the basis of more limited data [10, 22]. In contrast with other eucharitid genera which have a limited range of potential hosts and a marked specificity towards the host as far as genus is concerned [4–6], the diversity of host genera and species attacked by *Kapala* is impressive. The data reported here for French Guiana extend the number of reliable host species for *Kapala* to 24 (see Table 2), a diversity of host species only comparable to that found for the worldwide distributed orasemine genus *Orasema* Cameron [1, 6]. Such a broad range of potential hosts for *Kapala* is

also observed at the species level. For example, *K. iridicolor* (Cameron) (Table 2) parasitizes no less than five different species from three genera and two ant subfamilies [10, 22], and a similar phenomenon is likely to concern also some of the other species reported here as undescribed under the label “*Kapala* sp.”. Furthermore, *Kapala* species are known to parasitize ants in very diverse habitats including both highly anthropic modified environments (roadsides, college campus, agroecosystems, pastures) and well-preserved forests [1, 10, 22, 24, 25], [this work]. Combined with the fact that *Ectatomma*, *Gnamptogenys*, *Odontomachus*, and *Pachycondyla* are probably the four most widely distributed

genera among the Neotropical poneromorph ants [27–29], the wide host range of *Kapala* species and their ability to attack ants in diverse habitats could account, at least in part, for the dominant status of this genus among the eucharitine wasps of Central and South America. Moreover, though the sampling of ant nests in general is not really adequate to confidently discuss rates of parasitism, for four species (*E. brunneum*, *G. tortuolosa*, *O. haematodus*, and *P. stigma*), the number of collected nests is significant enough (see [18, 19] for a comparison) to give a good idea of the rates of parasitism at the population level. The rate of parasitism is low to medium (from 14.3% to 27.3%, see Table 1) in all of these four cases, but for certain associations, parasitism rate can reach significant values. Half of the nests were parasitized in the case of the association *Kapala* sp. and *O. hastatus* in French Guiana [this work] (but our sample limitation—only 6 nests—could result, in this specific case, in rates of parasitism relatively far from the natural figures) and up to 63% of the nests for the association between *K. iridicolor*/*K. izapa* (Carmichael) and *E. ruidum* Roger in Mexico [18]. Such high parasitism rates certainly contribute to explain why *Kapala* is one of the eucharitid genera most commonly collected by traps and aerial nets in the Neotropical region [1].

All of the eucharitids are parasitoids of ants, but the exact relationship between these wasps and their host is far from being understood, and the scenario might be more complicated than once thought. For example, from the 17 species already described in the genus *Kapala*, the complete life cycle is known for only one of them, *K. iridicolor* [10]. However, even for this species, the way planidia manage to enter ant nests is unknown. Instead of a direct attachment to a foraging ant worker, some *Kapala* planidia have been recently reported attached to different species of scorpions, suggesting the use of alternative phoretic transport [30]. However, such occasional phoretic attachments to scorpions more likely correspond to random attachment to any nearby living object and likely have nothing to do with getting into the ant nest. They would just give evidence in favour of the high mobility of the planidia. Eucharitids are known to attack five subfamilies of ants, and a correlation between the phylogenetic relationships of the parasitoid and host is suggested by both morphological and molecular evidence ([1], E. Murray and J. M. Heraty unpubl. data). Additional information about ant hosts and within-nest biology as well as about oviposition habits throughout the geographical range of *Kapala* is critical for further resolving the limits and phylogenetic relationships of the species of this genus.

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