REVISION OF XANTHOMICROGASTER CAMERON, 1911 (HYMENOPTERA: 
BRACONIDAE: MICROGASTRINAE)

BY

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THESIS

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ABSTRACT

Subfamily Microgastrinae (Hymenoptera: Braconidae) is one of the largest subfamilies of parasitoid wasps, both in terms of number of described species as well as estimated total number of species. Containing ~57 genera and exclusively attacking Lepidoptera, most of the diversity is concentrated within a few very large genera, with many smaller genera, including Xanthomicrogaster Cameron, 1911, existing with unknown morphological boundaries, life histories, and habitat use information. Containing only four described species, Xanthomicrogaster is one of the smallest genera, with extremely little information known. In addition to this lack of knowledge, Xanthomicrogaster is an extremely rarely collected genus, both in Malaise traps and rearing projects.

Through the large scale efforts of the Área de Conservación Guanacaste (ACG) project in Costa Rica, over 50 specimens of Xanthomicrogaster have been collected, both through Malaise traps and caterpillar rearing. In addition to these specimens, borrowed material of undescribed Xanthomicrogaster species from the Canadian National Collection (CNC) and Texas A&M University insect collection (TAMU) is examined in order to understand the variation and geographic range of the genus. Previous descriptions of the genus and the recognized species are examined and placed into context using the material from across the geographic range. Seven species are newly described here from the ACG project, identified using morphology, DNA sequences (COI, wingless, and 28S rDNA), and host caterpillar with host plant records. The morphological boundaries of the genus are proposed, and a dichotomous key to world species is presented to facilitate identification and future description of species. Two molecular phylogenies are produced, using appropriate outgroups: one for all newly described species using three genes, and one for all Xanthomicrogaster specimens obtained from the ACG project using the COI barcode region.

Host caterpillar use with host plant records is examined in the context of the phylogeny, revealing that Xanthomicrogaster specialize on concealed hosts, especially within superfamily Gelechioidea (Lepidoptera). In addition, sexual dimorphism is examined for the first time, as associations could be made using COI barcode information, revealing that males are often darker than females and are never
collected in Malaise traps.

Color patterns in *Xanthomicrogaster* are examined, especially as they vary by sex, geography, and phylogeny. The geographic range of *Xanthomicrogaster* is strictly Neotropical, apparently restricted by the Sierra Madre del Sur range in Mexico and the Andes between Argentina and Chile. In addition, the genus *Xanthomicrogaster* occurs in Trinidad, but it is unknown if its range extends to the island of Tobago or beyond. In terms of elevation, specimens of *Xanthomicrogaster* have been collected from 13 m to 1600+ m. This revision increases the knowledge about *Xanthomicrogaster*, synthesizing research from the past 100 years and setting the stage for future taxonomists to examine the group.
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CHAPTER 1. REVISION OF XANTHOMICROGASTER CAMERON, 1911 (HYMENOPTERA: BRACONIDAE: MICROGASTRINAE)

Introduction

The Microgastrinae (Insecta: Hymenoptera: Braconidae) is one of the largest subfamilies of insects and contains parasitoid wasps that exclusively attack lepidopteran hosts. This subfamily contains ~2,000 described species, but is estimated to contain 17,000 to 46,000+ species (Rodriguez et al. 2012). There are currently ~57 recognized genera of Microgastrinae. Xanthomicrogaster is one of the smallest genera, containing only four species. The Microgastrinae are known for their use in pest management (Whitfield 1997) and the genomic integration of bracoviruses (polydnaviruses) for use in host immune suppression (e.g., Stoltz & Whitfield 1992; Lapointe et al. 2007; Strand & Burke 2012).

Xanthomicrogaster Cameron, 1911 was created to house two species: X. fortipes and X. ruficollis (Cameron 1911). Since neither described species was designated as the type species for the genus, Viereck later designated X. fortipes as the type species (Viereck 1914). Wilkinson synonymized the genus Xanthomicrogaster with Microgaster, placing X. fortipes into Microgaster Latreille and X. ruficollis into Apanteles Foerster (Wilkinson 1930). (Apanteles ruficollis was later moved to Pseudapanteles by Mason [1981].) Muesebeck (1931) also placed X. fortipes into Microgaster, unaware that Wilkinson had done so a year prior. Nixon reevaluated the status of the genus, disagreeing with Wilkinson and Muesebeck, and reviving the genus to house the type as well as two newly described species, X. seres and X. pelides (Nixon 1965). The genus was redescribed by Mason, who noted that there were at least a dozen undescribed (Mason 1981), but did not describe any new species himself. The most recent addition to the genus was X. maculatus, described in 2002 (Penteado-Dias et al. 2002).

Notably, X. fortipes was described by Cameron, redescribed by Mason, and redescribed once more by Penteado-Dias et al. These redescriptions disagree in some ways, suggesting that our concept of X. fortipes may be too broad. There may be similar problems with other species, but at present, only the type series has been collected for the other three species of Xanthomicrogaster.

The genus is known from throughout Central and South America, with X. seres described from
Mexico, *X. pelides* and *X. maculatus* from Brazil, and *X. fortipes* from Guyana (then British Guiana) and reportedly found in Brazil and Suriname. Specimens of the genus are also known from Costa Rica due to the efforts of the Área de Conservación Guanacaste (ACG) project (Janzen 2000; Janzen 2004; Janzen et al. 2009; Janzen & Hallwachs 2011), which has been fundamental in establishing estimates of Neotropical diversity, especially within subfamily Microgastrinae. Since the late 1970s, researchers have been finding caterpillars, associating them with their native food plant species, and rearing them to adult. If a parasitoid emerged instead of an adult lepidopteran, it was inventoried as well, with the goal to discover as much natural history information as possible. Although more than 16,500 microgastrine samples have been reared or caught through the ACG project, only 69 specimens of *Xanthomicrogaster* have been found, making it one of the rarest genera of Microgastrinae found in Costa Rica. The genus is exclusively solitary, and, like other Microgastrinae, is a koinobiont endoparasitoid.

*Xanthomicrogaster* is generally recognized as monophyletic, with the following diagnosis: hind wing r-m delimiting a cell that is much taller than wide; ovipositor sheaths 0.3 - 1.0 times as long as hind tibia and setose over most of length; metasomal tergite 2 with deep crenulate grooves; propodeum with a conspicuous median carina (Whitfield 1997; Mason 1981).

Three of the four described species of *Xanthomicrogaster* are known for only one sex. *Xanthomicrogaster fortipes* and *X. maculatus* were described from only females, whereas *X. seres* was described only from males. *X. pelides* was described from a single female, with a possibly conspecific male collected at a different time in the same locality, though Nixon was not sure that it was correct, describing it as “? *pelides* sp. n.” (Nixon 1965). Sexual dimorphism has not been thoroughly examined in *Xanthomicrogaster*, and it may be difficult to associate newly found males and females. Thus, one component of this project is to associate males and females of the same species (determined via COI barcode) to explore potential sexual dimorphism within the genus.

Color pattern has been traditionally used for separation of species within the genus. The diagnostic value of color pattern variation will be evaluated in concert with COI haplotype information, obtained through the ACG project barcode inventory (Janzen et al. 2009; Janzen & Hallwachs 2011).
Other morphological characters will also be examined, and a three-gene molecular phylogeny will be constructed to examine the evolution of these species.

From an examination of 69 Costa Rican specimens, 54 CNC specimens, and 4 TAMU specimens, I will describe 7 new species of *Xanthomicrogaster*. In addition, I will address issues of sexual dimorphism as it relates to associating males and females of newly found species in the future. Host records from the ACG project are the first to be recorded, and will be presented, and information about the host caterpillars and their host plants synthesized. The currently known biogeographic distribution of *Xanthomicrogaster* is confirmed to be Neotropical, with new records presented from seven countries.
Materials and Methods

Specimens were examined from across the geographic range by using material from the ACG project and loaned material from the Canadian National Collection (CNC) and the Texas A&M University insect collection (TAMU) (Figure 1). Specimens from the ACG project were selected for DNA extraction and sequencing based on preliminary barcode species identifications; in total, nine Xanthomicrogaster specimens were used for molecular analyses, as well as a specimen of the ACG species found to be the sister group to the genus in a full COI analysis of all Microgastrinae, Choeras sp. “Whitfield04” (Table 1).

Whole genomic DNA was isolated from specimens using the QIAGEN DNEasy Blood & Tissue Kit, either from mid/hind legs or whole insects (Table 1). Primer sequences are available in Table 2, and PCR conditions are available in Table 3. All PCR was performed using the New England Biosciences TAQ 5X MasterMix. Enzymatic purification was performed using Exonuclease I and Shrimp Alkaline Phosphatase. Sequencing was performed by the W.M. Keck Center for Comparative and Functional Genomics, with BigDye termination reactions and Sanger sequencing using an Applied Biosystems 3730xl DNA Analyzer. Sequences were edited using Geneious R7.

