RESEARCH ARTICLE

Contribution to the bionomics of the pollen wasp *Quartinia canariensis* Blüthgen, 1958 (Hymenoptera, Vespidae, Masarinae) in Fuerteventura (Canary Islands, Spain)

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Abstract

Quartinia canariensis was recorded from three semidesertic sand habitats in Fuerteventura. All localities were sparsely covered by halophytic vegetation and characterized by large patches of flowering plants of *Frankenia laevis* (Frankeniaceae). Males and females were exclusively observed to visit flowers of *Frankenia laevis*. During flower visits the imagines often switched between nectar and pollen uptake. Pollen was consumed directly from the anthers or pollen uptake was indirect with pollen grains gathering on the frons being brushed towards the mouthparts with the fore legs. During nectar uptake the wasps protruded their long proboscis into the nectariferous pockets between the claws of the petals of the *Frankenia* flowers. Brood cell provisions consisted mainly of pollen from *Frankenia* but to a small amount also from *Polycarpaea* (Caryophyllaceae) suggesting that *Quartinia canariensis* is polylectic with strong preference. Males regularly stood on the ground in the vicinity of *Frankenia* plants and frequently performed patrol flights along the flowers. Flower visiting females avoided contact with the males and mainly offered resistance against the insertion of the male genitalia. The behavioural sequence during copulation of a species of *Quartinia* is described for the first time. The nest was a multicellular sub-vertical burrow surmounted by a short turret. The burrow was excavated by the female in friable sandy soil. The walls of the nest were stabilized by silk produced by the nest building female and applied with the mouthparts. Inconsistencies concerning the host-parasite-relationship between *Quartinia canariensis* and *Chrysis atrocomitata* established by Gusenleitner 1990 are discussed.

Introduction

The genus *Quartinia* is a monophyletic subtaxon of the Masarinae (Carpenter 1993, Krenn et al. 2002). It has a disjunct distribution with an Afrotropical and a Palaearctic range. Within the Masarinae *Quartinia* is the genus with the highest species diversity (Richards 1962), with 101 described species occurring in the Afrotropical region (Gess and Gess 2010, Gess 2011a, 2011b) and 42 species in the Palaearctic (Carpenter 2001, 2003, Gusenleitner 2010a, 2010b, 2012a, 2012b, Schmid-Egger 2015). *Quartinia* species are on average the smallest of the pollen wasps, ranging from ± 2–7 mm in length (Gess 2007, Gess and Gess 2010) with 80 % of the species measuring less than 5 mm (n = 80 species; female body length taken from Richards 1962). Information about flower visiting, nesting, sleeping and sheltering, mating and associated organisms is mainly available for some Afrotropical species of *Quartinia* that have been studied in detail by Gess (2007, 2008, 2009, 2011a, 2011b), Gess and Gess (1992), Gess (1996) and Gess and Gess (1989, 2003, 2006, 2008, 2010). In contrast, knowledge about the bionomics of the Palaearctic species of *Quartinia* is still very limited and mainly restricted to a small number of occasional flower visiting records relating to ten species published by Morice (1900), Benoist (1929), Bequaert (1940), Popov (1948), Gusenleitner (1973, 1990) and Carpenter (2003). A systematic survey of the flower associations of various aculeate Hymenoptera including three *Quartinia*-species was conducted by Hohmann et al. (1993) for the Canary Islands. Many of the Palaearctic species seem to be associated with members of the Asteraceae, but there are also records from another eight plant families and five species of *Quartinia* were not or rarely recorded from Asteraceae. The degree of specialisation of any Palaearctic *Quartinia* species with regard to its pollen source is unknown.

Quartinia canariensis was described in 1958 by Blüthgen from three females collected by H. Lindberg from Fuerteventura during the Finnish Canary-Expedition. Further material from the Canary Islands, which had been collected by K.M. Guichard between 1964 and 1966, led to the description of the previously unknown male of *Q. canariensis* by Richards (1969) yet again recorded from Fuerteventura. Up to now the species has been found at 23 localities exclusively situated in Fuerteventura and Lanzarote (Gusenleitner 1990, Hohmann et al. 1993), suggesting that it is probably endemic to these two islands of the Canaries. Two closely allied *Quartinia* species occur on neighbouring islands, with *Quartinia guichardi* Richards, 1969 being restricted to Gran Canaria and *Quartinia tenerifina* Richards, 1969 inhabiting Tenerife and La Gomera (Richards 1969, Hohmann et al. 1993).

Published information about the bionomics of *Quartinia canariensis* is very fragmentary. There are several records of males and females having been observed visiting flowers

of *Frankenia laevis* L. (Frankeniaceae) (Gusenleitner 1990, Hohmann et al. 1993), but there are also single flower visiting records from plants belonging to the Asteraceae, Boraginaceae, Caryophyllaceae and Fabaceae (Hohmann et al. 1993). Gusenleitner (1990) established *Q. canariensis* as a host of what he called "*Chrysis atracomitata* LINS." (Chrysididae) without giving any details (for inconsistencies and nomenclatural inaccuracies relating to this host record see below).

In the present study data concerning flower associations, flower visiting behaviour, nesting and mating of *Quartinia canariensis* are recorded for the first time, as an example for a *Quartinia* species from the Palaearctic. A comparison is made with published data on the bionomics of the Afrotropical species of the genus.

Material and methods

Investigations were carried out from 29 March to 5 April 2015 in the vicinity of Costa Calma in Fuerteventura (Canary Islands, Spain). Geographic coordinates (WGS 84) were measured using a Garmin GPS 12. *Quartinia canariensis* was studied at three localities [**I** Montaña Pelada, 2 km SW Costa Calma, eastward exposed slope W of a Barranco SW of the road to Los Gorriones, 28°08.325'N 14°14.999'W, 55 m a.s.l.; **II** SW Costa Calma between "Playa Esmeralda" and "Playa Paraíso" 28°08.677'N 14°14.368'W, 60 m a.s.l.; **III** Istmo de la Pared, 0.5 km NW Costa Calma 28°10.202'N 14°14.396'W, 90 m a.s.l.]. Most observations were made at locality I.

For all documentations of observations the local time (= Greenwich Mean Time + 1h) was used. Sunrise was approximately at 7h45, sun's zenith at 14h00 and sunset at 20h15. Time intervals were measured using a digital stop-watch. Observations were made with a close-up binocular (Pentax Papilio 8.5x21) and documented by using a Canon EOS 70D camera with a 180 mm macro lens and a 25 mm extension tube (scale more than 1:1, resolution 20 mega pixel) and macro flash-lights. In addition, in the course of one investigation interval during nest observations, the system was combined with a close-up lens (4 dioptre).

Specimens of all plant species flowering at locality I were collected and preserved dried. The material was placed in the herbarium of the Staatliches Museum für Naturkunde Stuttgart (Herbarium STU). The plant taxa were identified following Hohenester and Welss (1993). Flower preferences of imagines were studied by counting the number of sightings (= first observations) of flower visiting individuals while walking randomly across the area at localities I and III (total investigation time 9.5 h). Flower visiting behaviour of *Q. canariensis* at *Frankenia laevis* was investigated at various patches of this plant at locality I for 7 h in total. In addition, various other flowers were randomly scrutinized for visitors in a parallel study on *Hoplitis zandeni* (Teunissen and van Achterberg 1992) (Müller and Mauss in press). Pollen samples from five brood cell provisions from a single nest were prepared using the method outlined by Westrich and Schmidt (1986). The different pollen types were identified

under a light microscope at magnifications of times 400 or 1000 and determined to the genus level with the aid of a reference collection consisting of pollen samples of 500 mainly Mediterranean plant species and pollen samples from the collected plants. For characterizing different degrees of host-plant association among pollen wasp species, the categories defined by Müller and Kuhlmann 2008 (based on Cane and Sipes 2006) were used.

Activity and behaviour of the female of nest No.1 were observed on 6 days in the morning and in the afternoon for 18.75 h in total always including the onset and ending of the diurnal activity period. The nest was excavated on 5 April using a combination of two reading glasses that provided a sufficient magnification. In the field, nest dimensions were measured using a strip of millimetre paper (accuracy 1 mm). The cells with their content were separately stored in Eppendorf vials in a freezer until they were finally investigated under a Wild M3 stereomicroscope (maximum magnification times 60) on 6 August 2015. Micro-photos were taken with a Leica IC 80 HD camera mounted on a Leica MS 5 stereomicroscope (magnification times 80).

Results

Habitat

Quartinia canariensis inhabited semidesertic areas on sandy ground sparsely covered by halophytic vegetation with scattered shrubs of *Salsola divaricata* Masson ex Link in Buch (Amaranthaceae), *Launaea arborescens* (Batt.) Murb. (Asteraceae) and *Zygophyllum fontanesii* Webb & Berthel. (Zygophyllaceae) (Fig. 1). All localities were characterized by large patches of flowering plants of *Frankenia laevis*. Altogether at least 14 plant species were in flower at the study sites [Asteraceae: *Reichardia tingitana* (L.) Roth., *Asteraceae spec.*; Boraginaceae: *Heliotropium erosum* Lehm.; Caryophyllaceae: *Polycarpaea divaricata* (Aiton) Poir. ex Steud.; Cistaceae: *Helianthemum canariense* (Jacq.) Pers.; Convolvulaceae: *Cuscuta planiflora* Ten.; Fabaceae: *Astragalus hamosus* L., *Lotus glaucus* Sol., *L. glinoides* Delile, *L. lancerottensis* Webb and Berth., *Ononis natrix* L.; Frankeniaceae: *Frankenia laevis* L.; Resedaceae: *Reseda lancerotae* Webb and Berth. ex Delile; Scrophulariaceae: *Kickxia sagittata* (Poir.) Rothm]. Noteworthy abiotic factors were the nearly continuous, fresh and often cool northerly wind that led to a permanent sand movement and the only moderate air temperatures that rose only slightly above 20 °C during the diurnal flight period of *Q. canariensis*. A single nest (nest No. 1) was located at locality I on a slope exposed towards the south-east with an inclination of 10°. The nesting site was a sparsely covered area situated in the centre of a patch of 21 small to medium-sized *Frankenia* plants 1.2 m to the SSW of a *Salsola* shrub (Fig. 4). The nest was 2 cm away from a little dry stem of an annual plant jutting obliquely above the entrance. The soil was sandy and friable but relatively stable. Although a vast number of empty and sand filled snail shells was inspected, no nests of *Quartinia canariensis* were found in the shells.

Figures 1–5. 1 Habitat of *Quartinia canariensis* at locality III Istmo de la Pared, 0.5 km northwest of Costa Calma, Fuerteventura **2** Female of *Quartinia canariensis* resting on the ground near plant of *Frankenia* **3** Male of *Quartinia canariensis* standing on the ground close to *Frankenia* dwarf shrub **4** Nesting site at locality I Montaña Pelada. **5** Male resting in partly sand filled shell of the snail *Theba geminata*.

Flower associations

During random searching for flower visitation by *Q. canariensis* 15 sightings of flower visiting females, 2 sightings of flower visiting males as well as the sighting of 1 individual of unidentified sex of *Q. canariensis* were exclusively recorded at *Frankenia laevis*. Likewise, sightings of 41 females, 5 males and 7 individuals of unidentified sex were recorded during point observations at flowers of *F. laevis*. Visits to flowers of other plant species were not observed. In addition, males and females of *Quartinia canariensis* were often observed standing on the ground close to *Frankenia* plants (Figs 2, 3).

During pollen uptake at flowers of *Frankenia laevis* the females of *Quartinia canariensis* stood on the petals and occasionally also on parts of the androecium or gynoecium with their hind and mid legs, while the head was orientated towards the anthers (Fig. 6). Pollen was directly removed from the anthers through manipulation with the mandibles, and probably also the maxillae, and ingested (Fig. 6). This was repeatedly accompanied by brushing movements of the fore tarsi from the anthers towards the mouthparts (Fig. 9). In addition, the females performed indirect pollen uptake, when pollen accumulated on their frons as a result of contacts with the anthers during nectar uptake (Fig. 8b). In this case, the females remained for a short while on the margin of the corolla brushing pollen grains from the frons to the mouthparts by alternating movements of their fore legs (Fig. 7). To reach the nectar the females protruded their long proboscis down into the corolla tube (Fig. 8a) and moved their head deep down between the stamina and the wall of the corolla (Fig. 8b) indicating that the tip of the proboscis was probably pushed into the nectariferous pockets between the claws of the petals (Fig. 10). These nectariferous pockets are formed by the prominent and inwards projecting nectar scales on the adaxial sides of two adjacent claws each dividing the floral tube into five chambers (Brochmann et al. 1995, Kubitzki 2003, Fig. 10). During a visit to a particular flower the females often switched from pollen gathering to nectar uptake, or vice versa, or nectar uptake took place between two longer phases of pollen feeding.

The behaviour of the males during pollen gathering (Fig. 9) and nectar uptake (Fig. 10) from flowers of *Frankenia laevis* was similar to that of the females.

The pollen composition of the brood cell provisions of *Quartinia canariensis* is summarized in Table 1.

Mating

Males of *Quartinia canariensis* frequently stood on the ground close to flowering patches of *Frankenia laevis* (Fig. 3). They repeatedly took off from the ground and patrolled along the *Frankenia* plants in a rather rapid irregular flight closely above the flowers with several abrupt changes in direction before they alighted on the ground again. Whilst on the ground the males adopted a characteristic posture with their antennae raised and spread at an angle of approximately 45° to the longitudinal axis and their wings longitu-

Figures 6–10. Flower visiting behaviour of *Quartinia canariensis* at flowers of *Frankenia laevis*: **6** Female feeding on pollen directly from the anthers **7** Female brushing pollen from her frons with alternating movements of her fore legs **8** Nectar uptake by female: **a** Proboscis protruded into corolla **b** Head and proboscis pushed deeper down into corolla tube **9** Male feeding on pollen directly from the anthers **10** Male with protruded proboscis taking up nectar (np = nectariferous pocket).

Table 1. Details of the brood cells of nest No.1 of *Quartinia canariensis* investigated on 5 April, 2015 at locality I.

Cell No.	Orientation to the north (°)	Depth below ground surface (mm)	Condition	Content	Pollen composition
1	250	20	?	pollen loaf [egg or larva probably artificially lost, as cell had been damaged during excavation]	*Frankenia* >99%
2	340	20	?	egg at distal end of cell beyond pollen loaf	*Frankenia* 95%, *Polycarpaea* 5%
3	70/250	20	sealed	large larva, pollen loaf	*Frankenia* >99%
4	110/290	15	sealed	small larva, pollen loaf	*Frankenia* 80%, *Polycarpaea* 20%
5	70/250	23	sealed	large larva, small remnants of pollen loaf	*Frankenia* >99%

dinally folded (Fig. 3). Flower visiting females of *Q. canariensis* left the *Frankenia* plants immediately whenever they recognized the arrival of a patrolling male.

The behavioural sequence during copulation was subdivided into three phases: 1. initiation, 2. insertion, 3. separation. Initiation always started by a flying male pouncing on a female that was visiting flowers or resting on the ground. The male always alighted on the back of the female and managed to hold on and to orientate his longitudinal axis parallel to hers. Finally, the head of the male was situated above the mesonotum of the female, level with her tegulae. His antennae were orientated straight anterior-downwards. The fore legs of the male were placed on the female's tegulae or on adjacent parts of her mesonotum or metanotum and his mid and hind legs were wrapped around her wings and her metasoma (Figs 11, 15a). In this stage of the initiation the female offered successful resistance in 30 out of 31 observed copulation attempts. Characteristic behaviours of female resistance were raising of the fore, mid or hind legs above the body (Figs 11b–c, 13) and bending of the metasoma in an anterior-ventral direction to preclude the male from inserting his genitalia (Figs 11b, 12, 13). Antagonistic interactions between the male and the female were observed to continue for up to 121 s (median 28 s; n = 16). During this time, periods in which the male was just calmly holding on to the back of the female (Fig. 11a, c) alternated several times with periods of intensive "grappling", during which the male protruded his genitalia accompanied by vigorous wing vibrations (Fig. 12) and the pair often fell to one side (Figs 11b, 13). When initiation did not release insertion behaviour, both individuals finally detached from each other and flew off. The behavioural sequence of the single complete copulation observed is summarized in Table 2 and Fig. 15a–f.

Male-male interactions were only rarely observed: Twice a patrolling male was observed approaching and pouncing on a male that was on the ground. On both occasions this led to a short interaction before both males flew off. Furthermore, there

Figures 11–14. Initiation phase of copulation of *Quartinia canariensis*: **11a** Calm position of a male on the back of a female after mounting **b** Male trying to accomplish insertion of his genitalia while the female raises her fore legs and bends her metasoma anterior-ventrad. **c** Female raising hind leg against the male **12** Male vibrating vigorously with his wings during "grappling" between the partners while the female is bending her metasoma strongly anterior-ventrad **13** Female is raising her mid and hind legs against the male and bending her metasoma anterior-ventrad **14** Second male holding on to mounting male of a pair after alighting on his back.

Figure 15. Behavioural sequence of a complete copulation of *Quartinia canariensis* on a flower of *Frankenia laevis* (for details see Table 2).

are two observations of a second male alighting on a male that had already mounted a female and was holding on to her back (Fig. 14). In both cases the second male left the pair shortly thereafter and the first male remained on the female.

Table 2. Behavioural sequence of the copulation of *Quartinia canariensis* (reconstructed from a series of 16 photos).

Time (s)	Behaviour	Figure
0	*Initiation*: ♂ pounced on ♀ on *Frankenia* flower. ♂ alighted on back of ♀; body axis of ♂ parallel to hers; head of ♂ situated above mesonotum of ♀ level with her tegulae; ♂ directed antennae straight anterior-downwards, so that ventral side of distal end of antennal club came into contact with posterior parts of pronotum and anterior parts of mesonotum of ♀; fore legs of ♂ placed laterally on scutellum and wing base of ♀, mid and hind legs of ♂ wrapped around wings and metasoma of ♀. ♀ remained passive, with antennae orientated 45° to longitudinal axis.	15a
32	♂ moved slightly backwards and shifted antennae laterally-outwards (transverse to body axis); metasoma of ♂ was turned to the right side of ♀ and was curved anterio-ventrad; ♂ genital protruded. ♀ shifted antennae laterally-outwards and opened genital chamber.	15b
37	*Insertion*: ♂ moved antennae to a position 45° to longitudinal axis and inserted his genital in genital chamber of ♀.	15c
43	♂ changed his position on ♀ very rapidly. After that, body of ♂ curved around posterior end of ♀ metasoma, only connected to ♀ by genitalia. Head of ♂ protruded and erect, mandibles spread, antennae stretched straight forward; ♂ fore legs stretched forward, mid and hind legs bent but raised without contact to body of ♀. Wings of ♀ drooping obliquely downwards.	15d
52	Head of ♂ directed downwards, mandibles of ♂ open, touching posterior margin of metasomal tergum III of ♀, antennae of ♂ directed obliquely downwards; fore, mid and hind legs of ♂ pressed against distal end of ♀ metasoma.	15e
58	Head of ♂ protruded and erect, mandibles spread, antennae stretched straight forward; ♂ fore legs stretched forward, mid and hind legs bent but raised without contact with body of ♀.	as in 15d
79	Head of ♂ directed downwards, mandibles of ♂ open touching posterior margin of metasomal tergum III of ♀, antennae of ♂ directed obliquely downwards; fore, mid and hind legs of ♂ attached to distal end of ♀ metasoma.	as in 15 e
93	Head of ♂ protruded and erect, mandibles spread, antennae stretched straight forward; ♂ fore legs stretched forward, mid and hind legs bent but raised without contact with body of ♀.	as in 15d
144	Head of ♂ directed downwards, mandibles of ♂ open, touching posterior margin of metasomal tergum III of ♀, antennae of ♂ directed obliquely downwards; fore, mid and hind legs of ♂ pressed against distal end of ♀ metasoma.	as in 15e
152	*Separation*: ♂ genital removed from ♀ genital chamber. ♀ shifted antennae to a position 45° to longitudinal axis and moved slowly forward. ♂ dismounted ♀ postero-laterally. ♂ and ♀ flew off.	15f

Female brood care

Nest structure: The nest consisted of a subterranean burrow. The entrance was surmounted by a short cylindrical turret measuring about 2.5 mm in diameter and 1.5 mm in height (Figs 20, 22). The inner diameter of the turret opening was somewhat more than 1 mm wide, the same as that of burrow. On the first days of observation, when the female was excavating the nest, the wall of the turret was lower on the side orientated towards the adjacent sand dropping area (Figs 20, 22). Later on, this gap in the turret wall was closed (Fig. 21). The burrow consisted of a sub-vertical to oblique shaft that ran down in curves to a depth of 20 mm, where it terminated into a cell (Fig. 25, cell No. 2). A second cell was situated close to the end of the shaft (Fig. 25,
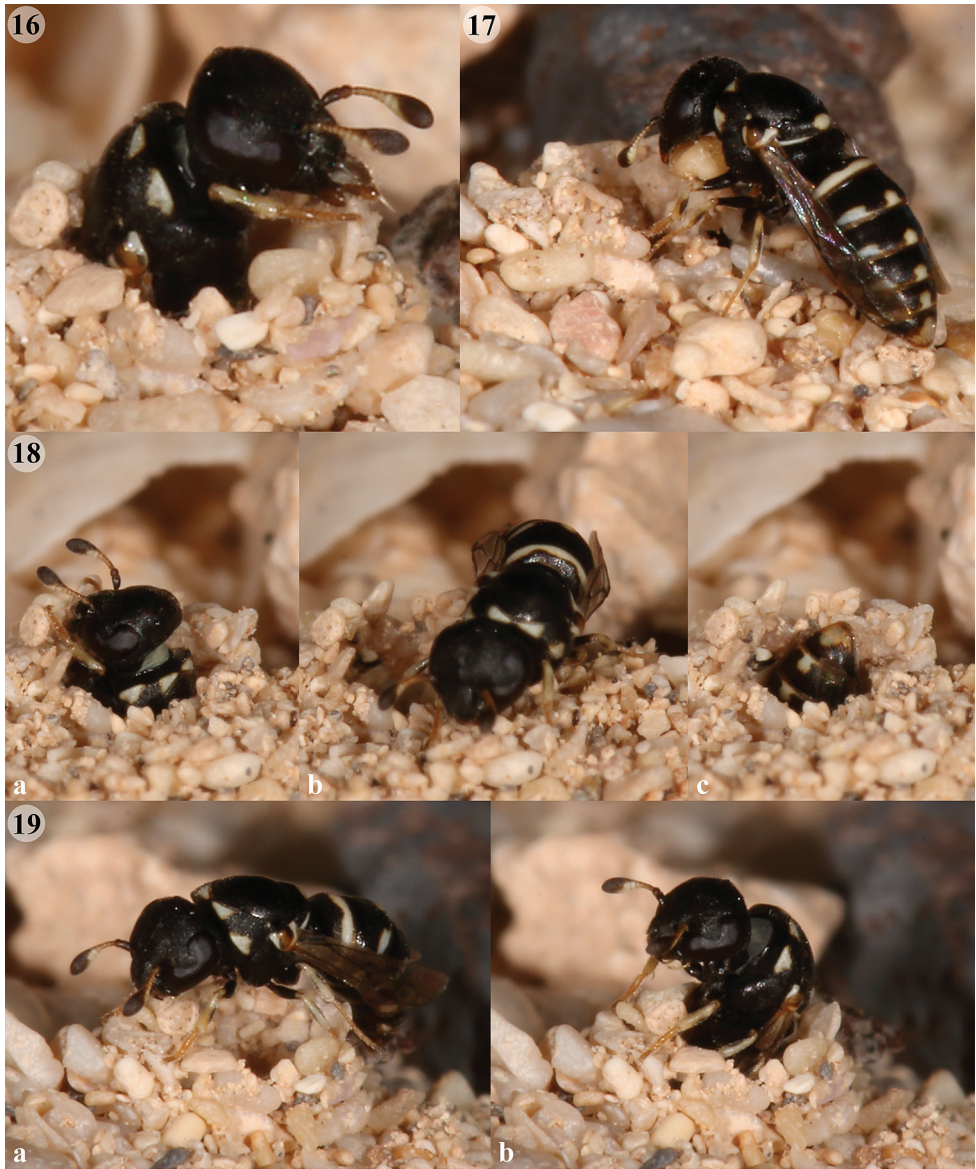
Figures 16–19. Behaviour of the nest owning female of *Quartinia canariensis* at nest No. 1: **16** Female "lining" of the turret rim with the mouthparts (mandible spread, labrum erected, part of maxilla visible) at the onset of activity in the morning **17** Female backing out of the shaft during nest excavation, carrying a large sand grain behind the mandibles **18** Female turning around outside of the nest prior to the start of flight activity in the morning: **a** Female "lining" the turret wall from the inside **b** Female turning quickly around after she has left the turret head first **c** Tip of the metasoma of the female is visible in the nest entrance after re-entering the nest head first **19** Female turning around outside of the nest at the end of activity in the afternoon: **a** Female situated above the turret after she has backed out of the nest and moved forward again **b** Female re-entering the nest backwards.
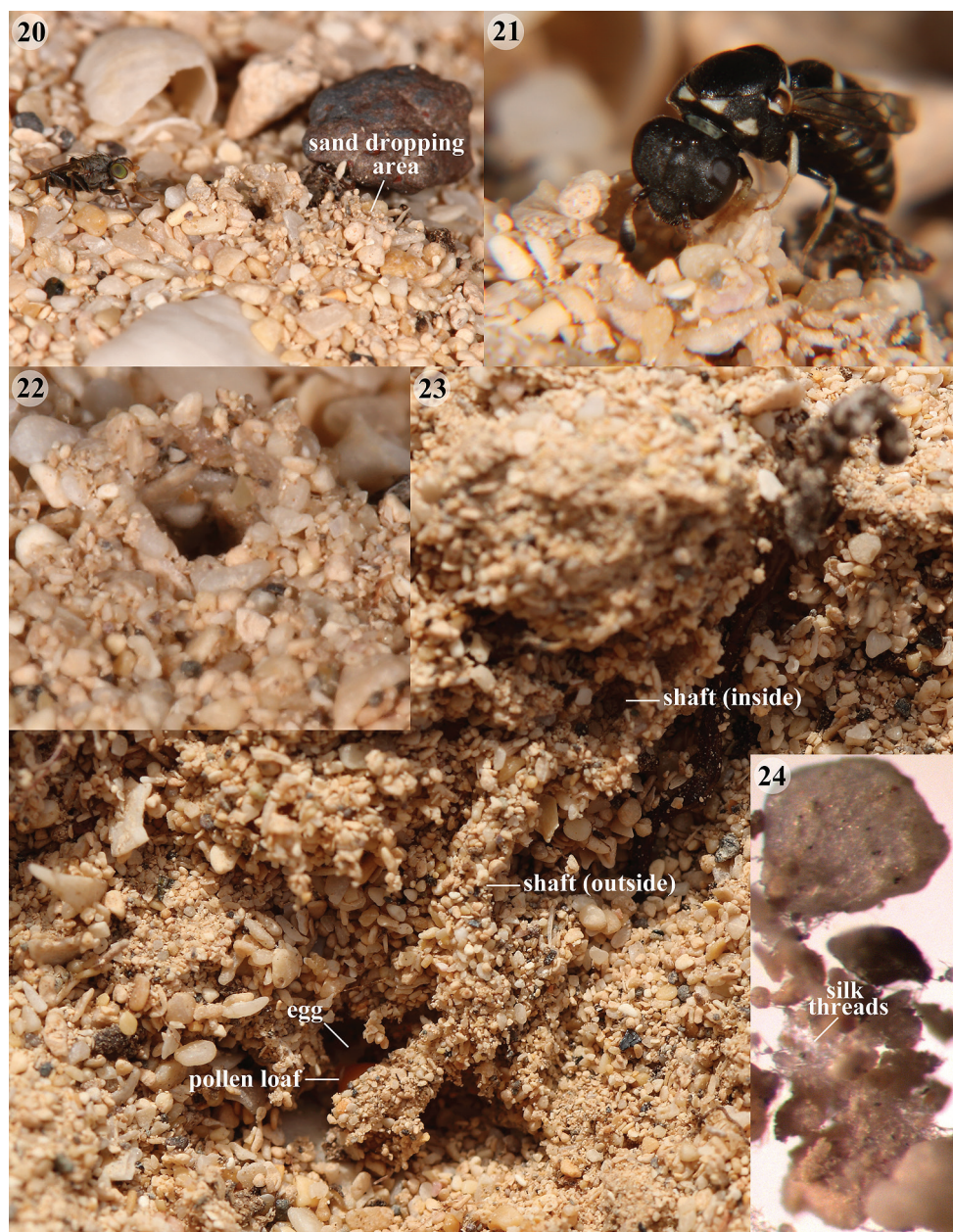
Figures 20–24. Nest No. 1 of *Quartinia canariensis*: **20** Close vicinity of the nest with a small fly (Diptera, Cyclorrhapha, Fam. indet.) probably inspecting the nest entrance **21** Female re-entering nest head first after backing out of the shaft prior to onset of flight activity in the morning **22** Nest entrance with dull whitish inner silken lining **23** Excavated burrow on 5 April, 2015 with turret removed and the shaft opened in the upper part to show the inner wall. The content of the opened brood cell No.2 is visible at the lower end of the shaft **24** Silk threads on and between sand grains from the wall of the nest.

cell No. 1). Another three cells were located at distances of up to 25 mm in a northerly direction from the shaft with no traceable connection to it (Fig. 25). The median depth of the cells below the ground was 20 mm (n = 5; Table 1). The inner dimensions of the brood cells measured approximately 3 mm in length and a little more than 1 mm in width.

The walls of the turret, the shaft and the brood cells consisted of sand grains (Figs 22, 23) bonded together with a dense, continuous lining of silk on the inside (Figs 22, 24). The silken lining of the shaft continued into the lining of the terminal cell.

Brood cell content: The content of the brood cells is summarized in Table 1. The provision consisted of an orange, more or less spherical loaf constituted of a mixture of pollen and a liquid, probably nectar, (Fig. 23) with a relatively firm surface adhering only weakly to the cell wall.

Behaviour at the nest: During nest excavation the female backed out of the shaft carrying a load of small sand grains or a single larger particle with her mouthparts (Fig. 17). The sand particles were positioned behind her mandibles and held with the aid of the elongated labial palpi. She moved a few steps backwards from the turret opening towards the sand dropping area where she stopped and discharged the sand particles curving her body downwards for a short moment. Then she moved rapidly forwards and re-entered the nest head first again. The female repeated the whole sequence of sand-load formation and sand dropping many times without interruption. The longest observed continuous phase of nest excavation lasted from 14h43 until 16h02. During these 79 min the female backed out the shaft 138 times. The time spent in the nest until the female reappeared with a new sand-load varied from 6.4 s to 123.3 s (median 17.4 s; n = 61). The sand-loads always appeared to be dry. The female always used the same sand dropping area, although she slightly modified the direction of her body axis when she was moving backwards resulting in the formation of a conical heap of excavated sand (Fig. 20). The sand dropping area was situated directly down slope as well as to the lee side of the nest entrance.

In the morning, at the start of diurnal activity, the female always appeared head first in the nest entrance continually treating the inner surface of the shaft and the turret with the mouthparts. These were moved slowly in close contact over the surface (Figs 16, 18a) while the female rotated gradually around her body axis. Throughout this process of "lining" the mandibles were moderately spread and the labrum was erected. Moreover, moistly shining, protruded parts of the epi- and hypopharynx were visible as well as distal parts of the maxillae performing some movements. At the margin of the turret the "lining"-behaviour led to the fixation of loose sand grains to the silken lining. After 3 to 7 min (median 6 min; n = 5) of "lining" the female left the turret head first, turned around and immediately re-entered the nest head first again (Figs 18a–c, 21). In the following 15 to 56 min (median 35 min; n = 4) the tip of the metasoma occasionally became visible in the nest entrance (Fig. 18c), indicating that the female was moving up and down inside the shaft. Finally, the female backed out of the nest entrance and remained for a short moment on the ground with her head above the turret before she flew off at last. On two occasions, after leaving the nest, she
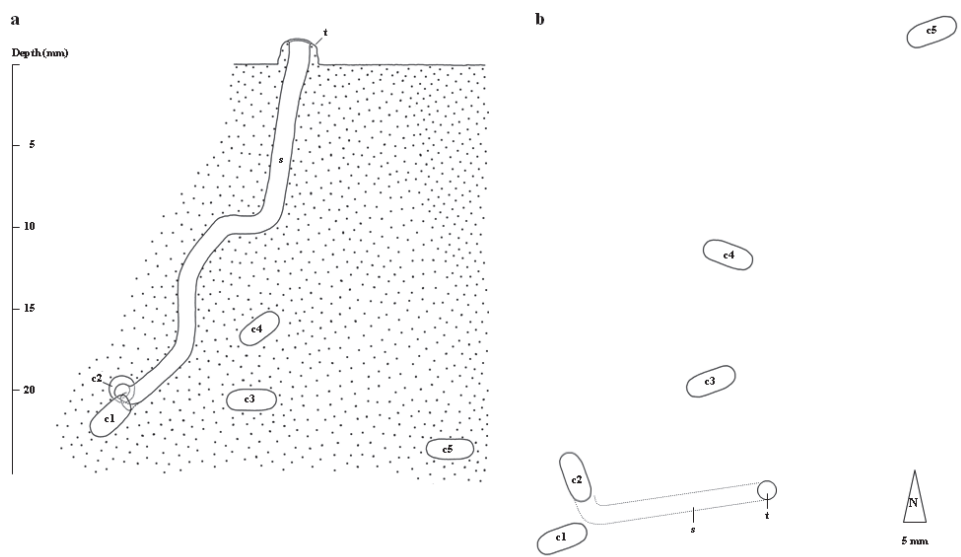
Figure 25. Nest architecture and brood cell arrangement of Nest No. 1 of *Quartinia canariensis* on 5 April, 2015: **a** schematic vertical cross section **b** schematic horizontal section (c = brood cell with cell number, s = main shaft, t = turret).

performed up to three arcs of a typical orientation flight. On two days it was observed at the end of the activity period that the female backed out of the shaft and then moved rapidly forwards again above the turret (Fig. 19a), where she curved her metasoma into the nest entrance (Fig. 19b) and moved backwards deep into the burrow with her head directed towards the nest entrance. The whole behavioural sequence took less than 2 s.

Activity, sleeping and sheltering

The diurnal activity of the female from nest No. 1 lasted for 4.8 to 6.0 h (median 5.6 h; n = 5) starting in the morning from 10h17 to 11h24 (median 10h53; n = 5) and finishing in the afternoon from 15h48 to 17h32 (median 16h22; n = 5). The female always spent the night within her burrow. The activity of males and females at flowers of *Frankenia* declined noticeably early in the afternoon and was mainly over around 15h00. On a single occasion at the end of the diurnal flight period, a male was observed to enter head first into an empty snail shell of *Theba geminata* (Mousson). The shell was approximately 10 cm away from a flowering patch of *Frankenia*. Within the shell the male first performed some movements then he rolled up his metasoma and remained motionless in a resting position (Fig. 5). However, after nine minutes the male became active again and reappeared, but this could have resulted from his being disturbed by the placing of a glass vial over the snail shell to prevent the male to escape unidentified.

Associated organisms

On a single occasion a small fly (Diptera, Cyclorrhapha, family indet.) was resting on the ground close to the turret, probably inspecting the nest entrance (Fig. 20). Other potential nest parasites were not observed.

Discussion

Flower associations

At all sites the only flowers that were observed to be visited by females and males of *Quartinia canariensis* were those of *Frankenia laevis*, indicating a close association with this plant that was used as a source of pollen and nectar. This is in congruence with the study by Gusenleitner (1990) in the neighbouring island Lanzarote, where members of the species were also recorded solely on flowers of or in close proximity to *Frankenia laevis*. However, the brood cell provisions of *Q. canariensis* consisted not only of pollen from *Frankenia* but also of small but substantial amounts of pollen from *Polycarpaea* that can not be explained by contamination. Therefore *Q. canariensis* is at least eclectic oligolectic, using at least pollen from two plant genera belonging to two different families that is Frankeniaceae and Caryophyllaceae. That *Q. canariensis* even may be polylectic with strong preference is supported by the results of Hohmann et al. (1993), who found the wasps mainly on flowers of *Frankenia laevis*, but recorded a specimen from *Polycarpaea* as well. Moreover, Hohmann et al. (1993) added single records from plants belonging to the families Asteraceae, Boraginaceae and Fabaceae. Such a broad spectrum of visited plant families and different flower types is unusual within the Masarinae for which various degrees of oligolecty (sensu Müller and Kuhlmann 2008) are more common (cf Gess 1996, Gess and Gess 2010). However, within the genus *Quartinia* the proportion of polylectic s.l. species seems to be comparatively high, as in Afrotropical *Quartinia* approximately 30% of the sufficiently examined species were recorded from more than two plant families (calculated from data by Gess and Gess 2010; n = 33). However, it is not known from how many of the plant families visited pollen is harvested.

During their visits to flowers of *Frankenia laevis* males and females of *Quartinia canariensis* usually came into contact with the anthers and stigmas of the flowers and there were often pollen grains on the exoskeleton of the wasps. Moreover, they showed a high flower fidelity to this plant. Therefore *Quartinia canariensis* probably acts as a pollinator of *Frankenia laevis*.

Mating

Males of *Quartinia canariensis* searched for females at flowers of *Frankenia laevis*, which was the main pollen source of the females. This is in congruence with mate searching in

Afrotropical species of *Quartinia* in which the males also frequently search for females at floral resources (Gess and Gess 1992, Gess and Gess 2010). However, the males of the Afrotropical *Quartinia* species commonly wait for females in flowers or rest on the ground in the vicinity of forage plants from where they rise up in response to the arrival of females, which they mount and copulate with on flowers (Gess and Gess 2010). In slight contrast, males of *Quartinia canariensis* were only observed to stand on the ground in the vicinity of the plants and not on the flowers (which is also reported for *Q. vagepunctata* by Gess and Gess 1992) and they frequently performed patrol flights along the flowers independent of the presence of females. Moreover, at least the initiation phase of the copulation in *Q. canariensis* took place both on flowers and on the ground as well as. Males of *Q. canariensis* were not observed at the nesting site whereas they were present in the nesting area of the Afrotropical *Q. vagepunctata* (Gess and Gess 1992). This might be explained by the formation of nesting aggregations in the latter species (Gess and Gess 1992) which makes it more predictable for the males to find potential mates in the vicinity of nests.

Females of *Quartinia canariensis* avoided contact with patrolling males at flowers and offered long lasting and predominantly successful resistance against insertion by males during the initiation phase. Since the females obviously bear considerable costs to withstand the male mating efforts, it can be assumed that insertion of the male genitalia is associated with high costs for the females of *Quartinia canariensis*, at least during the investigated period of the flight season. The nature of these costs is still unknown.

The copulation of a *Quartinia* species has not been described before in detail. Compared to photos of mating pairs of Afrotropical species of *Quartinia* in Gess and Gess (2010: 55) it seems that the position of the male on the female during the initiation phase is mainly similar in these taxa. The insertion phase has only been documented in *Quartinia femorata* (Gess and Gess 2010: 55). In this species the position of the male during the insertion seems to differ from *Q. canariensis* in that the male of *Q. femorata* is positioned less far posterior on the female with his head well above the posterior end of her mesosoma and the distal parts of his fore legs placed over the base of her wings. This is quite similar to the position in two species of the genus *Celonites* (Mauss 2006, Mauss and Müller 2014) the supposed sister group of *Quartinia* (Carpenter 1993, Krenn et al. 2002). In *Quartinia canariensis* the insertion phase lasted approximately 120 s. This is about ten times longer than the length of the insertion phase in members of the closely allied genera *Celonites* (Mauss 2006, Mauss and Müller 2014) and *Pseudomasaris* (Longair 1987). The significance and probable function of different insertion lengths is uncertain and should be investigated in detail.

Female brood care

Quartinia canariensis was found nesting in friable sandy soil close to its main forage plant. This is very similar to the nest situation recorded for two Afrotropical species, *Quartinia vagepunctata* (Gess and Gess 1992), nesting inland, and *Quartinia poecila*

(Gess 2009, Gess and Gess 2010), nesting on coastal dunes, from the Afrotropical region. In contrast utilization of sand-filled empty snail shells for nesting, as occurs facultatively or obligatorily in eight other Afrotropical species of *Quartinia* that also inhabit coastal and associated desert dune areas (Gess and Gess 1999, Gess and Gess 2008, 2010), seems to be absent in *Q. canariensis*.

As in all other Afrotropical *Quartinia* species for which nesting is known (Gess and Gess 1992, 1999, Gess and Gess 2010), the walls of the burrow and the cells of *Q. canariensis* were composed of non-rigid sand and silk structures with a silk lining. The silk was produced by the nest building female that apparently issued the material from the oral region and applied it with modified components of the mouthparts to the inner surface of the walls. Stabilization of the walls of the burrow by silk is unique among the Masarinae (Gess and Gess 1992, Mauss 2007), and can be regarded as an outstanding apomorphic trait of *Quartinia*. It probably had been the key adaptation for ground nesting in friable sandy soil that enabled the members of the stem-line of *Quartinia* to inhabit sand ecosystems. Within the evolution of the Masarinae the ability to exist in such sand habitats probably constituted a new adaptive zone for *Quartinia* and may at least partly explain the higher species diversity in *Quartinia* in relation to other genera of pollen wasps.

The short vertical turret surmounting the nest entrance of *Quartinia canariensis* is of the same form as in the Afrotropical *Quartinia* species (Gess and Gess 2010), exception being *Q. vagepunctata* that builds a horizontal, bag-like turret (Gess and Gess 1992), which is probably derived. The existence of a turret at the nest entrance is probably a plesiomorphic trait of *Quartinia* adopted from the ground pattern of the Masarini (Mauss 2007). It is of note that the focally observed female of *Quartinia canariensis* stabilized and repaired the turret walls from the inside of the turret while she was in the nest shaft with her head facing outwards. This situation is very unusual and it remains to be shown whether the turret is actually built and not only repaired in this position. In all other ground nesting pollen wasps in which the construction of the turret has been observed, i.e. *Priscomasaris namibiensis* (Gess 2001), several species of *Ceramius* (Gess and Gess 1980, Mauss et al. 2003, 2010), *Jugurtia* (Gess and Gess 1980, Gess and Gess 2010) and *Masarina* (Gess and Gess 1988a, Gess et al. 1997) as well as *Trimeria howardi* (Mechi 1999), the female is situated outside of the nest during turret building, standing on the ground or holding on to the outside of the walls of the growing turret with the mid and hind legs, simultaneously putting her head and her fore legs into the turret opening and curving her metasoma around the margin on the outside while she is adding mud with her mouthparts from the inside to the rim of the turret.

The nest of *Quartinia canariensis* consisted of a subterranean burrow terminated by a cell, which is principally similar to the nest architecture of *Quartinia vagepunctata* (Gess and Gess 1992). However, a minor difference between the nests of these species may exist in the depth of the cells varying between 15–23 mm in *Q. canariensis* and 25–30 mm in *Q. vagepunctata* (Gess and Gess 1992). Moreover, the nest of *Q. canariensis* was multicellular while all investigated nests of *Q. vagepunctata* contained only a single brood cell (Gess and Gess 1992). However, in one nest an additional blind

ending lateral shaft existed suggesting that *Q. vagepunctata* probably also constructs more than one cell per nest (Gess and Gess 1992). In all *Quartinia* species nesting in snail shells the burrow is multicellular with up to 20 or even more cells (Gess and Gess 2010). The distant and isolated position of the cells No. 3, 4 and 5 in the nest of *Quartinia canariensis* is remarkable. The developmental stages of the offspring in these cells clearly indicate that the cells had been excavated and provisioned by the female previous to the cells No. 1 and 2. Since the connection to the main shaft was not perceptible any more during nest excavation, it remains to be shown whether these cells were built either along a single earlier long lateral branch of the main shaft or at the end of three separate secondary shafts. Isolated brood cells at some distance from the main shaft have only been reported to occur in the subterranean burrows of the members of the species group 8 of *Ceramius* (summarized in Gess 1996) and of *Metaparagia angulata* (Gess et al. 1995). In these taxa each cell is probably built at the end of a relatively long separate secondary shaft connecting the brood cell to the main shaft. After the cell has been sealed by the female the secondary shaft is filled with soil particles to the point where it left the main shaft from which it is then sealed off (summarized in Gess 1996).

The behaviour of a *Quartinia* species during nest excavation has been observed for the first time. The female of *Q. canariensis* backed out of the shaft carrying soil particles with her mouthparts, which is similar to the behaviour of all other primarily ground nesting Masarine wasps, i.e. *Priscomasaris* (Gess 2001), *Paragia* (Houston 1984), *Metaparagia* (Gess et al. 1995, Houston 1995), *Ceramius* (Gess and Gess 1980, 1986, 1988b, Gess and Gess 2010, Mauss 1996, Mauss and Müller 2000, Mauss et al. 2003, 2006, 2010), *Trimeria* (Mechi 1999), *Jugurtia* (Gess and Gess 1980, Gess 1996) and *Masarina* (Gess and Gess 1988a). Therefore, these elements of the behaviour are probably plesiomorphic. However, the nest excavating behaviour of *Quartinia canariensis* differs from the ground pattern of the Masarinae (cf. Mauss 2007), in that no observable liquid was used during nest excavation. Liquid is probably not required, since firstly the friable sandy soil can be removed by the mandibles without softening it, and secondly bonding of the loose sand particles within the burrow is achieved by self-generated silk. This makes excavation more rapid as the necessity for interrupting excavation to fetch liquid is eliminated. In contrast, the other primarily ground nesting pollen wasps regularly have to interrupt nest excavation sequences to collect water, or rarely nectar, which is required for softening the soil and pellet formation.

The position of the egg at the distal end of the brood cell beyond the pollen loaf indicates that egg deposition precedes pollen provisioning in *Quartinia canariensis*. This is a plesiomorphic behavioural trait adopted from the ground pattern of the Masarinae and even the Vespidae (Gess 1996, Mauss 2007).

Associated organisms

In 1990 Gusenleitner established "*Chrysis atracomitata* LINS." as a cleptoparasite of *Quartinia canariensis*. Obviously, this is a misspelling of the name *Chrysis atrocomitata*

Linsenmaier, 1993 and the spelling has already been corrected in this sense by Hohmann et al. (1993: 109). Unfortunately, Gusenleitner used the name as a nomen nudum three years before the description of *Chrysis atrocomitata* was finally published by Linsenmaier (1993). Apparently Linsenmaier changed his opinion about the identity of the *Chrysis* taxon collected by Gusenleitner from the island Lanzarote as he described it as a separate species named *Chrysis umbofascialis* Linsenmaier, 1993. In fact, *Chrysis atrocomitata* sensu Linsenmaier (1993) does not occur in Lanzarote at all (Hohmann et al. 1993, Linsenmaier 1993), and the proposed parasite-host relationship refers to *Chrysis umbofascialis*, which was overlooked by Hohmann et al. (1993). However, the existence of a parasite-host relationship between *Chrysis umbofascialis* and *Quartinia canariensis* was in all probability only supported by the simultaneous occurrence of both taxa in the same habitat in Lanzarote and their matching small size, as Gusenleitner did not observe any behavioural interactions between them (Gusenleitner, pers. comm.). In contradiction, the geographic distribution of both taxa does not match with a close relationship between them. *Chrysis umbofascialis* has not been recorded from Fuerteventura, although most records of *Quartinia canariensis* come from this island. It was found in Tenerife instead, where *Q. canariensis* is missing (Hohmann et al. 1993, Linsenmaier 1993). Therefore, the existence of a parasite-host relationship between *Chrysis umbofascialis* and *Quartinia canariensis* seems doubtful at the moment. In this context it is of note that we did not observe any chrysidid wasp at the focally observed nest of *Quartinia canariensis*.

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RESEARCH ARTICLE

Revision of the genus *Promicrogaster* (Hymenoptera, Braconidae, Microgastrinae) from Area de Conservación Guanacaste, Costa Rica, with a key to all species previously described from Mesoamerica

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Abstract

The genus *Promicrogaster* (Hymenoptera, Braconidae, Microgastrinae) from Area de Conservación Guanacaste (ACG), Costa Rica, is revised. A key is provided to all new species as well as those previously described from Mesoamerica. A total of 21 species, all authored by Fernandez-Triana & Boudreault, are described as **species nova**: *alexmartinezi, andreyvallejosi, brandondinartei, daniellopezi, daretrizoi, eddycastroi, eimyobandoae, fabiancastroi, fabriciocambroneroi, hillaryvillafuerteae, kevinmartinezi, kiralycastilloae, leilycastilloae, liagrantae, luismendezi, monteverdensis, naomiduarteae, pablouzagai, ronycastilloi, sebastiancambroneroi, tracyvindasae*. A species previously described from India is considered as **incertae sedis**. *Promicrogaster* is considered to be restricted to the New World, with the vast majority of the species found in the Neotropics and a few extending north to the Nearctic. Almost 60% of the known species in ACG are found in cloud forests at over 1,000 m altitude. All of the verified and authenticated host records for *Promicrogaster* are from caterpillars living more deeply inside plant tissue than simply in rolled leaf structures – although no host data from ACG is available.

Introduction

The genus *Promicrogaster* was described by Brues and Richardson (1913) to accommodate a single female specimen from Guyana, which they considered to be unique based on several morphological characters. Half a century later Muesebeck (1958) and Nixon (1965) added 10 more new species of *Promicrogaster*, all from the Neotropics. An additional species was described from India by Sathe and Bhoje (1998), but we consider that a incertae sedis (see below for details). The true diversity of the genus remains unknown, although Mason (1981) considered that, in spite of being rare in collections, it might have more than 100 species overall. The highest diversity is in the Neotropics but a few, undescribed species reach the Nearctic. Biological information for the genus is very scarce: two host records from concealed caterpillars in the Lepidoptera families Sesiidae and Tineidae (Davis 1996, Garcia and Montilla 2010), an unidentified caterpillars infesting bracket fungus (Muesebeck 1958, Mason 1981).

This paper revises the genus *Promicrogaster* in Area de Conservación Guanacaste (ACG), northwestern Costa Rica (Janzen et al. 2009, Janzen and Hallwachs 2011), as part of comprehensive studies on the fauna of Microgastrinae from that region (e.g. Fernandez-Triana et al. 2013, 2014a–d). A key to all known species from Mesoamerica is also included, but the North and South American species are not dealt with in this paper.

Methods

Promicrogaster is a rarely collected genus (Mason 1981), and it is poorly represented in collections. This study is based on 120+ specimens, most of them collected in ACG, with a few additional specimens from other Mesoamerican countries available for study in the Canadian National Collection of Insects (CNC) in Ottawa. Some paratypes of the new species being described will be deposited in other collections with the following acronyms used: BMNH (The Natural History Museum, London, United Kingdom), INBio (Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica) and NMNH (National Museum of Natural History, the Smithsonian Institution, Washington DC, United States).

Four species of *Promicrogaster* had been described previously from Mesoamerica. The original descriptions and illustrations for three of them were sufficiently detailed to allow us to describe the new species with confidence. The only exception was *Promicrogaster apharea* Nixon, 1965 (Brazil and highlands of southwestern Mexico), which could not be reliably defined based on the original description alone, but in that case we examined the holotype.

Morphological terms and measurements of structures are mostly as used by Mason (1981), Huber and Sharkey (1993), Whitfield (1997), Karlsson and Ronquist (2012), and Fernández-Triana et al. (2014a). Mediotergites 1, 2, etc., are abbreviated as T1, T2, etc. Flagellomere 1 is the closest to pedicel while flagellomere 16 is the most apical one. Because the ovipositor in *Promicrogaster* is curved and crooked at the very apex, its length is difficult to measure accurately; the ovipositor length measurements provided for each new species are only intended as an approximation. In any case, the ovipositor and its sheaths are some of the longest observed in any Microgastrinae genera; they are usually two times longer than the metatibia length.

The dichotomous key and descriptions of the new species are based on the study of all available female specimens, so as to reflect intraspecific variation, but always include data from the holotype for the new species. Males of most species cannot be readily identified unless associated with females via rearing or molecular data.

The dichotomous key is mostly based on morphological characters, but in one couplet we used molecular characters to differentiate species that are morphologically similar to each other. In that case we used characteristic loci in the DNA barcoding region. The bases are numbered from the start of the COI gene according to the reference sequence U37541 (*Drosophila melanogaster*), and are only diagnostic within that couplet. The letters A, C, G, and T correspond to adenine, cytosine, guanine, and thymine respectively.

The descriptions include 21 characters that are commonly used in describing Microgastrinae (e.g., body measurements such as length of body and fore wing, ovipositor sheath; and also color of particular body areas). These characters follow a recent revision of the related genus *Sendaphne* (Fernandez-Triana et al. 2014d), so as to facilitate future comparisons between species in those two genera.

Photos were taken with a Keyence VHX-1000 Digital Microscope, using a lens with a range of 13–130×. Multiple images through the focal plane were taken of a structure and these were combined to produce a single in-focus image, using the software associated with the Keyence System.

Together with morphological studies, we also analyzed DNA barcodes (the 5' region of the cytochrome *c* oxidase I (CO1) gene, Hebert et al. 2003) whenever available. DNA barcodes were obtained using DNA extracts prepared from single legs using a glass fibre protocol (Ivanova et al. 2006). Briefly, total genomic DNA was re-suspended in 30 μl of dH2O, and a 658-bp region near the 5' terminus of the CO1 gene was amplified using standard primers (LepF1–LepR1) following established protocols (Smith et al. 2006, 2007, 2008). If the initial 658 bp amplification was unsuccessful, smaller sequences were generated using internal primers. If each amplification worked, a composite sequence was generated, however in cases where only one read amplified, this shorter sequence was used. All information for the sequences associated with each individual specimen can be retrieved from the Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007). A Neighbor-Joining tree based on Kimura 2-parameter was also generated (Fig. 160).

The new species described below received patronyms based on the winners of a school child nature awareness competition conducted by the Programa de Educación Biológica de ACG in the last half of 2015 (Kazmier 2015).

Results

Characterization of the genus *Promicrogaster*

Promicrogaster Brues & Richardson, 1913

Promicrogaster: Brues and Richardson 1913: 499.

Diagnosis. Glossa elongate and bilobate (Figs 4, 10, 16, 22, 28, 34, 40, 46, 70, 76, 82, 101, 107, 118, 130, 149). Lateral face of scutellum with polished area (=lunules) occupying most of the lateral face (Figs 12, 18, 24, 32, 36, 42, 62, 66, 72, 78, 84, 110, 114, 120, 126, 138, 147, 151). Propodeum clearly sculptured and usually with some carination (Figs 12, 18, 36, 42, 66, 90, 99, 114, 120, 132, 133, 157). Metacoxa very long, 0.8–1.0 × metafemur length and 0.6–0.8 × metatibia length (Figs 7, 15, 38, 45, 51, 57, 63, 74, 87, 106, 117, 129, 135, 146, 148, 154). Mediotergite 1 parallel-sided (Figs 8, 13, 19, 32, 60, 140) to slightly narrowing towards posterior margin (Figs 38, 44, 55, 67, 73, 85, 91, 105, 127, 132, 147). Mediotergite 2 transverse, its width at posterior margin 3.0–4.5 × (rarely 2.0 ×) its length medially. Ovipositor very long for a microgastrine wasp (approximately two times longer than metatibia length), strongly curved and with its apex sinuate (Figs 1, 5, 14, 15, 20, 26, 30, 37, 43, 50, 51, 56, 61, 63, 68, 69, 74, 86, 87, 92, 98, 104, 108, 116, 121, 123, 128, 139, 140, 144, 148, 154, 159). Fore wing usually with a small areolet, which is sometimes poorly defined (Figs 3, 17, 23, 29, 35, 47, 59, 65, 71, 77, 83, 89, 95, 108, 113, 119, 131, 137, 156); but some small species have no trace of areolet whatsoever (Figs 41, 102, 125, 150). Body and fore wing lengths ranging from 1.8–2.0 mm in the smallest species up to 4.9–5.3 mm in the largest species. Body length varying from slightly longer to slightly shorter than fore wing length.

