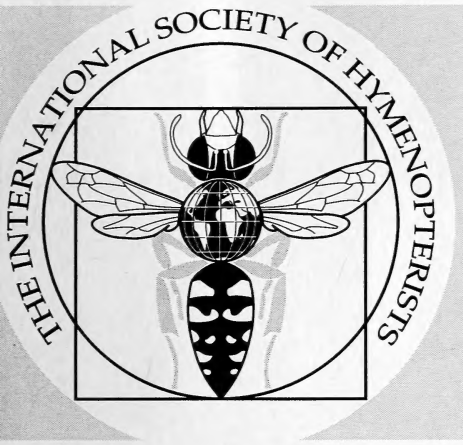
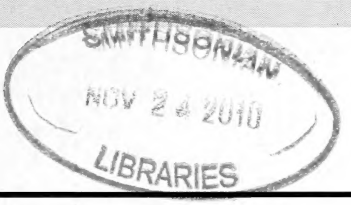


Journal of Hymenoptera Research



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OTHER CONTRIBUTIONS

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EDITORIAL

Persona of Roy

Volume 18, Issue 2 (2009) of this Journal was dedicated Roy R. Snelling, with an introduction by Longino and Snelling (2009) highlighting his life, some of his scientific adventures, and a bibliography of his publications. This issue of the Journal of Hymenoptera Research continues the dedication with seven more papers honoring Roy. Many of the contributors in both issues penned comments of inspirations Roy had given throughout their careers. On the personal side, everybody who knew Roy has one or many stories. Here we share a few of the stories exemplifying the essence of Roy.

Who Would Think The Name "Roy Snelling" Could Save Your Hide! – Almost four decades ago I was a graduate student working on my dissertation on the chemical ecology of Nearctic *Camponotus* species. In spring of 1973, I embarked on a collecting trip across the southern United States. After southern Texas, I headed westward collecting in West Texas, New Mexico, around Portal, Arizona, and westward to the Huachuca Mountains. Roy Snelling, a friend of my advisor, Murray Blum, had given directions to a location where I might be able to collect *Camponotus ulcerosus* Whr. I drove the rather desolate road to the Huachuca National Monument and remember thinking that I hoped my old car would not break down. When I found what I determined to be the collecting locality that Roy had given, I pulled off the road and began looking for foraging workers. I was probably a quarter to a half mile south of the dirt road when I located the entrance to a colony of *C. ulcerosus* under a rock and began to excavate. I probably dug a two foot deep hole 2–3 feet in diameter.

Preoccupied with the excavating, I didn't notice the approach of a pick-up truck that had driven close to me through the scrub. Two men had gotten out of the truck and were heading toward me. One was an older rugged looking cowboy and the other looked about twenty. The older one said "Stand up!" They surprised the daylights out of me. As I got up I could see that the younger one was wearing a holster with the largest revolver I had ever seen. It looked like the barrel was 18 inches long and the guy had his hand on its handle. The older guy asked me what I was doing. When I said I was digging up an ant colony, he asked "Why here?". I said a friend had told me about this location and that there was a particular species of ant that I was hoping to collect. He then demanded, "Who told you to come here?". I told him that he would not know the person, but I could see he was getting agitated. When he growled "I asked you who told you to collect at this location?", I blurted out 'Roy Snelling'. Immediately the older cowboy's demeanor changed. He turned to the younger guy who still had his hand on the handle of the revolver and said "He's OK, he is a friend of Roy's!" They had known Roy for some time and were friends. The rancher explained that he had been told that there was someone exhibiting suspicious behavior on his property. He further explained that drug dealers would cut his fences that parallel the US/Mexican border and drive trucks across the border loaded with marijuana. His cattle would inadvertently wander over the border into Mexico and were rustled or slaughtered as soon as they

crossed the border. It was costing him hundreds of dollars. The rancher thought I might have been a spotter for these people, or that I was digging up drugs buried at that location. The name Roy Snelling had a very long reach.

– Richard M. Duffield, Howard University

Roy and Big and Haires – In the 1990s I was out many nights alone in Willcox, AZ working on vinegaroon behavior. I was slowly walking around with a headlight scanning for vinegaroons – that is, acting exactly like a sick or disabled prey. To make matters worse, I would crawl under trees or in brush to examine critters or holes. Several nights I saw mountain lions in the beam of the headlight that was a fixture on my forehead. Mountain lions have a beautiful green eyeshine; all other North America cats have yellow eyeshine. One night I looked to the right and saw two large green eyes, and a little later looked to the left and saw two small green eyes about half the height above the ground. Needless to say these night adventures became less pleasant and more anxious. It is amazing what one's mind can do when alone for hours at night in a quiet environment.

Roy Snelling called a few days later and I relayed my story and asked how to deal with this situation. He matter of factly commented that the Indians in the US West routinely had that problem that they solved by making full neck-length chokers of closely fitting elk rib bones. They worked because the cats have rather short teeth, cannot puncture through the rib bones, kill by piercing the cervical spinal cord, and will flee if the prey is not quickly killed and puts up much of a fight. By blocking the success of an initial surprise attack, the warrior could turn and punch the cat in the belly or elsewhere and it would flee. I never had to test Roy's theory, but did run around thereafter with a thick roll of towel around my neck and a bicycle helmet. Roy's wisdom gave me piece of mind and I never became cat food!

– Justin O. Schmidt, Southwestern Biological Institute

Roy on the Phone – When I was a post doc at the Smithsonian, I had no phone, and my rare calls came to Arnold Menke's phone. One day Arnold stuck his head out in the hall and yelled gruffly "Chris, that Indian's on the phone." Well, it was kind of like being in England and hearing someone call "God save the Queen". I wouldn't ask which queen, and in this case it didn't occur to me to ask which Indian. So, I walked down the hall, picked up the phone and asked "You send-um smoke signal?", to which Roy responded "Ugh."

– Christopher K. Starr, University of West Indies

Horse – This final story was known to many. In 1973 Roy was attending the funeral for William S. Creighton, the great North American ant taxonomist of the middle of the 20th Century. Creighton had died of a heart attack. While at the service Roy found himself in the same hospital as Creighton had been in, in the same bed, with the same doctors, and with the same diagnosis. Having seen how Creighton ended up and sizing up the competence of the doctors, he decided it best to check himself out and return from Missouri to California, against the protests of the doctors who said he would never make it alive. Once

back, he sent the doctors a post card featuring the south end of a horse to assure them he had arrived safely. That was Roy!

– The editors

This Festschrift would not have been possible without the generous help of many people and the support of the International Society of Hymenopterists. Many reviewers selflessly interrupted their busy schedules to facilitate rapid reviews, often approaching record turn around times. A hearty thanks to the followings reviewers: John Alcock, Jeffery R. Aldrich, Craig M. Brabant, Stephen Buchmann, James H. Cane, James M. Carpenter, Martin Cooper, Robin Crewe, Cameron Currie, Richard M. Duffield, Pierre Escoubas, Fernando Fernández, Brian L. Fisher, Terry Griswold, Darryl T. Gwynne, Robert L. Jeanne, Robert A. Johnson, John T. Longino, William P. MacKay, Donald G. Manley, Robert L. Minckley, Andreas Mueller, John L. Neff, Michael Ohl, William L. Overal, John D. Oswald, Robert J. Paxton, Christian Rabeling, William L. Rubink, Ted R. Schultz, Stephen W. Taber, Richard S. Vetter, S. Bradley Vinson, Philip S. Ward, John W. Wenzel, Diana E. Wheeler, Alexander L. Wild, Douglas Yanega, and James R. Zimmerman. Special thanks to Gavin Broad, editor of the Journal of Hymenoptera Research, for generously and expertly shepherding the volume through to production.

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LITERATURE CITED

Longino, J. T. and G. C. Snelling. 2009. An inordinate fondness for things that sting. *Journal of Hymenoptera Research* 18: 125–135.

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Foraging Behavior and Colony Cycle of *Agelaia vicina* (Hymenoptera: Vespidae; Epiponini)

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Abstract.—The neotropical *Agelaia vicina* has the largest nest built among social wasps, yet little is known about nest construction, growth and structure. In this work, the development of two nests of *A. vicina* was followed. Studies were done through analysis of images to estimate the growth of nests. The material collected below the nests was examined to estimate colony productivity. Nests were collected to analyze their architecture and structure. Colony cycle was similar in the two colonies. Colonies increase in size throughout the dry season and into the rainy season, with a sudden drop in production at the end of the rainy season. The colonies doubled in size in about six months.

Social wasps are important to the study of social evolution. They fall into two groups according to how they initiate colonies (Jeanne 1991). In independent-founding species, one or a small group of queens start the construction of a new nest, without the aid of workers. In swarm-founding species, a new colony is initiated by a large group of workers and one or more queens. Patterns in nest construction vary. The independent-founders are characterized by continuous nest construction; that is, the size of the nest increases gradually throughout the founding and ergonomic stages of the colony cycle, and is closely correlated with oviposition rate (Richards and Richards 1951; Wenzel 1991).

In contrast, some several swarm-founding species engage in episodic nest construction, building the nest rapidly at the beginning of the founding stage. The new cells are constructed faster than the queens fill them with eggs. The nest is completed rapidly in this stage (Jeanne 1991; Wenzel 1991), and then the nest stays static for weeks or months, while the colony expands its population within the limits of its initial structure. Subsequent expansion of the nest in its following stage is equally quick, building hundreds or thousands of cells in a few days.

In tropical environments, the groups most studied for foraging behavior are *Polistes*, *Mischocyttarus*, and *Polybia* (Dapporto and Palagi 2006; Hermann and Chao 1984; Hrncir et al. 2007; Jha et al. 2006; O'Donnell and Jeanne 2002; Richter 2000). The importance of these wasps is related to how they act in a trophic network as herbivores (sugar and nectar collectors) and predators (Raposo Filho and Rodrigues 1983). Necrophorus feeding habits are known in *Agelaia* and *Angiopolybia* (O'Donnell 1995). *Agelaia* is very commonly found at flowers (Mechi 2005) and is among the most abundant genera in neotropical forests (Hunt et al. 2001; Silveira et al. 2005; Zucchi et al. 1995), indicating its ecological importance.

Agelaia vicina (Saussure) has the largest colony size among the social wasps. Von Ihering (1903, 1904) first offered information on this, reporting an *A. vicina* colony of with more than 108,000 individuals, but colonies may exceed one million adults

(Zucchi et al. 1995). The nests are built commonly in cavities, such as caverns or tree hollows. Built in protected places, they lack a nest envelope, as in many other *Agelaia* (Hunt et al. 2001; Wenzel 1991). The nest of *A. vicina* is composed of vegetable fibers without wax or resin. Some parts, such as the pedicels receive additional glandular secretion as a presumed reinforcement (Wenzel 1998). Workers build cells that form combs. During nest initiation, several combs are built separately, fixed by pedicels to the substrate (generally ceilings of cavities), so that the combs are parallel to the substrate. The combs are then expanded and merge to form a great expanse of cells. Besides the considerable amount of information regarding nest architecture in *A. vicina*, virtually nothing is known about its biology.

MATERIALS AND METHODS

We observed two nests in São Paulo state, Brazil, one in the municipality of Paulo de Faria Brazil (19°S 49°W) and the other in Pindorama (21°S 48°W). The Paulo de Faria nest was located in an abandoned wooden guard station, 3.5 m above the ground. The Pindorama nest was 2.5 m above the ground, inside a brick structure in the form of a shut tower in the back yard of an abandoned house.

Images were captured using a digital camera in order to measure nest growth. The images of the Paulo de Faria nest were captured from November 2005 to April 2006, those of the Pindorama nest from June 2006 to February 2007. Nest growth was estimated by Axiovision, software that calculates area increase from the images.

At the end of the observations, each nest was collected, weighed and dismantled comb by comb for a better understanding of its structure and composition (Fig. 1A–B). The Paulo de Faria nest was collected after natural decline, and the Pindorama nest was killed for collection. Subsequently, the combs of each nest were cut out in squares with areas of 100cm^2. We used these squares for counting and weighing nest cells.

In February 2007 we gathered 42 hours of video segments at the entrance of the Pindorama nest in order to record the departure and return of foragers. These images were studied then in slow motion. We recorded for one hour each at starting times of 06h, 14h, 18h and 24h.

To study foraging behavior, we offered baits of meat 15m from the nest. Arriving foragers were marked on the thorax with non-toxic ink. This allowed us to estimate round-trip times. To determine whether the presence of baits increases the number of workers leaving the nest, we noted the number of marked foragers present throughout the day. We designated the start of foraging when the first forager arrived in the bait.

It is known that *A. vicina* discards leftover food and the opercula of pupal cocoons below the nest (Zucchi et al. 1995). Because each operculum corresponds to an emergent adult, the number of opercula corresponds to the number of adults produced in a period of collection. Plastic trays were put below the nests in order to collect the discarded material (Fig. 1C).

RESULTS

Nest growth was continuous during the period of observation. From the image analyses, the Paulo de Faria nest initially had 459,143 cells, which increased to approximately 956,340 cells over the course of six months of observations, an increase of 108%. After nest collection, it weighed 13.8 kg with cells (or combs) organized in 28 layers (Fig. 1B), yielding an estimate of 69,300 cells per kg. Only the central area (about 30%) of the nest was used for the brood production, as seen in the presence of meconia in these cells. For the nest studied in Pindorama it was not possible to estimate nest growth. When the nest was collected, it had approximately 745,564 cells distributed in 41 layers and weighed 11.5kg (Fig. 1A). As in the Paulo de Faria

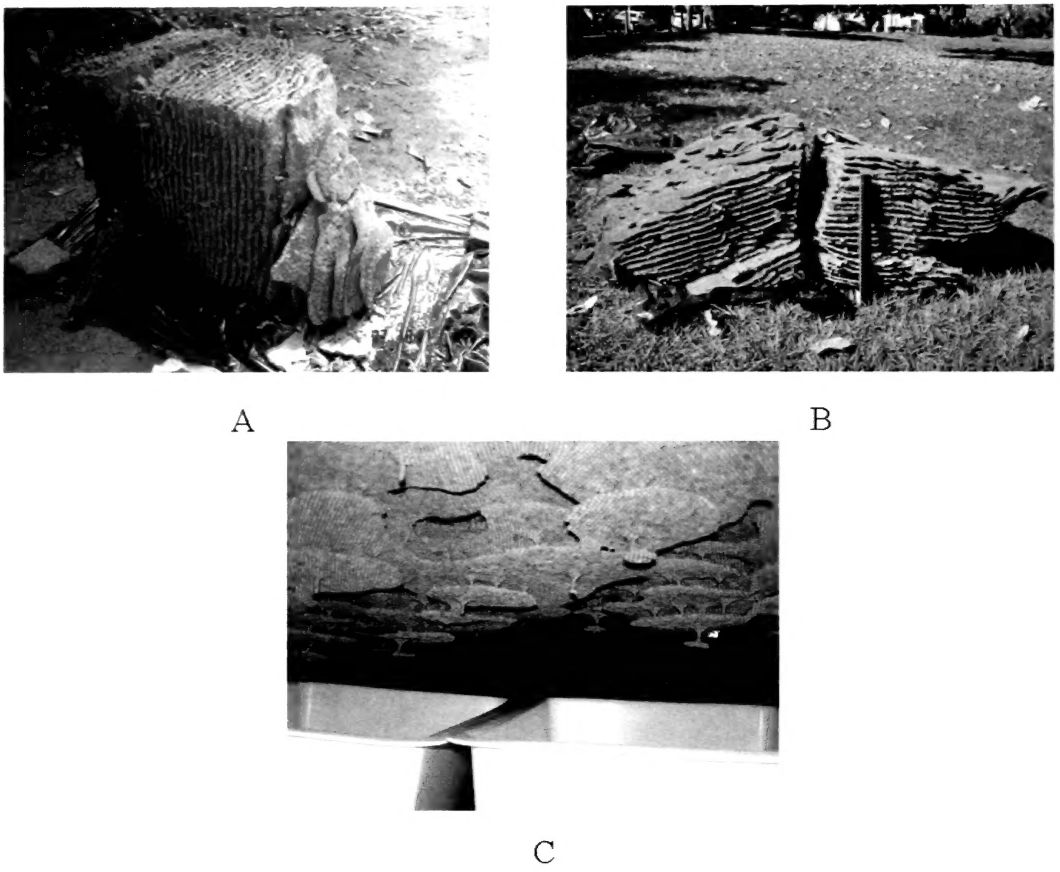

Fig. 1. Nests of *Agelaia vicina* from Pindorama (A) and Paulo de Faria (B), SP, Brazil. Position of trays beneath a nest to collect material discarded from the Paulo de Faria nest (C).

nest, a central area comprising about 30% of the nest was used for brood production. This nest had about 64,832 cells per kg.