In addition to the new sequences, outgroup sequences and one Xanthomicrogaster sequence were downloaded from GenBank, with accession numbers and original study listed in Table 4. Outgroups were selected by using BLAST, looking for the closest hits for each gene, and then prioritizing specimens with data for at least two of the three genes.

Alignment for wingless was performed by eye as it was trivial (no gaps). Alignment for 28S (D2 region) was performed using MAFFT v. 7.164b (Katoh & Standley 2013, Katoh et al. 2002). Alignment for COI sequences, sequenced as part of the ACG project, was also performed using MAFFT v. 7.164b. The total length of each gene’s sequence was 693 bp for COI, 502 bp for wingless, and 627 bp for 28S rDNA.

Phylogenetic analysis was performed using RAxML v. 7.2.6 (Stamatakis 2006). Five ML analyses were performed: one for each individual gene (totaling three), a concatenated analysis of all
three genes, and a full COI analysis using every sequence from the ACG. The same parameters were used for each run. A full analysis with rapid bootstrapping (-f a) was performed with 1000 rapid bootstrap replicates. A GTR+G model was used for the full ML analysis, while a GTR+CAT approximation was used for rapid bootstrapping.

In addition, a Bayesian analysis was completed for the concatenated dataset using MrBayes v. 3.2.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003; Ronquist et al. 2012). The dataset was partitioned by gene, with each gene having its own parameters free to vary using the GTR+G model. The analysis was done using 2 runs, each with 4 chains, for 2,000,000 generations, sampled every 1,000 generations. The default burn-in from Tracer v. 1.6 of 10% (200,000 generations) was used. Convergence between the two runs was verified using Tracer v. 1.6, and trees were summarized via Tree Annotator v. 1.8.1 using the Maximum Clade Credibility (MCC) method (Drummond et al. 2012).

A phylogenetic network was constructed in order to visualize phylogenetic signal and support for clades found in the ML and Bayesian analysis. Unlike phylogenetic trees, phylogenetic networks are able to display conflicting relationships, rather than simply reporting a low support value (Morrison 2011). Using the three-gene dataset, a Neighbor-Net was constructed with K2P distance correction in SplitsTree4 (Huson & Bryant 2006).
Results

Generic diagnosis

*Xanthomicrogaster* Cameron, 1911

(= *Microgaster* Latreille; Wilkinson 1930 and Muesebeck 1931)

Type: *Xanthomicrogaster fortipes* Cameron; in Natural History Museum, London. Collected British Guyana.

Diagnosis: Coloration ranging from yellow to black. Strictly Neotropical distribution. Size 2.8mm - 4.3mm. Flagellum of antennae light brown to dark brown. Forewing second submarginal cell closed distally by r-m, forming small cell or areolet. Hind wing r-m delimiting cell much taller than wide (longer measured on axis from anterior to posterior wing edge than on axis from basal to distal ends of wing).

Hind coxae enlarged. Propodeum with strong median carina, rarely incomplete posteriorly. Tergite 1 rugose or punctate, with deep furrow. Anterior, posterior and, occasionally, lateral margins of tergite 2 deeply crenulate. Tergite 2 two to four times as wide as long. Ovipositor sheath to hind tibia ratio 0.6 to 0.9, ovipositor sheath setose over most of length.

Remarks: Most easily recognized by the crenulate anterior and posterior margins of tergite 2, combined with the closed r-m cell of the forewing and yellow to black coloration. Commonly confused with *Diolcogaster*, but easily distinguished by the crenulate margins of tergite 2, which *Diolcogaster* lack. Also confused with *Promicrogaster*, due to convergent coloration, but easily distinguished by the deep median furrow of tergite 1, which *Promicrogaster* lack.

Morphological features used to distinguish the species of *Xanthomicrogaster* include color pattern, body size, width to length ratio of metasomal tergite 2, and hind tibia length to ovipositor length ratio. Other variable morphological characters were examined, including: a) punctation of the metasomal
tergites, b) sculpturing on the propodeum, c) wing venation, and d) hind tibial spurs. These characters are either too variable (a, b), diagnostically uninformative (d), or too subjective (a, b, c) to be of use in species-level separation.

In order to maintain consistency in species descriptions, all color patterns are described in terms of unpigmented, yellow, black, and brown. Unpigmented sections appear white, apparently lacking both yellow and dark pigments. Yellow varies in intensity, but always lacks dark pigment; it may be perceived as orange by some. Black is clearly dark, marked by areas of heavy deposition of dark pigment. Brown is the intermediate between the two, where some dark pigment is deposited, but not enough to color the section black.


The only species previously placed in *Xanthomicrogaster* is *Psuedapanteles ruficollis* (Cameron, 1911); this species was placed in genus *Apanteles* by Wilkinson (1930), and placed in *Pseudapanteles* by Mason (1981).

Recorded collection localities include Guyana (*X. fortipes*), Brazil (*X. maculatus, X. fortipes* and *X. pelides*), Mexico (*X. seres*), Suriname (*X. fortipes*), and French Guiana (unidentified material from Malaise trap; Braet et al. 2000). Examination of undescribed *Xanthomicrogaster* extends this list to include Costa Rica, Colombia, Venezuela, Trinidad and Tobago, Ecuador, Peru, and Argentina.

Previously described species

The four previously known species of *Xanthomicrogaster* are described first, along with notes compiled from their original descriptions as well as any redescriptions, and photographs of the type specimens.
This species is unique in that the body is fully yellow, including the hind tarsus, unlike any other described species. It is known to occur in Guyana as well as possibly Suriname and Brazil.

A photograph of the holotype provided by Gavin Broad of the Natural History Museum, London, was examined. The original description (Cameron 1911) and the first redescription (Nixon 1965) were both written using the type specimen (Figure 2A), and thus agree completely, though the language used by Nixon is more precise than that of Cameron. The most important note from these descriptions is that of the body and legs, as being “entirely honey-yellow” (Nixon 1965).

Penteado-Dias et al. recorded this species in Brazil and Suriname. After examining 54 wasps from the CNC collection across the range of Xanthomicogaster distribution, no wasp was found matching the original description of Cameron and the redescription of Nixon. Some wasps had similar overall color patterns, but upon detailed examination represent other, undescribed species. If this species is so widespread and apparently abundant (13 wasps across multiple states of Brazil, Suriname, and Guyana), and no other species were mentioned to be found by the authors, it would be expected that some of the Xanthomicogaster in the CNC collection from Brazil would be X. fortipes -- but this is not the case.

The description by Penteado-Dias et al. disagrees with the redescription by Nixon, in that the type has the 2nd metasomal tergite with “coarse but very superficial structure present only towards sides,” while Penteado-Dias et al. state that the second tergite was “medially coarsely punctate.” Nixon states that the legs were “entirely honey-yellow,” while Penteado-Dias state that the hind tarsus is brown. A photo of the type specimen (Figure 2A) show that the hind legs do appear to darken distally (though this
may be due to shadows), but the hind tarsus still appears yellow. Punctation on the 2\textsuperscript{nd} metasomal tergite could not be verified in the type, as it was not captured in the photograph.

The descriptions by Cameron and Nixon are sufficiently different from that of Penteado-Dias \textit{et al.} to conclude that Penteado-Dias \textit{et al.} are probably describing at least one different species, with careful examination possibly revealing many. Host data and molecular evidence may be necessary to discern how many species there are, and future research should include at least the COI barcode region as a species association tool.

\textit{Xanthomicrogaster pelides} Nixon, 1965


\textit{Xanthomicrogaster pelides} is recognized in the female by the anterior portion of the mesoscutum being darkened (as in Figure 3), with yellow hind coxa. In the male, it is recognized by its entirely black hind coxa, as well as predominantly mesosoma.

A photograph of the holotype provided by Gavin Broad of the Natural History Museum, London, was examined. There are no anomalies in the description of \textit{X. pelides}, with the exception of the coloration, which includes red. Due to the dark coloration of this wasp, the lighter colors are not clearly visible, yet it appears yellow rather than red (Figure 2B). Some freshly collected species appear to be more “orange,” but it is still closer to yellow, and is treated here as yellow.

Nixon tentatively associated a male with the female of the species, having been collected in the same locality three years apart. Though the male specimen has not been examined, Nixon's description of the male vs. the female is consistent with what is now known about sexual dimorphism in the genus, and thus should be considered correct for the time being.
*Xanthomicrogaster seres* Nixon, 1965


*Xanthomicrogaster seres* may be difficult to distinguish from other species, possessing a black metanotum, black propodeum, black episternum, and yellow epimeron, and in that the ventral portion of the hind coxa and ventral portion of the mesopleuron are black. It is unique among others with the same general pattern in the coloration of the hind coxa. The extent of the coloration of the hind coxa is such that the portion of the hind coxa abutting the mid coxa is black, and the area of black coloration present distally is nearly the same as that of the black coloration present anywhere else on the coxa (see Figure 4 for comparison).

Though Nixon describes *X. seres* as “predominantly bright reddish yellow,” the coloration is not significantly different from any of the other *Xanthomicrogaster* examined, and thus, as mentioned in the generic remarks, is considered yellow (Figure 2C).