    Promicrogaster is a very distinctive genus as defined by the combination of elongate and bilobate glossa, large polished areas on lateral face of scutellum, and ovipositor shape and length. Within Microgastrinae, it can only be confused with *Sendaphne*, but the later has a much less transverse mediotergite 2, the apex of ovipositor is not sinuate, the propodeum is entirely or mostly smooth, and the first discal cell is much wider (e.g., Fernandez-Triana et al. 2014d).

    We consider the described '*Promicrogaster*' from India as incertae sedis (see below for a detailed discussion on that species). Thus, *Promicrogaster* as defined here is restricted to the New World, with the vast majority of the species found in the Neotropics and a few extending north to the Nearctic (Mason 1981, and unpublished data from the CNC collection). This pattern of distribution is remarkably similar to that found in other genera recently revised in the New World, such as *Pseudapanteles* and *Venanus* (Fernandez-Triana et al. 2013, 2014b, 2014c). A total of 21 new species are described below, increasing the total known Mesoamerican species from 4 to 25, and the total number of described species for the genus from 11 to 32 (Table 1). We are aware of many additional undescribed species in collections, from North America (Canada/US) and South America, which will be dealt with in future papers.

As for habitat preference, 82% of the ACG species were collected in rain forests and cloud forests (with almost 60% restricted to cloud forests), while only 18% were found in dry forests. Around 40% of the species were found at low-mid elevation (0-500 m) whereas almost 60% of the species were collected at altitudes over 1,000 m. This strongly contrasts with the closely related genus *Sendaphne*, which has been mostly found at altitudes between 100–900 m with just a few species found in cloud forests (Fernandez-Triana et al. 2014d).

All of the verified and authenticated host records for *Promicrogaster* are from caterpillars living more deeply inside more or less woody plant material than simply in rolled leaf structures. It is possible that the sinuate ovipositor tip in all known species of *Promicrogaster* is an adaptation allowing the ovipositor to be steered through fissures in harder/more woody structures than mere leaf rolls (e.g., Quicke 2015).

Muesebeck (1958) described *Promicrogaster polyporicola* as reared from unidentified Lepidoptera larvae infesting a bracket fungus (*Fomes* sp.) in Panama. Davis (1996) reared an unidentified species of *Promicrogaster* from caterpillars of *Prosetomorpha fal-*

Table 1. Mesoamerican species of *Promicrogaster*. The presence of species in Area de Conservación Guanacaste is indicated below by adding 'ACG' after 'Costa Rica'. New country records for species previously described are marked with an asterisk (*).

Species	Distribution
Promicrogaster alexmartinezi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster andreyvallejosi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster apharea Nixon, 1965	Brazil, Mexico
Promicrogaster brandondinartei Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster daniellopezi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster daretrizoi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster eddycastroi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster eimyobandoae Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster fabiancastroi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster fabriciocambroneroi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster hillaryvillafuerteae Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster kevinmartinezi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster kiralycastilloae Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster leilycastilloae Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster liagrantae Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster luismendezi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster miranda Muesebeck, 1958	Panama, Trinidad (*)
Promicrogaster monteverdensis Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG and other localities
Promicrogaster munda Muesebeck, 1958	Costa Rica, Honduras, Mexico, Panama (*)
Promicrogaster naomiduarteae Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster pablouzagai Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster polyporicola Muesebeck, 1958	Panama
Promicrogaster ronycastilloi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster sebastiancambroneroi Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG
Promicrogaster tracyvindasae Fernandez-Triana & Boudreault, sp. n.	Costa Rica, ACG and other localities

cata (Tineidae) in Colombia; the larvae of this small moth are scavengers feeding on frass within the burrows made by larval Curculionidae in the stems of *Solanum quitoensis* (Solanaceae: 'Naranjilla'). Garcia and Montilla (2010) reared *Promicrogaster* as a parasitoid of cocoa fruit borers, *Carmenta* spp. (Sessidae) in Venezuela; *Carmenta* larvae mine through the pericarp of cocoa (Malvaceae: *Theobroma cacao*) fruit, and their damage leads to secondary phytopathogenic fungal infections (such as *Phytophthora* sp.) that cause the fruit to rot (e.g., Morrilo et al. 2009). The 21 species of *Promicrogaster* found in ACG have only been collected in Malaise traps. It is likely that those wasp species have not been reared yet because they are parasitizing small moth larvae concealed inside more or less woody plant or fungal tissues - the ACG inventory, while being the most comprehensive effort ever done to rear tropical caterpillars, has only focused on exposed feeders and rollers of green leaves.

Key to *Promicrogaster* species in Mesoamerica (female specimens)

1   Head entirely yellow-orange to orange-brown; anteromesoscutum and scutellar disc mostly orange-brown (Figs 129, 130, 133); antenna mostly orange-yellow (only apical 4–5 flagellomeres dark brown) ....
.... ***Promicrogaster pablouzagai*** **Fernandez-Triana & Boudreault, sp. n.**
–   Head entirely black to dark brown (except for clypeus and labrum orange-yellow in some species); anteromesoscutum and scutellar disc black; antenna dark brown to black (rarely some species with apical 5–7 flagellomeres yellow-white) **2**

2(1)   Lighter coloured species; clypeus entirely or mostly yellow to orange-yellow (as in Figs 4, 107, 118); all sternites and hypopygium yellow to orange-yellow (as in Figs 3, 5, 7, 57, 61, 106, 108, 117, 121); metasoma dorsally with T1–T4 entirely (rarely mostly) yellow, orange or red (as in Figs 8, 60, 109, 110, 119, 120) **3**
–   Darker coloured species; most sternites (usually) and hypopygium (partially to entirely) dark brown (as in Figs 14, 20, 26, 30, 43, 56); metasoma dorsally mostly dark brown to black (rarely some tergites with small areas orange to light brown) (as in Figs 13, 19, 25, 31, 38, 44, 48, 55); clypeus coloration variable, usually dark brown to black **6**

3(2)   Propodeum with complete, raised, and strongly defined median carina (partially visible in Fig. 110); ***and*** T1 entirely smooth (Fig. 109); ***and*** malar distance more than half eye length (Fig. 107); ***and*** clypeus large and entirely orange-yellow (Fig. 107) [Panama, Trinidad] ....
....***Promicrogaster miranda*** **Muesebeck, 1958**
–   Propodeum without a median carina but with central depression (Figs 62, 120, 122); ***either*** with T1 mostly rugose (Figs 119, 120) ***and*** with malar distance less than half eye length (Figs 4, 118); ***or*** with clypeus smaller and not entirely yellow-red (as in Fig. 58) [other Mesoamerican countries, mostly Costa Rica]..............**4**

4(3)   Metasoma dorsally entirely yellow-orange (Figs 119, 120); T1 with coarse sculpture on 0.7 or more its length; T2 relatively narrow, its width at posterior margin more than 3.0 × its length centrally (Figs 119, 120); scape entirely to mostly black to dark brown (partially visible in Fig. 118) [Costa Rica, Honduras, Mexico, Panama, mostly found at elevations over 1000m] . ... ***Promicrogaster munda* Muesebeck, 1958**

–   Metasoma dorsally with some red, brown or black coloration (Figs 8, 60); T1 smoother (Fig. 60), at most with sculpture on posterior 0.5 of its length (Figs 8); T2 broader, its width at posterior margin usually less than 3.0 its length centrally (Figs 8, 60, 62); scape mostly yellow (Fig 4, 58) [Costa Rica, ACG, dry forest, under 300m]..**5**

5(4)   Posterior margin of clypeus strongly concave (Fig. 58); lower face clearly elongate, malar distance at least 1.5 × mandible width (Fig. 58); fore wing vein 1M transparent (Fig. 59); T1 shape more or less rectangular (width at middle length, anterior or posterior margin about the same); T1–T4 entirely orange-yellow, T5+ mostly dark brown to black (Fig. 60)................***Promicrogaster fabriciocambroneroi* Fernandez-Triana & Boudreault, sp. n.**

–   Posterior margin of clypeus very slightly concave, almost straight (Fig. 4); lower face of normal length, malar distance 1.0 × mandible width (Fig. 4); fore wing with vein 1M brown (Fig. 3); T1 narrowing towards posterior margin; T1 mostly red with black margins (posterior 0.3 of T1 black sometimes), T2–T4 red-orange or yellow-orange, T5+ yellow with small central band brown (Fig. 8).. ....***Promicrogaster alexmartinezi* Fernandez-Triana & Boudreault, sp. n.**

6(2)   Antenna with most flagellomeres 10–16 yellow-white (Figs 33, 87)............**7**

–   Antenna entirely dark brown to black (rarely with flagellomeres 1–4 lighter in colour than rest of antenna)..**8**

7(6)   Antenna with flagellomeres 11–16 yellow-white (Fig. 87); propleuron, anterior 0.5 of metacoxa, sternites and hypopygium dark brown (Figs 87, 89); ovipositor strongly down curved on posterior 0.2 (Fig. 92) [Costa Rica, ACG, cloud forest over 1000m].. .....***Promicrogaster leilycastilloae* Fernandez-Triana & Boudreault, sp. n.**

–   Antenna with flagellomeres 1–8 and 15–16 dark brown, and flagellomeres 9–14 (sometimes only 10–14) yellow white (Fig. 33); propleuron, metacoxa, sternites and hypopygium mostly yellow to orange-yellow (Figs 33, 37); ovipositor relatively straight (Fig. 37) [Costa Rica, ACG, mid-elevation rain forests, 500-800m].. .... ***Promicrogaster daretrizoi* Fernandez-Triana & Boudreault, sp. n.**

8(6)   Fore wing without areolet (as in Figs 41, 53, 102, 125, 150), ***and*** hypopygium and sternites almost always entirely dark brown (at most hypopygium with small pale spot basally, and/or anterior 2-3 sternites yellow) (Figs 30, 43,

56, 100, 104, 128, 144, 153), **and** smaller size (body length 1.8–2.4 mm, fore wing length 2.0–2.6 mm) **9**

–   Fore wing with small areolet (as in Figs 137), **and/or** hypopygium and sternites usually mostly to entirely yellow, **and/or** larger size (body and fore wing lengths usually 3.0–4.0 mm)..**15**

9(8)   Propodeum mostly sculptured (except for polished areas postero-laterally) (Figs 42, 54, 103, 105, 127, 128) **10**

–   Propodeum mostly smooth (except for small striae around nucha) (Figs 32, 145, 147, 151)...**13**

10(9)   Smaller size, body length 2.0–2.1 mm, fore wing length 2.2 mm, metacoxa 0.45–0.46 mm; ocular–ocellar line 0.08–0.09 mm; T1 width/length 0.4–0.5 x; ten diagnostic characters in the DNA barcoding region: 79C, 235C, 346C, 364C, 386A, 415A, 421G, 562A, 607G, 622C ....
.....*Promicrogaster fabiancastroi* **Fernandez-Triana & Boudreault, sp. n.**

–   Larger size, body length 2.3–2.4 mm, fore wing length 2.4–2.6 mm, metacoxa 0.47–0.56 mm; ocular–ocellar line 0.11–0.15 mm (rarely 0.08); T1 width/length 0.5–0.7 x; different base pairs in the barcoding region : 79A or 79T, 235T, 346A or 346T, 364A or 364T, 386T, 415G, 421A or 421T, 562G or 562T, 607A or 607T, 622A or 622T **11**

11(10)   Ocular–ocellar line shorter than interocellar distance (0.9 x); T1 posterior width 1.3 × T2 central length; T2 width 3.2 × its length centrally ....
.......*Promicrogaster luismendezi* **Fernandez-Triana & Boudreault, sp. n.**

–   Ocular–ocellar line longer than interocellar distance (1.4–1.6 x); T1 posterior width 1.8–2.0 × T2 central length; T2 width 3.5–4.9 × (usually more than 4.0 x) its length centrally...**12**

12(11)   T2 width 4.9 × its length centrally; T1 length 1.9 × its posterior width; larger species, fore wing length 2.6 mm, metacoxa length 0.6 mm, metafemur length 0.7 mm, metatibia 0.9 mm ....
........*Promicrogaster eddycastroi* **Fernandez-Triana & Boudreault, sp. n.**

–   T2 width 3.5–4.0 × its length centrally; T1 length 1.5–1.7 × its posterior width; smaller species, fore wing length 2.3–2.4 mm, metacoxa length 0.5 mm, metafemur length 0.5–0.6 mm, metatibia 0.7–0.8 mm ....
..*Promicrogaster naomiduarteae* **Fernandez-Triana & Boudreault, sp. n.**

13(9)   Pterostigma with anterior 0.3 or more white, most veins of fore wing transparent or white (Fig. 29) [Costa Rica, ACG, dry forest under 300m] ....
.......*Promicrogaster daniellopezi* **Fernandez-Triana & Boudreault, sp. n.**

–   Pterostigma entirely brown or at most with anterior 0.1 pale, fore wing with veins mostly brown (Figs 143, 150) [Costa Rica, ACG, cloud forests over 1,000m]..**14**

14(13)   Posterior 0.6 of T1 sculptured (Fig. 147); clypeus, procoxa, most of sternites and laterotergites brown (Figs 141, 142, 144)..
......*Promicrogaster ronycastilloi* **Fernandez-Triana & Boudreault, sp. n.**

– Posterior 0.6 of T1 mostly smooth (at most with sculpture restricted to margins) (Fig. 152); labrum yellow-orange, procoxa yellow, sternites and laterotergites mostly to partially yellow (Figs 148, 149, 153) ....***Promicrogaster sebastiancambroneroi* Fernandez-Triana & Boudreault, sp. n.**

15(8) Posterolateral corners of anteromesoscutum orange (Fig. 138); hypopygium and sternites dark brown (Figs 137, 139); T1 hardly narrowing towards posterior margins; T1 relatively wide, its medial length barely longer than its width at anterior margin (Figs 138, 140) [Panama] ....
....***Promicrogaster polyporicola* Muesebeck, 1958**

– Anteromesoscutum entirely black; hypopygium and sternites usually mostly to entirely yellow; T1 usually narrowing towards posterior margin; T1 relatively narrower, its medial length much longer than its width at anterior margin [Brazil, Costa Rica, Mexico] **16**

16(15) Propleuron almost entirely yellow (Figs 45, 69, 70, 76), except for anterior 0.2 near head yellow-white (rarely propleuron partially yellow, partially light-brown); hypopygium, sternites and most laterotergites entirely yellow (hypopygium may have a dark spot on posterior 0.1 or less) (Figs 50, 69, 74, 81, 86)................**17**

– Propleuron almost entirely dark brown to black, except for anterior 0.2 near head yellow (Figs 9, 63, 111); hypopygium, sternites and laterotergites at least partially dark brown...**19**

17(16) Metacoxa dark brown on anterior 0.6 (Fig. 86); tegula brown; propleuron partially yellow, partially light-brown (partially visible in Figs 81, 82) ....
..***Promicrogaster kiralycastilloae* Fernandez-Triana & Boudreault, sp. n.**

– Metacoxa, tegula and propleuron entirely yellow (propleuron with anterior 0.2 near head yellow-white) (Figs 45, 46, 50, 69, 74, 76) **18**

18(17) T3 mostly yellow-white, with anterior 0.4 light brown, T4–7 brown anteriorly, white on posterior 0.3–0.5 (Figs 71, 73) [Costa Rica, ACG, cloud forest over 1,000m]...
... ***Promicrogaster kevinmartinezi* Fernandez-Triana & Boudreault, sp. n.**

– All tergites dark brown to black (Fig. 48) [Costa Rica, ACG, mid-elevation rain forest, 500m] ....
...***Promicrogaster eimyobandoae* Fernandez-Triana & Boudreault, sp. n.**

19(16) Fore wing without areolet (Fig. 11) ....
..***Promicrogaster andreyvallejosi* Fernandez-Triana & Boudreault, sp. n.**

– Fore wing with small areolet **20**

20(19) Flagellomeres 1–4 yellow-brown, clearly paler than rest of entirely brown flagellomeres (partially visible in Figs 63, 64); orange-yellow areas on metapleuron posterior 0.4, T1 anterior 0.6, T3 anterior 0.5 and small spot on mesopleuron posteriorly (Figs 63, 66–68) ....
..***Promicrogaster hillaryvillafuerteae* Fernandez-Triana & Boudreault, sp. n.**

– All flagellomeres same color (brown to dark brown); meso and metapleuron entirely dark brown to black, coloration of T1 and T3 variable but not as above **21**

21(20) Tegula and wing base dark brown to black (Fig. 114); clypeus black (same color as face) (Fig. 112); clypeus slightly protruding and labrum slightly depressed, giving the appearance of a circular opening between the margin of clypeus and mandibles (barely distinguishable in Fig. 112) ....
...*Promicrogaster monteverdensis* **Fernandez-Triana & Boudreault, sp. n.**
– Tegula and wing base yellow; clypeus entirely to partially orange-yellow or orange-brown (clearer than face) (Figs 16, 155); clypeus not protruding and labrum not depressed, not giving the appearance of a circular opening **22**
22(21) Flagellomere 15 length 1.6–1.7 × its width; *and* ovipositor tip strongly bent downwards; *and* clypeus entirely orange-yellow (different from dark brown to black face); *and* body length and fore wing length 4.0 mm; *and* T1 almost parallel-sided, very slightly narrowing towards posterior margin; *and* T2 mostly sculptured; *and* T3 with small yellow spot laterally [Brazil, Mexico]...
....*Promicrogaster apharea* **Nixon, 1965**
– Flagellomere 15 length 1.0–1.3 × its width; *and/or* ovipositor tip less strongly bent downwards; and/or clypeus entirely to partially dark brown to black (same color than face); *and/or* body length and fore wing length less than 4.0 mm; *and/or* T1 clearly narrowing towards posterior margin; *and/or* T2 mostly smooth; *and/or* T3 entirely dark brown to black [Costa Rica] **23**
23(22) Metacoxa with anterior 0.3–0.6 black (Figs 15, 19) [Costa Rica, ACG, cloud forests over 1,000m] ....
...*Promicrogaster brandondinartei* **Fernandez-Triana & Boudreault, sp. n.**
– Metacoxa entirely yellow (at most with small dark spot on anterior 0.1 or less, barely visible) (Figs 95, 154, 156) [Costa Rica, ACG, dry forest or mid-elevation rainforests, 300–500m]..**24**
24(23) T1 clearly narrowing towards posterior margin, its length 2.0 × its width at posterior margin; T2 mostly sculptured; T3 with yellow spots laterally (Figs 94, 99) .... *Promicrogaster liagrantae* **Fernandez-Triana & Boudreault, sp. n.**
– T1 almost parallel-sided, very slightly narrowing towards posterior margin, its length 1.7 × its width at posterior margin; T2 mostly smooth; T3 entirely dark brown to black (partially visible in Figs 156–158)................................
....*Promicrogaster tracyvindasae* **Fernandez-Triana & Boudreault, sp. n.**

Taxonomic treatment of species

Promicrogaster saraswatti Sathe & Bhoje, 1998, incertae sedis

Promicrogaster saraswatti Sathe & Bhoje, 1998: 105. Original description.

Holotype. Female, depository unknown. INDIA, Maharashtra, Kolhapur. Holotype not examined.

Comments. There are several issues that will require further study to clarify the status and identity of this species. First, all other *Promicrogaster* specimens that we have seen in collections (from either described or undescribed species) are restricted to the New World, and all published evidence (e.g., Mason 1981, Whitfield 1997) does not support this genus to be present in India. Second, *Promicrogaster saraswatti* was described by Sathe and Bhoje (1998) as a parasitoid of *Phytomyza atricornis* Meigen (Diptera: Agromyzidae), which is very suspicious, as all authenticated records of Microgastrinae are from Lepidoptera (e.g., Shaw and Huddleston 1991, Whitfield 1997, Quicke, 2015). Third, Sathe and Bhoje (1998) recorded in their paper the body size of the parasitoid wasp to be 4.64 mm and the wasp cocoon to be 4.5 mm; this is in strong contrast to a much smaller size for its supposed host: larvae of *Phytomyza atricornis* are only known to reach a maximum length of 3.5 mm and their puparia are even smaller at 2.1–2.5 mm (Cohen 1936). All of that points towards this species not being *Promicrogaster* but some other Microgastrinae (impossible to tell based on the unclear original description, which lacked any illustration); and the parasitoid's biology might well have also been misunderstood and should be considered as highly questionable. To complicate things further, no details about the institution storing the holotype and 33 paratypes (reportedly from the same locality and data as holotype) were provided by the authors. Because the original description of *P. saraswatti* is the only source of information currently available, this species remains unrecognizable.

Promicrogaster alexmartinezi Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/2392E300-06B5-44CB-B4DE-D54F90EF21E1
Figs 1–8

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa, Area Administrativa, 295m, 10.83764, -85.61871. DNA Voucher code: DHJPAR0031827.

Paratype. 1♀ (CNC), same locality as holotype. DNA voucher code: DHJPAR0031814.

Description. Head: mostly black, clypeus, labrum and mandibles yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: white. Metasoma (dorsally): T1 mostly red with black margins (posterior 0.3 of T1 black sometimes), T2–T4 red-orange or yellow-orange, T5+ yellow with small central band brown. Metacoxa: Orange. Malar distance: 0.3 × eye length. Fore wing areolet: present. T1 sculpture: mostly smooth, with posterior 0.3 sculptured. T2 sculpture: mostly smooth. Ocular–ocellar line: 0.14 mm. Interocellar distance: 0.12 mm. Posterior ocellus diameter: 0.11 mm. Body length: 4.20–4.97 mm. Fore wing length: 4.17–4.83 mm. Ovipositor length: 2.40–3.50 mm. Metacoxa length: 1.10–1.41 mm. Metafemur length: 1.11–1.32 mm. Metatibia length: 1.44–1.89 mm. T1 length/width at posterior margin: 0.56–0.73mm/ 0.32–0.40 mm. T2 length/width at posterior margin: 0.18–0.20 mm/ 0.42–0.63 mm.
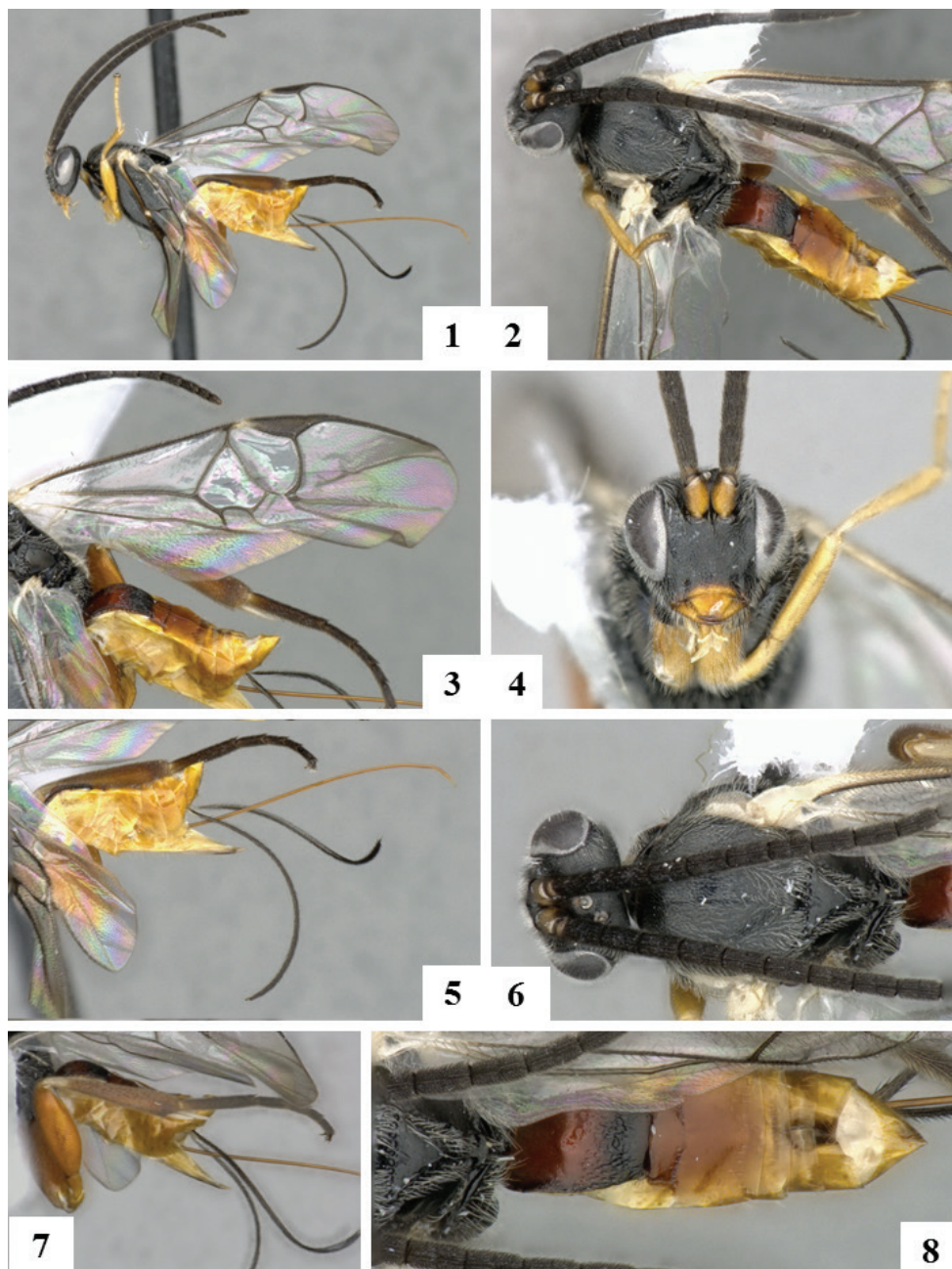
Figures 1–8. *Promicrogaster alexmartinezi* sp. n. holotype.

Distribution. Known only from the holotype locality in ACG, dry forest, Costa Rica.

Comments. The female holotype is larger and slightly darker than the paratype.

Etymology. *Promicrogaster alexmartinezi* is named in honor of 13-year-old Alex Geovanny Martínez López from the Colonia Bolaños school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster andreyvallejosi Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/42C8D3E2-34E6-424B-B594-F3CEB5AC3FB0
Figs 9–14

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Sendero Cima, 1460m, 10.93328, -85.45729. DNA Voucher code: DHJPAR0034152.

**Description.** Head: mostly black, labrum and mandibles yellow-orange. Flagellomeres: dark brown to black. Mesosoma color: black. Tegula: dark brown. Metasoma (dorsally): black to dark brown. Metacoxa: dark brown on anterior 0.5, yellow on posterior 0.5. Malar distance: less than 0.2 × eye length. Fore wing areolet: absent. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured. Ocular–ocellar line: 0.15 mm. Interocellar distance: 0.06 mm. Posterior ocellus diameter: 0.08 mm. Body length: 3.46 mm. Fore wing length: 3.34 mm. Ovipositor length: 2.18 mm. Metacoxa length: 0.76 mm. Metafemur length: 0.89 mm. Metatibia length: 1.06 mm. T1 length/width at posterior margin: 0.45mm/ 0.27 mm. T2 length/width at posterior margin: 0.14 mm/ 0.44 mm.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

Etymology. *Promicrogaster andreyvallejosi* is named in honor of 11-year-old Andrey Vallejos López from the La Garita Vieja school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Comments. The ovipositor was too curved and the metacoxa was partially hidden in the available specimen, so those measurements should be considered as approximate.

Promicrogaster apharea Nixon, 1965

Promicrogaster apharea Nixon, 1965: 234. Original description.

Holotype. Female, BMNH (examined). MEXICO, Guerrero, Omilteme, 2400 m.

Distribution. Mexico, Brazil. The two Mexican specimens were collected at altitudes of 1,400 and 2,400 m respectively, whereas the Brazilian specimen was collected at around 500 m (Nixon 1965).

Comments. The relatively long flagellomere 15, as well as body length and fore wing length over 4.0 mm are the most useful characters to separate the species from a

Figures 9–14. *Promicrogaster andreyvallejosi* sp. n. holotype.

few Costa Rican species that are otherwise similar morphologically (e.g., *P. brandondinartei, P. liagrantae* and *P. tracyvindasae*). *P. apharea* is only known from three female specimens, as mentioned in the original description Nixon (1965). The strange geographic and ecological distribution reported suggests it might actually comprise two different species, one from Mexico and one from Brazil. Because we only examined the holotype we cannot conclude about that.

Promicrogaster brandondinartei Fernandez-Triana & Boudreault, sp. n.

http://zoobank.org/BC14B161-CE15-4AA2-B24C-E9019D20759E
Figs 15–26

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Sendero Arenales, 1080m, 10.92471, -85.46738. DNA Voucher code: DHJPAR0031290.

Paratypes. 1♀ (NMNH), same locality as holotype; 2♀ 1♂ (CNC), Costa Rica, Guanacaste, ACG, Sector Cacao, Sendero Circular, 1185m, 10.92714, -85.46683; 1♂ (CNC). Panama, Cerro Campana, 850m, 8º 40' N 79º 55' W. DNA Voucher codes: CNCHYM 01985, DHJPAR0031203, DHJPAR0031206, DHJPAR0031258, DHJPAR0031326.

Description. Head: mostly black, labrum and mandibles light brown to yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: brown. Metasoma (dorsally): dark brown to black. Metacoxa: yellow. Malar distance: less than $0.2 \times$ eye length. Fore wing areolet: present. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.15 mm. Interocellar distance: 0.10 mm. Posterior ocellus diameter: 0.08 mm. Body length: 3.54 mm. Fore wing length: 3.70 mm. Ovipositor length: 2.89 mm. Metacoxa length: 0.85 mm. Metafemur length: 0.97 mm. Metatibia length: 1.27 mm. T1 length/width at posterior margin: 0.50 mm/ 0.31 mm. T2 length/width at posterior margin: 0.11 mm/ 0.47 mm.

Distribution. Costa Rica (ACG, cloud forest), Panama.

Etymology. *Promicrogaster brandondinartei* is named in honor of 12-year-old Brandon Josué Dinarte Barrientos from the Huacas school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Comments. There are two barcode divergent groups within what we call *Promicrogaster brandondinartei* (Fig. 160). The holotype (DHJPAR0031290, from the barcode BIN BOLD:ABZ2999) and three of the paratypes (DHJPAR0031203, DHJPAR0031258, DHJPAR0031206, from the barcode BIN BOLD:AAM9535) form two sequence clusters that are not monophyletic within the genus. A fourth paratype specimen (DHJPAR0031326) is represented by a short sequence that clusters with the holotype. These two BINS are separated by 2.3 % sequence divergence, four amino acid differences and are derived from specimens collected from Malaise traps placed at different elevations along Volcán Cacao (Arenales and Circular at approximately 1,000m and 1,200m respectively). This may suggest that there are multiple species
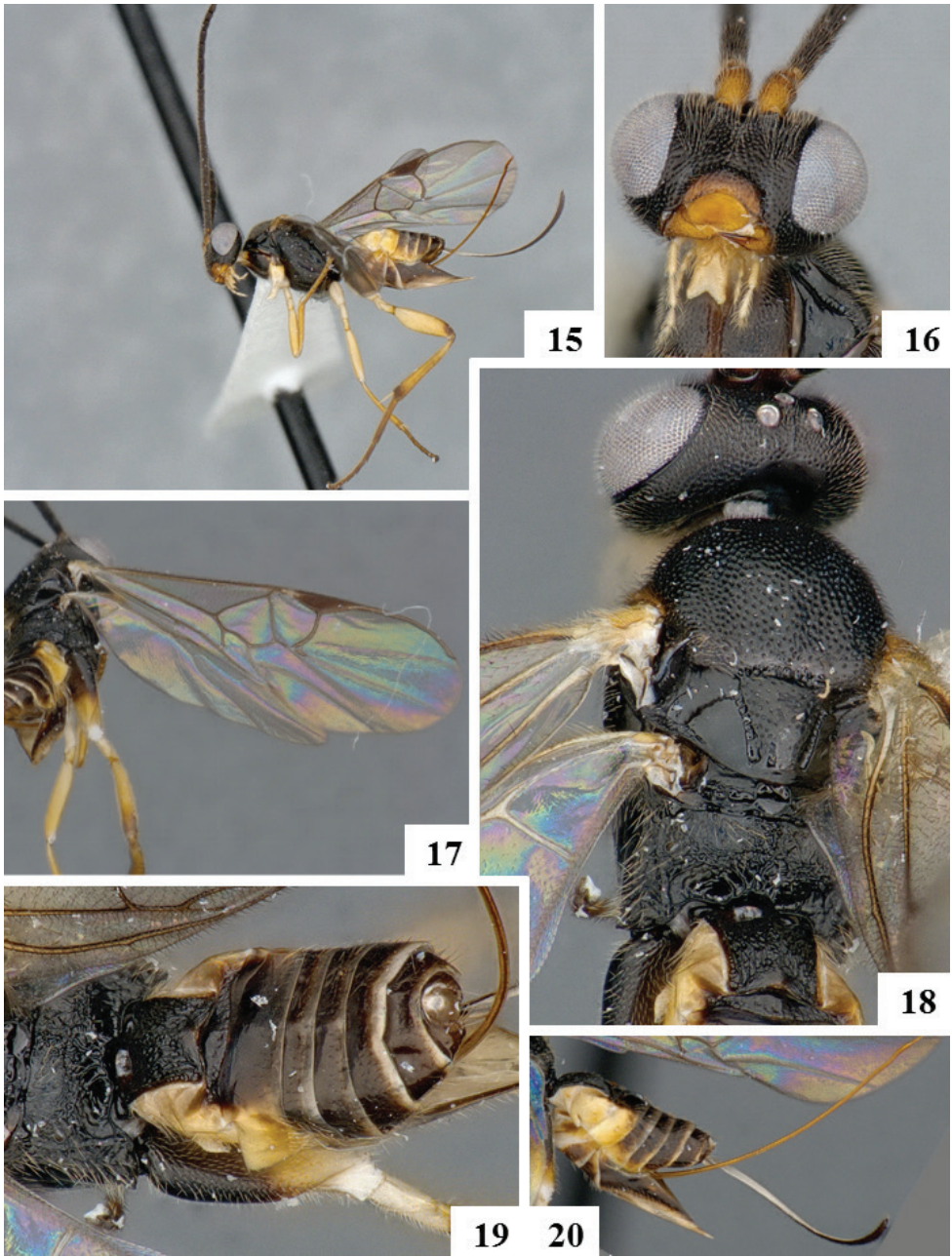
Figures 15–20. *Promicrogaster brandondinartei* sp. n. holotype.

Figures 21–26. *Promicrogaster brandondinartei* sp. n. paratype.

within this name. However, the trace files for the BIN associated with the holotype (BOLD:ABZ2999) contain ambiguities at the bases associated with the amino acid changes between the two BINS, a potential signal of co-amplification of a pseudogene or numt (Zhang and Hewitt 1996). Since the specimens are morphologically indistinguishable, we consider it likely that the barcode records for *P. brandondinartei* contain variation derived from a pseudogene rather than representing a true mitochondrial variant. However, clearly delineating between the hypotheses of morphologically cryptic species-level variation (two BINS) or pseudogene-derived barcode variation within *brandondinartei* will require further collections and specimens to be barcoded.

Promicrogaster daniellopezi Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/79CB6DA4-9678-408D-810F-DB276467FF2E
Figs 27–32

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa, Area Administrativa, 295m, 10.83764, -85.61871. DNA Voucher code: DHJPAR0031641.

   Paratype. 1♀ (CNC), same locality as holotype. DNA voucher code: DHJPAR0031819.

   Description. Head: mostly black, labrum and mandibles light brown to yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: dark brown. Metasoma (dorsally): black to dark brown. Metacoxa: mostly black to dark brown (posterior 0.1–0.2 yellow). Malar distance: less than 0.2 × eye length. Fore wing areolet: present. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.10 mm. Interocellar distance: 0.05 mm. Posterior ocellus diameter: 0.03 mm. Body length: 1.81 mm. Fore wing length: 2.02 mm. Ovipositor length: 1.47 mm. Metacoxa length: 0.31 mm. Metafemur length: 0.47 mm. Metatibia length: 0.58 mm. T1 length/width at posterior margin: 0.27 mm/ 0.13 mm. T2 length/width at posterior margin: 0.04 mm/ 0.24 mm.

   Distribution. Known only from the holotype locality in ACG, dry forest, Costa Rica.
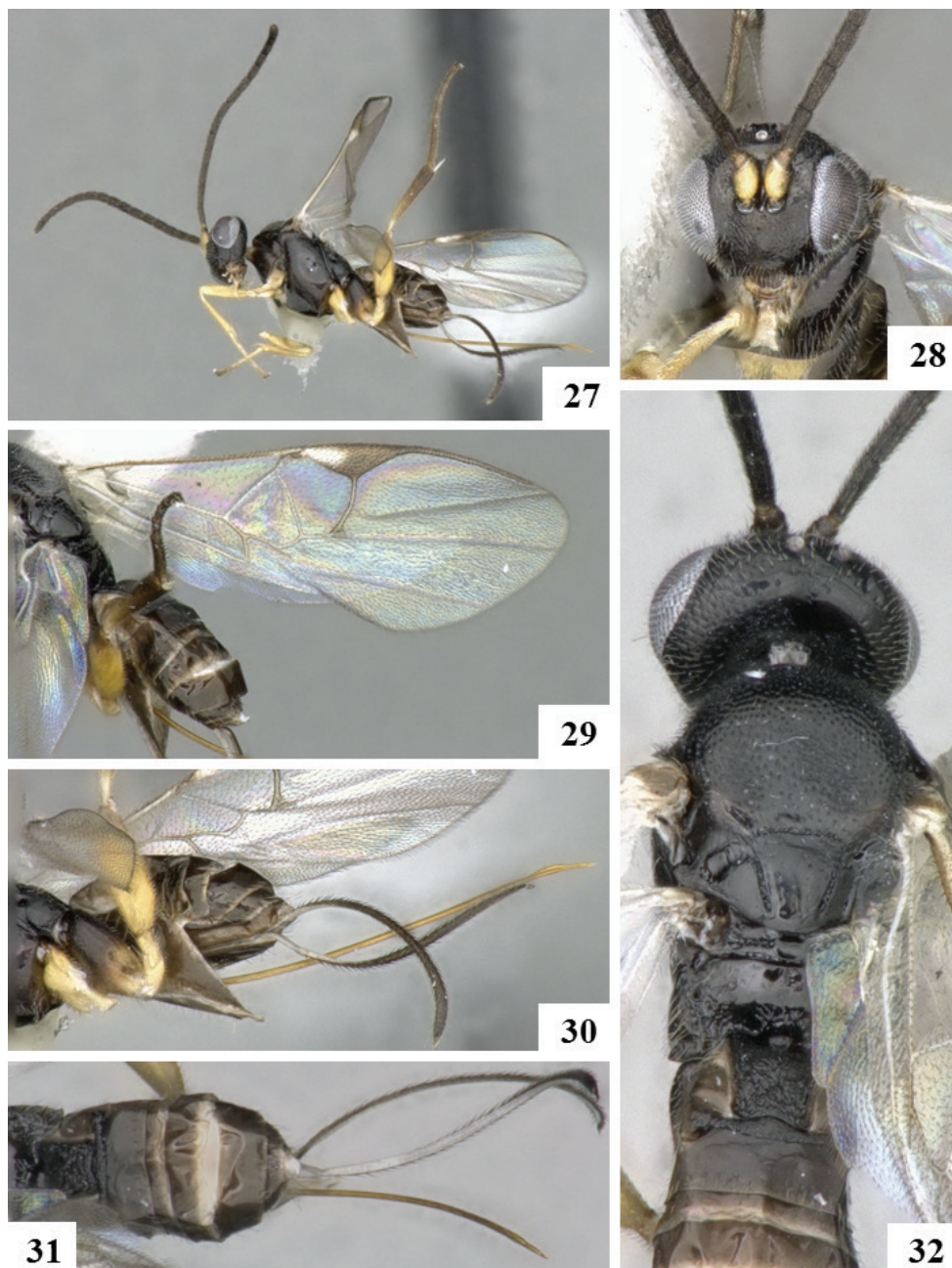   **Etymology.** *Promicrogaster daniellopezi* is named in honor of 13-year-old Migdonio Daniel López Martínez from the Colonia Bolaños school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster daretrizoi Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/F91D4DBE-0D0C-457E-9CF2-FD82F92E6523
Figs 33–38

Holotype. Female, CNC. COSTA RICA, Alajuela, Area de Conservación Guanacaste, Sector San Cristobal, Bosque Trampa Malaise, 815m, 10.86280, -85.38460. DNA Voucher code: DHJPAR0025899.

Figures 27–32. *Promicrogaster daniellopezi* sp. n. holotype.

Figures 33–38. *Promicrogaster daretrizoi* sp. n. holotype.

Paratypes. 12♀, 37♂ (CNC, NMNH, BMNH, INBio). Costa Rica, Alajuela, ACG, same locality than holotype; Sector San Cristóbal,   Río Blanco Abajo, 10.9, -85.373, 500m; Sector San Cristóbal, Potrero Argentina, 10.89, -85.388, 520m; Sector San Cristóbal, Estación San Gerardo, 10.88, -85.389, 575m; Sector Rincón Rain Forest, Vado Río Francia, 10.901, -85.289, 400m. DNA Voucher codes: DHJPAR0025506, DHJPAR0024792,   DHJPAR0025676,   DHJPAR0025820,   DHJPAR0025821, DHJPAR0025872,   DHJPAR0025873,   DHJPAR0025874,   DHJPAR0025908, DHJPAR0025945,   DHJPAR0025953,   DHJPAR0025963,   DHJPAR0025968, DHJPAR0025971,   DHJPAR0025973,   DHJPAR0025980,   DHJPAR0025986, DHJPAR0025989,   DHJPAR0025999,   DHJPAR0026006,   DHJPAR0026009, DHJPAR0026010,   DHJPAR0026011,   DHJPAR0026015,   DHJPAR0026023, DHJPAR0026025,   DHJPAR0026041,   DHJPAR0026044,   DHJPAR0026057, DHJPAR0026072,   DHJPAR0026077,   DHJPAR0027603,   DHJPAR0027604, DHJPAR0027611,   DHJPAR0027615,   DHJPAR0027617,   DHJPAR0027624, DHJPAR0027630,   DHJPAR0027634,   DHJPAR0027638,   DHJPAR0027640, DHJPAR0027642, DHJPAR0027643, DHJPAR0027662, DHJPAR0027665, DHJ-PAR0027674, DHJPAR0027677, DHJPAR0027694, DHJPAR0027702.

Description. Head: mostly black, labrum and mandibles yellow. Flagellomeres: flagellomeres 1–8 and 15–16 dark brown, flagellomeres 9–14 (sometimes only 10–14) yellow white. Mesosoma: black. Tegula: dark brown. Metasoma (dorsally): black to dark brown. Metacoxa: mostly orange-yellow but with small brown spot dorsally. Malar distance: less than 0.2 × eye length. Fore wing areolet: present. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.10–0.11 mm. Interocellar distance: 0.06–0.08 mm. Posterior ocellus diameter: 0.05–0.06 mm. Body length: 2.49–2.75 mm. Fore wing length: 2.55–2.86 mm. Ovipositor length: 1.67–1.90 mm. Metacoxa length: 0.63–0.72 mm. Metafemur length: 0.73–0.81 mm. Metatibia length: 0.89–1.01 mm. T1 length/width at posterior margin: 0.32–0.40 mm/ mm. T2 length/width at posterior margin: 0.06–0.10 mm/ 0.15–0.33 mm.

**Distribution.** Costa Rica (ACG, mid-elevation rain forest).

Etymology. *Promicrogaster daretrizoi* is named in honor of 12-year-old Daret Rizo Alemán from the Colonia Bolaños school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster eddycastroi **Fernandez-Triana & Boudreault, sp. n.**
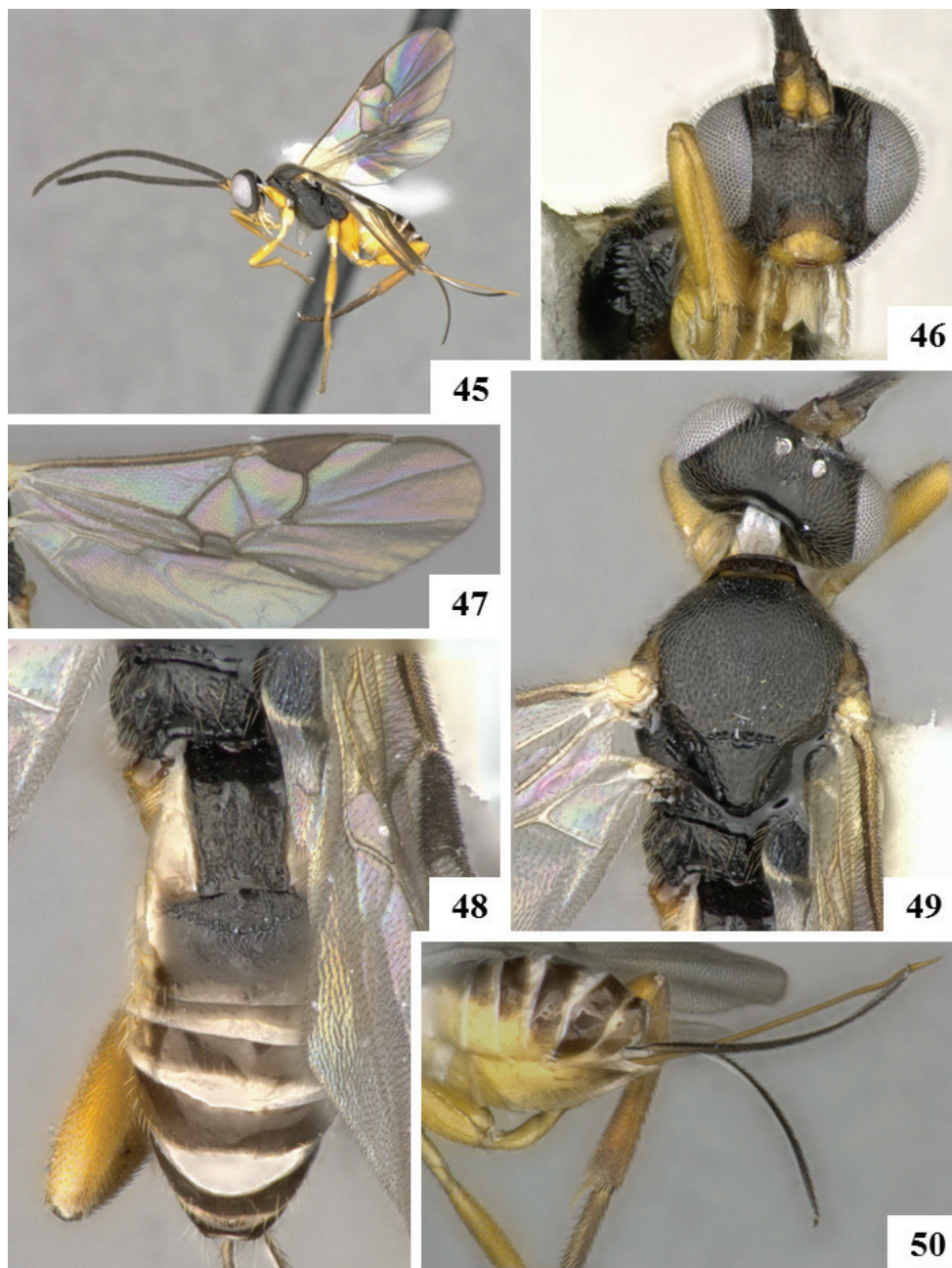http://zoobank.org/B2C0A188-C887-489F-A07F-5B0AF33180E9
Figs 39–44

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Sendero Arenales, 1080m, 10.92471, -85.46738. DNA Voucher code: DHJPAR0031320.
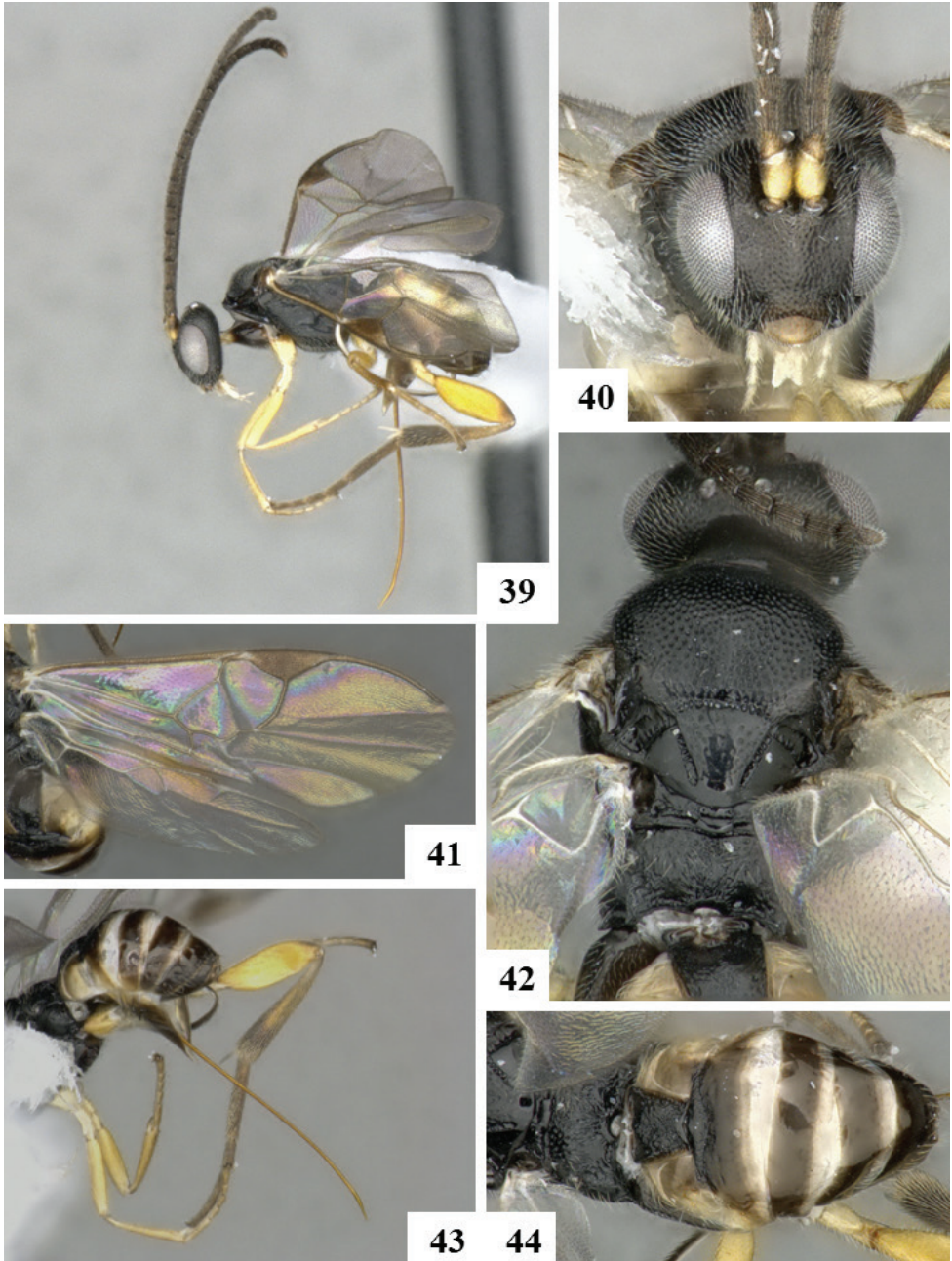
Figures 39–44. *Promicrogaster eddycastroi* sp. n. holotype.

Description. Head: mostly black, labrum and mandibles light brown to yellow. Flagellomeres: dark brown. Mesosoma: black. Tegula: brown. Metasoma (dorsally): black to dark brown. Metacoxa: mostly black to dark brown (posterior 0.1–0.2 yellow). Malar distance: less than 0.2 × eye length. Fore wing areolet: absent. T1 sculpture: anterior 0.5 smooth, posterior 0.5 sculptured.

T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.11 mm. Interocellar distance: 0.08 mm. Posterior ocellus diameter: 0.06 mm. Body length: 2.29 mm. Fore wing length: 2.65 mm. Ovipositor length: 1.77 mm. Metacoxa length: 0.56 mm. Metafemur length: 0.68 mm. Metatibia length: 0.89 mm. T1 length/width at posterior margin: 0.30 mm/ 0.16 mm. T2 length/width at posterior margin: 0.08 mm/ 0.39 mm.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

Etymology. *Promicrogaster eddycastroi* is named in honor of 12-year-old Eddy Alfredo Castro Detrinidad from the Huacas school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster eimyobandoae Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/8E3614AC-D86A-42FF-B97C-796C4841755F
Figs 45–50

Holotype. Female, CNC. COSTA RICA, Alajuela, Area de Conservación Guanacaste, Sector San Cristobal, Potrero Argentina, 520m, 10.89021, -85.38803. DNA Voucher code: DHJPAR0027520.

Paratypes. 1♀, 1♂ (CNC), same locality as holotype. 1♂ (CNC), ACG, Sector San Cristobal, Rio Blanco Abajo, 500m, 10.90037, -85.37254. DNA voucher codes: DHJPAR0025577, DHJPAR0025685, DHJPAR0026587.

Description. Head: mostly black, labrum and mandibles light brown to yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: brown. Metasoma (dorsally): black to dark brown. Metacoxa: orange-yellow. Malar distance: less than 0.2 × eye length. Fore wing areolet: present. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.10 mm. Interocellar distance: 0.08 mm. Posterior ocellus diameter: 0.06 mm. Body length: 2.78–2.80 mm. Fore wing length: 2.73–2.80 mm. Ovipositor length: 1.69–1.84 mm. Metacoxa length: 0.63 mm. Metafemur length: 0.69–0.71 mm. Metatibia length: 0.87–0.92 mm. T1 length/width at posterior margin: 0.32 mm/ 0.15–0.23 mm. T2 length/width at posterior margin: 0.11 mm/ 0.32–0.37 mm.

Distribution. Costa Rica (ACG, mid-elevation rain forest).

Etymology. *Promicrogaster eimyobandoae* is named in honor of 12-year-old Eimy Yuleisi Obando Zelaya from the La Garita Vieja school for her growing enthusiasm for understanding and protecting the wild nature that occurs in her homeland.

Figures 45–50. *Promicrogaster eimyobandoae* sp. n. holotype.

Promicrogaster fabiancastroi **Fernandez-Triana & Boudreault, sp. n.**
http://zoobank.org/726D9560-5CEE-46B6-BEF3-6355FC7FA78F
Figs 51–56

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Sendero Arenales, 1080m, 10.92471, -85.46738. DNA Voucher code: DHJPAR0031313.

Paratype. 1♀ (CNC), same locality as holotype. DNA voucher code: DHJPAR0031314.

Description. Head: mostly black, labrum and mandibles light brown to yellow. Flagellomeres: dark brown. Mesosoma: black. Tegula: brown. Metasoma (dorsally): black to dark brown. Metacoxa: mostly black to dark brown (posterior 0.1–0.2 yellow). Malar distance: less than 0.2 × eye length. Fore wing areolet: absent. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.08–0.10 mm. Interocellar distance: 0.08 mm. Posterior ocellus diameter: 0.05 mm. Body length: 1.98–2.14 mm. Fore wing length: 2.23–2.25 mm. Ovipositor length: 1.40–1.57 mm. Metacoxa length: 0.45–0.47 mm. Metafemur length: 0.52–0.56 mm. Metatibia length: 0.65–0.69 mm. T1 length/width at posterior margin: 0.24–0.27 mm/ 0.11 mm. T2 length/width at posterior margin: 0.06–0.07 mm/ 0.27–0.29 mm.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

Etymology. *Promicrogaster fabiancastroi* is named in honor of 8-year-old Fabián Castro Gutiérrez from Educarte school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster fabriciocambroneroi **Fernandez-Triana & Boudreault, sp. n.**
http://zoobank.org/812785CB-AAC1-4E96-A138-99C25043D5A4
Figs 57–62

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector El Hacha, Sendero Bejuquilla, 280m, 11.03004, -85.52699. DNA Voucher code: DHJPAR0012588.

