# The life history of Pseudometagea schwarzii, with a discussion of the evolution of endoparasitism and koinobiosis in Eucharitidae and Perilampidae (Chalcidoidea) 

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#### Abstract

The immature stages and behavior of Pseudometagea schwarzii (Ashmead) (Hymenoptera: Eucharitidae: Eucharitini) are described, and the presence of an endoparasitic planidium that undergoes growth-feeding in the larva of the host ant (Lasius neoniger Emery) is confirmed. Bayesian inference and parsimony ancestral state reconstruction are used to map the evolution of endoparasitism across the eucharitid-perilampid clade. Endoparasitism is proposed to have evolved independently three times within Eucharitidae, including once in Pseudometagea Ashmead, and at least twice in Perilampus Latreille. Endoparasitism is independent as an evolutionary trait from other life history traits such as differences in growth and development of the first-instar larva, hypermetamorphic larval morphology, and other biological traits, including koinobiosis.


## Keywords

Eucharitidae, endoparasitism, koinobiosis, hyperparasitism, Formicidae

## Introduction

Eucharitidae and Perilampidae form a monophyletic group within Chalcidoidea (Hymenoptera) (Munro et al. 2011, Heraty et al. 2013). Females lay their eggs away from the larval food source, and the sclerotized first-instar larvae (planidia) are active in
finding their hosts (Clausen 1940a, b). Planidia attack the host larval stage, but do not develop further until the final host larval instar or prepupal stage is reached and histolysis during pupal formation begins (Smith 1912, Clausen 1941). The number of larval instars is variable within Perilampidae, with four larval instars reported for Chrysolampinae (Darling and Miller 1991), and three (Smith 1912, Clancy 1946) or four (Parker 1924, Tripp 1962, Darling and Roberts 1999) for Perilampinae. Only three instars have ever been reported for Eucharitidae (Wheeler 1907, Clausen 1923, 1928, 1940a, Ayre 1962, Heraty et al. 1993, Heraty 1994, 2000).

Development on the host pupa is nearly identical for all taxa, with the first and later instars developing as ectoparasitoids typically on the posterior ventral thoracic region of the host pupa (Smith 1912, Clausen 1940a, Darling and Miller 1991, Darling 1992, 1999). A secondarily endoparasitic late instar larva and pupa is known only in Monacon Waterston (Perilampidae) (Darling and Roberts 1999). As currently recognized, the Perilampidae (Chrysolampinae, Philomidinae and Perilampinae) are parasitoids of Coleoptera, Neuroptera, Diptera (Tachinidae) and Hymenoptera (Apoidea, Ichneumonoidea and Tenthredinoidea), and are paraphyletic with respect to the Eucharitidae (Darling 1992, Munro et al. 2011, Heraty et al. 2013, Murray et al. 2013). Although paraphyletic to Eucharitidae, no changes in the classification of Perilampidae have been proposed without a more comprehensive review of the entire superfamily (Heraty et al. 2013). Eucharitidae (Akapalinae, Gollumiellinae, Oraseminae and Eucharitinae) are monophyletic and, except for Akapalinae for which the hosts are unknown, are all parasitoids of ants (Murray et al. 2013).

Oviposition, host location and planidial behaviors vary across Eucharitidae and Perilampidae. Eggs of Chrysolampinae are deposited in the flower head or seed pod, and larvae move to the weevil host, where they remain as ectoparasitoids until host pupation (Askew 1980, Darling and Miller 1991). The oviposition behavior, means of accessing the host and behavior on the host larva is unknown for Philomidinae, but the planidia are ectoparasitoids on the pupae of halictid bees (Darling 1992). Perilampinae oviposit in close proximity to the host, with planidia either becoming ectoparasitoids (e.g., Perilampus chrysopae Crawford (Clancy 1946), Steffanolampus salicetum (Steffan) (Darling 1999) and Monacon robertsi Bouçek (Darling and Roberts 1999), or endoparasitoids when primary parasitoids of Diprionidae or hyperparasitoids of Ichneumonoidea and Tachinidae (e.g. Perilampus hayalinus Say, Smith 1912, Ford 1922, Tripp 1962). Perilampid planidia are cannibalistic as ectoparasitoids on the host pupa, and only one parasitoid develops per host pupa (Darling 1992). Within Eucharitidae, eggs are deposited more remotely from the host, and planidia use a variety of behaviors to gain access to the host ant larva (Clausen 1940b, 1941, Heraty 2000). Eucharitid planidia can be either endoparasitic or ectoparasitic on their host ant larvae. Cannibalistic behavior has not been observed, and in some Eucharitinae, multiple parasitoids can develop on a single host pupa (Clausen 1923, Heraty and Barber 1990, Lachaud and Pérez-Lachaud 2012). In Gollumiellinae and Oraseminae, planidia are endoparasitic on Formicinae (Nylanderia) and Myrmicinae, respectively (Wheeler 1907, Heraty et al. 1993, 2004, Heraty 1994). Both Nylanderia Emery and Myrmicinae lack a cocoon,
and development occurs on exposed pupae in the brood pile. In Eucharitinae, development takes place within the host cocoon of Ponerinae, Ectatomminae, Formicinae or Myrmeciinae (Heraty 2002, Lachaud and Pérez-Lachaud 2012, Murray et al. 2013, Torréns 2013). Planidia of Eucharitinae are all ectoparasitoids, with one exception Pseudometagea schwarzii (Ashmead) was described by Ayre (1962) as having an internal planidium on larvae of Lasius neoniger Emery (Formicinae).

Both Eucharitidae and Perilampidae are koinobionts, that is, parasitoids that do not kill their host initially but instead transition through more than one host life history stage (Askew and Shaw 1986). Most koinobionts are internal parasitoids and therefore can more easily transition from one instar or life stage to another (Gauld and Hanson 1995). Very few switch their mode of parasitism once on their primary host. Endoparasitism by the planidia on the host larva is so far known only in some Perilampus (Perilampinae) and all known Gollumiellinae, Oraseminae and Pseudometagea (Eucharitinae). Because the endoparasitic planidia of Perilampidae do not feed, Darling and Roberts (1999) considered the term endoparasitoid inappropriate. However, at least in Eucharitidae, while in or on their larval host, planidia may exhibit sustenance feeding, at most becoming turgid, or may undergo what can be termed growth feeding in which the planida expand to several hundred times their original size (Wheeler 1907, Smith 1912, Tripp 1962). Therefore at least some feeding, and thus true endoparasitism, does takes place within Eucharitidae.

Hypermetamorphic larvae with both discrete morphologies and behaviors across different instars is uncommon within the Hymenoptera. Type I hypermetamorphism involves oviposition away from the food source and an active first-instar parasitoid (Pinto 2003). Both the terms triungulins (with legs) and planidia (without legs) have been used, but Pinto (2003) disputed the term triungulin (=three clawed) and lumped both forms under the category of planidium (= little or diminuitive wanderers). In contrast, Darling and Miller (1991) and Darling (1992) proposed that because of their unique structure and phylogenetic placement, the term planidium should be reserved for Perilampidae and Eucharitidae, with other [Type I] forms referred to as planidiaform. Type I hypermetamorphic larvae are rare, and appear to have evolved only twice in Hymenoptera, once in Ichneumonidae (Tripp 1961) and in a monophyletic Eucharitidae + Perilampidae (Heraty et al. 2013). For the Chalcidoidea that oviposit away from the host, not all of their larvae are hypermetamorphic (von Rosen 1956, Parnell 1963, Askew 1980). The planidia of Eucharitidae and Perilampidae share a suite of character states that is unique among insects and appear to have been derived only once within Chalcidoidea (Heraty and Darling 1984, Darling 1992, Munro et al. 2011, Heraty et al. 2013).

Both endoparasitism and koinobiosis are derived and likely independent traits within Hymenoptera (Askew and Shaw 1986, Gauld 1991, Whitfield 1992, Wahl and Sharkey 1993). Most koinobionts are endoparasites, and ectoparasitic koinobionts are rare (Gauld and Hanson 1995). However, both Perilampidae and Eucharitidae are koinobionts that are nearly always ectoparasitic in later instars, with oviposition away from the host and planidial larvae.

In this paper, we confirm the observation of endoparasitism within the genus Pseudometagea, and propose that endoparasitism may have developed at least five times within the perilampid-eucharitid lineage. We use these data to interpret the evolution of endoparasitism and koinobiosis within this specialized group of type I hypermetamorphic Chalcidoidea.

## Materials and methods

## Collections

A total of 46 colonies of Lasius neoniger were sampled from under stones along a roadside in the Ojibway Long Grass Prairie Nature Reserve, Windsor, Ontario, Canada ( $\left.42^{\circ} 15^{\prime} 42.9^{\prime \prime} \mathrm{N}, 83^{\circ} 04^{\prime} 02.2^{\prime \prime} \mathrm{W}\right)$ from $2-4$ June, 1982 . No attempt was made to sample entire colonies, but instead only the larvae, cocoons and representative adult ants that could be readily aspirated. Collections were stored in $70 \%$ ethanol. Cocoons were dissected and the contents examined for parasitized ant larvae, prepupae, ant pupae or parasitoid pupae. Representative adults and larval stages of both Pseudometagea and Lasius were dried using hexamethyldisilazane (HMDS, Heraty and Hawks 1998), card-mounted, and deposited in the UC Riverside Entomology Research Museum under museum barcode numbers UCRC_ENT 00352406-31.

## Endoparasitism trait mapping

Literature records for internal or external parasitism by planidia on their larval host are known for 27 species of Perilampidae (Chrysolampinae and Perilampinae) and Eucharitidae (Wheeler 1907, Smith 1912, Brues 1919, Ford 1922, Clausen 1923, 1928, 1940a, Wheeler and Wheeler 1937, Clancy 1946, Ayre 1962, Tripp 1962, Askew 1980, Laing and Heraty 1981, Heraty and Darling 1984, Darling and Miller 1991, Darling 1992, 1999, Heraty et al. 1993, Heraty 1994, 2000, 2002, Darling and Roberts 1999, Pérez-Lachaud et al. 2006, Carey et al. 2012, Lachaud and Pérez-Lachaud 2012, Torréns 2013) (cf. Table 1). We used Bayesian inference and parsimony methods to model the ancestral states and behavioral changes for the parasitoid larvae.

Exemplar trees for trait mapping were pruned from the Bayesian analysis of molecular data (18S, 28S, COI, COII) for 237 taxa by Murray et al. (2013). Except for Perilampus, larval behaviors are identical within genera. Thus, for those taxa with trait data for species that were not represented in the Murray et al. analysis, we matched these names to closely related species of the same genus (* on Fig. 11). BayesTraits Multistate v1.0 was used for ancestral host reconstruction in a Bayesian framework. Using a distribution of 10,000 trees, each chronogram was pruned from 237 taxa to 27 taxa, retaining the original topology and branch lengths of each phylogeny. For state reconstruction, an empirical Bayes approach was employed, where first the data were analyzed under maximum likelihood
Table I. Taxa used in reduced analysis, with references to the mode of parasitism and taxon substitutes (grey) from the matrix. Voucher codes and Genebank accession numbers are included. Classification abbbreviations: PEC Chrysolampinae; PEP Perilampinae; EUG Gollumiellinae; EUO Oraseminae; EUP Eucharitinae: Psilocharitini; EUE Eucharitinae: Eucharitini.

| Classif. | Reference taxon | planidial mode | Reference | Taxon in analysis | D_number | Genbank Accession Numbers |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| PEC | Chrysolampus sisimbryi |  |  |  |  | JN623326 | AY552188 | KC008309 | - |
| PEC | Chrysolampus thenae | ectoparasite | Askew 1979 | Chrysolampus sp. (Australia) | D0160 | JN623327 | AY552185, <br> JN624069 | - |  |
| PEP | Steffanolampus salicetum | ectoparasite | Darling 1999 | Steffanolampus salicetum | D0320 | JN623354 | AY552177, <br> JN624088 | KC008323 | - |
| PEP | Monacon robertsi | ectoparasite | Darling and Roberts 1999 | Monacon robertsi | D0318 | JN623340 | AY552181, <br> JN624078 | KC008315 | - |
| PEP | Perilampus chrysopae | ectoparasite | Clancy 1946 | Chrysolampus sp. (Australia) | D0113 | JN623345 | AY552178 | KC008319 | - |
| PEP | Perilampus fulvicornis | endoparasite | Laing and Heraty 1981 | Perilampus fulvicornis | D0713 | JN623342 | JN623717, <br> JN624080 | KC008217 | KC008489 |
| PEP | Perilampus hyalinus | endoparasite | Smith 1912, Tripp 1962 | Perilampus hyalinus | D0972 | AY552257 | AY552180 | KC008318 | - | AY552191, KC008166 KC008328 | AY672931 | - | - |
| :--- | :--- | :--- | | $\begin{array}{c}\text { AY552206, } \\ \text { JN624027 }\end{array}$ | KC008181 | - |
| :--- | :--- | :--- | | $\begin{array}{l}\text { KC008091, } \\ \text { KC008142 }\end{array}$ | KC008182 | - |
| :--- | :--- | :--- | | AY672955, | - | - |
| :--- | :--- | :--- |
| KC008493 | - | - | | KC008093, | - | - |
| ---: | :--- | :--- |
| KC008143 | - | - | | AY552195, |
| :--- | :--- | :--- |
| JN624034 |$\quad-\quad$ KC008334 KC008096, KC008186 KC008348 KC008109 KC008233 KC008412 AY671806 KC008220 KC008398


| Classif. | Reference taxon | planidial mode | Reference | Taxon in analysis | D_number | Genbank Accession Numbers |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  | 18S | 28S D2-D5 | COI | COII |
| EUE | Chalcura affinis | ectoparasite | Clausen 1940 | Chalcura sp. (Australia: NT) | D0647 | - | KC008099 | KC008211 | KC008387 |
| EUE | Dicoelothorax platycerus | ectoparasite | Torréns and Heraty 2012 | Dicoelothorax platycerus | D2512 | - | $\begin{aligned} & \text { KC008115, } \\ & \text { KC008149 } \end{aligned}$ | - | KC008431 |
| EUE | Eucharis adscendens | ectoparasite | Clausen 1940 | Eucharis adscendens | D0729 | JN623231 | AY552229, JN624007 | KC008189 | KC008353 |
| EUE | Galearia bruchii | ectoparasite | Torréns 2013 | Galearia bruchii | D2491 | KC008531 | KC008117 | - | - |
| EUE | Kapala terminalis | ectoparasite | Clausen 1940 | Kapala terminalis | D1270 | KC008561 | AY671891 | KC008290 | KC008479 |
| EUE | Latina rugulosa | ectoparasite | Torréns 2013 | Latina guriana (Argentina: SA) | D1073b | AY552319 | AY552242 | KC008246 | KC008433 |
| EUE | Pseudochalcura gibbosa | ectoparasite | Heraty and Barber 1990 | Pseudochalcura gibbosa | D0910 | AY552295 | AY552218 | KC008199 | KC008373 |
| EUE | Pseudometagea schwarzii | endoparasite | Ayre 1962 | Pseudometagea schwarzii | D0274 | AY552292 | AY552215 | KC008188 | KC008352 |
| EUE | Stilbula cyniformis | ectoparasite | Clausen 1940 | Stilbula sp. 1 (Nigeria) | D2692 | AY552301 | $\begin{aligned} & \text { GQ331923, } \\ & \text { KC008495 } \end{aligned}$ | - | KC008367 |
| EUE | Stilbula tenuicornis | ectoparasite | Clausen 1923 | Stilbula sp. 2 (Singapore) | D2837 | KC008517 | KC008097 | KC008196 | KC008368 |

analysis, and then these results informed the choice of Bayesian priors. For the Bayesian implementation, reversible-jump MCMC was used instead of specifying a model of character change. We designated a hyperprior on an exponential distribution, drawn from a uniform distribution on the interval 0 to 5 with a rate deviation of 15.500 million generations were run, sampling every 50,000 , with the first 100 million generations discarded as burn-in. Acceptance rates were considered as valid if they fell within a range of 0.2-0.4.

During analysis, BayesTraits picks one of the 10,000 trees randomly for each iteration and calculates state probabilities at designated nodes of interest. There are two nodes that are not present on all trees: Perilampinae + Eucharitidae, and Eucharitini excluding Pseudometagea. For trees without the node present, the probability of the ancestral states was set as uninformative at a 0.5 probability for each state. This incorporates uncertainty of the node in proportion to its appearance in the distribution of trees. Tracer v1.5.0 (Rambaut and Drummond 2007) was used to obtain the mean output value for at each node of interest.

Mesquite v2.73 (Maddison and Maddison 2010) was used for parsimony reconstruction of ancestral states by tracing the character on the maximum clade credibility tree from Murray et al. (2013).

## Results

Fourteen (30.4\%) of the 47 colonies of $L$. neoniger sampled were parasitized by $P$. schwarzii. From these parasitized colonies, we recovered 17 unparasitized mature ant larvae, 473 unparasitized ant pupae, and 115 parasitized cocoons. Of the parasitized cocoons, there were 15 mature ant larvae within the cocoon with an internal planidium of P. schwarzii (PS), 7 ant pupae with external PS planidia, 5 ant pupae with a second instar PS, 2 ant pupae with a third instar PS, and 86 PS pupae. Only one parasitoid per host larva or pupa was ever observed. Three larval instars were observed for $P$. schwarzii. The few mature larvae and numerous ant and parasitoid pupae suggest that sampling took place at the end of the overwintering generation of brood for that year. Numerous males of $P$. schwarzii flying over the ant colonies during collection also suggested a recent emergence. One female emerging from the nest entrance attracted several males that swarmed the female in a ball on the ground. The supposedly now mated female left the cluster of males and flew to the nearest host plant and began oviposition into flower heads of Erigeron strigosus Muhl. ex Willd. (Asteraceae).