Foraging began early from the Pindorama nest, so that during the 06–07h period when the colony was in an active phase too many workers were active to allow their number to be estimated, even with slow-motion playback (Table 1). Later, in the declining phase of the colony cycle, with fewer individuals and less activity, it was possible to identify more foragers exiting than returning. From 14h–15h to 18h–19h, there were more foragers returning. We observed that about 30% of the "foraging activity" was related to very brief absences that presumably brought nothing into the nest. This behavior gave rise to a cloud of workers outside the nest throughout the day while the colony was in an active phase.

Foraging times of exiting the nest, arriving at the bait, then returning to the nest in Paulo de Faria averages 2 min (1.19–3.47 min). The increase in the number of foragers in the baits was linear (Fig. 2), suggesting the absence of recruitment (Hrncir et al. 2007).

In October 2005, the colony of Paulo de Faria was active, producing males and workers, both of which are easily identified in this species. Using operculum numbers, we found a rise in the production of new individuals in the period from November 2005 to March 2006, reaching a peak in March, following by a decrease in April 2006 (Fig. 3A), with signs of nest desertion due to the absence of workers in the

Table 1. Mean ratio of *Agelaia vicina* foragers exiting by those returning per minute (values reported as exit/return) in different periods of the day at nest in Pindorama, SP, Brazil. These are recorded both when the colony was active and in apparent good health and later when it was in a state of decline.

	06h~07h	*14h~15h*	*18h~19h*	*24h~01h*
Active	>1000	53/73	150/145	00/00
Declining	30/11	03/06	07/04	00/00

external area of the nest. In front or above the nests of *A. vicina* we sometimes saw a cloud of foragers flying near the nest. This cloud disappeared after April 2006.

The colony cycle at Pindorama was similar to that from Paulo de Faria. From May to June 2006, there was little activity and almost no production of new individuals. After July 2006 males were found in the population. Adult production increased to a climax in January 2007, remained high up to the end of February (2007) when the population lessened drastically (Fig. 3B).

Agelaia vicina collects at least 10 different orders of insects: Lepidoptera, Coleoptera, Dermaptera, Hymenoptera, Heteroptera, Mantodea, Diptera, Neuroptera, Blattodae and Homoptera. In addition, we found many spiders (Arachnida: Araneae). In the two studied colonies, the taxonomic composition of the discarded prey parts was similar. Lepidoptera and Coleoptera, represented by remains of larval mandibles and adult body parts, were the most common. Spiders were also an important item in their diet. The other orders were found at much lower levels. In addition, we found two different seeds, one from a grass (*Panicum sp.*) and a *Cyperus sp.* Several balls of plant leaf hairs were found, wasp larvae, and some small pebbles and sticks.

DISCUSSION

Information on architecture of the observed nests corroborates that of Wenzel (1991) and Zucchi et al. (1995), in that the

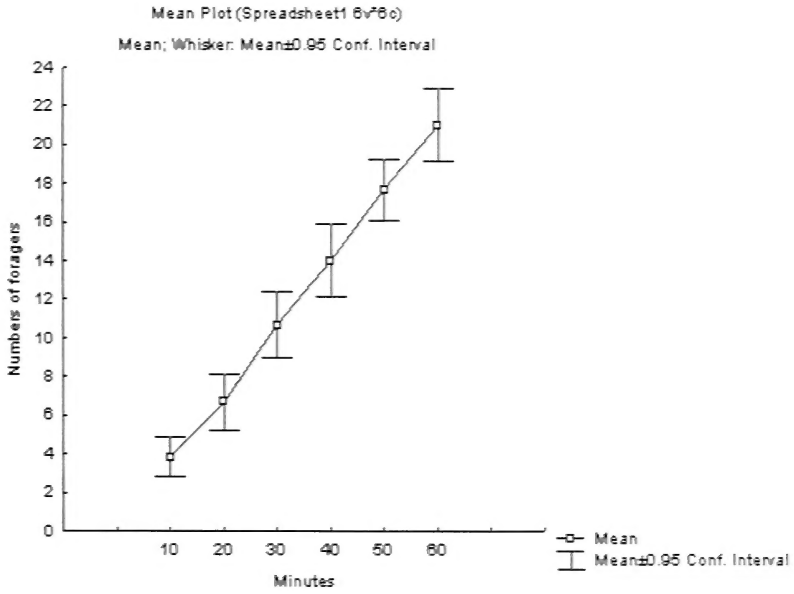

Fig. 2. Numbers of *Agelaia vicina* foragers per minute (mean ± SE) that found and collected meat baits at Pindorama, SP, Brazil.

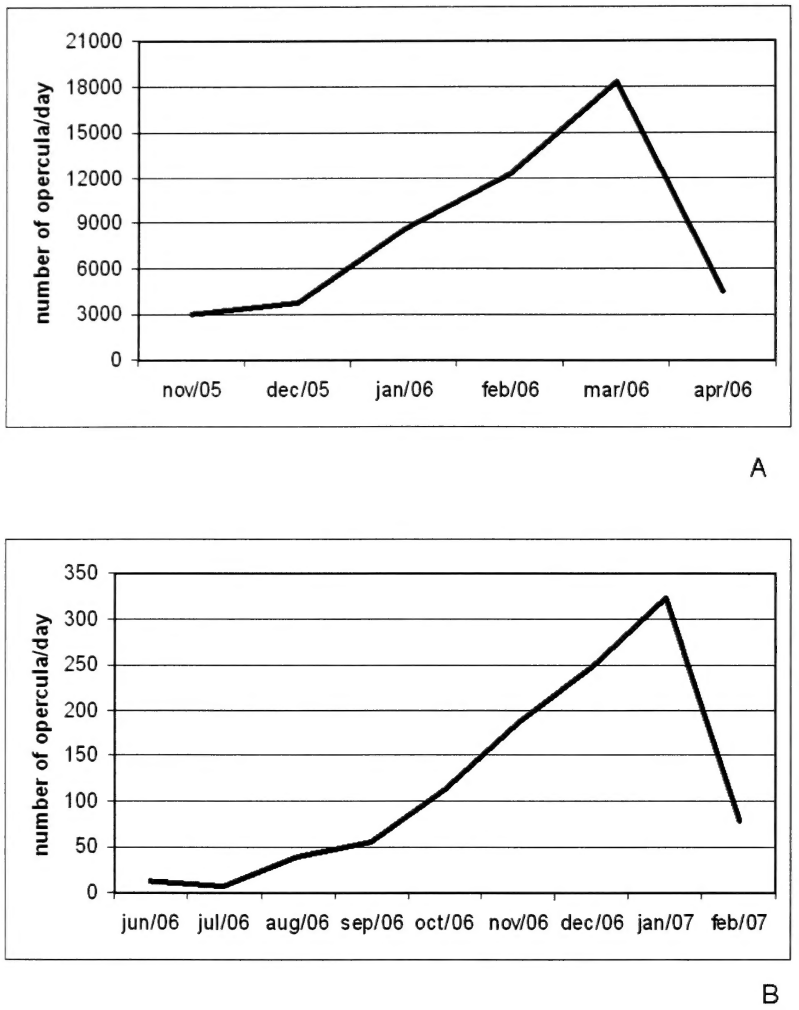

Fig. 3. Number of opercula/day collected during the months of study from nests of *Agelaia vicina* at Paulo de Faria (A) and Pindorama (B), SP, Brazil.

peripheral regions of combs do not fulfill a reproductive function but the act as an envelope. Detailed studies of nest development in swarm-founding wasps are largely limited to the genus *Polybia* (Jeanne and Bouwma 2004; Kudô et al. 2003, 2005; Loope and Jeanne 2008), which provides a baseline for comparison. In swarms of *P. occidentalis* (Oliver), for example, rapid construction in the founding stage completes the initial nest in two to three weeks, followed by almost no change during much of the ergonomic stage. Renewed expansion may occur several weeks or months later (Jeanne and Bouwma 2004).

In *A. vicina*, initial construction of the nest can also be considered rapid, with the construction of several combs. Approximately fifteen pedicels and initial cells may be built in the first five hours (Oliveira pers. obs). However, *A. vicina* then shows a continuous increase in the size of the nest, rather than alternating periods of stasis and sudden expansion. The growth rate found here shows that nests double in size in six months. Factors that allow nests of the great size of *A. vicina* include high growth rate, high population and large number of queens.

The large number of foragers producing a cloud of workers during the whole

activity period of the colony is visually impressive. As we observed, most exits from the nest lead to very short flights that appear unconnected with foraging. Hypotheses to explain this persistent cloud include that it a) serves a defensive function in obstructing the approach of predators or parasites, b) serves as a landmark in the orientation of returning foragers, or c) is simply a way of reducing crowding inside the nest during the active part of the day. The absence of feces on the substrate near the nest indicates that these are not defecation flights, as Richards (1978) suggested. If it is found that the cloud is composed of young workers who are not yet fully mature, this would be inconsistent with hypothesis (a) and consistent with (b) and (c).

No recruitment to meat baits was detected. This is in agreement with previous observations on *Agelaia* (Jeanne et al. 1995) and contrary to what was observed for *Polybia paulista* (Ihering) (Hrncir et al. 2007) in which authors found recruitment for sugar sources. In terms of diet, our results are similar to that from many other social wasps (Edwards 1980). *A. vicina* has a very broad diet, foraging for water (O. Oliveira pers. obs), plant tissues, proteins and carbohydrates. They use plant fibers (cellulose) for nest construction, proteins (from captured arthropods and carrion) and sugar from fruits (probably from the pulp of the seeds found) as energy source for the brood and adults (Akre 1982; Rossi and Hunt 1988; Spradbery 1973). *A. vicina* is a generalist predator of land arthropods, taking spiders and a broad range of insects. We can infer that it plays important roles in their ecosystem as a predator of large numbers of invertebrates (see daily productivity, below).

The colony cycle of the two studied colonies of *A. vicina* was similar. In the dry season, population increases possibly indicated preparations for reproductive swarming, which causes an abrupt fall in colony size, as is known in other Epiponini (Jeanne 1991). Based on Figure 3A–B, nests differ greatly in the number of individuals produced. The Paulo de Faria nest reached a production of 18,000 new individuals per day, but the Pindorama nest reached no more than 300 individuals per day at peak production. It is hard to account for this very large difference.

For less complex societies, like *Polistes*, feeding efficiency may not to be a limiting factor for nest size (Strassmann and Orgren 1983). In *A. vicina*, however, the fall in worker production may be a consequence of the difficulty of obtaining food in the rainy season, associated with the implications of a high relative moisture for the maintenance of the colony, an increase in predation, or appearance of fungus or parasitism (Hunt et al. 2001; Richards 1978). Because the forest remnant of Paulo de Faria (435 ha) is larger than that of Pindorama (128 ha), it may also provide more resources. Nevertheless, the differences presented regarding the production of new individuals may not be tied only to resource availability but also may relate to the differences in colony age and predation.

The term "keystone species" was coined by Paine (1969). A keystone species influences several organisms in an ecosystem with a effects on the other species out of proportion to its abundance. A keystone species may determine the types and numbers of various other species in a community. Several aspects of our results suggest that *A. vicina* may act as a keystone species. *A. vicina*, besides having the largest nests and colonies among social wasps, has a very high rate of brood production (up to several thousand individuals per day). The quantity of prey brought to the nest is evidently very substantial, especially if we take into account the rough rule of a 10% efficiency energy transfer between trophic levels. *A. vicina* preys upon an impressive diversity of arthropods and must impact their populations locally. We propose *A. vicina*

as a candidate keystone species, so that it would be fruitful if future studies were to evaluate its influence in neotropical environments.

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We dedicate this paper to Roy Snelling, who liked social wasps and helped to inspire young hymenopterists of every stripe. He was one of those rare people who excelled in doing difficult, dangerous, and sometimes unpleasant work if it would open doors to a provocative new view of the fascinating insects around us. We think he would have enjoyed returning a critique of this paper. This work was funded by FAPESP (2005/03569-8; 2008/07633-1).

LITERATURE CITED

Akre, R. D. 1982. Social wasps. Pp. 1–105 *in:* Hermann, H. R. ed. *Social Insects*, vol. 4. Academic, New York.

Dapporto, L. and E. Palagi. 2006. Wasps in the shadow: Looking at the pre-hibernating clusters of *Polistes dominulus*. *Annales Zoologici Fennici* 43: 583–594.

Edwards, R. 1980. *Social Wasps: Their Biology and Control*. Rentokil, East Grinstead. 398 pp.

Hermann, H. R. and J. T. Chao. 1984. Nesting Biology and Defensive Behavior of *Mischocyttarus (Monocyttarus) mexicanus cubicola* (Vespidae: Polistinae). *Psyche* 91: 51–65.

Hrncir, M., S. Mateus, and F. S. Nascimento. 2007. Exploitation of carbohydrate food sources in *Polybia occidentalis*: social cues influence foraging decisions in swarm-founding wasps. *Behavioral Ecology and Sociobiology* 61: 975–983.

Hunt, J. H., S. O'Donnell, N. Chernoff, and C. Brownie. 2001. Observations on two neotropical swarm-fonding wasps *Agelaia yepocapa* and *A. panamaensis* (Hymenoptera:Vespidae). *Annals of the Entomological Society of America* 94: 555–562.

Ihering, R. Von. 1903. Contributions à l'étude des Vespides de l'Amérique su Sud. *Annales de la Société Entomologique de France* 72: 144–155.

———. 1904. As vespas sociaes do Brasil. *Revista do Museu Paulista* 6: 97–309.

Jeanne, R. L. 1991. The swarm-founding Polistinae. Pp. 191–231 *in:* Ross, K. G., and R. W. Matthews eds. *The Social Biology of Wasps*. Cornell University Press, Ithaca.

——— and A. M. Bouwma. 2004. Divergent patterns of nest construction in eusocial wasps. *Journal of the Kansas Entomological Society* 77: 429–447.