Many of the characters that Nixon considered in the description of the male (the type) seem to be artifacts of preservation rather than actual diagnostic characters, so caution should be taken. His description of the “apical tergites very short and retracted beneath 3” is very similar to that of some other *Xanthomicrogaster*, but other individuals of the same species often have visible, substantial tergites, with a bloated metasoma apparently stretching the tergites such that unpigmented membrane can be seen underneath.

*Xanthomicrogaster maculatus* Penteado-Dias, Shimabukuro, & van Achterberg, 2002

*Xanthomicrogaster maculatus* Penteado-Dias, Shimabukuro, & van Achterberg, 2002: 42 (original description).

*Xanthomicrogaster maculatus* is the only described species in which the lateral lobes of the
mesoscutum are black while the central lobe is yellow.

The only material examined were the photographs included in the original description (Penteado-Dias et al. 2002).

The species description possibly refers only to the holotype, and does not strictly match the photographs provided by the authors. In fact, the two photographs provided are of different wasps, which have different color patterns (and thus may be different species). The wasp pictured in Figure 1 is much yellower, whereas the wasp in Figure 2 (figures in Penteado-Dias et al. 2002) is darker. The description, however, captures none of this variation, and describes a vague color pattern that could apply to many wasps of different species. As is the case with the redescription of *X. fortipes*, many different species of wasps could, in fact, be described as paratypes of *X. maculatus*.

The description states that the mesosoma is yellow, except for some regions which are black. The lateral and central lobes of the mesoscutum are described to be black; however, the central lobe is only black anteriorly in the wasps in Figures 1 and 2 (in Penteado-Dias et al. 2002), while the lateral lobe is very black in Figure 2, with a much lesser extent of black in Figure 1. The scutellum laterally (called “lunules” by them, also known as axillae) is also described to be black. The lower half of the mesopleuron, as well as the mesosternum and the metanotum, are described as black, which appears to be true in both figures, though the wings obscure the metanotum in both. “Some areas of the propodeum” are listed as black, though these areas are not enumerated. In Figure 1, it appears as though the propodeum itself is yellow, with the dorsal portion of the metapleuron being black; in Figure 2, the propodeum is obscured, though the ventral tip and dorsal portion of the metapleuron are black.

The metasoma description is consistent between the two wasps, though once again, the third tergite is listed as “mostly yellow,” which does not detail where the black coloration occurs. In Figure 2 (in Penteado-Dias et al. 2002), the third tergite appears to be entirely black; in Figure 1, the third tergite is yellow except for a black spot occurring medially.

These discrepancies may be due to intraspecific variation (that is not captured in the description) or the type series may comprise two or more species. A detailed examination and (possibly) molecular
evidence are necessary in order to resolve these discrepancies and produce a description capturing the variation of the species.

New species descriptions

*Xanthomicrogaster algentryi* sp. nov.

(Figure 5)


**Holotype**, ♀. 3.65 mm.
Head yellow; ocellar triangle yellow; inner portion of scape yellow, outer portion of scape brown; flagellomeres brown; mouthparts yellow.

Pronotum yellow; propleuron yellow; portion of mesopleuron anterior to mesepisternal groove yellow, rest black; metapleuron black. Mesoscutum yellow; scutellum black except for the axillae, which are yellow. Metanotum black; propodeum black, with relatively smooth median carina, and lateral carinae forming a Y encompassing yellow spiracle, as well as forming prominent extensions lateroposteriorly. Tegula yellow, humeral plate yellow. Foreleg and midleg yellow, with exception of tarsal claw, which is brown. Hind coxa yellow except for distal tip, which is sometimes brown; hind trochanter yellow; hind trochantellus yellow; hind femur yellow; hind tibia yellow; hind tarsus yellow with the exception of tarsal claw, which is brown.

Wings as in Figure 5B.

Metasoma: first tergite rugose and yellow or unpigmented, with deep furrow; second tergite rugose, black medially and brown laterally; anterior and posterior margins crenulate. Third tergite black medially, yellow laterally. Fourth through eighth tergites black medially, yellow laterally. Sternum yellow. Hypopygium yellow. Ovipositor sheath dark brown.

Hind tibia 1.28 mm long, and ovipositor sheath 1.00 mm long (ovipositor sheath to hind tibia ratio: 0.78). Metasomal tergite 2 is 0.30 mm long and 0.76 mm wide (2.53 times as wide as long).

Male.—Unknown.

Cocoon.—Unknown.

Host.—Unknown.

Etymology: Xanthomicrogaster algentryi sp. n. is dedicated to Dr. Al Gentry of the Missouri Botanical Garden in recognition of his serious taxonomic support for coming to know the plants of Área de Conservación Guanacaste.
Remarks: *Xanthomicrogaster algentryi* sp. n. is easily recognized due to its unique coloration, possessing a black propodeum, yellow metasomal tergite 1, and black metasomal tergite 2, a pattern that is not found on any known specimen.

This species is, by far, the most common *Xanthomicrogaster* species found in Malaise trap samples from the ACG, and its life history is completely unknown.

*Xanthomicrogaster ronliesneri* sp. nov.

(Figure 6)


Holotype, ♀. 3.65 mm.

Head yellow; ocellar triangle yellow; inner portion of scape yellow, outer portion of scape brown; flagellomeres brown; mouthparts yellow.

Pronotum yellow; propleuron yellow; dorsal ¾ of mesopleuron yellow, ventral ¼ of mesopleuron black; metapleuron yellow. Mesoscutum yellow; scutellum yellow. Metanotum yellow; propodeum yellow, with relatively smooth median carina, and lateral carinae forming a Y encompassing yellow spiracle, as well as forming prominent extensions lateroposteriorly. Tegula yellow, humeral plate yellow. Foreleg and midleg yellow, with exception of tarsal claw, which is brown. Hind coxa yellow except for posterior region, which is brown; hind trochanter yellow; hind trochantellus brown; hind femur yellow anteriorly, brown posteriorly; hind tibia very light yellow anteriorly, brown posteriorly; hind tarsus brown.

Wings as in Figure 6B.

Hind tibia 1.22 mm long, and ovipositor sheath 0.97 mm long (ovipositor sheath to hind tibia ratio: 0.79). Metasomal tergite 2 is 0.28 mm long and 0.84 mm wide (3 times as wide as long).

Male.—Unknown.

Cocoon.—Large, white, shaggy, single cocoon. Found in host cocoon.

Host.—Single record on undescribed species of Elachistidae, feeding on *Schnella glabra* (Fabaceae).

Etymology.—*Xanthomicrogaster ronliesneri* sp. n. is dedicated to Dr. Ron Liesner of the Missouri Botanical Garden in recognition of his serious taxonomic support for coming to know the plants of Área de Conservación Guanacaste.

Remarks: *Xanthomicrogaster ronliesneri* sp. n. is recognized by its mostly yellow body, with the ventral portion of the mesosoma and the ventral portion of the hind coxa being black.

This species is most similar in appearance to *X. fortipes* Cameron 1911, with the exception of the dark coloration on the ventral portion of the mesosoma and hind coxa, and of the distal portion of the hind tibia.

The description above is based on one specimen and may be broadened when other specimens are found.

*Xanthomicrogaster mikegrayumi* sp. nov.

(Figures 7 and 8)

Material.—**Holotype**, ♀, Costa Rica, Alajuela, ACG, Sector Rincon Rain Forest, Sendero Juntas (10.90661° N, 85.28784° W), 400 m. Coll. 5.vii.2010, Pablo Umaña Calderon. Voucher numbers:
DHJPAR0040528, 10-SRNP-42238. Reared from *Antaeotricha* sp. (Elachistidae), found on host plant *Inga oerstediana* (Fabaceae).


Holotype, ♀. 3.6 mm.

Head yellow; ocellar triangle yellow; inner portion of scape yellow, outer portion of scape brown; flagellomeres brown; mouthparts yellow.

Pronotum yellow; propleuron yellow; dorsal, anterior portion of mesopleuron yellow, while ventral, posterior portion of mesopleuron black, including along and dorsal to mesepisternal groove; scalloped, such that the black portion occupies an area laterally and medially, with yellow area between it, forming a W or M shape; metapleuron black. Mesoscutum yellow; scutellum yellow. Metanotum black, except for posterior margin between metanotum and propodeum, which is yellow; propodeum black, with relatively smooth median carina, and lateral carinae forming a Y encompassing yellow spiracle, as well as forming prominent extensions lateroposteriorly. Tegula yellow or brown, humeral plate yellow or brown.
Foreleg and midleg yellow, with exception of tarsal claw, which is brown. Hind coxa black; hind trochanter yellow; hind trochantellus brown; hind femur yellow anteriorly for first ⅛, brown posteriorly for last ⅜; hind tibia yellow; hind tarsus yellow anteriorly, gradually darkening to brown at tarsal claw.

Wings as in Figure 7B.