The unfed planidium (Fig. 1), taken from these same collections, was described by Heraty and Darling (1984) and earlier by Ayre (1962). The feeding and later stages are herein described as follows. On mature larvae within the cocoon, the planidia were found completely embedded in the thoracic region of the host (pl, Figs 2, 5, 9, 10). All of the internal planidia were in the growth phase, with the body greatly swollen and the tergites reduced to well-separated bands (Figs 2, 5). The entrance hole (eh) was marked by a sclerotic ring (Fig. 9). After pupation of the host, the enlarged planidium became ectoparasitic (exposed by molted exuvium) and then relocated to the ventral region of the thorax behind


Figures I-IO. Pseudometagea schwarzii. I planidium (first-instar), tp = tergopleural line $\mathbf{2}$ Lasius neoniger larva with internal planidium ( pl ), inset is full size ant larva (from cocoon) $\mathbf{3}$ female pupa $\mathbf{4}$ adult male in process of opening cocoon $\mathbf{5}$ Lasius larva with planidium, eh= entrance hole $\mathbf{6}$ Lasius pupa with external planidium 7 third instar $P$ seudometagea with attached planidial exuvium (plex) 8 Pseudometagea pupa 9 ant larva with entrance hole and broken to show internal planidium (apical segments), anthd = ant head $\mathbf{1 0}$ ant larva with dissection showing fed (expanded) internal planidium.


Figure II. Ancestral character reconstruction of mode of planidial parasitism. Terminal taxa coded as either ectoparasitic (orange) or endoparasitic (blue). Branches of phylogeny colored according to parsimony reconstruction, with gray branches indicating ambiguity. Pie charts at selected nodes show probabilities of each state from the Bayesian analysis. Taxa were coded directly from life history records except where indicated by asterisks, when taxa were substituted for those included in the analyses of Murray et al. (2013) as detailed in Table 1.
the legs (Fig. 6). The third-instar had a swollen dorsal prothoracic region, a single thoracic spiracle and a weakly pustulate dorsal surface, and retained the cast planidial exuvium (plex) as observed for other Eucharitidae (Fig. 7). The pupa lacks any ocellar ornamentation (found in some Eucharitinae) or petiolar nodules (found in Oraseminae), but does have lateral bladder-like abdominal processes (found in some Eucharitinae) (Figs 3, 4, 8) (cf. Brues 1919, Heraty et al. 1993, Heraty 1994, 2002). Adults emerge from the cocoon by cutting a transverse slit in the cocoon prior to the wings becoming fully expanded (Fig. 4).

Ancestral states reconstruction for ectoparasitism and endoparasitism was done using BayesTraits (Bayesian inference) and Mesquite (parsimony) (Fig. 1). Relationships and branch lengths were based on Murray et al. (2013). The acceptance rate for the Bayesian analysis reached 0.227 . Ectoparasitism is regarded as the ancestral trait for the perilampid-eucharitid lineage. The sister group relationship with this clade within Chalcidoidea is unclear (Munro et al. 2011, Heraty et al. 2013), but an ectoparasitic ancestor appears most likely given our selected taxa and using both Bayesian inference and parsimony (Fig. 11). Within Perilampinae, both Perilampus hyalinus and P. fulvicornis have internal planidia, whereas $P$. chrysopae and all other Perilampinae, are always external. In Eucharitidae, planidia shift to endoparasitism in Gollumiella Hedqvist (Gollumiellinae), all Oraseminae, and Pseudometagea (Eucharitinae). Although ambiguous under parsimony, BayesTraits suggests a slightly higher probability (>60\%) for ectoparasitism by the planidium on the host larva being plesiomorphic, followed by five independent derivations of an endoparasitic planidium in Perilampinae + Eucharitidae (Fig. 11).

## Discussion

Three types of feeding by planidia have been observed on the host larva. The planidia of Perilampidae are all considered as non-feeding (little to no expansion of body segments) while on or in the host larvae (Darling and Roberts 1999, Heraty et al. 2004). The endoparasitic planidia of Gollumiellinae and Oraseminae undergo sustenance feeding, at most becoming turgid with the tergites slightly separated (Heraty et al. 1993, Heraty 1994, 2000). Some ectoparasitic perilampid planidia also partake in limited host feeding, as evidenced by a slight expansion of the body and separation of the planidial tergites (Darling, pers. comm.). This sustenance-feeding by external planidia occurs in some Perilampinae and most Eucharitini (Eucharitinae) (Clausen 1928, 1940a, Heraty and Barber 1990, Lachaud and Pérez-Lachaud 2012 [note error in their fig. 2d, the expanded planidia is on an ant prepupa, not a larva; pers. comm. J.-P. Lachaud], Torréns and Heraty 2012, Torréns 2013). However, in Neolosbanus Heraty (Eucharitinae; Psilocharitini), the ectoparasitic planidia partakes in growth feeding and swells considerably while on the host larva, although not to their final immense size as occurs on the host pupa (Heraty 1994). Only the first instar larvae of Stilbula tenuicornis (Clausen) (Eucharitini) have been reported to growth feed and complete their development on the larval host (Clausen 1923). In Pseudometagea, planidia are not only endoparasitic, but they increase to their full swollen size while within the host larva (Figs 2, 5), and prior to their migration to the venter of the thorax of the host pupa (Fig. 6).

Our results confirm the report by Ayre (1962) that planidia of $P$. schwarzii are endoparasitic, and that they "burrowed into the ant larva in the dorsal or pleural region of the second or third thoracic segment". Ayre (1962) reported that planidia burrowed into the ant larva both prior to pupation and occasionally prior to the final host instar molt. Ayre (1962) also observed that the planidia overwintered and remain dormant within the host (presumably with minimal feeding) until the spring when they undergo a great increase in size "when the ant larvae commence feeding in the spring". From this, we interpret that growth feeding in the host larva occurs just prior to cocoon formation. This would agree with our observation of internal engorged planidia within host larvae in the cocoon (Figs 2, 5, 9, 10). The planidium of P. schwarzii attains full size while in the host larva. Such an advanced state prior to host pupation has only been observed for Stilbula tenuicornis, which apparently grew and moulted to the second instar while on the host larva, and then completed development on the host pupa (Clausen 1923, 1928). Eucharitinae can have expanded growth-feeding planidia while on the host larvae, but these reach at most only a third of the final first instar size (Torréns 2013). The development and feeding location of the enlarged planidium and later instars on the ventral region of the pupal thorax is otherwise similar across Eucharitidae and Perilampidae (Wheeler 1907, Clausen 1923, Darling and Miller 1991, Darling 1992, Heraty et al. 1993, Heraty 1994, 2000).

One of the important discoveries noted by Ayre (1962) is the presence of an endoparasitic first instar in Pseudometagea. In all other known Eucharitinae, the plan-
idium remains as an ectoparasite of both the larval and pupal host (Clausen 1923, Clausen 1928, Clausen 1940a, Heraty and Barber 1990, Heraty 1994, Lachaud and Pérez-Lachaud 2012, Torréns and Heraty 2012, Torréns 2013). Our results suggest that endoparasitism developed independently at least three times in Eucharitidae, and possibly at least twice in Perilampinae. Growth-feeding by the planidium on the host larva is not unique for Pseudometagea, and has been observed in both Neolosbanus and Galearia Brullè, which have external planidia. However, the degree of host feeding and attainment of a full size first instar by Pseudometagea within the host larva is unique.

The causes for developing an endoparasitic lifestyle in these taxa are unclear. For most koinobionts, endoparasitism avoids issues associated with detachment during host moults between instars. However, the majority of both Eucharitidae and Perilampidae are ectoparasitic during all life stages, and retain enough mobility to relocate and reattach to the host after each moult. In Perilampidae, endoparasitism is associated with hyperparasitism, with planidia entering the primary host and then locating and attacking the ichneumonid or tachinid parasitoid within (Smith 1912, Ford 1922, Tripp 1962). In Gollumiellinae and Oraseminae, the ant hosts lack a cocoon. Perhaps an endoparasitic lifestyle prevents detection of planidia on larvae in the open brood pile, although the same risks occur throughout the ant parasitic Eucharitidae with ectoparasitic planidia. As well, later development in both Gollumiellinae and Oraseminae occurs openly on the naked pupa. For Orasema Cameron attacking polymorphic Myrmicinae, possible control of larval growth through limited feeding by the internal planidia was suggested by Heraty (1990). However, Pseudometagea attacks a monomorphic ant host, and development of the later instars occurs within the host cocoon.

Potentially, endoparasitism could be associated with overwintering in the ant larval host.

Overwintering in the egg stage is known for some Eucharitinae (Clausen 1940b, Heraty and Barber 1990). Overwintering by planidia on their ant host has only been documented for Pseudometagea (Ayre 1962) and Austeucharis Bouçek (Eucharitinae; ectoparasitic and may overwinter on host larva or in cocoon) (Taylor et al. 1993). Overwintering as a planidium on the host may be more common in some groups such as Orasema that rely on the seasonal presence of their plant hosts and have no means of overwintering as adults.

Pseudometagea occupy a phylogenetically important position within the family as the sister group of the remaining Eucharitini (Fig. 11). Their planidia are endoparasitic and overwinter on the larvae of their host ant, and they have a growth phase of development while in the larval host. Endoparasitism in Perilampidae may be correlated with hyperparasitism. Within Eucharitidae, our results suggest that endoparasitism has developed multiple times (Fig. 11), with its appearance independent of other derived larval behaviors including growth feeding, association with ants that have a cocoon, and overwintering. The reasons for the derivation of each of these traits are unclear, and future studies of both eucharitid and ant biology are necessary to better understand the evolution of parasitoid developmental behaviors.

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# Food plants and life histories of sawflies of the families Argidae and Tenthredinidae (Hymenoptera) in Costa Rica, a supplement 

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#### Abstract

Food plants and information on life history are presented for six species of Argidae and four species of Tenthredinidae in Costa Rica. The Argidae include cocoons of Atomacera josefernandezi Smith, sp. n., found on Hampea appendiculata (Donn. Sm.) Standl. (Malvaceae) and likely feeding on its leaves before pupation, and larvae of Eriglenum tristum Smith feeding on Machaerium seemanii Benth. Ex Seem. (Fabaceae), Ptenos leucopodus (Cameron) feeding on Inga oerstediana Benth. and I. vera Willd. (Fabaceae), Ptilia peleterii (Gray) feeding on Cnestidium rufescens (Connaraceae), and Scobina lepida (Klug) and S. notaticollis (Konow) feeding on Sida rhombifolia L. (Malvaceae). The Tenthredinidae include larvae of Dochmioglene crassa (Cameron) feeding on the fern Lomariopsis vestita E. Fourn. (Lomariopsidaceeae), Dochmiogleme Smith03 feeding on Blechnum occidentale L. (Blechnaceae), Waldheimia laeta (Cameron) feeding on Cissus alata Jacq. (Vitaceae), and Waldheimia lucianocapellii Smith, sp. n., feeding on Davilla nitida (Vahl) Kubitzki (Dilleniaceae). Waldheimia lucianocapellii is described from specimens from both Panama and Costa Rica. Selandria crassa Cameron, 1883 is a comb. n. in Dochmioglene.


## Keywords

Symphyta, Area de Conservación Guanacaste, ACG, fern, tropical dry forest, tropical rain forest

## Introduction

Two previous papers presented food plants and life history notes on twelve species of Argidae (Smith and Janzen 2003a) and five species of Tenthredinidae and six species of Pergidae (Smith and Janzen 2003b). Since, several other species have been reared during the ongoing caterpillar inventory of Area de Conservación Guanacaste (ACG) in Guanacaste Province in northwestern Costa Rica. Here, we report on six additional species of Argidae and four additional species of Tenthredinidae.

## Materials and methods

Acronyms used are: USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; INBio, Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; BMNH, The Natural History Museum, London, U.K.

Images $1-15$ were obtained using an EntoVision Imaging Suite that included a firewire JVC KY-75 3CCD digital camera mounted to a Leica M16 zoom lens via a Leica z-step microscope stand. Multiple focal planes were merged using Cartograph 5.6.0 (Microvision Instruments, France) software. Images 16-22 are from the ACG website, cited below.

Voucher codes associated with each reared adult are expressed as, for example, "99-SRNP-4547" (year-Santa Rosa National Park-unique rearing number for that year). This code is unique for the event of finding and rearing the caterpillar, irrespective of what it produces. Full details of the voucher records and associated images may be obtained at http://janzen.sas.upenn.edu and in Janzen (2000, 2001), Burns and Janzen (2001), and Janzen and Hallwachs (2011). Most adult specimens have been DNA barcoded (see acknowledgments).

The format follows Smith and Janzen (2003a, 2003b).

## Results

Argidae

## Atomacera josefernandezi Smith, sp. n.

http://zoobank.org/8FBA5D7B-A71F-42D8-8EC3-FA2401840903
http://species-id.net/wiki/Atomacera_josefernandezi
Figs 1-3, 12, 16

Description. Female (Figs 1-3). Length, 4.0 mm . Head black, labrum and mandible whitish. Antenna black with first and second antennomeres dark orange. Thorax black with pronotum, tegula, mesoprescutum, and mesonotal lateral lobes red; mesosternum


Figures I-3. Atomacera josefernandezi. I Lateral $\mathbf{2}$ Dorsum of head and thorax $\mathbf{3}$ Face, front.
dark orange. Legs mostly white; tarsi black, tibiae with apex black and spot of black near base, black more distinct on hind tibia. Abdomen black. Wings darkly infuscated, slightly lighter toward apex; veins and stigma black.

Head smooth and shining, without punctures or other sculpture. Antennal length $1.3 \times$ head width. Lower interocular distance about $1.2 \times$ eye height. Distances between eye and hind ocellus, between hind ocelli, and between hind ocellus and posterior margin of head as $1.0: 1.2: 0.5$. Clypeus with shallow central emargination. Interantennal area rounded, without carina. Malar space about $1.3 \times$ diameter of front ocellus.

Postocellar area very short，almost non－existent，sloping downward just behind lateral ocelli；without lateral postocellar grooves．Forewing with 4 cubital cells，first cubital crossvein may be weak．Hind basitarsomere $0.9 \times$ length of remaining tarsomeres com－ bined．Sheath uniformly slender in dorsal view，straight above and rounded below in lateral view．Lancet（Fig．12）with serrulae moderately deep，with 1 or 2 anterior and 4－5 posterior subbasal teeth；annuli slightly curved in basal half，straighter in apical half；short hairs on annuli．

Male．Unknown．
Type material．Holotype female，labeled＂Voucher：D．H．Janzen \＆W．Hallwachs， DB：http：／／Janzen．sas．upenn．edu，Area de Conservación Guanacaste，Costa Rica， 11－SRNP－20098，＂＂legs away for DNA＂（USNM）．Paratypes：Same data except for voucher numbers，10－SRNP－22258（区），10－SRNP－22259（1 区），10－SRNP－22260 （1 邓），10－SRNP－22263（1 邓），10－SRNP－22264（1 区），10－SRNP－22265（1 『）， 10－SRNP－22266（1 『），10－SRNP－22269（1 区），10－SRNP－22272（1 区），10－SRNP－ 22273 （ $1 \boxtimes$ ），10－SRNP－22274（1 『），11－SRNP－20096（1 区），11－SRNP－20099（1『），11－SRNP－20104（1 『），11－SRNP－20105（1 『），11－SRNP－20109（1 『），11－ SRNP－20110（1 区）（USNM，INBio）．

Etymology．This species is named in honor of Jose Fernandez－Triana of Ottawa， Canada，in recognition of his outstanding efforts to describe and otherwise clarify the taxonomy of the many hundreds of species of microgastrine braconid wasps being reared by the same inventory that discovered this new sawfly．

Food plant and biology．All specimens of $A$ ．josefernandezi were found as tiny spun cocoons on the leaves of Hampea appendiculata（Donn．Sm．）Standl．（Malva－ ceae）．While the cocoons of all other species of sawflies reared by the ACG inventory have been ovoid in shape，the cocoons of $A$ ．josefernandezi are conspicuously squared off at both ends，making them look like small bricks（Fig．16）．The larvae were not seen，and this may not be the food plant．However，we suspect that it is the food plant because the many cocoons were all on one individual of $H$ ．appendiculata and not scat－ tered over other individual plants，and were accompanied by large areas of strongly skeletonized leaves．There were two sets，apparently broods，of wild－caught cocoons （2010 and 2011）in the same area on the same species of plant，again suggesting that this really is the food plant．

Remarks．The combination of the following characters will distinguish $A$ ．jo－ sefernandezi from other species of Atomacera：tegula，pronotum，and mesonotum （except mesoscutellum）red；mesosternum dark orange；tibiae mostly white with some black at base and apex；interantennal area rounded，without a carina；cl－ ypeus，supraclypeal area，and areas surrounding antennae smooth，shiny，with－ out sculpture；very short postocellar area，lacking lateral furrows；and lancet（Fig． 12）with distinct serrulae and short hairs on the annuli．With the red pronotum， tegula，and most of the mesonotum and mostly white tibiae，this species will run to couplet 10，Atomacera ebena Smith，in the key to Atomacera（Smith 1992）． Atomacera ebena is separated from $A$ ．josefernandezi by the presence of a short in－
terantennal carina, the clypeus, supraclypeal area, and interantennal area punctate, the postocellar area defined by lateral furrows, a red mesoscutellum, most of the hind tarsi white, and the lancet with very low serrulae and lacking annular hairs (Fig. 13). This species is also similar to $A$. nama Smith, but $A$. nama has the legs black, metascutellum and metascutellum orange, and flatter serrulae on the lancet (Smith 1992: fig. 113).

Atomacera josefernandezi DNA barcodes (Janzen and Hallwachs 2011) are very distinctively different from all other species of Argidae and Tenthredinidae reared to date in ACG. However, it is noteworthy that the 2010 rearing consistently differed by what appears to be 1 basepair from the 2011 rearing, a very shallow split that needs to be analyzed with a larger sample size. All the specimens found within a year, to date, are likely to be sibs, and therefore in one sense we have DNA barcoded only two specimens (= two broods).