———, J. H. Hunt, and M. G. Keeping. 1995. Foraging in social wasps: *Agelaia* lacks recruitment to food. *Journal of the Kansas Entomological Society* 68: 279–289.

Jha, S., R. G. Casey-Ford, J. S. Pedersen, T. G. Platt, R. Cervo, D. C. Queller, and J. E. Strassmann. 2006. The queen is not a pacemaker in the small-colony wasps *Polistes instabilis* and *P. dominulus*. *Animal Behaviour* 71: 1197–1203.

Kudô, K., R. Zucchi, and K. Tsuchida. 2003. Initial nest development in the swarm-founding paper wasp, *Polybia paulista* (Hymenoptera: Vespidae, Epiponini): cases of building multiple initial combs. *Journal of the New York Entomological Society* 111: 151–158.

———, S. Tsujita, K. Tsuchida, W. Goi, Sô. Yamane, S. Mateus, Y. Itô, S. Miyano, and R. Zucchi. 2005. Stable relatedness structure of the large-colony swarm-founding wasp Polybia paulista. *Behavioral Ecology and Sociobiology* 58: 27–35.

Loope, K. J. and R. L. Jeanne. 2008. A test of adaptive hypotheses for rapid nest construction in a swarm-founding wasp. *Insectes Sociaux* 55: 274–82.

Mechi, M. R. 2005. Comunidade de vespas Aculeata (Hymenoptera) e suas fontes florais. Pp. 256–265 *in:* Pivello, V. R., and E. M. Varanda eds. *O Cerrado Pé-de-Gigante: Ecologia e Conservação - Parque Estadual Vassununga*. Secretaria do Meio Ambiente, São Paulo.

O'Donnell, S. 1995. Necrophagy by neotropical swarm-founding wasps (Hymenoptera: Vespidae; Epiponini). *Biotropica* 27: 133–136.

——— and R. L. Jeanne. 2002. The nest as fortress: defensive behavior of *Polybia emaciata*, a mud-nesting eusocial wasp. *Journal of Insect Science* 2: 3–5.

Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103: 91–93.

Raposo Filho, J. R. and V. M. Rodrigues. 1983. Comportamentos tróficos de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Polistinae, Vespidae). I. Alimentação proteica. *Naturalia* (São Paulo) 8: 101–104.

Richards, O. W. and M. J. Richards. 1951. Observations on the social wasps of South America (Hymenoptera Vespidae). *Transactions of the Royal Entomological Society of London* 102: 1–170.

———. 1978. *The Social Wasps of the Americas,Excluding the Vespinae*. British Museum (Natural History), London. 580 pp.

Richter, M. R. 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annual Review of Entomology* 45: 121–150.

Rossi, A. M. and J. H. Hunt. 1988. Honey supplementation and its developmental consequences: evidence for food limitation in a paper wasp, *Polistes metricus*. *Ecological Entomology* 13: 437–42.

Silveira, O. T., M. C. Esposito, J. N. Santos Jr, and F. E. GemaqueJr 2005. Social wasps and bees captured in carrion traps in a rainforest in Brazil. *Entomological Science* 8: 33–39.

Spradbery, J. P. 1973. *Wasps: an Account of the Biology and Natural History of Social and Solitary Wasps.* University of Washington Press, Seattle. 408 pp.

Strassmann, J. E. and C. F. Orgren. 1983. Nest architecture and brood development times in the paper wasp *Polistes exclamans* (Hymenoptera:Vespidae). *Psyche* 90: 237–248.

Wenzel, J. W. 1991. Evolution of nest architecture. Pp. 480–519 *in:* Ross, K. G., and R. W. Matthews eds. *The Social Biology of Wasps.* Cornell University Press, Ithaca.

———. 1998. A generic key to the nest of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). *American Museum Novitates* 3224: l–39.

Zucchi, R., S. F. Sakagami, F. B. Noll, M. R. Mechi, S. Mateus, M. V. Baio, and S. N. Shima. 1995. *Agelaia vicina,* a swarm-founding polistine with the largest colony size among wasps and bees (Hymenoptera: Vespidae). *Journal of the New York Entomological Society* 103: 129–137.

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A Review of the Dacetine Ants of Guyana (Formicidae: Myrmicinae)

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Abstract.—The dacetine ants of Guyana are reviewed. One genus, *Acanthognathus*, is added to the three genera reported previously from Guyana. A total of 42 species are reported, 32 of which are new records for Guyana. Among these 32 species, the following five are new species: ***Pyramica dahlanae* sp. n.**, ***Pyramica mariae* sp. n.**, ***Strumigenys acarai* sp. n.**, ***Strumigenys royi* sp. n.**, and ***Strumigenys waiwai* sp. n**. *Pyramica dahlanae* is unusual for the genus because it lacks propodeal spines and possesses distinctive mandibular morphology. *Pyramica mariae* belongs to the *gundlachi* group and is apparently closely related to *P. denticulata* based on the length of the mandibles, the absence of spongiform tissue on the ventral margin of waist segments, general body pilosity, and general habitus. *Pyramica denticulata* is illustrated in order to show morphological differences from *P. mariae*. *Strumigenys royi* is a remarkable ant because its waist segments lack ventral spongiform tissue, it possesses short propodeal spines, its mandibles are long and with a minute denticle proximal to the apicodorsal tooth of the mandibular fork, and its coloration is distinctive. *Strumigenys acarai* is unusual because it possesses a minute denticle on the inner margin of the mandibles, distinctive rugulose sculpture on the dorsum of mesonotum that differs from sculpture found on other parts of the body, and a longitudinal median carina on the promesonotum. *Strumigenys waiwai* is easily recognized by the unusual multifurcate pilosity of the cephalic dorsum and small body size. Modifications of Bolton's (2000) keys to *Pyramica* and *Strumigenys* are provided to accommodate the newly described species.

Resumen.—En este artículo se revisaron las hormigas dacetinas presentes en Guyana. El género *Acanthognathus* se adiciona a los tres géneros de hormigas dacetinas conocidos anteriormente para Guyana. Se reportan un total de 42 especies, de las cuales 32 constituyen nuevos registros en este país. Dentro de estos 32 nuevos registros, cinco especies son nuevas: ***Pyramica dahlanae* sp. n.**, ***Pyramica mariae* sp. n.**, ***Strumigenys acarai* sp. n.**, ***Strumigenys royi* sp. n.**, y ***Strumigenys waiwai* sp. n**. *Pyramica dahlanae* es fácilmente reconocida por que carece de espinas en el propodeo y su morfología mandibular es distintiva. *Pyramica mariae* pertenece al grupo *gundlachi* y está probablemente relacionada con *P. denticulata* por la longitud de las mandíbulas, la ausencia de tejido en forma de esponja en la margen ventral del pecíolo y postpecíolo, la pilosidad en el cuerpo y por la forma del cuerpo en general. Tambien se ilustra *Pyramica denticulata* con el fin de mostrar las diferencias morfológicas que la separan de *P. mariae*. *Strumigenys royi* es una hormiga notable caracterizada por la carencia de tejido en forma de esponja en la parte ventral del pecíolo y postpecíolo, por la presencia de espinas propodeales cortas, por la presencia de mandíbulas largas y con un diminuto dentículo próximo al diente apicodorsal en la bifurcación apical, y por la coloración característica. *Strumigenys acarai* es una hormiga poco usual porque posee un diminuto dentículo en el borde interno próximo a la parte media de las mandíbulas, presenta una característica escultura rugulosa en el dorso del mesonoto la cual difiere de cualquier escultura presente en el resto del cuerpo, y presenta una carina media longitudinal en el promesonotum. *Strumigenys waiwai* es fácilmente reconocida por la pilosidad multi-furcada poco usual en el dorso

cefálico y por el reducido tamaño de las obreras. Modificaciones a las claves de Bolton (2000) para identificar las species de *Pyramica* y de *Strumigenys* son presentadas para incluir las nuevas especies.

Key words.—Dacetini, Hymenoptera, leaf-litter sampling, Neotropics, new species, *Pyramica*, *Strumigenys*, taxonomy

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Species of ants in the tribe Dacetini (Formicidae: Myrmicinae) vary greatly in size, morphology, and behavior (Hölldobler and Wilson 1990). They inhabit rotten wood, leaf litter, soil, and trees (Hölldobler and Wilson 1990; Bolton 1998) and feed on a diverse variety of small arthropods (Wilson 1953; Dejean 1985a; Bolton 1998). It has been hypothesized that the bizarre mandibular morphology of dacetines, including the different mandibular modes of action, and the conspicuous spongiform tissue located mostly on the waist segments are adaptations for attracting and capturing springtails (Collembola) on which most members of the tribe presumably feed (Brown and Wilson 1959; Dejean 1985a, b, 1987; Dietz and Brandão 1993; Gronenberg 1996; Kantarovich et al. 2006; Masuko 1984, 2009).

Guyana occupies a central position within the Guiana Shield, a large (~1,000,000 km^2), ancient (Proterozoic, ~2.5 billion years ago) geological area that was once attached to West Africa (Gibbs and Baron 1993) and that currently extends between the Amazon and the Orinoco River Basins. Unlike most tropical countries, ~70% of Guyana's land, including large tracts of primary rainforest, remains intact or is only marginally affected by human disturbance (Funk and Richardson 2002). Due to the creation of new roads, the influx of new inhabitants (especially from Brazil), and increased mining and timber-harvesting activity, this situation is rapidly changing. It is therefore imperative to gather the biological information necessary for identifying areas of conservation concern.

The ant fauna of Guyana remains largely unknown. Wheeler (1916, 1918) and LaPolla et al. (2007) have produced the only publications specifically addressing this fauna. Weber (1946) studied the fungus-growing ants (Attini) from Guyana; Kempf (1972) and Fernandez and Sendoya (2004), based primarily on literature reports, recorded ~350 described ant species from Guyana. LaPolla et al.'s (2007) study recorded 230 ant species (44 genera) collected from eight localities using leaf-litter mini-Winkler sampling. These figures clearly underestimate the actual number of species present in the country; for example, La Selva, a ~1500 ha Biological Reserve in Costa Rica, possesses at least 437 ant species (Longino et al. 2002). Bolton (2000) and Fernandez and Sendoya (2004) reported three dacetine genera and 10 species for Guyana. As a result of recent leaf-litter surveys in Guyana (Appendix 1), we increase the number of Guyana's dacetine ant species to 42, describe two new species in the genus *Pyramica* Roger and three new species in the genus *Strumigenys* F. Smith, and report for the first time species of *Acanthognathus* Mayr in Guyana (Appendix 2). Although Bolton's generic level classification of dacetines has recently been questioned (Baroni-Urbani and de Andrade 2007), we choose to follow it here for the sake of taxonomic stability in the face of indecisive phylogenetic data.

Despite Bolton's (2000) recent monograph of the dacetines, it is clear that many species remain to be discovered and described in this species-rich tribe. Fortunately, Bolton's study provides the context for rapidly identifying and describing new species as they are discovered (Deyrup 2006; Sosa-Calvo et al. 2006; Longino 2006; Azorsa & Sosa-Calvo 2008, Bolton et al.

2008). This study summarizes the current state of dacetine taxonomy in Guyana and describes several new species. While Guyana certainly contains many more dacetine species, both described and undescribed, we believe it is important to begin the process of documenting Guyanese dacetine diversity because (i) this information will facilitate the sorting and identification of material generated by ongoing ant surveys in Guyana, as well as in French Guiana, Suriname, and eastern Venezuela (Appendix 3); (ii) this information, combined with the information generated by those ongoing studies, will provide data urgently required by conservation efforts underway in Guyana and Suriname (LaPolla et al. 2007; Sosa-Calvo 2007; Alonso and Mol 2007; Alonso et al. 2008); and (iii) this information can be incorporated into ongoing studies aimed at understanding biodiversity patterns of the Guiana Shield, especially those generated by the Smithsonian's Biodiversity of the Guianas Program (Funk et al. 2002; Funk and Richardson 2002). This study increases our knowledge of the species that occur in Guyana and complements publications on other genera including *Acropyga* Roger (LaPolla 2004), *Lachnomyrmex* Wheeler (Feitosa and Brandão 2008), *Pheidole* Westwood (LaPolla and Cover 2005), and *Rogeria* Emery (LaPolla and Sosa-Calvo 2006).

MATERIAL AND METHODS

Specimens were examined and measured to the nearest 0.001 mm at various magnifications using a Leica MZ125 light stereomicroscope. All measurements are in millimeters unless noted otherwise. Specimens were photographed using a JVC KY-F70B video camera mounted on a Leica M420 stereomicroscope attached to an IBM Intellistation M Pro computer on which composite images were assembled using Auto- Montage Pro Version 5.03.0018 BETA software® (Synoptics Ltd.). Images were cropped and enhanced using Photoshop CS2 Version 9® (Adobe Inc.). Scanning electron micrographs (SEM) of uncoated specimens (*P. dahlanae*, *P. mariae*, and *S. royi*) were taken using a Philips XL-30 ESEM with Lanthanum Hexaboride (LaB6) source and a backscatter detector. *Strumigenys acarai* and *S. waiwai* were sputter-coated with 60:40 wt% Gold:Palladium alloy on a Cressington Scientific 108 auto/SE sputter coater to a thickness of 25-20 nm. Scanning electron micrographs for these specimens were taken using an Amray 1810 SEM with LaB6 source. Terminology for morphological features and surface sculpture, as well as abbreviations, follow Bolton (1994, 2000) and Harris (1979) with modifications where noted. Anatomical abbreviations are as follows:

EL — Eye Length: Maximum diameter of compound eye in lateral view.

GL — Gaster Length: Length of gaster in lateral view from anterior-most point of first gastral segment (third abdominal segment) to posterior-most point, excluding sting apparatus if protruding.

HL — Head Length: Length of head in full-face (dorsal) view, including occipital lobes and anterior clypeal margin but excluding mandibles.

HW — Head Width: Maximum measurable width of head in full-face view, excluding eyes.

ML — Mandible Length: Exposed length of closed mandibles, in full-face view, from anterior clypeal margin to apex of mandibles.

PL — Petiole Length: Straight line from posterior-most margin of petiole to posterior-most margin of metapleural lobe in lateral view.

PPL — Postpetiole Length: Maximum length of postpetiole in lateral view.

PW	Pronotal Width: Maximum measurable width of pronotum in dorsal view.
SL	Scape Length: Maximum length of antennal scape, excluding condylar bulb.
TL	Total Length: HL + ML + WL + PL + PPL + GL.
WL	Weber's Length: Maximum length of diagonal connecting, in lateral view, antero-dorsal angle of pronotum to posterior-most basal angle of metapleuron. (=Alitrunk Length in Bolton [2000].)
CI	Cephalic Index: (HW/HL) × 100.
MI	Mandibular Index: (ML/HL) × 100.
PI	Petiolar Length Index: (PL/WL) × 100.
SI	Scape Index: (SL/HW) × 100.

Specimens examined were borrowed from and/or have been deposited in the following institutions: The Natural History Museum, London, U.K. (BMNH); Centre for the Study of Biological Diversity, University of Guyana, Georgetown, Guyana (UGBC); Museum of Comparative Zoology, Harvard University, Cambridge, MA., U.S.A. (MCZC); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZSP); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM).