Metasoma: first tergite rugose and unpigmented (white) to yellow with deep furrow; second tergite rugose, with anterior and medioposterior portion dark brown to black, and lateroposterior portion yellow to dark brown (but always with less pigmentation than the anterior/medioposterior portion); anterior and posterior margins crenulate. Third tergite dark brown, except for posteriolaterally, where it is yellow (occasionally nearly entirely dark brown, but always with at least some yellow laterally). Fourth through eighth tergites yellow laterally and dark brown medially. Sternum yellow. Hypopygium yellow. Ovipositor sheath brown.

Hind tibia 1.02 mm long, and ovipositor sheath 0.92 mm long (ovipositor sheath to hind tibia ratio: 0.90). Metasomal tergite 2 is 0.32 mm long and 0.80 mm wide (2.5 times as wide as long).

Male.—3.25 mm. Head and mesosoma similar to female, with the following differences: separation between black and yellow on mesopleuron not as scalloped or well-defined as in female, though still somewhat scalloped.

Wings as in Figure 8B.

Metasoma: Similar to female, except for T4-T8, which is dark brown, and sternum, which is almost entirely yellow, except posteriorly, where it is brown.

Hind tibia 1.1 mm. Metasomal tergite 2 is 0.30 mm long and 0.76 mm wide (2.14 times as wide as long).

Cocoon.—White, cocoon, either shaggy or not. Found attached to leaf substrate (three) or in host cocoon (one). See Figure 9G-H.

Host.—All records from Antaeotricha (Elachistidae) feeding on two different species of Inga (Fabaceae), I. oerstediana and I. chocoensis.
Etymology.—*Xanthomicrogaster mikegrayumi* sp. n. is dedicated to Dr. Mike Grayum of the Missouri Botanical Garden in recognition of his serious taxonomic support for coming to know the plants of Área de Conservación Guanacaste.

Remarks: *Xanthomicrogaster mikegrayumi* sp. n. is most easily recognized by the coloration of the mesopleuron, in which the dorsal, anterior portion of mesopleuron yellow, while ventral, posterior portion of mesopleuron black, including along and dorsal to mesepisternal groove; scalloped, such that the black portion occupies an area laterally and medi ally, with yellow area between it, forming a W or M shape. In the male, this separation is not as well defined, and can also be recognized by the combination of a fully yellow propleuron and black metepimeron.

This species is most remarkable in that it lacks much sexual dimorphism, with the male and female looking remarkably similar. *X. mikegrayumi* sp. n. may be confused with *X. nelsonzamorai* sp. n., but is easily distinguished based on the coloration of the propleuron, which is yellow in *X. mikegrayumi* sp. n. and black or brown, at least in part, in *X. nelsonzamorai* sp. n.

*Xanthomicrogaster nelsonzamorai* sp. nov.

(Figures 10 and 11)


Holotype, ♀. 3.1 mm.

Head yellow; ocellar triangle yellow; inner portion of scape yellow, outer portion of scape brown; flagellomeres brown; mouthparts yellow.

Pronotum yellow; propleuron brown ventrally and posteriorly, yellow dorsally and anteriorly; mesopleuron black, with the exception of a small anteriodorsal splotch posterior to mesepisternal groove and the entire region anterior to mesepisternal groove, which are yellow; metapleuron black. Mesoscutum yellow; scutellum yellow, except for axillae, which are either yellow or black. Metanotum black; propodeum black, with relatively smooth median carina, and lateral carinae forming a Y encompassing yellow spiracle, though the more medial portion weakens anteriorly, as well as forming prominent extensions lateroposteriorly. Tegula yellow, humeral plate yellow. Foreleg and midleg yellow, with exception of tarsal claw, which is brown. Hind coxa black to dark brown dorsally, black ventrally; hind trochanter variable, yellow, dark brown, or black; hind trochantellus light brown to black; hind femur yellow anteriorly, brown posteriorly; hind tibia yellow; hind tarsus yellow, except for tarsal claw, which is brown.

Wings as in Figure 10B.

Metasoma: first tergite rugose and unpigmented (white) to yellow, with deep furrow; second tergite rugose and yellow, with the exception of the median, which is pale brown; anterior and posterior margins crenulate. Third tergite brown to black medially, with a small area laterally yellow, sometimes
moreso posteriorly than anteriorly. Fourth through eighth tergites brown to black medially, yellow laterally. Sternum yellow. Hypopygium brown to black ventrally, yellow dorsally. Ovipositor sheath dark brown.

Hind tibia 1.02 mm long, ovipositor sheath 0.9 mm long (ovipositor sheath to hind tibia ratio: 0.88). Metasomal tergite 2 is 0.28 mm long and 0.66 mm wide (2.36 times as wide as long).

Male.—2.8 mm. Head and mesosoma similar to female, with the following differences: humeral plate light brown. Hind coxa, trochanter and trochantellus black.

Wings as in Figure 11B.

Metasoma: first tergite rugose and brown with deep furrow, except for yellow spot posteriomedially. Second tergite rugose, brown, medially raised, with anterior and posterior margins crenulate and black. Third tergite brown medially, with a small splotch anteriolaterally yellow. Fourth through eighth tergites black. Sternum yellow anteriorly and black posteriorly.

Hind tibia 1.04 mm. Metasomal tergite 2 is 0.28 mm long and 0.60 mm wide (2.14 times as wide as long).

Cocoon.—White, shaggy cocoon.

Host.—Unknown caterpillar in family Gelechiidae, found on Celtis iguanaea (Ulmaceae).

Etymology.—Xanthomicrogaster nelsonzamorai sp. n. is dedicated to Dr. Nelson Zamora of the Costa Rica's INBio and national biodiversity inventory in recognition of his serious taxonomic support for coming to know the plants of Área de Conservación Guanacaste.

Remarks: Xanthomicrogaster nelsonzamorai sp. n. is recognized in the female by the combination of a medially brown, laterally yellow hypopygium and entirely black metanotum. The male is the only described species in which the medial lobe of the scutellum is yellow while the lateral lobes are black.

Xanthomicrogaster nelsonzamorai sp. n. may be confused with Xanthomicrogaster mikegrayumi sp. n. They are easily distinguished by the propleuron, which is yellow in X. mikegrayumi sp. n. and black or brown, at least in part, in X. nelsonzamorai sp. n.
Xanthomicrogaster clarkorum sp. nov.

(Figures 12 and 13)


Holotype, ♀. 3.60 mm.

Head yellow; ocellar triangle yellow; inner portion of scape yellow, outer portion of scape brown; flagellomeres brown; mouthparts yellow.

Pronotum yellow; propleuron yellow; mesopleuron yellow, except ventral portion, which is black; metapleuron yellow. Mesoscutum yellow; scutellum yellow. Metanotum yellow; propodeum yellow, with relatively smooth median carina, and lateral carinae forming a Y encompassing yellow spiracle, as well as forming prominent extensions lateroposteriorly. Tegula yellow, humeral plate dark brown. Foreleg and midleg yellow, with exception of tarsal claw, which is brown. Hind coxa yellow, except ventral portion, which is black; hind trochanter black outside, yellow inside; hind trochantellus black outside, yellow inside; hind femur yellow for proximal ⅛, brown distally; hind tibia yellow for proximal ¾, brown distally; hind tarsus brown.

Wings as in Figure 12B.

Metasoma: first tergite rugose and yellow, with deep furrow; second tergite rugose and yellow, anterior and posterior margins crenulate. Third tergite variable – yellow, light brown, or yellow with light brown spots laterally, such that the medial portion and lateral edges are yellow. Fourth through eighth tergites brown medially (though it may be a very small spot or nearly the entire tergite), yellow laterally. Sternum yellow. Hypopygium brown ventrally, yellow dorsally. Ovipositor sheath black.

Hind tibia 1.44 mm long, ovipositor sheath 1.00 mm long (ovipositor sheath to hind tibia ratio: 0.69). Metasomal tergite 2 is 0.36 mm long and 0.86 mm wide (2.38 times as wide as long).
Male.—3.65 mm. Head similar to female.

Mesosoma similar to female, with the following differences: mesopleuron yellow, except ventral portion and dorsal tip between forewing and hindwing articulations, which is black. Metepisternum black, metepimeron yellow, and area between mid and hind coxae black. Lateral lobes of mesoscutum occasionally light brown. Metanotum black, except median lobe, which is yellow. Propodeum dark brown to black, with more sculpturing along median carina than female. Hind tibia variable, either yellow for proximal ¾ and brown distally, or mottled brown/yellow in proximal ⅛ and brown distally.

Wings as in Figure 13B.

Metasoma: first tergite variable: either yellow, except for small brown tinges along lateral margins, which are black, or nearly entirely black, except for medioposterior yellow spot, and rugose, with deep furrow. Second tergite variable: either yellow, except for lateral margins, which are black, or entirely black, except for medial yellow spot which is rarely absent, and rugose with anterior and posterior margins crenulate and black. Third tergite black. Fourth through eighth tergites black. Sternum yellow. Genitalia brown.