Description. Head: mostly black, clypeus, labrum and mandibles yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: white. Metasoma (dorsally): T1–T4 entirely orange-yellow, T5+ mostly dark brown to black. Metacoxa: orange. Malar distance: more than 0.3 × eye length. Fore wing areolet: present. T1 sculpture: smooth. T2 sculpture: smooth. Ocular–ocellar line: 0.19 mm. Interocellar distance: 0.13 mm. Posterior ocellus diameter: 0.10 mm. Body length: 5.28 mm. Fore wing length: 4.96 mm. Ovipositor length: 4.26 mm. Metacoxa length: 1.18 mm. Metafemur length: 1.29 mm. Metatibia length: 1.71 mm. T1 length/width at posterior margin: 0.48 mm/ 0.56 mm. T2 length/width at posterior margin: 0.26 mm/ 0.58 mm.

Distribution. Known only from the holotype locality in ACG, dry forest, Costa Rica.
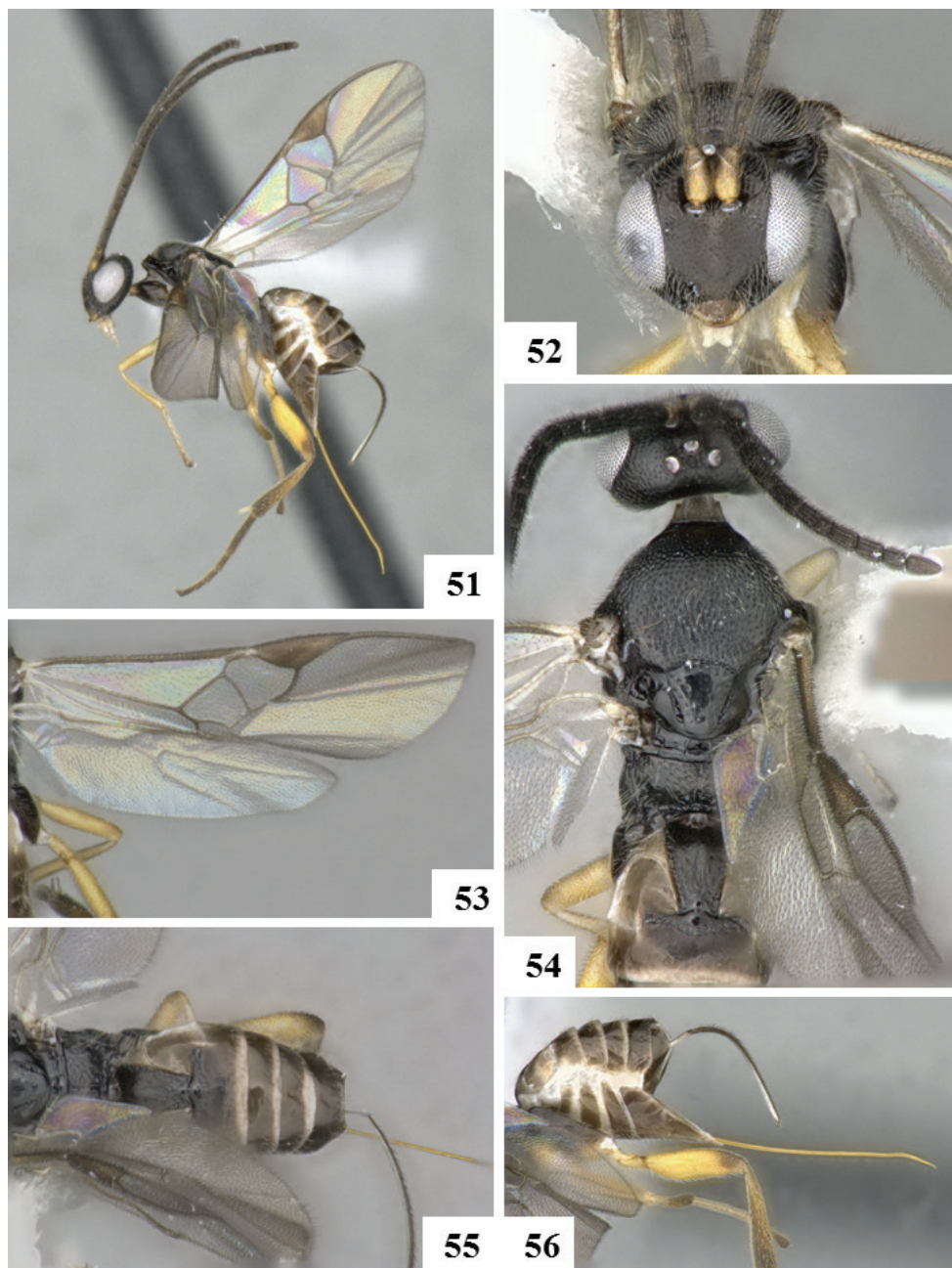
Figures 51–56. *Promicrogaster fabiancastroi* sp. n. holotype.
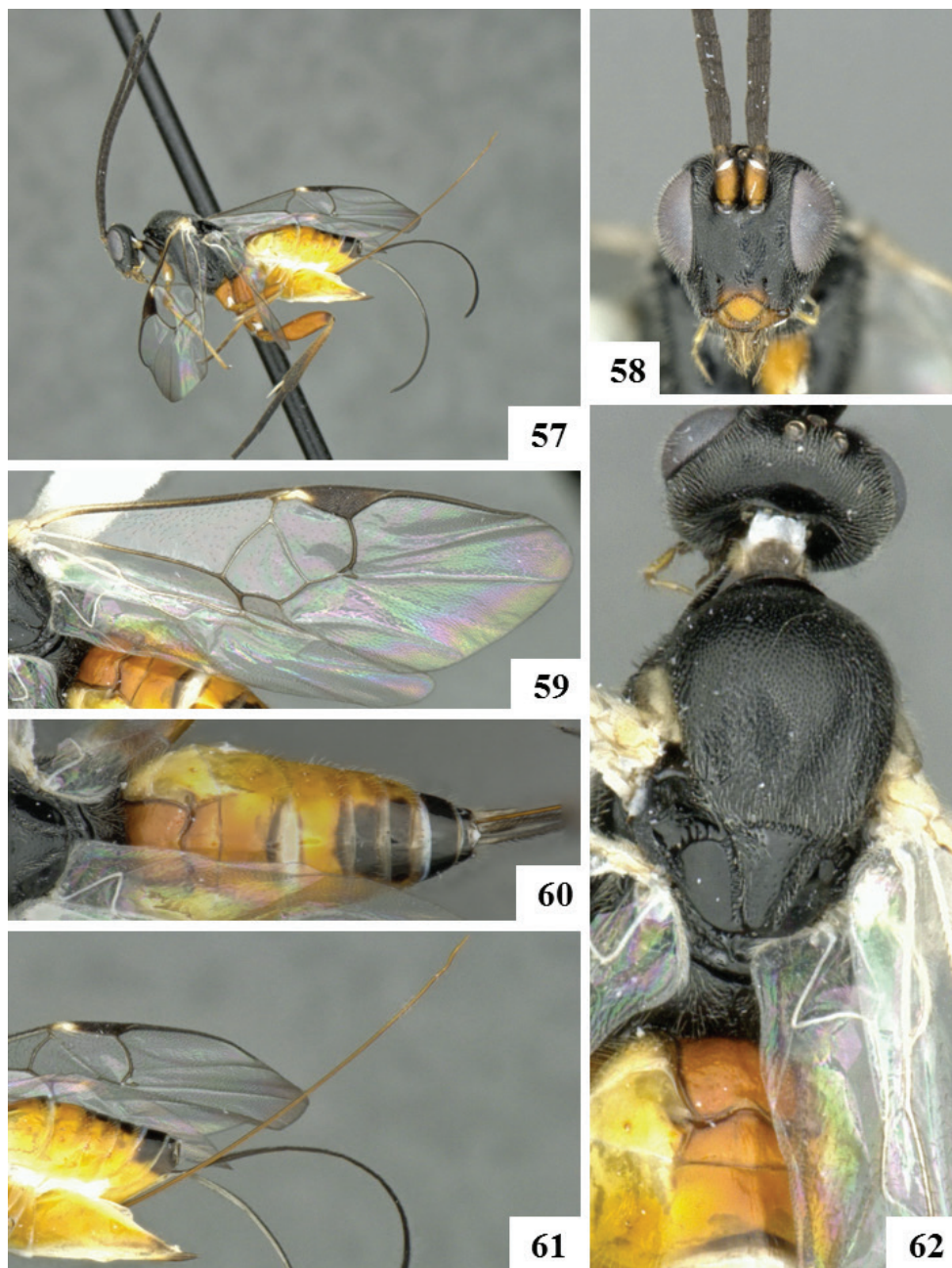
Figures 57–62. *Promicrogaster fabriciocambroneroi* sp. n. holotype.

Etymology. *Promicrogaster fabriciocambroneroi* is named in honor of 11-year-old Félix Fabricio Cambronero Mendoza from the Colonia Bolaños school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster hillaryvillafuerteae Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/F736CEEE-A2C6-4457-82E3-DAC19BCC6752
Figs 63–68

Holotype. Female, CNC. COSTA RICA, Alajuela, Area de Conservación Guanacaste, Sector San Cristobal, Rio Blanco Abajo, 500m, 10.90037, -85.37254. DNA Voucher code: DHJPAR0026620.

Description. Head: mostly black, labrum and mandibles yellow. Flagellomeres: flagellomeres 1–4 yellow-brown, flagellomeres 5–16 dark brown. Mesosoma: black. Tegula: black. Metasoma (dorsally): mostly dark brown, with orange-yellow areas on anterior 0.6 of T1 and anterior 0.5 of T3. Metacoxa: orange-yellow. Malar distance: less than 0.2 × eye length. Fore wing areolet: present. T1 sculpture: mostly smooth, with posterior 0.3 sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.11 mm. Interocellar distance: 0.08 mm. Posterior ocellus diameter: 0.06 mm. Body length: 2.47 mm. Fore wing length: 2.52 mm. Ovipositor length: 2.02 mm. Metacoxa length: 0.60 mm. Metafemur length: 0.65 mm. Metatibia length: 0.84 mm. T1 length/width at posterior margin: 0.34 mm/ 0.15 mm. T2 length/ width at posterior margin: 0.08 mm/ 0.31 mm.

Distribution. Known only from the holotype locality in ACG, mid-elevation rain forest, Costa Rica.

Etymology. *Promicrogaster hillaryvillafuerteae* is named in honor of 11-year-old Hillary Massiel Villafuerte Villegas from the Santa Rosa school for her growing enthusiasm for understanding and protecting the wild nature that occurs in her homeland.

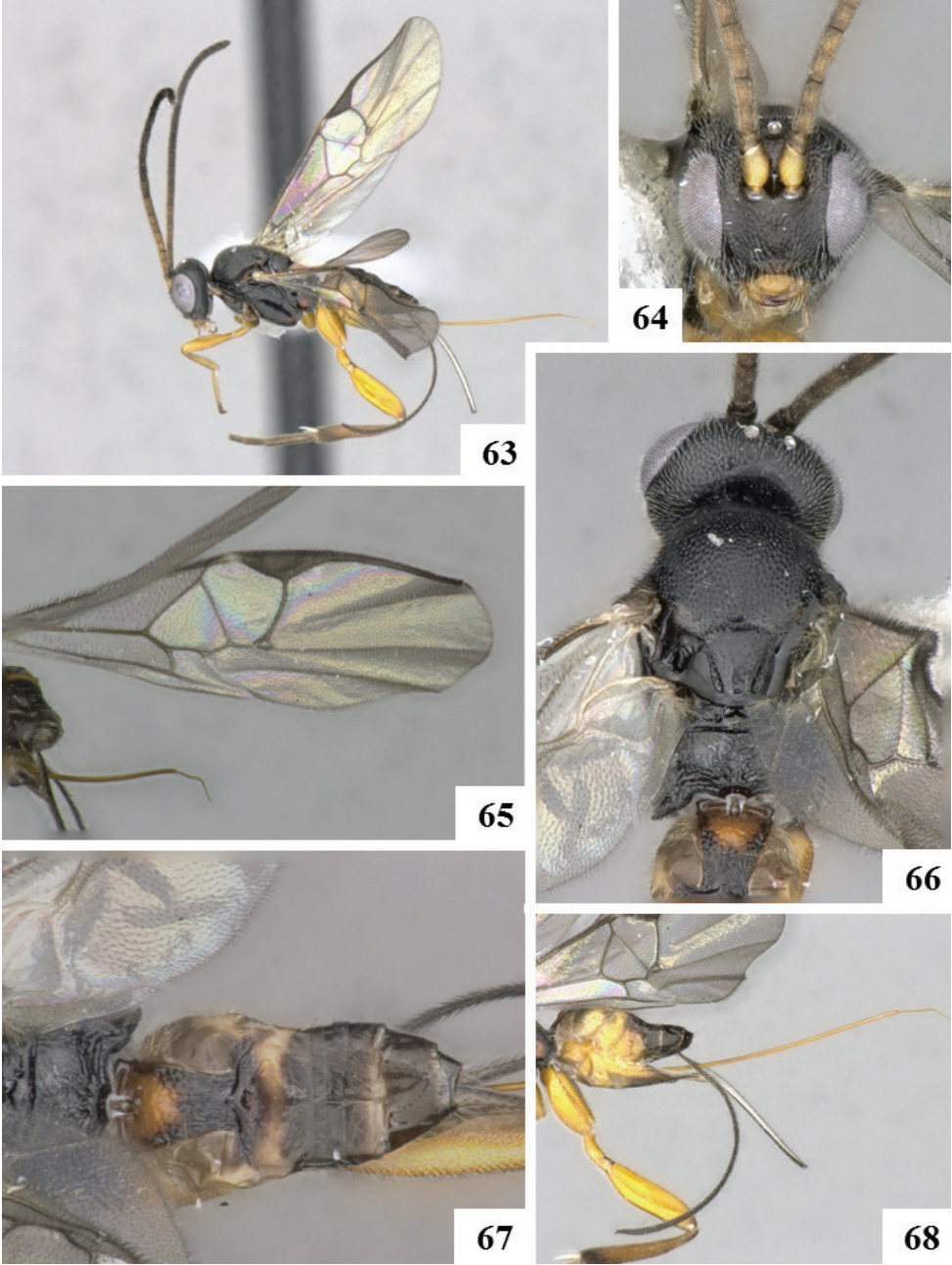## *Promicrogaster kevinmartinezi* Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/BA30242A-0A37-40D9-891A-3C4F09FADD9C
Figs 69–80

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Sendero Arenales, 1080m, 10.92471, -85.46738. DNA Voucher code: DHJPAR0031319.

Paratypes. 1♀, 1♂ (CNC), same locality as holotype. DNA voucher codes: DHJPAR0031274, DHJPAR0031318.

Description. Head: mostly black, clypeus, labrum and mandibles yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: yellow. Metasoma (dorsally): T1–T2 dark brown to black, T3 mostly yellow, with anterior 0.2 light brown, T4–7 brown anteriorly, white on posterior 0.3–0.5. Metacoxa: orange-yellow. Malar distance:

Figures 63–68. *Promicrogaster hillaryvillafuerteae* sp. n. holotype.

Figures 69–74. *Promicrogaster kevinmartinezi* sp. n. holotype.
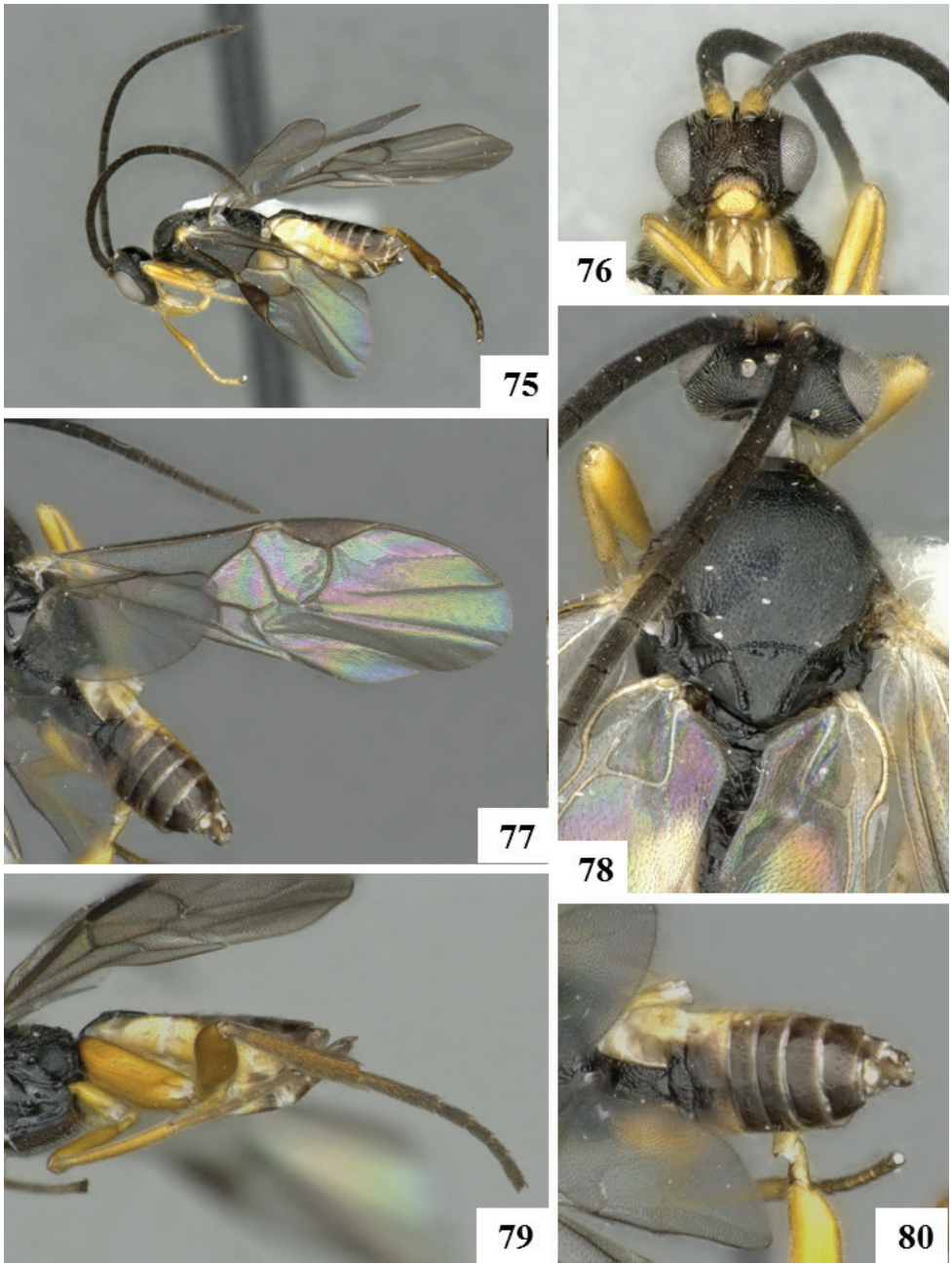
Figures 75–80. *Promicrogaster kevinmartinezi* sp. n. male paratype.

0.2–0.3 × eye length. Fore wing areolet: present. T1 sculpture: anterior 0.5 smooth, posterior 0.5 sculptured. T2 sculpture: mostly sculptured. Ocular–ocellar line: 0.14–0.15 mm. Interocellar distance: 0.10 mm. Posterior ocellus diameter: 0.07–0.08 mm. Body length: 2.85–3.37 mm. Fore wing length: 3.47–3.67 mm. Ovipositor length: 2.49–3.38 mm. Metacoxa length: 0.81–0.85 mm. Metafemur length: 0.89 mm. Metatibia length: 1.13–1.18 mm. T1 length/width at posterior margin: 0.40–0.56 mm/ 0.21–0.24 mm. T2 length/width at posterior margin: 0.11 mm/ 0.40–0.47 mm.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

Etymology. *Promicrogaster kevinmartinezi* is named in honor of 12-year-old Kevin Olivier Martínez Pérez from the Colonia Bolaños school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster kiralycastilloae Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/55057CB5-20C4-4AF8-B401-8306916B4773
Figs 81–86

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Sendero Arenales, 1080m, 10.92471, -85.46738. DNA Voucher code: DHJPAR0031288.

Description. Head: mostly black, clypeus, labrum and mandibles yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: dark brown. Metasoma (dorsally): mostly dark brown, with T3+ white on posterior 0.2–0.5. Metacoxa: dark brown on anterior 0.7, yellow-white on posterior 0.3. Malar distance: 0.2–0.3 × eye length. Fore wing areolet: present. T1 sculpture: anterior 0.5 smooth, posterior 0.5 sculptured. T2 sculpture: mostly sculptured. Ocular–ocellar line: 0.13 mm. Interocellar distance: 0.13 mm. Posterior ocellus diameter: 0.08 mm. Body length: 3.51 mm. Fore wing length: 3.80 mm. Ovipositor length: 2.95 mm. Metacoxa length: 0.82 mm. Metafemur length: 0.89 mm. Metatibia length: 1.10 mm. T1 length/width at posterior margin: 0.37 mm/ 0.22 mm. T2 length/width at posterior margin: 0.10 mm/ 0.47 mm.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.
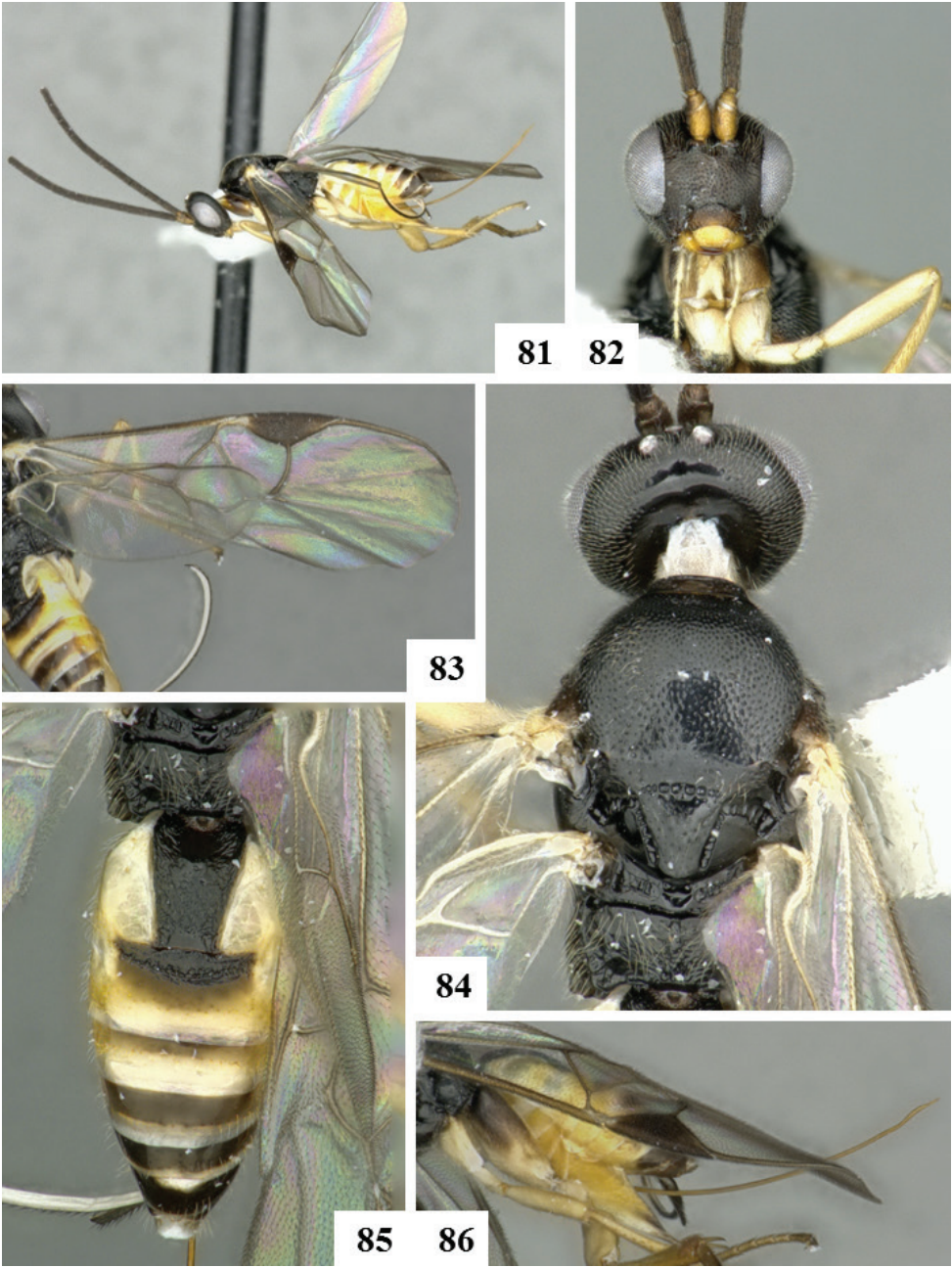
Etymology. *Promicrogaster kiralycastilloae* is named in honor of 12-year-old Kiraly Castillo García from the Colonia Bolaños school for her growing enthusiasm for understanding and protecting the wild nature that occurs in her homeland.

Promicrogaster leilycastilloae Fernandez-Triana & Boudreault, sp. n.
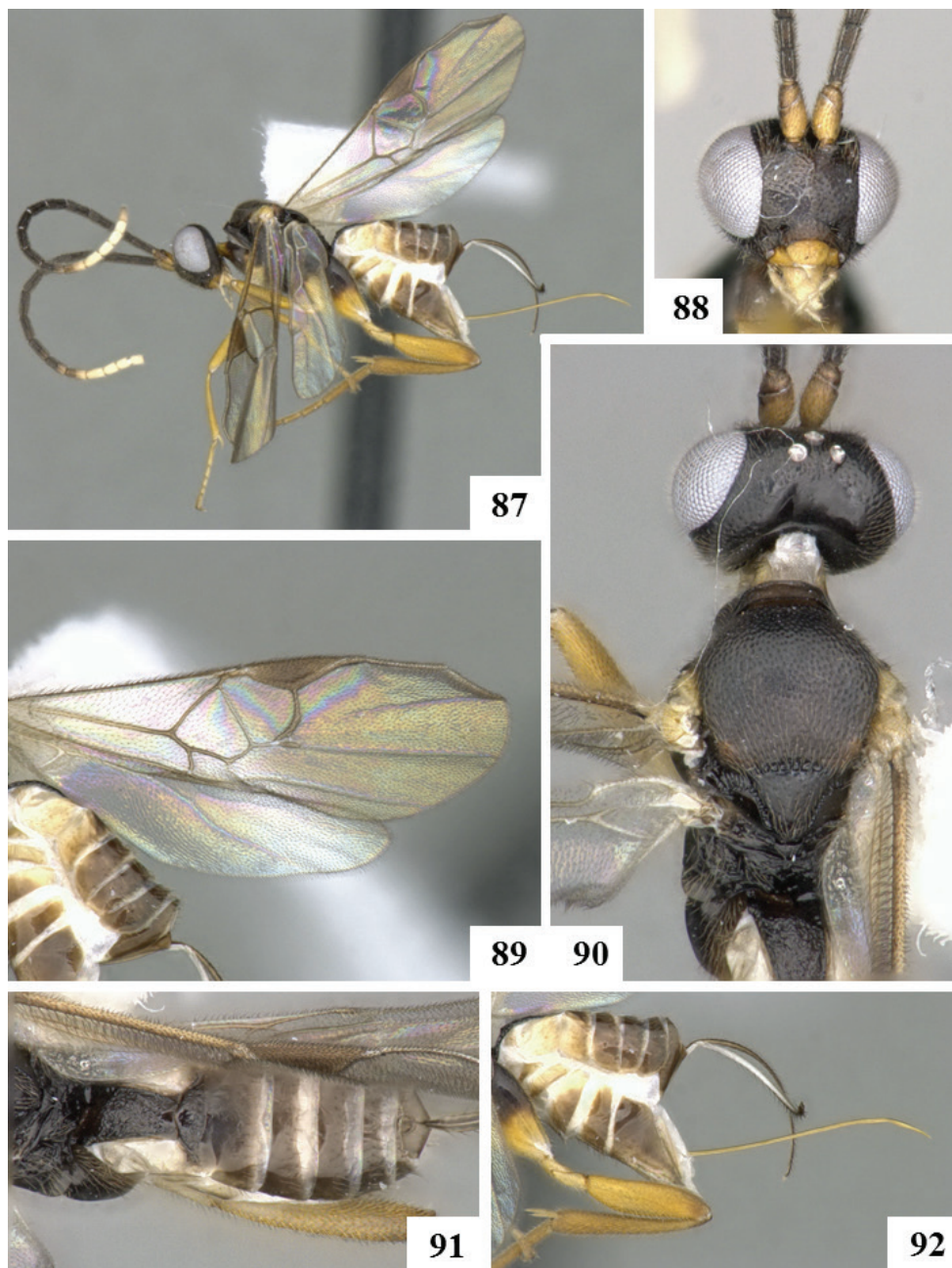http://zoobank.org/20043702-F698-4670-BB16-69EDC7DE4CEE
Figs 87–92

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Cerro Pedregal, 1080m, 10.92767, -85.47449. DNA Voucher code: DHJPAR0031431.

Figures 81–86. *Promicrogaster kiralycastilloae* sp. n. holotype.

Figures 87–92. *Promicrogaster leilycastilloae* sp. n. holotype.

Description. Head: mostly black, labrum and mandibles yellow. Flagellomeres: first 10 flagellomeres dark brown to black, flagellomeres 11–16 yellow-white. Mesosoma: black. Tegula: white. Metasoma (dorsally): dark brown to black. Metacoxa: dark brown on anterior 0.5, yellow on posterior 0.5. Malar distance: less than 0.2 × eye length. Fore wing areolet: present. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.10 mm. Interocellar distance: 0.06 mm. Posterior ocellus diameter: 0.06 mm. Body length: 2.16 mm. Fore wing length: 2.02 mm. Ovipositor length: 1.30 mm. Metacoxa length: 0.65 mm. Metafemur length: 0.77 mm. Metatibia length: 0.97 mm. T1 length/width at posterior margin: 0.32 mm/ 0.15 mm. T2 length/width at posterior margin: 0.10 mm/ 0.26 mm.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

Etymology. *Promicrogaster leilycastilloae* is named in honor of 12-year-old Leily María Castillo Mora from the Colonia Bolaños school for her growing enthusiasm for understanding and protecting the wild nature that occurs in her homeland.

Promicrogaster liagrantae Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/3CD68CCD-A608-4B7F-9F04-0EE3D44FEBA8
Figs 93–99

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa, Bosque San Emilio, 300m, 10.84389, -85.61384. DNA Voucher code: DHJPAR0013138.

Paratypes. 2♀ (CNC), Costa Rica, ACG, Sector El Hacha, Sendero Bejuquilla, 280m, 11.0.004, -85.52699. DNA Voucher codes: DHJPAR0012586, DHJPAR0012587.

Description. Head: mostly black, labrum and mandibles yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: yellow. Metasoma (dorsally): mostly dark brown to black, T3 with yellow spots laterally. Metacoxa: yellow. Malar distance: less than 0.2 × eye length. Fore wing areolet: present. T1 sculpture: anterior 0.5 smooth, posterior 0.5 sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.11–0.14 mm. Interocellar distance: 0.08–0.10 mm. Posterior ocellus diameter: 0.06–0.07 mm. Body length: 2.95–3.28 mm. Fore wing length: 3.11–3.15 mm. Ovipositor length: 2.66–2.70 mm. Metacoxa length: 0.73–0.76 mm. Metafemur length: 0.77–0.82 mm. Metatibia length: 0.97–1.03 mm. T1 length/width at posterior margin: 0.48–0.52 mm/ 0.24–0.27 mm. T2 length/width at posterior margin: 0.10–0.11 mm/ 0.40–0.45 mm.

Distribution. Costa Rica (ACG, dry forest).

Etymology. *Promicrogaster liagrantae* is named in honor of 12-year-old Lia Thamara Grant Chacón from the Huacas school for her growing enthusiasm for understanding and protecting the wild nature that occurs in her homeland.
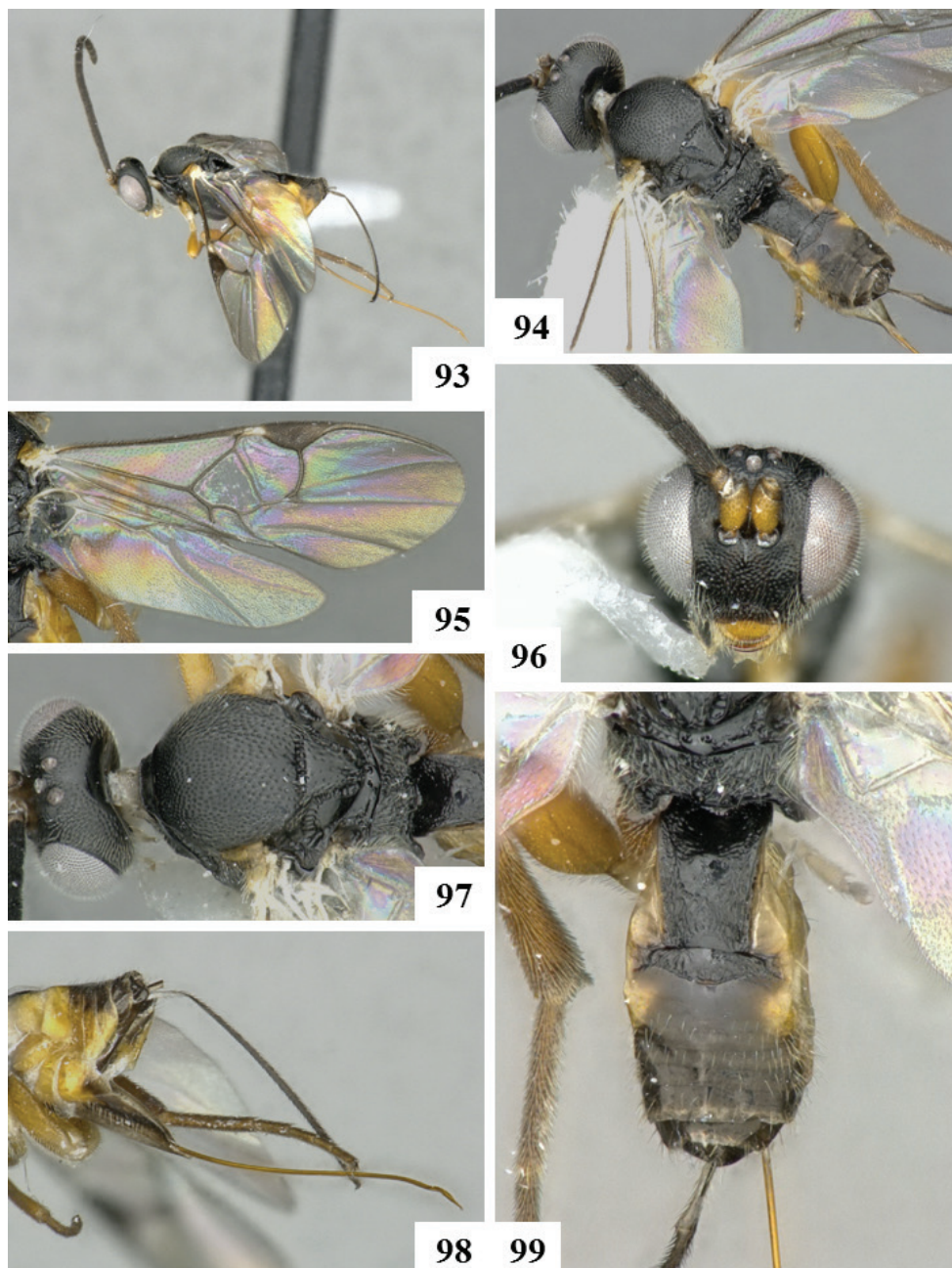
Figures 93–99. *Promicrogaster liagrantae* sp. n. holotype.

Promicrogaster luismendezi Fernandez-Triana & Boudreault, sp. n.

http://zoobank.org/FA0AFC58-103C-433B-95A8-388A9667B0D6

Figs 100–105

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Sendero Circular, 1185m, 10.92714, -85.46683. DNA Voucher code: DHJPAR0031207.

Description. Head: mostly black, labrum and mandibles light brown. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: brown. Metasoma (dorsally): black to dark brown. Metacoxa: mostly black to dark brown (posterior 0.1–0.2 yellow). Malar distance: less than 0.2 × eye length. Fore wing areolet: absent. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.08 mm. Interocellar distance: 0.09 mm. Posterior ocellus diameter: 0.05 mm. Body length: 2.33 mm. Fore wing length: 2.37 mm. Ovipositor length: 1.67 mm. Metacoxa length: 0.50 mm. Metafemur length: 0.58 mm. Metatibia length: 0.76 mm. T1 length/width at posterior margin: 0.23 mm/ 0.13 mm. T2 length/width at posterior margin: 0.10 mm/ 0.32 mm.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

Etymology. *Promicrogaster luismendezi* is named in honor of 12-year-old Luis Eduardo Méndez from the Santa Rosa school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster miranda Muesebeck, 1958

Figs 106–110

Promicrogaster miranda Muesebeck, 1958: 421. Original description.

Holotype. Female, NMNH (not examined). PANAMA, Barro Colorado Island, Canal Zone. Voucher code: USNM 63052.

Material examined. 1♀ (CNC), TRINIDAD, Curepe, viii.1978, Malaise Trap; 1♀ (CNC), TRINIDAD, St. Augustine, x.1946, collected on *Cordia* (Boraginaceae).

Distribution. Panama, Trinidad.

Comments. Previously known only from the holotype, we consider here two specimens from Trinidad (in the CNC collection) to be conspecific based on morphological similarities with the original description -thus expanding the known distribution of the species. However, future study of the holotype will be needed to corroborate our present decision. The photos provided in this paper were taken from one of the Trinidad specimens.
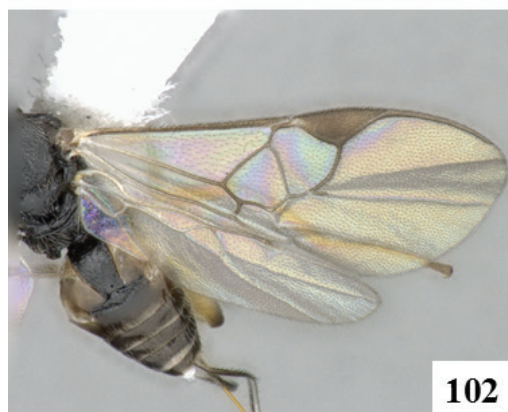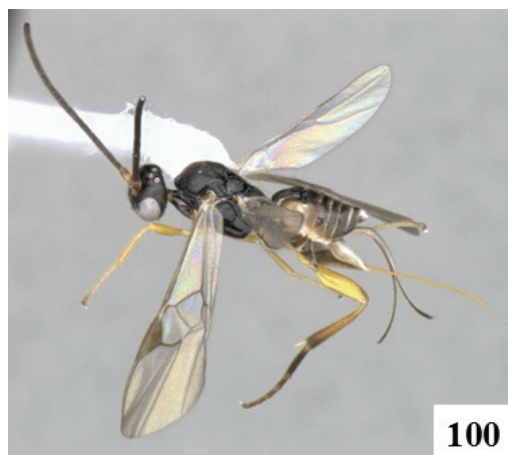
Figures 100–105. *Promicrogaster luismendezi* sp. n. holotype.
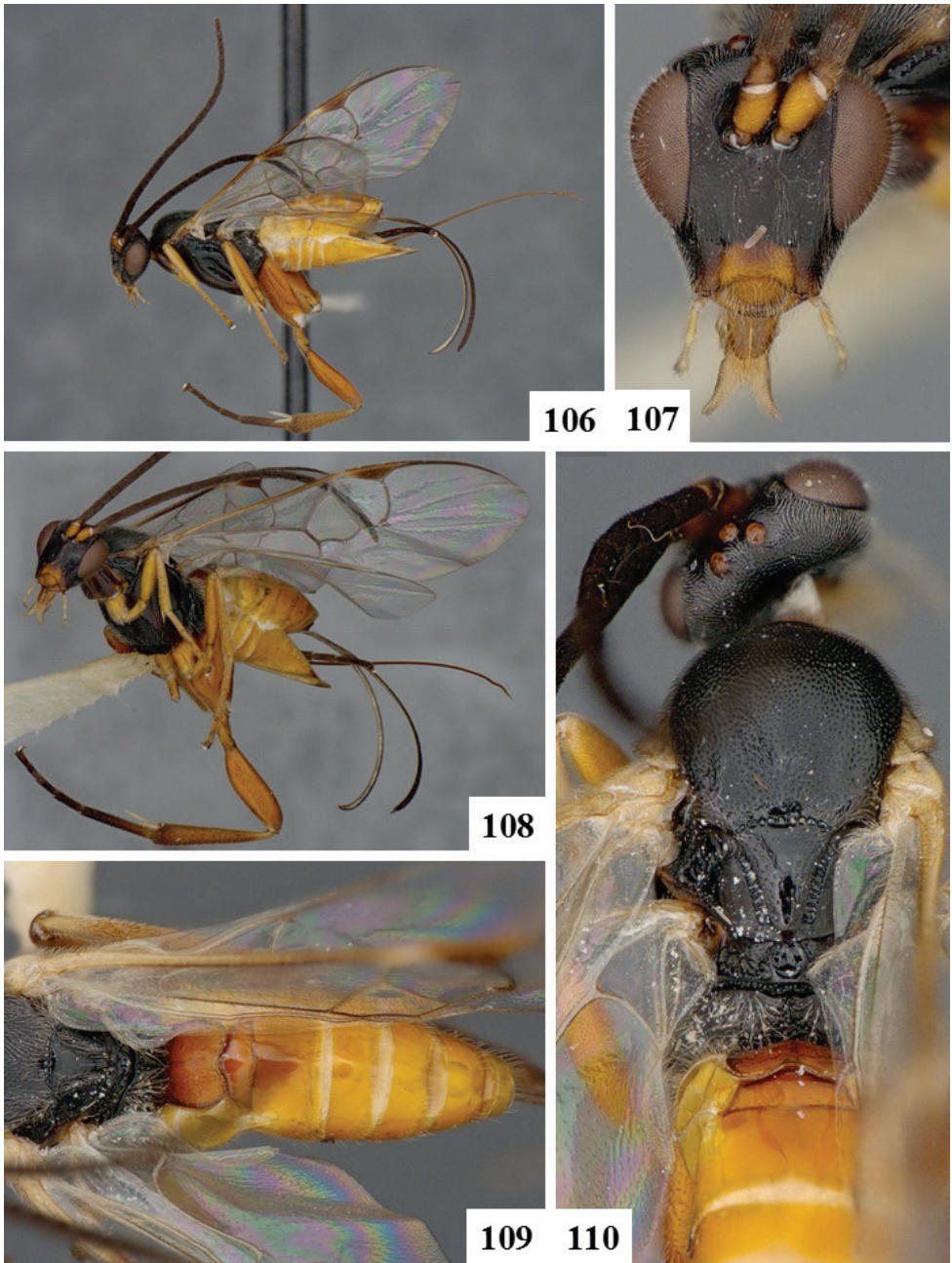
Figures 106–110. *Promicrogaster miranda.*

***Promicrogaster monteverdensis* Fernandez-Triana & Boudreault, sp. n.**
http://zoobank.org/8FDEF466-0376-424A-8D82-C295D7C43D77
Figs 111–116

Holotype. Female, CNC. COSTA RICA, Puntarenas, Monteverde. Holotype labels: COSTA RICA, Puntarenas, Monteverde, v.1990, D. Goulet, FIT [Flight Interception Trap], cloud forest. Voucher code: CNC 483494

Paratype. 1♀ (CNC), Costa Rica, Alajuela, ACG, Sector San Cristobal, Bosque Trampa Malaise, 815m, 10.86280, -85.38460. DNA voucher code: DHJPAR0025917.

Description. Head: mostly black, labrum and mandibles yellow to light brown. Flagellomeres: dark brown. Mesosoma: black. Tegula: dark brown to black. Metasoma (dorsally): black to dark brown. Metacoxa: orange-yellow. Malar distance: less than 0.2 × eye length. Fore wing areolet: present. T1 sculpture: mostly sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.10–0.11 mm. Interocellar distance: 0.08–0.10 mm. Posterior ocellus diameter: 0.06 mm. Body length: 3.18–3.19 mm. Fore wing length: 2.95–3.34 mm. Ovipositor length: 2.60–2.96 mm. Metacoxa length: 0.60–0.70 mm. Metafemur length: 0.73–0.82 mm. Metatibia length: 0.92–1.05 mm. T1 length/width at posterior margin: 0.27–0.35 mm/ 0.18–0.24 mm. T2 length/width at posterior margin: 0.09–1.00 mm/ 0.39–0.45 mm.

Distribution. Costa Rica, mid-elevation rain forest in Monteverde and ACG.
Etymology. Named after the type locality, Monteverde.

***Promicrogaster munda* Muesebeck, 1958**
Figs 117–122

Promicrogaster munda Muesebeck, 1958: 422. Original description.

Holotype. Female, NMNH (not examined). HONDURAS, Tegucigalpa. Voucher code: USNM 63052.

Material Examined. 2♀ (CNC), COSTA RICA, Puntarenas, San Vito, Las Cruces Biological Station, ~1,200m, 8.7853, -82.9589, voucher code: CNCH3316; 5.vii.1983, B. Gill (coll.); 2♀ (CNC), PANAMA, Chiriquí Province, 15km NW of Hato del Volcán, 1200m, 24–31.v.1977, Peck & Howden (colls.).

Description. Head: mostly black, clypeus, labrum and mandibles yellow. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: yellow. Metasoma (dorsally): T1 orange-yellow, T2+ yellow (some specimens with small brown spot centrally on T4+). Metacoxa: orange-yellow. Malar distance: 0.2–0.3 × eye length. Fore wing areolet: present. T1 sculpture: mostly smooth, with posterior 0.3 sculptured. T2 sculpture: smooth. Ocular–ocellar line: 0.15–0.18 mm. Interocellar distance: 0.11–0.14 mm. Posterior ocellus diameter: 0.10–0.11 mm. Body length: 4.33–5.12 mm. Fore wing length: 4.00–4.95 mm. Ovipositor length: 3.44–4.58 mm. Metacoxa length: 1.08–1.41 mm. Metafemur length: 1.14–1.51 mm. Metatibia length: 1.43–
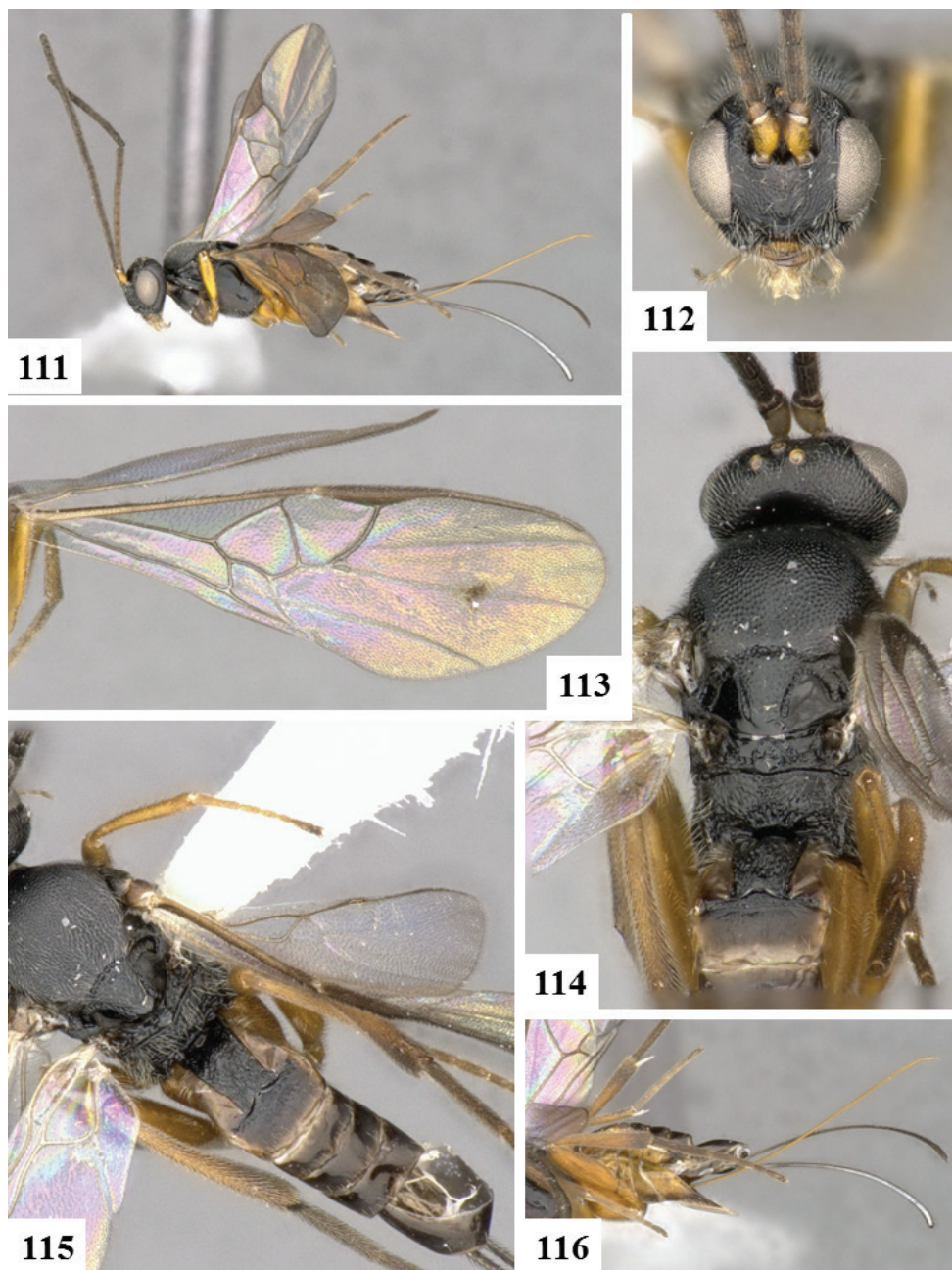
Figures 111–116. *Promicrogaster monteverdensis* sp. n. holotype.

1.89 mm. T1 length/width at posterior margin: 0.45–0.74 mm/ 0.29–0.40 mm. T2 length/width at posterior margin: 0.10–0.15 mm/ 0.39–0.60 mm.

Distribution. Costa Rica, Honduras, Mexico, Panama.
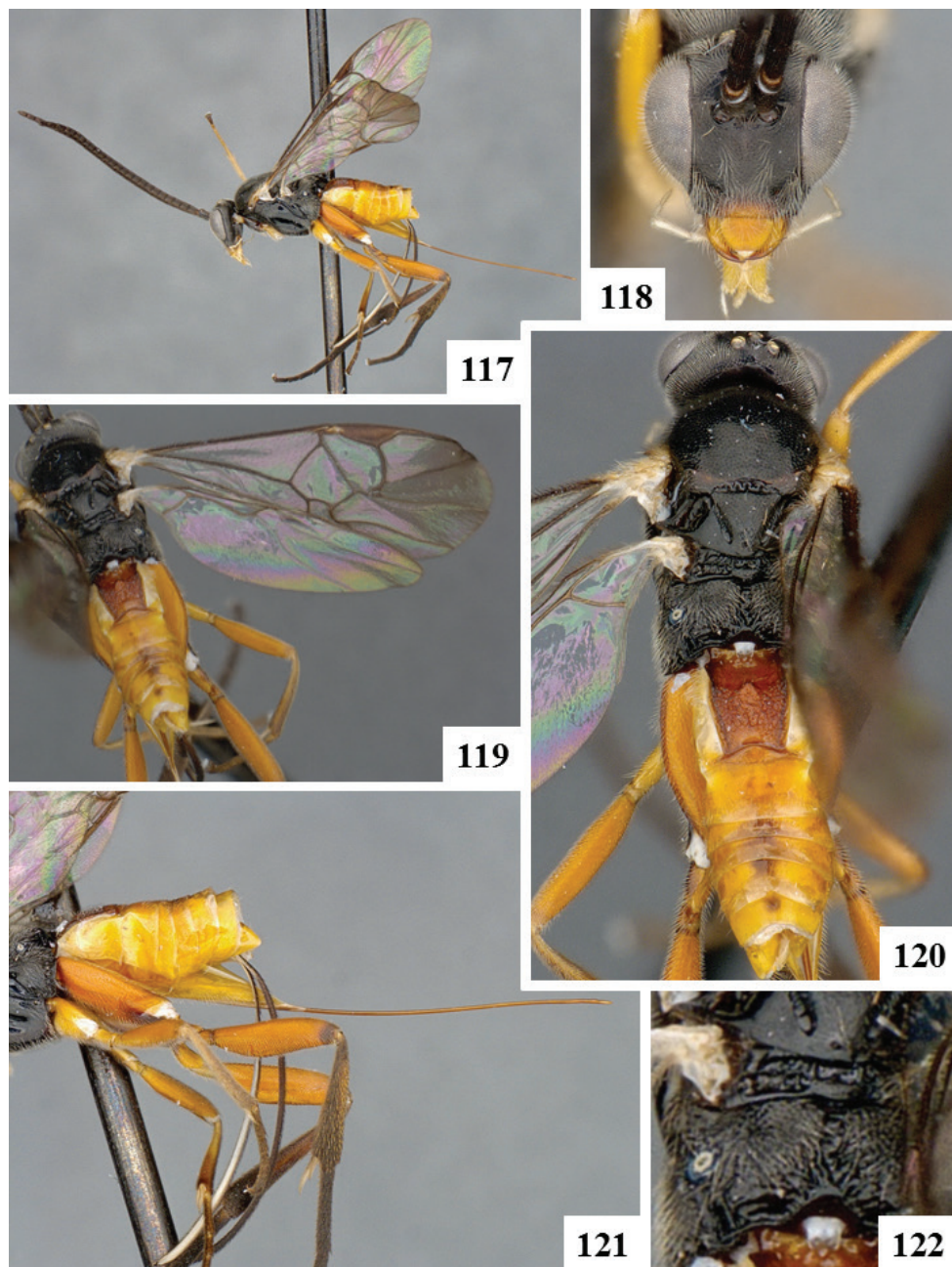
Figures 117–122. *Promicrogaster munda.*

Comments. The description and photos provided above are based on the CNC specimens studied, not the holotype–which was not examined. However, we suspect that *P. munda* is actually a complex of at least 2 morphologically similar species. We found variable coloration of the metatibia (entirely black vs mostly orange-yellow) and

fore wing (hyaline vs infumated) among the specimens seen, as well as significant differences in size (with specimens from Panama being smaller than those of Costa Rica, with body and fore wing lengths 0.6-0.8 mm shorter) and relative length of T1. Until more material becomes available for study we prefer to keep all specimens as *P. munda*.

Promicrogaster naomiduarteae Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/6C89EDBD-6AAC-4798-AF9E-745D9DA66EC1
Figs 123–128

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Cerro Pedregal, 1080m, 10.92767, -85.47449. DNA Voucher code: DHJPAR0031409.

Paratype. 1♀ (CNC), same locality as holotype. DNA voucher code: DHJPAR0031404.

Description. Head: mostly black, labrum and mandibles light brown. Flagellomeres: dark brown. Mesosoma: black. Tegula: brown. Metasoma (dorsally): black to dark brown. Metacoxa: mostly black to dark brown (posterior 0.1–0.2 yellow). Malar distance: less than 0.2 × eye length. Fore wing areolet: absent. T1 sculpture: anterior 0.5 sculptured, posterior 0.5 sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.11–0.14 mm. Interocellar distance: 0.07–0.09 mm. Posterior ocellus diameter: 0.06 mm. Body length: 2.33–2.39 mm. Fore wing length: 2.31–2.47 mm. Ovipositor length: 1.41–1.92 mm. Metacoxa length: 0.47–0.53 mm. Metafemur length: 0.52–0.61 mm. Metatibia length: 0.66–0.79 mm. T1 length/width at posterior margin: 0.24–0.30 mm/ 0.16–0.18 mm. T2 length/width at posterior margin: 0.08–0.10 mm/ 0.32–0.34 mm.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

Etymology. *Promicrogaster naomiduarteae* is named in honor of 11-year-old Naomi Duarte Cerdas from the Huacas school for her growing enthusiasm for understanding and protecting the wild nature that occurs in her homeland.