RESULTS AND DISCUSSION

Pyramica dahlanae Sosa-Calvo, Schultz, and LaPolla, **n. sp.**
(Figs 1–5)

Material examined.—Holotype: worker, labeled: "GUYANA: Mabura Hill camp at end of Rd. from Georgetown to Lethem Rd.; 64 m; 58° 41.982′ W 5° 9.313′ N; 29 x 2002; *J.S. LaPolla* et al.; primary forest; litter sample. (JSL021029-LS04)" USNM ENT No. 00442119 (UGBC). *Paratype:* worker, labeled: "GUYANA: Calm Water Creek along Essequibo River nr. Bartica; 58° 37.16′ W 6° 28.06′ N; 23 ix 2002; *J.S. LaPolla*; primary forest; litter sample. (JSL020923-LS02)" USNM ENT No. 00441577 (USNM).

Diagnosis (worker).—Very small (TL = 1.38–1.42); eyes absent; mandibles linear, elongate, and in closed position with gap between basal mandibular teeth and anterior portion of clypeus; propodeum unarmed; ventral portion of petiole lacking spongiform tissue.

Description (worker).—*Head:* in full-face view, clypeus slightly concave anteriorly, with long apical spoon-shaped hairs extending over mandibular gap; mandibles sublinear and elongate; at full closure mandibles contacting only in apical halves of their lengths, leaving gap between them basally; mandibles with 10 teeth, basal tooth acute, all other teeth rounded and flattened; teeth 1, 3, 5, 7, 9, and 10 (from base to apex) larger than other teeth; lateral dorsum of mandible with appressed simple hairs; eyes absent; sculpture on clypeal plate imbricate; sculpture on cephalic dorsum areolate and covered with squamate hairs; hairs on anterior margin (leading edge) of scape spoon-shaped and directed basad; antennal scape narrowed basally, anterior margin abruptly expanded, distinctly widest at point of expansion; apicoscrobal hair absent. *Mesosoma:* dorsum of anterior portion of pronotum glabrous; pronotal humeral hair absent; dorsum of promesonotum and dorsum and declivity of propodeum entirely areolate; propodeum lacking spines or denticles at its posterior margin; mesopleuron and metapleuron smooth and shining; dorsal portion of mesosoma covered with appressed spoon-shaped hairs (as on head) without erect hairs of any kind, lateral portions glabrous. *Metasoma*: petiole lacking ventral spongiform lobe, petiolar disc areolate and covered with slightly appressed spatulate hairs; lateral surface of petiolar peduncle smooth and shining; ventral surface of side of petiole weakly sculptured; disc of postpetiole

weakly sculptured and shining, covered with hairs similar to those on petiole but narrower; ventral surface of postpetiole with well-developed spongiform lobe that extends throughout its entire length; lateral spongiform tissue overhanging ventral spongiform lobe; dorsal surface of first gastral segment smooth with some longitudinal basigastral costulae. *Color:* individuals light yellow to dark yellow. Hairs throughout body lighter than integument.

Measurements: holotype (and paratype): GL = 0.3 (0.32), HL = 0.34, HW = 0.27 (0.28), ML = 0.09, PL = 0.17, PPL = 0.12 (0.11), PW = 0.19 (0.18), SL = 0.16, TL = 1.42 (1.38), WL = 0.39 (0.36). Indexes: CI = 82 (79), MI = 26, PI = 47 (44), SI = 59 (57). (n = 2)

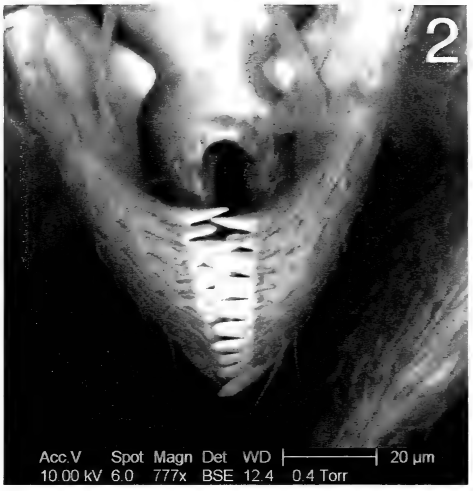
Gyne and male.—Unknown.

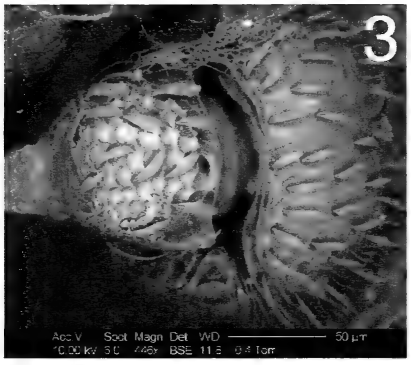
Etymology.—Named after Ms. Nor Faridah Dahlan in recognition of her expertise and hard work in support of Smithsonian ant research and in gratitude for her consistent good will and friendship. JS-C is deeply grateful to Faridah for all her help and care when he first arrived in the United States.

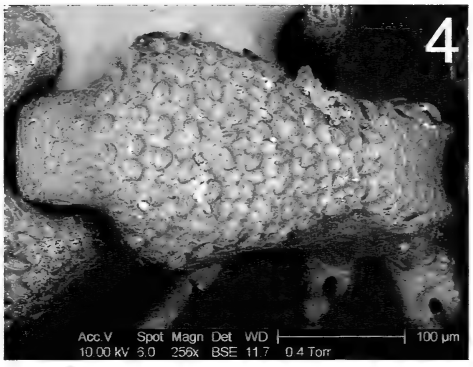
Comments.—*Pyramica dahlanae* n. sp. is most similar to members of the Nearctic *pergandei*-group, which includes *P. angulata* (M.R. Smith), known from the southeastern United States and Illinois, and *P. pergandei* (Emery), widely distributed in Canada and the United States. *Pyramica dahlanae* shares with those species the following characters: (i) mandibles short (MI 25–35) and, in frontal view, narrow and elongate, dentate only at the apical portion where they are in contact leaving an edentate gap between them; (ii) specialized mandibular dentition (alternating pattern of longer and shorter mandibular teeth); (iii) lateral clypeal margins, in dorsal view, extending beyond the line of the outer margin of the mandibles when closed; and (iv) preocular carina broad and conspicuous. *Pyramica dahlanae* differs from the species in the *pergandei*-group in four character states: (i) 10 mandibular teeth (15–16 in the *pergandei*-group), (ii) absence of triangular teeth on the propodeum (present in the *pergandei*-group), (iii) absence of a well-developed spongiform tissue on the ventral portion of the petiole (present in the *pergandei*-group), and (iv) shorter antennal scape, SI 57–59 (SI 65–84 in the *pergandei*-group).

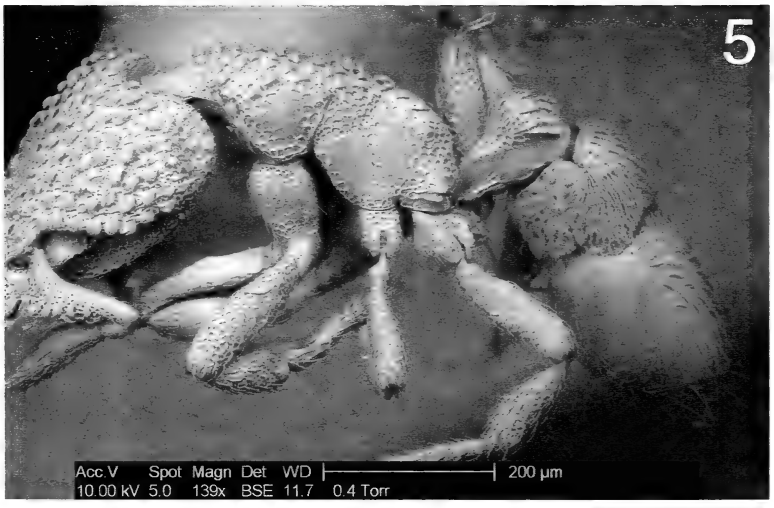
The mandibles of *P. dahlanae* are similar to those within the *pergandei*-group in that they contact in the apical third, producing a basal gap between the mandibles. This condition is different from the one found in species in the *ohioensis*-group, in which the masticatory margins contact through almost their entire lengths and in which the mandibles are triangular rather than elongate. Elongate mandibles can be found in the *gundlachi*- and *argiola*-groups, the latter an Old World group introduced into the United States (*P. hexamera* (Brown)). Mandibles in *P. hexamera* are highly distinctive with an elongate and spiniform apicodorsal tooth and two long preapical teeth (see Bolton 2000 for further information). Species of the *gundlachi*-group share with *P. dahlanae* the absence of a spongiform lobe on the ventral surface of the petiole but differ from *P. dahlanae* in: (i) mandibular length and morphology, (ii) the presence of a pair of triangular teeth or short spines on the propodeum, and (iii) the presence of pronotal humeral hairs and, in almost all species, a pair of laterally projecting apicoscrobal hairs.

Pyramica dahlanae may also be related to *P. paradoxa* Bolton, known from a single worker collected in Costa Rica. Both species share the absence of propodeal spines; however, *P. dahlanae* differs from *P. paradoxa* by the shape of the mandibles, and the head and mesosoma strongly areolate with the meso- and metapleuron smooth and shining. The head and mesosoma are mostly smooth and shining in *P. paradoxa*. Although *P. dahlanae* shares a number of character states with some members of the aforementioned groups, this species is not easily placed in any of the species groups defined by Bolton (2000).









Figs 1–5. Scanning electron micrographs of the holotype worker of *Pyramica dahlanae*, new species. 1, Full-face (dorsal) view. 2, Closed mandibles. 3, Dorsal view of petiole and postpetiole. 4, Dorsal view of mesosoma. 5, Lateral view.

MODIFIED VERSION OF KEY IN BOLTON (2000)

Pyramica dahlanae will not key out to any known species of *Pyramica* in either the Nearctic or the Neotropical keys of Bolton (2000). The key to Neotropical species can be modified as below to include *P. dahlanae*. The numbering of couplets follows Bolton (2000).

7.	Dorsum of postpetiole (= disc) smooth and with weak costulae	**7b**
–	Dorsum of postpetiole entirely reticulate-punctate	couplet 12 in Bolton (2000)
7b.	Cephalic dorsum with 1 or 2 pairs of standing hairs. Apicoscrobal and pronotal humeral hairs present...	couplet 8 in Bolton (2000)
–	Cephalic dorsum lacking standing hairs. Apicoscrobal and pronotal humeral hairs absent	***P. dahlanae* new species**

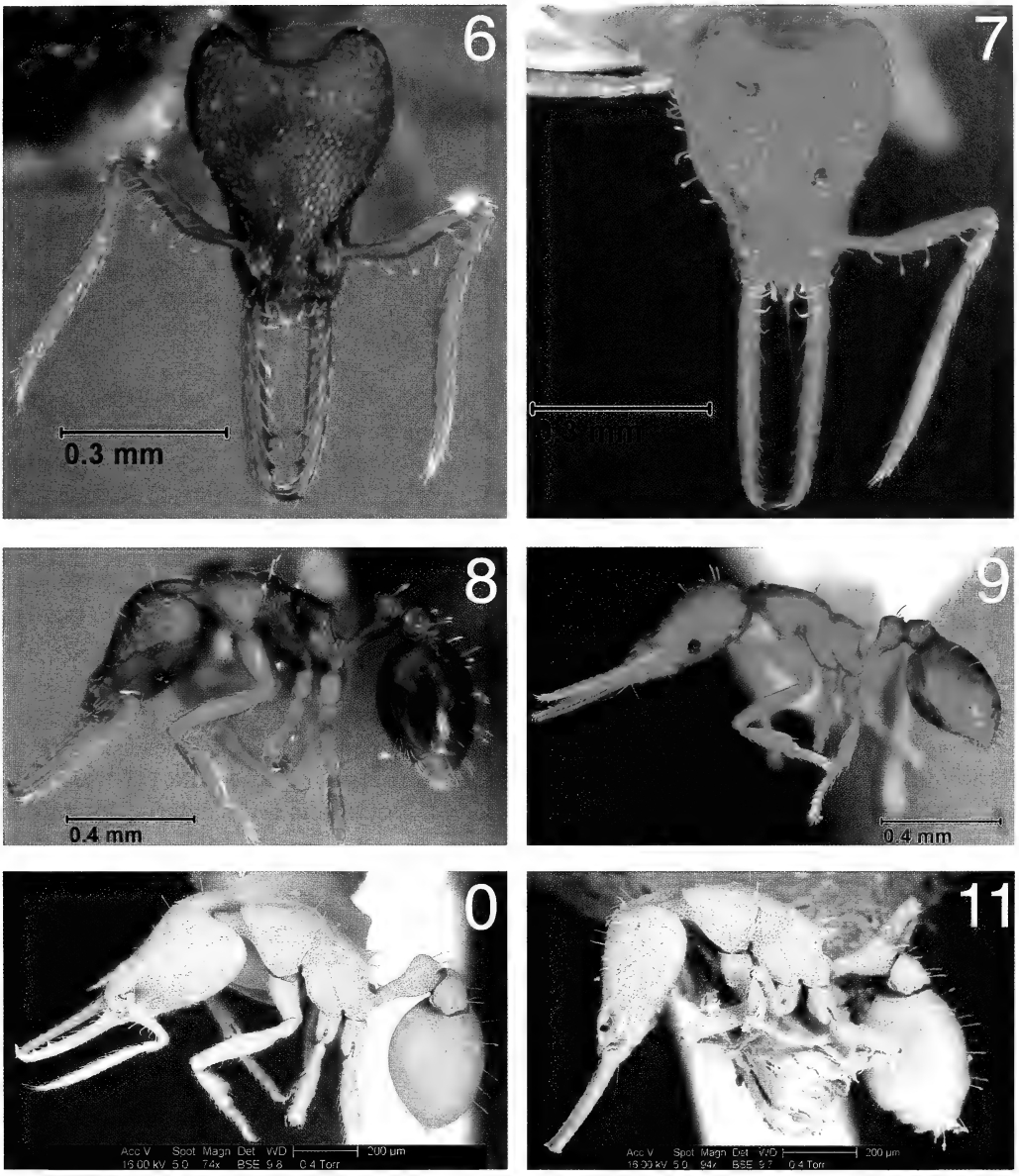
Pyramica mariae Sosa-Calvo, Schultz, and LaPolla, **n. sp.**
(Figs 6, 8, and 10)

Material examined.—Holotype: worker, labeled "GUYANA: Mt. Ayanganna montane forest; 1300 m; 59° 57.969' W 5° 22.483' N; 13.x.2002; *T.R. Schultz, J. LaPolla, C. Marshall, R. Williams*; litter sample." USNM ENT No. 00413858. (UGBC). *Paratypes*: 3 workers, same locality as in holotype. USNM ENT No. 00413859, 00442882, 00442883. (USNM).

Diagnosis (worker).—Mandibles linear, elongate, and narrow; inner margin of mandibles with two clearly defined teeth, which are larger than the rest; labral lobes short with long trigger hairs at their apices; metapleuron smooth and shining; ventral portions of petiole and postpetiole lacking spongiform tissue.