The New World genus Atomacera includes about 32 species, 30 of which are Neotropical and were keyed by Smith (1992). It occurs from Canada to Argentina. Only five species apart from the one recorded here have been associated with food plants. Atomacera pubicornis (Fabricius) from northern South America feeds on Ipomoea sp. (Convolvulaceae) (Smith 1992), A. petroa Smith has been reared from Miconia calvescens DC (Melastomataceae) in Costa Rica (Badenes-Perez and Johnson 2007), and Atomacera raza (99-SRNP-4547), also reared by the ACG inventory (Smith and Janzen 2003a), was feeding on leaves of Malvaviscus palmanus (Malvaceae). The Nearctic species $A$. debilis Say feeds on Desmodium sp. (Fabaceae), and A. decepta Rohwer feeds on Hibiscus sp. (Malvaceae) (Smith 1969).

## Eriglenum tristum Smith

http://species-id.net/wiki/Eriglenum_tristum
Figs 16, 18
Eriglenum tristum Smith, 1992: 53.

Remarks. This species was described from a single female from Cartago, Turrialba, Costa Rica. Another species, E. crudum Konow, was reared from Maechaerium acuminatum Kunth (Fabaceae) in ACG (Smith and Janzen 2003a). Eriglenum occurs from Mexico to northern Argentina; see Smith (1992) for separation of the four species.

Distribution. Known only from Costa Rica.
Food plant and biology. Nine specimens from two broods were reared, with voucher codes 03-SRNP-11949, 03-SRNP-11951, 03-SRNP-11952, 03-SRNP11953, 08-SRNP-70547, 08-SRNP-70548, 08-SRNP-70549 (Fig. 16), 08-SRNP70550, and 08-SRNP-70551. They were reared from larvae feeding on leaves of Machaerium seemannii Benth. Ex Seem. (Fabaceae). The tough, oval cocoon was formed on a leaf (Fig. 18).

## Ptenos leucopodus (Cameron)

http://species-id.net/wiki/Ptenos_leucopodus
Sericocera leucopoda Cameron, 1883: 48, pl. 3, fig. 3.
Hemidianeura leucopoda: Smith 1992: 120.
Ptenos leucopodus: Taeger et al. 2010: 169.

Remarks. Specimens in USNM from Venezuela bear a label "caterpillar on Inya sp." (Smith 1992). This is probably a misspelling for Inga. Ptenos occurs from southwestern United States and Dominica to Argentina; about 31 species are known, which were keyed by Smith (1992) under the name Hemidianeura. Host plants are not known for the other species.

Distribution. Costa Rica, Ecuador, Guyana, Honduras, Mexico (Chiapas, San Luis Potosi, Tabasco, Veracruz), Panama, Surinam, Venezuela (Smith 1992).

Food plant and biology. Nine ACG specimens were reared, with voucher codes 99-SRNP-17561, 99-SRNP-17562, 01-SRNP-22641, 06-SRNP-31799, 06-SRNP31799.1, 06-SRNP-31799.2, 06-SRNP-31799.3, 06-SRNP-317799.4, and 06-SRNP-31799.5. Larvae were feeding on foliage of Inga vera Willd. (ACG dry forest) and Inga oerstediana Benth (Fabaceae) (ACG rain forest).

## Ptilia peleterii (Gray)

http://species-id.net/wiki/Ptilia_peleterii
Schizocerus Peleterii Gray, 1831 in Gray 1831-1832: 403, pl. 66, fig. 1.
Ptilia peletieri: Smith 1992: 137.

Remarks. This species was reared from Cnestidium rufescens Planch. (Connaraceae) in Panama, and the larva was described and biological notes given by Kimsey and Smith (1985). Ptilia occurs from Mexico to Brazil; seven species are known (Smith 1992).

Distribution. Brazil (Amazonas, Mato Grosso); Colombia; Costa Rica; Guyana; Panama; Surinam; Trinidad and Tobago (both islands); Venezuela (Smith 1992).

Food plant and biology. One ACG specimen was reared (03-SRNP-20546), feeding on very young foliage of the rain forest woody vine Cnestidium rufescens, confirming the report by Kimsey and Smith (1985). A related species, Ptilia versicolor (Klug), feeds on Rourea glabra Kunth (Connaraceae) in ACG (Smith and Janzen 2003a).

## Scobina lepida (Klug)

http://species-id.net/wiki/Scobina_lepida
Fig. 19
Hylotoma lepida Klug, 1834: 239.
Scobina lepida: Smith 1992: 26.

Remarks. This is one of the more common species of Scobina in Central America, but the host plant was not known. Scobina includes about 50 species from Mexico to Argentina, and they were keyed by Smith (1992). Host information was known for only three species, S. guatemalensis (Dalla Torre), S. consobrina (Norton), and S. notaticollis (Konow), all of which fed on the foliage of Sida (Malvaceae).

Distribution. Costa Rica, El Salvador, Guatemala, Honduras, Mexico (Chiapas, Oaxaca, Veracruz), Nicaragua, Panama (Smith 1992).

Food plant and biology. One larva (07-SRNP-40019) was found eating mature leaves of rain forest Sida rhombifolia L. (Malvaceae), a common pasture and roadside woody herb. The fibrous, oval cocoon was on a leaf (Fig. 19).

## Scobina notaticollis (Konow)

http://species-id.net/wiki/Scobina_notaticollis
Fig. 20
Labidarge notaticollis Konow, 1899: 310.
Scobina notaticollis: Smith 1992: 29.

Remarks. Costa Rica is the northernmost record for this species.
Distribution. Bolivia; Colombia, Costa Rica, Ecuador, Panama, Peru, Venezuela (Smith 1992).

Food plant and biology. One larva (Fig. 20) was found feeding on foliage of ACG rain forest Sida rhombifolia (06-SRNP-44107) .

## Tenthredinidae

Dochmioglene crassa (Cameron), comb. n.
http://species-id.net/wiki/Dochmioglene_crassa
Figs 4-6
Selandria crassa Cameron, 1883: 19, pl. 1, fig. 5.

Remarks. Dochmioglene includes about 11 species distributed from Central America to Argentina (Smith, unpublished). The genus has not been revised. The reared specimen (Figs 4-6) agrees with $D$. crassa except for the lack of a black mark on the mesoprescutum. This mark, however, is faint to absent in some other specimens examined.

Dochmioglene belongs in the subfamily Selandriinae, which includes many species associated with ferns. This rearing, and that of the following species, confirms that larvae of many Neotropical selandriine species may be feeding on fern foliage.

Cameron (1883) described the female from "Guatemala, San Isidro 1600 feet" and mentioned that a male from El Tumbador may be the male of the species. Because


Figures 4-6. Dochmioglene crassa. 4 Lateral 5 Dorsum of head and thorax 6 Face, front.

Cameron did not designate a holotype, apparently included a male, and did not state how many specimens were available, a lectotype is here designated. The female of Se landria crassa in in BMNH, labeled "Type H.T.," "B.M. type :Hym. 1.266," "B.C.A. Hymen. I, Selandria crassa Cam.," "San Isidro, 1600 ft., Champion" and "Selandria crassa Cam., type, BCA Hy 1, 10 " is designated the lectotype. The combination in Dochmioglene has not been published and is based on study of the type by DRS.

Distribution. Costa Rica, Guatemala, Panama, Surinam (Smith, unpublished).
Food plant and biology. One specimen, 09-SRNP-32388, was found feeding on the foliage of an ACG rain forest fern, Lomariopsis vestita E. Fourn. (Lomariopsidaceae).

## Dochmioglene Smith03

Remarks. Only parts of the reared adult are stored in a gelatin capsule. They are sufficient to place it in Dochmioglene, but there is not enough left to tell if this is the same as $D$. crassa or another species. Since the host plant is different than that of $D$. crassa and we cannot be sure it is the same, we here consider it as a second reared species of the genus in ACG, with the interim name of Dochmioglene Smith03.

Distribution. Known only from the single specimen from ACG.
Food plant and biology. One specimen, 09-SRNP-21528, was found feeding on the foliage of a rain forest fern, Blechnum occidentale L. (Blechnaceae).

## Waldheimia laeta (Cameron)

http://species-id.net/wiki/Waldheimia_laeta
Monophadnus laetus Cameron, 1883: 22.

Remarks. Waldheimia is a large genus of nearly 100 species and occurs from southwestern United States to Argentina. Waldheimia laeta is separated by its black head, wings yellow with apices black, abdomen orange with apex black, and the very short, triangular lancet with indiscernible serrulae.

The host plants of five species of Waldheimia in Costa Rica are now known: W. laeta and W. lucianocapellii are treated here. Waldheimia suturalis (Cameron) feeds on very young leaves of Cissus rhombifolia Vahl, W. fascipennis (Norton) feeds on very young leaves of Cissus pseudosicyoides Croat (Vitaceae), and W. interstitialis (Cameron) feeds on leaves of Hamelia patens Jacq. (Rubiaceae) (Smith and Janzen 2003b).

Distribution. Bolivia, Colombia, Costa Rica, Panama, Peru, Trinidad, Venezuela (Smith, unpublished)

Food plant and biology. One specimen, 09-SRNP-6456, found feeding on very young leaves of ACG dry forest Cissus alata Jacq. (Vitaceae), the same host genus as W. suturalis and W. fascipennis (Smith and Janzen 2003b). This sawfly did not spin a cocoon, but rather pupated naked in the leaf litter.

## Waldheimia lucianocapellii Smith，sp．n．

http：／／zoobank．org／D281ED64－E3C0－4F27－A155－F24009AA67A5
http：／／species－id．net／wiki／Waldheimia＿lucianocapellii
Figs 7－11，14，21， 22

Description．Female（Figs 7－9）．Length， 7.0 mm ．Antenna black with antenno－ meres 1 and 2 and basal $2 / 3$ of 3 rd yellow．Head yellow with area just in front of anterior ocellus to posterior margin of head and hind orbits above eyes black；apex of mandible reddish．Thorax yellow with triangular black spot on mesoprescutum． Abdomen yellow with apical segments and sheath black．Legs yellow，apex of fore－ tarsus and apex of midtarsus infuscated；apical $2 / 3$ of hind tibia，apical $2 / 3$ of hind basitarsomere，and apical 4 hind tarsomeres black．Wings fasciated，area apical to apex of stigma and area basal to intercostal veins darkly infuscated，center yellow； extreme base of costa yellow；stigma yellow；veins in yellow area，yellow；veins in infuscated area，black．

Antenna $2.0 \times$ head width，apical 4 segments longer than broad and shorter than segments 4 and 5 combined．Lower interocular distance $0.8 \times$ eye length；distances between eye and hind ocellus，between hind ocelli，and between hind ocellus and posterior margin of head as 1．0：1．0：1．0．Malar space absent．Hind basitarsomere longer than following tarsomeres combined．Sheath rounded at apex in lateral view． Lancet（Fig．14）with serrulae flat，each with 7－9 fine subbasal teeth；annular hairs dense，short．

Male．Length， 7.0 mm ．Similar in color to female．Male genitalia in Figs 10，11； harpe tapering to rounded apex；parapenis rounded on inner margin，almost straight on outer margin；valviceps of penis valve with long，rounded dorsal lobe．

Type material．Holotype female labeled，＂Barro Colorado，CZ，Pan．，R．C．Shan－ non，VII－19－23＂（USNM）．Paratypes：Panama，Canal Zone，Barro Colorado Is．， $9^{\circ} 9^{\prime}$ N， $79^{\circ} 51^{\prime}$ W， $8-15$ Feb．1995，J．Pickering（1 『）；same data except 3 May， 1995 （1邓），19－26 Jan． 1994 （1 区）；Panama，Canal Zone，Barrow Colorado Is．， 9 May 1978， in Malaise trap， 20 m up in Tachigaua，Rainer Krell（1 $\mathbb{\text { ）}}$（USNM）．

Other specimen．Costa Rica，Area de Conservación Guanacaste，lat11．01926 long－85．40997，14 Oct 2005，05－SRNP－33935（1 区，USNM）（http：／／Janzen．sas． upenn．edu）．

Etymology．This species in named in honor of Luciano Capelli of San Jose， Costa Rica，for his intense and generous efforts to publicize ACG conservation with outstanding video and photographs for the Costa Rican and international public．

Food plant and biology．One specimen，05－SRNP－33935），was reared from Davilla nitida（Vahl）Kubitzki（Dilleniaceae）．The larva（Figs 21，22）is very similar to that of W．interstitialis，illustrated by Smith and Janzen（2003b：fig．3）．

Remarks．The specimen reared from Costa Rica is not complete and is not in－ cluded in the type series．However，enough is present，including the lancet，to show it


Figures 7-II. Waldheimia lucianocapellii. 7 Lateral 8 Dorsal 9 Face, front 10 Male genital capsule, ventral II Male penis valve, lateral.


Figures 12-15. Lancets. 12 Atomacera josefernandezi 13 A. ebena 14 Waldheimia lucianocapellii 15 W. fascipennis.
is the same as the specimens from Panama. It DNA barcodes as far from the other 4 species of Waldheimia that were DNA barcoded, as they do from each other.

This species is similar to Waldheimia duckei Konow of South America, but W. lucianocapellii is separated by the mostly black mesoprescutum, white base of the hind tibia and base of the hind basitarsomere, yellow antennomeres 1 and 2 and base of $3^{\text {rd }}$, head pale from above antennae to clypeus, and low flat serrulae of the lancet (Fig. 14). The only other species with which it might be confused in Costa Rica is W. fascipennis, which also has the wings broadly black at the base and apex and yellow at the center; however, W. fascipennis has an entirely orange head, entirely white hind basitarsomere, and deeper serrulae on the lancet (Fig. 15).


Figures 16-22. 16 Adult of Eriglenum tristum 17 Cocoon of Atomacera josefernandezi on leaf 18 Cocoon of Eriglenum tristum on leaf 19 cocoon of Scobina Lepida 20 Larva of Scobina notaticollis 21, 22 Larvae of Waldheimia lucianocapellii.

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# Function of the Dufour's gland in solitary and social Hymenoptera 

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#### Abstract

The poison gland and Dufour's gland are the two glands associated with the sting apparatus in female Apocrita (Hymenoptera). While the poison gland usually functions as an integral part of the venom delivery system, the Dufour's gland has been found to differ in its function in various hymenopteran groups. Like all exocrine glands, the function of the Dufour's gland is to secrete chemicals, but the nature and function of the secretions varies in different taxa. Functions of the Dufour's gland secretions range from serving as a component of material used in nest building, larval food, and pheromones involved in communicative functions that are important for both solitary and social species. This review summarizes the different functions reported for the Dufour's gland in hymenopterans, illustrating how the Dufour's gland secretions can be adapted to give rise to various functions in response to different challenges posed by the ways of life followed by different taxa. Aspects of development, structure, chemistry and the evolution of different functions are also touched upon briefly.


## Keywords

Dufour's gland, function, structure, chemistry, evolution, Hymenoptera

## Introduction

The poison gland and Dufour's gland are the two glands associated with the sting apparatus in female Apocrita (Hymenoptera) (Fig 1). The Dufour's gland is generally found in most Apocrita, and in Symphyta a homologous gland may exist (Robertson 1968, Van Marle and Piek 1986).

[^1]

Figure I. Diagram showing position of the Dufour's gland among other abdominal organs in the polistine wasp Ropalidia marginata. (Drawing: author, not to scale)

Hymenopterans probably originated during the Triassic period (about 250 to 200 million years ago), and the oldest fossils found are similar to sawflies of the family Xyelidae (Symphyta) (Rasnitsyn 2002). The Hymenoptera started diversifying during the Cretaceous (about 150 to 70 million years ago), and this diversification took place simultaneously with other major insect groups like the Lepidoptera, Coleoptera and Diptera, in conjunction with the the rise of the flowering plants, signifying plant-insect coevolution (Hoell et al. 1998, Grimaldi and Engel 2005). The first social Hymenoptera are also believed to have evolved in the Cretaceous. Although the establishment of the major hymenopteran categories like Apocrita, Aculeata and non-aculeate Apocrita, and the subsequent split between ancestors of present day aculeates (Apoidea, Vespoidea and Chrysidoidea) appears to have taken place earlier, in the Jurassic (about 200 to 150 million years ago) (Rasnitsyn and Zhang 2010, Heraty et al. 2011), much of the diversification appears to have taken place in the Cretaceous, when the major Aculeate clades became established (Brady et al. 2009). Thus the Dufour's gland may have been evolving for over more than 200 million years to give rise to the variety of functions it exhibits in modern hymenopterans.

While the poison gland usually functions as an integral part of the venom delivery system, used for paralyzing prey to be used as food as well as in defense, the Dufour's gland has been found to differ in its function in various hymenopteran groups. Like all exocrine glands, the function of the Dufour's gland is to secrete chemicals, but the nature and function of the secretions varies in different taxa. Functions of the Dufour's gland secretions range from serving as a component of material used in nest building, larval food, and various communicative functions like host marking, nest recognition, nestmate recognition, kin recognition, fertility signaling, as a trail pheromone and as a
sex pheromone. These are important for both solitary and social species. The purpose of this review is to summarize the different functions reported for the Dufour's gland secretions in hymenopterans. This will further the understanding and appreciation of how an organ can be adapted for different functions in different lineages, and how differences in the mode of living has led to an organ being adapted for diverse functions. Aspects of development, structure and chemistry are also touched upon briefly.