Promicrogaster pablouzagai Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/1B87199D-93D4-448B-B0EB-E2AC9490B64A
Figs 129–134

Holotype. Female, CNC. COSTA RICA, Alajuela, Area de Conservación Guanacaste, Sector San Cristobal, Bosque Trampa Malaise, 815m, 10.86280, -85.38460. DNA Voucher code: DHJPAR0025926.

Paratypes. 6♂ (CNC, NMNH), same locality as holotype; 1♂ (CNC), from Costa Rica, Guanacaste, ACG, Sector Cacao, Cerro Pedregal, 1080m, 10.92767, -85.47449. DNA Voucher codes: DHJPAR0025962, DHJPAR0025964, DHJPAR0025993, DHJPAR0026085, DHJPAR0026089, DHJPAR0027659, DHJPAR0031406.
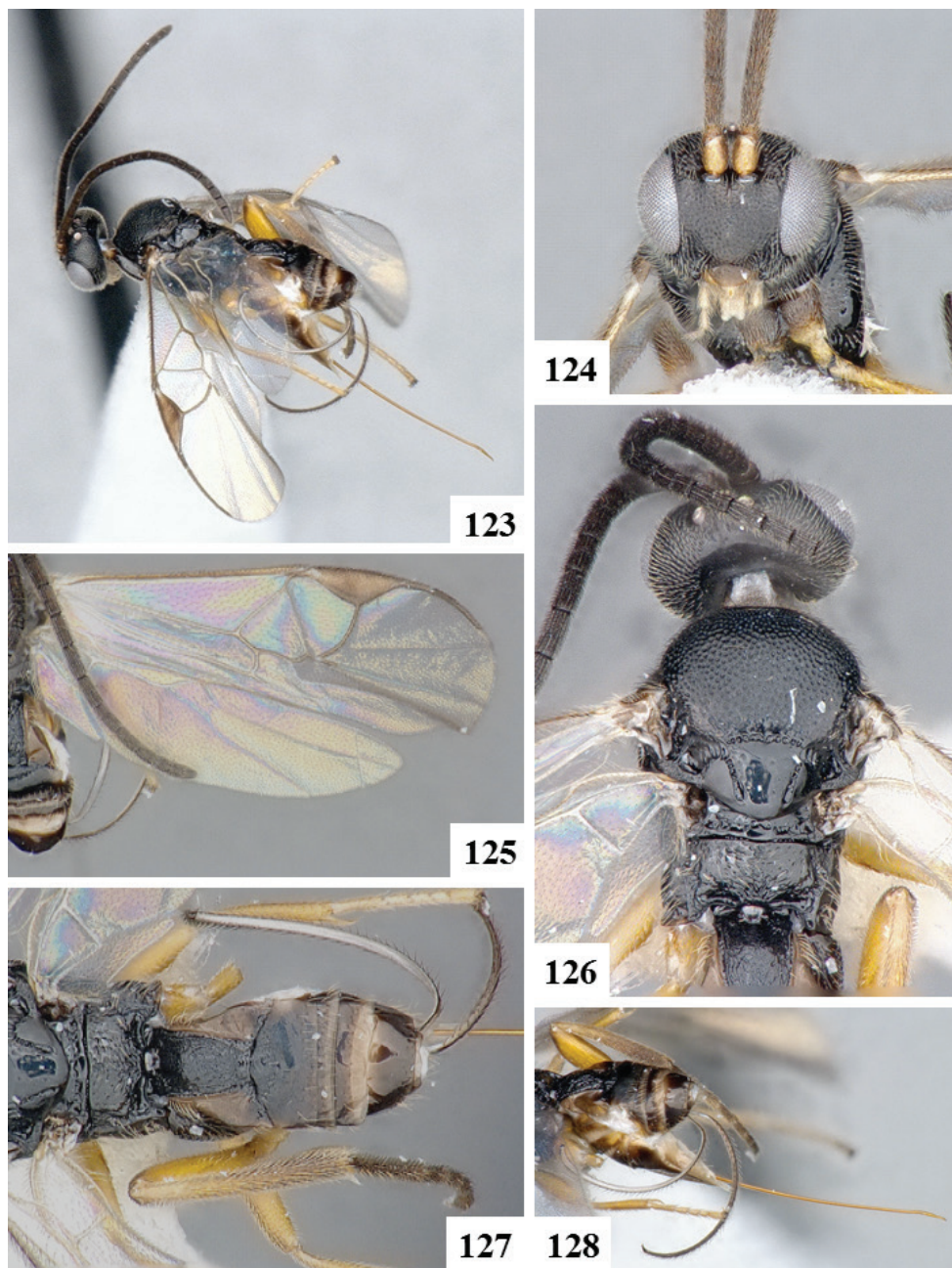
Figures 123–128. *Promicrogaster naomiduarteae* sp. n. holotype.

Description. Head: orange-yellow. Flagellomeres: flagellomeres 1–2 light brown, flagellomeres 3–11 orange-yellow, flagellomeres 12–16 dark brown. Mesosoma: mostly black, with anteromesoscutum, scutellar disc and part of the axillar complex orange-brown.
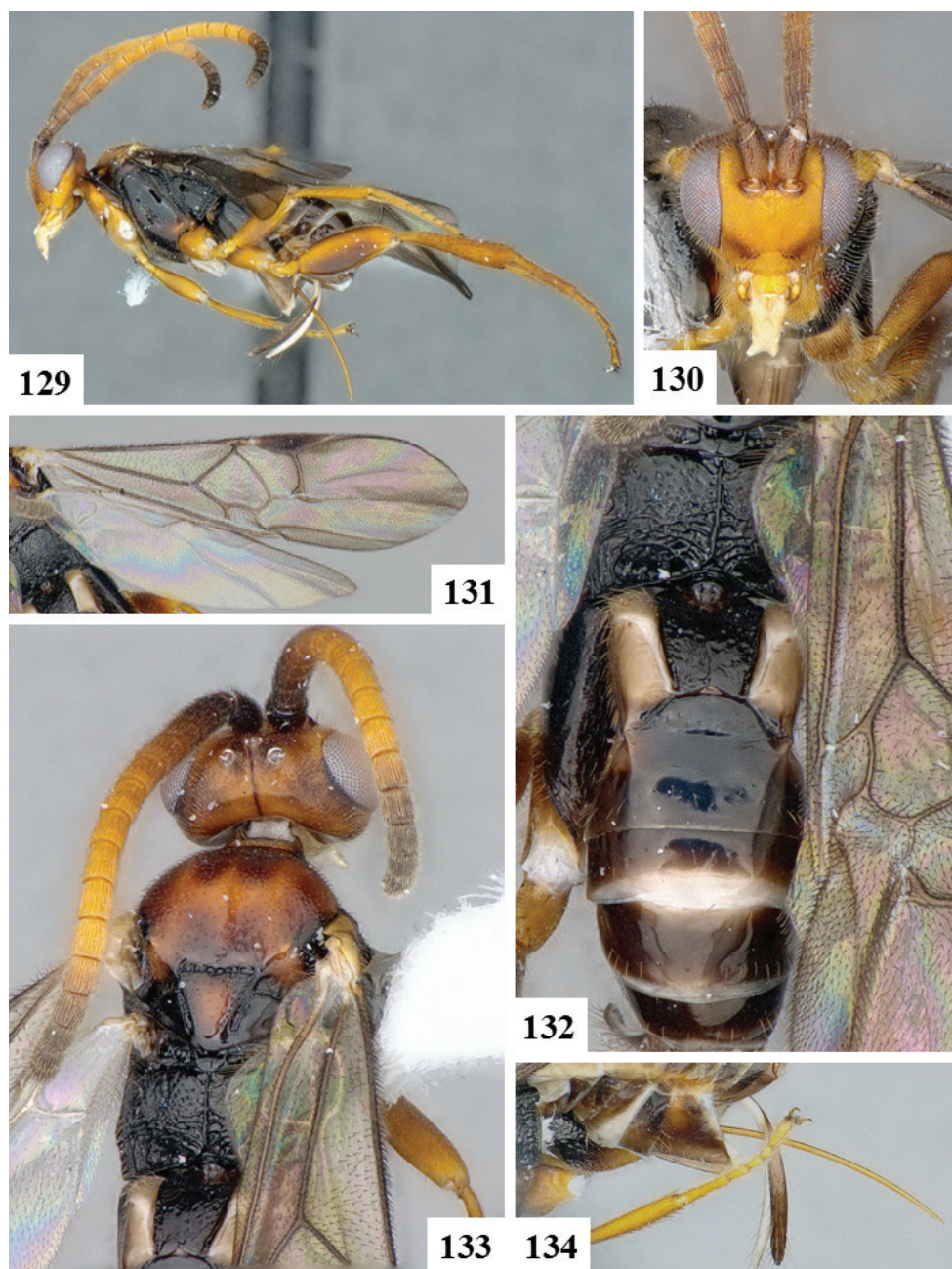
Figures 129–134. *Promicrogaster pablouzagai* sp. n. holotype.

Tegula: yellow. Metasoma (dorsally): dark brown to black. Metacoxa: orange dorsally, brown ventrally. Malar distance: 0.2–0.3 × eye length. Fore wing areolet: present. T1 sculpture: smooth. T2 sculpture: smooth. Ocular–ocellar line: 0.11 mm. Interocellar dis-

tance: 0.10–0.11 mm. Posterior ocellus diameter: 0.06–0.07 mm. Body length: 2.65 mm. Fore wing length: 2.99 mm. Ovipositor length: 1.28 mm. Metacoxa length: 0.77 mm. Metafemur length: 0.90 mm. Metatibia length: 1.06 mm. T1 length/width at posterior margin: 0.48 mm/ 0.21 mm. T2 length/width at posterior margin: 0.11 mm/ 0.40 mm.

Distribution. Costa Rica (ACG, mid-elevation rain forest and cloud forest).

Etymology. *Promicrogaster pablouzagai* is named in honor of 14-year-old Juan Pablo Uzaga López from the Colonia Bolaños school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Comments. Based in body color, propodeum sculpture, and shape of areolet in fore wing, this is the most distinctive *Promicrogaster* among all species studied.

Promicrogaster polyporicola Muesebeck, 1958
Figs 135–140

Promicrogaster polyporicola Muesebeck, 1958: 423. Original description.

Holotype. Female, NMNH (not examined). PANAMA, Barro Colorado Island, Canal Zone. Voucher code: USNM 63053.

Material examined. 1♀, paratype (CNC), same locality than holotype; 1♂ (CNC), PANAMA, Panama, Cerro Campana, 850m, 8°40'N, 19°50W; 1♂ (CNC), PANAMA, Panama, no further locality information.
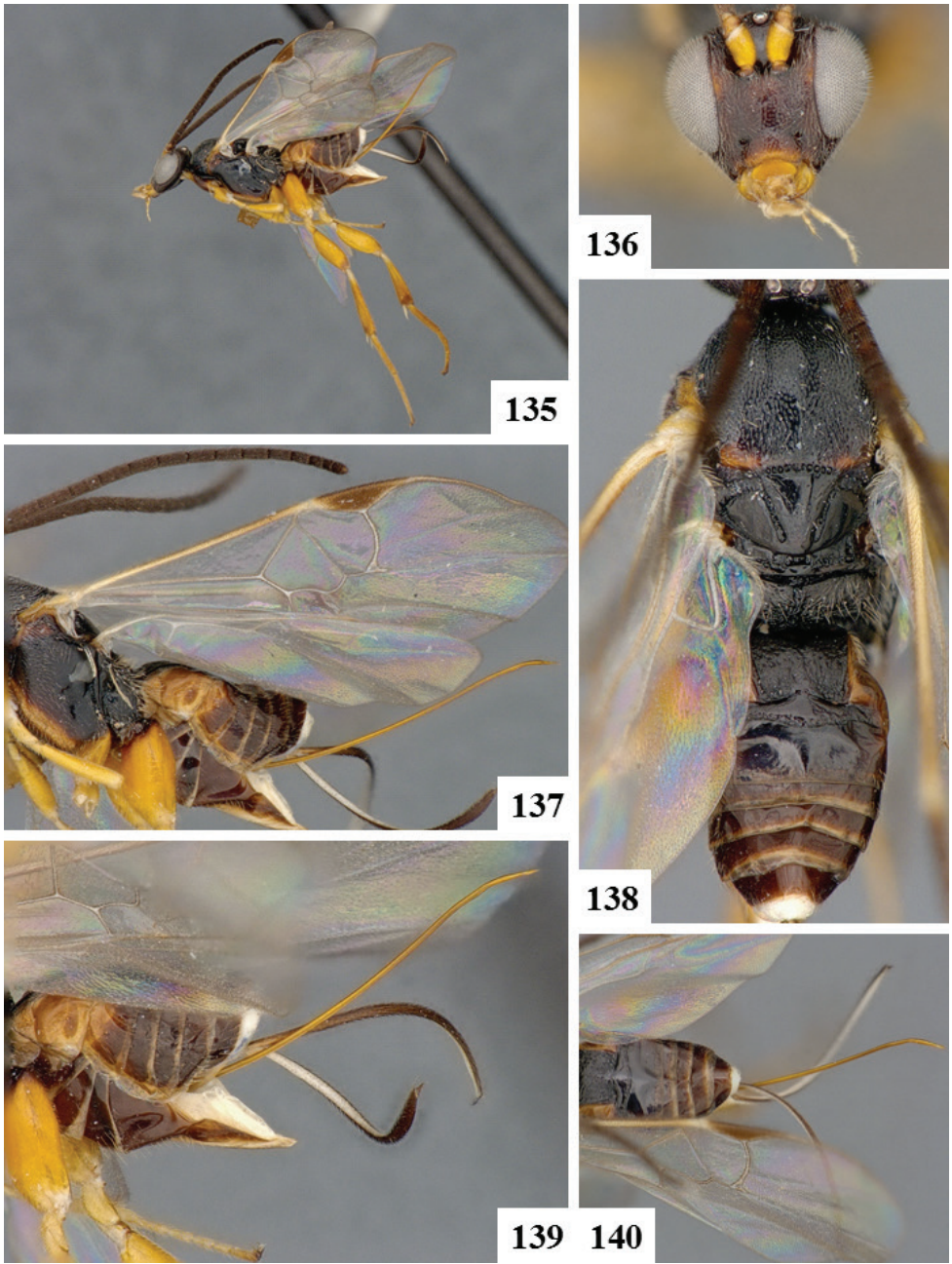
Distribution. Panama.

Promicrogaster ronycastilloi Fernandez-Triana & Boudreault, sp. n.
http://zoobank.org/D7B8BB92-E509-405E-B6FF-F0401634F6E9
Figs 141–147

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Sendero Arenales, 1080m, 10.92471, -85.46738. DNA Voucher code: DHJPAR0031345.

Description. Head: mostly black, labrum and mandibles light brown. Flagellomeres: dark brown to black. Mesosoma: black. Tegula: dark brown. Metasoma (dorsally): black to dark brown. Metacoxa: mostly black to dark brown (posterior 0.1–0.2 yellow). Malar distance: less than 0.2 × eye length. Fore wing areolet: absent. T1 sculpture: mostly smooth, with some sculpture laterlally. T2 sculpture: mostly smooth with some sculptured near posterior margin. Ocular–ocellar line: 0.07 mm. Interocellar distance: 0.08 mm. Posterior ocellus diameter: 0.06 mm. Body length: 1.94 mm. Fore wing length: 2.21 mm. Ovipositor length: 1.56 mm. Metacoxa length: 0.47 mm. Metafemur length: 0.48 mm. Metatibia length: 0.68 mm. T1 length/width at posterior margin: 0.23mm/ 0.15 mm. T2 length/width at posterior margin: 0.06 mm/ 0.21 mm.

Figures 135–140. *Promicrogaster polyporicola.*
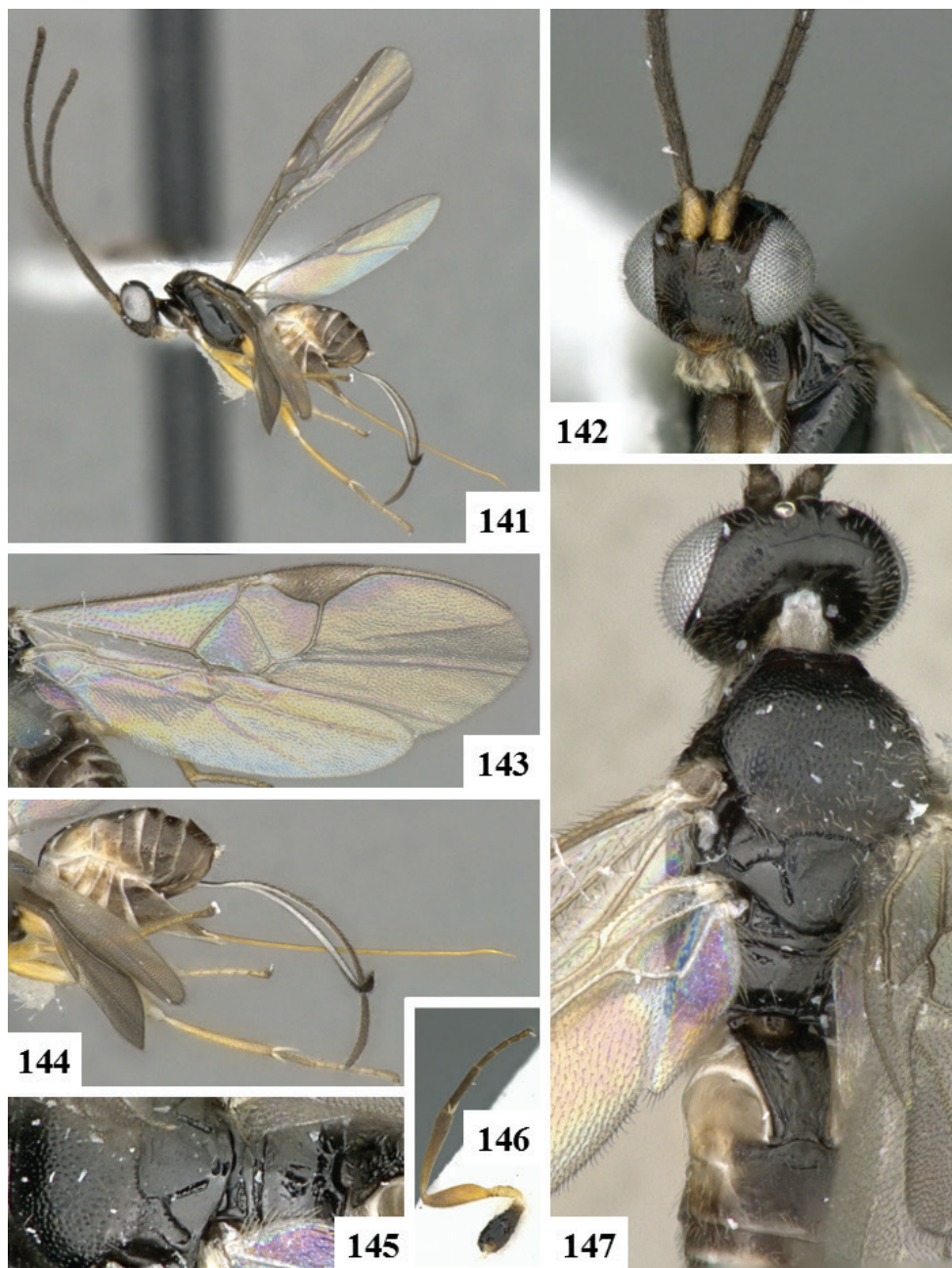
Figures 141–147. *Promicrogaster ronycastilloi* sp. n. holotype.

Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

Etymology. *Promicrogaster ronycastilloi* is named in honor of 10-year-old Rony Castillo Martínez from the Colonia Bolaños school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster sebastiancambroneroi **Fernandez-Triana & Boudreault, sp. n.**

http://zoobank.org/1EEA621A-D68F-495B-98B9-809993983FEE

Figs 148–153

Holotype. Female, CNC. COSTA RICA, Guanacaste, Area de Conservación Guanacaste, Sector Cacao, Cerro Pedregal, 1080m, 10.92767, -85.47449. DNA Voucher code: DHJPAR0033736.

    Description. Head: mostly black, labrum and mandibles orange-brown. Flagellomeres: dark brown. Mesosoma: black. Tegula: dark brown. Metasoma (dorsally): black to dark brown. Metacoxa: mostly black to dark brown (posterior 0.1–0.2 yellow). Malar distance: 0.2–0.3 × eye length. Fore wing areolet: absent. T1 sculpture: anterior 0.5 smooth, posterior 0.5 sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.10 mm. Interocellar distance: 0.08 mm. Posterior ocellus diameter: 0.05 mm. Body length: 2.43 mm. Fore wing length: 2.37 mm. Ovipositor length: 1.73 mm. Metacoxa length: 0.50 mm. Metafemur length: 0.56 mm. Metatibia length: 0.69 mm. T1 length/width at posterior margin: 0.22 mm/ 0.16 mm. T2 length/width at posterior margin: 0.08 mm/ 0.27 mm.

    Distribution. Known only from the holotype locality in ACG, cloud forest, Costa Rica.

    Etymology. *Promicrogaster sebastiancambroneroi* is named in honor of 12-year-old Erick Sebastián Cambronero Narváez from the Colonia Bolaños school for his growing enthusiasm for understanding and protecting the wild nature that occurs in his homeland.

Promicrogaster tracyvindasae **Fernandez-Triana & Boudreault, sp. n.**

http://zoobank.org/60402B64-D1CF-4E15-9718-16B4466D5930

Figs 154–159

Holotype. Female, CNC. COSTA RICA, Alajuela, Area de Conservación Guanacaste, Sector Rincón Rain Forest, Vado Rio Francia, 400m, 10.90093, -85.28915. DNA Voucher code: DHJPAR0025529.

    Paratypes. 1♀, 1♂ (CNC), Costa Rica, Alajuela, ACG, Sector San Cristobal, Potrero Argentina, 520m, 10.89021, -85.38803; 1♀ (CNC), Costa Rica, Braulio Carrillo National Park, 500m, 10.10, -84.07; 1♀ (CNC), Costa Rica, San Vito, Las Cruces. DNA voucher codes: CNCHYM 01515, DHJPAR0025572, DHJPAR0025660.
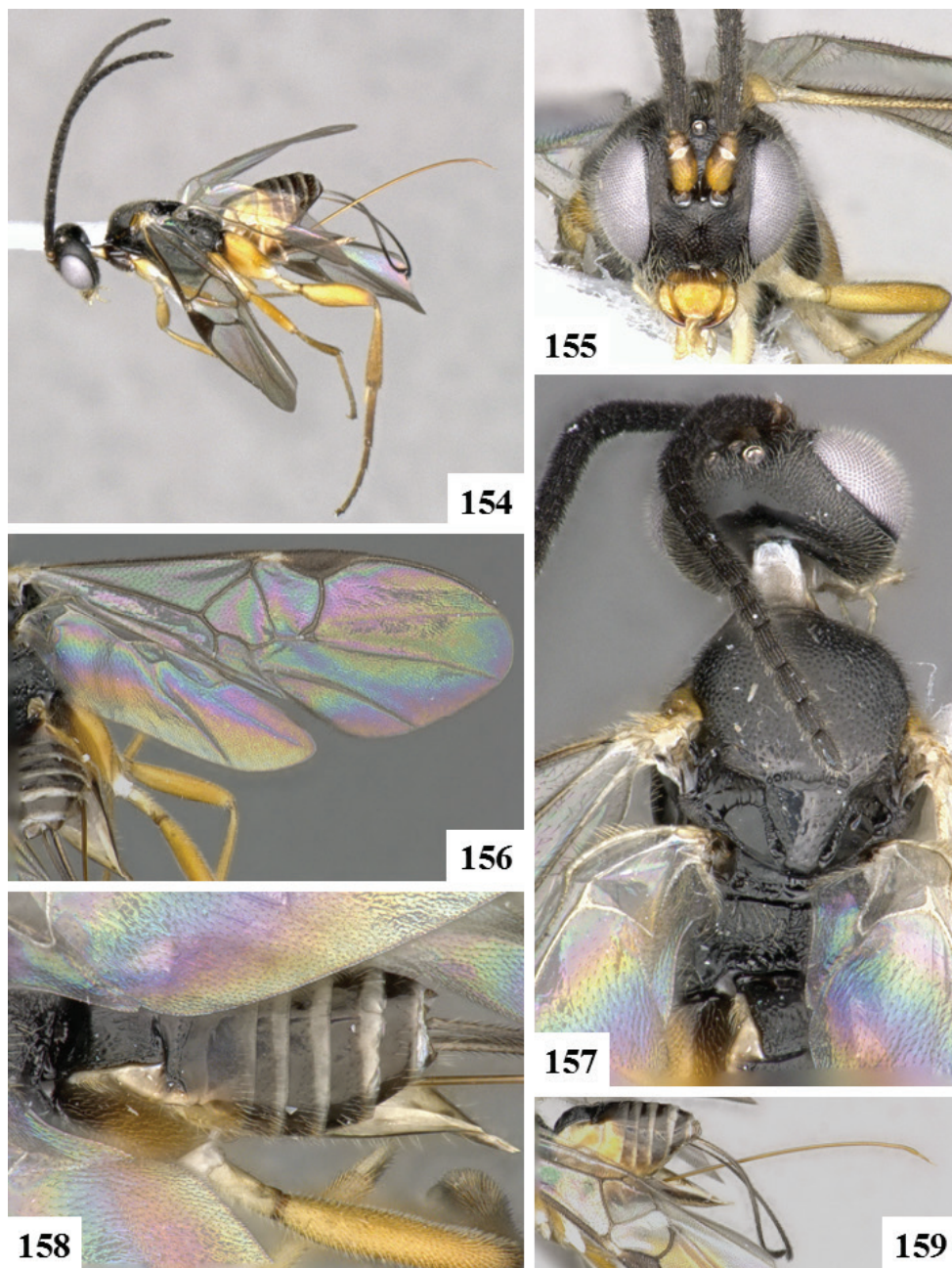
    Description. Head: mostly black, labrum and mandibles yellow to orange-brown. Flagellomeres: dark brown to black. Mesosoma color: black. Tegula: yellow. Metasoma (dorsally): black to dark brown. Metacoxa: orange-yellow. Malar distance: less than 0.2 × eye length. Fore wing areolet: present. T1 sculpture: anterior 05. Smooth, posterior 0.5 sculptured. T2 sculpture: mostly sculptured, except for smooth central area. Ocular–ocellar line: 0.13–0.14 mm. Interocellar distance: 0.08–0.10 mm. Posterior ocellus diameter: 0.08 mm. Body length: 3.61–3.93 mm. Fore wing length: 3.57–4.08 mm. Ovipositor length: 2.50–2.96 mm. Metacoxa length: 0.82–0.90 mm. Metafemur length: 0.89–1.03 mm.
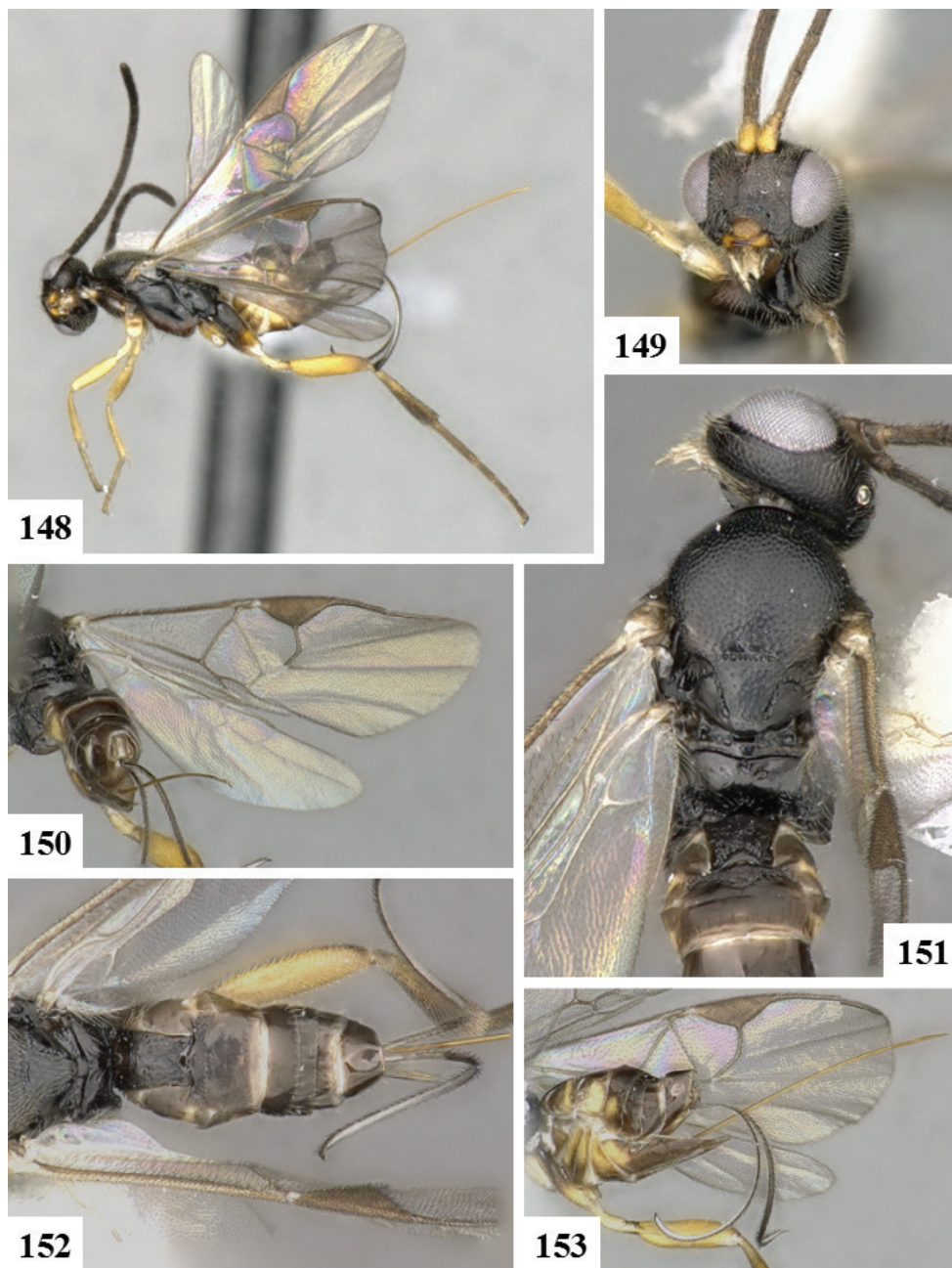
Figures 148–153. *Promicrogaster sebastiancambroneroi* sp. n. holotype.

Metatibia length: 1.04–1.29 mm. T1 length/width at posterior margin: 0.50–0.55 mm/ 0.30–0.32 mm. T2 length/width at posterior margin: 0.10–0.14 mm/ 0.45–0.58 mm.

Distribution. Costa Rica, mid-elevation rain forest.

Figures 154–159. *Promicrogaster tracyvindasae* sp. n. holotype.

Etymology. *Promicrogaster tracyvindasae* is named in honor of 11-year-old Tracy Johana Vindas Espinoza from the Huacas school for her growing enthusiasm for understanding and protecting the wild nature that occurs in her homeland.
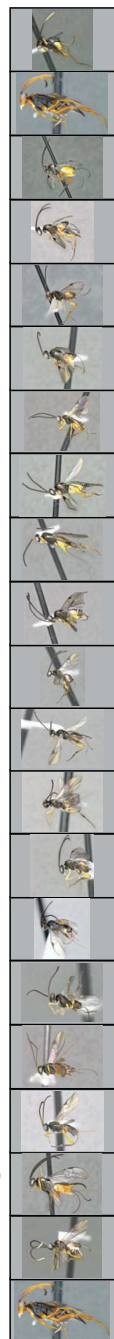
Promicrogaster daretrizoi|DHJPAR0025968
Promicrogaster daretrizoi|DHJPAR0026057
Promicrogaster daretrizoi|DHJPAR0025980
Promicrogaster daretrizoi|DHJPAR0025506
Promicrogaster daretrizoi|DHJPAR0027638
Promicrogaster daretrizoi|DHJPAR0026072
Promicrogaster daretrizoi|DHJPAR0024792
Promicrogaster daretrizoi|DHJPAR0025676
Promicrogaster daretrizoi|DHJPAR0025820
Promicrogaster daretrizoi|DHJPAR0025821
Promicrogaster daretrizoi|DHJPAR0025899
Promicrogaster daretrizoi|DHJPAR0025945
Promicrogaster daretrizoi|DHJPAR0025963
Promicrogaster daretrizoi|DHJPAR0025986
Promicrogaster daretrizoi|DHJPAR0025989
Promicrogaster daretrizoi|DHJPAR0025999
Promicrogaster daretrizoi|DHJPAR0026009
Promicrogaster daretrizoi|DHJPAR0026015
Promicrogaster daretrizoi|DHJPAR0026041
Promicrogaster daretrizoi|DHJPAR0027665
Promicrogaster daretrizoi|DHJPAR0025953
Promicrogaster daretrizoi|DHJPAR0026006
Promicrogaster daretrizoi|DHJPAR0026077
Promicrogaster daretrizoi|DHJPAR0027604
Promicrogaster daretrizoi|DHJPAR0027640
Promicrogaster daretrizoi|DHJPAR0026011
Promicrogaster daretrizoi|DHJPAR0026025
Promicrogaster daretrizoi|DHJPAR0027674
Promicrogaster daretrizoi|DHJPAR0027694
Promicrogaster daretrizoi|DHJPAR0025873
Promicrogaster daretrizoi|DHJPAR0025874
Promicrogaster daretrizoi|DHJPAR0025973
Promicrogaster daretrizoi|DHJPAR0027677
Promicrogaster daretrizoi|DHJPAR0027603
Promicrogaster daretrizoi|DHJPAR0025971
Promicrogaster daretrizoi|DHJPAR0026023
Promicrogaster daretrizoi|DHJPAR0027642
Promicrogaster daretrizoi|DHJPAR0027702
Promicrogaster daretrizoi|DHJPAR0027630
Promicrogaster daretrizoi|DHJPAR0027615
Promicrogaster daretrizoi|DHJPAR0027662
Promicrogaster daretrizoi|DHJPAR0026044
Promicrogaster daretrizoi|DHJPAR0025872
Promicrogaster daretrizoi|DHJPAR0027611
Promicrogaster daretrizoi|DHJPAR0027634
Promicrogaster daretrizoi|DHJPAR0027643
Promicrogaster daretrizoi|DHJPAR0025908
Promicrogaster daretrizoi|DHJPAR0026010
Promicrogaster daretrizoi|DHJPAR0027617
Promicrogaster daretrizoi|DHJPAR0027624
Promicrogaster pablozagai|DHJPAR0025351
Promicrogaster pablouzagai|DHJPAR0025829
Promicrogaster fabriciocambroneroi|DHJPAR0012588
Promicrogaster tracyvindasae|DHJPAR0025660
Promicrogaster tracyvindasae|DHJPAR0025772
Promicrogaster tracyvindasae|DHJPAR0025529
Promicrogaster brandondinartei|DHJPAR0031290
Promicrogaster brandondinartei|DHJPAR0031326
Promicrogaster brandondinartei|DHJPAR0031203
Promicrogaster brandondinartei|DHJPAR0031206
Promicrogaster brandondinartei|DHJPAR0031258
Promicrogaster liagrantae|DHJPAR0012587
Promicrogaster liagrantae|DHJPAR0012586
Promicrogaster liagrantae|DHJPAR0012725
Promicrogaster liagrantae|DHJPAR0013138
Promicrogaster liagrantae|DHJPAR0024707
Promicrogaster eimyobandoae|DHJPAR0025685
Promicrogaster eimyobandoae|DHJPAR0027520
Promicrogaster eimyobandoae|DHJPAR0025577
Promicrogaster eimyobandoae|DHJPAR0026587
Promicrogaster kiralycastilloae|DHJPAR0031288
Promicrogaster kevinmartinezi|DHJPAR0031274
Promicrogaster kevinmartinezi|DHJPAR0031318
Promicrogaster andreyvallejosi|DHJPAR0034086
Promicrogaster andreyvallejosi|DHJPAR0034152
Promicrogaster andreyvallejosi|DHJPAR0031432
Promicrogaster fabiancastroi|DHJPAR0031313
Promicrogaster fabiancastroi|DHJPAR0031314
Promicrogaster fabiancastroi|DHJPAR0031310
Promicrogaster luismendezi|DHJPAR0031207
Promicrogaster sebastiancambroneroi|DHJPAR0033736
Promicrogaster sebastiancambroneroi|DHJPAR0031377
Promicrogaster eddycastroi|DHJPAR0031320
Promicrogaster naomiduarteae|DHJPAR0031404
Promicrogaster naomiduarteae|DHJPAR0031409
Promicrogaster daniellopezi|DHJPAR0031819
Promicrogaster daniellopezi|DHJPAR0031641
Promicrogaster monteverdensis|DHJPAR0025917
Promicrogaster hillaryvillafuerteae|DHJPAR0026620
Promicrogaster alexmartinezi|DHJPAR0031814
Promicrogaster alexmartinezi|DHJPAR0031827
Promicrogaster leilycastilloae|DHJPAR0031431
Promicrogaster pablouzagai|DHJPAR0026085
Promicrogaster pablouzagai|DHJPAR0027659
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Promicrogaster pablouzagai|DHJPAR0025962
Promicrogaster pablouzagai|DHJPAR0025926
Promicrogaster pablouzagai|DHJPAR0025964
Promicrogaster pablouzagai|DHJPAR0025993
Promicrogaster pablouzagai|DHJPAR0031406

0.01

Figure 160. Neighbor-Joining (NJ – Saitou and Nei 1987) tree based on Kimura 2-parameter distances (K2P – Kimura 1980) made using MEGA6 (Tamura et al. 2013) for all currently barcode specimens of *Promicrogaster* in ACG. Tip labels include species name and specimen accession number. Panel on the right contains a single lateral image of each species. The order of the photographs within this panel from top to bottom corresponds to the order of the species within the tree from top to bottom.

Acknowledgments

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RESEARCH ARTICLE

Morphology of the male genitalia of *Brachymyrmex* and their implications in the Formicinae phylogeny

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Abstract

The male genitalia of *Brachymyrmex* are examined and terminology clarified. We document two conformation groups based on the lateral carina, conformation 1 has a complete lateral carina that reaches the apex of the valviceps and in conformation 2 the lateral carina is broken with the apical end projected dorsally. Previously documented species are evaluated in the context of this new information. We offer support for the movement of *Brachymyrmex* into the resurrected tribe Myrmelachistini based on the morphology of the penisvalvae, and offer definitive methods of assigning unknown specimens to this genus. This study provides histological methodologies for the preparation, differentiation, and permanent storage of minute ant genitalia structures and the associated musculature.

Introduction

The ant genus *Brachymyrmex* Mayr, 1868 exists in a state of taxonomic confusion. The small workers are notably devoid of good species delineating characters, and their distributions are not well represented in collections. This "miserable little genus" (Creighton 1950) has been largely ignored in systematic myrmecological works. Currently there are 60 valid species, of which only 21 contain male descriptions, and five of these have genitalia illustrations. The male genitalia offer species level characters that are desperately needed for this taxonomically challenging group (Quirán et al. 2004). In order to utilize the characters to the best of our ability we must first understand their morphology. Boudinot (2013) has provided a comprehensive review of the morphological structures and musculature associated with ant male genitalia, allowing for comparative studies across ants as a group.

Taxonomic history of Brachymyrmex

Brachymyrmex was described by Mayr (1868) from the type species *Brachymyrmex patagonicus*. Forel (1878) included *Brachymyrmex* in the subfamily Camponotinae, and in the tribe Plagiolepidini (Forel 1893). Ashmead (1905) included the Plagiolepidini in the subfamily Formicinae. Forel (1912) erected the tribe Myrmelachistini and defined the tribe as having females with an atennomere count of 9 or 10, males being 10 or 11-merous, and included the genera *Aphomyrmex*, *Brachymyrmex*, *Myrmelachista,* and *Rhopalomyrmex*. Emery (1925) redefined the Myrmleachistini as having fewer than 12 antennomere, with a distinct antennal club. This redefinition removed *Brachymyrmex* from the Myrmelachistini and Emery placed it in the tribe Dimorphomyrmicini. Emery included along with *Brachymyrmex*, the genera *Aphomomyrmex, Cladomyrma, Dimorphomyrmex*, and *Gesomyrmex*, based on the 8 to 9 merous antennomere count lacking an antennal club, short frontal carinae, and large eyes. Emery further considered *Aphomyrmex, Brachymyremx*, and *Cladomyrma* to be closely related and had them comprise the subtribe Brachymyrmicini. Wheeler (1929) treated *Dimorphomyrmex* as a junior synonym of *Gesomyrmex*, and concluded that *Gesomyrmex* was not closely related to the other members of Dimorphomyrmicini. As a result Wheeler raised Emery's subtribe Brachymyrmicini to tribal status, and resurrected Gesomyrmicini to include *Gesomyrmex*. Wheeler and Wheeler (1976, 1985) concluded *Aphomomyrmex, Brachymyrex, Cladomyrma, Euprenolpis, Paratrechina, Petelomyrmex, Prenolepis*, and *Stigmacros* to be in the Brachymyrmicini, using larval characters. Agosti (1991) placed *Brachymyremx* within the *Pseudolasius* genus-group defined by widely separated hind coxae, the petiole ventrally u-shaped, a simple helcium which is antero-ventraly often concealed by the anteriorly fused sternite and tergite. Bolton (2003) transferred *Brachymyrmex* to the Plagiolepidin. Recently Ward et al. (2016) transferred both *Brachymyrmex* and *Myrmelachista* to the Myrmelachistini, which they resurrected. Ward et al. define this group as having the following shared worker characters: a reduced antennomere count (9–10-merous), five mandibular teeth, petiolar node inclined anteriorly, with the base of abdominal segment III completely

fused tergosternally on each side of the helcium, and a plesiomorphic 6,4 palp formula that is reduced to 5,4 in some *Myrmelachista* (Ward et al. 2016).

Santschi (1923) provided the last revision of the group, designating many new species and subspecies. His descriptions, however, are of little value, as they are short and include few comparative characters. In his revision Santschi erected the subgenus *Bryscha,* which he defined by having dimorphic workers, short and flared sepals of the proventriculus, and erect hairs on the scape and legs. *Bryscha* was provisionally synonymized under *Brachymyrmex* by Brown (1973). Although most *Brachymyrmex* have monomorphic workers; at least two species are dimorphic and *Bryscha* may need to be resurrected (Ortiz and Fernández 2014).

The genus has a wide diversity of life histories. Most species are generalist nesters that nest in leaf litter, under stones, or under bark; at least two species have a distinct replete caste; while others are arboreal nesting under epiphyte mats or in small plant cavities. By contrast, the closely-related *Myrmelachista* are obligate arboreal nesting ants (Longino 2006).

As our understanding of ant evolution progresses, the need for additional taxonomic and systematic information is increasing. The primary source for morphological characters in ants is worker morphology. This trend is easy to understand as workers are ubiquitous in the environment, often being the only caste collected and certainly the most prevalent. Queens and males on the other hand are less-frequently encountered, as they are usually within nests or produced only for brief periods. The reproductive casts have thus been largely neglected. Males are largely ignored, and therefore represent an untapped source of morphological characters for taxonomic and phylogenetic use. Moreover, when collected, males may be difficult or even impossible to associate with their workers. However, males may be associated through careful collecting and molecular phylogenies. A recent movement among ant researchers has been to pay more attention to males, both when collecting in the field and unassociated males (Boudinot 2013, Boudinot 2015, Deyrup and Cover 2004, LaPolla et al. 2012, and Yoshimura and Fisher 2007, 2009, 2012).

The most useful character for males are arguably the genitalia, and males, like workers, range in size from the *Dorylus* "sausage flies" to remarkably small *Brachymyrmex.* Viewing and manipulating the male genitalia of larger species is often simple enough; most genitalia are even large enough to point mount for permanent storage. Smaller species, however, are neither simple to manipulate nor store. This has led some authors to not fully dissect the genitalia from small males obtaining images *in situ* either through compound microcopy or scanning electron microscopy (SEM) (LaPolla et al. 2012, and Ortiz and Fernández 2014). With the high cost and low availability of SEM, stereoscopic microscopy is more available, although resolution at 40× is often poor. Due to the low resolution at this magnification, small genitalic structures tend to blend together and become difficult to interpret *in situ*. While there is value in the structure of an intact genital capsule, there remains a large portion of both the volsella, and penisvalva that cannot be viewed, losing potentially important characters.

Here we present methods for dissection and permanent storage via slide mounting of small ant genitalia, with an additional option for muscle fixture and the ability to

clear structures for SEM. Slide mounting genitalia allows examination at much higher magnifications than under stereoscopic microscopy, without the need for sputter coating or environmental SEM prep. Additionally the remainder of the specimen remains intact, losing, at most, only the last three segments. Notes on the genitalia of *Brachymyrmex* and their implications on the Formicinae phylogeny are presented using the described dissection methodologies. It is our hope that this paper provides a greater understanding of the male genitalia characters for *Brachymyrmex*, and encourages renewed interest in this "miserable little genus".

Materials and methods

Tissue sampling

For this study we sampled 16 species/morphospecies of *Brachymyrmex*, specimens were taken from the first author's personal collection (CMWC), the Sam Houston State University Entomology Collection (SHSUE), the John T. Longino collection (JTLC), or accessed via AntWeb.org. Specimens from the collections were either in 95% EtOH or dried. Once dissected, bodies without genitalia were returned to the collections dried and point mounted, with the genitalia deposited in the CMWC on slides. The genitalia where dissected under an Olympus SZX12 dissecting microscope with a maximum 115× magnification mounted with a Olympus DP72 camera. Examined under an Olympus BX53 compound microscope with 10×, 40×, and 60× planapochromatic objectives with differential interference contrast prism mounted with a Olympus DP72 camera, and an Olympus B-Max 41 compound microscope with 10×, 40×, and 60×, with universal and planapochromatic objectives with either bright-field or phase-contrast condenser mounted with a Olympus DP-12 camera. Additional specimens were prepared for SEM using a Vega Scan high vacuum micrograph. Photos taken with the aforementioned cameras were stacked by hand using Adobe Photoshop CS6.

Microtechnique

The procedures for the unstained whole mounts are as follows. The terminal segments of male reproductive organs were removed with a surgical scalpel and size 000 insect pins. Tissues were transferred and presoaked in a 20% sodium hydroxide (NaOH) solution for ca. 30 minutes to dissolve muscle and soft tissues. The remaining sclerites were neutralized with a 20% solution of Acetic acid ($C_2H_4O_2$) for 5 minutes. Dehydration of tissues was initiated in 70% ethanol and continued at 20 min intervals through a graded series of ethanol washes, ending in two final washes with 100% ethanol. Tissues were cleared to near transparency with an initial introduction to xylene via a 50:50 solution of xylene:ethanol, and two 20 minutes washes in histological grade xylene. Prepared specimens were permanently mounted with dammar balsam mounting me-

dia. Alternatively, specimens can be directly taken form 100% ethanol and mounted in euparal. Slides are placed on a pre-warmed slide warmer and allowed to cure overnight.

The procedures for stained whole mounts are as follows. The terminal segments of male reproductive organs were removed with a surgical scalpel and size 000 insect pins. In order to examine the insertion and attachment sites for all muscles, excised tissues were not dissolved. Hydration of reproductive tissues were initiated in 70% ethanol and regressed to a final wash in deionized water. Prepared tissues were stained for 20 minutes in Harris Hematoxylin (without counterstain), and washed in an acid alcohol de-stain for 5–10 seconds. Stained tissues were then dehydrated with ethanol through an ascending graded series, cleared in xylene and permanently mounted with Damar Balsam mounting media. Examination of prepared tissue mounts follows the description above. The figures presented here are grouped by similar morphology and grouping statements accompany the respective figures.

Results

The terminology herein follows Boudinot (2013). The genital capsule is composed of three paired valves, sternum IX, and the cupula. Working from medial to lateral we find a paired median valve termed the penisvalva, each segment of the penisvalva is composed of an arm-like apophysis termed the valvura, and the distal components or valviceps. The paired penisvalvae are joined dorsomedially by the penisvalva membrane. On either side of the penisvalva are the paired volsellae, which are attached to the basimere via the basivolsella and volsellar membrane. The volsellae themselves are composed of the parossiculus, the cuspis, and the digitus which is basolaterally articulated with the parossiculus. The lateral most paired valves are the parameres, which are composed of a large dish like basimere, and an elongated distal telomere. The cupula is a small thin sclerite attached to abdominal tergum IX and the vollsella, and is easily left behind when removing the genital capsule. We have not examined the cupula of *Brachymyrmex*.

Penisvalvae

The paired penisvalvae of *Brachymyrmex* show tremendous variation in general shape, ranging from scimitar, to sickle-shaped, and quadrate. All species in which the males have been examined show dentition on the ventral ridge of the penisvalvae, which is conspicuously absent in *Myrmelachista* (though it should be noted that dentition is present throughout many of the formicids) (Fig. 1).

LaPolla and Longino (2006) suggest that the dorsal placement of the apodemal ridge in *Brachymyrmex*, *Cladomyrma*, and *Myrmelachista* as a potential synapomorphy for these three genera. A clarification of terms is needed. The penisvalva is composed of two parts, the valvura and the valviceps. The valvura bears all of the muscular insertions, and is an internal aphophysis while the valviceps is an external blade like
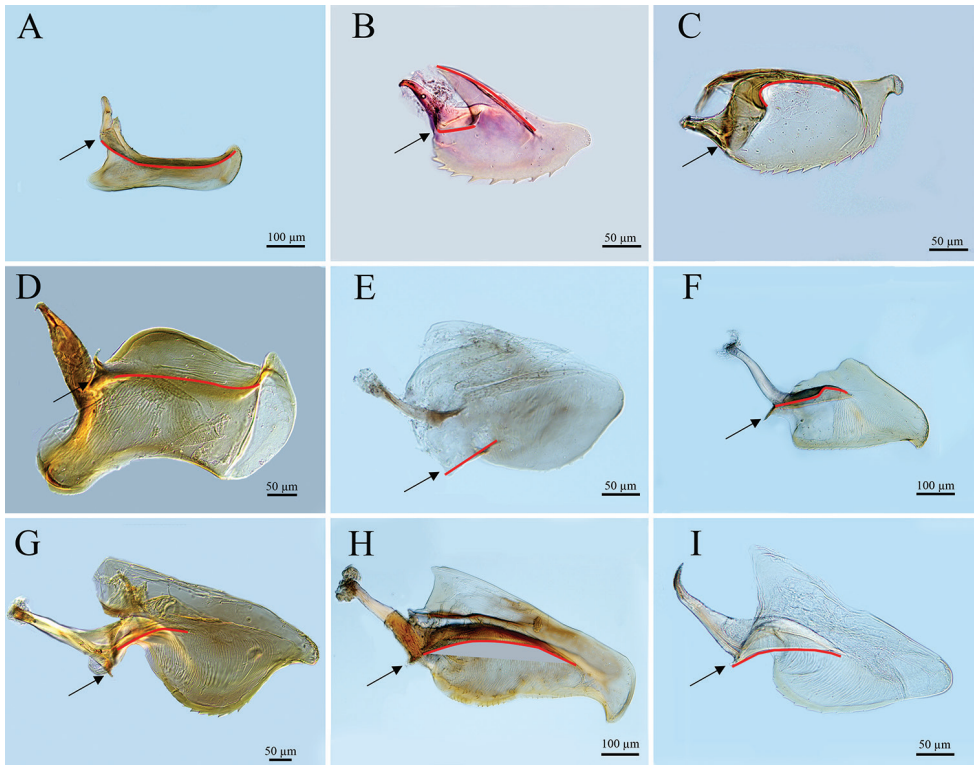
Figure 1. Ectal views of the right penisvalvae of *Myrmelachista* sp. **A** *Brachymyrmex* CMW-012 **B** *Brachymyrmex patagonicus* **C** *Acropyga exsanguis* **D** *Stigmacros sp.* **E** *Camponotus tonduzi* **F** *Lasius* sp. **G** *Gigantiops destructor* **H** *Prenolepis impairs* **I** Black Arrows lateral apodeme, Red Lines lateral carinae.

structure. The insertion of muscle *k* (= dorsal gonostyle/volsella complex penisvalval muscle) delimits the valvura posterodorsally.

As the base of the valvura is produced laterally, it may be referred to as the "lateral apodeme" (Fig. 1). Muscles *i* (= ventroapical parameral-penisvalvar muscle) and *l* (= lateral parameral-penisvalvar muscle) attach to the penisvalva via the lateral apodeme. The apodeme and its associated musculature allow the penisvalvae to pivot on the mediosagittal plane. The lateral apodeme in most ants is situated at the anterior end of a lateral carina (referred to by Lapolla and Longino as the "apodemal ridge"). This lateral carina is on the external surface of the valviceps (i.e. is not internal) and therefore cannot be an apodeme. The lateral carina cups the volsella dorsally *in situ*, and is a structure which displays taxonomically valuable variation. Additionally the "dorsally placed" carina ("apodemal ridge") interpretation of Lapolla and Longino (2006) is anatomicaly imprecise and suggest that the lateral caraina has migrated dorsally to a position which is dissimilar to other Formicinae. Instead, it is apparent that the lateral carina is unmodified in position and that, rather, the anterodorsal region of the valviceps has been reduced such that the lateral apodeme delimits the valviceps anterodorsally.
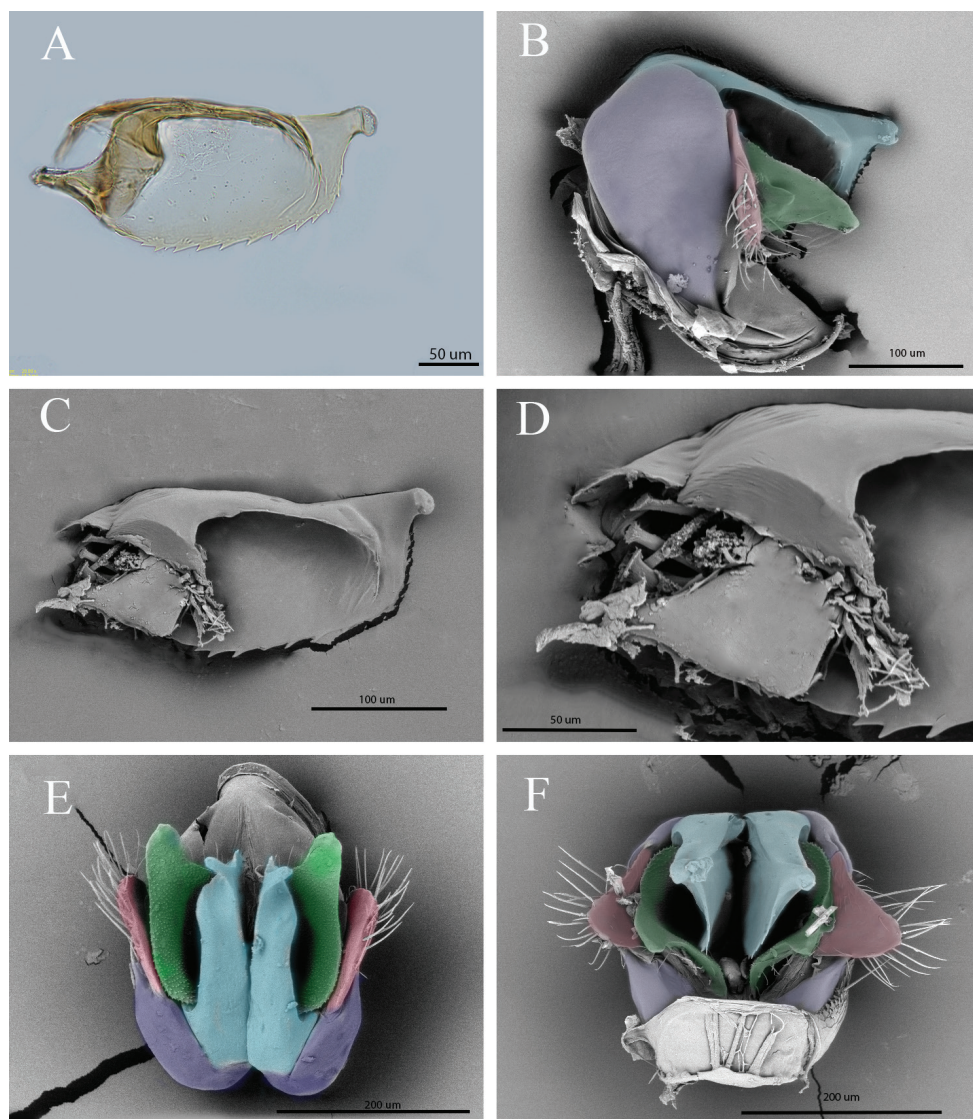
Figure 2. External genitalia of *Brachymyrmex patagonicus*, compound light microphotograph of the penisvalva in ectal view **A** lateral view of the genital capsule with the telomere pulled back to reveal the volsella and penisvalva **B** SEM of the penisvalva in ectal view **C** magnified ectal view of the penisvalva showing the separation of the valvura, the proximal end of the lateral carina, and severed muscular tissue form muscles *k,* and *i* **D** dorsal view of the genital capsule **E** apical view of the genital capsule **F** Colors: **Blue** penisvalvae; **Green** volsella; **Red** telomere; **Purple** baismere.