Description (worker).—Possessing characters of the *gundlachi*-group and *gundlachi*-complex (Bolton 2000). *Head:* in full-face view nearly as broad as long; inner margin of elongate mandibles slightly concave to more or less straight, with 4 teeth on left mandible and 3 on right mandible, of which a pair of teeth are larger on each mandible (same in paratypes); with 2 minute intercalary denticles between apicodorsal and apicoventral fork teeth; labral lobes short, almost invisible in full-face view; trigger hairs long; eyes with 3 ommatidia in longest row, with 6–7 ommatidia in total. Cephalic dorsum with two pairs of erect hairs: one pair located close to occipital margin and another pair located close to highest point of vertex; each upper scrobal margin with a short apicoscrobal hair that projects laterally. *Mesosoma*: pronotum with a pair of short humeral hairs that project laterally; mesonotum with a pair of short, erect, stiff hairs; mesopleuron and metapleuron mostly smooth and shining; dorsum of promesonotum, propodeum, and propodeal declivity strongly reticulate. *Metasoma*: peduncle of petiole long, length of petiole 3–3.5 times longer than its disc; petiolar disc reticulate-punctate, with a pair of erect hairs on posterior portion of disc; ventral portion of petiole lacking spongiform tissue; disc of postpetiole reticulate, ventral portion of postpetiole lacking spongiform tissue; posterior portion of postpetiole disc with a row of 4 erect hairs; first gastral tergite almost entirely reticulate except for a small portion at posterior portion of tergite. Individuals light brown to brown.

Measurements: holotype (and paratype): GL = 0.59 (0.48), HL = 0.52 (0.48–0.50), HW = 0.42 (0.38–0.46), ML = 0.36 (0.36–0.38), PL = 0.28 (0.24–0.27), PPL = 0.12, PW = 0.27 (0.23–0.24), SL = 0.30 (0.30–0.31), TL = 2.47 (2.24–2.28), WL = 0.58 (0.55–0.56). Indexes: CI = 81 (78–92), MI =



Figs 6–11. Full-face (dorsal) and lateral views of the holotype worker of *Pyramica mariae*, new species (6, 8, 10) and *P. denticulata* (7, 9, 11).

73 (72–75), PI = 48 (43–49), SI = 71 (65–82). (n = 4)

Gyne and male.—Unknown

Etymology.—Named in honor of the first author's mother, Maria del Carmen Calvo, in gratitude for her encouragement and support.

Comments.—*Pyramica mariae* n. sp. is clearly a member of the *gundlachi*-group (refer to Bolton [2000: 176–179 p.] for further information). Within the *gundlachi*-group, Bolton (2000) identified two complexes, *crassicornis* and *gundlachi*. *Pyramica mariae* belongs to the *gundlachi* complex and resembles *P. denticulata* (Mayr), *P. enopla* Bolton, and *P. vartana* Bolton. *Pyramica mariae* shares with *P. vartana* the smooth and shining mesopleuron and

metapleuron, but *P. mariae* can be distinguished from *P. vartana* by the form of the apicoscrobal and pronotal humeral hairs, both short and stiff (*mariae*) rather than long and filiform (*vartana*), and the disc of the postpetiole is reticulate (*mariae*) rather than smooth and shining (*vartana*).

Pyramica mariae is of similar size and color as *P. enopla*. However, *P. mariae* differs from *P. enopla* in that the apicoscrobal, humeral, and mesonotal hairs are short, erect, and stiff (*mariae*) rather than long and filiform (*enopla*); the metapleuron is smooth and shining (*mariae*) rather than reticulate (*enopla*); the dorsum of the petiole bears a single pair of hairs (*mariae*) rather than two pairs of hairs (*enopla*); and the dorsum of the postpetiole lacks an anterior pair of hairs (*mariae*), present *in enopla*.

Pyramica mariae can easily be confused with *P. denticulata* (Figs 7, 9, and 11) with which it shares the most character states. However, the species can be separated by: (i) mandibular dentition: *P. denticulata* has 5–10 preapical denticles of similar size, whereas *P. mariae* has 3–4 preapical denticles, two of which are larger than the rest. In *Pyramica mariae*, at least in the four specimens examined, there are 4 teeth on the left mandible and 3 teeth on the right mandible; (ii) mesosomal sculpture: the metapleuron in *P. denticulata* is reticulate, whereas in *P. mariae* it is smooth and shining; (iii) petiole proportions: the petiolar peduncle in *P. denticulata* is relatively shorter (PI 38–42) than in *P. mariae* (PI 43–49) (Figs 12–13).

The four specimens known of *P. mariae* were collected in a leaf-litter sample extracted with a mini-Winkler. The sample was collected in a primary lower montane forest (1300 m). Other species in the *gundlachi*-group have been recorded from wet forest habitats and from lowland rainforest to cloud forest and some in agroecosystems. *Pyramica denticulata*, the species perhaps most closely related to *P. mariae*, has been collected in lowland (< 1000 m) forests in Panama (Sosa-Calvo et al. 2006) to subtropical forests in the wet Chaco region of Argentina (Theunis et al. 2005). Nothing is known about the biology of *P. mariae* other than the collection data.

MODIFIED VERSION OF KEY IN BOLTON (2000)

In Bolton's (2000) key, *Pyramica mariae* keys out to *P. denticulata*. The key can be modified as below to include *P. mariae*. Numbering of couplets follows Bolton (2000).

23.	In lateral view, postpetiole lacking ventral spongiform lobe; sometimes a minute vestige visible; mesonotum with a pair of erect hairs	**23b**
–	In lateral view, postpetiole with reduced ventral spongiform lobe but distinct; if lobe very shallow then mesonotum with pair of straggly (i.e., laid out in an irregular, untidy way) flagellate hairs	couplet 25 in Bolton (2000)
23b.	Mandibles long, MI 72–85. Dorsum of pronotum lacking pair of stiff erect hairs	**23c**
–	Mandibles short, MI 58–65. Dorsum of pronotum with pair of stiff erect hairs	***eggersi***
23c.	Inner margin of mandibles with 5–10 preapical denticles of similar size. Metapleuron densely reticulate. Peduncle of petiole short, PI 38–42	***denticulata***
–	Inner margin of mandibles with 3–4 preapical denticles, two distinctly larger than rest. Metapleuron smooth and shining. Peduncle of petiole elongate, PI 48–49	***mariae*** **new species**

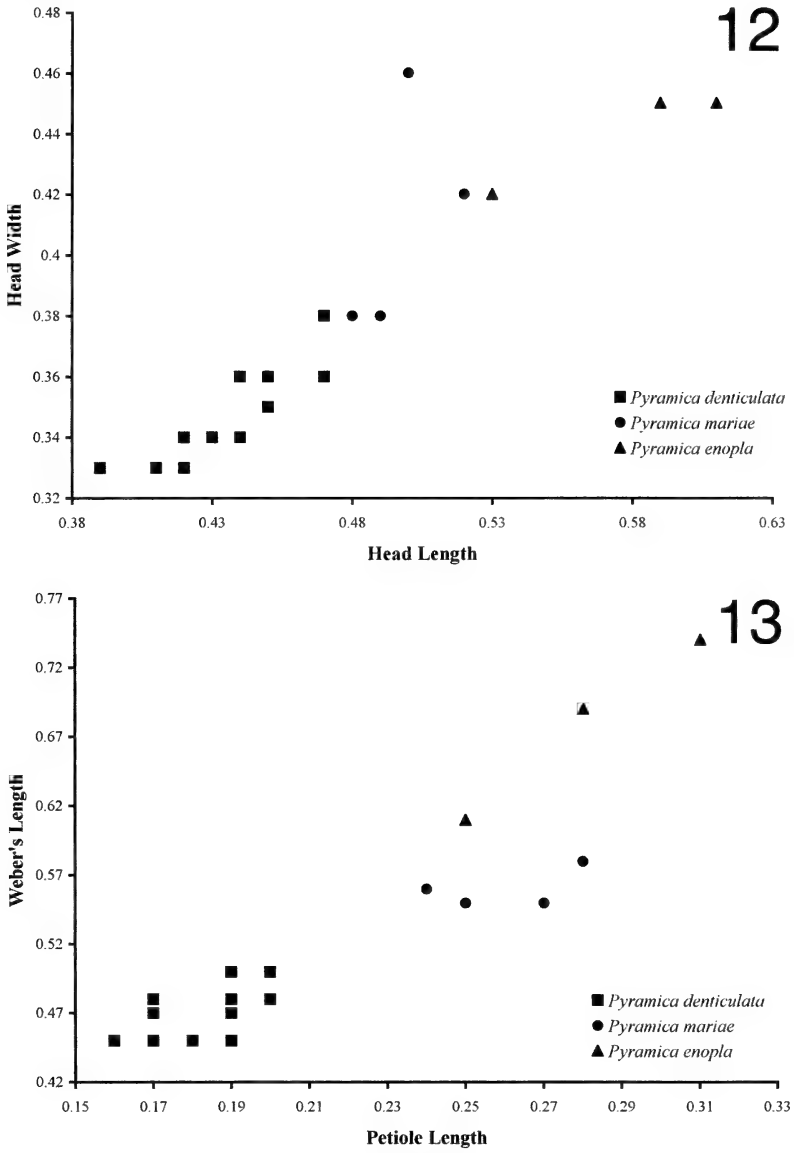


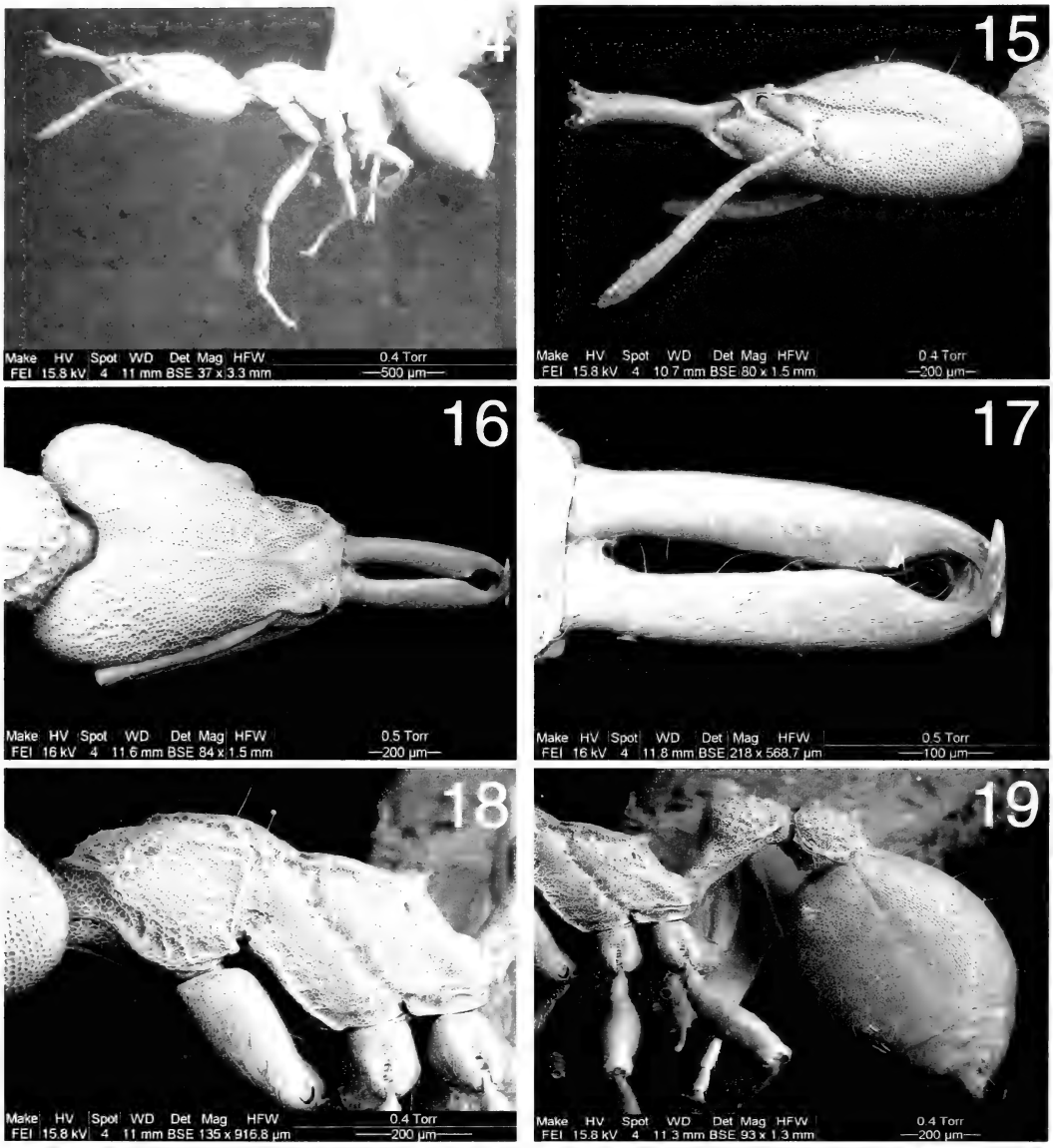
Fig. 12. Relationship between head width and head length among *Pyramica denticulata*, *P. mariae*, and *P. enopla*. Measurements in millimeters.

Fig. 13. Relationship between petiole length and Weber's length among *Pyramica denticulata*, *P. mariae*, and *P. enopla*. Measurements in millimeters.

Strumigenys royi Sosa-Calvo, Schultz, and LaPolla, **n. sp.** (Figs 14–25)

Material examined.—*Holotype*: worker, labeled "GUYANA: Kanuku Mts.: Nappi Creek. camp; 128 m; 59°33.963′ W, 3°21.018′ N; 24.x.2002; *J.S. LaPolla*; forest; on tree trunk. (JSL021024-08)" USNM ENT No. 00537288. (UGBC). *Paratype*: 1 worker, same locality as in holotype. USNM ENT No. 00537289. (USNM).