Hind tibia 1.56 mm. Metasomal tergite 2 is 0.38 mm long and 0.86 mm wide (2.26 times as wide as long).

Cocoon.—White, shaggy cocoon. See Figure 9A-E.

Host.—Specialist on Ethmia catapeltica (Depressariidae) found on Cordia alliodora (Boraginaceae).

Etymology.—Named in honor of Dr. Francis M. and Mrs. Harlie M. Clark. Dr. Francis M. Clark was a microbiologist and professor at University of Illinois, and an award named in his and his wife’s honor made the phylogenetic component of this research possible.

Remarks: The female of Xanthomicrogaster clarkorum sp. n. is recognized by a medially brown, laterally yellow hypopygium and entirely yellow metapleuron. The male is identified by its partially brown propleuron (at the ventral tip), and the coloration of the hind coxa. The extent of the coloration of the hind coxa is such that the area of black coloration present distally is greater than that of the black coloration present anywhere else on the coxa (see Figure 4 for comparison).
The male is nearly identical to Xanthomicrogaster barryhammeli sp. n., described below. The most useful character for separating these species is the coloration of the ventral tip of the propleuron, which is yellow in X. barryhammeli sp. n. and partially brown in X. clarkorum sp. n. Both the male of X. clarkorum sp. n. and the male of X. barryhammeli sp. n. look very similar to X. seres Nixon 1965, and are differentiated from X. seres by the coloration of the distal portion of the hind coxa; in X. clarkorum sp. n. and X. barryhammeli sp. n., the portion of the coxa that is colored black is larger at the distal tip of the coxa than anywhere else on the coxa; in X. seres, it is nearly the same size as anywhere else on the coxa (see Figure 4).

Xanthomicrogaster barryhammeli sp. nov.

(Figure 14)

Material.—Holotype, ♂, Costa Rica, Guanacaste, ACG, Sector Pitilla, Leonel (10.99637° N, 85.40195° W), 510 m. Coll. 17.ii.2010, Dinia Martinez. Voucher numbers: DHJPAR0039072, 10-SRNP-70551. Reared from Dichomeris sp. (Gelechiidae), found on host plant Calea pittieri (Asteraceae).


(where deposited… USNM, CNC, INBio, INHS if enough material)

Holotype, ♂. 3.30 mm.
Head yellow; ocellar triangle yellow; inner portion of scape yellow, outer portion of scape brown; flagellomeres brown; mouthparts yellow.

Pronotum yellow; propleuron yellow dorsally, brown ventrally; mesopleuron yellow, except ventral portion and dorsal tip between forewing and hindwing articulations, which is black or brown. Metepisternum black; metepimeron yellow anteriorly and black dorsally; area between mid and hind coxae black. Mesoscutum yellow, except for lateral lobes, which are brown or yellow; scutellum yellow. Metanotum black, except for median lobe, which is black or yellow; propodeum black, with relatively smooth median carina, and lateral carinae forming a Y encompassing yellow spiracle, as well as forming prominent extensions lateroposteriorly. Tegula yellow, humeral plate brown. Foreleg and midleg yellow, with exception of tarsal claw, which is brown. Hind coxa yellow dorsally and black ventrally on proximal half, and completely black on distal half; hind trochanter black; hind trochantellus black; hind femur yellow for proximal 7/8, brown distally; hind tibia yellow for proximal ⅞, brown distally; hind tarsus brown.

Wings as in Figure 14B.

Metasoma: first tergite rugose and yellow to unpigmented with deep furrow, sometimes with brown splotches between furrow and margin posteriorly; second tergite rugose, either completely black or black with a posteriomedial yellow spot; anterior and posterior margins crenulate. Third tergite either completely black or black with a posteriomedial yellow spot. Fourth through eighth tergites variable -- either black with yellow medially, light brown medially with a yellow posteriomedial spot and yellow laterally, or dark brown except for yellow lateral edges. Sternum yellow. Genitalia brown.

Hind tibia 1.02 mm long. Metasomal tergite 2 is 0.32 mm long and 0.66 mm wide (2.06 times as wide as long).

Female.—Unknown.

Cocoon.—White, shaggy cocoon. See Figure 9I.
Host.—Undescribed caterpillar in *Dichomeris* (Gelechiidae) found on two plants in family Asteraceae: *Koanophyllon hylonoma* and *Calea pittieri*.

Etymology.—*Xanthomicrogaster barryhammeli* sp. n. is dedicated to Dr. Barry Hammel of the Missouri Botanical Garden in recognition of his serious taxonomic support for coming to know the plants of Área de Conservación Guanacaste.

Remarks: This species is recognized by its fully yellow propleuron and the coloration of the hind coxa. The extent of the coloration of the hind coxa is such that the area of black coloration present distally is greater than that of the black coloration present anywhere else on the coxa (see Figure 4 for comparison).

This species is nearly identical to the male of *Xanthomicrogaster clarkorum* sp. n., described above. See the remarks for the description of *X. clarkorum* sp. n. and Figure 4 for the differences between the species.

*Xanthomicrogaster peterraveni* sp. nov.

(Figure 15)


(where deposited… USNM, CNC, INBio, INHS if enough material)

Holotype, ♀. 4.3 mm.
Head yellow; ocellar triangle yellow; inner portion of scape yellow, outer portion of scape brown; flagellomeres brown; mouthparts brown.

Pronotum yellow; propleuron black ventrally and yellow dorsally; mesopleuron black, with the exception of a small anteriodorsal splotch, which is yellow; metapleuron black. Mesoscutum yellow; scutellum yellow. Metanotum black; propodeum black, with relatively smooth median carina, and lateral carinae forming a Y encompassing yellow spiracle, as well as forming prominent extensions lateroposteriorly. Tegula yellow, humeral plate brown. Fore coxa brown ventrally, yellow dorsally; fore trochanter brown ventrally, yellow dorsally; fore trochantellus brown; fore femur yellow, except for small brown spot ventrally and proximally; fore tibia yellow; fore tarsus yellow, except claw, which is brown and expanded, containing a white pad. Mid coxa brown; mid trochanter brown; mid trochantellus brown; mid femur brown; mid tibia yellow proximally and brown distally; mid tarsus yellow, except for last tarsomere, which is brown, and claw, which is brown and expanded, containing a white pad. Hind coxa black; hind trochanter black; hind trochantellus black except for ventral portion, which is yellow; hind femur black except for proximal ventral tip, which is yellow; hind tibia black except for proximal tip, which is yellow; hind tarsus black, claw not expanded and lacking white pad.

Wings as in Figure 15B.

Metasoma: first tergite rugose and black with deep furrow. Second tergite rugose and black, with anterior and posterior margins crenulate. T3-T8 black and very smooth. Sternum black and very smooth. Hypopygium black. Ovipositor sheath black.

Hind tibia 1.52 mm long, and ovipositor sheath 1.44 mm long (ovipositor sheath to hind tibia ratio: 0.95). Metasomal tergite 2 is 0.38 mm long and 1.28 mm wide (3.37 times as wide as long).

Male.—Unknown.

Cocoon.—White, not very shaggy cocoon. See Figure 9F.

Host.—One record from Palpusia cf. plumipes (Crambidae) found on Coutarea hexandra (Rubiaceae). One record from Anacrusis nephrodes (Tortricidae) found on Trichospermum grewiifolium (Malvaceae).
Etymology.—*Xanthomicrogaster peterraveni* sp. n. is dedicated to Dr. Peter Raven of the Missouri Botanical Garden in recognition of his serious taxonomic support for coming to know the plants of Área de Conservación Guanacaste.

Remarks: *Xanthomicrogaster peterraveni* sp. n. is very distinctive, being nearly entirely black, including the entirety of the hypopygium, and being over 4.0 mm long.

Though this species is exceptional among *Xanthomicrogaster*, it clearly belongs to *Xanthomicrogaster* based on molecular evidence (COI, wingless, and 28S ribosomal) and morphological synapomorphies, including closed forewing areolet, anterior and posterior margins of the second metasomal tergite crenulate, second metasomal tergite much longer than wide, and closed r-m cell on the hindwing that is taller than wide. It is, however, significantly different from the rest of *Xanthomicrogaster*, including all undescribed borrowed material, and may represent a different subgenus or species-group – more wasps from different regions are needed to confirm this species’ relationship to the other *Xanthomicrogaster*.