## Development and structure

The Dufour's gland (often referred to as "alkaline gland" in the older literature) was first described by Dufour (1841). It is an ectodermal abdominal gland located near the proximal end of the abdomen (Fig. 1), and is believed to be a homologue of the colleterial gland of other insects, i.e. an accessory reproductive gland (Carlet 1884, Maschwitz and Kloft 1971, Hermann 1969, Hermann and Blum 1967a, 1967b, 1981, Abdalla and Cruz-Landim 2001). The sting apparatus in Hymenoptera is ectodermal in origin and arises as a modification of the female reproductive system, as evidenced from developmental ontogeny. Buds of genitalia develop on the $8^{\text {th }}$ and $9^{\text {th }}$ abdominal sterna of hymenopteran larvae, and these develop into the ovipositor (sting). The spermatheca, poison gland and Dufour's glands develop as invaginations of valves of the sternum (D'Rozario 1942, Robertson 1968). The duct of the Dufour's gland opens into the sting in ants, while in wasps and bees it opens into the dorsal vaginal wall. The duct opening into the vaginal wall has been proposed as the ancestral state, while opening into the sting has been proposed as a derived state (Billen 1987). However, in a digger wasp, it has been reported that the Dufour's gland opens into the sting, thereby raising doubts about the earlier hypothesis (Gnatzy et al. 2004).

The morphology of the Dufour's gland can vary between groups, but the structure is essentially a single layered epithelial tube. It is partially covered by a muscular layer and is associated with tracheoles and nerves (Hermann and Blum 1967a, 1967b, Landolt and Akre 1979, Downing and Jeanne 1983, Billen 1986a, 1986b, Abdalla and Cruz-Landim 2004, Abdalla et al. 1999). Since there is a single layer of glandular epithelium, the Dufour's gland is a "class I" epidermal gland, as described by Noirot and Quennedy (1974). The gland cells are abundant in smooth endoplasmic reticulum, secretory vesicles, mitochondria, and electron dense granules, consistent with their role in secretion (Billen 1982, 1986a, 1986b). The cells secrete material into the lumen of the gland, which is then carried outwards. Muscles located around the opening of the gland's duct may help in controlling the flow of secretion.

## Chemistry

The Dufour's gland is believed to have evolved from the colleterial gland. Therefore in the ancestral state, the Dufour's gland secretions might be similar to colleterial gland
secretions, found to be glucosides, proteins and enzymes in Lepidoptera and Blattodea, consistent with its role in reproduction (Pau et al. 1971, Sugumaran and Nellaiappan 1990, Jin et al. 2006). Unfortunately the chemistry of the colleterial gland/Dufour's gland in basal hymenopterans (Symphyta) and in many other non-aculeate hymenopterans remains unexplored. The Dufour's gland secretion has generally been found to contain long chain saturated and unsaturated hydrocarbons in most taxa that have been examined. In addition to hydrocarbons, various other volatile, semi-volatile and non-volatile compounds like terpenoids, alcohols, esters, long chain fatty acids, sugars, quinones, various aromatic compounds, traces of cholesterol and aldehydes have been reported. Fig. 2 lists the types of compounds that have been reported from different groups of hymenopterans.

It can be seen that secretion of long chain hydrocarbons is the most ubiquitous trait amongst all hymenopterans whose Dufour's gland chemistry has been analyzed (Fig. 2). Thus secretion of hydrocarbons is likely to be an ancestral trait common to all hymenopterans, while other categories of compounds that have been reported are likely to be derived traits. In Apoidea, Andrenidae, Colletidae and Halictidae are closely related clades that share esters with terpene derivatives (Hefetz et al. 1979, Duffield et al. 1981, Hefetz 1987).The Colletidae and Halictidae are sister clades that share macrocyclic lactones. The Megachilidae is sister to the Apidae and has triglycerides, a trait shared with Anthophorini, which is basal to other apids (Cane 1981, Cane and Carlson 1984, Kronenberg and Hefetz 1984, Cardinal et al. 2010). This trait is absent in other apids, who share esters as a common trait, suggesting that ester production may be a trait that evolved early during the diversification of the Apidae (Vinson et al. 1978, Duffield et al. 1984, Kronenberg and Hefetz 1984, Katzav-Gozansky et al. 1997, Abdalla et al. 2004, Amsalem et al. 2009). In the Vespoidea, again hydrocarbons are the trait common to most taxa, while the Formicidae show the presence of categories of compounds not found in other vespoids (see Fig. 2). Since the Formicidae show considerable adaptive radiation and occupy diverse ecological microhabitats, it is not surprising to see several derived traits with respect to Dufour's gland chemistry in the Formicidae. Hydrocarbons are likely to be the conserved trait in Dufour's gland chemicals of Hymenoptera, and different clades show appreciable differences in the composition of their Dufour's gland compounds, with the majority of clades presenting an admixture of ancestral and derived traits.

## Function

The Hymenoptera form a basal sister clade with respect other insect orders like the Lepidoptera, Trichoptera, Siphonaptera and Diptera (Kristensen 1981, Whiting 2002, Kjer 2004). Since the Dufour's gland is believed to have evolved from the colleterial gland (an accessory reproductive gland) that is present in other insects (Carlet 1884, Maschwitz and Kloft 1971, Hermann 1969, Hermann and Blum


Figure 2. Diagram listing the categories of compounds reported from the Dufour's gland in various hymenopteran taxa, also showing the inter-relationships of the taxa. Dendrogram made following Brothers (1998), Schmitz and Moritz (1998), Whitfield and Cameron (1998), Grimaldi and Engel (2005), Brady et al. (2009), Vincent et al. (2010), and Cardinal et al. (2010). References cited in parenthesis below the names of compounds. Branch lengths do not have any significance.

1967a, 1967b, 1981, Abdalla and Cruz-Landim 2001), the ancestral function of the gland could be similar to roles performed by the colleterial gland in other insects, like forming a protective casing (ootheca) over the eggs, or producing cementing material for attaching eggs to the substrate (Brunet et al. 1952). Colleterial glands in a moth (Lepidoptera, a sister clade of Hymenoptera) have been found to function in attaching eggs to leaves of plants (Chaudhuri and Sinha 1994). The colleterial gland in Symphyta has been reported as the homologue of the Dufour's gland (Robertson 1968, Van Marle and Piek 1986) but unfortunately, the function of this gland in symphytans (basal Hymenoptera) remains unexplored (Fig 3). With the exception of Orussidae, which is parasitic and basal to the apocritans, other symphytans are phytophagous, with Xyelidae being the clade basal to all other Hymenopetra (Davis et al. 2010). Perhaps the colleterial gland in Symphyta may be involved primarily in cementing eggs to plants, as in other phytophagous insects. In the older literature the Dufour's gland was often referred to as the "alkaline gland" and its secretions were assumed to be alkaline in nature in contrast to the poison gland, whose secretions were deemed acidic. It was often assumed that the general function of the Dufour's gland secretion is to lubricate the sting or ovipositor, lubricate passage of eggs during oviposition, glue eggs to the substratum, or to provide a protective coating to eggs, but experimental evidence for these postulated functions is absent (Dufour 1841, Billen 1987, Howard and Baker 2003, Gnatzy et al. 2004). The Dufour's gland is reported to serve various communicative purposes in social apocritans (Fig. 3).

Figure 3. Diagrammatic summary of the known functions of the Dufour's gland in various hymenopteran taxa, also showing the inter-relationships of the taxa. Dendrogram made following Brothers (1998), Schmitz and Moritz (1998), Whitfield and Cameron (1998), Grimaldi and Engel (2005), Brady et al. (2009), Vincent et al. (2010), and Cardinal et al. (2010). Figures in parenthesis beside each function denote references cited. Branch lengths do not have any significance.
References: $\mathbf{1}$ Rosi et al. (2001), $\mathbf{2}$ Mehrnejad and Copland (2007), $\mathbf{3}$ Vardal (2006), 4 Guillot et al. (1974), $\mathbf{5}$ Vinson and Guillot (1972), $\mathbf{6}$ Lawrence and Akin (1990), $\mathbf{7}$ Vinson (1978), $\mathbf{8}$ de Freitas et al. (2004), $\mathbf{9}$ Marris et al. (1996), $\mathbf{1 0}$ Huang et al. (2008), $\mathbf{1 1}$ Cane (1981), $\mathbf{1 2}$ Duffield et al. (1983), 13 Hefetz (1987), $\mathbf{1 4}$ Ayasse et al. (1990b), $\mathbf{1 5}$ Hefetz et al. (1979), $\mathbf{1 6}$ Albans et al. (1980), $\mathbf{1 7}$ Cane (1981), 18 Guedot et al. (2006), 19 Cane (1981), 20 Brooks and Cane (1984), 21 Ayasse et al. (1990a), 22 Smith et al. (1985), 23 Barrows (1975a), 24 Barrows et al. (1975b), 25 Ayasse et al. (1993), 26 Hefetz et al. (1986), 27 Hefetz (1987), 28 Smith and Wenzel (1988), 29 Cane and Carlson (1984), 30 Duffield et al. (1984), 31 Norden et al. (1980), $\mathbf{3 2}$ Hefetz et al. (1982), 33 Shimron et al. (1985), 34 Frankie and Vinson (1977), 35 Vinson et al. (1978), 36 Katzav-Gozansky et al. (2002), 37 Sole et al. (2002), 38 Oldroyd et al. (2002), 39 Katzav-Gozansky et al. (2007), 40 Malka et al. (2008), 41 Tengö et al. (1991), 42 Oldham et al. (1994), 43 Ayasse et al. (1999), 44 Amsalem et al. (2009), 45 Amsalem and Hefetz (2010), 46 Abdalla and Cruz-Landim (2004), 47 Downing and Jeanne (1983), 48 Downing (1991), 49 Dani et al. (1996a), 50 Dani et al. (1996b), 51 Mitra et al. (2011), 52 Mitra and Gadagkar (2011), 53 Mitra and Gadagkar (2012a), 54 Mitra and Gadagkar (2012b), 55 Jeanne (1977), 56 Reed (1982), 57 Reed and Akre (1982), 58 Barr-Nea et al. (1976), 59 Sledge et al. (2000), 60 Fortunato and Turillazzi (2012), 61 Turillazzi (1989), $\mathbf{6 2}$ Cervo et al. (2002), 63 Law et al. (1965), 64 Hölldobler and Wilson (1970), 65 Williams et

al. (1981), 66 Blatrix et al. (2002), 67 Jeanson et al. (2003), 68 Greene and Gordon (2007), 69 Morgan (2009), 70 Cammaerts et al. (1977), 71 Wilson and Regnier (1971), 72 Whitehouse and Jaffe (1996), 73 Topoff et al. (1988), 74 Mori et al. (2000), 75 Hölldobler and Wilson (1990), 76 Ayasse et al. (2001).

## a) Parasitic wasps

The evolution of the parasitic life history has been considered to be an important factor that led to the massive divergence and adaptive radiation of the Hymenoptera (Heraty et al. 2011). Unfortunately, the function of the Dufour's gland remains poorly explored in parasitic Hymenoptera that are basal to the more advanced groups of aculeates. Among various non-aculeate parasitic apocritans the function of the Dufour's gland may range from host marking (oviposition site marker), sex attractant, coating the egg surface or facilitating oviposition. In Chalcidoidea, the Dufour's gland region has been found to elicit a male courtship response in the chalcid wasps Brachymeria lasus and B. intermedia (Chalcididae) and thereby it has been proposed that Dufour's gland secretions may act as a sex pheromone (Simser and Coppel 1980). There is some evidence of Dufour's gland secretion acting as host marking chemicals in Psyllaephagus pistaciae (Encyrtidae) that can be used to avoid ovipositing in a parasitized host (Mehrnejad and Copland 2007). The function of Dufour's gland remains unexplored in fig wasps (Agaonidae). In Ichneumonoidea, Dufour's gland hydrocarbons have been implicated in host marking in Cardiochiles nigriceps and Micropletis croceipes (Braconidae) (Guillot et al. 1974, Vinson and Guillot 1972), and also in Nemeritis canescens and Itoplectis naranyae (Ichneumonidae) (Mudd et al. 1982, Hubbard et al. 1987, Ueno 1994). It has been found that not only may the Dufour's gland function in host marking in Venturia canescens (Ichneumonidae), but females may also discriminate between hosts parasitized by other closely related females versus those parasitized by unrelated females, thereby ensuring that their offspring do not have to compete with other genetically similar larvae in the same host (Marris et al. 1996). In Diadegma semiclausum (Ichneumonidae), Dufour's gland secretions have been reported to be added along with venom gland secretions to mature eggs that are ready to be laid (Huang et al. 2008). The Dufour's gland has been reported to act as a female sex pheromone in Cardiochiles nigriceps and Cotesia flavipes (Braconidae) (Vinson 1978, Syvertsen et al. 1995, de Freitas et al. 2004). In Biosteres longicaudatus (Braconidae), virus-like particles have been reported to accumulate in the Dufour's gland, which are injected into the host during parasitization, and may serve in suppressing the immune system of the host during development of parasitic larvae in the host's body (Lawrence and Akin 1990). In Platygastroidea, evidence for host marking has been found in Trissolcus basalis (Scelionidae) (Rosi et al. 2001).

The function of the Dufour's gland remains to be studied in Cephranoidea, Evanoidea, Megalyroidea, Mymarommatoidea, Proctotrupoidea, Stephanoidea, and Trigonaloidea, while recent evidence suggests that the Dufour's gland may be absent in Cynipoidea (Vardal 2006).

## b) Aculeata

All social hymenopterans belong to the Aculeata, a clade which has received much attention over the years. Consequently, most of the information on the function of the

Dufour's gland comes from aculeates. Aculeates are characterized by the development of the stinging apparatus, which leads to a separation of the sting from any oviposition related functions (Hunt 2007). In aculeates, the speculations regarding ancestral functions of the Dufour's gland include sting lubrication, venom constituent or role in oviposition (Dufour 1841, Billen 1987, Howard and Baker 2003, Gnatzy et al. 2004), but definitive demonstrations are lacking. Many studies have looked at the function of the Dufour's gland in the two well studied groups: the Apoidea and Vespoidea. Among solitary aculeates, the function of Dufour's gland remains unknown in the Chrysidoidea (cuckoo wasps). Since this group is basal to other aculeates, it would be of interest to investigate the role of the Dufour's gland in this group. Since the Chrysidoidea is comprised mostly of parasitoids, perhaps the role of the Dufour's gland here is similar to that in the parasitoid non-aculeates. The Dufour's gland probably underwent further modifications that were possible with the development of the stinging apparatus of the Aculeata, which removes any constraints related to oviposition from the stinging apparatus (Whitfield 1992), and thereby with the evolution of the sting, the Dufour's gland can be freed from prior evolutionary constraints. Indeed, structural modifications whereby the Dufour's gland no longer remains connected to the reproductive tract but opens instead into the sting has been documented (Billen 1987, Gnatzy et al. 2004). The function of the Dufour's gland in the Aculeata varies widely with variation in mode of living.

In Apoidea, the primary role of the Dufour's gland in various ground nesting bees appears to be producing the brood cell lining. Dufour's gland secretions have been found to be involved in forming a protective lining of the brood cells in various ground dwelling bees in Colletidae, Andrenidae, Halictidae, and some Apidae (Anthophorini and Eucerini), and sometimes they also form a hydrophobic lining for their pollen balls (Hefetz et al. 1979, Albans et al. 1980, Cane 1981, Duffield et al. 1981, 1983, Cane and Carlson 1984, Hefetz et al. 1982, 1986, Hefetz 1987). Ground dwelling bees face the challenge of keeping their larval food free from microbial growth, desiccation, and soaking by water. They have evolved to respond to this challenge by coating their brood cell with a hydrophobic lining that forms a sheath around the larval food. Secretions of the Dufour's gland have been found to be involved in forming this cell lining. Consequently the Dufour's gland has been found to become hypertrophied with the increase in activity during the nest construction phase (Lello 1971a, 1971b, Kronenberg and Hefetz 1984). Production of brood cell lining is an important adaptation for mass provisioners, ensuring that the food remains fresh and suitable for consumption by the larvae. Unfortunately, it is not known whether a similar function is served by the Dufour's gland in ground dwelling digger wasps, sand wasps and bee wolves (Sphecidae and Crabronidae), which utilize similar nest substrates. In the Crabronidae there is evidence for the post pharyngeal gland being involved in prey embalming, which may serve the same function as served by the protective hydrophobic cell lining of ground dwelling bees (Strohm et al. 2001). In the melittid bee Hesperapis the Dufour's glands are tiny and appear to be secondarily derived, as they are correlated with the absence of cell lining or with producing cell lining from
exogenously derived substances (Cane 1983). In communally nesting mining bees of genus Andrena (Andrenidae), Dufour's gland compounds have been found to vary with genetic relatedness, thereby implying a possible role in kin recognition (Ayasse et al. 1990b). Such compounds have also been implicated in marking the nest entrance, helping in locating the nest within the nesting site (Hefetz 1987). In the sweat bee Lasioglossum malachurum (Halictidae), the pattern of Dufour's gland compounds was found to differ between virgin and mated queens, suggesting a possible involvement in mating and courtship (Ayasse et al. 1993). Mated queens had higher proportion of macrocyclic lactones (used in nest construction), and lower proportion of isopentyl esters (volatiles), as compared to virgin queens, and the composition of Dufour's gland compounds was found to change within one day of mating (Ayasse et al. 1993). In the same species, L. malachurum (Halictidae), the pattern of ester composition has also been found to differ between young virgin queens and old nesting queens, and the pattern has also been correlated with volume of fat body and status of ovarian development, implying possible involvement in sex pheromonal communication and in nest recognition (Ayasse et al. 1990a). Dufour's gland lactones have been found to act as a sex pheromone in L. zephyrum (Smith et al. 1985, Barrows 1975a, Barrows 1975b). Dufour's gland compounds have been implied in nestmate recognition and kin recognition as well in halictine bees (Hefetz et al. 1986, Hefetz 1987, Smith and Wenzel 1988, Soro et al. 2011). In Halictus hesperus (Halictidae) Dufour's gland secretion has been found to impart structural strength to the opening of the nest (Brooks and Cane 1984). In Eucera palestinae (Apidae: Eucerini), in addition to serving as a cell lining, Dufour's gland compounds also serve to mark the nest entrance and are used by individuals to locate their nest within dense nest aggregations (Shimron et al. 1985). A similar function has been proposed for Colletes cunicularius (Colletidae) and Osmia lignaria (Megachilidae) as well (Guédot et al. 2006). To serve as a semiochemical used in nest recognition, the Dufour's gland chemicals must show considerable inter-individual variability. Such variability has indeed been reported in some species (Kronenberg and Hefetz 1984, Hefetz 1987). In some Megachile species (leaf cutter bees) (Megachilidae), Dufour's gland compounds have been found mixed with larval food (bee bread), implying that they may serve as larval nutrition, or possibly to protect the larvae from fungal or bacterial attack (Cane and Carlson 1984, Duffield et al. 1984). Among short-tongued bees (Colletidae, Halictidae, Andrenidae and Melittidae) chemosystematic analysis suggests that Colletidae, Oxaeinae, Nomiinae and Halictinae comprise a monophyletic group (lactone producing bees), sharing macrocyclic lactones that are not found in any other hymenopterans. The other short-tongued bees (Andrenidae, Melittidae and Dufoureinae (currently Systrophinae)) form another monophyletic clade, sharing hydrocarbons (Cane 1983). The function of Dufour's gland in other solitary Apoidea like the Sphecidae (digger wasps), Crabronidae (sand wasps and bee wolves), and Ampulicidae (cockroach wasps) remains unexplored. Thus in addition to forming the cell lining, nest recognition seems to be another widespread function of Dufour's gland chemicals in bees. The same chemicals that are already in use for lining the nest surface can also be used by the organisms to identify their nests.