Two main conformation patterns can be seen in the penisvalval morphology among the *Brachymyrmex* we sampled. In conformation 1 the lateral carina is complete, running from the lateral apodeme to the apex of the valviceps. In this conforma-
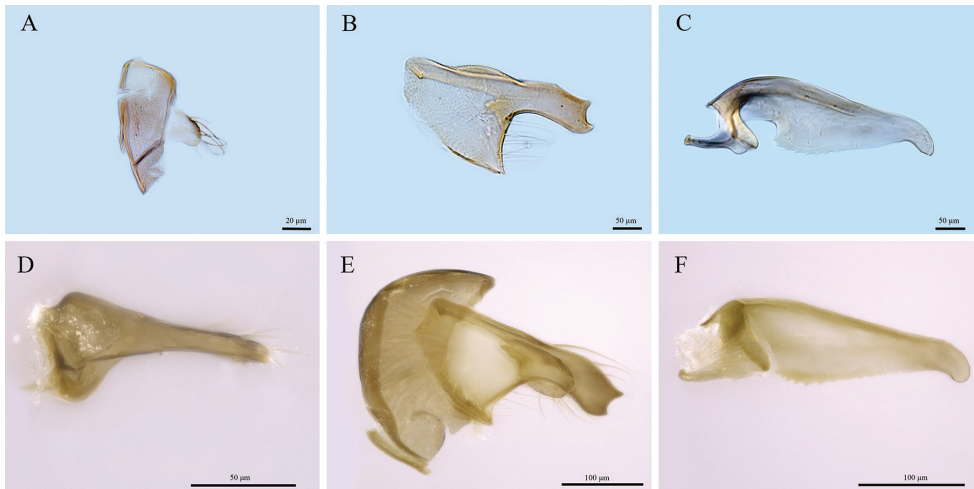
Figure 3. Paramere, volsella, and penisvalva of *Brachymyrmex obscurior* **A–C** *Brachymyrmex coredmoyi* (basimere not present) AntWeb.org, CASENT0740911 Photograped by Veronica M. Sinotte **D–F** Grouping: lateral carinae complete; digitus elongate and bifurcate apicaly; valvura parallel to the long axis of the valviceps.

tion group the lateral carina forms a sharp curve dorsally near the carina's base (Fig. 1C). This group includes *Brachymyrmex cordemoyi* Forel, 1895, *B. patagonicus* and *Brachymyrmex obscurior* Forel, 1893 (Figs 2A, 3C, F). The general shape, most notably the lack of a raised anterior portion along the valvicpes blade, can also be seen in the illustrations of *Brachymyrmex brevicronis* Emery, 1906 (Quirán 2005), *Brachymyrmex bruchi* Forel, 1912, and *Brachymyremx oculatus* Santschi, 1919 (Quirán et al. 2004). This conformation is rather distinct among the Formicinae which tend to have a fairly flat, or gently forming a convex lateral carinae (Fig. 1D–I).

The lateral carina of conformation 2 is incomplete being broken apically of the lateral apodeme into an anterior portion, which is continuous with the lateral apodeme, and a posterior portion that is raised dorsally above the blade of the valviceps (Fig. 1B). This conformation group includes all other taxa we examined (Figs 4–6). The broken lateral carina is almost certainly unique and is likely to be a synapomorphy for species with this morphology. Though this is a tentative evaluation that requires further sampling to fully elucidate.

Quirán's (2007) illustration of *Brachymyrmex australis* Forel, 1901 is difficult to place in either conformation group. The penisvalvae illustration lacks a raised anterior portion, however the lateral carina is not indicated, furthermore the volsella is similar to those in conformation 2, with a medial concavity (see discussion of the volsella below). Ortiz and Fernández's (2014) description, and accompanying figure for the male of *Brachymyrmex pilipes* Mayr, 1887 is inconclusive. The majority of the valviceps is covered by the telomere, and the volsella is completely hidden. That being said, the dorsum of the apical end of the valviceps does appear to be projected upwards, as we see in conformation 2.
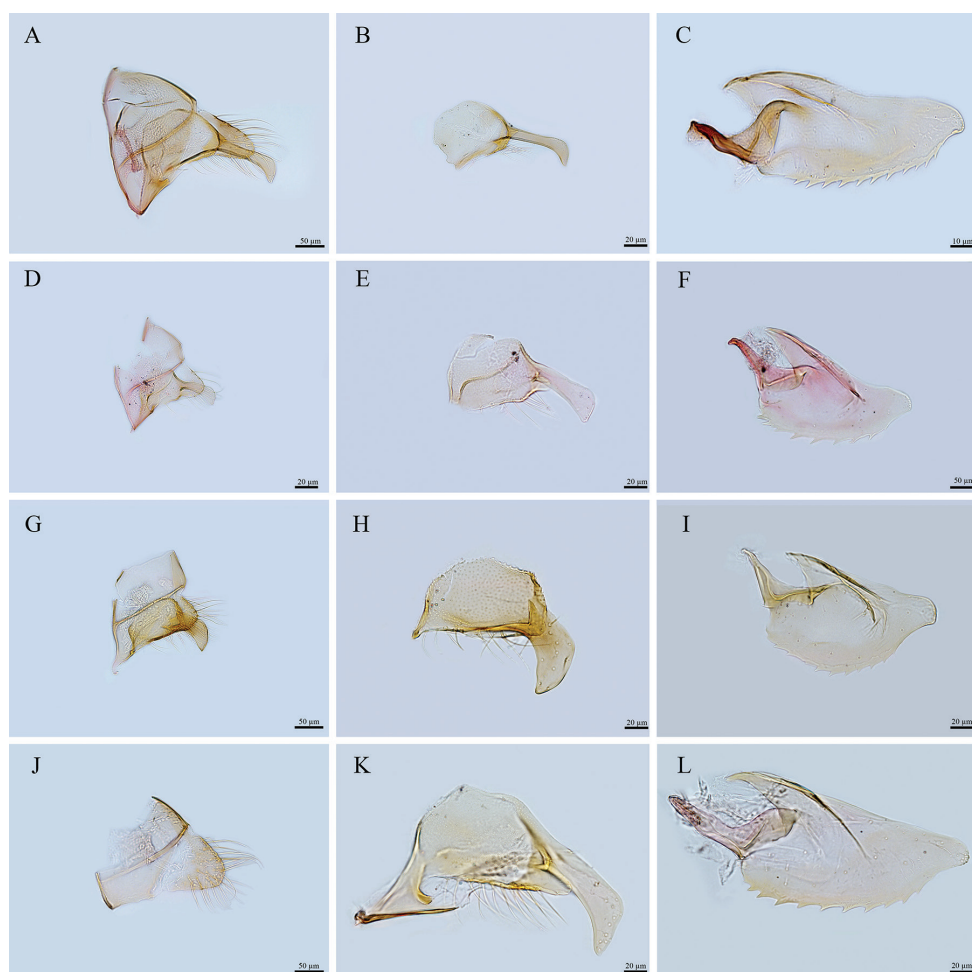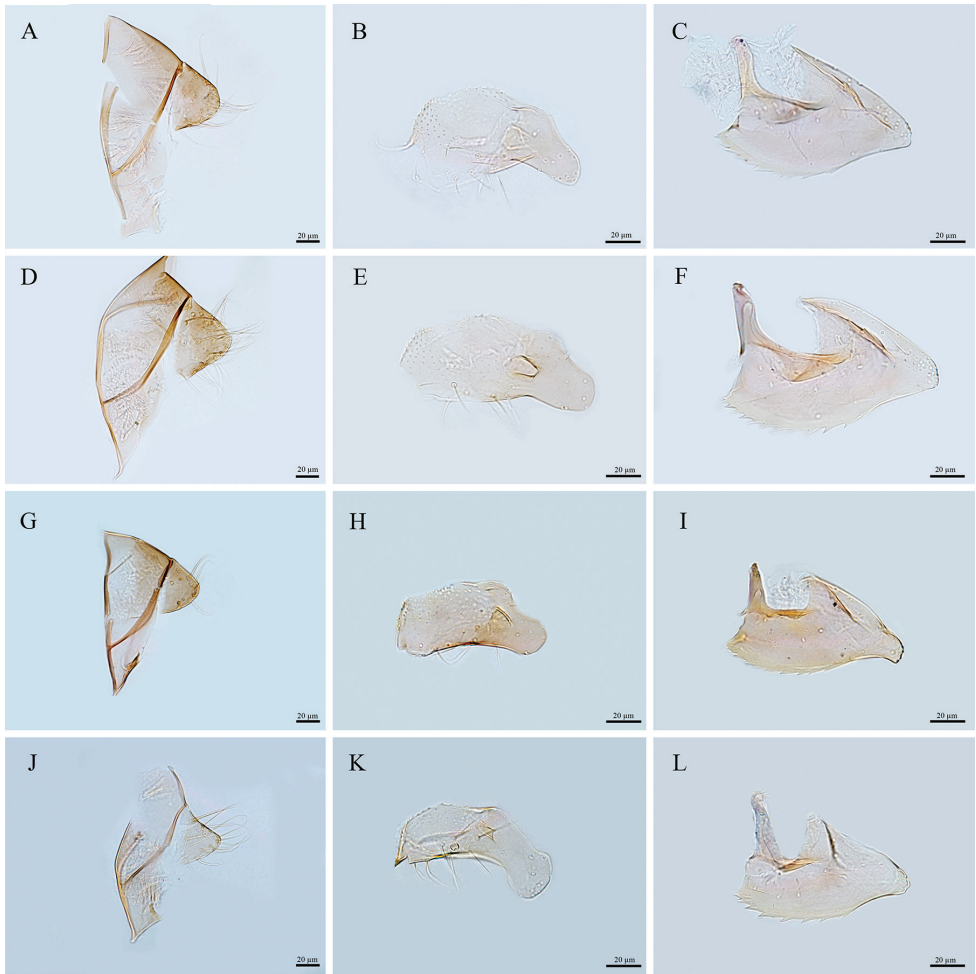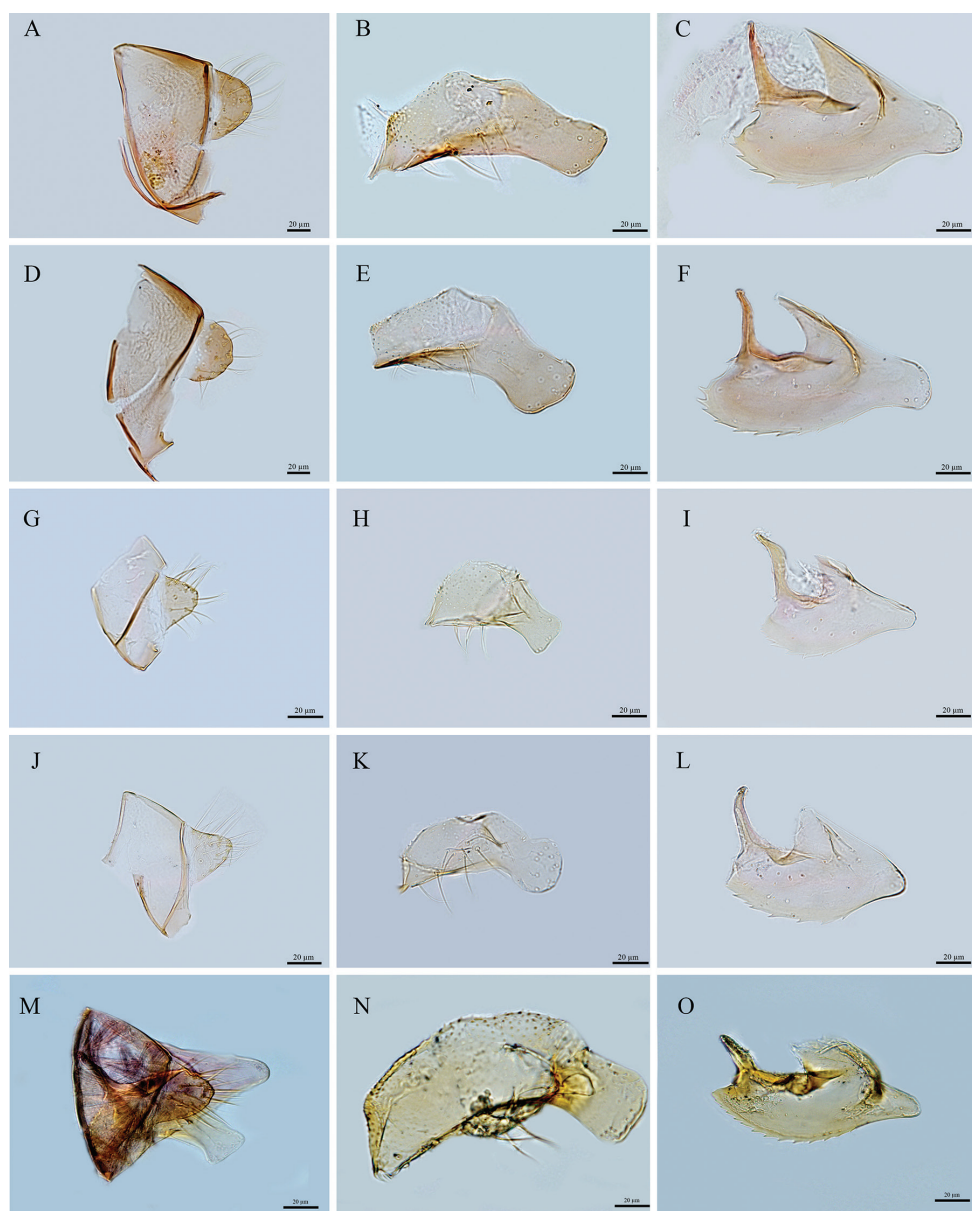
Figure 4. Paramere, volsella, and penisvalva of *Brachymyrmex* CMW-011 (basivolsella fragmented) **A–C** *Brachymyrmex* CMW-012 (basivolsella fragmented) **D–F** *Brachymyrmex cavernicola* **G–I** *Brachymyrmex heeri* **J–L** Grouping: lateral carinae broken; digitus elongate, apex curving ventrad and not bifurcate apically; valvura oblique to the long axis of the valviceps.

Volsella

The volsella of *Brachymyrmex* follows the pattern of some *Myrmelachista* where the cuspis is reduced to a small triangular protrusion affixed to the wall of the digitus (*B. obscurior*, (Fig. 3B) *B.* CMW-006, *B.* CMW-003, *B.* CMW-008, *B.* CMW-010, (Fig. 5B, E, H, K) *B.* JTL-004, *B.* JTL-005, and *Brachymyrmex depilis* Emery, 1893 (Fig. 6H, K)), or completely absent (*B.* CMW-007, *B.* CMW-009 (Fig. 6B, E)). Unlike *Myrmelachista*, there is little variation in the cuspis, though in some species the cuspis is slightly protruded (*B.* CMW-011, *B.* CMW-012, *Brachymyrmex cavernicola* Wheeler, 1938 and *Brachymyrmex heeri* Forel, 1874 (Fig. 4B, E, H, K)). *Brachymyrmex*

Figure 5. Paramere, volsella, and penisvalva of *Brachymyrmex* CMW-006 (basivolsella fragmented) **A–C** *Brachymyrmex* CMW-003 **D–F** *Brachymyrmex* CMW-008 **G–I**: *Brachymyrmex* CMW-010 **J–L** Grouping: lateral carinae broken; digitus lobate; valvura perpendicular to the long axis of the valviceps.

cordemoyi is unique amongst the specimens we examined, the cuspis is ovate, and well developed (in regards to *Brachymyrmex*), and a number of flexuous setae are present (Fig. 3E). In addition the digitus also bears setae, which is similarly unique. A row of flexuous setae is present ventromedially on the basivolsella in all taxa we examined and can serve as a method of orienting the dissected volsella. The shape of the digitus ranges from a subtriangular, or subquadrate short broad projection (*B. patagonicus* (Fig. 7C), *B.* CMW-006, *B.* CMW-003, *B.* CMW-008, *B.* CMW-010 (Fig. 5B, E, H, K)) to a long narrow structure with the apical portion either curving ventrad (*B.* CMW-0011, *B.* CMW-0012, *B. cavernicola*, and *B. heeri* (Fig. 4B, E, H, K)), or bifurcate (*B. cordemoyi, and B. obscurior* (Fig. 3B, E)). The basivolsella is broadly flattened bending to

Figure 6. Paramere, volsella, and penisvalva of *Brachymyrmex* CMW-007 (basivolsella fragmented) **A–C** *Brachymyrmex* CMW-009 (basivolsella fragmented) **D–F** *Brachymyrmex* JTL-004 (basivolsella fragmented) **G–I** *Brachymyrmex* JTL-005 (basivolsella fragmented) **J–L** *Brachymyrmex depilis* (basivolsella fragmented) **M–O** Grouping: lateral carinae broken; digitus lobate; valvura perpendicular to the long axis of the valviceps.

curve around the penisvalva (Fig. 2E, F), as a result of disarticulating the volsella from the baimere the basivolsellae are prone to fragmentation this has been noted in the figure legends were it has occurred.
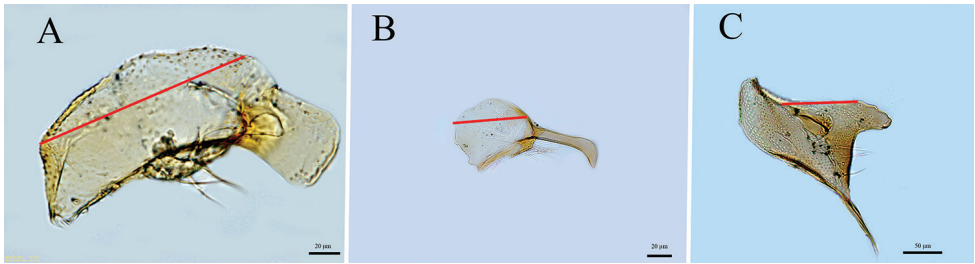
Figure 7. Ectal views of the volsella in *Brachymyrmex depilis* **A** *Brachymyrmex* CMW-011 **B** *Brachymyrmex patagonicus* **C** Red lines running from the dorsum of both the distal and apical ends of the volsella not including the digitus.

The modification to the lateral carina of the valviceps seen in both conformation groups seem to be related to the method in which the volsella rests against the valviceps *in situ*. As a result the dorsal surface of the volsella in conformation 1 is unbroken, while the dorsal surface of conformation 2 has a distinct concavity medially (Fig. 7)

Paramere

The telomeres are separated from the basimere by a membrane. Of the structures associated with the genital capsule, the telomeres of *Brachymyrmex* show the least variation in terms of overall shape and size. They are generally short and broad with numerous elongate flexuous setae. Of the taxa we examined, the telomeres of *B.* CMW-007, and *B.* CMW-009 (Fig. 6A, D) are as broad as long and hemispherical in shape; those of *B. cavernicola, B. heeri,* (Fig. 4G, J) *B.* CMW-006, *B.* CMW-003 *B.* CMW-008, *B.* CMW-010 (Fig. 5A, D, G, J), *B.* CMW-012 (Fig. 4D), *B.* JTL-004, *B.* JTL-005, and *B. depilis* (Fig. 6G, J, M) are slightly longer than broad and subtriangular; and those of *B. cordemoyi, B. obscurior* (Fig. 3A, D) and *B.* CMW-11 (Fig. 4A) are longer than broad, and finger like in shape. The basimere of *Brachymyrmex* are sub-triangular, and broad dorsally. The basimere are also difficult to separate from the volsella completely intact and often fragment.

Discussion

Our findings demonstrate that males of this genus may offer more taxonomic information for understating the evolution within the genus, and for species delineations than their worker counterparts. The morphology of the penisvalva lateral carina displayed in the two conformation groups seen in *Brachymyrmex* likely represent two distinct clades within the genus, and when compared on an intraspecific level there seems to be little variation in genital morphology. Of course additional sampling is needed to confirm this. In regard to the tribal position of *Brachymyrmex* in light of the conclu-

sive phylogeny of Blaimer et al. (2015) the characters that have previously been used to unite various genera with *Brachymyrmex*, namely that of the reduced antennomere count, and the reduction of the anterodorsal region of the valviceps must be considered homoplasious.

Within *Brachymyrmex* Ortiz and Fernández (2014) redescribed two dimorphic species of *Brachymyrmex*, *B. pilipes*, and *Brachymyrmex micromegas* Emery, in Santschi, 1923. While these ants do fall within the current definition of the genus, the authors raised questions as to the generic placement of these species. As noted previously their figure for the male of *B. pilipes* is inconclusive, however it does outwardly resemble the morphology seen in our conformation 2. Unfortunately the male of *B. micromegas* is unknown. We hope that our work here stimulates future studies on these dimorphic species to include dissected male genitalia, as these traits may help to accurately place dimorphic species.

Future researchers collecting *Brachymyrmex* are encouraged to exhaustively, and carefully hunt for males along with associated workers. Those running Malaise and UV light traps should also be alert for male specimens. To that regard *Brachymyrmex* holds a number of invasive ant species, *B. patagonicus* for example is a widespread and has reached pest status in the United States (MacGown et al. 2007). The males of this species can accumulate in UV light traps in the hundreds (Danny McDonald personal communication). Our results here should be useful in obtaining a definitive genus diagnosis, and in the United States our native species, *B. depilis*, belongs to conformation group 2 which is easily separated from the invasive *B. patagonicus*, and *B. obscurior* both of which belong to conformation group 1. Outside of the United States the uniqueness of *Brachymyrmex* genitalia should serve as a valuable tool for invasive species detection with the implementation of general collecting methods.

Acknowledgments

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Supplementary material 1

Specimen locality data
Authors: Christopher M. Wilson, Autumn Smith-Herron, Jerry L. Cook
Data type: Specimen locality data
Explanation note: Locality data for dissected specimens.

RESEARCH ARTICLE

Differential impact of two dominant *Formica* ant species (Hymenoptera, Formicidae) on subordinates in temperate Europe

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Abstract

Competition is one of the basic mechanisms shaping ant assemblages. Dominant territorial species are known to restrictively influence the traits of subordinates in various ways. However, there could be differences in the effects of dominants due to differences in their colony structure, lifestyle and also behaviour. We tested this hypothesis in natural circumstances in an area where a *Formica exsecta* Nyl. supercolony neighbours a strong population of the European slave-maker *F. sanguinea* Latr. For the purpose of our study three different sites were selected: one dominated by *F. exsecta*, a neighbouring site dominated by *F. sanguinea*, and a third site where both species co-occurred. We analyzed the structure of subordinate ant communities based on nest counts, and by recording the activity of ants at baits. Based on our findings the structure of ant communities differed significantly among the three sites. The *F. exsecta* site was characterized by the lowest nest density of subordinates, especially in the case of aggressive species as *Lasius platythorax* Seifert. At baits even the simple presence of the dominant limited the abundance and occurrence of subordinates. In contrast, no such negative effect could be revealed at the *F. sanguinea* site. The community of the mixed site showed intermediate features in many respects. Generally, the supercolonial

F. exsecta had a bigger influence on the ant community than the slave-making *F. sanguinea*. On the other hand, our findings revealed a slight protective role of the territorial *F. exsecta* for potential slave species to *F. sanguinea*. The current study underlines the importance of differences between dominant ant species in shaping differentially ant communities even within the same restricted area.

Keywords

Formica exsecta, *Formica sanguinea*, baits, community structure, competition, interspecific hierarchy, nest density, slavery, territoriality

Introduction

Most of the concepts regarding the assembly rules of animal communities point to competition as a crucial factor in shaping their composition and structure (MacArthur 1972, Wiens 1983, Farris et al. 2015, McFarlane Tranquilla et al. 2015, Sunarto et al. 2015). This is supported for ants as well by several case studies (e.g. Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989, Cerdá et al. 1998, Parr and Gibb 2010, Czechowski et al. 2013, Maák et al. 2014, Ślipiński et al. 2014, Dejean et al. 2015, Spotti et al. 2015) and the work reviewed quite recently by Cerdá et al. (2013). Specifically, ant communities in temperate zones are organized hierarchically and a crucial role in shaping them can be attributed to ecologically and behaviourally dominant species. Dominant species can restrictively structure local communities in various ways, from interference and exploitative competition to direct predation on lower-ranked species, both quantitatively (decreasing nest densities and colony sizes of subordinates) and qualitatively (reducing species richness by competitive exclusion and altering the dominance structure), but also with regards to the spatial patterns of the nests (e.g. by forced resource partitioning, nest moving, etc.) (Higashi and Yamauchi 1979, Cherix and Bourne 1980, Pisarski 1982, Pisarski and Vepsäläinen 1989, Savolainen and Vepsäläinen 1988, 1989, Savolainen et al. 1989, Savolainen 1990, 1991, Vepsäläinen and Savolainen 1990, Hölldobler and Wilson 1990, Punttila et al. 1991, 1996, Sanders and Gordon 2003, Czechowski and Markó 2005, Adler et al. 2007, Czechowski et al. 2013, Markó et al. 2013, Rzeszowski et al. 2013, Ślipiński et al. 2014).

Typically, at least in Euro-Asian boreal and temperate zones, the top dominants of ant communities are territorial species (sensu Pisarski 1982), i.e. those which actively protect the boundaries of their whole foraging areas against other territorials (Pisarski 1980, Vepsäläinen and Pisarski 1982, Pisarski and Vepsäläinen 1989). In temperate Europe, such territorial dominants, already well-known for their competitive impact on subordinate ants, are the wood ant species of the *Formica rufa* group (subgenus *Formica* s. str. L.) (Savolainen and Vepsäläinen 1988, 1989, Savolainen et al. 1989, Savolainen 1990, 1991, Punttila et al. 1991, 1996, Czechowski and Markó 2005), species of the subgenus *Coptoformica* Müll. (genus *Formica* L.) (Czechowski 1975, Pisarski 1982, Pisarski and Vepsäläinen 1989), the dendrophilic *Lasius* (*Dendrolasius*) *fuliginosus* (Latr.) (Czechowski et al. 2013, Markó et al. 2013, Ślipiński et al. 2014),

and *Liometopum microcephalum* (Panzer) (Petráková and Schlagamerský 2011). Colonies of territorial species (either allo- or conspecific) do not share the same territory, but non-territorial species can nest and forage within the dominant's territory, however with diverse limitations. Their colonies are the centres of the spatial organization in ant communities through their differential effects on subordinate species, which are 'allowed' only to nest at certain distances from the nest of the territorial species – the farther away are the nests of the subordinates, the stronger could be the competition between the two species (Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989). The impact of territorials on subordinates may further be enhanced by specific social strategies, such as the formation of new colonies through budding, which leads to the development of a network of related nests over a larger area (so-called supercolonies – see e.g. Helanterä et al. 2009, Robinson 2014 for reviews), a well-known strategy in many territorial wood ants (Higashi and Yamauchi 1979, Cherix and Bourne 1980, Rosengren et al. 1985), but also in members of the subgenus *Coptoformica* (Pisarski 1982, Czechowski 1975, 1977, Markó et al. 2012).

Within subordinates, two competition levels are distinguished: (a) encounter species, which are fairly aggressive and usually manage to monopolize (defend) single food sources, and (b) submissive species, which defend only their nests (Vepsäläinen and Pisarski 1982). Although they can manage to survive in the territory of dominants, subordinates are restrictively affected by territorials, and, in general, they fare better outside than within territories of dominant species (Savolainen 1990, 1991). On the other hand, in certain situations, nesting inside a dominant territory can even be good for certain species. Members of the subgenus *Serviformica* For. (genus *Formica*) are slave species for the facultative slave-maker *Formica* (*Raptiformica*) *sanguinea* Latr. Potential slave colonies may profit from the proximity of strong dominants since these can stop the raiding columns of *F. sanguinea* or force them to change their route when protecting their own territory. Such a positive effect of territorials has been reported for several species of wood ants of the *F. rufa* group (*F. rufa* L., *F. polyctena* Först., *F. aquilonia* Yarr., *F. lugubris* Zett.) for *F. fusca* L. and *F. lemani* Bondr., and known slave species *F. sanguinea* (Punttila et al. 1996, Czechowski 1999, 2000, Czechowski and Vepsäläinen 2001, Czechowski and Markó 2006, Väänänen et al. 2010). A similar mechanism may also work, at least to some extent, in the case of *Serviformica* species enslaved by the obligate slave-maker *Polyergus rufescens* (Latr.) (Czechowski 2006).

The differences among dominant species regarding their effect on subordinates may vary depending on their lifestyle (slave-maker vs non-slave-maker), colony structure (mono- vs polydomous), and on their foraging strategies (narrow vs wide food spectrum). The differential effect of dominants on subordinates are best revealed when dominant species occur syntopically (in the same habitat), consequently, the basic species pool that could make up the ant community is the same. Therefore, if the differences between the dominants are negligible, the differences between the ant communities occurring in their territories/areas should also be minor. In order to test this hypothesis, an appropriate natural set-up is needed, with the long-term co-occurrence of territorial allospecific neighbours (see e.g. Czechowski et al. 2013). Recent field

studies performed on the largest European polydomous system of the territorial *Formica exsecta* (Markó et al. 2012) yielded the discovery of a large population of the slave-maker *F. sanguinea*, also a dominant species, neighbouring the above-mentioned supercolony. This unique natural set-up of two dominant neighbours from the same genus, yet with a different colony structure (supercoloniality vs mono- or oligodomy) and lifestyle (non slave-maker vs slave-maker) offered the chance to perform a comparative study. In the framework of the current study, we proposed an analysis of the structure of ant communities in the area of these two dominants, and formulated the following questions: (1) are there any differences between the structure of ant communities of the two neighbouring dominant *Formica* species' territory/area, (2) are there any differential effects of these two dominants on the foraging strategies of subordinate species, (3) do the abundance and foraging strategy of members of the subgenus *Serviformica*, known as a slave species of *F. sanguinea*, differ within and outside the *F. sanguinea* area?

Materials and methods

Study species and sites

The main subjects of the study are two dominant ant species: *Formica* (*Coptoformica*) *exsecta* and *Formica* (*Raptiformica*) *sanguinea*.

Formica exsecta is a fairly common North-Palaearctic mound-building territorial species, a typical forest-ecotone polytope dwelling in forest margins and clearings, thinned young growth, overgrowing meadows and glades, etc. Its colonies number several thousand to tens of thousands of workers and occur in two, mono- and polygynous social forms. Polygynous colonies may grow through nest splitting into polydomous systems, often with more than 100 nests (so-called supercolonies). Additionally, colonies may be established through the temporary social parasitism of members of the subgenus *Serviformica*. The optimal home range of foraging workers from a single nest does not exceed a few meters. They are aggressive and predacious ants, which also feed on honeydew (Pisarski 1982, Seifert 2000, Hughes 2006, Erős et al. 2009, Csata et al. 2012).

Formica sanguinea is a common South-Palaearctic species, a polytope of warm and dry habitats, both forested and open areas; generally its ecological preferences widely overlap with those of the former species. It nests in decaying tree stumps, partly covered with dry plant material and also in the ground, often under stones. In general, colonies, usually functionally monogynous, number up to several tens of thousands of workers. It is a facultative socially parasitic species which enslaves workers of the subgenus *Serviformica*; the range of its slave raids may reach 100 m (usually < 50 m). They are very aggressive and predatory ants; during their raiding period they do not respect the boundaries of other species' territories (Czechowski 2000, Hughes 2006). The territoriality of *F. sanguinea* is a moot point (see the Discussion).

As habitat niches of *Formica exsecta* and *F. sanguinea* overlap each other to a considerable degree, colonies of these two species often co-occur.

Our study area was a vast semi-moist meadow of the *Molinion caeruleae* W. Koch alliance [with, among others, *Molinia caerulea* (L.) Moench, *Deschampsia caespitose* (L.) P. B., *Festuca pratensis* Huds., *Nardus stricta* L. and *Juncus* sp.], densely overgrown with small birch saplings, located in the southern part of the Giurgeului depression (46°36'N; 25°36'E; 780 m a.s.l.) in the eastern Carpathians, Transylvania, Romania. The meadow is fairly intensely grazed by cows for most of the year. This is the location of the largest known European polydomous system of *Formica exsecta*. The supercolony contains 3,347 permanent nests over an area of nearly 22 ha (i.e. the nest density is ca. 153/ha) (Markó et al. 2012). A population of *F. sanguinea* was recently detected, with a small number of *F. cunicularia* Latr. and *F. rufibarbis* F. slaves, within the same habitat near the area occupied by the supercolony.

Three sites were selected within the area for the purpose of our study (Fig. 1): (1) a site clearly dominated by *Formica sanguinea* right at the border of the *F. exsecta* polydomous system (referred to as the *F. sanguinea* site; 32 *F. sanguinea* nests on ca. 3210 m² with 0.01 nests/m², and four *F. exsecta* nests with 0.001 nests/m²), (2) a neighbouring patch within the *F. exsecta* territory with a single *F. sanguinea* nests (referred to as the *F. exsecta* site; 68 nests on ca. 5780 m² with 0.012 *F. exsecta* nests/m², and one *F. sanguinea* nest with 0.0002 nest/m²) and (3) a site with interspersed nests of both *F. sanguinea* and *F. exsecta* (referred to as the mixed site; eight *F. sanguinea* on ca. 2685 m² with and 0.003 nests/m², and 80 *F. exsecta* nests with 0.03 nests/m²). Within the whole study area, the meadow was homogeneous in respect of the vegetation, surface configuration and sun exposure.

The study area was not part of any nature protection area and no specific permits were required to carry out the field studies.

Sampling methods

Nest densities of different subordinate ant species were obtained using the biocoenometric method, by carefully investigating 15 quadrats of 9 m² at each of the three study sites. The quadrats were randomly selected by a blindfolded person in the field, they did not border each other, and they were at least 2 m from any *Formica exsecta* nest (Fig. 1). A sample of workers was collected for precise identification from each nest found. Identification of ant species was carried out with the key of Czechowski et al. (2012). Field work was carried out between 17 and 21 June 2010.

Baiting is commonly used to study the foraging pattern of ants around their nests and species' foraging strategies. It is also an appropriate method for determining the hierarchical positions of particular species within an assemblage (e.g. Czechowski 1979, 1985, Czechowski and Pisarski 1988, Parr and Gibb 2010, Petráková and Schlaghamerský 2011, Markó and Czechowski 2012). As the food preferences of ants may change seasonally, we provided a mixture of two different kinds of bait:
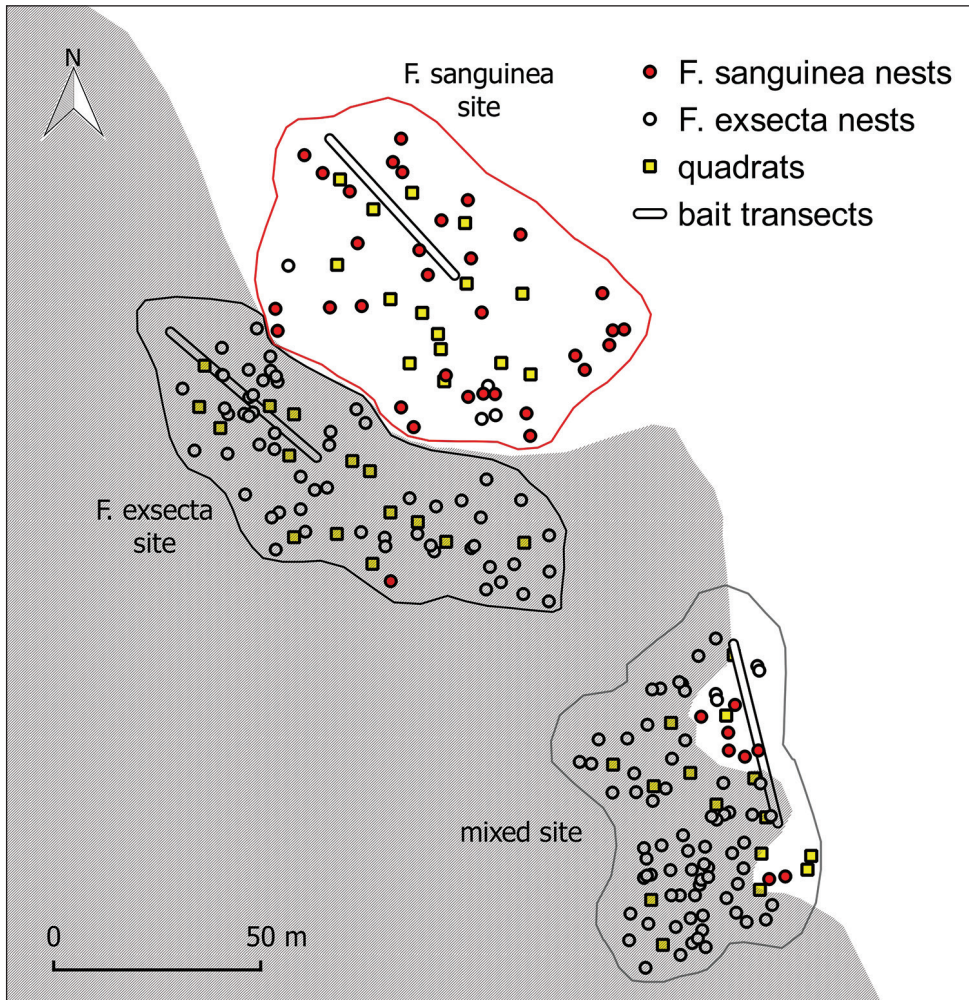
Figure 1. Map of the study area (*F. exsecta* nests outside the delineated sites are not marked out; grey area – compact area of the *F. exsecta* supercolony).

tuna fish flakes as a source of animal protein food and a water solution of mixed-flower honey as a source of carbohydrates. Altogether, 10 observation plots were distributed along linear transects at each of the three study sites (Fig. 1), and the baits were put out in the centre of each plot, separated from the next plot by 2 m, and placed at least 2 m from any *Formica exsecta* or *F. sanguinea* nest and any previously surveyed plot. The bait portions of ca. 3 cm diameter were placed in the centre of a round green plastic plate of 10 cm diameter. Baiting observations were carried out on 8 July 2010. Observations were carried out in two periods: between 10^{00} and 12^{00} AM, and between 5^{20} and 7^{20} PM. Each period consisted of six observations of

1 min, separated by 20 minute breaks. During each observation, the number and species of ants appearing at the baits were recorded, with the exception of *Myrmica* spp., where species level identification could not be performed under field conditions. The baits were put out 10 minutes before each period of observation (morning and afternoon) and left there until the end of the period when they were retrieved and the plates cleaned.

Data analyses

The differences in the abundance of different ant species among sites were revealed by the use of the Kruskal-Wallis test, followed by Tukey and Kramer post-hoc tests. The diversity of ant communities was calculated with the Shannon-Wiener entropy index ($\log_2$), using data for individual quadrats and baits respectively for nest count and bait data, while differences among sites for these parameters were revealed by using the Kruskal-Wallis test, followed by the Tukey and Kramer post-hoc tests separately for nest count and bait data. In order to determine the differences among the ant assemblages of the three sites, permutational multivariate ANOVA (perMANOVA, 10000 permutations) was applied both for nest count and bait data, while Nonmetric Multidimensional Scaling (NMDS) was used to visualize the three assemblages, both in the case of nest and bait data. The SIMPER test was performed to determine the contribution of each species to dissimilarities between ant communities.

The Generalized Linear Mixed Model approach (GLMM, binomial, maximum likelihood) was applied to analyze the effect of dominant species on the presence and absence of subordinate species at baits. The abundance of *Formica sanguinea* and *F. exsecta* workers present at baits were introduced as variables, along with their presence vs absence data as factors, next to the type of the site (*F. sanguinea*, *F. exsecta*, mixed) as a factor. The period and time of the observation as well as bait ID were introduced as nested random factors. A similar approach (GLMM, Poisson error, maximum likelihood) was applied to separately test the effect of dominants on the abundance of subordinates. The number of all subordinates was pooled together, since they showed a low abundance separately (see the Results). The same model structure was used as above.

All statistical analyses were carried out using the R 3.1.2 statistical package (R Core Team 2015). Multiple pairwise comparisons in the case of the Kruskal-Wallis tests concerning diversity indices were performed using the Tukey and Kramer post-hoc test after Nemenyi with the *PMCMR* R-package (Pohlert 2015). Permutational multivariate ANOVA, NMDS and the SIMPER test were carried out with the *vegan* R-package (Oksanen et al. 2013). GLMMs were performed using the *glmer* function in the *lme4* R-package (Bates et al. 2014). Post-hoc Tukey-tests for sequential comparison among factor levels when performing GLMM were carried out with the *glht* function in the *multcomp* R-package (Hothorn et al. 2015).

Results

Species composition and abundance

During the quadrat survey, 171 nests were found belonging to 11 subordinate ant species in addition to the two dominant species (i.e. *Formica sanguinea* and *F. exsecta*) (Table 1). Five subordinate species occurred at every site studied [*Tetramorium* cf. *caespitum* (L.), *Myrmica scabrinodis* Nyl., *M. vandeli* Bondr., *M. schencki* Viereck, and *Lasius flavus* (F.)]. Total nest density of co-occurring ant species was 1.8 times higher at the *F. sanguinea* than at the *F. exsecta* site, whereas it was intermediate at the mixed site (Table 1). The most abundant subordinate species was the subterranean *L. flavus* followed by *M. scabrinodis* on every study site (Table 1).

Only three aggressive encounter species were found: *Lasius platythorax*, *Tetramorium* cf. *caespitum* and *Formica rufibarbis*, and none of them were present in high densities at the site (territory) of *F. exsecta*. The three sites differed mainly in the nest density of two encounter species: *L. platythorax* and *T.* cf. *caespitum* (Table 1). Nest density of the former was relatively high at the *F. sanguinea* site, whereas the latter had a higher density at the mixed site. Nest density of all submissive species [*Myrmica* spp., *Leptothorax acervorum* (F.) and *Serviformica* spp.] taken together was the highest at the *F. sanguinea* site, owing mainly to the trends noticeable in *Myrmica* species (Table 1).

The ant community of the *Formica sanguinea* site was significantly more diverse than the *F. exsecta* site, while the mixed site had an intermediate position (Kruskal-Wallis χ^2 = 7.83, *p* = 0.02; Fig. 2). The structure of the ant assemblages also differed significantly among the three studied sites (perMANOVA $F_{1,40}$ = 3.51, *p* = 0.006), mostly with regards to the ant community of the *F. sanguinea* site, while seemingly the communities of the other two sites were quite similar (Fig. 3). According to the results of the SIMPER analysis, most of the dissimilarities (ca. 70%) among the three sites could be contributed mostly to three common species: *Lasius flavus*, *Myrmica scabrinodis* and *L. platythorax*, except for the *F. exsecta* vs mixed site, where *T.* cf. *caespitum* took the place of *L. platythorax* in this respect (Table 2).

Foraging strategies and competitive effects

Besides *Formica sanguinea* and *F. exsecta*, foragers of other species were also present at the baits (Table 3). The highest abundance of ants at baits was observed at the *F. exsecta* site, exclusively due to the efficient recruitment of *F. exsecta* workers to the food sources (Table 3). As expected, *F. sanguinea* was present at baits in its site, though in a surprisingly low number, whereas it was totally absent from the *F. exsecta* site; in turn, *F. exsecta* was absent in the *F. sanguinea* site. Both species exploited baits, though, at the mixed site (Table 3).

Different trends were detected in the abundance of two aggressive (encounter) species: *Lasius platythorax* and *Tetramorium* cf. *caespitum*. The former occurred in similar

Table 1. Nest densities (mean number per 9 m² ± SD) of subordinate ant species and their proportions (%) in the three study sites.

Species	F. sanguinea site mean ± SD %	F. exsecta site mean ± SD %	Mixed site mean ± SD %
Tetramorium cf. *caespitum* (L.)	0.33 ± 0.49 6.4	0.2 ± 0.56 7	0.67 ± 1.05 20
Leptothorax acervorum (F.)	–	0.07 ± 0.26 2.3	–
Myrmica scabrinodis Nyl.	1.13 ± 1.13 21.8	0.53 ± 0.92 18.6	0.73 ± 1.1 22
Myrmica vandeli Bondr.	0.47 ± 0.99 9.0	0.47 ± 0.74 16.3	0.13 ± 0.35 4.0
Myrmica schencki Viereck	0.27 ± 0.8 5.1	0.07 ± 0.26 2.3	0.13 ± 0.35 4
Myrmica lobicornis Nyl.	–	0.13 ± 0.35 4.7	0.07 ± 0.26 2
Myrmica ruginodis Nyl.	0.07 ± 0.26 1.3	–	–
Lasius flavus (F.)	2.00 ± 1.81 38.5	1.33 ± 1.54 46.5	1.40 ± 0.99 42
Lasius platythorax Seifert	0.87 ± 0.74 16.7	0.07 ± 0.26 2.3	–
Formica cunicularia Latr.	0.07 ± 0.26 1.3	–	0.13 ± 0.35 4
Formica rufibarbis F.	–	–	0.07 ± 0.26 2
All subordinate species	5.21	2.87	3.33
All epigean subordinate species	3.21	1.54	1.93

Table 2. Results of the SIMPER analysis: the overall dissimilarity between study sites, the average contribution of subordinated ant species to overall dissimilarity (Dissimilarity contribution), their mean abundances in the compared sites (Mean 1 and Mean 2), and the cumulative percentages of contributions.

| Sites (dissimilarity)	Species	Dissimilarity contribution (%)	Mean 1	Mean 2	Cumulative contribution (%)
F. sanguinea vs. F. exsecta (70.13)	*L. flavus*	20.95	2	1.54	29.88
	M. scabrinodis	13.49	1.13	0.62	49.13
	L. platythorax	12.27	0.87	0.08	66.63
	M. vandeli	9.44	0.47	0.54	80.11
	T. cf. *caespitum*	6.13	0.33	0.23	88.85
F. sanguinea vs. Mixed (67.83)	*L. flavus*	18.83	2	1.5	27.76
	M. scabrinodis	13.11	1.13	0.78	47.1
	L. platythorax	12.21	0.87	0	65.11
	T. cf. *caespitum*	9.33	0.33	0.71	78.88
	M. vandeli	6.18	0.47	0.14	88
F. exsecta vs. Mixed (65.81)	*L. flavus*	20.35	1.54	1.5	30.92
	M. scabrinodis	14.38	0.62	0.79	52.79
	T. cf. *caespitum*	11.16	0.23	0.71	69.75
	M. vandeli	8.48	0.54	0.14	82.64
	M. schencki	3.46	0.08	0.14	87.91
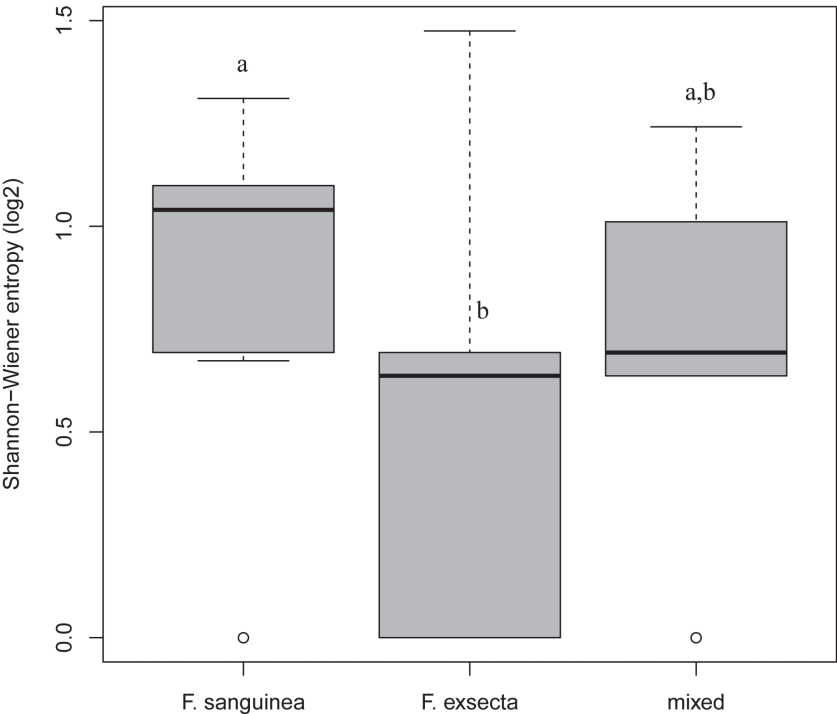
Figure 2. Diversity of the ant communities within the study sites based on nest surveys (medians, quartiles, min–max values and outliers). Survey performed on 9 m² quadrats (N = 15 in each site). Different letters indicate significant differences among groups.

Table 3. Mean number of ant individuals per baits (± SD) for each study site and their relative proportions (%) to other ant species at the same site.

Species	*F. sanguinea* site mean ± SD %	*F. exsecta* site mean ± SD %	Mixed site mean ± SD %
Tetramorium cf. *caespitum*	31.6 ± 96.78 36.5	–	10.6 ± 21.49 32.0
Myrmica spp.	2.1 ± 3.96 2.4	0.2 ± 0.42 0.1	4.0 ± 3.83 12.1
Lasius platythorax	52.2 ± 83.48 60.3	52.2 ± 120.86 29.6	–
Formica cunicularia	0.6 ± 1.9 0.7	3.4 ± 4.03 1.9	1.8 ± 3.16 5.4
Formica sanguinea	0.1 ± 0.32 0.1	–	1.9 ± 2.56 5.7
Formica exsecta	–	120.4 ± 100.65 68.3	14.8 ± 35.67 44.7
All subordinate species	86.5 ± 111.43 99.9	55.8 ± 121.5 31.6	16.5 ± 22.75 49.7
All species	86.6 ± 111.35 100	176.6 ± 102.94 100	33.2 ± 36.19 100
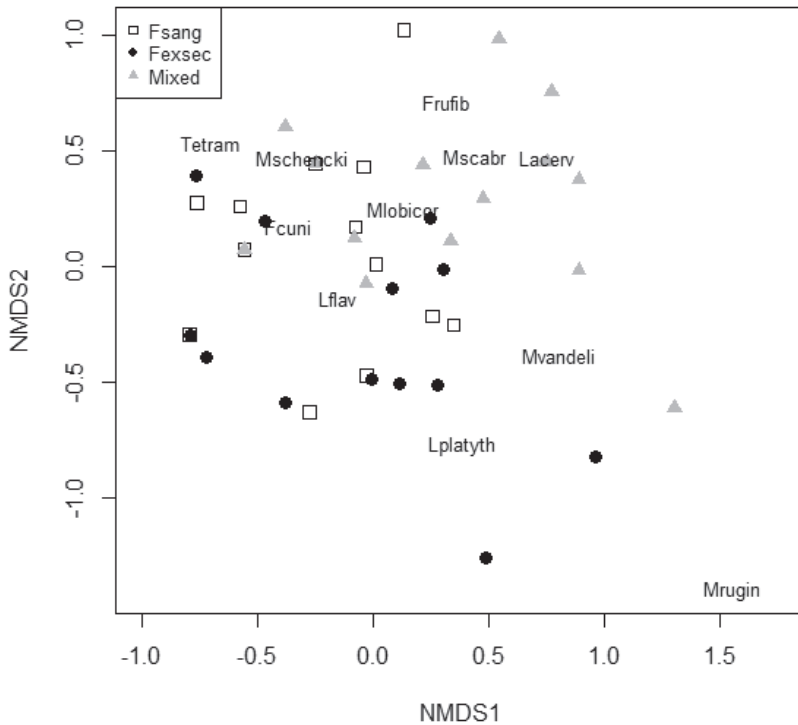
Figure 3. NMDS graph of the ant communities within the study sites based on nest survey (stress = 0.172).

numbers at baits in the *Formica exsecta* and *F. sanguinea* sites, whereas it was absent from the mixed site (Table 3). In turn, *Tetramorium* cf. *caespitum* was absent from the *F. exsecta* site, while it was the second most abundant ant in the two other sites (Table 3). The abundance of potential *F. sanguinea* slave species, such as *F. cunicularia*, gradually increased from the *F. sanguinea* site to the mixed one and then to the *F. exsecta* site (Table 3).

The highest diversity was found at baits in the mixed site (Kruskal-Wallis χ^2 = 9.11, p = 0.011) followed by the significantly lower diversities of *Formica sanguinea* and *F. exsecta* sites, which did not differ significantly from each other based on the post-hoc test result (Fig. 4). There were no differences between the three sites in the qualitative-quantitative composition of foraging ants (perMANOVA $F_{1,29}$ = 1.83, p = 0.12), however, baits in the *F. exsecta* territory seemed to stand apart from all other sites due to the marked presence of *F. exsecta*, while the presence of subordinate species was more characteristic for the *F. sanguinea* and the mixed sites (Fig. 5).

According to the results of the GLMM analysis, *Formica exsecta*'s abundance (z = −3.09, p = 0.002) and presence (z = −2.32, p = 0.02) had a significant negative effect on the occurrence of subordinates at baits, while the abundance of *F. sanguinea* did not play a major role (z = −1.72, p = 0.08), but its presence did have a positive influence on the occurrence of subordinates (z = 2.13, p = 0.033). There were no differences
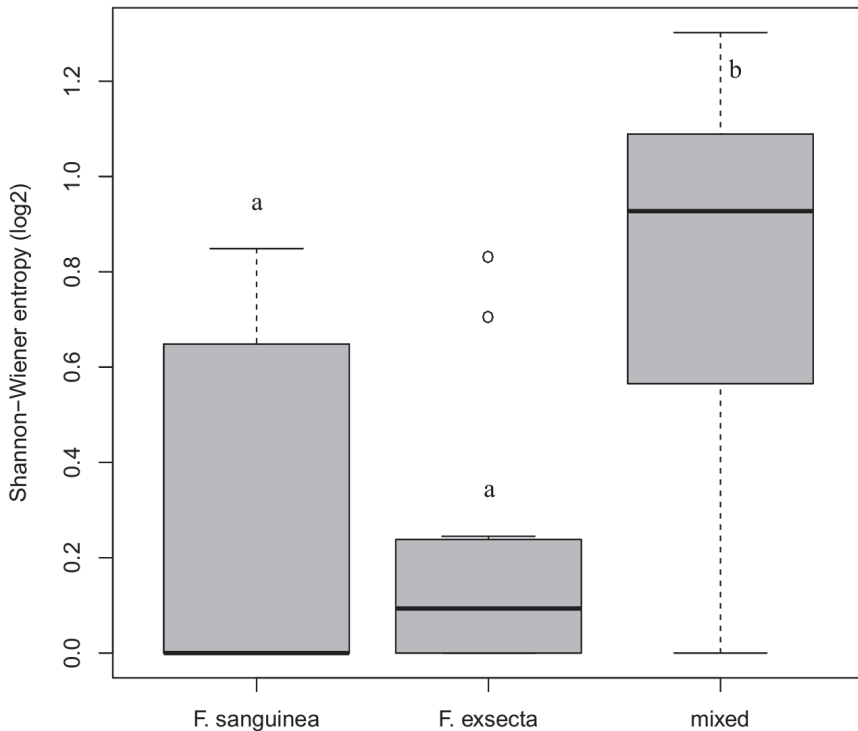
Figure 4. Diversity of the ant communities within the study sites based on bait observations (medians, quartiles, min–max values and outliers). Different letters indicate significant differences among groups.

between the *F. sanguinea* and the *F. exsecta* sites with regards to the frequency of the occurrence of subordinates ($z = 1.99$, $p = 0.11$). Also, no difference was found between the *F. sanguinea* and the mixed site in this respect ($z = -1.8$, $p = 0.16$), but subordinates were significantly less frequent at baits in the mixed site compared to the *F. exsecta* site ($z = -3.18$, $p = 0.004$).