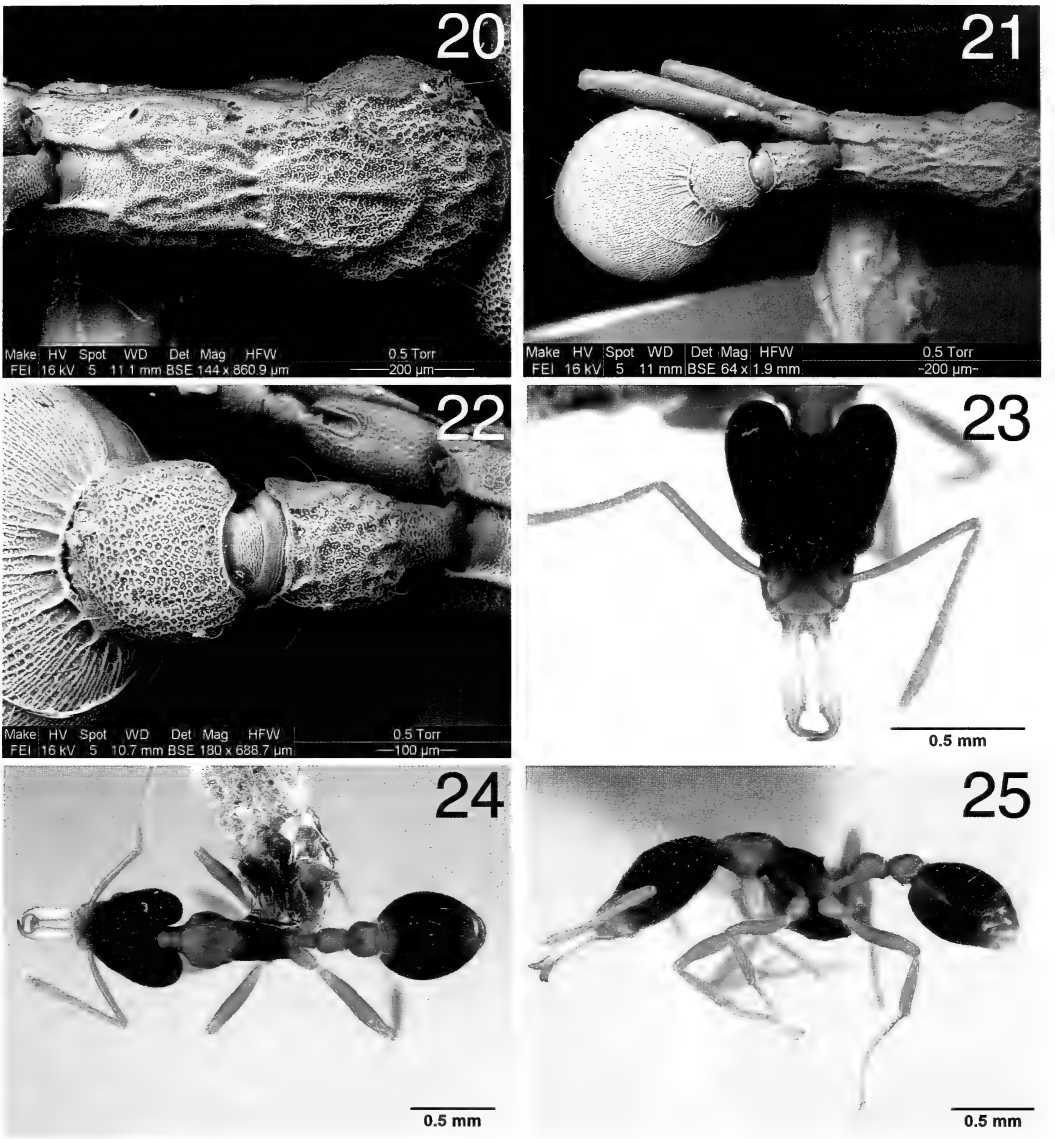
Diagnosis (worker).—Leading edge of antennal scape with all hairs curving to apex, lacking hairs that curve to the base of segment; mandibles long and linear with a small, but conspicuous preapical tooth



Figs 14–22. Scanning electron micrographs of the holotype worker of *Strumigenys royi*, new species. 14, Lateral view. 15, Lateral view of head. 16, Full-face view. 17, Closed mandibles. 18, Lateral view of mesosoma. 19, Lateral view of petiole, postpetiole, and gaster. 20, Dorsal view of mesosoma. 21, Dorsal view of mesosoma, waist segments, and first gastral tergite. 22, Dorsal view of waist segments (petiole and postpetiole).

close to the apicodorsal teeth; propodeum with small denticles; segments of the waist with ventral margin lacking spongiform tissue of any kind; first gastral sternite lacking spongiform pad; body strongly reticulate and with area within each reticulation verrucose; coloration distinctive: mandibles mostly whitish, antennae and legs yellowish, mesosoma mostly ferruginous, waist segments light brown, and head and gaster mostly dark brown or black.

Description (worker).—*Head:* in full-face view, mandibles thick throughout most of their length and abruptly narrowing just before apex by sudden oblique divergence of inner margin, a minute but conspicuous preapical denticle arising on this oblique



Figs 23–25. Automontage images of a paratype of *Strumigenys royi*, new species. 23, Full-face view. 24, Dorsal view. 25, Lateral view.

section; mandibles with intercalary denticle that arises from dorsal base of apicoventral tooth; in full-face view, anterior margin of clypeus transverse to very slightly concave and with at least 6 narrowly spatulate elongate hairs; dorsum of clypeus finely reticulate-punctate and with short, appressed, simple hairs; ocular carina short, ending at eye level; leading edge of scapes with all hairs curved or inclined toward apex of scape; funicular segments II and III long [holotype: 2^{nd} = 0.073, 3^{rd} = 0.092; paratype: 2^{nd} = 0.079, 3^{rd} = 0.092], their lengths, when combined, almost as long as funicular segment IV; occipital margin deeply emarginate, forming prominent rounded cephalic lobes; dorsum of head with two pairs of erect fine hairs: one pair close to margin of occipital concavity and another close to highest point of vertex, clearly differing from appressed simple ground-pilosity

(*sensu* Bolton 2000:998: referring to "the short pilosity often present on cephalic dorsum, dorsolateral margins of head, promesonotum and its margins. These hairs could be simple or spatulate to orbicular, usually decumbent to appressed and may rarely be elevated"); eye with 13–14 ommatidia on longest row; apicoscrobal hair elongate and simple (this hair lacking on holotype due to damage); dorsum of head strongly reticulate and with areas within each reticulation verrucose (i.e., containing wart-like protuberances). *Mesosoma:* humeral hair elongate and simple, similar in shape to apicoscrobal hair but longer; pilosity on dorsum of pronotum consisting of decumbent hairs; dorsum of pronotum with irregular rugae and markedly reticulate with areas within reticulation verrucose; mesonotum, in lateral view, raised and separated from pronotum by transverse or rounded carina; mesonotum, in lateral view, with pair of erect elongate simple hairs and pair of short erect simple hairs; dorsum of mesonotum with conspicuous longitudinal rugae and strongly reticulate with area within reticulation verrucose; mesopleuron and metapleuron separated by deep scrobiculate constriction that extends to dorsum of alitrunk to form metanotal groove; in lateral view, constriction extends backward from propodeum throughout base of propodeal denticles, before beginning of propodeal declivity; propodeum with small denticles; declivity of propodeum with thin reticulate carina; mesopleuron mostly reticulate and with area within reticulation verrucose; proximal to border with metapleuron (and especially upper portion of katepisternum), reticulations fading leaving only verrucose sculpture visible; anepisternum mostly verrucose; metapleuron reticulate and with areas within reticulation verrucose. *Metasoma:* waist segments lacking ventral spongiform tissue; petiole with anterior acute process; node of petiole, in lateral view, rounded; pilosity on petiole, in frontodorsal view, consisting of anterior pair of elongate, simple suberect hairs and posterior transverse row of four elongate, simple suberect hairs (hair on each side of petiole and pair on posterior dorsum of petiole); posterior margin of petiolar node with low spongiform crest; disc of petiole, in dorsal view, rugose-reticulate and with area within reticulation verrucose. Postpetiole, in lateral view, globose and in fronto-dorsal view, with two transverse rows of four elongate, simple suberect hairs, located on anterior and posterior portions of postpetiole. (Distribution of these hairs similar to that of posterior row on petiole.) Anterior margin of postpetiole, in dorsal view, concave; postpetiole wider than long [length = 0.205, width = 0.238]; posterior margin of postpetiolar disc with small spongiform crest; disc of postpetiole reticulate with areas within reticulations verrucose. First gastral tergite finely reticulate-substrigulate with some verrucose sculpture confined to basigastral area; dorsum of first gastral tergite with widely spaced elongate erect simple hairs. Similar hairs on gastral sternite but more abundant; first gastral sternite reticulate, differing from sculpture on tergite; basigastral costulae longitudinal, spaced, and very short but conspicuous. *Color*: anterior portion of head yellowish and gradually increasing in color to ferruginous by level of eyes and dark brown on rest of head. Mandibles mostly whitish with tips ferruginous to dark brown. Mesosoma ferrugineous; petiole and postpetiole light brown; legs and antennae yellowish, slightly lighter in color than waist segments; first gastral tergite black or dark brown, second and third gastral tergites ferrugineous, fourth gastral tergite yellowish; first to third gastral sternites ferrugineous, fourth gastral sternite yellowish.

Measurements: holotype (and paratype): EL = 0.16 (0.14), GL = 0.79 (0.78), HL = 0.86, HW = 0.65, ML = 0.49 (0.52), PL = 0.40 (0.37), PPL = 0.19 (0.20), PW = 0.36 (0.35), SL = 0.57 (0.59), TL = 3.53, WL = 0.79 (0.80). Indexes: CI = 75, MI = 57 (60), PI = 51 (46), SI = 88 (90). (n = 2)

Gyne and male.—Unknown.

Etymology.—This species is named in honor of Roy Snelling to acknowledge his numerous contributions to the taxonomy of ants, bees, and wasps. He will live on through the solid foundation he provided for ant taxonomy and through the thousands of specimens that he left behind for myrmecologists to ponder over for many years to come.

Biology.—*Strumigenys royi* was collected from an upright, living tree trunk in a small dirt tunnel (likely made by termites) that ran up the side of the tree.

Comments.—This large species is easily distinguished from any other species in the genus *Strumigenys* (*sensu* Bolton 2000) by lacking the spongiform tissue on the ventral margin of the waist segments (petiole and postpetiole) and lacking a spongiform pad on the first gastral sternite, by having the apical fork of the mandibles with an intercalary denticle that arises from the dorsal base of apicoventral tooth, by having antennal funicular segments II and III, when combined, almost as long as funicular segment IV (shared with *S. fairchildi* Brown), by having a minute denticle close to the apicodorsal tooth (similar in *S. lanuginosa* Wheeler), and by having marked body sculpture. Due to this combination of characters it is difficult to place this species in any of the species groups given by Bolton (2000).

Strumigenys royi differs from *S. idiogenes* Bolton, to which it keys out in Bolton's (2000) key, as the latter possesses: a larger and conspicuous lobe on ventral margin of postpetiole, a narrow spongiform pad on the base of first gastral sternite, asymmetrical dentition on the mandibles, and a pair of narrow spines on the propodeum.

MODIFIED VERSION OF KEY IN BOLTON (2000)

Strumigenys royi will key out to *S. idiogenes* in Bolton's (2000) "key to Neotropical-Nearctic *Strumigenys* species." The key for the species of *Strumigenys* can be modified as below to include *S. royi*. Numbering of couplets follows Bolton (2000).

4. Mandibles without intercalary teeth or denticles that arise between apicodorsal and apicoventral teeth of apical fork, nor arise from dorsal base of apicoventral tooth ..... couplet 5 of Bolton (2000)
– Mandible with 1 or 2 intercalary teeth or denticles that arise between apicodorsal and apicoventral teeth of apical fork, or arise from dorsal base of apicoventral tooth ..... couplet 10 of Bolton (2000)
10. Mandibles without, or with only one, preapical tooth or denticle couplet 11 of Bolton (2000)
– Mandible with 2 preapical teeth or denticles ..... couplet 15 of Bolton (2000)
11. Preapical dentition consisting of single tooth on one or both mandibles; preapical tooth conspicuously dentiform and located close to apicodorsal tooth **12**
– Preapical dentition absent from both mandibles or single minute denticle present; if the latter denticle located close to midlength, not near apicodorsal tooth **14**
12. First gastral tergite very densely clothed with long fine flagellate hairs. Dorsolateral margin of head with 2 freely laterally projecting long flagellate hairs, one at level of eye, other apicoscrobal ..... ***lanuginosa***
– First gastral tergite with stout curved hairs that are remiform or apically spatulate or simple erect standing hairs. Dorsolateral margin of head without projecting flagellate hairs or with single hair, in apicoscrobal position **13**
13. Scape strongly dorsoventrally flattened and very broad; in full-face view maximum width of scape greater than maximum width of mandible. First gastral tergite

unsculptured. Pronotal humeral hairs stiff and stout. With head in profile highest point of vertex without erect hairs ..... ***platyscapa***

– Scape subcylindrical; in full-face view maximum width of scape less than maximum width of mandible. First gastral tergite with sculpture present other than basigastral costulae. Pronotal humeral hairs elongate or flagellate. With head in profile highest point of vertex with pair of erect hairs **13b**

13b. Ventral surface of postpetiole with large and distinct spongiform lobe. Propodeal spines long. Mandibles with asymmetrical preapical dentition (left mandible without trace of preapical dentition, right mandible with small slender preapical tooth located close to apicodorsal tooth and slightly smaller than intercalary tooth) ..... ***idiogenes***

– Ventral surface of postpetiole without spongiform lobe or crest. Propodeal spines short. Mandibles with symmetrical preapical dentition (both mandibles with small preapical tooth located close to apocidorsal tooth) ..... ***royi* new species**

Strumigenys acarai Sosa-Calvo, Schultz, and LaPolla, **n. sp.**
(Figs 26–39)

Material examined.—Holotype: worker, labeled "GUYANA: Upper Takutu-Upper Essequibo, Acarai Mountains, New Romeo Camp, 1069 m., 58°57.828'W, 1°19.938'N; 14.x.2006; *T.R. Schultz, J. Sosa-Calvo, C.J. Marshall, R. Williams*; 1° upland forest; leaf-litter sample. (JSC061014-01)" USNM ENT No. 00537294. (UGBC). *Paratypes*: 9 workers, labeled "GUYANA: Upper Takutu-Upper Essequibo, Acarai Mountains, New Romeo Camp, 1069 m., 58°57.828'W, 1°19.938'N; 14.x.2006; *T.R. Schultz, J. Sosa-Calvo, C.J. Marshall, R. Williams*; 1° upland forest; leaf-litter sample. (JSC061014-02, JSC061014-03). USNM ENT No. 00537295–00537303. (BMNH (1), MCZC (1), and USNM (6))

Diagnosis (worker).—Small (TL 1.62–1.79); eyes vestigial, consisting of one or two ommatidia; masticatory margin of mandibles with an inconspicuous tooth, visible under high magnifications; leading edge of antennal scapes with some hairs that curve toward the base of scape; dorsum of promesonotum rugulose and with a conspicuous median longitudinal ruga that extends for entire length of promesonotum; petiole lacking a ventral process or spongiform tissue of any kind.

Description (worker).—*Head:* mandibles elongate with outer margin convex; inner margin of mandibles with minute inconspicuous preapical denticle in mandible's midlength, visible under high magnification; apical fork of mandibles lacking intercalary teeth; anterior margin of clypeus slightly concave or transverse; dorsum of antennal scape imbricate; anterior edge of antennal scape with at least 3 narrowly spatulate hairs curving toward base, some hairs on scape multi-furcate (Fig. 30); hairs on upper margin of scrobe narrowly spatulate and curving anteriorly; apicoscrobal hair flagellate; dorsum of head strongly areolate; ocular carina failing to reach level of eyes; eyes minute, with only 1 (one paratype, most of them with two) or 2 ommatidia; dorsum of head with fine subdecumbent hairs, some of which curve medially and with pair of erect hairs present on cephalic margin (very difficult to see). *Mesosoma:* humeral hair flagellate; anterior portion of pronotum, in dorsal view, strongly reticulate; dorsum of promesonotum rugulose and with conspicuous median longitudinal ruga or carina that extends for entire length of promesonotum; areas between rugae smooth and shining; dorsum of promesonotum with subdecumbent hairs that curve medially, most hairs directed backwards; posterior half of promesonotum areolate; mesonotum with pair of flagellate simple hairs; dorsum of propodeum and declivity of

propodeum areolate; mesopleuron and metapleuron mostly smooth and shining; mesopleuron and metapleuron divided by strip of aerolate sculpture that originates at ventral margin of mesopleuron and metapleuron and extends dorsally in direction of metanotal groove, this strip incomplete, fading before it connects with metanotal groove; propodeal spines long; declivity of propodeum with a thin carina. *Metasoma:* dorsum and sides of petiole strongly areolate; ventral margin lacking spongiform tissue or process of any kind; node of petiole, in lateral view, with two transverse rows each consisting of four long subdecumbent and simple hairs and composed of two hairs medially and two hairs distally (Fig. 35); posterior margin of petiolar node with small spongiform crest, best seen in fronto-dorsal view; in dorsal view, lateral projections of crest conspicuous and triangular; postpetiole with ventral and lateral spongiform lobes well developed; dorsum of postpetiole with longitudinal rugae, areas between rugae smooth and shining; base of first gastral sternite bearing conspicuous pad of spongiform tissue; basigastral costulae longitudinal and sharply defined, longer than maximum length of disc of postpetiole; dorsum of first gastral tergite with numerous long flagellate hairs; entire tergite posterior to basigastral costulae smooth and shining.