*Key to world species of Xanthomicrogaster*

1. Female .......................................................... 2
1’. Male ................................................................... 10

2. Body size over 4 mm; mouthparts brown; hypopygium entirely black (as in Figure 16). Costa Rica. .......................... Xanthomicrogaster peterraveni* sp.n. 2’. Body size under 4 mm; mouthparts yellow; hypopygium entirely or partially yellow. ............. 3

3. Mesoscutum entirely yellow. .......................................................... 4
3’. Anterior portion of medial lobe of mesoscutum darkened (as in Figure 3) ................................................. 9
4. Hypopygium entirely yellow (as in Figure 5C). .......................................................... 5

4’. Hypopygium medially brown, laterally yellow (as in Figure 10C)............................... 8

5. Mesosoma and hind coxa entirely honey-yellow. Guyana. (Possibly Suriname and Brazil) .......... Xanthomicrogaster fortipes Cameron 1911

5’. Mesosoma and/or hind coxa entirely or partially black or dark brown............................ 6

6. Hind coxa entirely black (as in Figure 7C). Costa Rica........ Xanthomicrogaster mikegrayumi sp.n.

6’. Hind coxa yellow with brown distal tip (as in Figures 5C, 6C). ..................................... 7

7. Metapleuron entirely black (as in Figure 5C). Costa Rica.........Xanthomicrogaster algentryi sp.n.

7’. Metapleuron entirely yellow (as in Figure 6C). Costa Rica....... Xanthomicrogaster ronliesneri sp.n.

8. Metapleuron entirely black (as in Figure 10C). Costa Rica....Xanthomicrogaster nelsonzamorai sp.n.

8’. Metapleuron entirely yellow (as in Figure 7C). Costa Rica. .... Xanthomicrogaster clarkorum sp.n.

9. Hind coxa black (as in Figure 7C). Brazil .................................................................

……………………………………………………………………………………………………….. Xanthomicrogaster maculatus Penteado-Dias, Shimabukuro & van Achterberg 2002

9’. Hind coxa yellow. Brazil ................................................................. Xanthomicrogaster pelides Nixon 1965

10. Ventral tip of propleuron yellow (as in Figure 13C). Costa Rica .................................... 11

10’. Ventral tip of propleuron black or brown (as in Figure 11C or Figure 17) ...................... 12

11. Metepimeron yellow (as in Figure 14C). Costa Rica........... Xanthomicrogaster clarkorum sp. n.

11’. Metepimeron black. Costa Rica.............................. Xanthomicrogaster mikegrayumi sp. n.
12. Hind coxa entirely black. ................................................................. 13

12’. Hind coxa yellow, except for the ventral portion, which is black. .......................... 14


.................................................................Xanthomicrogaster nelsonzamorai sp.n.

13’. Body predominantly black. Brazil ............................................... Xanthomicrogaster pelides Nixon 1965

14. Distal black pigmentation of hind coxa extending dorsally, such that a larger portion of the coxa is
black near the trochanter than anywhere else on the coxa (Figure 4, middle/top). Costa Rica ..........

.................................................................Xanthomicrogaster barryhammeli sp.n.

14’. Distal black pigmentation of hind coxa not extending dorsally, such that the same portion of the
coxa is black near the trochanter as anywhere else on the coxa (Figure 4, bottom). Mexico............

.................................................................Xanthomicrogaster seres Nixon 1965

**Biogeography, host use, and phylogeny**

Collection records of *Xanthomicrogaster* from across its geographic range are presented in Figure
1. Collections records of *Xanthomicrogaster* from the ACG rearing project in Costa Rica are presented in
Figure 18. *Xanthomicrogaster* has a recorded elevational range of 13 m to 2100 m, though the genus
seems to be more abundant at lower elevations.

The undescribed material of *Xanthomicrogaster* examined reveals the diversity of the genus.

Though rare, *Xanthomicrogaster* seems speciose, with no identical specimens being found at different
localities. Since most of the species are represented by only one specimen, it is difficult to draw
conclusions or to try to describe the species. There are some color pattern elements that are consistently
found in different undescribed species from different localities, though it is not certain whether these
patterns are homologous or whether the underlying genes determining color pattern are responsible. A
change in expression in one gene may influence the color pattern in a specific place, and these changes
may be very common, given the striking diversity of color patterns among the genus.

There is one host record from the undescribed species, with five wasps being pinned with cocoons (Figure 9J-K). These wasps were collected in Trinidad, and the recorded host is Dichomeris larva on Cordia. These host records are congruent with the records from Costa Rica, where X. barryhammeli sp. n. attacks Dichomeris (albeit on a different host plant) and X. clarkorum sp. n. on Cordia (albeit on a different host caterpillar).

Of the seven described species, host information is known for six. Three of these six have been reared from only one species of host caterpillar that apparently feeds on only one species of plant (X. ronliesneri sp. n., X. clarkorum sp. n., and X. nelsonzamorai sp. n.). Two of the six species (Xanthomicrogaster mikegrayumi sp. n. and X. barryhammeli sp. n.) have been found on one species of host caterpillar that feeds on two or more species of plant. The remaining species, Xanthomicrogaster peterraveni sp. n., has been found on two or more species of caterpillar found on two or more species of plant. Host caterpillars are from five different families: Gelechiidae, Depressariidae, Crambidae, Tortricidae, and Elachistidae. Host plants for the various caterpillars are from six different families: Boraginaceae, Rubiaceae, Malvaceae, Asteraceae, Fabaceae, and Ulmaceae.

The resulting phylogenies for the three-gene analysis using ML and Bayes are presented in Figures 19 and 20, respectively. Support values were very low for all relationships except for that of X. clarkorum sp. n. and X. barryhammeli sp. n., which are sister species. The monophyly of Xanthomicrogaster is strongly supported. The phylogenetic network (Neighbor-Net) is also presented in Figure 21, and also shows little support for any of the relationships outside of X. clarkorum sp. n. and X. barryhammeli sp. n. This may be due to a rapid radiation within the genus Xanthomicrogaster, or it may be due to the limited number of characters used in the alignment.

The full COI tree, under ML, shows similar results, with very little support for most of the inferred relationships (Figure 22).
Discussion

Sexual dimorphism and color patterns

Sexual dimorphism is present among all three newly described species for which both a male and a female are known, with sex associations confirmed by COI haplotype information. In every case, the male is darker than the female in some way (Figures 7 and 8; 10 and 11; 12 and 13). This ranges from only slightly darker, in the case of X. mikegrayumi sp. n. (T2-T8 darker in male than in female), to ostensibly darker, in the case of X. clarkorum sp. n. (propodeum and metanotum yellow in female, black in male, among other differences). This is also true for unassociated material from across the geographic range, where male specimens from a given region are darker than the females of that region.

The most consistent color pattern elements between males and females are in the mesosoma, while the least consistent are in the metasoma. The propleuron, mesopleuron, and hind coxa, in particular, seem particularly useful for associating males and females. The metasoma itself shows intraspecific variation and should not be used in isolation for species identification or sex association.

Sexual dimorphism is not limited to morphology, and appears to have a consequence in terms of flight patterns, dispersal, or predation avoidance, evident in Malaise trap samples. No male Xanthomicrogaster have ever been retrieved from Malaise traps, while females have. Several possibilities exist to explain this discrepancy: 1) sampling error, although this is unlikely, as evidenced by equal ratios of males and females from reared material and a large number of Malaise trap caught wasps; 2) flight patterns, males may tend to fly higher than females, thus avoiding usual Malaise trap placement; 3) dispersal, males do not fly very far, and thus are unlikely to be caught in Malaise traps, while females must fly further to seek out appropriate hosts; and 4) predation avoidance, males do not fly up into the collecting head when in the Malaise trap, and instead tend to fly away from a trap once its flight is interrupted. Due to the rarity of Xanthomicrogaster, it is unlikely that an answer could be found for this phenomenon without dedicated research.

Color pattern commonalities abound among Xanthomicrogaster species, and appear especially present in males. Fewer males have been recorded than females, yet, male color pattern variation
(especially of the metasoma) is more extensive than in females. One explanation is that the haploid males tend to express recessive genes affecting color pattern more often than the diploid females. The females display more color pattern variation between species than within species, suggesting that male color patterns may be either convergent or have not diverged.

One particularly striking example is that of *X. clarkorum* sp. n., *X. barryhammeli* sp. n., and an undescribed male *Xanthomicrogaster* from Guayas, Ecuador (CNC material; voucher CNCHYM007177) (Figure 4). The two main differentiating features are: 1) black portion of hind coxa greater distally than anywhere else (as in undescribed male, *X. clarkorum* sp. n., and *X. barryhammeli* sp. n.), and 2) proximal portion of hind coxa black, such that the portion abutting the mid coxa is black (as in *X. clarkorum* sp. n. and *X. barryhammeli* sp. n.). The combination of these two characters is sufficient to distinguish the currently known color variants of this male pattern (aside from the sister species *X. barryhammeli* sp. n. and *X. clarkorum* sp. n., which are separated based on the color of the propleuron).

There are various color pattern characters that appear throughout *Xanthomicrogaster* spp., across the entire geographical range. It is unknown whether there is a phylogenetic basis for these, if this is a result of homology in the underlying genes determining color pattern, or whether there is massive convergence within these patterns. These elements probably do not represent the ancestral color pattern, as many of them are mutually exclusive; without a well-resolved phylogeny sampled across the geographic range, it will be impossible to determine how the most recent common ancestor of *Xanthomicrogaster* appeared. They may instead indicate that similar genes control the expression of pigmentation in each species.