Various communicative roles of the Dufour's gland like kin recognition and nestmate recognition are reported in communally nesting species of Andrenidae and Colletidae, and social Halictidae (Fig. 3).

In the Apidae, the role of the Dufour's gland in producing brood cell lining is found in ground dwelling bees of the genera Anthophora (Anthophorini) and Eucera (Eucerini) (Stephen and Torchio 1961, Norden et al. 1980, Cane and Carlson 1984, Shimron et al. 1985) and in ground dwelling carpenter bees as well (Xylocopa olivieri, Apidae: Xylocopini) (Kronenberg and Hefetz 1984). Xylocopines generally nest in wood (mostly tree trunks), and ground nesting strategy is an exception for this group. Thus the Dufour's gland secretions may have secondarily gained the function of producing brood cell lining in xylocopines. The function of the Dufour's gland in secreting a cell lining in the various ground nesting Apidae can be the result of the retention of a function present in ancestors of this group who diversified to form the different present day phyla. However, cases of convergent evolution owing to similarity in ecological habits cannot be ruled out. Similar to its suggested role in the Megachilidae, the role of the Dufour's gland in producing larval food has been demonstrated in Anthophora abrupta (Norden et al. 1980). In carpenter bees (Xylocopini), Dufour's gland has been implicated in foraging site marking, i.e. marking flowers that have been visited for pollen or nectar collection (Fig. 3). This marking is temporary and fades away over a short period of time, over which the flower is able to replenish its nectar. In Xylocopa virginica (Xylocopini) Dufour's gland secretions are deposited on flowers visited by bees, and serves to deter visits by conspecifics on a short term (Frankie and Vinson 1977, Vinson et al. 1978). In kleptoparasitic Nomadini, male mandibular gland secretion has been found to mimic the Dufour's gland secretion of their hosts. Males have been found to coat females with their mandibular gland secretion, which renders the chemical profile of the female similar to the cell lining of their host, thereby facilitating kleptoparasitism (Tengö and Bergström 1977).

Among the corbiculate apids (Apini, Bombini, Meliponini and Euglossini), communicative functions for the Dufour's gland secretions have been reported in various taxa. In bumble bees (Bombini), the Dufour's gland has been found to increase in size and activity with the reproductive activity and age of queens, and queen worker differences in gland size have also been reported, implying a possible role as an egg marking pheromone (Abdalla et al. 1999). Queen signaling and nestmate recognition through Dufour's gland has also been implied (Tengö et al. 1991, Oldham et al. 1994, Ayasse et al. 1999). In Bombus terrestris it has been found that workers may advertise their sterility through esters secreted in their Dufour's gland, and thereby avoid being policed by queens or other egg laying workers. These esters disappear when an individual starts to develop ovaries (Amsalem et al. 2009, Amsalem and Hefetz 2010). Cuckoo bumblebees (subgenus psithyrus) can be attracted by the Dufour's gland odors of their hosts (other Bombus) to parasitize them (Fisher et al. 1993). In stingless bees (Meliponini) it has been found that reproductively active queens may have larger Dufour's glands than virgin queens and the gland may be absent in workers; however the function remains unknown and has been speculated as involvement in reproduction or in queen
signaling, and it has been suggested that the Dufour's gland secretions may act as a queen pheromone, as virgin queens have hydrocarbons in their Dufour's gland, while mated physogastric queens have esters in addition to hydrocarbons (Abdalla and CruzLandim 2004, Abdalla et al. 2004). In honey bees (Apini), there are multiple evidences for Dufour's gland esters functioning in pheromonal queen signaling. Such esters are initially absent in workers, but start being secreted in egg laying workers (KatzavGozansky et al. 2002, Oldroyd et al. 2002, Katzav-Gozansky et al. 2007, Malka et al. 2008). It has been proposed that multiple mating of queens triggers the production of esters from the Dufour's gland (Richard et al. 2011), while in the case of workers it is probably triggered by the absence of queen pheromone. The egg laying workers of Apis mellifera capensis, who act as social parasites of $A$. mellifera scutellata, produce Dufour's gland secretions that have been found to mimic the queen gland secretion better than that of egg laying $A$. m. scutellata workers, thereby increasing the efficiency of their social parasitism (Sole et al. 2002). The role of Dufour's gland in Euglossini remains unknown. Thus in honey bees (Apini), bumble bees (Bombini), and stingless bees (Meliponini) the Dufour's gland serves communicative functions like fertility signaling (queen pheromone) and nestmate recognition (Fig. 3).

The Vespoidea contains two major groups of social Hymenoptera: the Formicidae and Vespidae. Apart from these two families, the function of Dufour's gland remains unexplored in other Vespoidea (Tiphiidae, Sapygidae, Mutillidae, Pompilidae, Rhopalosomatidae, Scoliidae, and Sierolomorphidae). In ants (Formicidae), Dufour's gland secretions have often been found to act as a trail pheromone in Formicinae and Ponerinae (Law et al. 1965, Hölldobler and Wilson 1970, Williams et al. 1981, Bestmann et al. 1995, Blatrix et al. 2002, Jeanson et al. 2003). They have a recruitment effect, serve in territorial marking, or in setting foraging direction (Cammaerts et al. 1977, Greene and Gordon 2007). Often the Dufour's gland acts in unison with other glands, like the poison gland, in communicating recruitment signals for recruitment of workers to food or nesting sites. Secretions of the Dufour's gland are often applied on the substrate by extruding the sting and dragging it (Hölldobler and Wilson 1970, Morgan 2009). However, other glandular sources of trail pheromone originating in the metasoma (hindgut, pygidial gland, post-pygidial gland) or legs (tibial glands, footprint glands on the hind pre-tarsi) are also known (Morgan 2009). The Dufour's gland secretion can have colony specificity and species specificity, thereby ensuring fidelity of the trail (Traniello 1980, Haak et al. 1996). The Dufour's gland has also been implicated as a storage site for chemicals involved in the alarm-defense system of ants, whereby the same chemicals can produce an alarm reaction among nestmates, while simultaneously acting as repellents to intruders (Wilson and Regnier 1971, Whitehouse and Jaffe 1996). In slave making ants of the genus Polygerus Dufour's gland chemicals have been found to be used in manipulating the behavior of the host species. Dufour's gland compounds facilitate the new queen of the slave making ant to invade a host colony, and reduce any aggression shown by the host workers towards the usurper (Topoff et al. 1988, Mori et al. 2000). Such compounds may also act as a repellent and thereby facilitate usurpation of a host colony (Ruano et al. 2005). Another function of

Dufour's gland in slave making ants is to act as a source of propaganda substances that elicit panic among defending host workers, thereby increasing the efficiency of slave capturing raids (Brandt et al. 2006). Dufour's gland compounds have also been found to act as sex pheromones, and can also be involved in the calling behavior exhibited by females, whereby virgin gynes place themselves in strategic positions outside their nests and "call" for mates by releasing sex pheromones (Hölldobler and Wust 1973, Hölldobler and Wilson 1990, Ayasse et al. 2001).

In the hover wasps (Vespidae: Stenogastrinae) the Dufour's gland substances act as a substrate on which eggs are laid and food is placed for subsequent consumption by larvae and adults (Sledge et al. 2000, Fortunato and Turillazzi 2012). The secretion of a jelly-like substance by the Dufour's gland that functions in larval nutrition has been proposed as an important step towards the evolution of sociality in this lineage. It enables anchoring eggs and larvae, and the storage of liquid food in the nest, subsequently facilitating the evolution of behavioral mechanisms that facilitate social interaction (Turillazzi 1989, Cervo et al. 2002). Apart from these functions, Dufour's gland secretions also serve as ant repellents. They are used to construct sticky barriers which serve as ant guards around the nest (Sledge et al. 2000, Fortunato and Turillazzi 2012). These aid in preventing predation of immature brood by ants. Dufour's gland compounds may also function in nestmate recognition (Cervo et al. 2002). Additionally, the Dufour's gland secretions serve as food for both larvae and adults and can be stored for future consumption. This seems to be an important development that may have facilitated the evolution of sociality in this group (Turillazzi 1989, Cervo et al. 2002, Fortunato and Turillazzi 2012). The Dufour's gland secretions function as ant repellants (Sledge et al. 2000), and this should be another important factor facilitating progressive provisioning of brood. Progressive provisioning of brood is a character shared by most eusocial Hymenoptera, and is important for the evolution of sociality (Hunt 2007). Evidence for Dufour's gland compounds acting in nestmate recognition in stenogastrines reinforces the idea of chemicals having other primary functions being secondarily involved in chemical communication. Since the gland secretions have to be applied inside cells, and also outside and around the nest, to repel ants, this should facilitate nest or nestmate recognition by nest odor. Thus the Dufour's gland secretions can be intertwined with the coevolution of brood rearing, avoiding brood predation, and maintaining colony fidelity, and appear to have an important role in the evolution of sociality in hover wasps.

Among other vespids, in the Vespinae the Dufour's gland has been postulated to facilitate social parasitism by increasing acceptance of parasites among host individuals, or by acting as an alarm pheromone, eventually serving as a means of usurping and controlling the host colony (Jeanne 1977, Reed 1982, Reed and Akre 1982). The Dufour's gland secretion of Vespa orientalis has been reported to be slightly lethal to honey bees, thereby implicating a role in venom secretion (Barr-Nea et al. 1976). This may be another example of an adaptation of Dufour's gland secretions for a function not reported in other hymenopteran taxa. In Polistinae, Dufour's gland compounds have been implicated in dominance interactions, egg marking, nestmate recognition,
and queen signaling (Downing and Jeanne 1983, Downing 1991, Dani et al. 1996a, 1996b, Mitra et al. 2011, Mitra and Gadagkar 2011, Mitra and Gadagkar 2012a, 2012b). In the polistine wasp Ropalidia marginata the Dufour's gland has been shown to be involved in producing the queen pheromone, using which the queen conveys her presence to workers and thereby maintains reproductive monopoly (Mitra et al. 2011). It has also been found that the Dufour's gland hydrocarbon composition varies as a function of ovarian development, thereby suggesting that such chemicals can act as an honest signal of the queen's fertility (Mitra and Gadagkar 2011, Mitra and Gadagkar 2012a, 2012b). Interestingly it has been found that the cuticle and the haemolymph of $R$. marginata also contain the same set of hydrocarbons as found in the Dufour's gland, thereby implying that these hydrocarbons can be synthesized in the oenocytes of fat bodies, from where they enter circulation in the haemoplymph and are finally sequestered and stored in the Dufour's gland or secreted on the cuticle (Mitra and Gadagkar: in press). The function of the Dufour's gland remains unexplored in other Vespidae like potter wasps (Eumeninae) or pollen wasps (Masarinae). Examples of chemical communication through Dufour's gland in vespids, like dominance signaling, queen signaling, nestmate recognition or social parasitism (Fig. 3), again suggest adaptations in a case specific manner. The ability to perceive chemicals secreted from the Dufour's gland should be necessary to facilitate the evolution of adaptive communicative functions. Interestingly, in a polistine wasp it was found that dominance signaling through Dufour's gland secretions may act via egg marking (Downing and Jeanne 1983, Downing 1991), perhaps exemplifying the ancestral function of egg coating giving rise to novel communicative roles. The role of the Dufour's gland in communication in vespids may have coevolved with the evolution of various behavioral and chemical communication systems exhibited by vespids, or it may also have evolved coincidentally with the evolution of vespid sociality.

## Concluding remarks

It can be seen that the Dufour's gland secretion has undergone a variety of shifts in its functionality in various hymenopteran lineages. The ancestral function related to egg coating and attachment of eggs to the substrate might be retained (or perhaps secondarily gained) only in stenogastrines, in addition to a few extant clades like ichneumonids and perhaps a few polistines (Fig. 3). In parasitic wasps, it has gained the function of host marking, which may be the most widespread function of the Dufour's gland in non-aculeates (Fig. 3). Dufour's gland secretions form a chemical mark on the host body, which can be used by the parasites as a recognition cue, thereby preventing overinfection of the same host. In these groups, the ovipositor is long, sting-like, and the precursor of the sting of Aculeata, and thereby secretions of the Dufour's gland (perhaps involved in oviposition and other reproductive functions) can get co-opted to be used as semiochemicals used to avoid oviposition in a host that is already parasitized. This is particularly interesting from the perspective of evolution of semiochemicals, be-
cause chemicals that already exist for other purposes often get co-opted later for being used as a signal (Stoka 1999). Since the Dufour's gland chemicals may be involved in oviposition, they will inadvertently get deposited on the host when the parasite injects her eggs. With the evolution of the signaling system, which requires developing the ability to detect these chemicals, these chemicals can advertise the unavailability of a host to other potential parasites. The Dufour's gland secretions have also been reported to act as sex pheromone in braconids (Fig. 3). Unsaturated hydrocarbons have been reported in Dufour's gland secretions of braconids and ichneumonids (Fig. 2), and it is possible that the ability to secrete such semi-volatile compounds is a necessary prerequisite for evolving the function of sex pheromones or other semiochemicals that are detected at a distance. The presumed ancestral role of involvement in oviposition or egg coating appears to have been retained in ichneumonids (Huang et al. 2008), but it may well be that such a role is present in other taxa as well, awaiting discovery.

In some non-apid bees (Colletidae and Halictidae), the gland has primarily acquired the role of producing cell linings, which are essential for preserving provisions for the brood. This clearly has arisen in response to the challenges faced for keeping food unattended and unspoiled in cells constructed in the soil, where food is always prone to becoming over-hydrated and being attacked by microbes. The chemistry of Dufour's gland secretions have been altered accordingly in these two groups of ground nesting bees and consist of terpenoid esters and other esters, and macrocyclic lactones in addition to hydrocarbons (Fig. 2). These chemicals often form a natural polyester lining inside the brood cells, acting as an effective water repellent. It is possible that this function of producing the brood cell lining from Dufour's gland secretions may have arisen simultaneously with diversification of the ground nesting bees into their present state. Interestingly, there are also ground nesting basal melittids and megachilids that do not line their cell walls (Cane 1983). Hence it is possible that this trait has arisen independently multiple times. The function of producing cell lining from Dufour's gland secretions is again found in ground nesting apid bees (Anthophorini and Eucerini), although the chemistry of the secretions is different, comprising of hydrocarbons and esters (Fig. 2). The function of producing brood cell lining is lost in social bees of Apini, Bombini and Meliponini, where communicative functions take precedence, and unsaturated hydrocarbons and esters seem to be involved in this function. Members of Apini, Bombini and Meliponini generally construct their nests from wax produced from abdominal wax glands (cuticular exocrine glands), sometimes also using cellulose and other material collected from their surroundings in the nest construction process. Hence it is not surprising to find that the Dufour's gland no longer plays a role in lining their cells or producing material for nest construction. Communicative roles are also seen in other social bees like the Halictidae, and in various vespoids. The Dufour's gland may have played an important part in the evolution of sociality in stenogastrines, as the conditions necessary for successful social living would have to be fulfilled in other ways in the absence of the Dufour's gland. The ancestral function of attachment of eggs to the substrate through Dufour's gland secretions may also have been retained in stenogastrines (however secondary gain of such function cannot be ruled out). The Dufour's gland plays communicative roles in polistines as well, emphasiz-
ing the utility for developing modes of chemical communication in conjunction with the evolution of social life. In the Formicidae there is enormous variation in the communicative roles played by the Dufour's gland, concomitant with the wide ranging adaptive radiation and speciation undergone by this group. The Formicidae show appreciable variation in communicative roles of the Dufour's gland ranging from trail pheromone and territory marking to alarm-defense, slave making, and serving as sex pheromones (Fig. 3). The role of the gland in trail formation has been demonstrated in many trail forming species. The ability of the ants to perceive Dufour's gland chemicals should be a prerequisite for involvement of such chemicals in trail marking. Accordingly the chemical composition of the Dufour's gland also includes various volatile and semi-volatile compounds like unsaturated hydrocarbons, terpenoids, alcohols, acids, quinones and aromatic compounds. The involvement of the Dufour's gland in the alarm-defense system or in slave making, may be secondary adaptations. Perhaps the involvement of Dufour's gland chemicals as an alarm pheromone has been exploited by slave making species to give rise to this special kind of social parasitism. The involvement of the Dufour's gland in sex pheromone production in ants is reminiscent of a similar role in non-aculeate hymenopterans.