Generally, a similar pattern with smaller adjustments was found when analyzing the effect of dominants on the abundance of subordinates at baits. In addition to the abundance of *Formica exsecta* ($z = -8.33$, $p < 0.0001$), even its simple presence ($z = -2.01$, $p = 0.044$) had a significant negative effect on the abundance of subordinates. On the other hand, *F. sanguinea*'s abundance ($z = 0.04$, $p = 0.96$) and presence ($z = 0.96$, $p = 0.33$) had no significant effect. The abundance of subordinates also showed significant differences among the three study sites ($z \geq 9.92$, $p < 0.0001$).

Discussion

The main factors which shape biodiversity and structure of animal communities are, besides habitat heterogeneity (see e.g. MacArthur and MacArthur 1961, Hölldobler
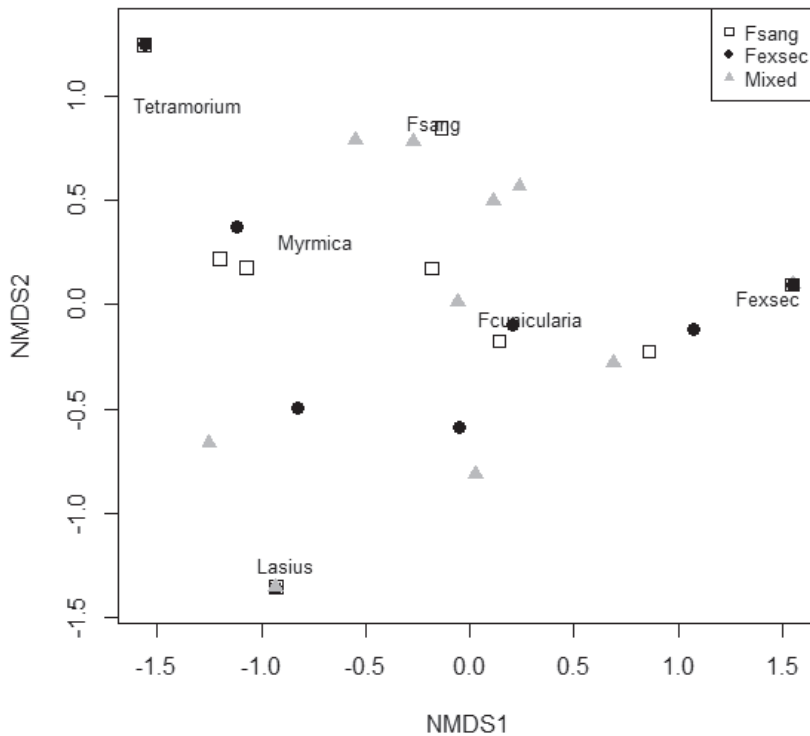
Figure 5. NMDS graph of the ant communities within the study sites based on bait observations (stress = 0.114).

and Wilson 1990, Tews et al. 2004, Ossola et al. 2015), intra- and interspecific relationships, such as competition and social parasitism. The importance of the latter is well known in ants (Savolainen and Vepsäläinen 1988, Hölldobler and Wilson 1990, Andersen 1992, Ryti and Case 1992, Cerdá et al. 1997, Czechowski and Markó 2006, Scharf et al. 2011, Ślipiński et al. 2011, 2014). Colonies of dominant species, especially territorial ones, play a crucial role, as organizing centres of the ant community, by limiting the establishment of colonies of subordinate species within dominant territories or by managing their accessibility to various resources (Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989, Andersen 1992, Bestelmeyer 2000, Lester et al. 2010, Cerdá et al. 2012, 2013, Czechowski et al. 2013). In our study, we revealed considerable differences among ant communities living in areas within the same habitat, but dominated by two dominant species with clearly different features.

The species composition of the studied ant communities was quite similar among all three sites, but differences were found in the abundance of different ant species, and also in the diversity of ant communities. In almost all respects the *Formica sanguinea site* was superior housing the most diverse ant community. Thus, despite the low chance of interaction with *Lasius flavus* due to its subterranean lifestyle, the lowest density of *L. flavus* nests was recorded in the *Formica exsecta* territory, which could be

the result of the establishment of *F. exsecta* colonies on the top of their soil mounds, with the gradual extermination of *L. flavus* colonies (Pisarski 1982). This species was followed by *Myrmica* spp. with a low level of aggression compared to *L. platythorax* and *Tetramorium* cf. *caespitum*, while the lowest abundance was recorded for members of the subgenus *Serviformica*, being both a slave species to *F. sanguinea* and the host of temporary social parasitism caused by *F. exsecta* fundatrices (Czechowski et al. 2012). Generally speaking, there was an increase in the abundance of aggressive and submissive species in the mixed territory where *F. exsecta* and the slave maker species showed lower abundance or were absent.

Usually, the exploitation patterns of food resources at the *Formica exsecta* site was in agreement with the general rules concerning hierarchy patterns, where the dominant species, especially a territorial one, monopolizes the area and its resources (Savolainen and Vepsäläinen 1988, Savolainen et al. 1989). In the *F. exsecta* site the absence of *T.* cf. *caespitum* at baits, known as an aggressive species (e.g. Brian et al. 1966, 1979) with a quick reaction towards intruders (Dobrzański and Dobrzańska 1975) and with the ability to exploit habitat resources effectively (Brian et al. 1966), might have been caused by its general avoidance of the dominant species during foraging (see Cerdá et al. 2012). On the other hand, contrary to *Formica exsecta*, as other authors have already shown before (e.g. Czechowski 1999, 2000, Czechowski and Markó 2006, Ślipiński et al. 2011), *F. sanguinea* behaved as a considerably weaker competitor, exploiting the baits much less actively than e.g. *Lasius platythorax* and *Tetramorium* cf. *caespitum*, which succeeded in exploiting the baits within its area quite heavily. The strongest difference in the exploitation pattern of baits is shown by the results obtained from the mixed territory, where the presence of almost all species at baits increased, with the exception of *Formica exsecta*, which exhibited the highest frequency and abundance in its own exclusive territory.

The low number of *Formica sanguinea* foragers at baits, especially in relation to the numbers of workers of other ant species, requires additional explanations. Recent studies on the foraging strategy of *F. sanguinea* have already shown, that this species seems to be less competitive towards subordinates to the south (e.g. Romania) than in the northern parts of the species range in Europe (e.g. Finland) (P. Ślipiński et al., in prep). One of the major signs of its weaker competitiveness is its reduced presence at artificial baits, as also confirmed by our present observations. However, it is possible that at least some of the *F. cunicularia* workers present at baits were individuals enslaved by *F. sanguinea*, and these *de facto* acted as foragers of the latter. Since, generally, slaves fulfill intranest tasks in colonies (Kharkiv 1979a,b, see also Czechowski 1996), the abundance of slaves foraging at baits could anyhow be quite low.

Territorial ants can hold off raiding columns of *Formica sanguinea* to some extent, and in this way directly protect possible slave species against their enslaver. This protective effect would manifest itself when there was a significantly greater abundance of slave species within, rather than outside of wood ant territories of the *F. rufa* group (Punttila et al. 1996, Czechowski 2000, Czechowski and Vepsäläinen 2001, Czechowski and Markó 2006, Väänänen et al. 2010). However, this is not generally valid for all territorials, since, e.g., no measurable protective effect of the territorial *Lasius fuliginosus*

towards the *F. fusca* slave species was detected by Ślipiński et al (2014), despite cases of direct interference of the latter during *F. sanguinea* raids (Czechowski 1999, 2000). In our study area, two potential slave ant species (and, at the same time, potential hosts of the temporary social parasitism of *F. exsecta*) occurred, both members of the subgenus *Serviformica*: *F. cunicularia* and *F. rufibarbis*. The former is a typical submissive species, the latter is an aggressive encounter species. Due to this, the relations of each of them with both local dominant species, i.e. *F. exsecta* and *F. sanguinea*, might proceed differently. On one hand, the submissive, weakly competitive *F. cunicularia* should be less restrictively treated by the territorial *F. exsecta* than the more competitive *F. rufibarbis*. On the other hand, colonies of the aggressive *F. rufibarbis* (see Mori et al. 2001) should be much less prone to being destroyed by *F. sanguinea*, and they should also be more resistant to being taken over by young *F. exsecta* queens than colonies of the submissive *F. cunicularia.* So, one could expect that these differences in behaviour might be reflected in differences in the distribution of the two subordinate species. However, both species were very scarce in the study area. In total, only three nests of *F. cunicularia* and one nest of *F. rufibarbis* were found. At the baits, only *F. cunicularia* foragers occurred, most abundantly within the *F. exsecta* site. At the remaining sites (both with *F. sanguinea*), they were generally scarce, and what is more, at least some of them may have been *F. sanguinea* slaves. This result may suggest some type of protective effect of the territorial *F. exsecta* on this slave species against the slave-maker.

While the decisive effect of *Formica exsecta* as a typically territorial species on the structure of ant communities is quite evident, this question still remains open regarding *F. sanguinea*. In the literature, the latter is commonly handled in a similar manner as the territorial *Formica* s. str. and *Coptoformica* species (Vepsäläinen and Pisarski 1982, Savolainen et al. 1989, Punttila et al. 1996, Czechowski 2000, Czechowski and Markó 2006, Väänänen et al. 2010). However, our findings seem to contradict the similarly strong territorial (*sensu* Pisarski 1982) nature of *F. sanguinea*. The fact that some *F. sanguinea* nests can occur in the vicinity of *F. exsecta* nests (see the mixed site) also emphasizes the reduced territoriality of *F. exsecta*. Other field observations point in this direction as well. For example, in the Białowieża Forest (N-E Poland), a very strong *F. sanguinea* colony was observed to peacefully coexist with a fairly large *F. exsecta* colony over several years, nesting just ca. 3 m from an edge of the mound of the latter (W. Czechowski, unpubl.). Also, the above mentioned recent case study on the competitive strategy of *F. sanguinea* (P. Ślipiński et al., in prep.) strongly suggests the non-territoriality of this aggressive and undoubtedly influential species.

The results of this study underscore the importance of differences between dominant ant species in differentially shaping ant communities, even within the same limited area.

Acknowledgements

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RESEARCH ARTICLE

Foraging behavior and Preferences for Alternative Supplementary Feeds by the African Weaver Ant, *Oecophylla longinoda* Latreille (Hymenoptera, Formicidae)

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Abstract

Weaver ants, *Oecophylla* spp, are effective predators that control a wide range of insect pests in multiple crops when maintained at high population. Supplementary feeding, particularly during reduced food availability is one of the management practices that maintain and boost weaver ants' populations. Experiments were conducted between September and October 2013, January and February, 2014 to determine the type of food preferred by weaver ants, *O. longinoda*. Twenty colonies of *O. longinoda* were provided with four types of food to determine their feeding preferences. These include anchovy, chicken intestine, fish intestines and earthworms. We examined food preferred by ants based on weight of the food removed and activity of the ants on foods. Furthermore, we examined foraging behavior of ant workers on anchovy food (fresh-ground and dry-ground) in nine *O. longinoda* colonies. Thereafter, small and large particles of dried-ground anchovy were tested. The results showed that *O. longinoda* preferred anchovy to other foods provided. However, the results of Analytical Hierarchy Process showed that earthworm and fish intestine were the most accessible food types by farmers, as determined by availability, affordability and applicability. We observed more ants on fresh-ground as opposed to dry anchovy; similarly, large particles were more easily removed than was the case with small particles. Thus, during reduced food availability, farmers in the study area should use earthworms and fish intestines feeds to supplement *O. longinoda* colonies. Fresh moist anchovy or dry anchovy of large particle sizes can be used where available.

Introduction

Two species of weaver ants, *Oecophylla longinoda* Latreille and *Oecophylla smaragdina* Fabricius are generalist predators that protect crops against insect pests (Way and Khoo 1991; Peng and Christian 2007; Van Mele 2008; Materu et al. 2014). The use of *Oecophylla* as a biocontrol can lead to increased fruit yield and quality (Barzman et al. 1996; Peng and Christian 2005; Olotu et al. 2013a). The ants prey directly on insect pests and obtain energy from honeydew produced by homopterans or from plant nectaries (Way and Khoo 1992). Crop protection is therefore more successful when there is a high and stable population of weaver ants. For instance, Stathers (1995) revealed that cashew trees colonized by high number of *O. longinoda* (>500 foraging *O. longinoda* workers) recorded lower damage by coreid bugs (*Helopeltis anacardii* Miller and *Pseudotheraptus wayi* Brown) than those with few *O. longinoda* (1-20). Adequate palm protection is realized when two or more nests of *O. longinoda* are found in the palm crown (Way 1953) or when 60–70% of the palms are colonized by *O. longinoda* (Way and Khoo 1992). As Sporleder and Rapp (1998) reported, the population of *P. wayi* sinks to zero after a long and stable occupation of palm trees by *O. longinoda*.

In addition to biocontrol, *Oecophylla* is used as a valuable source of food for humans (Sribandit et al. 2008), contributing directly to food security (Offenberg and Wiwatwitaya 2010) and also serve as a feed for song birds in Indonesia (Césard 2004). Populations of weaver ants in crop fields are, however, not stable, as they can commonly drop to very low levels in the field, resulting in inadequate crop protection. This can be caused by many factors one of which is movement of colonies to non-agricultural fields. Different management practices are being developed in order to maintain, boost, and expand the existing colonies to optimum levels. These management practices include artificial nests, (Offenburg 2014), the use of pesticides that are less harmful to the ants, protection of ants from competitors like black ant *Dolichoderus thoracicus* (Smith), facilitation of colony expansion by using strings and poles to connect trees (Van Mele and Cuc 2000; 2007) and maintenance of ground vegetation to control *Pheidole* spp (Way and Khoo 1992; Seguni et al. 2011). Furthermore, technologies for rearing weaver ants in nurseries are being developed (Peeters and Andersen 1989; Ouagoussounon et al. 2013)

Social insect populations are negatively affected when food is scarce (Dusstour and Sympson 2012). Weaver ant colonies may even move among trees in search of forage (Van Mele and Cuc 2007). The goal of biocontrol is to have large and stable colonies thus food supplementation may help to boost population size.

The feeding preferences of *Oecophylla longinoda* are not well known. In Vietnam, farmers provide fish and chicken intestines to *O. smaragdina* as supplementary foods during scarcity (Van Mele and Cuc 2000). Food supplementation (Van Mele and Cuc 2000; Lim 2007) or feeding (Offenburg and Wiwatwitaya 2010) of weaver ants

is reported to increase weaver ant populations. Furthermore, population increase of *O. longinoda* was reported in fed colonies (Abdula et al. 2015). However, weaver ants consume food in order of preference. *O. smaragdina* prefer mealworm to fish, honey or weaver ant formula (Lim 2007).

The practice of food supplementation for *O. longinoda* is limited by inadequate knowledge on food preference (based on cheap local available feeds), forms or states as well as particle sizes. Therefore, the objective of this study was to determine the type of food preferred by weaver ants in terms of form and size. A good understanding of food preferences by weaver ants and their foraging behavior is essential for effective management of *O. longinoda* during food scarcity.

Materials and methods

We conducted experiments at Naliendele Agricultural Research Institute (NARI), Mtwara Region, in Southern Tanzania (40°09'57.05"E, 10°21'22.49"S, 140 m asl). The region has a unimodal rainfall pattern, starting from November/December to April/May, with a single peak in January. The annual rainfall ranges from 810 to 1090 mm, whereas mean temperature ranges from 23°C in July to 27°C in December. Relative humidity ranges from 79% in October to 87% in March.

The study was approved by the Directorate of Research and Postgraduate Studies (DRPG) of SUA, a body responsible for monitoring and evaluating compliance to ethical conduct of staff and students undertaking research. The research complied with Code of Conduct for Research Ethics of Sokoine University of Agriculture (SUA) available at www.drpgs.suanet.ac.tz. Food preferences were tested for 10 days in orchards colonized by weaver ants. The tests were conducted for two seasons, between September and October 2013 (dry season), and between January and February 2014 (rainy season). Two orchards one of cashew, *Anacardium occidentale* L. and another of orange, *Citrus sinensis* L were selected.

In each orchard we selected trees with at least 40% of branches occupied by ants (as assessed by as per Peng et al. (2008). Each tree had between 5 and 25 nests. Each colony was provided with four types of foods; (i) earthworm (ii) chicken intestine (iii) fish intestine and (iv) anchovy.

Intestines and anchovy were ground by locally made mortar and pestle. Earthworms were dug out of wet soils (close to water ponds and irrigated fields) and chopped into small pieces (approximately 0.5–1 cm in length) by a kitchen knife. About 6 g of each food type were placed in a 0.01×0.1 m bowl, set on a feeding platform. Ants could access the bowls by crawling through a guiding stick. Feed bowls were placed equidistant from the middle of the feeding platform. Feeds and water were provided *ad libitum* throughout the experimental period. All the food types were tested in 10 colonies in each orchard. Preferences were determined by i) counting all foraging workers observed on food station and inserting their mouths into a food type and ii) weighing the amount of each food removed by the ants. Counting started 60 minutes after more

than one forager had discovered each food type. Thereafter, the weight of the remaining food in each bowl was determined. The amount of food type removed by the ants was determined by establishing the difference in weight between the food supplied and the food which remained in the bowl. In each case, the weight loss due to evaporation was deducted. Weight loss due to evaporation was determined in the control food types that were inaccessible by ants.

A sample of each food type was analyzed for nutrient compositions at the University of Dar es Salaam. The total carbohydrate, crude protein, total lipids (Fat) and vitamin A were determined according to the procedures described by Allen (1989). The total flavonoids were determined based on the procedures described by Bonvehi et al. (2001); the moisture content was determined gravimetrically after oven has dried at 105°C for 24 hours.

Furthermore, we used anchovy food to test for food forms and particle sizes that can be preferred by *Oecophylla longinoda*. Anchovy was used because it is processed in a standard form. We hypothesized that anchovy type (dry and fresh) affected the foraging behavior of workers. We also hypothesized that the particle size of dry anchovy affects the foraging behavior of workers. The experiments were conducted between May and July 2014. The first experiment involved two different forms of anchovy, dried and fresh. This experiment was conducted for 10 days, with the observation starting around 0900 am each day. The anchovy was sun dried (27–29 °C) for 7 days before grinding. We used fresh-ground anchovy of approximately similar size as the dried one. A Y- shaped feeding arena made up of wood was used as a feeding platform. A feeding bowl was placed on top of a board tied at each end of the Y shaped arena. This gave an equal chance for the workers to access each of the anchovy food types. Nine colonies were used. Each colony occupied at least two citrus trees. One bowl of each anchovy food was supplied per colony. The foraging behavior was assessed by counting workers carrying food particles from the source. The counting was done ten times at an interval of one minute (ten observations) every day per each colony for 10 days consecutively. In the end, we calculated the average number of foraging workers per minute per colony for a given food form.

The second experiment involved dried-ground anchovy of different particle sizes. The particles were measured by using laboratory test sieves (Wagtech International Ltd UK). Two particles sizes were selected; particles ranging from 0.5 to 1 mm in diameter (referred hereinafter as small particles) and; particles of 2 mm d (referred hereinafter as large particles). The experiment was conducted on six weaver ant colonies for 10 days using similar procedures for testing food types (above).

Thereafter, Analytic Hierarchy Process (AHP) (Saaty 1980) was used to determine the food type that would be accessed by the farmers. The set of evaluation criteria consisted of affordability, availability and applicability. The set of alternative options among which the decision was made consisted of four food types. The weights for each evaluation criterion were generated. The score for each criterion was assigned according to the pair wise comparisons of the options (on a scale of 1 – 9). Finally, the criteria weights and the options scores were used to compute the global score for a given option, as a weighted sum of the scores obtained with respect to all the criteria.

Data analysis

The analyses were performed using JMP 10.00 software. A non parametric one way ANOVA was used followed by Multiple Comparison-Wilcoxon Each Pair for counting forage workers and the amount of food removed under food preferences. Mann-Whitney tests were performed to compare the number of forage workers on dried and fresh anchovy; similar comparisons were done for small and large particle sizes.

Results

Nutrients composition of the feeds fed to the ants are presented in Table 1. Crude protein ranged from 47.7% (from fish intestine) to 31.2% (chicken intestine). All tested feeds, except earthworms contained flavonoids. The highest amount of flavonoids was 0.013 mg/g.

The numbers of workers foraging on food types were significantly (p=0.05) different in both citrus and cashew orchards, during both dry and rainy seasons (Tables 2, 3). Significantly, (p=0.05) more workers foraged on anchovy than they did on other food types. However, in citrus during dry season, the numbers of workers foraging on anchovy and chicken intestine were not significantly (p=0.05) different. The preference was the highest for anchovy and fish intestine and the least for earthworm and chicken intestine across both seasons and orchards except in citrus during the dry season (Figure 1a, 1b). The quantities of food types taken by ant workers were significantly (p=0.05) different in citrus but not in cashew orchard during the dry season (Tables 2, 3). In contrast, the quantities of food taken by ant workers in both orchards were statistically different (p=0.05) during the rainy season. Workers took significantly (p=0.05) more anchovy than they did to other food types. In all situations, the preference was the lowest for chicken and fish intestine (Fig. 2a, b). The results show further that more workers foraged on fresh-ground than they did on dried-ground anchovy (Fig. 3a). Similarly, more workers foraged on large particles than they did on small particles of ground-dried anchovy (Fig. 3b). The results of the AHP show that of the three criteria, earthworm ranked the highest followed by fish and chicken intestine.

Table 1. Nutrients composition of the feeds fed to ants.

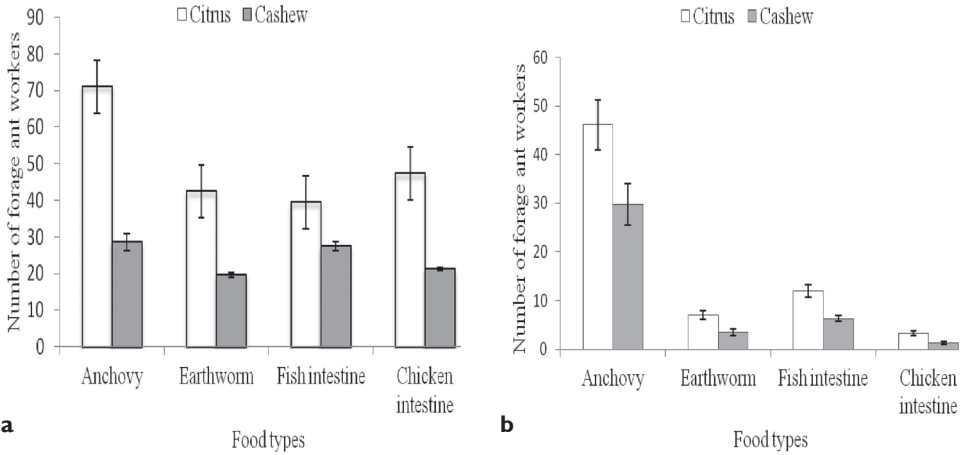| Parameters	Food type Anchovy	Fish intestine	Chicken intestine	Earthworm
Crude Protein (%)	44.6	47.68	31.2	45.6
Total carbohydrate (g/100g)	0.2	3.1	6.21	0.01
Fat content(g/g)	0.059	0.078	0.087	0.005
Moisture content(%)	89.4	52.7	78.4	92.9
Vitamin A(mg/100g)	4.5	3.4	5.6	0
Flavonoids(mg/g)	0.013	0.0002	0.001	0.00
Energy(kj/g	9.711	11.414	9.553	7.834

Figure 1. Number of Weaver Ant workers at food sources after 60 minutes foods supplied daily for 10 days between (**a**) September-October 2013 (dry season), and (**b**) January-February 2014 (rainy season) at Naliendele Citrus and Cashew orchard, Tanzania.

Table 2. The p-values for weaver ant counting and amount of food removed (g)/hour in 20 days between September and October 2013 and January and February 2014 in citrus orchard, Naliendele, Tanzania. (Kruskal-Wallis Multiple Comparison-Wilcoxon Each Pair test).

Food types	Citrus dry season		Citrus rainy season	
Pairwise comparison	Weaver ant counting (P-values)	Amount of food removed (g) (P-values)	Weaver ant counting (P-values)	Amount of food removed (g) (P-values)
Anchovy versus Chicken intestine	0.054	0.042	0.0002	0.0011
Anchovy versus Earthworm	0.021	0.108	0.0002	0.0011
Anchovy versus Fish intestine	0.014	0.0018	0.0003	0.0011
Chicken intestine versus Fish intestine	0.121	0.0095	0.0002	0.0011
Chicken intestine versus Earthworm	0.68	0.77	0.004	0.0011
Earthworm versus Fish intestine	0.33	0.014	0.0155	0.0011

Table3. The p-values for weaver ant counting and amount of food removed (g)/hour in 20 days between September and October 2013 and January and February 2014 in cashew orchard, Naliendele, Tanzania. (Kruskal-Wallis Multiple Comparison-Wilcoxon Each Pair test).

| Food types	Cashew dry season		Cashew rainy season	
Pairwise comparison	Weaver ant counting (P-values)	Amount of food removed (g) (P-values)	Weaver ant counting (P-values)	Amount of food removed (g) (P-values)
Anchovy versus Chicken intestine	0.0013	0.51	0.0002	0.0002
Anchovy versus Earthworm	0.0006	0.817	0.0002	0.0002
Anchovy versus Fish intestine	1.00	0.86	0.0002	0.0002
Chicken intestine versus Fish intestine	0.0008	0.76	0.0002	0.0002
Chicken intestine versus Earthworm	0.068	0.84	0.023	0.0002
Earthworm versus Fish intestine	0.0003	0.92	0.005	0.0002
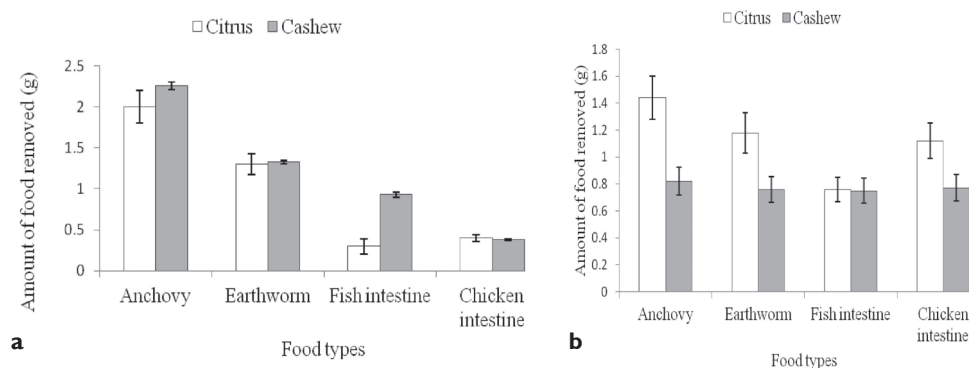
Figure 2. The average amount of food removed by the forage workers after 60 minutes foods supplied/day for 10 days between (**a**) September-October 2013 (dry season), and (**b**) January-February 2014 (rainy season) at Naliendele Citrus and Cashew orchard, Tanzania.
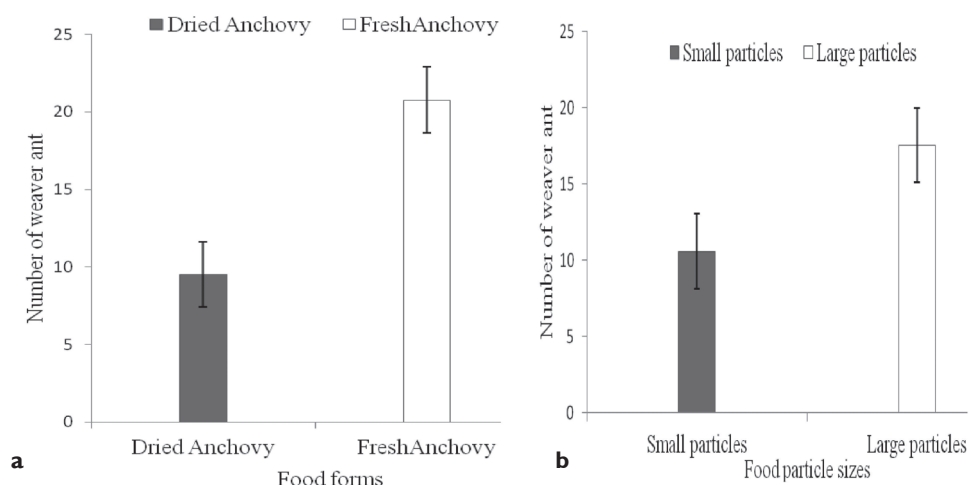

Figure 3. Food forms (**a**): Wilcoxon test; N=90; Prob.<0.0001, Food particle sizes (**b**) Wilcoxon test; N=60; Prob.<0.0001. Number of Weaver Ant counting /10 minutes for 10 days between May and July, 2014 for the given anchovy food forms and different particle sizes at Naliendele Citrus orchard, Tanzania, 2014. Large particle sizes refer to all particles that do not pass on a sieve of less or equal to 1mm, where as small particle sizes are those particle passes on 0.5 or 1 mm sieves.

Table 4. Analytical Hierarchy Process results on farmers access to food types for weaver ants.

Alternatives	Weights (Eigen Vector)*			Global score
	Affordability (0.539)	Availability (0.0845)	Applicability (0.126)	
Earthworm	0.59	0.63	0.41	0.42
Fish intestine	0.25	0.19	0.27	0.18
Chicken intestine	0.13	0.28	0.22	0.12
Anchovy	0.04	0.054	0.11	0.04

*Maximum Eigen Value = 0.24, CI = -1.09, CR = -0.27

Discussion

This study revealed that food preferences and foraging behavior by the *Oecophylla longinoda* can be influenced by food type, form, as well as particle size. Anchovy was highly preferred by *O. longinoda* in both citrus and cashew orchards during both dry and rainy seasons. The reason for forage workers' preference on anchovy is however not clear and could not be confirmed by this study. High preference for anchovy could be due to nutritional composition, particularly flavonoids or proteins. The foraging rate of *Pheidole megacephala* (Fabricius) depends on the type of protein (Cornelius and Grace 1997). It has also been reported that the velvety tree ant, *Liometopum occidentale* Emery prefers anchovy to earthworm (Hoey-Chamberlain and Rust 2014).

Anchovy was the highest preferred food across orchards and seasons but the order of preference for other food types in both orchards varied between seasons.

Chicken intestine was the least preferred during the rainy season. This is probably due to the fact that individual ant workers more easily remove fish intestine and earthworm than chicken intestine. Chicken intestine became stickier and bound to the food bowl during the rainy season. Thus, the removal of chicken intestine by foragers was difficult. Foragers spent time trying to take sticky-bound food items but they often failed. A temporal change in foraging activities was observed when the food became sticky and bound to the feeding bowl. At 15-30 minutes after food introduction, many ants were recruited and foraging activities increased with more ants observed on chicken intestine. However, as the food became stickier and bound to the feeding bowl, workers shifted to other food sources. It can be concluded that the nature of food at a particular time determines the foraging behavior of *Oecophylla longinoda* workers, and thereby influences preferences. Previous studies have shown that a large number of nest mates are recruited when ants are facing a non-transportable food items such as shrimps (Cerdá et al. 2009), but, foraging shifts were observed when other food sources were present. According to Lim (2007), ants choose food types which are easier to transport, that is, requiring less energy to remove and transport.

More anchovy was removed by ants as opposed to other feeds across seasons and orchards. The probable reason for this could be the form that anchovy assumes after being ground. Anchovy in the field became moist and grainy and could be removed without difficulty unlike the other food types. According to Hoey-Chamberlain and Rust (2014), the ease with which foragers are able to carry a particular type of food influences the amount of food to be consumed apart from food quality. However, inconsistency was observed for the rest of foods across seasons or orchards. For instance, similar amounts of earthworm and chicken intestine were removed in citrus during the dry season. On the other hand, ants removed more chicken intestine than fish intestine in citrus orchard during the rainy season. Furthermore, similar amounts of food types were removed during the dry season in the cashew orchard. A possible cause of the observed differences in food preferences across seasons could be colony needs at a particular time (Rust et al. 2000; Dussutour and Simpson 2008).

The quantities of food taken did correspond with the number of foraging workers, except for fish intestine in citrus orchard. We recorded more foraging workers on fish intestine than on chicken intestine and earthworm but the amount of food removed was smaller. Sometimes more ants visit particular feed but remove less (Neff et al. 2011).

In this study, we observed higher foraging activities on ground-fresh than on dry anchovy. These results support previous studies whereby three ants, *Linepithema humile* Mayr, *Anoplolepis custodiens* F. Smith and *Crematogaster peringueyi* Emery foraged more on liquid or moist food bait than on dry food bait (Nyamukondiwa and Addison 2014). Similarly, more activities for the ant, *L. lumile* were recorded on a 25% sugar solutions or honey than was the case with solid based protein foods such as tuna (Baker et al. 1985). It can be argued that, *Oecophylla longinoda* prefer fresh, moist foods than dried solid particles.

However, fresh-ground foods become sticky after some time, making it difficult for ant workers to remove them. Therefore, fresh-ground anchovy should be replenished to avoid stickiness; otherwise dried-ground anchovy should be used.

Forage workers easily collected and took large particles back to their nests in their mouthparts. However, they faced difficulties in collecting small particles and spent more time at the food bowl. A similar finding was reported for the fire ant *Solenopsis invicta* Buren (Neff et al. 2011).

Flavonoids have phytochemical properties against fungal, virus, and bacteria (Cushnie and Lamb 2005). They possess pharmacological activities such as antioxidant, anticancer and inhibition of tumor growth in mice (Shama 2006). They are considered to be an integral part of human diet (Arrabi et al. 2004). Therefore, flavonoid rich food types such as anchovy can be regarded as the best food to feed weaver ants. However, results of the AHP indicate that earthworm ranked the highest. This means farmers are more inclined to adopt the food type that is affordable and readily available. Earthworm is a cheap and widely available source of protein in the study area.

Conclusion

The results showed that all four tested feeds were removed by *Oecophylla longinoda* workers but anchovy was the most preferred. Considering the availability and affordability of the tested food sources, earthworms and fish intestine would be recommended as supplements during scarcity to boost weaver ants colonies on understanding that farmers preferred the less costly and sustainable option. All in all, fresh or dried-ground anchovy with particle sizes greater than 1 mm remains the best choice if availability and affordability are not subjects of concern.

Acknowledgements

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RESEARCH ARTICLE

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First confirmed record of the ant genus *Myrmecina* (Hymenoptera, Formicidae) from the Malay Peninsula: description of a new species and a key to *Myrmecina* species from Sundaland

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Abstract

We present the first confirmed record of the little known and uncommon ant genus *Myrmecina* for the Malay Peninsula. *Myrmecina magnificens* **sp. n.**, a new species displaying unique anteriorly pointing propodeal spines, is described from specimens of the worker caste collected in a selectively logged primary rainforest in Singapore. We also provide the first key to *Myrmecina* species of the Sundaland region.

Keywords

Myrmecina, Southeast Asia, Malay Peninsula, Singapore, Leaf litter

Introduction

Ants of the myrmicine genus *Myrmecina* are generally encountered in leaf litter samples where they live in small colonies of 30 to less than 150 individuals (Buschinger and Schreiber 2002; Terayama et al. 2014). Little is known about their biology, although specialized predation on oribatid mites has been observed in two Japanese species (Masuko 1994). Some *Myrmecina* species are also known to exhibit queen polymorphism, where two different phenotypes of reproductive females occur within a colony (Steiner et al. 2006). The genus contains 51 valid species (excluding the current description) and 1 valid subspecies (Bolton 2016). These ants are distributed throughout the Nearctic, Palearctic, Indomalayan and Austral regions, and apparently absent from Central and South America, sub-Saharan Africa and most of the Middle East (Antmaps 2016). Within the Indomalayan region, *Myrmecina* has been recorded from India and Sri Lanka (4 species), China and Taiwan (10 species), Myanmar (1 species) as well as the Sundaland (6 species) (Antmaps 2016). Most of the recent taxonomic work on *Myrmecina* has focused on Chinese species (Huang et al. 2008, Zhou et al. 2008), while other Oriental members of the genus from tropical regions were described nearly a century ago, in particular species from the Sundaland region. Here, we describe a new *Myrmecina* species possessing distinct anteriorly pointing propodeal spines, which was discovered in a selectively logged primary forest of Singapore. The discovery of *Myrmecina magnificens* sp. n. represents the first confirmed record of the *Myrmecina* genus from the Malay Peninsula. We also provide a key for *Myrmecina* species from Sundaland and highlight the need for more extensive sampling of ant communities in this part of the world.

Methods

Pictures of specimens were obtained with an incorporated digital camera, Leica DFC450, mounted on a Leica M205C dissecting microscope through the Leica Application Suite V4 software. A total of 24 to 86 images were taken and stacked together. Measurements of specimens were taken in mm (accurate to 0.001mm and rounded to the nearest 0.01mm for presentation) with the *Measure Tools* function of the Leica Application Suite V4 software on imaged specimens after proper placement for each body part measured. Measurements and morphological terminology follow: Shattuck (2009) for HW, HL, SL and WL; Fischer et al. (2014) for PNH and PTH; Baroni Urbani (1977) for PI and PPI.

The abbreviations used for the measurements and indices are as follows:

HW   Head Width. Maximum width of head in full-face view excluding the eyes.
HL   Head Length. Maximum head length in full-face view, measured from the anterior-most point of the clypeal margin to the midpoint of a line drawn across the posterior margin of the head.

MaL   Mandible Length. Maximum length of mandible from the anterolateral margin of clypeus at outer side of mandibular insertion to mandibular apex.

SL   Scape Length. Scape length, excluding the basal radicle.

EL   Eye Length. Maximum diameter of eye measured in lateral view.

TL   Total Length. Maximum length of specimen measured from the tip of the mandibles to the tip of the abdominal segment VII, not including sting. Due to the position of the specimen, total length was measured as the sum of head length + thorax, petiole and postpetiole length + gaster length.

WL   Weber's length measured from the anterior-most point of the pronotal collar to the posterior-most point of the propodeal process.

PNH   Pronotum Height. Maximum height of pronotum, measured in profile from the posterior base of the lateral sides of pronotum, where procoxa is attached, to the highest point of the pronotum.

PNW   Pronotal Width. Maximum width of pronotum measured in dorsal view.

MW   Mesonotal Width. Maximum width of the mesonotum measured in dorsal view.

PSL   Propodeal Spine Length. Maximum length of propodeal spines measured in profile view from the tip of the propodeal spine to the closer outward margin of the propodeal spiracle.

PTL   Petiole Length. Maximum diagonal length of petiole, measured in lateral view, from most anteroventral point of the peduncle, at or below the propodeal lobe, to most posterodorsal point at the junction with helcial tergite.

PTH   Petiole Height. Maximum height of petiole, measured in lateral view from the highest (median) point of the node, orthogonally to the ventral outline of the node.

PTW   Petiole Width. Maximum width of the petiole in dorsal view.

PPL   Postpetiole Length. Maximum length of postpetiole, measured in lateral view.

PPH   Postpetiole Height. Maximum height of postpetiole, measured in lateral view from the highest point of the node.

PPW   Postpetiole Width. Maximum width of the postpetiole in dorsal view.

CI   Cephalic Index. Calculated as: HW / HL ×100.

SI   Scape Index. Calculated as: SL / HW ×100.

MaI   Mandibular Index. Calculated as: MaL / HW ×100.

PI   Petiolar Index. Calculated as: PTW / PTL ×100.

PPI   Postpetiolar Index. Calculated as: PPW / PPL ×100.

Abbreviations of the type depositories and others are as follows:

LKCNHM Lee Kong Chian Natural History Museum, Singapore.

SBSHKU Insect Biodiversity and Biogeography Laboratory, School of Biological Sciences, The University of Hong Kong, Hong Kong SAR.

Results

Description of new species

Myrmecina magnificens Wong & Guénard, sp. n.
http://zoobank.org/DA28E247-B301-4642-8250-729C0F05AC66
Figs 1–5

Holotype. Worker from SINGAPORE, Seletar Trail, Central Catchment Nature Reserve, 1.395141°N, 103.802595°E, 47m, 02.IX.2015, leaf litter, leg. Mark K. L. Wong, label "MW020915-L1.1" (ANTWEB1009004) deposited in LKCNHM.

    Paratypes. Four workers in total (ANTWEB1009005, ANTWEB1009006, ANTWEB1009007, ANTWEB1009008), all with the same collection data as holotype (deposited at SBSHKU).

Figure 1. Full-face view of *Myrmecina magnificens* (Holotype, ANTWEB1009004, LKCNHM) from Singapore.

Figure 2. Head view focusing on mandibles of *Myrmecina magnificens* (Holotype, ANTWEB1009004, LKCNHM) from Singapore.

Measurements and indices. Holotype: HL 0.98 mm; HW 1.12 mm; MaL 0.63 mm; SL 0.90 mm; EL 0.20 mm; WL 1.37 mm; PNW 0.71 mm; PNH 0.62 mm; MW 0.65 mm; PSL 0.24 mm; PTL 0.36 mm; PTW 0.32 mm; PTH 0.35 mm; TL 4.42 mm (stinger not included); PPL 0.23 mm; PPW 0.34 mm; PPH 0.39 mm; CI 114, SI 80, MaI 56, PI 88, PPI 149.

Paratypes (n=4): HL 0.94–0.98 mm; HW 1.06–1.11 mm; MaL 0.55–0.63 mm; SL 0.89–0.91 mm; EL 0.20–0.21 mm; WL 1.22–1.36 mm; PNW 0.70–0.74 mm; PNH 0.57–0.62 mm; MW 0.61–0.65 mm; PSL 0.23–024 mm; PTL 0.34–0.36 mm; PTW 0.29–0.31 mm; PTH 0.31–0.33 mm; TL 4.36–4.57 mm (stinger not included); PPL 0.22–0.24 mm; PPW 0.32–0.35 mm; PPH 0.34–0.36 mm; CI 113–116, SI 80–86, MaI 51–57, PI 83–87, PPI 141–151.

Worker description. Head. Head in full-face view slightly shorter than wide (CI 113–116) and maximum HW occurs behind the eyes, sides convex, occipital corners triangular, occipital margin strongly convex (Fig. 1). Thin lamella finely rugulose present on the anterolateral margin of the clypeus (Fig. 2). Eyes relatively large with EL approximately 1/5 of HL. Antennal scape long (SI 80–86); antenna with 12 segments, last three segments forming indistinct club. Clypeus short, anterior clypeal margin broadly convex with two angular projections on either sides. Mascitory margin
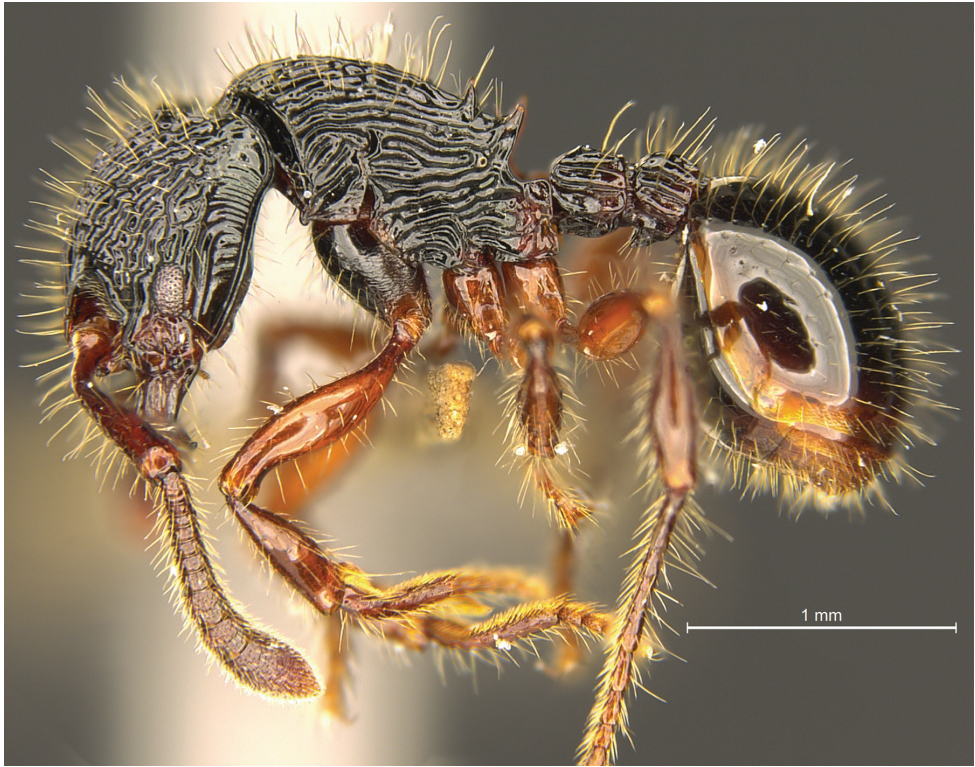
Figure 3. Profile view of *Myrmecina magnificens* (Holotype, ANTWEB1009004, LKCNHM) from Singapore.

of mandible with two apical teeth followed by a series of extremely reduced blunt denticles (n=5).

Mesosoma. In profile view, dorsal outline of promesonotum flat to broadly convex, sloping along anterodorsal part of propodeum (Fig. 3). In profile view, propleuron angular and forming a distinct acute tooth. Two distinct propodeal spines both slightly longer than broad and pointing anteriorly (Fig. 4). Propodeal declivity strongly concave before terminating at a right angle with a rounded edge.

Metasoma. In profile view (Fig. 4), anterodorsal face of petiolar node broadly convex, posterodorsal face of petiolar node flat to weakly concave; overall dorsal outline of petiolar node triangular. Ventral outline of petiolar node rounded. Dorsal outline of postpetiole flat to weakly convex, sternopostpetiolar process well-developed and triangular, almost as long as broad and pointing anteriorly. Petiolar node is longer than postpetiole. In dorsal view (Fig. 5), petiolar node is broader than long and exhibits trapezoid shape; petiolar node is distinctly broader at posterior margin than at anterior margin. Postpetiole is broader than long and exhibits rectangular shape; width of postpetiole is similar at both the anterior and posterior margins.

Figure 4. Profile view focusing on the propodeum, petiole and subpetiole of *Myrmecina magnificens* (Holotype, ANTWEB1009004, LKCNHM) from Singapore.

Sculpture. Sculpturing on head and thorax running longitudinally. Sculpture on head parallel on its middle portion and divergent on the sides and posterior portions. Groove on head with latitudinal sculptures present on most of its length. In profile view, sculpture on thorax presenting a complex pattern with parallel or and convergent sculptures (Fig. 3). Parallel sculptures present on the entire length of the petiole and postpetiole. Gaster smooth and shiny. In dorsal view, thorax entirely sculptured with a single median carina separating in two symmetrical portions the dorsal sculptures (Fig. 5). Other sculptures converging posteriorly to reach the median carina on the dorsum of the thorax.

Pubescence. Almost all of body covered in abundant erect long hairs (0.2–0.25 mm) with the exception of the propodeal junction and ventral surface of the petiole where pubescence is absent.

Coloration. Most of head, mesosoma and gaster black; antenna, clypeus and mandibles dark red to dark brown; legs, posterior portion of propodeum light amber to light brown; pubescence and margins of gastral tergites yellow to light gold.

Castes. Male and gyne castes unknown.

Etymology. The species epithet is derived from the English word 'magnificent', referencing the beautiful appearance of this species, which makes it truly magnificent to behold. The species epithet is a noun, and thus invariant.

Distribution. Southeast Asia. Only known from Singapore.

Ecology. Almost nothing is known about the ecology of *M. magnificens*. All specimens were collected from a selectively logged lowland primary rainforest. Based on the

Figure 5. Dorsal view of *Myrmecina magnificens* (Holotype, ANTWEB1009004, LKCNHM) from Singapore.

collection methods used to collect several workers (N=5), we suspect that *M. magnificens* probably forages within the leaf litter and topsoil. This is based on our collection of the species via a Berlese extraction of sifted leaf litter and topsoil, as well as from a subterranean pitfall trap baited with tuna and buried at a depth of 5 cm underground. No other conspecifics were found in similar traps buried at greater depths (i.e. 15, 20, 25 cm) within the same locality.

Diagnosis. With the exception of *M. sulcata* for which body size was not recorded in the species description, the new species *M. magnificens* can quickly be distinguished from other *Myrmecina* species in the Sundaland region by its large overall size (TL 4.2–4.6 mm) and its distinctly long and forward-pointing propodeal spines. While *M. nesaea*, *M. semipolita*, *M. sulcata* and *M. undulata* also possess relatively long propodeal spines, their spines are posteriorly oriented. The other two species, *M. bandarensis* and *M. butteli* have relatively short propodeal spines, and are also notably smaller in their overall sizes (TL 1.9–2.2 mm), which by comparison would be approximately half that of *M. magnificens*.

Synoptic species list of *Myrmecina* species known from Sundaland

Myrmecina bandarensis Forel, 1913 (Sumatra)
Myrmecina butteli Forel, 1913 (Sumatra)
Myrmecina magnificens sp. n. (Singapore)
Myrmecina nesaea Wheeler, 1924 (Sumatra) – described from gyne only
Myrmecina semipolita Forel, 1905 (Java)
Myrmecina sulcata Emery, 1887 (Java)
Myrmecina undulata Emery, 1900 (Borneo, Sumatra)

Key to *Myrmecina* species from Sundaland based on worker caste

A new key to *Myrmecina* species from Sundaland based on descriptions of the worker caste was developed from scrutinizing the respective taxonomic descriptions for the worker caste of *M. butteli* (Forel 1913, p.71), *M. semipolita* (Forel 1905, p.15), *M. sulcata* (Emery 1887, p.449) and *M. undulata* (Emery 1900, p.678). For two other Sunda *Myrmecina* species, specimens of the worker caste were examined. These included: *M. bandarensis*, one imaged specimen on Antweb.org (Syntype, Forel, 1913, Bandar Barae, Sumatra, CASENT0908953); *M. magnificens* sp. n., three mounted type specimens, all with same collection data, "M. Wong, 02.IX.2015, Seletar Trail, Singapore" (Holotype ANTWEB1009004, Paratypes ANTWEB1009005 to ANT-WEB1009008). In an effort to be comprehensive, we also tentatively incorporated the description of *M. nesaea*, which was described from the gyne caste only (Wheeler 1924, p.247). For this last species, we only included characters on pilosity that might be shared between the gyne and worker castes into our comparative analyses. However a more detailed study of the type specimens of this species including a complementary description would represent an interesting contribution in the future.

|	
1	In profile view propodeal spines pointing posteriorly **2**
–	In profile view propodeal spines pointing anteriorly; large sized species (TL > 4 mm) (Singapore)...***M. magnificens* sp. n.**
2	In profile view propodeal spines small with length shorter than or equivalent to basal width **3**
–	In profile view propodeal spines distinct with length exceeding basal width... **4**
3	In profile view pro-mesonotum weak to moderately convex (Fig. 6b); in full-face view anterior edge of clypeus straight, eyes large, approximately 1/4 of HL (Fig. 6a) (Sumatra) ....***M. bandarensis* Forel**
–	In profile view pro-mesonotum strongly convex; in full-face view anterior edge of clypeus slightly concave (Sumatra) .... ***M. butteli* Forel**
4	In full-face view clypeus with distinctly concave anterior edge (Borneo, Sumatra)...***M. undulata* Emery**
–	In full-face view clypeus with straight anterior edge **5**
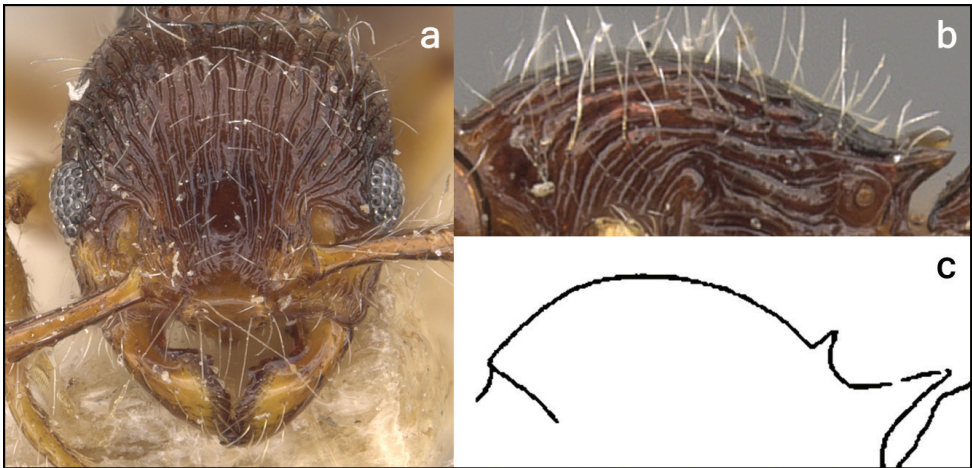
Figure 6. Photographs of *M. bandarensis* from AntWeb (CASENT0908953, photos by Will Ericson) in **a** full-face view showing large eyes and straight anterior edge of clypeus **b** profile view, close-up of thorax showing weak to moderately convex pro-mesonotum and short propodeal spine. Original illustration of *M. sulcata* in profile view **c** with close-up of thorax showing strongly convex pro-mesonotum and long propodeal spine pointing posteriorly at approximate forty-five degree angle (from Emery 1887, p.449, pl. 1, fig. 11)

5   In profile view pro-mesonotum strongly convex (Fig. 6c); propodeal spine with length that is almost twice of basal width, and pointing posteriorly at an approximate forty-five degree angle (Fig. 6c) (Java)..........***M. sulcata* Emery**

–   In profile view pro-mesonotum weakly convex; propodeal spines with length slightly exceeding basal width and pointing posteriorly at a nearly horizontal angle **6**

6   Pilosity on entire body long and white in colour (Sumatra) .... ***M. nesaea* Wheeler** (Described from gyne only)

–   Pilosity on entire body short and yellow in colour (Java)....***M. semipolita* Forel**

Discussion

Myrmecina magnificens represents the first *Myrmecina* species described from the Malay Peninsula and completes the distribution of the genus in the Sundaland region. Although several records of *Myrmecina* have been reported from ecological work in this region, most of them have not been formerly identified. For example, many unidentified *Myrmecina* species were previously reported from Peninsular Malaysia: Negeri Selemban and Selangor provinces in Malaysia (Agosti et al. 1994; Malsch 2000), as well as Narathiwat, Songkhla and Trang provinces in Thailand (Noon-anant et al. 2005; Watanasit et al. 2007; Sakchoowong et al. 2015). In this regard, the key provided here is by no means exhaustive and it is likely that new *Myrmecina* species will be described in the future. Nevertheless, in light of the characteristic morphology of the new species

described here, we took the opportunity to present a primary baseline for future work on this genus in the Sundaland region. Notably, while populations of *M. magnificens* have yet to be discovered in other parts of Singapore, the apparent abundance of this species within Seletar forest is surprising; thus far several specimens have been collected with a variety of methods including Berlese extractions of understorey material as well as baited subterranean pitfall traps. In conclusion, the present discovery of a new ant species that is non-cryptic, of relatively large body size (TL > 4 mm) and perhaps not uncommon in a small forest remnant (ca. 2000 ha) of a highly urbanized city (i.e. Singapore) clearly highlights the shortage of extensive sampling in Southeast Asia, and is very encouraging to future myrmecological research in this part of the world.