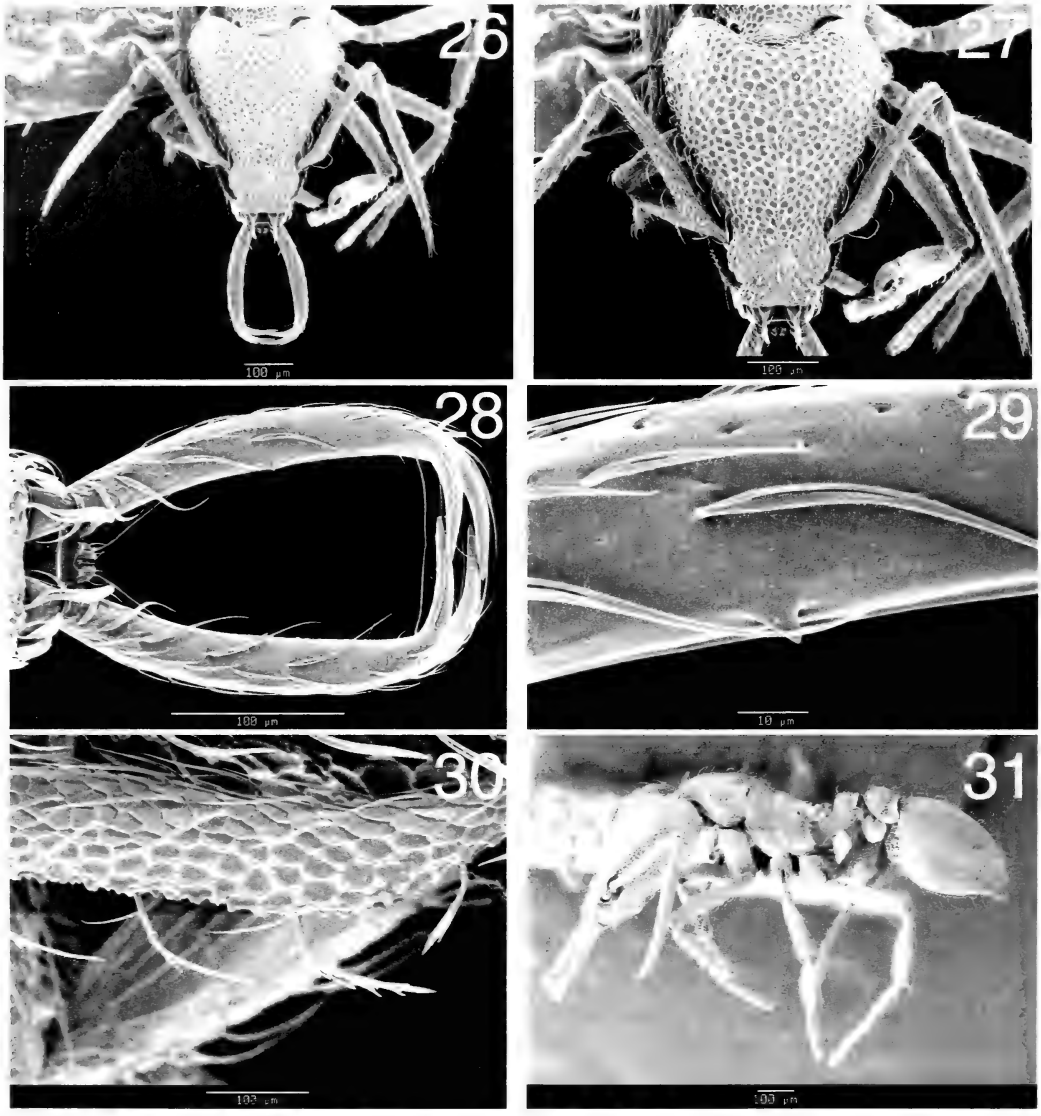
Measurements: holotype (and paratypes): GL = 0.40 (0.35–0.41), HL = 0.42 (0.39–0.41), HW = 0.31 (0.29–0.33), ML = 0.25 (0.24–0.25), PL = 0.20 (0.15–0.19), PPL = 0.09 (0.08–0.11), PW = 0.18 (0.17–0.19), SL = 0.29 (0.27–0.30), TL = 1.77 (1.62–1.79), WL = 0.41 (0.38–0.42). Indexes: CI = 73 (74–81), MI = 59 (58–64), PI = 48 (38–51), SI = 94 (88–96). (n = 10)

Gyne and male.—Unknown.

Etymology.—The name of this species refers to the Acarai Mountains, in the Upper Takutu-Upper Essequibo region of southern Guyana, where specimens of this species were collected.

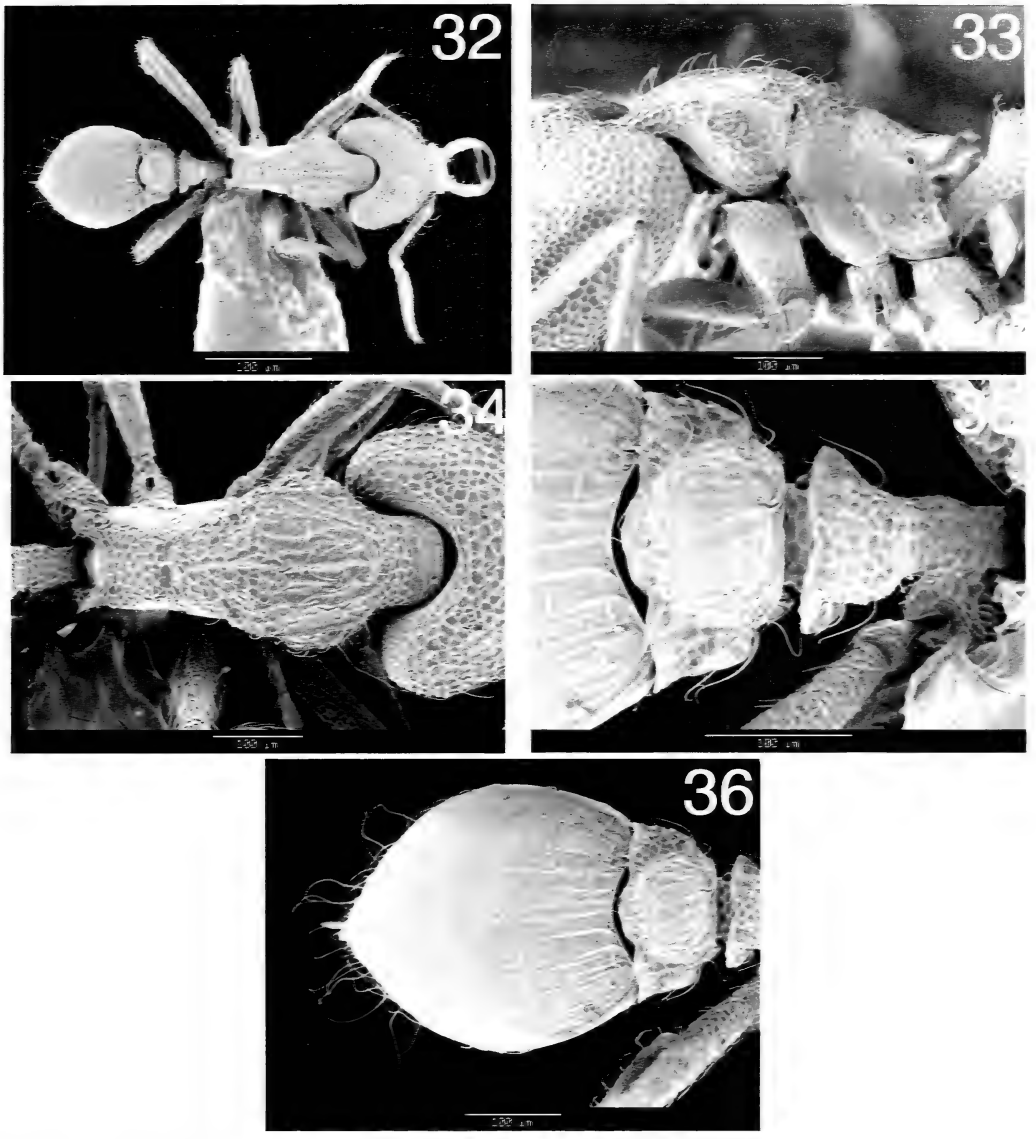
Comments.—*Strumigenys acarai* seems to belong to the *S. silvestrii* species group (*sensu* Bolton 2000), sharing with some members of that group: (i) the ventral margin of petiole lacking spongiform tissue; (ii) the small worker size (HL 0.39–0.43, HW 0.29–0.33, TL 1.62–1.79, WL 0.38–0.42 in *S. acarai*, HL 0.36–0.52, HW 0.28–0.44, TL 1.5–2.2, WL 0.36–0.56 in the *S. silvestrii* group); (iii) the apical fork of mandibles lacking intercalary denticles; (iv) the leading edge of the antennal scapes having two or more hairs that are curved or inclined toward the base of the scape; (v) the eyes minute, usually with only 1–3 ommatidia in total; (vi) the preocular carina short and ending before the level of the eye; (vii) the propodeal spines usually present; and (viii) the head and alitrunk usually sculptured but the mesopleuron and metapleuron entirely smooth and shining.

Strumigenys acarai shares with *S. carinithorax* Borgmeier, in addition to the character states mentioned above, the presence of a median fine longitudinal carina on the mesonotum. *Strumigenys acarai* differs from *S. carinithorax*, however, by having the ground-pilosity of the head, from above level of eye to close to occipital margin, very narrowly spatulate (almost simple) rather than spatulate as in *S. carinithorax*; the mandibles with a pair of minute inconspicuous preapical denticles proximal to the midlength of the mandibles rather than with a pair of spiniform preapical teeth as found in *S. carinithorax*, which are located in the distal third, and with a minute pair of denticles that may be difficult to see that are just proximal to the midlength of the mandibles (Bolton 2000); the leading edge of the antennal scapes with some multifurcated narrowly spatulate hairs rather than spoon-shaped hairs of *S. carinithorax*. *Strumigenys acarai* shares with *S. waiwai* (described here) the presence of multifurcated hairs. In the former species, however, these hairs seem to be restricted to the leading edge of the



Figs 26–36. Scanning electron micrographs of a paratype worker of *Strumigenys acarai*, new species. 26, Head and mandibles in full-face view. 27, Cephalic capsule in full-face view. 28, Mandibles in dorsal view. 29, Tooth on inner margin of mandibles in dorsal view. 30, antennal scapes and hairs on leading edge of scape in full-face view. 31, Lateral view. 32, Dorsal view. 33, Lateral view of mesosoma. 34, Dorsal view of mesosoma. 35, Dorsal view of waist segments (petiole and postpetiole). 36, Dorsal view of postpetiole and first gastral tergite.

antennal scapes, whereas in the latter these hairs are present on the dorsum of the head. The two species described here (*S. acarai* and *S. waiwai*) also differ from each other in mandibular dentition (inconspicuous pair of teeth at midlength of mandibles in *S. acarai*, and having a pair of spiniform teeth and a minute, but conspicuous pair of teeth at midlength of mandibles in *S. waiwai*), in the sculpture of the dorsum of the promesonotum (rugulose and with a conspicuous median longitudinal ruga in *S. acarai*, and strongly aerolate in *S. waiwai*), and in the length of the costulae on first gastral tergite (longer than the maximum length of the disc of postpetiole in *S. acarai*, and barely as long as the disc of postpetiole in *S. waiwai*).

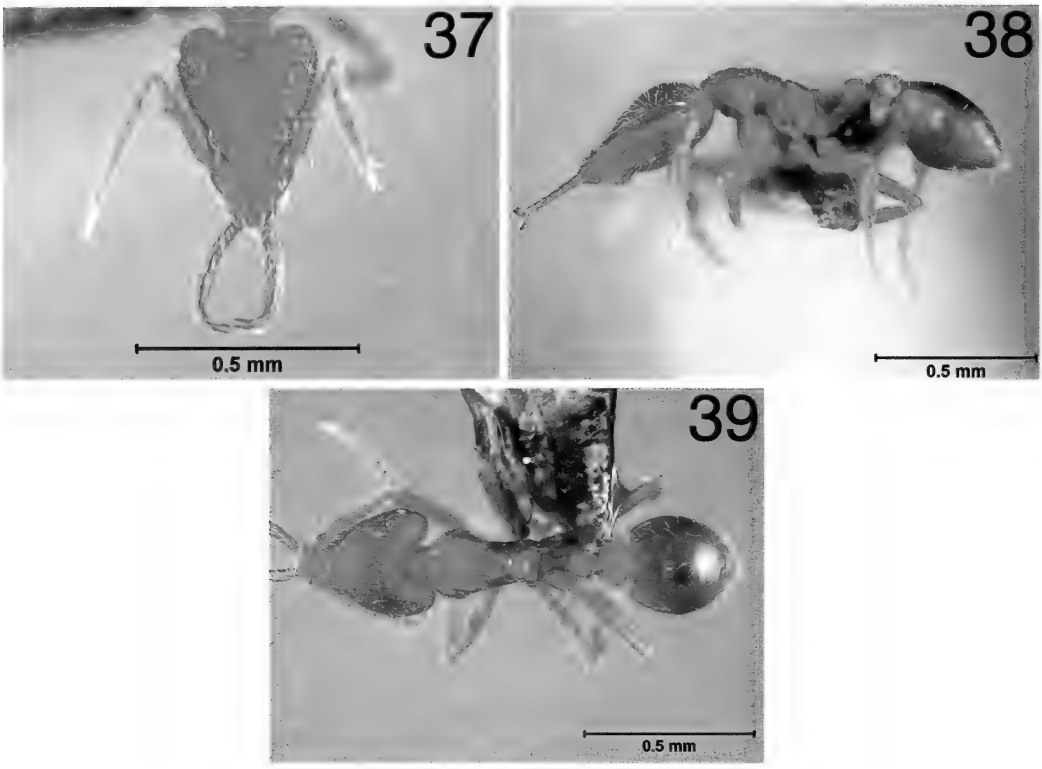


Figs 26–36. Continued.

MODIFIED VERSION OF KEY IN BOLTON (2000)

In Bolton's (2000) key, *Strumigenys acarai* will not key out to any of the known species. The key for the species of *Strumigenys* of the Neotropics can be modified as below to include *S. acarai*. Numbering of couplets follows Bolton (2000).