Thus the Dufour's gland secretions display a fair degree of functional plasticity, in conjunction with the diversity of ecological habits followed by different groups of Hymenoptera (Fig. 3). The basic function of the gland in all Hymenoptera remains the secretion of chemicals, but the nature of secretions and the function of the secreted chemicals have undergone appreciable modification in various taxa. This illustrates how an organ can evolve to give rise to various functions in response to challenges posed by the way of life followed by a lineage. The function of the Dufour's gland remains unexplored in various basal Hymenoptera, especially the Symphyta. Future explorations in that direction should be able to provide a clearer picture of the role of the gland in the ancestral condition. This will result in a comprehensive view of the evolution of Dufour's gland function in the Hymenoptera.

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# Factors influencing the foraging activity of the allodapine bee Braunsapis puangensis on creeping daisy (Sphagneticola trilobata) in Fiji 

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## Keywords

Bees, invasive plants, pollinators, South Pacific

## Introduction

There is growing concern regarding the global decline of honey bee populations and the implications of this demise for the pollination of entomophilous crops (Potts et al. 2010, Groom and Schwarz 2011; Cornman et al. 2012). In the future we may rely on other insect species to perform crop pollination services, including naturally-occurring native or introduced species of bees (e.g. Rader et al. 2009). Pollination success of generalist plants tends to be positively related to pollinator diversity, so any habitat modifications that increase the number of pollinating species present at a site would
tend to be of some inherent value (Hoehn et al. 2008, Albrecht et al. 2012). The deliberate sub-planting of crops, orchards or vineyards with flowering plants (such as buckwheat, Phacelia and Alyssum) is already employed as a means of attracting beneficial invertebrates by providing a nectar or pollen reward (Irvin et al. 2006). A similar process involves the leaving of field margins fallow to allow a higher diversity of flowering 'weeds' to grow, which again promotes a higher diversity of invertebrate predators and pollinators to occur (Cowgill et al. 1993).

The situations described above give the impression that the presence of some exotic flowering plants may be of benefit by encouraging higher numbers of pollinating species to occur at a site. Outside of agro-ecological systems, many studies have indicated that even flowering plants considered as invasive may have positive effects on insects, especially on nectar and pollen feeding species. For example, in Europe and North America, the exotic highly invasive Himalayan balsam (Impatiens glandulifera Royle) is visited by a high diversity of native pollinating insects, including bumble bees (Bombus spp), solitary bees, and domestic honey bees (Apis mellifera L.) (Showler 1989, Stary and Tkalcu 1998, Nienhuis et al. 2009).

Sphagneticola trilobata (L.) Pruski (Asteraceae) is an emerald-green creeping plant that has bright yellow daisy-like flowers. The plant is of Central/South American origin and is now found in many South Pacific island states, where it has become established on disturbed sites, such as waste land, road sides, riverbanks and the sea shore (Whistler 1995). The species is thought to have been introduced to Fiji sometime in the early 1970s as a garden ornamental near Suva Point, on the main island of Vitu Levu (Thaman 1999). A recent survey in the Suva area reported over 100 species of arthropods associated with road side patches of S. trilobata, including Hymenoptera such as parasitoid wasps, honey bees and solitary bees (Prasad and Hodge in press). One species of solitary bee, Braunsapis puangensis (Cockerell, 1929) (Apidae: Allodapini) was locally abundant on patches of S. trilobata in the Laucala Bay area of Suva. This bee species is probably of Indian origin and was most likely carried to Fiji by anthropogenic means (Groom and Schwarz 2011, Davies et al. in press). The genus Braunsapis is listed in the Fijian fauna provided by Evenhuis (2007), but does not appear in the older lists of Michener (1965), Fullaway (1957) and Turner (1919). Shenoy and Borges (2008) examined the diurnal activity patterns and pollination behaviour of this species in India and the phylogeny of the group has received some detailed attention (Bull et al. 2003, Schwarz et al. 2004, Fuller et al. 2005). The genus has also been studied in terms of its social parasite behaviour (Reyes and Sakagami 1990, Batra et al. 1993).

The aim of this study was to obtain empirical data on the activity and distribution of Braunsapis puangensis in the Suva area of Fiji and examine its association with Sphagneticola trilobata. We studied spatial patterns on a local scale by recording its presence or absence on patches of S. trilobata along roadsides, and carried out long term sampling over 14 months to gain information on patterns in seasonal occurrence. A more detailed study was performed at a single site to investigate daily foraging patterns and examine the effects of environmental conditions on B. puangensis activity.

## Methods

## Field survey of patches of Sphagneticola trilobata in the Suva area

Twenty-two patches of Sphagneticola trilobata were selected to give widespread coverage of the Greater Suva area (including Lami and Nasinu) and the surrounding area (Rewa Delta, Nukulau Island) (Table 1). All the patches of S. trilobata sampled were greater than $4 \mathrm{~m}^{2}$ in area and close to roadsides or tracks. Insects were either sampled using a sweep net or obtained directly from the flowers using a battery-powered aspirator. To avoid over sampling the bees, only the presence/absence of Braunsapis puangensis was recorded at some locations. The coordinates of each site were recorded using a geographical positioning system ['etrex'; Garmin Ltd, Southampton, UK] and these used to plot a map of the sites using Microsoft MapPoint (Figure 1).

## Seasonal activity patterns of Braunsapis puangensis

Long term monitoring of Braunsapis puangensis was carried out using yellow pan traps placed out under the eaves of a house on The University of the South Pacific (USP)

Table I. The presence or absence of Braunsapis puangensis on twenty two patches of Sphagneticola trilobata in the Greater Suva area visited in April 2011.

| Site no. | Site Identification | Latitude | Longitude | B. puangensis |
| :---: | :---: | :---: | :---: | :---: |
| 1 | USP, Campus library | -18.150 | 178.445 | $\checkmark$ |
| 2 | USP, Lower Campus | -18.150 | 178.453 | $\checkmark$ |
| 3 | USP, Upper Halls | -18.149 | 178.445 | $\checkmark$ |
| 4 | Colo-i-Suva | -18.091 | 178.458 | $\checkmark$ |
| 5 | Bowling Club | -18.149 | 178.423 | - |
| 6 | Muanikau | -18.150 | 178.450 | $\checkmark$ |
| 7 | Vatuwaqa Cemetery | -18.141 | 178.456 | - |
| 8 | FNU Hospitality | -18.163 | 178.431 | $\checkmark$ |
| 9 | Lami rubbish dump | -18.114 | 178.425 | - |
| 10 | Lami town | -18.114 | 178.409 | - |
| 11 | Laucala Beach | -18.112 | 178.478 | - |
| 12 | Golf course | -18.127 | 178.462 | - |
| 13 | Khalsa Road | -18.087 | 178.465 | - |
| 14 | Savura | -18.082 | 178.443 | - |
| 15 | Namadi heights | -18.109 | 178.446 | - |
| 16 | Nadawa | -18.102 | 178.499 | - |
| 17 | Kalabo | -18.087 | 178.494 | - |
| 18 | Caubati | -18.104 | 178.469 | - |
| 19 | Ram Lakhan Park | -18.128 | 178.441 | - |
| 20 | Cunningham Road | -18.100 | 178.456 | - |
| 21 | Nukulau Island | -18.173 | 178.514 | $\checkmark$ |
| 22 | Rewa Delta | -18.074 | 178.574 | - |



Figure I. Maps of major Fiji Islands showing general location of study area, and of Greater Suva indicating locations of patches of Sphagneticola trilobata sampled in the current study. Dark circles indicate presence and white circles indicate absence of Braunsapis puangensis.

Upper Campus within a patch of Sphagneticola trilobata (and a few other low-lying plants). The traps consisted of $30 \mathrm{~cm} \times 25 \mathrm{~cm}$ rectangular plastic bowls ( 20 cm deep) that were half filled with water to which a few drops of household detergent had been added. Sampling was continuous, using two traps at all times which were emptied once each week. The insects collected in each calendar month were then pooled. Collecting was carried out for 14 months, from May 2010 to June 2011.

## Daily activity patterns of Braunsapis puangensis and the effect of environmental parameters

A single patch of Sphagneticola trilobata on The USP Upper Campus was used to monitor daily activity patterns of Braunsapis puangensis. Activity was estimated by dividing the patch of flowers into three sectors (each $2 \mathrm{~m} \times 2 \mathrm{~m}$ ) and performing a 30 second count of individuals in each sector. A mean of the three counts was then obtained. Attempts were made not to count the same individual more than once. This process was repeated every hour, from just prior to dawn and to just after dusk, and was repeated over five separate days (during April 2011). Light intensity, relative humidity and temperature were measured on each occasion using electronic meters.

The whole procedure was repeated in May 2011, but on this occasion the activity of the bees was measured during dry periods and during rain until there were five replicates of bee activity for each hourly interval for both dry and wet conditions.

## Results

Braunsapis puangensis was recorded at eight of the twenty two sites sampled (Table1; Figure 1). There was a cluster of sites where B. puangensis was present at Suva Point, but


Figure 2. Braunsapis puangensis activity from 7am to 6pm on a single Sphagneticola trilobata patch at The University of the South Pacific, Laucala Campus (individuals counted in 30 s ; mean $\pm \mathrm{SE}, n=5$ ). Observations were made during sunny weather in April 2011, and during sunny and rain conditions in May 2011.

Table 2. Correlation of environmental factors and activity of Braunsapis puangensis in a single patch of Sphagneticola trilobata on the USP Laucala campus (April 2011). Values given are $r_{s}$, Spearman's rank correlation coefficient ( $n=60 ; P<0.001$ in all cases).

|  | Relative Humidity | Light Intensity | Bee Activity |
| :--- | :---: | :---: | :---: |
| Temperature | -0.79 | 0.85 | 0.87 |
| Relative Humidity | - | -0.77 | -0.78 |
| Light Intensity | - | - | 0.86 |

other sites were quite widespread, from the coastal sites in Laucala and Nukulau Island to the inland forests at Colo-i-Suva (Figure 1).

The activity of Braunsapis puangensis observed in May was generally lower than that observed in the April survey at any given time point, but the daily patterns in activity were similar (Figure 2). In fine weather, the activity of the bees increased steadily from 8 am , reached a peak around mid-day and then decreased through the afternoon. No B. puangensis were observed on the patch of Sphagneticola trilobata on the USP campus prior to 7 am and after 6 pm .

The environmental parameters measured were all co-correlated, with high mid-day temperatures being associated with high light and low relative humidity, and lower temperatures recorded early morning and late afternoon being associated with lower light levels and higher relative humidity (Table 2). Therefore the activity of Braunsapis puangensis displayed an association with a set of environmental conditions, activity having a strong positive correlation with temperature and light intensity, and a strong negative correlation with relative humidity (Figure 3; Table 2). The activity of the bees virtually ceased during periods of rain (Figure 2), although bees were often observed foraging soon after the rain had stopped.


Figure 3. The relationship between activity of Braunsapis puangensis (counts in 30 s ) and a light intensity b relative humidity and $\mathbf{c}$ temperature at a single patch of Sphagneticola trilobata on the USP Laucala campus during fine weather in April 2011.

Braunsapis puangensis was recorded in all 14 monthly samples, indicating that adults were present and active in the Suva area over the whole annual cycle. However, the use of water traps as a collecting method for these bees was largely unsuccessful. Braunsapis puangensis was only recorded in very low numbers (between 1 and 4
individuals each month: data not shown), even when foraging activity was observed to be high in the surrounding area. Thus, due to the constant low catch, there were no obvious seasonal patterns in B. puangensis abundance revealed by this method.

## Discussion

The frequency of occurrence of Braunsapis puangensis over the sample sites (8 of 22) was lower than we had anticipated. Our initial expectations were based on observations of foraging activity on patches of Sphagneticola trilobata in or near the USP campus in Laucala Bay, where B. puangensis was common (see Figure 1), often seen in high numbers (see Figure 2) and found regularly throughout the year. The road-side samples were all taken around mid-day in fine weather so, based on the activity patterns observed for this species, if adults were present they would likely have been active when collecting was performed. Braunsapis puangensis has been observed on S. trilobata at other locations on the south of Viti Levu (e.g. Pacific Harbour and Sigatoka; S. Hodge 2011 pers. obs.), and Davies et al. (in press) give a record of $B$. puangensis to the north of Viti Levu. Our observations likely represent a 'snap shot' of the bee distribution among patches of $S$. trilobata on those sampling days: revisiting the same patches in the future may reveal a different, dynamic aspect, to patch occupancy. However, the occupation level of patches ( $36 \%$ ) indicates that B. puangensis may not be as ubiquitous on this species of flower as we had first thought, and that further work is required to establish what factors are influencing the distribution of B. puangensis, both among patches of $S$. trilobata, on other species of flowering plant, and over the island as a whole.

The daily activity patterns of Braunsapis puangensis are similar to those recorded for other bee species. Shenoy and Borges (2008) also found that B. puangensis was active throughout the day in Western Ghats of India, although visits of the bee to flowers of Humboldtia brunonis Wall. (Fabaceae) appeared more frequent in the morning, with no records beyond early afternoon. Foraging of wild bees and wasps can be strongly correlated to environmental factors (Vicens and Bosch 2000, Wang et al. 2009) and the high levels of B. puangensis activity around midday indicated that this species preferred high light levels and warmer conditions (even considering the lowest temperature recorded was $26^{\circ} \mathrm{C}$ ). The virtual cessation of activity during rain can also be linked to these findings: during many of the periods of (sometimes intense) tropical rain we encountered in Suva light levels dropped considerably and relative humidity naturally reached saturation levels. The onset of rain can dramatically reduce foraging activity in Hymenoptera, although, as seen in our study, activity often recovers once bouts of rain have ceased (Vicens and Bosch 2000, Kasper et al. 2008). The daily activity pattern of bees has implications for sampling protocols when attempting to analyze the details of pollinator networks. If the various pollinating species have different diurnal patterns, and respond differently to climatic factors, then the pollinator assemblage recorded could be specific to the immediate weather conditions and the time of day the sample is taken (Baldock et al. 2011).

Solitary and/or native bee species are considered an important resource in terms of pollination of crop species (Groom and Schwarz 2011) and Braunsapis is already known to be an important pollinator of native plants (Anderson and Symon 1988, Shenoy and Borges 2008). The most conspicuous Hymenoptera we recorded on Sphagneticola trilobata were Apis mellifera and Braunsapis puangensis, both introduced species in Fiji. Thus it is important to realize that although S. trilobata is considered an invasive 'nuisance weed' in one context, it may be of value to crop growers, and commercial honey producers, by attracting and augmenting local populations of pollinating insects.

There has been some fairly wide-ranging, albeit sporadic, published work on the Hymenoptera of Fiji. Turner (1919), Brues (1922) and Fullaway (1957) provided early checklists of species in the islands, which has recently been updated by Evenhuis (2007). There has been the occasional publication on honey bees and bee products (e.g. Anon 1985, Anderson 1990, Prasad 2007, Saraf et al. 2009) and consideration of the ecology of the Formicidae (e.g. Ward 2008, Sarnat 2008). Recently, the biogeography and evolutionary pathways of South Pacific bees have been the focus of detailed investigation (Groom and Schwarz 2011, Groom et al. 2013, Davies et al. in press). Our investigation represents preliminary ecological work on aspects of the ecology of an introduced bee utilizing a naturalized invasive plant. Our results indicate that adult Braunsapis puangensis are present in Fiji throughout the year, and its abundance on patches of Sphagneticola trilobata varies both temporally and spatially. Future work should extend these studies by examining the nesting behaviour of B. puangensis in Fiji, exploring the residence time and 'departure rules' of foraging bees on S. trilobata (and other species of flowers), and attempt to gain similar basic data on native species of pollinators and their natural and agricultural host plants.

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# Taxonomic review of the ant genus Paratrechina, with a description of a new species from Africa 

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#### Abstract

With the recent finding of Paratrechina (broad sense) paraphyly, only Paratrechina longicornis remained in a redefined genus. As one of the most widely distributed ant species due to human transfer around the world, there is much interest in the biology of $P$. longicornis. One issue concerning P. longicornis has been as to where exactly the species is native, with both African and Asian native ranges being invoked in the literature. Here we report the discovery of a second species within Paratrechina. This species, P. zanjensis, is native to Africa (known from Angola, Mozambique and Tanzania), where it appears to be a dry miombo woodland species. Given the discovery of this new species, a reevaluation of the morphological definition of Paratrechina is provided; also provided is an updated generic level identification key. Given the available distribution information on P. longicornis, we conclude that P. longicornis remains most likely native to southeastern Asia, and that the discovery of a new species native to Africa makes Paratrechina yet another example of an ant genus that possesses an Afro-Asian distribution.


## Keywords

Invasive species, miombo woodland, new species, Nylanderia, Prenolepis, Zatania

## Introduction

Recently the ant genus Paratrechina (broad sense) was found to be paraphyletic, with all but one species being transferred to the revived genera Nylanderia and Paraparatrechina (LaPolla et al. 2010a; LaPolla et al. 2010c; LaPolla et al. 2011a). The sole remaining species within Paratrechina was P. longicornis (see LaPolla et al. 2010b). The discovery of Paratrechina (broad sense) paraphyly was not particularly surprising, because P. longicornis possesses a morphology that had long been noted as being different from other members of the genus with especially elongated scapes, head and tibiae, coupled with a distinctly shaped mesosoma and unusual mesosomal setal pattern (Trager 1984; LaPolla et al. 2010a).