Common color pattern elements include: 1) dark coloration of the lateral lobes of the mesoscutum, often in combination with a faint dark area in the anterior portion of the medial lobe (as in *X. maculatus* Penteado-Dias, Shimabukuro, and van Achterberg 2002); 2) dark coloration of the ventral portion of the mesopleuron as well as the ventral portion of the hind coxa (as in Figures 4, 12C, and 14C); 3) dark coloration of the ventral portion of the mesopleuron as well as a small dorsal portion, between the forewing and hindwing articulations (as in Figures 4, 8C, and 14C); 4) dark coloration of the metanotum
and propodeum (as in Figures 5A, 7A, 8A, 10A, 11A, 13A, 14A, and 15A); 5) dark coloration of the entirety of metasomal T1, occasionally lacking dark pigment along the furrow (as in Figures 11A, 13A, and 15A); 6) dark coloration of metasomal T2-T8 (or T3-T8), occasionally lacking dark pigment either medially or laterally (as in Figures 5A, 7A, 8A, 10A, 11A, 12A, 13A, 14A, and 15A); 7) dark coloration of the distal tip of the hind femur (as in Figures 7C and 12C); and 8) dark coloration of the metanotum and propodeum (see 4 above) and the metepisternum, such that the metepimeron is yellow and bordered by dark coloration (as in Figure 4).

Biogeography of Xanthomicrogaster

In addition to previously reported countries (Suriname, Guyana, Mexico, Brazil, and French Guiana), the genus has been found in 7 other countries (Costa Rica, Colombia, Venezuela, Trinidad and Tobago, Ecuador, Peru, and Argentina) (Cameron 1911; Nixon 1965; Penteado-Dias et al. 2002; Braet et al. 2000). Examining collection records can indicate biogeographical barriers for dispersal of Xanthomicrogaster or its host caterpillars (for all collection records, see Figure 1).

Xanthomicrogaster seres represents the northernmost collection record of the genus (Veracruz, Mexico). One more specimen was collected from Mexico, and is located in the CNC, though it is from Chiapas, which is southeast of Veracruz. This suggests a northern/western barrier for Xanthomicrogaster of the Sierra Madre del Sur of Mexico.

In terms of the northeastern border of the range, Xanthomicrogaster is known from the island of Trinidad (Trinidad and Tobago), but extensive collecting has not been done to attempt to locate Xanthomicrogaster in Tobago or beyond, into the Lesser and Greater Antilles. As Trinidad is the closest island to mainland South America, it is possible (and perhaps likely) that this is the northeastern limit of the genus.

Xanthomicrogaster is not known from Chile, though no extensive sampling has been done in this country. This suggests that the Andes form a geographic barrier for the generic range. The southernmost record for Xanthomicrogaster is from central Argentina.
Maximum elevational distributional range is unclear. Within the ACG, elevation ranges from 335 m to 540 m; using the localities from CNC specimens, this range is extended to 13 m to 2100 m. The lowest elevational records are from Curepe, Trinidad, and Silva Jardim, Rio de Janeiro, Brazil. The highest are from San Cristobal de Las Casas, Chiapas, Mexico; Merida, Venezuela; and Santo Domingo, Pichincha, Ecuador. Most records occur below 1000 m.

In looking at other rearing projects for Microgastrinae, no Xanthomicrogaster have been reared in the duration of the Yanayacu Biological Station rearing project. Located in Ecuador, Yanayacu Biological Station is at an elevation of 2100 m, on an altitudinal gradient. As of 2009, 258 Microgastrinae had been reared, representing 14 genera (Whitfield et al. 2009). Using the rate of discovery for the ACG specimens, it would be expected that one Xanthomicrogaster would be reared by now if the two rearing projects had similar compositions of Microgastrinae. This is obviously left up to chance and sampling error, so no real conclusions can be drawn from the genus’s absence at Yanayacu Biological Station.

Phylogenetic relationships of Xanthomicrogaster

The low support values in the phylogeny, regardless of analysis method (Figures 19, 20, 21, and 22), indicate that a rapid radiation may have occurred during the diversification of the genus, leading to short internal branches and long terminal branches, and possibly long branch attraction artifacts. There is one highly supported relationship, that of X. clarkorum sp. n. and X. barryhammeli sp. n. as sister groups, recovered in 100% of bootstrap replicates in full ML analysis and with a posterior probability of 1.0 in the Bayesian analysis.

While the female for X. barryhammeli sp. n. is unknown, the male of X. barryhammeli sp. n. and the male of X. clarkorum sp. n. look very similar, being mainly separated by the coloration of the propleuron. They are similar in size (X. clarkorum sp. n. is 3.65 mm, while X. barryhammeli sp. n. is 3.30 mm), and are difficult to distinguish from one another. X. seres and an undescribed specimen from Ecuador (CNC material) also look very similar (see Figure 4).

In terms of host use, X. barryhammeli sp. n. has been found on Dichomeris sp. (Gelechiidae) on
two plants in the Asteraceae, whereas *X. clarkorum* sp. n. has been found on *Ethmia catapeltica* (Depressariidae) on one plant, *Cordia alliodora* (Boraginaceae). The undescribed species from Trinidad has been recorded on *Dichomeris* found on *Cordia*; it is impossible to confirm these records, but one can easily imagine host switching either to a different caterpillar on a closely related plant or to a closely related caterpillar on a different plant. The difference in host use between these two species points to specialization being a driver of speciation within this genus, and the few morphological differences in the males may be due to recent speciation. When the female *X. barryhammeli* sp. n. are found, it will shed light on this situation, with a similar appearance to *X. clarkorum* sp. n. indicating recent speciation, and a different appearance indicating lack of morphological differentiation in males.

*Constraints on host use*

In terms of host caterpillar family, *Xanthomicrogaster* prefers to attack members of superfamily Gelechioidea. For the six described species with recorded host information, only one species deviates from this superfamily, attacking both Tortricidae (Tortricoidea) and Crambidae (Pyraloidea). It thus seems most likely that *Xanthomicrogaster* diversified on Gelechioid lineages, with host switching to other lepidopteran families following. There is an argument that the ancestral host lineage for *Xanthomicrogaster* is not the Gelechioidea, and that the most recent common ancestor was more generalist, based on the COI tree (Figure 22) placing *X. peterraveni* sp. n. as the sister group to the rest of the genus. This is not supported by any other analysis, however, and it appears that the exceptionality of *X. peterraveni* sp. n. may be derived rather than plesiomorphic.

In terms of the host plants of these host caterpillars, records span across six families from wildly different superfamilies, and it is difficult to see the implications for the biology of *Xanthomicrogaster*.

Although *Xanthomicrogaster* is not restricted to host caterpillars based on phylogenetic relationships, the genus does seem to have an ecological constraint in the form of parasitizing concealed hosts. All known hosts belong to families that often conceal themselves. The cocoons, often found on the leaf substrate or even within the host cocoons, are usually attached to the edge of the leaf, such that the
leaf will roll up as it dries. The cocoons are most similar to those of *Prasmodon*, with both genera producing “messy,” shaggy, white cocoons.
Table 1 The vouchers used for DNA extraction are listed above, as well as their species identification (which serves as their labels on phylogenetic trees) and whether an entire wasp (whole) was used for DNA extraction or just one leg (usually hind leg, post-coxa, but occasionally mid leg, post-coxa).

<table>
<thead>
<tr>
<th>Species</th>
<th>DHJPAR Voucher Number</th>
<th>Extraction of whole specimen or leg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Choeras sp.</td>
<td>DHJPAR0012590</td>
<td>whole</td>
</tr>
<tr>
<td>X. ronliesneri sp. n.</td>
<td>DHJPAR0034285</td>
<td>leg</td>
</tr>
<tr>
<td>X. nelsonzamorai sp. n.</td>
<td>DHJPAR0039452</td>
<td>whole</td>
</tr>
<tr>
<td>X. barryhammeli sp. n. A</td>
<td>DHJPAR0045288</td>
<td>leg</td>
</tr>
<tr>
<td>X. barryhammeli sp. n. B</td>
<td>DHJPAR0043160</td>
<td>leg</td>
</tr>
<tr>
<td>X. clarkorum sp. n. A</td>
<td>DHJPAR0039924</td>
<td>whole</td>
</tr>
<tr>
<td>X. clarkorum sp. n. B</td>
<td>DHJPAR0040582</td>
<td>leg</td>
</tr>
<tr>
<td>X. algentryi sp. n.</td>
<td>DHJPAR0025166</td>
<td>whole</td>
</tr>
<tr>
<td>X. peterraveni sp. n.</td>
<td>DHJPAR0048213</td>
<td>leg</td>
</tr>
<tr>
<td>X. mikegrayumi sp. n.</td>
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<td>whole</td>
</tr>
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<td>Direction</td>
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<td>wgAbRZ</td>
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<td>28SF</td>
<td>Forward</td>
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<tr>
<td></td>
<td>28S-PM</td>
<td>Reverse</td>
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</table>