Acknowledgments

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REVIEW ARTICLE

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The life, publications and new taxa of Qabir Argaman (Carol Nagy)

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Abstract

This biography of the Hungarian/Romanian/Israeli hymenopterist Qabir Argaman (= Carol Nagy) provides a list of his publications (except for newspaper articles) and the new taxa and new replacement names he proposed. Dr. Argaman began his career in Hungary, publishing under the name Carol Nagy. He later moved to Romania and finally moved to Israel, where he assumed the name Qabir Argaman. In total, he published 84 articles on the order Hymenoptera and described 348 new taxa (2 families, 11 subfamilies, 58 tribes, 153 genera or subgenera, and 125 species or subspecies) in 15 families, as well as 1 new species of Scarabaeidae (Coleoptera).

Introduction

The majority of insect taxonomists tend to focus on a single family group for the majority of their careers. However, others have more diverse interests. The taxonomist Qabir Argaman (Fig. 1) worked on a wide diversity of Hymenoptera families during his career between 1965 and 2003, and he did so under different names. Early on he published under the names Carol Nagy or Károly Nagy and later under the name

Figure 1. Qabir Argaman at work in Israel (photo courtesy of the Israeli Ministry of Agriculture).

Qabir Argaman. In total he published new taxa in 15 hymenopteran families, Ampulicidae, Bethylidae, Braconidae, Bradynobaenidae (as Apterogynidae), Dryinidae, Heterogynaidae, Kislevidae, Mutillidae, Perilampidae, Plumariidae, Sclerogibbidae, Scolebythidae, Scoliidae, Sierolomorphidae and Tiphiidae (mostly as Myzinidae), as well as one new species of Scarabaeidae (Coleoptera). Because of his changes of surname, the obscure nature of some of the journals he published in and the diversity of families involved, it is difficult to find many of his publications. We have attempted to do so here, and also give a brief account of his life based on many (sometimes conflicting) sources.

Károly (Karol/Carol) György (George) Nagy was born on January 15, 1940 in Oradea, Romania (the region was transferred to Hungary later that year, but restored to Romania after the war). In the early 1960's he attended university in Romania where he developed an interest in wasp taxonomy. In 1965 he began publishing on the Mutillidae, Bethylidae and "heterogyne Hymenoptera" of Romania. He graduated in 1967 from Babeş-Bolyai University, in Cluj-Napoca, Romania with an MSc degree in biology. He then studied under László Móczár at the University of Szeged in Hungary, where he received his PhD in 1968. Thereafter he held a position at the Marine Research Institute, in Agigea-Constantza, Romania, where he studied the taxonomy, biology and zoogeography of the Romanian wasp fauna. He obtained his DSc in 1974

from the University "Al. I. Cuza" in Iaşi, his thesis on the scolioids of Romania being supervised by Mihai Constantineanu.

In 1980 Carol Nagy moved from Agigea, Romania to Israel (Menke 1980). According to a note in Sphecos (Menke 1981) he and his family left Romania with only 40 kg of baggage, which consisted mostly of clothes for their baby. He had to leave behind his entomological library and collections in Romania, lived for a time in a camp for immigrants, and started a new life in a new country with all the attendant challenges - learning a new language, trying to find employment (difficult for a wasp taxonomist in such a small country and without his literature resources), and trying to find a permanent home. During this period he briefly changed his surname from Nagy to Grosman, but was required by Israeli immigration regulations to adopt a Hebrew name (Menke 1982). He then became Qabir Argaman (ריבכ ןמגרא), and from the mid 1980's his papers were all published under this name. In 1981 he began working as an insect taxonomist for the Israeli Ministry of Agriculture, Plant Protection Department, in Bet Dagan, working on insects of agricultural importance. However, he also continued his work on a diversity of wasp families, but suffered from shortages of basic supplies such as pins and boxes, an initial lack of a collection and constraints on field work (the threat of terrorism being a concern) (Menke 1987). He worked for the Ministry of Agriculture until his death in October 2003 at the age of 63.

Nagy's research interests changed over the years. Between 1965 and 1968 his studies focused primarily on the Romanian fauna. In 1968 he described a new species of Mutillidae from Sudan (Nagy1968b) and this began the expansion of his research interests into other parts of the world. In the 1970's he began working on the European bethylid and mutillid faunas and small collections of ampulicids from Africa, tiphiids, scolebythids, South American Plumariiidae and Mongolian scoliids. There is a gap in his publications between 1980 and 1986, which is the period when he moved his family to Israel. In the remainder of the 1990's he began new studies of Perilampidae, Sierolomorphidae and Scoliidae and continued his work on the Bethylidae, Sclerogibbidae and Tiphiidae. He produced several papers dealing with the higher-level classification of various groups, describing many new genera and other higher taxa supposedly based on phylogenetic principles requiring naming of monophyletic groups, but never provided any cladistic or other analyses justifying his decisions. His publications were primarily limited to descriptions of new taxa and faunal lists. He never produced any taxonomic revisions. Subsequent workers have generally rejected his excessively split approach and synonymized most of his names, or else deliberately ignored them (e.g. Osten 2005). His idiosyncratic approach and involvement with such a diversity of groups means that any workers having to deal with his taxa and names should be aware of these complexities to be able to evaluate them properly.

According to an unpublished obituary provided by the Israeli Ministry of Agriculture, Argaman's personal collection, primarily accumulated once he arrived in Israel, also included some materials dating from his early work in Hungary and Romania. According to Laibale Friedman (in Romano 2012), after Argaman's death the collection was broken up, part being sold privately, and the remainder being

donated by his family to the Israeli Ministry of Agriculture and transferred to the Tel Aviv University Collection. For unknown reasons, Argaman apparently removed labels from some specimens, including types, leaving them without any labels at all, and making the identification of such type specimens essentially impossible. (When DJB briefly visited him in Tel Aviv in 1985, he gained the impression that Argaman was suspicious of the motives of others and jealously guarded his specimens, not being willing to let them out of his sight; this attitude probably resulted from the personal difficulties he had endured, and may explain the removal of labels.) Repositories of his types, according to his publications and information provided by collection managers, include the following:

Argaman Coll. – much of his personal collection now resides in Tel Aviv (see below), the location(s) and extent of the remainder are unknown.
Bar Ilan – Department of Life Sciences, Bar Ilan University, Ramat Gan, Israel.
Berlin – Museum für Naturkunde, Berlin, Germany.
Brussels – Royal Belgian Institute of Natural Sciences, Brussels, Belgium.
Budapest – Magyar Természettudományi Múzeum, Budapest, Hungary.
Cluj – Zoological Museum, Universitatea Babeș-Bolyai, Cluj-Napoca, Romania.
Copenhagen – Statens Naturhistoriske Museum, Copenhagen, Denmark.
Fruhstorfer Coll. – Museum für Naturkunde, Berlin, Germany.
Geneva – Muséum d'histoire naturelle de la Ville, Geneva, Switzerland.
Genoa – Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy.
Hamburg – Zoologisches Museum, Hamburg, Germany.
Nagy Coll. – a small part of this collection resides in Tel Aviv (see below), the location of the rest is unknown.
Nonveiller Coll. – the private collection of the late Guido Nonveiller, Zemun, Serbia, now housed in Biologiezentrum, Oberösterreichs Landesmuseum, Linz, Austria.
Pagliano Coll. – the private collection of Guido Pagliano, Turin, Italy
Paris – Muséum National d'Histoire Naturelle, Paris, France
Senckenberg – Senckenberg Deutsches Entomologisches Institut, Berlin, Germany.
Tel Aviv – The Steinhardt Museum of Natural History and National Research Center, Tel Aviv University, Tel Aviv, Israel.
Washington – U. S. National Museum of Natural History, Washington, D. C., USA.

Lists of his theses and publications are given below (compiled from various sources, importantly using information provided by Laibale Friedman which unfortunately had all titles translated into English). A complete tabulation of new taxa described by him is given in Table 1, followed by an Appendix comprising a detailed list of his new taxa and new names, including type locality and repository for each species. If the repository has been confirmed by the date of this publication it is indicated as such. Others are yet to be confirmed. This is another problem to be resolved; it has not been possible to determine the location of most of the aculeate wasp types described by him. Some, particularly the aculeates, may still be in Romania.

Table 1. Summary of new taxa described by Nagy/Argaman; new families are indicated by asterisks (*), new replacement names are given between parentheses ( ), and unavailable names between square brackets [ ].

Order	Family	Subfam.	Tribe	Genus/ Subgen.	Species/ Subsp.	Geographic Region of New Species				
						Europe	Asia	Africa	Americas	Australia
Coleoptera	Scarabaeidae				1		1			
Hymenoptera	Ampulicidae				5		5			
	Bradynobaenidae		4	7	1			1		
	Bethylidae	3	3	12	29	10	11	8		
	Braconidae			1						
	Dryinidae				2	1	1			
	Heterogynaidae*			2	2	1	1			
	Kislevidae*			1	1		1			
	Mutillidae	1	2	3	30	8	5	1	16	
	Perilampidae			26	26 (+3)		5	12	9	
	Plumariidae				5				5	
	Sclerogibbidae	2	2	1	2	1		1		
	Scolebythidae			1	1			1		1
	Scoliidae	1	22	61 (+3)	3 [+3]	1	2			
	Sierolomorphidae				2		2			
	Tiphiidae	4	25	38	15	7	4	4		
Totals	2	11	58	153 (+3)	125 (+3) [+3]	29	38	28	30	1

Unpublished theses by Carol Nagy (The information on these appears in the list from Friedman; we have not been able to locate them to confirm the details or original titles, however, so several peculiarities are evident.)

Nagy CG (1967) [Contributions to the knowledge of the heterogynoid Hymenoptera from the fauna of Romania.] Master of Science Thesis, University "Babeş-Bolyai" in Cluj, 1–87. [Romanian]

Nagy CG (1968) [The Hymenoptera Proctotrupoidea in the fauna of Romania.] Doctor of Philosophy Thesis, Constantza-Szeged-Budapest. 1–70. [Romanian]

Nagy CG (1974) [Contributions to the study of Scolioidea (Hymenoptera) from the fauna of Romania, from systematical, biological, ecological and economical viewpoints.] Doctor of Science Thesis, Universitatea "Alexandru Ioan Cuza" din Iaşi, 1–300, 302 figs. [Romanian]

Publications by Carol Nagy/Qabir Argaman

This list includes all publications in books, journals or magazines for which page numbers are available, but it excludes his many (at least 117, from 1967 to 1978) "popular" contributions to newspapers or small local periodicals on a very wide range of subjects (butterflies, snakes, honey bees, birds, scientific expeditions, biological control, ants in

forests, scientific methods, oceanology, sea snakes, Antarctic exploration, obituaries, physics of the universe, linguistics, conference reports, turtle conservation, human development, psychoanalysis, archeology, environmental conservation, pogonophorans, black widow spiders, human facial expressions, yogis in ancient India, marine rescues, fossil corals, hare behavior, vitamins, human social behavior, animal suicides, *Drosophila* cultures, beach events, forest mammals, Oriental archeology, energy sources, noise pollution, ecological non-equilibria, species concepts, concept of life, scientific literature, sea gulls, sand-nesting wasps and bees, general theory of relativity, wildlife conservation, crows, biospeleology and meiobenthal faunas, autobiography, guppies, pollution, medusas, blue-green algae, shipwrecks, lunar orbits, coffee cultivation, scientific ethics, biological systems, animal intelligence, calendars, lagoons, importance of stinging wasps, pheromones, bee pollination ecology, hedgehogs, biology of cancer, dolphins, cybernetics of life, ocean plankton, hypochondria, human genetics, and dogs). The more cultural publications included below were generally authored by "Nagy G Károly", reflected here as "Nagy KG". Where easily available, actual dates of publication are provided, and the sequence attempts to reflect the temporal sequence of publication (primarily based on the sequence in the list mentioned above). Unfortunately, we have been unable to obtain copies of all of the entries and have therefore not been able to provide the original titles for those non-English papers we have not seen, but indicate the original language. His papers were in Romanian, German, Hungarian, French, English and Hebrew; English translations of Hungarian and Romanian titles are given in addition to the originals since these are less familiar languages to most, but only English translations of the Hebrew titles are given. Articles we have not been able to locate are indicated by an asterisk (*).

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Nagy CGh (1966b) Neue Bethyliden-Arten für die Fauna Rumäniens (Hymenoptera). Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa" 6: 165–169.

Nagy CGh (1966c) Contribuţii la cunoaşterea himenopterelor heterogine din rezervaţiile naturale ale Dobrogii [Contributions to the knowledge of heterogyne Hymenoptera of nature reserves of Dobruja]. Ocrotirea Naturii 10(2): 223–228.

Nagy CGh, Stamp HM (1966) Katalog der Heterogyniden (Hymenoptera) aus der Sammlung Brukenthalmuseums in Sibiu. Rovartani Közlemények Folia Entomologica Hungarica (Series Nova) 19(27): 491–500.

Nagy CGh (1967a) Gonatopodine noi pentru fauna României (Hymenoptera: Dryinidae) [Gonatopodines new to the fauna of Romania]. Studia Universitatis Babeş-Bolyai (Series Biologica) 1: 123–125.

Nagy CGh (1967b, April 20) Une nouvelle espèce du genre *Myrmilla* Wesm. de la faune de la Roumanie (Hymenoptera, Mutillidae). Bollettino della Società Entomologica Italiana 97(3–4): 50–54.

Nagy CGh (1967c, June 21) Systematisches Studium der Tiphiiden Rumäniens. Reichenbachia 8(24): 175–204.

Nagy CGh (1967d, June 21) Beiträge zur Kenntnis der rumänischen Scoliiden-Arten (Hymenoptera, Scoliidae). Reichenbachia 8(28): 221–226.

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Nagy CGh (1967g) Description du mâle de *Myrmilla subcornuta* Mor. (Hym. Mutillidae). Deutsche Entomologische Zeitschrift (Neue Folge) 14(5): 473–476.

Nagy CGh (1967h) Contributions à la connaissance des hyménoptères Bethylidae de la faune roumaine. Rovartani Közlemények Folia Entomologica Hungarica (Series Nova) 20(8): 87–94.

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Nagy CG (1968b) Une nouvelle espèce du genre *Dolichomutilla* Ashm. (Hym., Mutillidae). Rovartani Közlemények Folia Entomologica Hungarica (Series Nova) 21(10): 147–151.

Nagy CGh (1968c, June 20) Quelques espèces nouvelles de Myrmillines dans la faune de la Roumanie (Hymenoptera, Mutillidae). Bollettino della Società Entomologica Italiana 98(3–6): 65–69.

Nagy CG (1968d) Observations écologiques sur l'espèce *Smicromyrme septentrionalis* Hffr. (Hym., Mutillidae). Acta Entomologica Bohemoslovaca 65: 375–378.

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Appendix 1

New taxa described and new names proposed by Argaman/Nagy. It has not been possible to check the accuracy of all of Argaman/Nagy's type designations, so the information on these is derived directly from his publications. Synonymies have been indicated where known to us; some may, however, have been missed, so this listing should not be considered authoritative.

Order Hymenoptera

Family Ampulicidae
   Species:
   Chlorampulex sciophanes Nagy, 1971c: 104. Holotype male; Formosa (Taiwan): Takao (Nagy Coll.). =*Ampulex sciophanes* (Nagy). Transferred by Bohart & Menke (1976: 78).
   Dolichurus alorus Nagy, 1971c: 106. Holotype male; Formosa (Taiwan): Taihorin (Nagy Coll.).
   Dolichurus dromedarius Nagy, 1971c: 106. Holotype male; Formosa (Taiwan): Takao (Nagy Coll.).
   Dolichurus ombrodes Nagy, 1971c: 106. Holotype male; Formosa (Taiwan): Taihorin (Nagy Coll.).
   Dolichurus oxanus Nagy, 1971c: 107. Holotype male; Celebes (Sulawesi): Bua-Kraeng (Nagy Coll.).

Family Bradynobaenidae, Subfamily Apterogyninae [treated as Family Apterogynidae by Argaman]
   Tribe: Doryleikini Argaman, 1994a: 45. Type genus: *Doryleika* Argaman, 1994. =Apterogyninae André, 1899. Synonymy implied by Pagliano (2002) in not recognizing higher taxa within Apterogyninae.
   Tribe: Gynecapterini Argaman, 1994a: 46. Type genus: *Gynecaptera* Skorikov, 1935. =Apterogyninae André, 1899. Synonymy implied by Pagliano (2002) in not recognizing higher taxa within Apterogyninae.
   Tribe: Icalanticini Argaman, 1994a: 47. Type genus: *Icalantica* Argaman, 1994. =Apterogyninae André, 1899. Synonymy implied by Pagliano (2002) in not recognizing higher taxa within Apterogyninae.
   Tribe: Pauxorculini Argaman, 1994a: 48. Type genus: *Pauxorcula* Argaman, 1994. =Apterogyninae André, 1899. Synonymy implied by Pagliano (2002) in not recognizing higher taxa within Apterogyninae.
   Genus: *Doryleika* Argaman, 1994a: 46. Type species: *Doryleika mahunkai* Argaman, 1994. =*Macroocula* Panifilov, 1954. Synonymized by Pagliano (2002: 125).
   Genus: *Icalantica* Argaman, 1994a: 48. Type species: *Apterogyna lateritia* Morawitz, 1890. = *Apterogyna* Latreille, 1809. Synonymized by Pagliano (2002: 26).

Genus: *Micatagla* Argaman, 1994a: 45. Type species: *Apterogyna schultzei* André, 1909.

Genus: *Mutillariola* Argaman, 1994a: 47. Type species: *Apterygyna bimaculata* André, 1898. = *Gynecaptera* Skorikov, 1935. Synonymized by Pagliano (2002: 101).

Genus: *Pauxorcula* Argaman, 1994a: 49. Type species: *Apterogyna bulawayona* Peringuey, 1914. = *Micatagla* Argaman, 1994. Synonymized by Pagliano (2002: 204).

Genus: *Utapitoca* Argaman, 1994a: 48. Type species: *Apterogyna latreillei* Klug, 1829. = *Apterogyna* Latreille, 1809. Synonymized by Pagliano (2002: 26).

Genus: *Zarabayca* Argaman, 1994a: 49. Type species: *Apterogyna miniaticornis* Enderlein, 1901. = *Apterogyna* Latreille, 1809. Synonymized by Pagliano (2002: 26).

Species:

Doryleika mahunkai Argaman, 1994a: 51. Holotype male; Tunisia: Boughrara (Budapest, confirmed). =*Macroocula mahunkai* (Argaman). Transferred by Pagliano (2002: 160).

Family Bethylidae

Subfamily: Afgoiogfinae Argaman, 1988b: 140. Type genus: *Afgoiogfa* Argaman, 1988. =Pristocerinae Dalla Torre, 1898. Synonymy implied by Gordh & Moczar (1990: 198) in placing *Afgoiogfa* Argaman in Pristocerinae.

Subfamily: Galodoxinae Nagy, 1974c: 126. Type genus: *Galodoxa* Nagy, 1974. =Epyrinae Kieffer, 1914. Synonymized by Azevedo & Lanes (2009: 847).

Subfamily: Protopristocerinae Nagy, 1974c: 126. Type genus: *Protopristocera* Brues, 1923. =Pristocerinae Dalla Torre, 1898. Synonymy implied by Perrichot & Nel (2008: 101) in placing *Protopristocera* Brues in Pristocerinae.

Tribe: Domonkosini Argaman, 2003: 66, 79. Type genus: *Domonkos* Argaman, 2003. =Mesitiinae Kieffer, 1914. Synonymy implied by Gordh & Moczar (1990) in not recognizing higher taxa within Mesitiinae.

Tribe: Heterocoeliini Argaman, 2003: 66, 67. Type genus: *Heterocoelia* Dahlbom, 1854. =Mesitiinae Kieffer, 1914. Synonymy implied by Gordh & Moczar (1990) in not recognizing higher taxa within Mesitiinae.

Tribe: Triglenusini Argaman, 2003: 66, 72. Type genus: *Triglenus* Marshall, 1905. =Mesitiinae Kieffer, 1914. Synonymy implied by Gordh & Moczar (1990) in not recognizing higher taxa within Mesitiinae.

Genus: *Afgoiogfa* Argaman, 1988b: 141. Type species: *Afgoiogfa olmiana* Argaman, 1988.

Genus: *Botoryan* Argaman, 2003: 66, 69. Type species: *Mesitius discolor* Nagy, 1968.

Genus: *Clytrovorus* Nagy, 1972a: 10. Type species: *Mesitius horvathi* Kieffer, 1906.

Genus: *Codorcas* Nagy, 1972a: 10. Type species: *Mesitius cursor* Kieffer, 1906.

Genus: *Domonkos* Argaman, 2003: 67, 79. Type species: *Mesitius capensis* Kieffer, 1911.

Genus: *Galodoxa* Nagy, 1974c: 126. Type species: *Galodoxa torquata* Nagy, 1974.

Genus: *Gerbekas* Argaman, 2003: 66, 71. Type species: *Mesitius carcelii* Westwood, 1874.

Genus: *Hamusmus* Argaman, 2003: 66, 72. Type species: *Mesitius punctatus* Kieffer, 1906

Genus: *Itapayos* Argaman, 2003: 67, 77. Type species: *Mesitius spinosus* Kieffer, 1906.

Genus: *Topcobius* Nagy, 1972a: 17. Type species: *Mesitius punctaticollis* Fouts, 1930.

Genus: *Ukayakos* Argaman, 2003: 66, 68. Type species: *Mesitius obscurus* Kieffer, 1906.

Genus: *Zimankos* Argaman, 2003: 67, 80. Type species: *Mesitius alluaudi* Kieffer, 1913.

Species:

Afgoiogfa olmiana Argaman, 1988b: 143. Holotype male; Somalia: Afgoi (Pagliano Coll.).

Bethylus antipai Nagy, 1968h: 1033. Holotype male; Romania: Bistriţa, Station de Recherches Biologiques d'Arcalia (Nagy Coll.).

Bethylus paradoxus Nagy, 1970e: 63. Holotype female; Romania: Cluj, Fînaţele Clujului (Nagy Coll.)

Dissomphalus claudivani Argaman, 1989b: 9. Holotype female; Israel: Galilea, below Safad (Geneva).

Epyris carbunculus Nagy, 1970j: 267. Holotype male; Romania: Agigea (Tel Aviv [Nagy Coll.], confirmed).

Galodoxa torquata Nagy, 1974c: 127. Holotype female; Philippines: Palawan, Mantalingajan, Pinigisan 600m (Copenhagen, confirmed).

Holepyris napocaensis Nagy, 1968g: 409. Holotype male; Romania: Cluj (Nagy Coll.)

Mesitius andriescui Nagy, 1970c: 207. Holotype female; Morocco: "Tanger" (Geneva).

Mesitius bridwelli Nagy, 1968a: 170. Holotype female; Nigeria: Lagos (Washington, confirmed).

Mesitius caspicus Nagy, 1969i: 291. Holotype female; "Umgebung des Kaspischen Meeres" (Paris, confirmed).

Mesitius cerasinus Nagy, 1970c: 208. Holotype female; Morocco: "Maroc" (Geneva).

Mesitius clavicornis Nagy, 1968a: 173. Holotype female: India (Nagy Coll., Tel Aviv, confirmed).

Mesitius concii Nagy, 1972a: 8. Holotype male; Spain: "Palma de Mallorca" (Nagy Coll.).

Mesitius discolor Nagy, 1968a: 174. Holotype male; Country?: "Arallan or Arauan" (Washington).

Mesitius foenarius Nagy, 1968a: 171. Holotype female; Romania: Cluj (Nagy Coll.).

Mesitius kiefferi Nagy, 1970g: 205. Holotype male; Algeria: Bildah-Médéah (Berlin).

Mesitius krombeini Nagy, 1968a: 175. Holotype male; India: Mangalore (Washingon).

Mesitius moczari Nagy, 1968a: 172. Holtoype female; Afghanistan: Kandahar-Kuna (Budapest).

Mesitius orcus Nagy, 1972a: 9. Holotype male; Israel: "Palestina" (Nagy Coll.).

Mesitius viator Nagy, 1968a: 171. Holotype female; Russia: Sarepta (Berlin, confirmed).

Parascleroderma cisnora Argaman, 1988b: 147. Holotype male; West Bank: Bethlehem, Wadi-Tekoa (Argaman Coll.).

Parascleroderma fiturcata Argaman, 1988b: 150. Holotype male; Italy: Napoli, Volcano Stromboli (Argaman Coll.).

Parascleroderma hindola Argaman, 1988b: 151. Holotype male; Israel: Tell-Zakarja Junction (Argaman Coll.).

Parascleroderma norcasta Argaman, 1988b: 147. Holotype male; Italy: Liguria, Savona (Argaman Coll.).

Parascleroderma oriana Argaman, 1988b: 148. Holotype male; Israel: Hawwat Eden (Argaman Coll.).

Parascleroderma varlinda Argaman, 1988b: 148. Holotype male; Israel: Sharon Plain, Hofit, Nahal Alexander (Argaman Coll.)

Parasierola swirskiana Argaman, 1992: 195. Holotype female; Israel: Central coastal plain, Mikhmoret, Miramare hotel garden (Tel Aviv, confirmed).

Sulcomesitius hilarius Nagy, 1972a: 16. Holotype female; Ethiopia: "N. Galla, Aberasch" (Tel Aviv [Nagy Coll.], confirmed).

Subspecies:

Mesitius africanus lugubris Nagy, 1970c: 207. Holotype female; Morocco: Tangier (Geneva).

Family Braconidae

Genus: *Kollasmosoma* Achterberg & Argaman, 1993: 64, 66. Type species: *Elasmosoma platamonense* Huddleston, 1976.

Family Dryinidae

Species:

Bocchus scobiolae Nagy, 1967e: 334. Holotype female; Romania: Agigea, Dobroudja (Tel Aviv, confirmed).

Bocchus pedunculatus Nagy, 1969e: 323. Holotype male; Philippines: Palawan, Pinigisan, Mantalingajan (Copenhagen, confirmed).

Family: Heterogynaidae Nagy, 1969b: 299. [Emended from Heterogynidae by ICZN (1987), nec Heterogynidae, Lepidoptera]. Type genus: *Heterogyna* Nagy, 1969.

Genus: *Daycatinca* Argaman, 1986a: 7. Type species: *Heterogyna fantsilotra* Day, 1984. =*Heterogyna* Nagy, 1969. Synonymized by Melo (1999: 34).

Genus: *Heterogyna* Nagy, 1969b: 300. Type species: *Heterogyna protea* Nagy, 1969.

Species:

Heterogyna kugleri Argaman, 1986a: 8. Holotype female; Israel: Nazareth (Argaman Coll.).

Hete*rogyna protea* Nagy, 1969b: 300. Holotype male; Greece: Rhodes, Ixia (Nagy Coll.?).

Family: Kislevidae Argaman, 2002. Type genus: *Kisleva* Argaman, 2002.

Genus: *Kisleva* Argaman, 2002: 112. Type species: *Kisleva ohalona* Argaman, 2002.

Species:

Kisleva ohalona Argaman, 2002: 112. Holotype subfossil head; Israel: Galilee, Locus No. 1, Ohalo II excavation (Bar Ilan).

Family Mutillidae

Subfamily: Ticoplinae Nagy, 1970f: 84. Type genus: *Ticopla* Nagy, 1970.

Tribe: Smicromyrmillini Argaman, 1988c: 36. Type genus: *Smicromyrmilla* Suárez, 1965.

Tribe: Ticoplini Nagy, 1970f: 84. Type genus: *Ticopla* Nagy, 1970.

Genus: *Ticopla* Nagy, 1970f: 85. Type species: *Ticopla yoca* Nagy, 1970. =*Nanomutilla* André, 1900. Synonymized by Mitchell and Brothers (1998: 193 & 2002: 313).

Subgenus: *Arcasina* Nagy, 1970g: 88, 95. Type species: *Ephuta* (*Arcasina*) *chendisa* Nagy, 1970.

Subgenus: *Rhombotilla* Nagy, 1966a: 113. Type species: *Smicromyrme* (*Rhombotilla*) *riparia* Nagy, 1966.

Species:

Dolichomutilla cribraria Nagy, 1968b: 147. Holotype female; Sudan: Khartoum ("Chartoum") (Cluj?).

Ephuta (*Arcasina*) *chendisa* Nagy, 1970g: 88, 96. Holotype male; Surinam (Nagy Coll.).

Ephuta (*Ephuta*) *anephuta* Nagy, 1970g: 88, 92. Holotype female; Brazil: Santa Catarina, Boiteuxburgo (Hamburg).

Ephuta (*Ephuta*) *bilunata* Nagy, 1970g: 87, 89. Holotype female; Brazil: São Paulo, Estancio Mayrink (Hamburg).

Ephuta (*Ephuta*) *buftex* Nagy, 1970g: 88, 91. Holotype female; Brazil: São Paulo, Estancio Mayrink (Hamburg).

Ephuta (*Ephuta*) *bulmaca* Nagy, 1970g: 88, 93. Holotype male; Brazil: São Paulo, Estancio Mayrink (Hamburg).

Ephuta (*Ephuta*) *cumba* Nagy, 1970g: 88, 90. Holotype female; Brazil: Rio de Janeiro, Petropolis (Hamburg).

Ephuta (*Ephuta*) *dorida* Nagy, 1970g: 88, 93. Holotype male; Costa Rica: "Pacific-Seite" (Hamburg).

Ephuta (*Ephuta*) *elanora* Nagy, 1970g: 88, 94. Holotype male; Costa Rica: San José de Costa Rica (Hamburg).

Ephuta (*Ephuta*) *minerva* Nagy, 1970g: 88, 93. Holotype male; Brazil: São Paulo, Estancio Mayrink (Hamburg).

Ephuta (*Ephuta*) *novacula* Nagy, 1970g: 88, 90. Holotype female; Brazil: São Paulo (Nagy Coll.).

Ephuta (*Ephuta*) *olma* Nagy, 1970g: 88, 92. Holotype male; Brazil: Rio Grande do Sul, Santa Cruz (Hamburg).

Ephuta (*Ephuta*) *serapia* Nagy, 1970g: 89, 95. Holotype male; Costa Rica: "Pacific-Seite" (Hamburg).

Ephuta (*Ephuta*) *sicona* Nagy, 1970g: 87, 89. Holotype female; Ecuador: Guyaquil (Nagy Coll.).

Ephuta (*Ephuta*) *verbena* Nagy, 1970g: 89, 94. Holotype male; Costa Rica: San José de Costa Rica (Hamburg).

Ephuta (*Ephuta*) *weidneri* Nagy, 1970g: 87, 89. Holotype female; Brazil: São Paulo (Hamburg).

Ephuta (*Ephuta*) *yarasirda* Nagy, 1970g: 88, 92. Holotype male; Argentina: District Mendoza (Hamburg).

Myrmilla atalanta Nagy, 1967b:52. Holotype male; Romania: Dobroutcha, "dunes maritimes d'Agigea" (Nagy Coll.). =*Myrmilla* (*Pseudomutilla*) *atalanta* Nagy. Subgenus specified by Lelej (2002: 36).

Myrmilla labecua Nagy, 1968c: 68. Holotype female; Romania: Cluj (Nagy Coll.).

Myrmilla macrura Nagy, 1968c: 65. Holotype female; Romania: Cluj (Nagy Coll.).

Nanomutilla nadae Argaman, 1988c: 38. Holotype female; south Spain (Argaman Coll.). Spelling of specific name fixed by Mitchell & Brothers (2002: 313).

Smicromyrme borceai Nagy, 1968f: 220. Holotype female; Romania: Agigea (Nagy Coll.). Placed in subgenus *Erimyrme* Lelej, 1985 by Lelej (2002: 68).

Smicromyrme (*Edrionotus*) *ursina* Nagy, 1972c: 4. Holotype female; Turkey: Ankara, Salt Lake (Tuz-Gölü) (Nagy Coll.). =*Dentilla ursina* (Nagy). Transferred by Lelej & Kabakov (1980: 195).

Smicromyrme (*Rhombotilla*) *riparia* Nagy, 1966a: 115. Holotype female; Romania: Agigea (Nagy Coll.).

Smicromyrme (*Rhombotilla*) *vinuta* Nagy, 1972c: 5. Holotype male; Afghanistan, Kabul vicinity (Nagy Coll.). =*Promecilla vinuta* (Nagy). Transferred by Lelej & Kabakov (1980: 192).

Smicromyrme (*Smicromyrme*) *terricola* Nagy, 1972b: 29. Holotype female; Greece: "Nea Peramos" (Nagy Coll.). Considered incertae sedis by Lelej (2002: 79).

Smicromyrme (*Smicromyrme*) *tumidula* Nagy, 1972b: 27. Holotype female; Greece: "Parnals" (Nagy Coll.). Considered incertae sedis by Lelej (2002: 79).

Smicromyrme (*Smicromyrme*) *weidneri* Nagy, 1971a:167. Holotype female: Iran ("Persien") (Hamburg, confirmed). =*Dentilla weidneri* (Nagy). Transferred by Lelej & Kabakov (1980: 195).

Ticopla parila Nagy, 1970f: 85. Holotype male; Jordan: Amman (Nagy Coll.). =*Nanomutilla parila* (Nagy). Transfer implied by Mitchell & Brothers (2002: 313).

Ticopla yoca Nagy, 1970f: 85. Holotype male; Jordan (Nagy Coll.) =*Nanomutilla yoca* (Nagy). Transferred by Mitchell & Brothers (2002: 313).

Family Perilampidae

Genus: *Bagdasar* Argaman, 1990a: 212, 250. Type species: *Bagdasar amnonius* Argaman, 1990. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 120).

Genus: *Balintos* Argaman, 1990a: 205, 241. Type species: *Perilampus parvus* Howard, 1896. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 107).

Genus: *Bukbakas* Argaman, 1990a: 229, 261. Type species: *Perilampus microgastris* Ferrière, 1930. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 126).

Genus: *Dekterek* Argaman, 1990a: 230, 262. Type species: *Perilampus granulosus* Crawford, 1914. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 124).

Genus: *Durgadas* Argaman, 1990a: 205, 239. Type species: *Durgadas pappi* Argaman, 1990. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 114).

Genus: *Ecalibur* Argaman, 1990a: 228, 260. Type species: *Perilampus robertsoni* Crawford, 1914. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 122).

Genus: *Fifirtiz* Argaman, 1990a: 225, 259. Type species: *Perilampus noemi* Nikolskaya, 1952. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 117).

Genus: *Fulaytar* Argaman, 1990a: 208, 243. Type species: *Perilampus singaporensis* Rohwer, 1923. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 110).

Genus: *Goyurfis* Argaman, 1990a: 205, 242. Type species: *Perilampus platigaster* Say, 1836. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 114).

Genus: *Ihrambek* Argaman, 1990a: 213, 252. Type species: *Perilampus chrysonotus* Foerster, 1859. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 124; misspelled as *Ihambrek*).

Genus: Itonayis Argaman, 1990a: 211, 248. Type species: *Perilampus micans* Dalman, 1820. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 119).

Genus: *Kekender* Argaman, 1990a: 201, 233. Type species: *Kekender bouceki* Argaman, 1990. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 107).

Genus: *Lufarfar* Argaman, 1990a: 232; 1991a: 3. Type species: *Lufarfar rainerius* Argaman, 1990. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 125).

Genus: *Mivarhis* Argaman, 1990a: 219, 255. Type species: *Perilampus laevifrons* Dalman, 1822. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 127).

Genus: *Naspoyar* Argaman, 1990a: 228, 261. Type species: *Perilampus fulvicornis* Ashmead, 1886. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 121).

Genus: *Nilgator* Argaman, 1990a: 207, 242. Type species: *Perilampus mirabeaui* Girault, 1930. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 108).

Genus: *Olarlar* Argaman, 1990a: 214, 252. Type species: *Chalcis aenea* Rossi, 1790 and *Olarlar cocegus* Argaman, 1990. *Chalcis aenea* Rossi was designated as the type species by Darling (1996: 114, 116). =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 116).

Genus: *Pondoros* Argaman, 1990a: 230; 1991a: 1. Type species: *Perilampus tristis* Mayr, 1905. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 125).

Genus: *Sicatang* Argaman, 1990a: 225, 257. Type species: *Sicatang catilus* Argaman, 1990. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 117).

Genus: *Taltonos* Argaman, 1990a: 201, 234. Type species: *Perilampus hyalinus* Say, 1828. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 113).

Genus: *Tiboras* Argaman, 1990a: 208, 243. Type species: *Perilampus maurus* Walker, 1852. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 110).

Genus: *Tondolos* Argaman, 1990a: 208, 243. Type species: *Perilampus tasmanicus* Cameron, 1911. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 110).

Genus: *Vadramas* Argaman, 1990a: 223, 255. Type species: *Perilampus nigriviridis* Girault, 1912. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 116).

Genus: *Vaktaris* Argaman, 1990a: 211, 248. Type species: Cynips auratus Panzer, 1798. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 119).

Genus: *Yertatop* Argaman, 1990a: 207, 242. Type species: *Perilampus emersoni* Girault, 1930. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 107).

Genus: *Zuglavas* Argaman, 1990a: 212, 251. Type species: *Perilampus stygicus* Provancher, 1888. =*Perilampus* Latreille, 1809. Synonymized by Darling (1996: 122).

Species:

Afroperilampus delbotor Argaman, 1990a: 211, 247. Holotype female; Uganda: Mujenje (Budapest, confirmed). =*Perilampus delbotor* (Argaman). Transfer implied by Darling (1996: 111, 127).

Afroperilampus horocos Argaman, 1990a: 210, 246. Holotype male; "Africa Or.[ientale]": Arusha (Budapest, confirmed). =*Perilampus horocos* (Argaman). Transfer implied by Darling (1996: 111, 127).

Afroperilampus hurap Argaman, 1990a: 209, 245. Holotype female; Uganda: Bussu (Genoa, confirmed). =*Perilampus hurap* (Argaman). Transfer implied by Darling (1996: 111, 127).

Afroperilampus liliae Argaman, 1990a: 210, 245. Holotype male; Algeria: Biskra (Genoa, confirmed). =*Perilampus liliae* (Argaman). Transfer implied by Darling (1996: 111, 127).

Bagdasar amnonius Argaman, 1990a: 212, 251. Holotype female; South Africa: Natal, Pietermaritzburg, Ashburton (Argaman Coll.). =*Perilampus amnonius* (Argaman). Transfer implied by Darling (1996: 120).

Bukbakas casevitzi Argaman, 1990a: 229, 262. Holotype male; South Africa: Pretoria (Argaman Coll.). =*Perilampus casevitzi* (Argaman). Transfer implied by Darling (1996: 126).

Durgadas pappi Argaman, 1990a: 205, 239. Holotype female; Brazil: Para, Rio Acara (Budapest, confirmed). =*Perilampus pappi* (Argaman). Transfer implied by Darling (1996: 114).

Fifirtiz mavricus Argaman, 1990a: 227, 260. Holotype female; Egypt: "H.-I. Sinai, Ofira" (Argaman Coll.). =*Perilampus mavricus* (Argaman). Transfer implied by Darling (1996: 117).

Fifirtiz turpiculus Argaman, 1990a: 226, 259. Holotype male; Israel: Upper Galilee, Hula Valley Natural Reserve (Argaman Coll.). =*Perilampus turpiculus* (Argaman). Transfer implied by Darling (1996: 117).

Goyurfis dobnos Argaman, 1990a: 199. New replacement name for *Perilampus antennatus* Cameron, 1897 nec *Perilampus antennatus* Walker, 1834. =*Perilampus dobnos* (Argaman). Transfer implied by Darling (1996: 114).

Kekender bouceki Argaman, 1990a: 201, 233. Holotype male; Kenya: Muto-Berg (Argaman Coll.). =*Perilampus bouceki* (Argaman). Transfer implied by Darling (1996: 107).

Lufarfar nimrodus Argaman, 1990a: 232; 1991a: 4. Holotype female; "Africa or.[ientale]": Assab (Budapest, confirmed). =*Perilampus nimrodus* (Argaman). Transfer implied by Darling (1996: 125).

Lufarfar rainerius Argaman, 1990a: 232; 1991a: 4. Holotype female; Egypt: Gebel Asfar (Genoa, confirmed). =*Perilampus rainerius* (Argaman). Transfer implied by Darling (1996: 125).

Olarlar cocegus Argaman, 1990a: 214, 252. Holotype female; South Africa: "Meester-Cornelis, Transvaal" (Argaman Coll.). =*Perilampus cocegus* (Argaman). Transfer implied by Darling (1996: 116).

Perilampus uris Argaman, 1990a: 199. New replacement name for *Perilampus carinifrons* Mani et Kaul, 1973 nec *Perilampus carinifrons* Crawford, 1914.

Pondoros kittenbergeri Argaman, 1990a: 230; 1991a: 2. Holotype female; Uganda: Mujenje (Budapest, confirmed). =*Perilampus kittenbergeri* (Argaman). Transfer implied by Darling (1996: 125).

Pondoros moczari Argaman, 1990a: 232; 1991a: 2. Holotype female; Afghanistan: Nuristan, Bashgul-Tal, Achmede Dewane (Budapest, confirmed). =*Perilampus moczari* (Argaman). Transfer implied by Darling (1996: 125).

Sicatang catilus Argaman, 1990a: 225, 258. Holotype male; Turkey: Anatolia, "Tschukur-hissar" (Argaman Coll.). =*Perilampus catilus* (Argaman). Transfer implied by Darling (1996: 117).

Sicatang picpus Argaman, 1990a: 225, 258. Holotype female; Korea: Gang-von, Ondzong, Kum-gang san, along Ok-ru dong (Budapest, confirmed). =*Perilampus picpus* (Argaman). Transfer implied by Darling (1996: 117).

Taltonos azureus Argaman, 1990a: 203, 235. Holotype female; Argentina: Tucuman (Budapest, confirmed). =*Perilampus azureus* (Argaman). Transfer implied by Darling (1996: 113).

Taltonos birous Argaman, 1990a: 203, 237. Holotype female; Brazil: Santa Cruz (Budapest, confirmed). =*Perilampus birous* (Argaman). Transfer implied by Darling (1996: 113).

Taltonos dumcas Argaman, 1990a: 203, 236. Holotype female; Argentina: Tucuman (Budapest, confirmed). =*Perilampus dumcas* (Argaman). Transfer implied by Darling (1996: 113).

Taltonos jolaus Argaman, 1990a: 204, 238. Holotype female; [Brazil:] Sao Paulo (Budapest, confirmed). =*Perilampus jolaus* (Argaman). Transfer implied by Darling (1996: 113).

Taltonos sirsiris Argaman, 1990a: 199. New replacement name for *Perilampus cyaneus* Brullé, 1846 nec *Perilampus cyaneus* Fabricius, 1798. =*Perilampus sirsiris* (Argaman). Transfer implied by Darling (1996: 113).

Taltonos tutubas Argaman, 1990a: 202, 235. Holotype female; Argentina: Mendoza (Budapest, confirmed). =*Perilampus tutubas* (Argaman). Transfer implied by Darling (1996: 113).

Taltonos xirgus Argaman, 1990a: 203, 236. Holotype male; Brazil: Para, Faro (Budapest, confirmed). =*Perilampus xirgus* (Argaman). Transfer implied by Darling (1996: 113).

Vadramas tetar Argaman, 1990a: 225, 257. Holotype male; Nicaragua: "Sierra di Managua" (Genoa, confirmed). =*Perilampus tetar* (Argaman). Transfer implied by Darling (1996: 116).

Vaktaris ganuz Argaman, 1990a: 212, 249. Holotype male; Israel: near Dead Sea (Tel Aviv). =*Perilampus ganuz* (Argaman). Transfer implied by Darling (1996: 119).

Vaktaris ilvauber Argaman, 1990a: 211, 249. Holotype female; Guatemala: Punta Gorda (Argaman Coll.). =*Perilampus ilvauber* (Argaman). Transfer implied by Darling (1996: 119).

Family Plumariidae

Species:

Plumarius argentinus Nagy, 1973c: 259, 266. Holotype male; Argentina: Rio Negro, Norquinco (Budapest, confirmed).

Plumarius baloghi Nagy, 1973c: 258, 259. Holotype male; Chile: Tarapaca Prov., Azapa (Budapest, confirmed).

Plumarius chilensis Nagy, 1973c: 258, 262. Holotype male; Chile: Tarapaca Prov., Azapa (Budapest, confirmed).

Plumarius densepunctatus Nagy, 1973c: 259, 265. Holotype male; Chile: Coquimbo Prov., El Tangue (Nagy Coll.).

Plumarius topali Nagy, 1973c: 258, 260. Holotope male; Argentina: Rio Negro, Norquinco (Budapest, confirmed).

Family Sclerogibbidae

Subfamily: Caenosclerogibbinae Argaman, 1988a: 178. Type genus *Caenosclerogibba* Yasumatsu, 1958. =Sclerogibbidae Ashmead, 1902. Synonymy implied by Olmi (2005) in not recognizing higher taxa within Sclerogibbidae.

Subfamily: Probethylinae Argaman, 1988a: 178. Type genus *Probethylus* Ashmead, 1902. =Sclerogibbidae Ashmead, 1902. Synonymy implied by Olmi (2005) in not recognizing higher taxa within Sclerogibbidae.

Tribe: Tanynotini Argaman, 1988a: 178. Type genus *Tanynotus* Cameron, 1904. =Sclerogibbidae Ashmead, 1902. Synonymy implied by Olmi (2005) in not recognizing higher taxa within Sclerogibbidae.

Tribe: Parasclerogibbini Argaman, 1988a: 178. Type genus *Parasclerogibba* Hamann, 1958. =Sclerogibbidae Ashmead, 1902. Synonymy implied by Olmi (2005) in not recognizing higher taxa within Sclerogibbidae.

Genus: *Poggiana* Argaman, 1993: 540, 541. Type species: *Poggiana pilosella* Argaman, 1993. =*Sclerogibba* Riggio & De Stefani-Perez, 1888. Synonymized by Olmi (2005: 120).

Species:

Poggiana pilosella Argaman, 1993: 543. Holotype female; Italy: Sardinia, Tavolara Archipelago, Isola Molarotto (Genoa, confirmed). =*Sclerogibba berlandi* Benoit, 1963. Synonymized by Olmi (2005: 129).

Prosclerogibba dessarti Argaman, 1993: 550. Holotype male; Togo: Sokode (Brussels, confirmed). =*Sclerogibba vagabunda* (Bridwell, 1919). Synonymized by Olmi (2005: 180).

Family Scolebythidae

Genus: *Ycaploca* Nagy, 1975c: 75. Type species: *Ycaploca evansi* Nagy, 1975.

Species:

Ycaploca evansi Nagy, 1975c: 75. Holotype female; South Africa: Cape, Kirstenbosch (Nagy Coll.).

Family Scoliidae (Argaman (1996) was deliberately not taken into account by Osten (2005) in compiling his checklist of Scoliidae of the world. Elliott (2011) recognized that Osten (2005) implicitly synonymized some Argaman genera by placing their type species in other genera or subgenera, and we have followed this approach, although some of Argaman's type species may have been misidentified since he did not examine their type material. Argaman's (1996) numerous new names and other nomenclatural acts thus still need more critical evaluation beyond that possible here.)

Subfamily: Colpinae Argaman, 1996: 180. Type genus: *Colpa* Dufour, 1841. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Agombardini Argaman, 1996: 193. Type genus: *Agombarda* Argaman, 1996. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 27).

Tribe: Ascoliini Argaman, 1996: 187. Type genus: *Ascolia* Argaman, 1996. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 37).

Tribe: Austroscoliini Argaman, 1996: 191. Type genus: *Austroscolia* Betrem, 1928. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 26).

Tribe: Betremiini Argaman, 1996: 197. Type genus: *Betremia* Bradley, 1948. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 26).

Tribe: Carinoscoliini Argaman, 1996: 191. Type genus: *Carinoscolia* Betrem, 1927. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 26).

Tribe: Colpacampsomerini Argaman, 1996: 209. Type genus: *Colpacampsomeris* Betrem, 1941. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Colpini Argaman, 1996: 184. Type genus: *Colpa* Dufour, 1841. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Curtaurgini Argaman, 1996: 182. Type genus: *Curtaurga* Argaman, 1996. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Dasyscoliini Argaman, 1996: 181. Type genus: *Dasyscolia* Bradley, 1951. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Dielidini Argaman, 1996: 212. Type genus: *Dielis* Saussure & Sichel, 1864. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Discoliini Argaman, 1996: 197. Type genus: *Discolia* Saussure, 1863. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 26).

Tribe: Dobrobetini Argaman, 1996: 205. Type genus: *Dobrobeta* Argaman, 1996. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 22).

Tribe: Hangasornini Argaman, 1996: 197. Type genus: *Hangasorna* Argaman, 1996. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 41).

Tribe: Heterelini Argaman, 1996: 183. Type genus: *Heterelis* Costa, 1887. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Lisocini Argaman, 1996: 199. Type genus: *Lisoca* Costa, 1858. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 26).

Tribe: Megacampsomerini Argaman, 1996: 211. Type genus: *Megacampsomeris* Betrem, 1928. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Megascoliini Argaman, 1996: 199. Type genus: *Megascolia* Betrem, 1928. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 26).

Tribe: Pseudotrielidini Argaman, 1996: 205. Type genus: *Pseudotrielis* Betrem, 1928. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Tetrascitonini Argaman, 1996: 201. Type genus: *Tetrasciton* Betrem, 1927. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 8).

Tribe: Trisciloini Argaman, 1996: 201. Type genus: *Trisciloa* Gribodo, 1893. =Campsomerini Betrem in Betrem & Bradley, 1972. Synonymy implied by Osten (2005: 3).

Tribe: Triscoliini Argaman, 1996: 193. Type genus: *Triscolia* Saussure, 1863. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 26).

Tribe: Ycasbraini Argaman, 1996: 191. Type genus: *Ycasbraia* Argaman, 1996. =Scoliini Latreille, 1802. Synonymy implied by Osten (2005: 42).

Genus: *Agombarda* Argaman, 1996: 194. Type species: *Scolia atra* Illiger, 1802. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 27).

Genus: *Ascolia* Argaman, 1996: 188. Type species: *Scolia flavifrons* Fabricius, 1775. Intended as an emendation of *Ascoli* Guérin-Méneville, 1838 but that name is not available since it was proposed for a hypothetical taxon (Guérin-Méneville 1838) and *Ascolia* must thus be regarded as a new genus. =*Regiscolia* Betrem & Bradley, 1964. Synonymy implied by Osten (2005: 37). (The name *Ascoli* has had a checkered history, being cited in synonymy of *Triscolia* Saussure, 1863 by Saussure & Sichel (1864) but being used as valid by Betrem (1926) and thereby technically being made available (ICZN 1999, Article 11.6.1). It has not been used as valid since, and a type species has never been designated. Jacot-Guillarmod et al. (1963) requested the International Commission on Zoological Nomenclature to suppress *Ascoli* as used by Guérin-Ménéville (1838) and Betrem (1926), but an Opinion on this has never been issued, which means that prevailing usage (which regards it as unavailable) should be maintained (ICZN 1999, Article 82.1).)

Genus: *Bagonasuna* Argaman, 1996: 186. Type species: *Trielis tartara* Morawitz, 1897. =*Crioscolia* Bradley, 1951. Synonymy implied by Osten (2005: 23); Morawitz ("1897") dealt with *Trielis tartara* (Saussure, 1880) var. *mongolica* Morawitz, 1889, however (Morawitz's paper was actually published in 1896, see Oshanin (1910)).

Genus: *Batalanga* Argaman, 1996: 205. Type species: *Elis phalerata* Saussure, 1858. Proposed as a new replacement name for *Phalerimeris* Betrem, 1967 not Betrem, 1966. =*Phalerimeris* Betrem, 1967. *Batalanga* is an objective synonym of *Phalerimeris* Betrem, 1967 because "*Phalerimeris* Betrem, 1966" is not an available name, merely appearing without any description and stated to be a nomen nudum (Bradley & Betrem 1966: 74), and therefore cannot be a senior homonym of *Phalerimeris* Betrem, 1967. (For "*Phalerimeris* Betrem, 1966" Argaman (1996: 205) used "*Phaleromeris* Bradley, 1964" but that too is not an available name, having no description (Bradley 1964: 193); *Annulimeris* Betrem, 1967 should be used for that taxon.)

Genus: *Borongorba* Argaman, 1996: 213. Type species: *Scolia habrocoma* Smith, 1855. =*Megacampsomeris* Betrem, 1928. Synonymy implied by Osten (2005: 12).

Genus: *Burgamurga* Argaman, 1996: 194. Type species: *Scolia cyanipennis* Fabricius, 1804. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 30).

Genus: *Buzatlana* Argaman, 1996: 200. Type species: *Scolia fuciformis* Scopoli, 1786. =*Scolia* Fabricius, 1775. Synonymy implied by Osten (2005: 33).

Genus: *Citberaysa* Argaman, 1996: 192. Type species: *Scolia ebenina* Saussure, 1858. =*Austroscolia* Betrem, 1928. Synonymy implied by Osten (2005: 31).

Genus: *Curtaurga* Argaman, 1996: 183. Type species: *Scolia aliena* Klug, 1832. Proposed as a new replacement name for *Guigliana* Betrem, 1967 not Bradley, 1964. =*Guigliana* Betrem, 1967. *Curtaurga* is an objective synonym of *Guigliana* Betrem because "*Guigliana* Bradley, 1964" is not an available name, merely appearing as "*Scolia* (*Guigliana*) *azurea azurea* Christ" without any description (Bradley 1964: 192), and therefore cannot be a senior homonym of *Guigliana* Betrem. (Osten (2005: 27) placed *S. azurea* Christ in *Megascolia* (*Regiscolia*); there is thus no need for another name for Argaman's concept of "*Guigliana* Bradley, 1964".)

Genus: *Dobrobeta* Argaman, 1996: 206. Type species: *Campsomeris socotrana* Kirby, 1900. =*Cathimeris* Betrem, 1972. Synonymy implied by Osten (2005: 22).

Genus: *Elpaholta* Argaman, 1996: 194. Type species: *Scolia fulvifrons* Saussure, 1854. =*Regiscolia* Betrem & Bradley, 1964. Synonymy implied by Osten (2005: 33).

Genus: *Fiharbuxa* Argaman, 1996: 212. Type species: *Scolia prismatica* Smith, 1855. =*Megacampsomeris* Betrem, 1928. Synonymy implied by Osten (2005: 19).

Genus: *Gondiconda* Argaman, 1996: 210. Type species: *Elis vittata* Sichel, 1864. =*Pygodasis* Bradley, 1957. Synonymy implied by Osten (2005: 25).

Genus: *Hangasorna* Argaman, 1996: 197. Type species: *Scolia quadripustulata* Fabricius, 1782. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 41).

Genus: *Haralambia* Argaman, 1996: 215. Type species: *Tiphia dorsata* Fabricius, 1787. =*Dielis* Saussure & Sichel, 1864. Synonymy implied by Osten (2005: 10).

Genus: *Hayderiba* Argaman, 1996: 209. Type species: *Colpa peregrina* Lepeletier, 1845. New replacement name for *Colpa* Lepeletier, 1845 not Dufour, 1841. =*Campsomeris* Guérin-Ménéville, 1838. Synonymy implied by Osten (2005: 19).

Genus: *Hitfoidra* Argaman, 1996: 192. Type species: *Scolia carnifex* Coquerel, 1855. =*Austroscolia* Betrem, 1928. Synonymy implied by Osten (2005: 29).

Genus: *Iforborha* Argaman, 1996: 203. Type species: *Tiphia collaris* Fabricius, 1775. =*Campsomeriella* Betrem, 1941. Synonymy implied by Osten (2005: 8).

Genus: *Iksalonca* Argaman, 1996: 199. Type species: *Scolia jurinei* Saussure, 1854. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 36).

Genus: *Ilkamilka* Argaman, 1996: 212. Type species: *Campsomeris luzonensis* Rohwer, 1921. =*Megacampsomeris* Betrem, 1928. Synonymy implied by Osten (2005: 16).

Genus: *Jupadora* Argaman, 1996: 193. Type species: *Scolia cerberia* Bradley, 1959. =*Microscolia* Betrem, 1927. Synonymy implied by Osten (2005: 29); the specific name is also spelled "*cereberia*" in Bradley (1959), the spelling used by Osten.