One particularly interesting and important aspect of Paratrechina longicornis biology is that it is perhaps the most widespread ant species in the world (Wetterer 2008), owing to the ease with which it is spread by human activities and the ability to survive even in extremely anthropogenically changed environments. This species has literally been spread around the planet, being found in almost every urban center in the tropics; it can also widely be found in greenhouses and other manmade structures in cool temperate climates (Wetterer 2008). Where exactly the species is native has been a source of debate and uncertainty, although the evidence seems to suggest it is native to Southeast Asia (Wetterer 2008; LaPolla et al. 2010a).

The unusual morphology of $P$. longicornis, coupled with its widespread tramp status, makes the discovery of a new species within the genus particularly important. Here we report on such a discovery from Africa (records from Angola, Mozambique and Tanzania). The discovery of this new species of Paratrechina now requires a reevaluation of the previous morphological definition of the genus (LaPolla et al. 2010a) and may contribute to our understanding of the native range of $P$. longicornis.

## Materials and methods

Specimens examined for this study are deposited in the following institutions:

AFRC AfriBugs, Pretoria, South Africa
ANIC Australian National Insect Collection, Canberra, Australia
CASC California Academy of Sciences, San Francisco, CA, USA
MCZC Museum of Comparative Zoology, Cambridge, MA, USA
NMKE National Museum of Kenya, Nairobi, Kenya
SAMC Iziko South African Museum, Cape Town, South Africa
USNM National Museum of Natural History, Washington, DC, USA

Measurements were taken using an eyepiece graticule with a Leica MZ16 microscope mounted on an axial shift carrier to avoid parallax errors, recorded to the nearest $1 / 10$ graticule unit and lengths calculated using calibration data from a stage
micrometer for each magnification. All measurements are given in millimeters. Digital color images of a $P$. longicornis male were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage (v 5.0) software; color images of P. zanjensis and P. longicornis workers were created using a Leica DFC425 digital camera and Leica LAS Montage (v3.8) software. Morphological terminology for measurements and indices employed throughout are defined (following LaPolla et al. 2011b) as:

EL (Eye Length): maximum length of compound eye in full-face view
GL (Gaster Length): the length of the gaster in lateral view from the anteriormost point of the first gastral segment (third abdominal segment) to the posteriormost point
HL (Head Length): the length of the head proper, excluding the mandibles; measured in full-face view from the midpoint of the anterior clypeal margin (a line is drawn between the projecting lateral portions of the clypeus to accommodate the anterior margin which is medially indented in Paratrechina) to a line drawn across the posterior margin from its highest points
HW (Head Width): the maximum width of the head in full-face view, excluding eyes
MSC (Mesonotal Setal Count): the number of erect macrosetae on mesonotum to one side of the sagittal plane
PW (Pronotal Width): the maximum width of the pronotum in dorsal view
PrFL (Profemur Length): the length of the profemur from its margin with the trochanter to its margin with the tibia
PSC (Pronotal Setal Count): the number of erect macrosetae on pronotum to one side of the sagittal plane
SSC (Scape Setal Count): the number of erect macrosetae on one antennal scape, excluding the terminal setal cluster
SL (Scape Length): the maximum length of the antennal scape excluding the condylar bulb
TL (Total Length): HL+WL+GL
WL (Weber's Length): in lateral view, the distance from the posteriormost border of the metapleural lobe to the anteriormost border of the pronotum, excluding the neck.
CI (Cephalic Index): (HW/HL) • 100
REL2 (sensu Ward 2006): (EL/HW) • 100
SI (Scape Index): (SL/HW) • 100

## Results

## Diagnosis of the genus

Since the new species described here is only known from the worker, we provide only a worker-based definition for the genus pending the discovery of males and queens for Paratrechina zanjensis.

Monomorphic, medium sized (2.1-3.2 mm in total length) formicine ants; brown to dark brown in color, with lighter mandibles, antennae (especially funicular segments towards tips) and legs (especially distal portion of tibiae and tarsi). Head with medially erect macrosetae roughly paired, extending through the medial portion of clypeus. Cuticle on the head smooth and shining, with faint shagreenate sculpture, especially towards the posterior margin. Antennae 12 segmented; scapes very long, with scape index above 180, usually above 200 (SI 183-220). Scapes with a dense layer of pubescence. Head is distinctly longer than wide, with cephalic index below 100 (CI 71-94); posterolateral corners rounded, with straight posterior margin. Eyes large relative to head width (REL2 greater than 35); eyes distinctly convex, extending beyond head margin in full frontal view; three small but distinct ocelli present. Mandibles typical for Prenolepis genus-group (Fig. 9), with 5 teeth; mandalus large and anteriorly placed; palps very long ( $0.70-0.75 \mathrm{~mm}$ ); palp formula 6:4; segments 3-6 are longest (numbered from basal segment (1) to apical segment (6). Mesosoma distinctly elongated; in profile pronotum and mesonotum long; propodeal dorsal face either nearly flat or moderately convex (Figs 2, 5); propodeum without macrosetae, anteriorly occasionally with a sparse layer of pubescence; pronotal setal count 5-10 (both sides of notum); mesonotal setal count 4-8 (both sides of notum). Petiole cuneate, broadly rounded dorsally, with much longer posterior face and not surpassing the height of the propodeum. Legs distinctly long (profemur length $0.6-1.0 \mathrm{~mm}$ ). Gaster robust, covered in abundant erect macrosetae.

## Synopsis of Paratrechina species

Paratrechina longicornis (Latreille, 1802) Pantropical tramp, origin uncertain = Paratrechina currens Motschoulsky, 1863. Junior synonym of longicornis by Emery, 1892: 166. Neotype designated by LaPolla et al. 2010b: 1.
= Paratrechina gracilescens (Nylander, 1856). Synonymy with longicornis by Roger 1863: 10.
= Paratrechina longicornis hagemanni (Forel, 1901). Junior synonym of longicornis by Wheeler 1922: 942. Revived from synonymy by Emery, 1925: 217. Junior synonym of longicornis by LaPolla et al. 2010a: 128.
= Paratrechina vagans (Jerdon, 1851). Junior synonym of longicornis by Dalla Torre 1893: 179; Forel 1894: 408.
Paratrechina zanjensis, sp. n. Angola, Mozambique and Tanzania

## Key to Paratrechina workers

For a genus-level key see LaPolla et al. (2012). The only modification for that key would be that the last statement in the second lug of couplet 4 would need to be removed.

It currently states: " ....scapes always lacking erect setae" which is true for all Paraparatrechina (except the morphologically unusual Paraparatrechina bufona) and P. longicornis. The discovery of P. zanjensis demonstrates that there is at least one species of Paratrechina that does possess erect macrosetae on the scapes.

1 Scapes without erect macrosetae (Fig. 7); in lateral view propodeal dorsal face almost flat (Fig. 2) longicornis

- $\quad$ Scapes with erect macrosetae (Fig. 8); in lateral view propodeal dorsal face convex (Fig. 5) zanjensis sp. n .


## Species accounts

## Paratrechina longicornis (Latreille, 1802)

http://species-id.net/wiki/Paratrechina_longicornis
Figs 1-3, 7 (worker); Figs 12-17 (male)
Formica longicornis Latreille, 1802: 113 (worker described). Neotype worker, THAILAND: Bangkok, 18 November 1970 (P. Jolivet) (ANIC32-053687) (ANIC) [examined]. For complete taxonomic history see Bolton (2013).

Worker diagnosis. Scapes without erect macrosetae.
Species description. WORKER. Measurements in millimeters ( $\mathrm{n}=4$ ): TL: 2.12.5; HW: 0.46-56; HL: 0.49-0.7; EL: 0.17-0.23; SL: 0.98-1.16; PW: 0.34-0.43; WL: 0.82-0.98; PrFL: 0.6-0.9; GL: 0.83-0.9.

Indices: CI: 73-94; REL2: 38-42 ; SI: 182-226.
Overall coloration pale to very dark brown, often with a distinct blueish iridescent sheen, especially on the mesosoma and gaster. Mandibles, antennae and legs (especially the trochanters of all legs, which are a strongly contrasting very pale yellow-brown) much lighter in color; cuticle smooth and moderately shining with faint shagreenate sculpture, which is most obvious on head and gaster. Head narrow, distinctly longer than broad, with abundant pale (yellow-brown to almost white), erect macrosetae; anterior clypeal margin with a shallow medial indentation; scapes with a dense layer of very fine pubescence but lacking erect macrosetae; eyes large and convex, extending beyond head lateral margin in full frontal view; posterior head margin with rounded posterolateral corners; three distinct ocelli present. Mesosoma with scattered pale erect macrosetae (PSC = 3; MSC $=3$-4); in profile pronotum and mesonotum almost flat dorsally, with a broadly angled junction; metanotal area relatively indistinct, medially about $1 / 5$ the length of the mesonotum but longer laterally than medially; dorsum of propodeum almost flat to very shallowly domed, rounding evenly into the short declivitious face; anterolateral portion of dorsal face with some scattered pubescence. Gaster with abundant erect pale macrosetae.

Material examined. The authors have examined hundreds of specimens of $P$. longicornis from around the world for this and other related studies. These are not


Figures I-9. Paratrechina workers in various views (left to right: full frontal, lateral and dorsal views for figs I-6): I-3 P. longicornis (CASENT0250003) 4-6 P. zanjensis holotype (SAM-HYM-C020685) $\mathbf{7}$ P. longicornis scape (CASENT0250003) 8 P. zanjensis holotype scape (SAM-HYM-C020685) 9 P. zanjensis paratype mandible (CASENT0250002).
listed here. The four specimens measured for this study were from: MADAGASCAR: Prov. Mahajanga; Mahavavy River; 6.2 km 145 SE Mitsinjo (CASENT0490165); 1603.1'S, $45^{\circ} 54.5^{\prime} \mathrm{E}$ (BLF6931); MAURITIUS: Pte d'Esny; 20²5.52'S, $57^{\circ} 43.44^{\prime} \mathrm{E}$ (CASENT0055961).

## Paratrechina zanjensis sp. n.

http://zoobank.org/B8FE1331-6242-44AB-8E31-BBE08175E83E
http://species-id.net/wiki/Paratrechina_zanjensis
Figs 4-6, 8, 9 (worker)

Holotype worker, TANZANIA: Ruvuma Region, Namtumbo District, Mkuju River, $855 \mathrm{~m}, 10.07400 \mathrm{~S}, 36.57959 \mathrm{E} \pm 100 \mathrm{~m}, 27-29 . x i .2011$, MKU2011-3.1 (P Hawkes, J Fisher) (SAMC: SAM-HYM-C020685). 13 paratypes with same data as holotype, 7 paratypes, TANZANIA: Ruvuma Region, Namtumbo District, Mkuju River, 831m, 10.08380 S, $36.57267 \mathrm{E} \pm 100 \mathrm{~m}, 2-4 . x i i .2011$, MKU2011-5.1 (P Hawkes, J Fisher) (AFRC, CASC, MCZC, NMKE, SAMC, USNM).

Worker diagnosis. Scapes with abundant erect macrosetae.
Species description. WORKER. Measurements in millimeters ( $\mathrm{n}=18$ ): TL: 2.63.2; HW: 0.50-0.59; HL: 0.68-0.77; EL: 0.19-0.23; SL: 1.07-1.24; PW: 0.41-0.5; WL: 0.94-1.20; PrFL: 0.78-0.91; GL: 0.92-1.30.

Indices: CI: 71-79; REL2: 37-44; SI: 198-220.
Overall coloration dark brown with lighter mandibles, antennae (especially funicular segments towards tips) and legs (especially trochanters of mid and hind legs, and distal portions of tibiae and tarsi); cuticle smooth, shining, and with very faint shagreenate sculpture, which is more obvious on head and gaster. Head narrow, distinctly longer than broad, with abundant dark, erect macrosetae; anterior clypeal margin with a shallow medial indentation; scapes with a dense layer of pubescence and scattered erect macrosetae $(S S C=17-29)$; eyes large and convex, extending beyond head lateral margin in full frontal view; posterior head margin with rounded posterolateral corners; three distinct ocelli present. Mesosoma with scattered dark erect macrosetae (PSC = 2-5; MSC = 2-3); in profile pronotum and mesonotum shallowly convex dorsally, presenting a uniform overall curvature through their junction; metanotal area distinct, about $1 / 3$ the length of the mesonotum; dorsal face of propodeum rounded, with short declivitious face; anterior portion of dorsal face with thin layer of pubescence. Gaster with abundant erect dark macrosetae.

Etymology. The specific epithet is derived from the ancient Arabic name for the stretch of East African coast that encompasses parts of modern day Kenya, Mozambique, and Tanzania.

Non-type specimens examined. ANGOLA: Huambo, Mont. Moko, 1725 m , $12^{\circ} 27.20^{\prime} \mathrm{S}, 15^{\circ} 07.45^{\prime} \mathrm{E}, 7 . \mathrm{vi} .2007$, miombo woodland (BLFisher) (CASENT0128086); MOZAMBIQUE: Sofala Prov., Gorongosa N.P., Ravine (18.63407S, 34.80689E), 172 m, 12.vi. 2012 (P Naskrecki); Sofala Prov., Gorongosa N.P., Gorongosa Mountain, road to waterfall (18.49764S, 34.04975E), $800 \mathrm{~m}, 19 . \mathrm{vi} 2012$ (GD Alpert).

Natural history and distribution. Very little is known about the natural history of P. zanjensis; the 23 specimens collected in the Mkuju River region of the Selous Game Reserve in Tanzania were all found in 48-hour pitfall trap samples (present in 8 of a total of 60 samples from two sites separated by about 1.3 km ) while none were found in the 40 Winkler-extracted leaf litter samples collected during daytime along the same transects. The two Tanzanian sites in which $P$. zanjensis were found were representative of mature dry miombo woodland, while they appeared to be absent from both dry and moist closed canopy forest sites nearby. The Angola and Mozambique specimens were also collected in miombo woodlands; this, in combination with the absence of $P$. zanjensis from 15 forest sites surveyed by one of us (PH) in the Eastern Arc Mountains and Coastal Forests of Tanzania, suggests that the species prefers open woodland rather than forest habitats.

## Discussion

The worker of $P$. zanjensis can easily be separated from P. longicornis based on the presence of erect macrosetae on the scapes. There are several other notable differences
between the two species (see Figs 1-6). The propodeal dorsal face of P. zanjensis is more convex than is observed in P. longicornis. Similarly, the pronotum and to a lesser degree the mesonotum are more convex in P. zanjensis, being almost flat in P. longicornis. The metanotal area is also longer and more distinct in P. zanjensis, being more strongly separated from the mesonotum and propodeum. Paratrechina zanjensis has erect macrosetae that are dark rather than pale as in P. longicornis, the body is glossier, and largely lacks the opalescent sheen / iridescence that is characteristic of P. longicornis. Unfortunately, the male and queen for $P$. zanjensis remain unknown. Paratrechina zanjensis is superficially similar to Nylanderia silvula (see images in LaPolla et al. 2011b), but can readily be distinguished from this species by its mandibular dentition ( 5 teeth in Paratrechina, 6 in Nylanderia), larger eyes, longer limbs and less strongly domed propodeum.

Paratrechina has been shown to be a distinct lineage within the Prenolepis genusgroup (LaPolla et al. 2010a), but with the discovery of P. zanjensis, some modifications need to be made to the genus diagnosis. The biggest change comes from the fact that P. zanjensis possesses erect macrosetae on their scapes, so the lack of erect macrosetae is no longer diagnostic for the genus. This is not particularly surprising; for instance, even though most Nylanderia species possess erect macrosetae on the scapes, a few species do not (Kallal and LaPolla 2012). This trait is also variable within Zatania as well, although the erect macrosetae when present in this genus are short (LaPolla et al. 2012), and despite the fact that nearly every species of Paraparatrechina lacks erect macrosetae on the scape, at least one species (Paraparatrechina bufona) possesses them (LaPolla et al. 2010c). With a scape index above 180 , and with most specimens registering above 200, Paratrechina possess among the longest scapes relative to head width within the genus-group (Fig. 10). The same can be said for their eye length relative to their head width (Fig. 11). Only species within the genera Prenolepis and Zatania seem to have such long scapes and eyes relative to their head width (Figs 10, 11).

The similarity of the scapes of Paratrechina, Prenolepis and Zatania extends to other aspects of overall worker morphology within these genera, and these three genera are the most likely members of the Prenolepis genus-group to be confused with each other. This is because workers from these genera generally possess elongated heads, scapes, mesosomata, and legs. Whether or not the elongated state of these morphological features represents the plesiomorphic state (as might be suggested by the basally diverging position of Prenolepis within the clade, see LaPolla et al. 2010a and LaPolla et al. 2012) within the genus-group or has been independently derived several times is unclear. There are diagnostic features, however, that separate workers in these genera. Paratrechina can be separated from Prenolepis by the fact that Paratrechina lack a constriction immediately behind the pronotum. From Zatania, where a constriction behind the pronotum is variable, the number of mandibular teeth is an important diagnostic character. When a constriction is not present in a Zatania species those species also possess 6 teeth versus the 5 teeth found in Paratrechina.

As was found in Zatania (LaPolla et al. 2012), the male morphology of Paratrechina does provide some important features that show it to be a distinct lineage based on morphological characters. In both Prenolepis and Zatania the parameres


Figure IO. Scape length versus head width of various Prenolepis genus-group taxa. Measurements are based on results from this study and LaPolla 2009; LaPolla et al. 2011a; Kallal and LaPolla 2012; LaPolla et al. 2012.


Figure II. Eye length versus head width of various Prenolepis genus-group taxa. Measurements are based on results from this study and LaPolla 2009; LaPolla et al. 2011a; Kallal and LaPolla 2012; LaPolla et al. 2012.