Table 2 The primers above were used to sequence all specimens. COI barcode data was provided by the ACG project.
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<th>Time</th>
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<td>95° C</td>
<td>30 s</td>
</tr>
<tr>
<td></td>
<td>30 cycles of</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Denaturation</td>
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<td></td>
<td>Annealing</td>
<td>50° C</td>
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<td>90 s</td>
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<td></td>
<td>Final extension</td>
<td>68° C</td>
<td>5 min</td>
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<td>30 s</td>
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<tr>
<td></td>
<td>25-30 cycles of</td>
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<td>Denaturation</td>
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<tr>
<td></td>
<td>Final extension</td>
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<td>5 min</td>
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Table 3 PCR conditions for each gene (using the primers in Table 1) are listed above. For 28S, two rounds were done: one with an annealing temperature of 48° C and one with an annealing temperature of 51° C.
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<th>COI</th>
<th>Original source</th>
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<td>Apanteles fumiferanae</td>
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<td>HQ552704</td>
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<td>Apanteles canarstiae</td>
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<td>AF102703</td>
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<td>DQ538986</td>
<td>DQ538832</td>
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<td>Glyptapanteles porthetriae</td>
<td>DQ538594</td>
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<td>DQ538828</td>
<td>Banks &amp; Whitfield 2006 (wg &amp; COI) Mardulyn &amp; Whitfield 1999 (28S)</td>
</tr>
<tr>
<td>Diolcogaster schizurae</td>
<td>DQ538591</td>
<td>AF102741</td>
<td>DQ538825</td>
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<td>Pholetesor ornigis</td>
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<td>Pseudapanteles sp. JCB-2006</td>
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<td>Venanus sp. JCB-2006</td>
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<td>Xanthomicrogaster sp. JCB-2006</td>
<td>DQ538612</td>
<td>DQ538996</td>
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</tr>
</tbody>
</table>

Table 4 GenBank accession numbers for all previously published data is provided in the table above. Along with outgroups, one set of sequences for an undescribed species of *Xanthomicrogaster* was also available.
Figure 1 Each dot represents a collection record of *Xanthomicrogaster*. For records with only the country reported, a dot was placed in the center of the country (Suriname, Guyana, and French Guiana). Map made using Google Maps.
Figure 2 Photos of the type specimens of the first three described species of *Xanthomicrogaster*, provided by Gavin Broad, Natural History Museum of London. A: *Xanthomicrogaster fortipes* Cameron 1911, holotype of genus. Labeled “*Xanthomicrogaster fortipes* Cam. Type. B. Guyana.” Collection label: “P. Cameron Coll. 1914-110.” (this probably refers to the date that it was deposited in the Natural History Museum, London, as it was described in 1911.) B: *Xanthomicrogaster pelides* Nixon 1965. Labeled “*Xanthomicrogaster pelides* Nixon. Type ♀, 19.” (the rest of the year is omitted.) Collection label: “Brasilien. Nova Teutonia. 27˚ 11’ B. 52˚ 23’ L. Fritz Plaumann. VIII – 1935.” Deposition label: “Brit. Mus. 1937-47.” C: *Xanthomicrogaster seres* Nixon 1965. Labeled “*Xanthomicrogaster seres* Nixon. Type ♂, 19.” (the rest of the year is omitted.) Two collection labels: “Atoyac, Vera Cruz. May. H.H.S.” “Godman-Salvin Coll. 1904 – 1.”
Figure 3 Dorsal view of undescribed *Xanthomicrogaster* species, showing the darkened anterior portion of the central lobe of the mesoscutum (voucher CNCHYM007168, from the CNC material). Collected: Represa Rio Grande, Guanabara, Brazil 1972.
Figure 4 Lateral views of the mesosoma of *Xanthomicrogaster* sp. (CNCHYM007177, Ecuador; top), *Xanthomicrogaster barryhammeli* sp. n. (middle), and *Xanthomicrogaster seres* Nixon 1965 (bottom).
Figure 5 Holotype of *Xanthomicrogaster algentryi* sp. n. A: Dorsal view of mesosoma (partial) and metasoma. B: Wing. C: Lateral view.
Figure 6 Holotype of *Xanthomicrogaster ronliesneri* sp. n. A: Dorsal view of mesosoma (partial) and metasoma. B: Wing. C: Lateral view.
Figure 7 Holotype (female) of *Xanthomicrogaster mikegrayumi* sp. n.  
A: Dorsal view of mesosoma (partial) and metasoma.  
B: Wing.  
C: Lateral view.
Figure 8 Allotype (male) of *Xanthomicrogaster mikegrayumi* sp. n. A: Dorsal view of mesosoma (partial) and metasoma. B: Wing. C: Lateral view.
Figure 9 Cocoons of Xanthomicrogaster. A-E: Each is from a different specimen of *Xanthomicrogaster clarkorum* sp. n.; F: *Xanthomicrogaster peterraveni* sp. n.; G-H: Each is from a different specimen of *Xanthomicrogaster mikgegrayami* sp. n.; I: *Xanthomicrogaster baryhummeli* sp. n.; J-K: Pinned cocoons from the Canadian National Collection, vouchers CNCHYM007151 (J) and CNCHYM007150 (K). In total, there were five specimens from the CNC with similar cocoons; some lack labels, but all are mounted in the same fashion. Three specimens are labeled “Trinidad. F.D. Simmonds.” One specimen is labeled “From *Dichomeris* larva on *Cordia*. 7 January 1951. Collector: F.J. Simmonds.” One specimen is unlabeled.
Figure 10 Holotype (female) of Xanthomicrogaster nelsonzamorai sp. n. A: Dorsal view of mesosoma (partial) and metasoma. B: Wing. C: Lateral view.
Figure 11 Allotype (male) of *Xanthomicrogaster nelsonzamorai* sp. n. A: Dorsal view of mesosoma (partial) and metasoma. B: Wing. C: Lateral-ventral view of propleuron and mesopleuron.
Figure 12 Holotype (female) of *Xanthomicrogaster clarkorum* sp. n. **A**: Dorsal view of mesosoma (partial) and metasoma. **B**: Wing. **C**: Lateral view.
Figure 13 Allotype (male) of *Xanthomicrogaster clarkorum* sp. n. A: Dorsal view of mesosoma (partial) and metasoma. B: Wing. C: Lateral-ventral view of mesosoma.
Figure 14 Holotype of *Xanthomicrogaster barryhammeli* sp. n. A: Dorsal view of mesosoma (partial) and metasoma. B: Wing. C: Lateral view.
Figure 15 Holotype of *Xanthomicrogaster peterraveni* sp. n. A: Dorsal view of mesosoma (partial) and metasoma. B: Wing. C: Lateral view.
Figure 16 Lateral oblique view of metasoma of holotype for *Xanthomicrogaster peterraveni* sp. n., showing the black hypopygium.
Figure 17 Oblique ventral view of holotype of *Xanthomicrogaster barryhammeli* sp. n., showing the darkened ventral tip of the propleuron.
Figure 18 Each dot represents a location where *Xanthomicrogaster* specimens have been recovered through the ACG rearing project, in Costa Rica. Map made using Google Maps.
Figure 19 Phylogenetic tree recovered from the RAxML analysis using three genes, with bootstrap support values for 1000 rapid bootstrap replicates.
Figure 20 Maximum clade credibility tree recovered from Bayesian analysis of three-gene dataset. The analysis was run in MrBayes. 2 runs with 4 chains each, for 2,000,000 generations, sampled every 1,000 generations, with a burn-in of 10%, and summarized using TreeAnnotator.
Figure 21 Neighbor-net analysis for the three-gene dataset for the newly described species. This phylogenetic network shows that the internal branches separating *Xanthomicrogaster* from one another are extremely short in comparison to the terminal branches, with the exception of *X. clarkorum* sp. n. and *X. barryhammeli* sp. n. This is reflected in low bootstrap support values (Figure 19) and low posterior probabilities (Figure 20) for the internal branches.
Figure 22 Phylogenetic tree from the full ML analysis of COI barcode data, with bootstrap support shown (removed for extremely small branches). Correct generic labels for the top clade are shown above the branch leading to that clade. The bottom clade contains all of the Xanthomicrogaster reared through the ACG project, with their proper species names. The undescribed species “Xanthomicrogaster_Janzen09” (voucher number DHJPAR0049936) was reared after the descriptions of the other species, and represents a sister species to Xanthomicrogaster_roeliesneri sp. n.
REFERENCES


APPENDIX A: THREE GENE DATASET

The three gene dataset, in NEXUS format, containing genes COI (1-693), wingless (694-1195), and 28S rDNA (1196-1822), used for analyses in this thesis, may be found in a supplemental file named XanthomicrogasterThreeGene.nex.
APPENDIX B: FULL COI DATASET

The data set containing all of the COI barcode data for *Xanthomicrogaster* and selected outgroups, in NEXUS format, used for an analysis presented in this thesis, may be found in a supplemental file named *XanthomicrogasterFullCOI.nex*. 