Genus: *Katapolda* Argaman, 1996: 198. Type species: *Scolia desidiosa* Bingham, 1896. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 30).

Genus: *Kokarevta* Argaman, 1996: 200. Type species: *Scolia histrionica* Fabricius, 1787. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 35).

Genus: *Kukkiya* Argaman, 1996: 187. Type species: *Scolia moricei* Saunders, 1901. =*Crioscolia* Bradley, 1951. Synonymy implied by Osten (2005: 17).

Genus: *Lacosia* Argaman, 1996: 199. Type species: *Scolia pygmaea* Saussure, 1858. Proposed as an emendation of *Lacosi* Guérin-Méneville, 1838, but must be considered as a new genus different in concept, since Bequaert (1926) had correctly designated the type species of *Lacosi* as *Scolia quadripunctata* Fabricius, 1775, and *S. pygmaea* was not an originally included species of *Lacosi* Guérin-Méneville. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 35).

Genus: *Laskariska* Argaman, 1996: 188. Type species: *Scolia haemorrhoidalis* Fabricius, 1787. =*Regiscolia* Betrem & Bradley, 1964. Synonymy implied by Osten (2005: 37).

Genus: *Lobhargita* Argaman, 1996: 208. Type species: *Scolia aureola* Klug, 1832. =*Micromeriella* Betrem, 1972. Synonymy implied by Osten (2005: 5).

Genus: *Molzinarda* Argaman, 1996: 192. Type species: *Scolia nitida* Smith, 1858. =*Austroscolia* Betrem, 1928. Synonymy implied by Osten (2005: 39).

Genus: *Mookitena* Argaman, 1996: 215. Type species: *Campsomeris hesterae* Rohwer, 1927. =*Xanthocampsomeris* Bradley, 1957. Synonymy implied by Osten (2005: 12).

Genus: *Murahutka* Argaman, 1996: 190. Type species: *Scolia quadriceps* Smith, 1859. =*Diliacos* Saussure & Sichel, 1864. Synonymy implied by Osten (2005: 41).

Genus: *Naysebwa* Argaman, 1996: 200. Type species: *Scolia fulvofimbriata* Burmeister, 1853. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 33).

Genus: *Niyaranta* Argaman, 1996: 213. Type species: *Scolia aurulenta* Smith, 1855. =*Phalerimeris* Betrem, 1967 (not Bradley, 1974). Synonymy implied by Osten (2005: 6).

Genus: *Nokbibula* Argaman, 1996: 191. Type species: *Scolia vittifrons* Sichel, 1864. =*Carinoscolia* Betrem, 1927. Synonymy implied by Osten (2005: 45).

Genus: *Noybarilta* Argaman, 1996: 211. Type species: *Scolia hoffmannseggii* [sic] Klug, 1805. =*Lissocampsomeris* Bradley, 1957. Synonymy implied by Osten (2005: 13).

Genus: *Onkoknoa* Argaman, 1996: 195. Type species: *Scolia bilunulata* Saussure, 1858. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 28).

Genus: *Ordatirga* Argaman, 1996: 185. Type species: *Dielis mima* Buysson, 1897. =*Heterelis* Costa, 1887. Synonymy implied by Osten (2005: 17).

Genus: *Orlovinga* Argaman, 1996: 199. Type species: *Scolia gussakovskii* Steinberg, 1953. =*Scolia* Fabricius, 1775. Synonymy implied by Osten (2005: 34).

Genus: *Oscalosca* Argaman, 1996: 214. Type species: *Elis pilipes* Saussure, 1858. =*Dielis* Saussure & Sichel, 1864. Synonymy implied by Osten (2005: 19).

Genus: *Paconzitva* Argaman, 1996: 196. Type species: *Scolia alecto* Smith, 1858. =*Regiscolia* Betrem & Bradley, 1964. Synonymy implied by Osten (2005: 26).

Genus: *Pardesiya* Argaman, 1996: 200. Type species: *Scolia neglecta* Cyrillo, 1787. =*Scolia* Fabricius, 1775. Synonymy implied by Osten (2005: 29).

Genus: *Pupunhuga* Argaman, 1996: 203. Type species: *Campsomeris sauteri* Betrem, 1928. =*Scolia* Fabricius, 1775. Synonymy implied by Osten (2005: 42).

Genus: *Rahosmula* Argaman, 1996: 190. Type species: *Scolia sicheli* Saussure, 1859. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 43).

Genus: *Rihamlika* Argaman, 1996: 195. Type species: *Scolia venusta* Smith, 1855. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 45).

Genus: *Rostopasca* Argaman, 1996: 187. Type species: *Scolia erivanensis* Radoszkowski, 1879. =*Scolia* Fabricius, 1775 (?). Possible synonymy implied by Osten (2005: 31).

Genus: *Rucarcana* Argaman, 1996: 206. Type species: *Campsomeris congener* Turner, 1909. =*Pseudotrielis* Betrem, 1928. Synonymy implied by Osten (2005: 9).

Genus: *Sisakrosa* Argaman, 1996: 204. Type species: *Dielis angulata* Morawitz, 1888. =*Micromeriella* Betrem, 1972. Synonymy implied by Osten (2005: 13).

Genus: *Sobolpiha* Argaman, 1996: 190. Type species: *Scolia ribbei* Betrem, 1928. =*Diliacos* Saussure & Sichel, 1864. Synonymy implied by Osten (2005: 41).

Genus: *Stiboranna* Argaman, 1996: 198. Type species: *Scolia hova* Saussure, 1891. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 35).

Genus: *Sugorpilfa* Argaman, 1996: 196. Type species: *Scolia philippinensis* Rohwer, 1921. =*Regiscolia* Betrem & Bradley, 1964. Synonymy implied by Osten (2005: 40).

Genus: *Susaynata* Argaman, 1996: 212. Type species: *Camposmeris cochinensis* Betrem, 1928. =*Megacampsomeris* Betrem, 1928. Synonymy implied by Osten (2005: 8).

Genus: *Tatusdayca* Argaman, 1996: 208. Type species: *Scolia ephippium* Say, 1837. =*Pygodasis* Bradley, 1957. Synonymy implied by Osten (2005: 10).

Genus: *Titbisayda* Argaman, 1996: 213. Type species: *Campsomeris binghami* Betrem, 1928. =*Megacampsomeris* Betrem, 1928. Synonymy implied by Osten (2005: 6).

Genus: *Tonsoygata* Argaman, 1996: 192. Type species: *Scolia verticalis* Fabricius, 1775. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 45).

Genus: *Torbesula* Argaman, 1996: 211. Type species: *Elis columba* Saussure, 1858. =*Lissocampsomeris* Bradley, 1957. Synonymy implied by Osten (2005: 8).

Genus: *Turturayca* Argaman, 1996: 190. Type species: *Scolia fulgidipennis* Smith, 1859. =*Liacos* Guérin-Ménéville, 1838. Synonymy implied by Osten (2005: 33).

Genus: *Ululanca* Argaman, 1996: 189. Type species: *Scolia nigrita* Fabricius, 1782. =*Liacos* Guérin-Ménéville, 1838. Synonymy implied by Osten (2005: 38).

Genus: *Uthakkara* Argaman, 1996: 202. Type species: *Campsomeris celebensis* Betrem, 1928. =*Megacampsomeris* Betrem, 1928. Synonymy implied by Osten (2005: 8).

Genus: *Vardombra* Argaman, 1996: 198. Type species: *Scolia picteti* Saussure, 1854. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 40).

Genus: *Vobalayca* Argaman, 1996: 201. Type species: *Scolia hortorum* Fabricius, 1787. =*Scolia* Fabricius, 1775. Synonymy implied by Osten (2005: 35).

Genus: *Wogungela* Argaman, 1996: 198. Type species: *Scolia micromelas* Sichel, 1864. =*Discolia* Saussure, 1863. Synonymy implied by Osten (2005: 38).

Genus: *Xirgoniqua* Argaman, 1996: 196. Type species: *Scolia capitata* Fabricius, 1804. =*Regiscolia* Betrem & Bradley, 1964. Synonymy implied by Osten (2005: 29).

Genus: *Ycasbraia* Argaman, 1996: 193. Type species: *Scolia rufiventris* Fabricius, 1804. =*Hesperoscolia* Bradley, 1974. Synonymy implied by Osten (2005: 42); actually an objective synonym.

Genus: *Yohaida* Argaman, 1996: 186. Type species: *Scolia klugi* van der Linden, 1829. =*Colpa* Dufour, 1841. Synonymy implied by Osten (2005: 14).

Genus: *Zazilayza* Argaman, 1996: 188. Type species: *Scolia rubida* Gribodo, 1893. =*Regiscolia* Betrem & Bradley, 1964. Synonymy implied by Osten (2005: 42).

Species:

[*Discolia kugleri* Nagy, 1979. This is an unavailable manuscript name and date on several specimens in the Tel Aviv Collection, which evidently has never been published; it was given as a synonym of *Scolia fallax* Eversmann, 1849 by Osten (2002: 347).]

[*Megascolia flavifrons* f. *vernalis* Nagy, 1967d: 223. "Holotype" female; Romania: Nicolina near Iaşi (Nagy Coll.). Name not available (Article 15.2, ICZN 1999).]

[*Megascolia flavifrons* f. *vespertina* Nagy, 1967d: 223. "Holotype" female; Romania: Agigea (Nagy Coll.). Name not available (Article 15.2, ICZN 1999).]

Scolia (*Scolia*) *incana* Nagy, 1970k: 322. Holotype female; Mongolia: Bajanchongor aimak, Echin gol, cca 90 km NO von Grenzposten Caganbulag (Budapest, confirmed). =*Scolia* (*Scolia*) *concolor* Eversmann, 1849. Synonymized by Osten (1997: 517).

Scolia (Discolia) mongolina Nagy, 1970k: 323. Holotype female; Mongolia: Bulgan aimak, 4 km S von Somon Daschinĕilen (Budapest, confirmed). =*Scolia hirta* Schrank, 1781. Synonymized by Osten (1997: 515).

Scolioides alutus Nagy, 1967d: 224. Holotype male; Romania: Murta, Oltenia (Nagy Coll.). =*Scolia hirta* Schrank, 1781. Synonymized by Hamon (1993: 95).

Family Sierolomorphidae

>Species:
>
>*Sierolomorpha isis* Nagy, 1971b: 247. Holotype female; Samarkand (Nagy Coll.).
>
>*Sierolomorpha atropos* Nagy, 1971b: 248. Holotype female; N. China: Kerulen (Nagy Coll.).

Family Tiphiidae [many treated under Family Myzinidae by Nagy/Argaman, but generally considered as subfamily Myzininae Ashmead, 1899]

Subfamily: Iswarinae Argaman, 1994b: 89. Type genus: *Iswara* Westwood, 1850. =Meriina Argaman, 1994. Synonymized by Boni Bartalucci (2004a: 1245).

Subfamily: Meriinae Argaman, 1994b: 91. Type genus: *Meria* Illiger, 1807. Considered as tribe Meriini Argaman, 1994 by Boni Bartalucci (2004a: 1218).

Subfamily: Mesinae Argaman, 1994b: 90. Type genus: *Mesa* Saussure, 1892. Considered as tribe Mesini Argaman, 1994 by Boni Bartalucci (2004a: 1218).

Subfamily: Silifkinae Argaman & Özbek, 1992: 5. Type genus: *Silifka* Argaman & Özbek, 1992. Considered as tribe Silifkini Argaman & Özbek, 1992 by Yildirim & Boni Bartalucci (2009: 2054).

Tribe: Acblasini Argaman & Özbek, 1992: 10. Type genus: *Acblasa* Argaman in Argaman & Özbek, 1992. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Burdufini Argaman & Özbek, 1992: 11. Type genus: *Burdufa* Argaman in Argaman & Özbek, 1992. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Cabaraxini Argaman & Özbek, 1992: 10. Type genus *Cabaraxa* Nagy, 1974. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Epomidiopterini Argaman & Özbek, 1992: 8. Type genus *Epomidiopteron* Romand, 1835. =Silifkini Argaman & Özbek, 1992. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Siflikini.

Tribe: Hylomesini Agaman, 1994b: 90. Type genus: *Hylomesa* Krombein, 1968. =Mesini Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in not recognizing higher taxa within Mesini.

Tribe: Icronathini Argaman & Özbek, 1992: 11. Type genus: *Icronatha* Nagy, 1967. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Illoswiini Argaman, 1994b: 92. Type genus: *Illoswia* Argaman, 1994. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Iswarini Argaman, 1994b: 89. Type genus: *Iswara* Westwood, 1850. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Jaynesiini Argaman & Özbek, 1992: 10. Type genus: *Jaynesia* Allen, 1969. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Komarowiini Argaman, 1994b: 92. Type genus: *Komarowia* Radoszkowski, 1886. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Krombeiniini Argaman & Özbek, 1992: 10. Type genus: *Krombeinia* Pate, 1947. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Luditini Argaman & Özbek, 1992: 10. Type genus *Ludita* Nagy, 1967. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Macromeriini Argaman, 1994b: 94. Type genus: *Macromeria* Saunders, 1850. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Meriini Argaman, 1994b: 95. Type genus: *Meria* Illiger, 1807.

Tribe: Mesini Argaman, 1994b: 90. Type genus: *Mesa* Saussure, 1892.

Tribe: Myzinellini Argaman, 1994b: 89. Type genus: *Myzinella* Guiglia, 1959. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Neotiphiini Argaman & Özbek, 1992: 9. Type genus: *Neotiphia* Malloch, 1918. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Parameriini Argaman, 1994b: 92. Type genus: *Parameria* Guérin-Méneville, 1837. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Paratiphiini Argaman & Özbek, 1992: 9. Type genus: *Paratiphia* Sichel, 1864. =Silifkini Argaman & Özbek, 1992. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Siflikini.

Tribe: Poecilotiphiini Argaman, 1994b: 93. Type genus: *Poecilotiphia* Cameron, 1902. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Pseudotiphiini Argaman & Özbek, 1992: 9. Type genus: *Pseudotiphia* Ashmead, 1903. =Tiphiini Leach, 1815. Synonymy implied by Yildirim & Boni Bartalucci (2009) in not recognizing higher taxa within Tiphiini.

Tribe: Silifkini Argaman & Özbek, 1992: 9. Type genus: *Silifka* Argaman & Özbek, 1992.

Tribe: Warayoini Argaman, 1994b: 91. Type genus: *Warayoa* Argaman, 1994. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Weerpagini Argaman, 1994b: 92. Type genus: *Weerpaga* Argaman, 1994. =Braunsomeriina Boni Bartalucci, 2004. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Tribe: Yooloini Argaman, 1994b: 92. Type genus: *Yooloa* Argaman, 1994. =Meriina Argaman, 1994b. Synonymy implied by Boni Bartalucci (2004a) in recognizing only two tribes within Meriini.

Genus: *Acblasa* Argaman in Argaman & Özbek, 1992: 10. Type species: *Tiphia abrupta* Turner, 1908.

Genus: *Arapatka* Argaman, 1994b: 94. Type species: *Myzine arabica* Guérin-Méneville 1837. =*Meria* Illiger, 1807. Synonymized by Boni Bartalucci (2001: 3).

Genus: *Burdufa* Argaman in Argaman & Özbek, 1992: 11. Type species: *Tiphia colombiana* Allen, 1972.

Genus: *Cabaraxa* Nagy, 1974d: 103. Type species: *Cabaraxa compedita* Nagy, 1974.

Genus: *Cocovasna* Argaman, 1994b: 86. *Myzine flavopicta* Smith, 1855. =*Myzinum* Latreille, 1803. Synonymized by Boni Bartalucci (2004a: 1225).

Genus: *Ekepirka* Argaman, 1994b: 88. Type species: *Myzine robusta* Burmeister, 1876. =*Myzinum* Latreille, 1803. Synonymized by Kimsey 2009.

Genus: *Fikoplesa* Argaman, 1994b: 88. Type species: *Myzine elegans* Burmeister, 1876. =*Myzinum* Latreille, 1803. Synonymized by Kimsey 2009.

Genus: *Foforoxia* Argaman in Argaman & Özbek, 1992: 11. Type species: *Tiphia ordinaria* Smith, 1873.

Genus: *Fongiba* Argaman, 1994b: 93. Type species: *Myzine aegyptiaca* Guérin-Méneville, 1837. =*Poecilotiphia* Cameron, 1902. Synonymized by Boni Bartalucci (2001: 28).

Genus: *Fukpokta* Argaman, 1994b: 95. Type species: *Scolia cylindrica* Fabricius, 1793. =*Meria* Illiger, 1807. Synonymized by Boni Bartalucci (2001: 3; misspelled as *Fukpotka*).

Genus: *Gebuipala* Argaman in Argaman & Özbek, 1992: 11. Type species: *Icronatha nuristana* Nagy, 1975.

Genus: *Gonordula* Argaman, 1994b: 87. Type species: *Myzine lateralis* Cresson, 1865. =*Myzinum* Latreille, 1803. Synonymized by Boni Bartalucci (2004a: 1225).

Genus: *Hahiya* Argaman, 1994b: 94. Type species: *Meria brevicauda* Morawitz, 1890. =*Poecilotiphia* Cameron, 1902. Synonymized by Boni Bartalucci (2001: 28).

Genus: *Icronatha* Nagy, 1967c: 193. Type species: *Tiphia olcesei* Tournier, 1889.

Genus: *Illoswia* Argaman, 1994b: 92. Type species: *Myzine braunsi* Turner, 1912. =*Myzinella* Guiglia, 1959. Synonymized by Boni Bartalucci (2001: 23).

Genus: *Ivazuga* Argaman, 1994b: 94. Type species: *Dermasothes trjapitzini* Gorbatovsky, 1979. =*Poecilotiphia* Cameron, 1902. Synonymized by Boni Bartalucci (2001: 28).

Genus: *Jurja* Argaman, 1994b: 93. Type species: *Jurja limpida* Argaman, 1994. =*Poecilotiphia* Cameron, 1902. Synonymized by Boni Bartalucci (2001: 28).

Genus: *Keyovaska* Argaman, 1994b: 88. Type species: *Myzine frontalis* Cresson, 1875. =*Myzinum* Latreille, 1803. Synonymized by Boni Bartalucci (2004a: 1225).

Genus: *Locodamia* Argaman & Özbek, 1992: 10. Type species: *Tiphia sulcata* Roberts, 1930.

Genus: *Ludita* Nagy, 1967c: 197. Type species: *Tiphia morio* Fabricius, 1787.

Genus: *Nurmiya* Argaman, 1994b: 94. Type species: *Meria contrastata* Guiglia, 1963. =*Poecilotiphia* Cameron, 1902. Synonymized by Boni Bartalucci (2001: 28).

Genus: *Nyuka* Argaman, 1994b: 90. Type species: *Plesia picticollis* Morawitz, 1890. =*Mesa* Saussure, 1892. Synonymized by Boni Bartalucci (2004a: 1228).

Genus: *Ocasasla* Argaman in Argaman & Özbek, 1992: 10. Type species: *Tiphia vandervechti* Allen, 1972.

Genus: *Pandasaria* Argaman in Argaman & Özbek, 1992: 11. Type species: *Tiphia latipes* Walker, 1871.

Genus: *Sasmarila* Argaman in Argaman & Özbek, 1992: 11. Type species: *Tiphia cinchonae* Allen, 1975.

Genus: *Serpapinta* Argaman in Argaman & Özbek, 1992: 9. Type species: *Tiphia scabrosa* Gerstaecker, 1858.

Genus: *Silifka* Argaman & Özbek, 1992: 5. Type species: *Silifka fatima* Argaman & Özbek, 1992.

Genus: *Taywola* Argaman, 1994b: 91. Type species: *Mesa palestinella* Guiglia, 1963. =*Mesa* Saussure, 1892. Synonymized by Boni Bartalucci (2004b: 365).

Genus: *Tilkuya* Argaman, 1994b: 96. Type species: *Myzine spinosa* Fischer de Waldheim, 1843. =*Meria* Illiger, 1807. Synonymized by Boni Bartalucci (2001: 3).

Genus: *Tokoparta* Argaman, 1994b: 88. Type species: *Plesia sexmaculata* Guérin-Méneville, 1838. =*Myzinum* Latreille, 1803. Synonymized by Kimsey 2009.

Genus: *Upaterka* Argaman, 1994b: 95. Type species: *Myzine latifasciata* Palma, 1869. =*Meria* Illiger, 1807. Synonymized by Boni Bartalucci (2001: 3).

Genus: *Vacacunda* Argaman in Argaman & Özbek, 1992: 10. Type species: *Tiphia quincemila* Allen, 1972.

Genus: *Warayoa* Nagy, 1994b: 91. Type species: *Warayoa citreosigna* Argaman, 1994. =*Braunsomeria* Turner, 1912. Synonymized by Boni Bartalucci (2011: 371).

Genus: *Weerpaga* Argaman, 1994b: 92. Type species: *Weerpaga udomanca* Argaman, 1994.

Genus: *Xilunka* Nagy, 1994b: 90. Type species: *Cosila donaldsoni* Fox, 1896. =*Mesa* Saussure, 1892. Synonymized by Boni Bartalucci (2004b: 365).

Genus: *Yooloa* Argaman, 1994b: 92. Type species: *Yooloa vircola* Argaman, 1994. =*Parameria* Guérin-Méneville, 1837. Synonymized by Boni Bartalucci (2001: 27).

Genus: *Zezelda* Nagy, 1994b: 90. Type species: *Myzine stigma* Turner, 1912.

Subgenus: *Sierocolpa* Nagy, 1967c: 177. Type species: *Tiphia minuta* van der Linden, 1827

Species:

Cabaraxa compedita Nagy, 1974d: 104. Holotype male; Ethiopia: Dire-Dana (belongs in Budapest, but not deposited there).

Dermasothes ponderopardalis Nagy, 1970d: 191. Holotype male; South Africa: Cape Prov., Willowmore (Nagy Coll.).

Icronatha nuristana Nagy, 1975a: 17. Holotype female; Afghanistan: Nuristan (Nagy Coll.).

Jurja limpida Argaman, 1994b: 96. Holotype male; Yemen: Wadi Zabid (belongs in Budapest, but not deposited there).

Ludita andromeda Nagy, 1967c: 198. Holotype female; Romania: Babadag (Nagy Coll.).

Ludita consobrina Nagy, 1967c: 202. Holotype male; Romania: Rarău Gebirge (Nagy Coll.).

Ludita ramispinosa Nagy, 1967c: 203. Holotype male; Romania: Caraorman, Rayon Tulcea (Nagy Coll.).

Methoca [sic] *sisala* Nagy, 1968e: 82. Holotype male; Romania: near Oradea, Băile Felix forest (Nagy Coll.).

Silifka fatima Argaman & Özbek, 1992: 6. Holotype female; Turkey: Silifke (Argaman Coll.)

Tiphia (*Tiphia*) *bexar* Nagy, 1967c: 187. Holotype female; Romania: Oituz (Nagy Coll.).

Tiphia (*Tiphia*) *copidosoma* Nagy, 1967c: 189. Holotype female; Romania: Băile Victoria (Nagy Coll.)

Tiphia (*Tiphia*) *iracunda* Nagy, 1967c: 182. Holotype male; Romania: Agigea (Nagy Coll.).

Warayoa citreosigna Argaman, 1994b: 91. Holotype male = paratype of *Braunsomeria quadraticeps* Turner, 1912; South Africa: "Cape Colony", Willowmore (London) [although Argaman considered this a replacement name, it must rather be treated as the proposal of a new species since he retained Turner's name for the female; although Boni Bartalucci (2011) designated the female specimen as the lectotype, this is invalid since Turner (1912) had specified "the female is the type", effectively designating it as the holotype]. = *Braunsomeria quadraticeps* Turner, 1912. Synonymized by Boni Bartalucci 2011.

Weerpaga udomanca Argaman, 1994b: 98. Holotype female; Cameroon: Guetale (Nonveiller Coll.).

Yooloa vircola Argaman, 1994b: 97. Holotype male; Israel: Mikhmoret, Miramare Hotel garden (Argaman Coll.). = *Parameria femorata* Guérin, 1837. Synonymized by Boni Bartalucci (2001: 27).

Order Coleoptera

Family Scarabaeidae

Species:

Maladera matrida Argaman, 1986b: 43, 68. Holotype male; Israel: Rehovot (Tel Aviv University). = *Maladera insanabilis* (Brenske, 1894). Synonymized by Ahrens (2000: 202, as *Autoserica insanabilis*).

SHORT COMMUNICATION

Trogus parasitoids of *Papilio* butterflies undergo extended diapause in western Canada (Hymenoptera, Ichneumonidae)

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Abstract

Diapause that extends across multiple years is considered a bet-hedging strategy in insect species that are exposed to unfavorable environmental conditions. The dynamics of extended diapause in herbivores can be complicated when their parasitoids can also extend diapause, although our knowledge of these dynamics is based primarily on pest species. Here, we report on regional variation in the phenology and life history of *Trogus* parasitoids of *Papilio machaon* group swallowtail butterflies in western Canada. We observed flexible phenological patterns in this interaction, with both hosts and parasitoids undergoing extended diapause. Additionally, we documented parasitism of earlier instar larvae in these *Trogus* species, which to our knowledge has not been observed in North America. Our observations provide a foundation for studying the potential evolutionary consequences of extended diapause in these multispecies interactions.

Keywords

Trogus lapidator, *Trogus fulvipes*, *Papilio machaon*, *Papilio zelicaon*, extended diapause, phenology

Introduction

Diapause is a vital life history characteristic for many insects that cope with harsh environmental conditions (Chapman 1998). At northern latitudes this period of developmental delay facilitates winter survival and is usually initiated or terminated by photoperiod and/or temperature cues (Denlinger 2002). Although the temporal dynamics of diapause are predictable and regular in some species, others exhibit plasticity where some individuals go through prolonged diapause periods that last multiple years (Tauber et al. 1986, Danks 1987, Hanski 1988). Such extended diapause is considered an adaptive "bet-hedging" strategy, providing long-term evolutionary gains at the expense of short-term costs (e.g. Menu and Debouzie 1993, Danforth 1999, Hopper 1999, Soula and Menu 2005).

The dynamics of facultative extended diapause are complicated by multispecies interactions, such as those between parasitoids and their hosts, each of which may exhibit extended diapause (Hanski 1988). In some cases these diapause periods are tied to similar external cues (Annila 1981), while in others the parasitoids simply follow the phenology of their host, whether it is simple or prolonged (Martinek 1985). Population modeling of these systems shows that length of diapause and proportion of parasite and host individuals extending their diapause can positively or negatively influence the stability of host-parasitoid interactions (Ringel et al. 1998, Corley et al. 2004). These predictions and most knowledge of extended diapause dynamics in host-parasitoid systems come primarily from insect pest systems, where population dynamics can be eruptive (Wallner 1987). The diverse ecology of parasitoids, particularly in Hymenoptera (LaSalle and Gauld 1993), underlines the importance of incorporating the dynamics of non-pest species into our understanding of extended diapause.

Trogus is a genus of large koinobiont parasitoid wasps that specialize on swallowtail butterflies (Lepidoptera: Papilionidae) (Sime and Wahl 2002). Single eggs are laid in caterpillars that develop normally through pupation; at this point the wasp larva begins feeding, develops, and pupates within the host pupa. Adults then emerge from the host pupa through the wing pad using primarily liquid secretions to dissolve the host tissue, creating a distinctive exit hole (Shaw et al. 2015). *Trogus* are frequently encountered due to widespread collecting and rearing of swallowtail larvae by lepidopterists, and so their host records are reliable (Wahl and Sime 2006). Despite this, the taxonomy of Nearctic *Trogus* has been contentious, with estimates of the number of species in the Nearctic ranging from one to a dozen (Heinrich 1962, Carlson 1979, Wahl and Sime 2006). Apart from their oviposition and direct interaction with swallowtail butterfly caterpillars (e.g. Sime 2005), the biology of these wasps is relatively unknown.

Here we report phenology and life history observations of *Trogus* spp. in Alberta and British Columbia. Extensive sampling of larvae of the *Papilio machaon* Linnaeus species group in population genetic and phylogeographic surveys (Dupuis and Sperling 2015, Dupuis and Sperling in review) resulted in a substantial number of *Trogus* specimens. We observed several novel life history features for *Trogus*, including extended diapause, absence of diapause, and parasitism of caterpillar hosts at earlier

instars than previously documented in this region. This life history information led us to consider the evolutionary consequences of parasitism and phenology in this host-parasitoid interaction.

Methods

During the summers of 2010–2012, *Papilio* larvae and eggs were hand-collected from larval hostplants in three geographic regions of Alberta and northeastern British Columbia, each of which contained a different member of the *P. machaon* species group (Figure 1). Two regions had subspecies of *P. machaon* whose larvae fed on *Artemesia dracunculus* L.: *Papilio machaon dodi* McDunnough, 1939 in the Red Deer River valley in southern Alberta, and *P. m. pikei* Sperling, 1987 in the Peace River valley in northwestern Alberta and northeastern British Columbia. The third region was the foothills of the Rocky Mountains, where *P. zelicaon* Lucas, 1852 and putative hybrids between *P. machaon* and *P. zelicaon* (see Dupuis and Sperling 2015; here referred to as *P. zelicaon*) were collected on *Heracleum lanatum* Bartr. from southwestern Alberta to northeastern British Columbia. Larval instar of caterpillars at the time of collection was estimated visually by JRD.

Caterpillars were reared on host plant clippings with a lighting regime of 16 hours light: 8 hours dark, and temperature maintained at 22°C (± 2°C). After pupation, an overwintering diapause period was simulated by storing pupae in a refrigerator held at 4°C (± 2°C) in total darkness for 16-20 weeks; pupae were misted with water every 1-2 weeks to maintain humidity. Following diapause, eclosion was induced by a return to their former light and temperature regimes, with daily water misting. Particularly at northern latitudes, members of the *P. machaon* group are known to undergo extended natural diapause spanning several winter seasons (Sperling 1987). Therefore if pupae did not eclose after 12-16 weeks but appeared viable (normal color, weight, etc.), the cycle of diapause/eclosion conditions was repeated. Dates of collection, pupation, eclosion, and number of diapause periods were recorded for butterflies and emerged parasites. All *Trogus* specimens were deposited in the E.H. Strickland Entomological Museum at the University of Alberta (UASM#270880-270946).

All data was examined for normality with visualization plots and Shapiro-Wilks tests. The number of days to emergence was measured from the date pupae were removed from the refrigerator, regardless of whether the pupae had previously undergone a simulated diapause regime. The number of days to emergence was transformed (ln(x)) to approach the assumptions of normality. To determine if number of days to emergence differed between sex for either *Papilio* or *Trogus,* the data was pooled across geographic regions. Separate ANOVAs were conducted on both *Papilio* and *Trogus,* with number of days to emergence specified as the response variable and sex specified as the explanatory variable. Another ANOVA was conducted to determine if number of days to emergence differed between *Papilio* and *Trogus,* successive diapause events, or geographic regions. Days to emergence was specified as the response variable and species (*Papilio/Trogus*), number of diapause events, geographic region, and their interaction
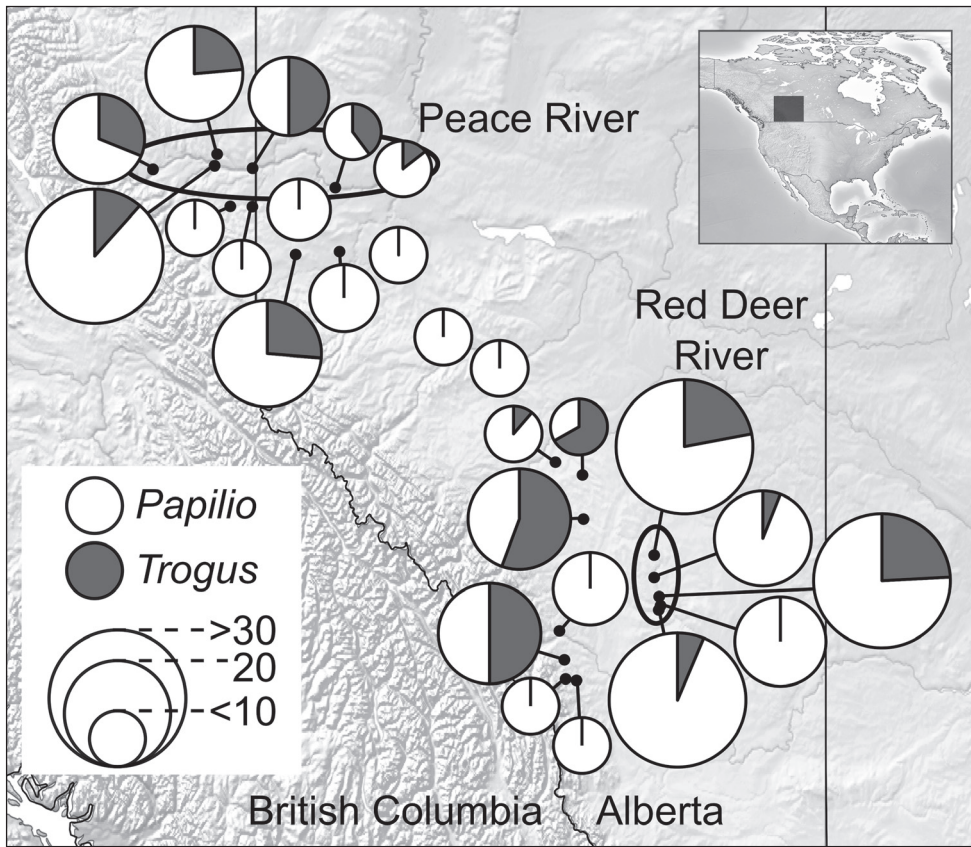
Figure 1. Map of *P. machaon* group larval sampling localities in Alberta and British Columbia. Pie charts represent relative numbers of reared *Papilio* butterflies (white) and *Trogus* parasitoids (grey) per locality (ignoring pupae that did not produce either), and pie chart size reflects sample size of *Papilio* and *Trogus* combined (see inset). Collection regions for *P. machaon* are indicated by ovals: Red Deer River, for *P. m. dodi,* and Peace River, for *P. m. pikei*. All other localities represented *P. zelicaon* collections. Map image is public domain from: www.simplemappr.net.

terms were specified as the explanatory variables. The model was simplified by removal of non-significant variables in a step-wise manner based on the Akaike information criterion (AIC). All statistical analyses were conducted in R 3.2.4 (R Core Team 2016).

Results

In total, 102 eggs and 826 caterpillars were collected during three field seasons. Of these 928 individuals, 685 successfully pupated and produced 290 butterflies and 75 parasites, 66 of which were *Trogus*. Following Wahl and Sime (2006), and after examination of 68 specimens from the Canadian National Collection included in Wahl and

Sime's (2006) revision, 60 individuals that we collected were identified as *T. lapidator* (Fabricius 1787) and the remaining six as *T. fulvipes* Cresson 1868. These species are known to display high variability in western Canada, and putative hybrids between *T. lapidator* and *T. fulvipes* have been collected from some of the same locations as the individuals in this study (Wahl and Sime 2006). This variability and intermediacy between the two species precluded confident species delimitation, and so we conducted statistical analyses on all specimens combined. More detailed taxonomic research is needed to determine the extent of hybridization between these *Trogus* species.

The majority of butterflies went through a single diapause period before eclosion, irrespective of species or collecting region (Table 1). Confirming previous rearing efforts (Sperling 1986), individuals of *P. m. pikei* in the Peace River were more likely than other populations to go through extended diapause before eclosion. One *P. zelicaon* individual did not undergo any diapause and eclosed 43 days after pupation. Although rare at northern latitudes, this is a common phenology in the southern part of the range of *P. zelicaon* where it has multiple flights per year (Scott 1986). Most *Trogus* eclosed after a single diapause period (Table 1), and all identified *T. fulvipes* followed this pattern. However, two individuals of *T. lapidator* reared from *P. zelicaon* did not go through a diapause period, and 11 individuals of *T. lapidator*, mostly reared from subspecies of *P. machaon*, went through two diapause periods before eclosing. To our knowledge, there is only a single previous record of *Trogus* going through multiple diapause periods in this region (Sperling 1986), and we have the first record of *Trogus* species not undergoing overwintering diapause in western Canada. Most *Trogus* were reared from host larvae collected at later larval instars (fourth-fifth); however, several *T. lapidator* were reared from *P. zelicaon* caterpillars collected during their first and second larval instars at Saskatoon Hill, Alberta. *Trogus pennator* (Fabricius 1793), a conspicuous species in eastern North America, is known to oviposit in caterpillars of any age (Sime and Wahl 2002), and *T. violaceus* Mocsáry 1883 (a synonym of *T. lapidator* found in Europe: Wahl and Sime 2006), has been shown to parasitize *P. hospiton* Géné 1839 as early as its second instar (Prota 1962). However, *T. lapidator* and *T. fulvipes* have only been documented from caterpillars collected during later (fourth and fifth) larval instars in western Canada (Sperling 1986, Wahl and Sime 2006). To our knowledge, this is the first record of such early parasitism in these species in North America.

For all *Papilio*, males emerged significantly earlier than females ($F_{1,284}$ = 9.62, $P <$ 0.01). However, there was no significant difference in emergence time of *Trogus* based on sex ($F_{1,62}$ = 1.53, $P >$ 0.05). When both *Papilio* and *Trogus* were examined together there was a significant host/parasite (*Papilio*/*Trogus*) by region interaction (Table 2). In the Red Deer River region *Trogus* adults emerged slightly later than *P. m. dodi* adults, whereas in the Peace River region there was no difference in emergence time between *Trogus* and *P. m. pikei* (Figure 2a). In the foothills region, *Trogus* emerged much later then *P. zelicaon* adults. Interestingly, there was no difference in days to emergence in *Papilio* or *Trogus* when number of diapause events was taken into account (Figure 2b). However, the number of days to emergence declined when both *Papilio* and *Trogus* underwent subsequent diapauses (Table 2, Figure 2b).

Table 1. Number of diapause periods for *Papilio* butterflies and *Trogus* parasitoids, summarized by region. RDR: Red Deer River, PR: Peace River.

Host or parasitoid	Region, species/host species	No. diapause periods				Total
		0	1	2	3	
Papilio (host)	RDR, *P. m. dodi*	0	82	29	6	117
	PR, *P. m. pikei*	0	48	22	1	71
	Foothills, *P. zelicaon*	1	75	24	2	102
	Total	1	205	75	9	290
Trogus (parasitoid)	RDR, *P. m. dodi*	0	11	5	0	16
	PR, *P. m. pikei*	0	18	4	0	22
	Foothills, *P. zelicaon*	2	26	1	0	29
	Total	2	55	10	0	67
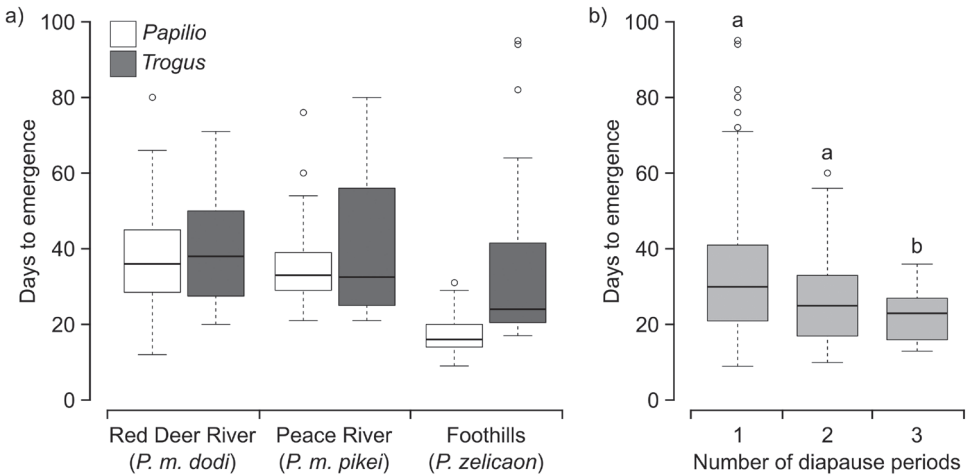
Figure 2. ANOVA results. **a** Number of days to emergence after simulated diapause for *Papilio* and *Trogus* in three geographic regions. There was a significant interaction between number of days to emergence and host/parasite ($P < 0.05$) **b** Number of days to emergence after simulated diapause by number of diapause periods for both *Papilio* and *Trogus* combined. Different letters above boxplots indicate significant differences (Tukey HSD test, $P < 0.05$). For both a and b sections of the figure, the median is indicated by the midline and the bottom and top of the box represent the first and third quartiles, respectively. Whiskers indicate the minimum/maximum values or 1.5 times the interquartile range, whichever is smaller, and circles represent outliers. Untransformed data is presented.

Discussion

Our work on *Papilio machaon* group swallowtail butterflies has fortuitously provided an opportunity to observe the phenology of their *Trogus* spp. parasitoids in western Canada. In addition to observing parasitism in earlier instar hosts than previously

Table 2. ANOVA test results. ANOVA test results for differences in the number of days to emergence between host versus parasite, geographic region, and number of diapause events.

Explanatory variable	DF	*F*-value	*P*-value
host/parasite (*Papilio/Trogus*)	1	25.08	< 0.0001
geographic region	2	154.19	< 0.0001
number of diapause events	2	17.52	< 0.0001
host/parasite*geographic region	2	13.95	< 0.0001
residual	343		

reported for these *Trogus* spp. in this region (Sperling 1987), we have documented a flexible emergence pattern for *T. lapidator*. We collected individuals that did not undergo any overwintering diapause period, as well as several that went through extended diapause before eclosion. *Trogus* emerged later than their hosts, as would be expected given that adult *Trogus* need to oviposit in larval *Papilio*, but this delay varied geographically. This variable phenological pattern of *Trogus* can be interpreted in terms of a potential evolutionary strategy.

Facultative extended diapause is commonly observed in the *P. machaon* group (present study, Sperling 1986), and can be interpreted as an evolutionary strategy for species living in unpredictable environments to withstand unfavorable environmental conditions (drought, irregular precipitation, etc.: Tauber et al. 1986, Danks 1987, Hanski 1988). Although we observed this phenology in all geographic regions in this study, the highest proportion of individuals undergoing extended diapause was observed in *P. m. pikei* in the Peace River region (Table 1). Interestingly, some of the localities in this region also experience very high rates of parasitism by *Trogus* wasps, where similar numbers of *Trogus* and butterflies eclose from reared pupae (Figure 1). Sperling (1986) observed similar patterns at the same localities, and hypothesized that the extended diapause observed in *P. m. pikei* may be an evolutionary strategy to counteract high parasitism rates by decoupling host and parasite phenology. If this is the case, then our observation of extended diapause in *Trogus* parasitoids may indicate that an evolutionary arms race is underway in this system. Under this scenario, *P. m. pikei* are undergoing multiple-year diapauses to avoid parasitism, and *Trogus* are mimicking the same strategy to increase successful parasitism.

In addition to highly parasitized localities in the Peace River region, we observed high parasitism (>50% of reared specimens being *Trogus*) in several populations in the foothills region (Figure 1), a pattern that was not found by Sperling (1986). Despite their comparable rates of parasitism, as well as comparable occurrences of extended diapause in the host, *P. zelicaon*, fewer *Trogus* went through extended diapause in these populations (Table 1). Thus *Trogus* are present in these populations, the hosts may be exhibiting parasite avoidance (following the hypothesis of an arms race), but the parasitoids have not responded with the same phenological flexibility as with *P. m. pikei*. However, we also observed the largest delay between host and parasitoid emergence in

the foothills region (Figure 2a), which may indicate that the overall phenology of these regions differs enough to preclude direct comparison.

Several lines of evidence may explain the overall phenological discrepancies between hosts and parasitoids in these regions. The most obvious is that environmental cues for initiation and termination of diapause may differ between host species/ subspecies, as well as between hosts and parasitoids. In the *P. machaon* species group, photoperiod has been identified as the main factor affecting diapause induction (*P. machaon*: Shimada 1983; *P. zelicaon*: Sims 1980; *P. polyxenes* Fabricius 1775: Oliver 1969, Sims 2007), but termination of diapause may also be affected by photoperiod and temperature (*P. polyxenes*: Oliver 1969). Regional differences in diapause dynamics (including degree days required for development) and voltinism are evident across the ranges of the species in this group, but populations in western Canada generally exhibit highly variable and overlapping phenological characteristics (Sperling 1987). Less is known about hymenopteran parasitoids, particularly species without obvious economic impacts. Temperature, combined with variables such as photoperiod and host instar, predominately affects diapause induction and termination in some parasitoids (Ichneumonidae: Griffiths 1969, Eliopolous and Stathas 2003; Trichogrammatidae: Laing and Corrigan 1995), however these effects can vary with the life stage of the insect (Trichogrammatidae: Ivanov and Reznik 2008). It is likely that differences in diapause cues can explain, at least in part, the variable phenologies we observed here. However, if diapause in *Papilio* and *Trogus* depends on regionally variable and species specific combinations of photoperiod and temperature, then extensive research efforts will be required to disentangle those effects.

Several additional factors affect the interpretation of these results. First, documenting *Trogus* phenology was not the main purpose of our collecting efforts. Although we aimed for standardized rearing conditions, we did not tailor rearing conditions of individuals to that of their respective regional environments. Dedicated experimentation mimicking more natural conditions, along with larger sample sizes and collections at particular larval instars, will be valuable for advancing understanding of this interaction. Second, although *Trogus* are specialist parasitoids on swallowtail butterflies, another swallowtail butterfly, *Papilio canadensis* Rothschild and Jordan 1906, also inhabits these areas (Scott 1986). While *Trogus lapidator* has not been reared from *P. canadensis*, there are records of *T. fulvipes* from this host (Sime and Wahl 2002), which adds another layer of complexity to the population dynamics of these parasitoids. Finally, as noted earlier, the taxonomy of these *Trogus* spp. is not well resolved in western Canada, and hybridization between *T. lapidator* and *T. fulvipes* may be widespread; this process may also parallel hybridization between *P. machaon* and *P. zelicaon* (Sperling 1987, Sperling 1990, Dupuis and Sperling 2015, Dupuis and Sperling in review). Detailed taxonomic research will be essential to expanding the hypothesis of an evolutionary arms race, as well as general life history knowledge of these charismatic parasitoids. Our natural history observations should provide a foundation for future work on the *Papilio-Trogus* interaction in western Canada.

Acknowledgements

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SHORT COMMUNICATION

First record of the parasitoid *Gonatopus flavipes* Olmi, 1984 (Hymenoptera, Dryinidae) in Brazil's Amazon forest

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Abstract

This study reports for the first time the occurrence of *Gonatopus flavipes* Olmi, 1984 in Pará State, Brazil. Specimens were collected on upland rice crops of Cambará variety in Novo Progresso (7°07'45.71"S 55°23'21.13"W). A sampling of insects with pitfall traps was conducted between November 2010 and March 2011. Specimens of *G. flavipes* were identified, illustrated and deposited in the Entomological Collection of the Department of Zoology, Federal University of Paraná, Curitiba, Brazil (DZUP/UFPR). This record indicates that rice crops may represent important habitats for this species.

Keywords

Introduction

Gonatopus Ljung, 1810 is one of the 11 genera belonging to the subfamily Gonatopodinae (Hymenoptera, Dryinidae). With about 440 worldwide described species, among which 120 known in the Neotropics and 32 in Brazil (Olmi and Virla 2014; Martins et al. 2015a, b), this genus is divided into 12 groups (nine registered for the Neotropics and five for Brazil) (Olmi and Virla 2014). Little is known about the biology of parasitoids belonging to the genus *Gonatopus*. The few studies report the association of the genus with some families of leafhoppers and planthoppers (Hemiptera, Auchenorrhyncha): Acaloniidae, Caliscelidae, Cicadellidae, Cixiidae, Delphacidae, Dictyopharidae, Flatidae, Issidae, Lophopidae, Meenoplidae and Tropiduchidae (Guglielmino et al. 2013; Olmi and Virla 2014).

Gonatopus flavipes Olmi, 1984, broadly distributed from Mexico to Argentina, belongs to group seven, which is the largest group of *Gonatopus* with exactly 61 described species. Both sexes of *G. flavipes* are known (Olmi and Virla 2014). The following species of Cicadellidae (Hemiptera, Auchenorrhyncha) are reported as hosts: *Mendozellus asunctia* Cheng in Argentina; *Dalbulus maidis* (DeLong and Wolcott) in Piaui, Brazil; *Dalbulus elimatus* (Ball), *Planicephalus flavicosta* (Stål) and *Graminella comata* (Ball) in Mexico (Guglielmino and Olmi 1997, 2006; Meneses et al. 2013; Moya-Raygoza 1990, 1993; Olmi and Virla 2014; Virla 1992).

The Companhia Nacional de Abastecimento do Brasil (CONAB 2016) records rice cultivation in Pará State since 1976–1977, mainly in the North, with recent planting of upland rice in the Southwest (less than 10 years) (Azevedo 2009; Krinski 2014; Lopes et al. 2004; Silva and Magalhães 1981). For this reason, a few entomological studies have been conducted on rice cultivars of this region. This study reports for the first time the occurrence of *G. flavipes* in upland rice crop in Southwestern region of Pará State (Brazil).

Materials and methods

A sampling of insects was conducted with pitfall traps on upland rice crops (Cambará variety), in Novo Progresso, State of Pará, Brazil (7°07'45.71"S 55°23'21.13"W) (Fig. 1), between November 2010 and March 2011. The sampling effort included 16 collecting points visited weekly, covering 400 meters in four transects of 100 meters, distant 25 meters from each other.

The collected specimens of *Gonatopus* were sent to the Laboratory of Comparative Hymenoptera Biology at Federal University of Paraná (UFPR), where they were identified to species level using a stereo-microscope LEICA M125 coupled to digital camera LEICA DFC295. The images were processed by Zerene Stacker software (1.04 version build). Digital scanning electronmicroscope (SEM) photographs were taken with a TESCAN VEGA3 LMU in low vacum mode. The figures were prepared using Adobe Photoshop (version 11.0). Specimens are deposited in the Entomological Collection of the Department of Zoology, Federal University of Paraná (DZUP).
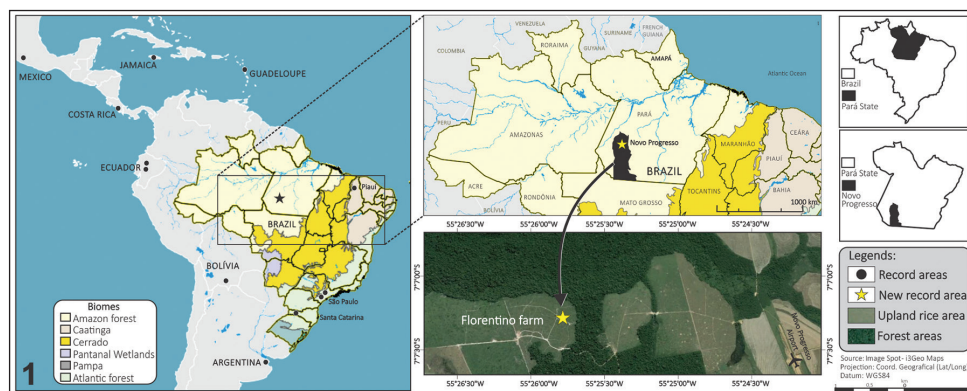
Figure 1. Distribution map of *Gonatopus flavipes*. Black circle: record areas in Argentina, Bolivia, Brazil (Piauí, São Paulo and Santa Catarina), Costa Rica, Ecuador, Guadeloupe, Jamaica and Mexico; Star: new record of occurrence (Florentino farm – municipality of Novo Progresso, Pará State, Brazil). Source: i3Geo (free software). Licensed as General Public License (GNU) and created by Ministry of Environment (MMA).

Results and discussion

Gonatopus flavipes **Olmi, 1984**

Gonatopus flavipes Olmi, 1984: 1752.

Note. Only two female specimens were collected (Figs 2–5). They present the following diagnostic features:

Diagnosis. Completely yellow testaceous except petiole black and metasoma partly brown (Fig. 2). Pronotum shiny, unsculptured, crossed by strong transverse furrow. Scutum shiny, unsculptured, laterally with two pointed apophyses (Fig. 3). Meso-metapleural suture obsolete (Fig. 2). Head with frontal line complete; occipital carina absent; OL (distance between the inner edges of a lateral ocellus and the median ocellus)/POL (distance between the inner edges of the lateral ocelli) = 1.5/1.0 (Fig. 4). Enlarged claw with one small subapical tooth and one row of six peg-like hairs. Segment 5 of protarsus with two rows of 22 + 12 lamellae (Fig. 5). Tibial spurs 1/0/1.

Material examined. Two females: Brazil, PA, Novo Progresso, Florentino Farm, Upland rice crop, 7°08'41"S 55°22'43"W,09.ii.2011, D. Krisnki, Pitfall traps (DZUP).

Gonatopus flavipes was recorded for Argentina, Bolivia, Brazil (Piaui, São Paulo and Santa Catarina States), Costa Rica, Ecuador, Guadeloupe, Jamaica and Mexico (Olmi and Virla 2014) (Fig. 1). In addition we record for the first time the presence of this species from Pará State, Brazil, in upland rice crop.

Therefore, considering the economic importance of rice crops in Brazil, we recommend careful monitoring in rice areas and studies on the biology, morphology and ecology of *G. flavipes* in different rice crops.
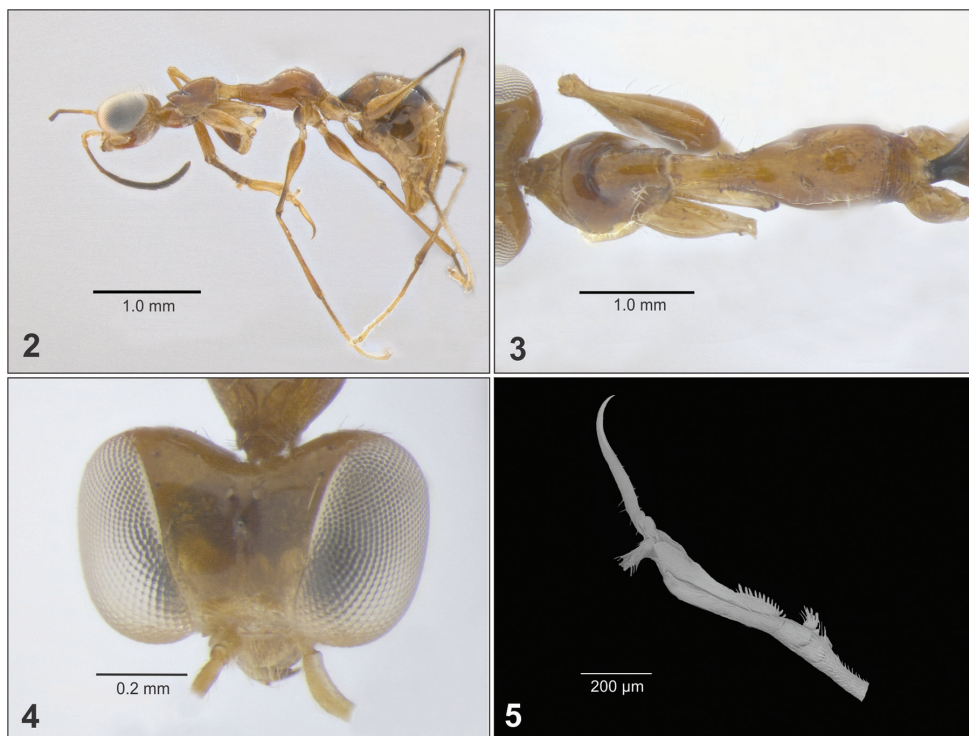
Figures 2–5. *Gonatopus flavipes*. **2** Habitus **3** Mesosoma in dorsal view **4** Head in dorsal view **5** Chela.

In addition, more studies are needed to assess the population fluctuation of this parasitoid in different rice varieties, mainly to investigate if this species can be used in the future for the biological control of Auchenorrhyncha (Guglielmino 2002; Mita et al. 2012). In fact, research out of Brazil have reported the occurrence of *Gonatopus* species associated with important pests of rice (Mita and Pham 2014).

Acknowledgements

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