Figures I2-I7. Paratrechina longicornis male (14-17 are scanning electron microscope images): $\mathbf{1 2}$ lateral view $\mathbf{1 3}$ full frontal view $\mathbf{1 4}$ genitalia dorsal view $\mathbf{1 5}$ genitalia ventral view $\mathbf{1 6}$ genitalia lateral view 17 close-up view of digitus and cuspis.
for instance are thin and elongated. While the male is only known for Paratrechina longicornis, in that species the parameres are unique and quite different from either Prenolepis or Zatania. In P. longicornis the male parameres are shorter and more robust (Figs 14, 16), with a more overall dorsal orientation, and the parameres are curved. This is a unique conformation observed among Prenolepis genus-group species to date, but exploration of male genitalic diversity among Pseudolasius, a close relative of Paratrechina, would be warranted. Among Euprenolepis, the putative sister group of Paratrechina (LaPolla et al. 2010a), the parameres of some species such as E. procera and $E$. wittei also curve entad (LaPolla 2009), but they are not as extended dorsally as in P. longicornis (Fig. 14).

Paratrechina zanjensis is certainly native to Africa, to date only being found in natural or minimally disturbed habitats. The presence of a new species of Paratrechina in Africa is interesting because P. longicornis is thought to be native to Asia (although some authors have considered it native to Africa, see Wetterer 2008 for review). Wetterer (2008) argued that P. longicornis is native to Southeast Asia, because it is only in this region, despite the extremely wide distribution of the species globally, that $P$. longicornis is found in native, undisturbed habitats. LaPolla et al. (2010a) also argued for a Southeast Asian origin of the genus (then thought to be monotypic) based on the fact that Paratrechina was found within a clade of largely Southeast Asian species (Euprenolepis and Pseudolasius; a few species of Pseudolasius are known outside of SE Asia extending into Australia). Regardless, the presence of another Paratrechina species in Africa is potentially important to interpreting the biogeography of P. longicornis. Certainly it is not unusual to have ant genera that span Africa and Asia, and this appears to be another example of an Afro-Asian genus. Since we know that Paratrechina is not monotypic the question becomes, are there additional new species awaiting discovery within the genus? There have been two monographic revisions of Prenolepis genus-group genera within Africa: Nylanderia (LaPolla et al. 2011b) and Paraparatrechina (LaPolla et al. 2010c). These studies did not find evidence of additional Paratrechina species, despite the fact these two studies examined thousands of Prenolepis genus-group specimens from the across the continent. Southeast Asia may very well be the place to look for new Paratrechina species because, other than Euprenolepis (LaPolla 2009), the other genera within the Prenolepis genus-group remain unrevised within the region.

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# First record of Chiasmognathus from the Kingdom of Saudi Arabia (Hymenoptera, Apidae) 

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#### Abstract

The cleptoparasitic bee genus Chiasmognathus Engel (Nomadinae: Ammobatini) is recorded from Saudi Arabia for the first time. Chiasmognathus nearchus Engel was previously known from specimens collected in the United Arab Emirates and Oman. Here we report and figure two individuals captured in central Saudi Arabia.


## Keywords

Apoidea, Anthophila, cleptoparasitism, cuckoo bees, biodiversity, Ammobatini

## Introduction

The cleptoparasitic bee genus Chiasmognathus Engel comprises some of the smallest and most distinctive species of the tribe Ammobatini, and at lengths as low as 2 mm are among the tiniest of all Anthophila (Engel 2006, 2009). Species of Chiasmognathus are found in the east from Central Asia to Sri Lanka, extending from their westward through the Middle East into northern Africa and marginally in southeastern Europe (Engel 2006, 2007, 2008a, 2008b, 2009, 2010; Straka and Engel 2012; Engel and Packer 2013) (Map 1). The
largest species, Chiasmognathus batelkai Straka and Engel, is endemic to the Cape Verde Islands and also marks the westernmost occurrence of the genus as it is presently understood (Straka and Engel 2012) (Map 1). Where known, species are cleptoparasites of the equally diminutive bees of the tribe Nomioidini (Engel 2006, 2007, 2009; Rozen 2008; Straka and Engel 2012). Nomioidini are widespread throughout the Old World and it is likely that Chiasmognathus is similarly distributed, with its currently more restrictive range an artifact of sampling. Given that these cleptoparasites are in lower abundance than their hosts, minute in their proportions (even the giants of the genus are scarcely over 4 mm in total length), and frequently sampled only from nesting aggregations of their hosts. Accordingly, records of the genus are scant at present and much remains to be discovered about their systematics, diversity, biogeography, and biology. Rozen (2008) provided information on the immature stages and biology of C. pashupati Engel in Pakistan, and this remains the most extensive source of information regarding the genus.

During recent sampling efforts across Saudi Arabia two specimens of Chiasmognathus were captured, both from central Saudi Arabia near Riyadh. One female and one male of C. nearchus Engel, previously known from the United Arab Emirates and Oman and known to victimize Nomioides rotundiceps Handlirsch (Engel 2009). Herein we provide details on these new records, adding the genus to the list of supraspecific bee taxa occurring in the Kingdom, and drawing the attention of melittologists in the region to the species in the hopes of learning more about these minute and elusive cleptoparasites.

## Material and methods

Material discussed herein was collected as part of general wild bee surveys underway by the authors throughout the Kingdom of Saudi Arabia, ongoing since 2011. Specimens were compared with the original type series of $C$. nearchus deposited in the Division of Entomology, University of Kansas Natural History Museum (Engel 2009). Photomicrographs were prepared with a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens.

## Systematics

## Genus Chiasmognathus Engel

## Chiasmognathus nearchus Engel

http://species-id.net/wiki/Chiasmognathus_nearchus
Figs 1-10

Material. 1区 (Figs 1-3), Saudi Arabia: Riyadh, Al Amariah, Majra [Mazra’ah], AlGasim [farm], 2.viii. 2011 [2 August 2011], I. Naser; 1『 (Figs 4-6), Saudi Arabia:


Map I. Distribution of currently described species of Chiasmognathus Engel (Ammobatini); numbered subsets refer to inserts in primary map at top.


Figures I-3. Female of Chiasmognathus nearchus Engel from Amariah, Saudi Arabia. I Lateral habitus 2 Facial view 3 Dorsal habitus.

Riyadh, Honeybee Queen Breeding Station, Ministry of Agriculture, Namar, 9.x. 2012 [9 October 2012], M.A. Hannan. The female is deposited in the King Saud University Museum of Arthropods, Plant Protection Department, College of Food and Agriculture Sciences, King Saud University, Riyadh, Kingdom of Saudi Arabia, while the male is deposited in the Division of Entomology, Snow Entomological Collections, University of Kansas Natural History Museum, Lawrence, Kansas, USA.

Comments. The new material does not differ in any significant manner from the diagnosis and description of the species as provided by Engel (2009). Unfortunately,


Figures 4-10. Male of Chiasmognathus nearchus Engel from Namar, Riyadh, Saudi Arabia. 4 Lateral habitus 5 Facial view 6 Dorsal habitus 7 Seventh metasomal sternum 8 Eighth metasomal sternum 9 Genital capsule, dorsal view 10 Genital capsule, ventral view.
the sole Saudi male is not preserved in the best condition, with some distortion of the antennae and much of the body matted resulting from the mode of collection and subsequent preparation (Figs 4-6). Nonetheless, it was suitable for dissection and the terminalia are presented here for the first time (Figs 7-10) and for comparison with those structures depicted for other species (e.g., Engel 2006, 2007, 2010; Straka and Engel 2012; Engel and Packer 2013).

Presently there are only three species of Chiasmognathus recorded from the Arabian Peninsula: C. aurantiacus Engel from the United Arab Emirates, C. himyarensis Engel from southwestern Yemen, and $C$. nearchus from Oman, the United Arab Emirates, and now central Saudi Arabia. A key to these species was provided by Engel (2009). The new records presented herein push the distribution of $C$. nearchus and the genus
as a whole westerly into the central desert region of Saudi Arabia. This is not surprising given the broader distribution of the group as well as that of its hosts. Species of Nomioides Schenck and Ceylalictus Strand are both present throughout the peninsula (Pesenko and Pauly 2009) and there is therefore every reason to suspect that with continued intensive sampling additional records will be forthcoming. Moreover, given that there are at least 20 species of Nomioidini present in the region it is possible that new species of Chiasmognathus may be recovered. Given the more varied habitats to the southwest, it is possible that endemic species of the genus may be found in the mountainous regions such as the Asir and Sarawat ranges south from Makkah (Mecca) and Taif, or in the low elevation plain of the Tihamah bordering the Red Sea. Unfortunately, at present none of the Saudi specimens have been collected in a context from which a positive host association can be made. Given that aggregations of N. rotundiceps are in the area, as well as other nomioidine species, it is possible that this is the host of the Saudi populations of $C$. nearchus just as is the case for those in the United Arab Emirates (Engel 2009).

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# Intraspecific variability of the Lygodium sawfly, Neostromboceros albicomus (Konow, I900) (Hymenoptera, Tenthredinidae, Selandriinae) 

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#### Abstract

The intraspecific variation of Neostromboceros albicomus (Konow, 1900) in a restricted area in Thailand is described. The value of characters, some of which are used for separating species and species groups in Neostromboceros, is discussed. The male of $N$. albicomus is described here for the first time.


## Keywords

Intraspecific variability, Selandriinae, Thailand

## Introduction

Neostromboceros Rohwer, 1912, originally described as a subgenus of Stromboceros Konow, 1885, comprises today 154 nominal taxa of which about 135 are currently considered to be valid (Taeger et al. 2010, and unpublished data). Eighty one (53\%) of the nominal taxa were described after 1998. Most species were recorded from the Oriental and eastern Palaearctic regions, and a few species from Australasia (e.g., Schmidt and Smith 2009).

The identification of Neostromboceros species is difficult, and usually great uncertainties remain. The most comprehensive keys to species were published by Malaise (1944; all known 41 taxa keyed), Saini (2006; 53 taxa from India keyed) and Haris (2006; 24 taxa from Malaysia, Indonesia and Papua New Guinea keyed).

Smith et al．（2002）discussed N．albicomus as a potential biological control agent for the Old World climbing fern，Lygodium microphyllum（Cav．）R．Brown，an invasive species in Florida．According to Rodgers et al．（2012），N．albicomus is still awaiting a permit for use as a biological control agent．As a second host plant，Smith et al．（2002） recorded Lygodium flexuosum（Linnaeus）Swartz．Furthermore，according to Smith et al．（2002）＂larvae fed and completed their live cycle on L．salicifolium Presl，but adults did not oviposit on this species＂．According to Smith et al．（2002）there are two bio－ types of $N$ ．albicomus，each feeding on a different host plant，and genetically differing by a single base in the $28 S-\mathrm{D} 2 \mathrm{rDNA}$ gene region．In the same paper，Smith clarified the synonymy of the species，and synonymized the type species of Neostromboceros， Stromboceros（Neostromboceros）metallica Rohwer，1912，with N．albicomus．Hitherto， the species is known from Malaysia，Philippines，Singapore，Thailand，and Vietnam （Smith et al．2002）．

## Material and methods

For this study， 39 specimens of Neostromboceros albicomus were examined from Thai－ land，Chiang Mai Province，collected by Saowapa Sonthichai with Malaise traps，with the following label data：

1－10 August 1997： $18.692^{\circ} \mathrm{N}, 98.816^{\circ} \mathrm{E}, 270 \mathrm{~m}$ ．Pa Huay Thong：Thambon Nam Bo Luang．Amphur Sampatong（7 『）．
10－20 August 1997： $18.542^{\circ} \mathrm{N}, 98.954^{\circ} \mathrm{E}, 250 \mathrm{~m}$ ．Pa Huay Thong：Thambon Nam Bo Luang．Amphur Sampatong，in field at edge of mixed deciduous forest（ $2 \boxtimes$ ）．
1－10 September 1997：Rim Pa Huay Tong， $18^{\circ} 48.07^{\prime} \mathrm{N}, 98^{\circ} 57.27^{\prime} \mathrm{E}\left[=18.801^{\circ} \mathrm{N}\right.$ ， $98.955^{\circ} \mathrm{E}$ ］， 270 m ．Thambon Bo Luang［sic！］．Amphur Sampatong，at edge of deciduous forest（11 区，2区）．
10－20 September 1997：Rim Pa Huay Tong， $18^{\circ} 48.07^{\prime} \mathrm{N}, 98^{\circ} 57.27^{\prime} \mathrm{E}$［ $=18.801^{\circ} \mathrm{N}$ ， $98.955^{\circ} \mathrm{E}$ ］， 270 m ．Thambon Bo Luang［sic！］．Amphur Sampatong，at edge of deciduous forest（ 12 区， $2 \boxtimes$ ）．
20－30 September 1997：Rim Pa Huay Tong， $18.801^{\circ} \mathrm{N}, 98.938^{\circ} \mathrm{E}, 250 \mathrm{~m}$ ．Thambon Nam Bo Luang．Amphur Sampatong，in mixed deciduous forest（3 $\mathbb{D}$ ）．

Photos were taken with a Leica DFC 495 digital camera attached to a M205 C stereo microscope．The penis valve was photographed with a Leica DFC 450 digital camera mounted on an Olympus BX． 51 microscope．Extended depth of field images were created with CombineZ5．3 and finally arranged and partly enhanced with Ulead PhotoImpact X3．The pictures reproduced in this paper，as well as views on other specimens，are accessible at full resolution under doi： $10.6084 / \mathrm{m} 9$ ．figshare． 798854. The specimens examined are housed in the entomological collection of Utah State University，Logan，USA，and in the Senckenberg Deutsches Entomologisches Institut， Müncheberg，Germany．

## Results

Of the 39 examined specimens, 19 with partly yellow-red abdomen run in the keys (Malaise 1944, Haris 2006) rather smoothly to N. albicomus, whereas 19 specimens with a black abdomen did not fit any of the keyed species. The remaining $39^{\text {th }}$ specimen is a very unusual intermediate female with the abdomen color longitudinally separated in a black left side and a right yellow-red side (Fig. 1a). This specimen strongly supports the hypothesis that the two alternative colorations of the abdomen (below called 'color forms') are a result of color dimorphism of the same species. The fairly large series of specimens was used to check the intraspecific variation of $N$. albicomus in a restricted area (the four localities listed above are no further apart from each other than 30 kilometers):

- Both color forms were found at all four localities; the clypeus is in most cases completely blue-black, but at all localities specimens with a pale marked clypeus also occur (Fig. 1c),
- the depth of the apical emargination of the clypeus varies about between 15 and $30 \%$ of its length (Fig. 1c),
- the pale marked clypeus may be found in both color forms (Table 1),
- specimens with a pale marked clypeus usually also have more extensively pale marked legs,
- the specimens with the palest legs have hind tibiae with more than the basal third pale, whereas in the darker forms only about the basal quarter is pale (Fig. 1e),
- the trochanters become paler from the front to the hind legs,
- the hind trochanters are usually more or less darkened on the inner side, but in pale specimens may also be completely pale; the tegulae are usually completely blue-black, in several specimens the basal area is more or less pale,
- the blue or more or less purple metallic luster is sometimes reduced on larger parts of the body and simply appears black (Fig. 1b),

Table I. Color patterns of clypeus and abdomen in $N$. albicomus, sorted by collecting event and sex. Intermediate female from 1-10 September not included.

| collecting event <br> (date and site) | specimens, <br> sex | abdomen and <br> clypeus blue- <br> black | abdomen blue- <br> black and clypeus <br> pale marked | abdomen mainly <br> pale and clypeus <br> blue-black | abdomen mainly <br> pale and clypeus <br> pale marked |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $1-10$ August | $7 \boxtimes$ | 2 | 1 | 3 | 1 |
| $10-20$ August | $2 \boxtimes$ | 1 |  | 1 |  |
| $1-10$ September | $10 \boxtimes$ | 1 | 3 | 5 | 1 |
| $1-10$ September | $2 \boxtimes$ | 2 |  |  |  |
| $10-20$ September | $12 \boxtimes$ | 5 | 1 | 6 |  |
| $10-20$ September | $2 \boxtimes$ | 1 |  |  | 1 |
| $20-30$ September | $3 \boxtimes$ | 1 | 1 | 1 |  |



Figure I. Neostromboceros albicomus, various specimens, both sexes. a color of abdomen (females, scale $2 \mathrm{~mm}) \mathbf{b}$ color and density of pits on mesonotum $\mathbf{c}$ color and shape of clypeus $\mathbf{d}$ shape of apical antennomeres $\mathbf{e}$ color of hind tibia.

- the size and density of the pits on the thorax and head are variable, but in a large majority of specimens the pits are scattered and small (Fig. 1b),
- the apical antennomeres are variable in size,
- the number of antennomeres is 9 or 10 (Fig. 1d) and frequently differs between antennae of a single specimen,
- intraspecific variation seems to be independent of the sex.


## Male

The male of $N$. albicomus was undescribed (Haris 2006). Among the material discussed above four males were found. Apart from the sexual differences, the male fits the characters of the female, including the variation described above. Smith (pers. comm.) noted that after 2002 he received some males from Thailand, most of them with orange on the abdomen but one more brownish. Images of two males are reproduced in Fig. 2.


Figure 2. Neostromboceros albicomus, males. a-f pale specimen a dorsal (scale 2 mm ) $\mathbf{b}$ ventral $\mathbf{c}$ lateral d face $\mathbf{e}$ head and thorax, dorsal $\mathbf{f}$ claw of hind $\operatorname{leg} \mathbf{g}-\mathbf{h}$ dark specimen $\mathbf{g}$ penis valve $\mathbf{h}$ ventrolateral view (scale 2 mm ).

## Discussion

The available material revealed an unexpected high level of intraspecific variation in $N$. albicomus. This is an example of a phenomenon that may be more widespread within the taxonomically very difficult genus Neostromboceros. Unfortunately, the characters that were shown to be highly variable are frequently used for the separation of species or species groups in Neostromboceros. The present study demonstrates that the description of new taxa from only few specimens or singletons, a common practice in the past, should be avoided because of the high risk of describing variants of known species. The inclusion of genetic information could help to solve problems related to color variation in the future.

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