48. Cephalic dorsum with two pairs of short erect hairs that differ from other cephalic ground-pilosity, one pair close to occipital margin, other close to highest point of vertex. Ventral surface of petiole with curtain or fringe of spongiform tissue, or at least with spongiform lobes linked by carina . . . . . couplet 49 of Bolton (2000)



Figs 37–39. Automontage images of the holotype worker of *Strumigenys acarai*, new species. 37, Full-face view. 38, Lateral view. 39, Dorsal view.

– Cephalic dorsum without or with one pair of short erect hairs that differs from other cephalic ground-pilosity, when one present it is close to occipital margin. Ventral surface of petiole without spongiform tissue, sometimes with rounded or angular anteroventral cuticular process . . . . . **52a** (different to couplet 52 in Bolton 2000)

52a. Mandible with minute inconspicuous denticle close to midlength . . . . ***acarai* new species**

– Mandible with 1 or 2 very conspicuous spiniform preapical teeth, distal one in apical third, proximal one close to midlength . . . . . couplet 52 in Bolton (2000)

Strumigenys waiwai Sosa-Calvo, Schultz, and LaPolla, **n. sp.** (Figs 40–47)

Material examined.—Holotype: worker, labeled "GUYANA: Upper Takutu-Upper Essequibo, Acarai Mountains, camp edge Kamoa River, 394 m., 58°49.929′ W, 1°32.786′ N; 22.x.2006; *J. Sosa-Calvo, T.R. Schultz*; 1° forest; leaf-litter sample. (TRS 061022-LS04)" USNM ENT No. 00537291. (UGBC). *Paratypes*: 2 workers, same locality as in holotype. USNM ENT No. 00537290, 00537292; 1 worker, labeled "GUYANA: Upper Takutu-Upper Essequibo, Acarai Mountains, camp edge Kamoa River, 530 m., 58°50.299′ W, 1°33.046′ N; 24.x.2006; *J. Sosa-Calvo, T.R. Schultz, C.J. Marshall, R. Williams*; 1° forest; leaf-litter sample. (JSC 061024-LS10)" USNM ENT No. 00537293. (USNM).

Diagnosis (worker).—Small (TL 1.35–1.45); cephalic margin with multi-furcate hairs; leading edge of antennal scapes at least with one hair that curves towards base of scape; eyes small, consisting of two

or three ommatidia; inner margin of mandibles with a pair of spiniform teeth and a minute but conspicuous pair of teeth at midlength of mandibles; ventral margin of petiole with angular ventral process. In some workers (paratypes) ventral process of petiole very reduced.

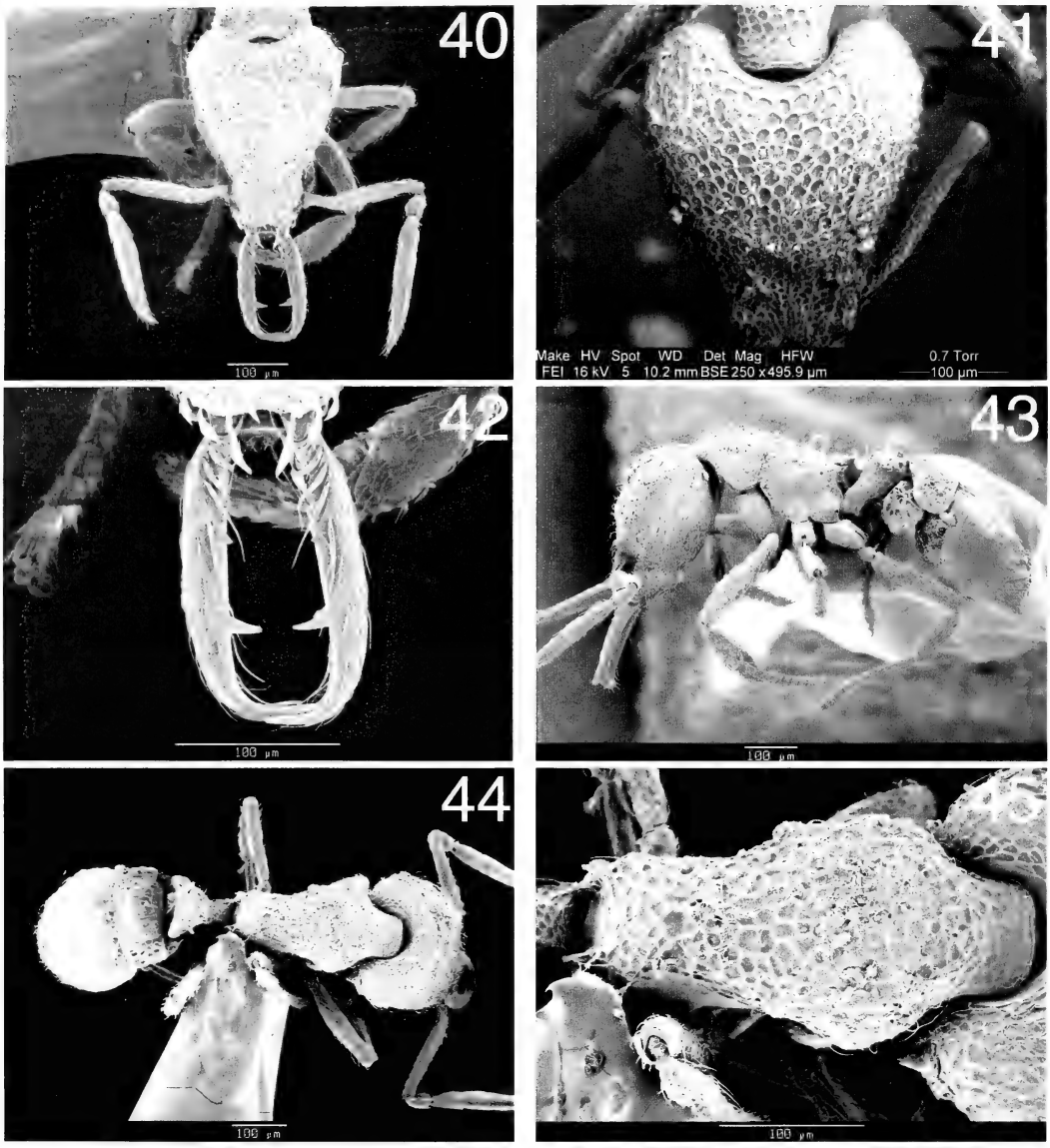
Description (worker).—*Head:* leading edge of antennal scapes with at least one hair curving toward base of antennal scape; hairs on leading edge of antennal scapes narrowly spatulate or simple; inner margin of mandibles with pair of preapical spiniform teeth close to apicodorsal tooth and minute but conspicuous pair of teeth at midlength of mandibles; anterior margin of clypeus slightly concave (Figs 40, 42); dorsum of clypeus finely reticulate; dorsum of head markedly areolate and with multi-furcate hairs on posterior occipital portion (Figs 40–41, 43); upper margin of scrobes with row of simple hairs that curve anteriorly and with two flagellate hairs, one of which is in apicoscrobal position; eyes very reduced, with 2 or 3 ommatidia; ocular carina weakly developed, short and not reaching level of eyes; cephalic dorsum, in profile, with 2 pairs of inconspicuous erect simple hairs, very difficult to see and perhaps fragile and easily lost but differing from bifurcating pilosity that surrounds them. *Mesosoma:* dorsum of promesonotum, propodeum, and declivity of propodeum strongly areolate; dorsum of pronotum with elongate pair of hairs in addition to those at humeri; humeral hair flagellate; promesonotal spiracle in dorsal view projecting laterally, giving pronotum wider appearance and mesonotum and propodeum narrower appearance; mesonotum with pair of elongate hairs; sides of pronotum and anepisternum strongly areolate; mesopleuron and metapleuron mostly smooth and shining; dorsum of promesonotum and propodeum with simple subdecumbent hairs; propodeal spines minute and acute, subtended by broad lamella on declivity. *Metasoma:* dorsum of peduncle, disc, and sides of petiole strongly areolate; in lateral view, petiole with long ventral process. In one worker (paratype) ventral process reduced to small tooth (Fig. 43); petiole, in lateral view, subquadrate; sides of petiole, in dorsal view, with conspicuous triangular crest; postpetiole, in lateral view, with large ventral spongiform lobes; disc of postpetiole with some longitudinal rugae; areas between rugae smooth and shining; dorsum of postpetiole with decumbent hairs; first gastral sternite with pad of spongiform tissue; first gastral tergite smooth and shining, with some conspicuous longitudinal basigastral costulae, barely as long as disc of postpetiole; first gastral tergite mostly with subdecumbent and decumbent hairs and some erect hairs (lacking in some paratype specimens. It is probable that these hairs are very fragile and lost easily).

Measurements: holotype (and paratypes): GL = 0.31 (0.28–0.31), HL = 0.33 (0.31–0.34), HW = 0.26 (0.25–0.26), ML = 0.18 (0.18–0.19), PL = 0.17, PPL = 0.08 (0.08–0.09), PW = 0.16 (0.14–0.16), SL = 0.21 (0.19–0.21), TL = 1.44 (1.35–1.45), WL = 0.36 (0.32–0.36). Indexes: CI = 79 (76–80), MI = 55 (53–58), PI = 48 (47–51), SI = 81 (77–82). (n = 4)

Gyne and male.—Unknown

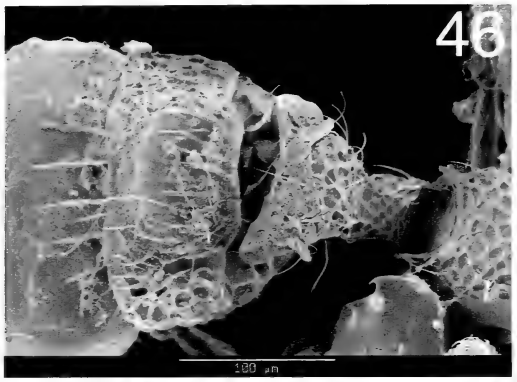
Etymology.—This species is named after the Wai-Wai indigenous people, who depend on the area where we collected this species for their sustenance. Without their guidance, support, and permission to conduct research on their land, this work would not have been possible.

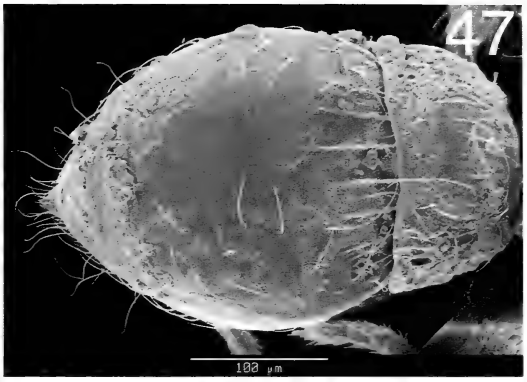
Comments.—*Strumigenys waiwai* is most similar to members of the Neotropical *silvestrii*-group. *Strumigenys waiwai* shares with most of the 18 known species in this group the following characters: (i) the small size (HL 0.31–0.34, HW 0.25–0.26, TL 1.35–1.45, WL 0.32–0.36. In members of the *silvestrii*-group HL 0.36–0.52, HW 0.28–0.44, TL 1.5–2.2, WL 0.36–0.56); (ii) the absence of intercalary tooth between the apicodorsal and apicoventral teeth in the apical fork of the mandibles (this character



Figs 40–47. Scanning electron micrograph of a paratype worker of *Strumigenys waiwai*, new species. 40, Head and mandibles in full-face view. 41, Cephalic capsule in full-face view. 42, Mandibles in dorsal view. 43, Lateral view. 44, Dorsal view. 45, Dorsal view of mesosoma. 46, Waist segments in dorsal view. 47, Postpetiole and first gastral tergite in dorsal view.

state is shared with all the species in the group, except for *S. xochipili* Bolton from Mexico, which possesses a single intercalary tooth); (iii) the presence, on the inner margin of mandibles, of a spiniform pair of preapical teeth close to the apicodorsal tooth of the apical fork and, in addition, a minute pair of denticles on the midlength of the mandibles that may be difficult to see; (iv) the antennal scapes short to moderate (SI 76–80. In members of the *S. silvestrii* species group the SI 62–91), and with some hairs on the leading edge of the antennal scape that are curved toward the base of the scape; (v) the eyes very small, commonly formed by 1–3 ommatidia in total (some members of the *S. silvestrii* species group with 6 or more ommatidia);





Figs 40–47. Continued.

(vi) the preocular carina short or weakly developed, ending before level of the eye; (vii) the propodeum, in profile, usually with a triangular pair of teeth that are subtended by a lamella or carina that extends down the declivity; and (viii) ventral surface of petiole lacking spongiform tissue instead with a small, but conspicuous crest or ventral process (members of the *silvestrii*-group usually lack spongiform tissue on ventral margin of petiole except for the species *S. nastata* Bolton, *S. perdita* Bolton, and *S. calamita* Bolton).

Variations in the presence of standing erect hairs on the cephalic dorsum were observed in the specimens studied (holotype and paratypes). In the material examined, some workers of *S. waiwai* have the two pairs of erect simple hairs on the dorsum of head that differ from the cephalic ground-pilosity, of which one pair is located close to occipital margin and the other is located close to the highest point of vertex. Among the variations observed in other specimens are: the two pairs of standing hairs are present, but curving at the tips, or only one pair of hairs is visible, or the hairs are difficult to see, or the hairs are missing. Apparently these hairs are very fragile and can be easily lost; therefore specimens may appear to have no hairs. Within the *silvestrii*-group, only individuals in the species *S. calamita*, *S. nastata*, *S. perdita*, and *S. timicala* Bolton, all endemic to Central America, share with individuals of *S. waiwai* the presence of two pairs of erect hairs on the cephalic dorsum, but these species differ from *S. waiwai* by having a fringe or curtain of spongiform tissue on the ventral margin of the petiole, whereas *S. waiwai* has an angular crest or small ventral process. In addition, *S. waiwai* differs from: *S. nastata* by having the antennal scape without a projecting narrow cuticular lamella that arises proximal to the subbasal bend; *S. timicala* by having the preapical tooth of the mandible separated from the apicodorsal tooth by a distance twice its length, rather than having the preapical tooth very close to the apicodorsal tooth; *S. calamita* and *S. perdita* by having the first gastral tergite generally with subdecumbent or decumbent simple hairs (in some specimens it is possible to see, in addition, a few erect simple hairs) rather than entirely short stout hairs that are remiform to claviform (in *S. calamita*) or simple erect and stiff (in *perdita*); and from all four species and any other species in the *S. silvestrii*-group by: (i) having the dorsolateral margin of the head with two freely laterally projecting elongate or short flagellate hairs, one of which is located at the level of the vestigial eye and the other the apicoscrobal hair. This character state is also shared with *S. lanuginosa* but these hairs are shorter in *S. waiwai* than in *S. lanuginosa*; (ii) having hairs on the upper margins of the antennal scrobe simple and curving anteriorly rather than spoon-

shaped, spatulate, or narrowly spatulate and curving anteriorly (except for *perparva* in which case these hairs are posteriorly curved); and (iii) the cephalic ground-pilosity composed of short erect or subdecumbent multifurcated hairs rather than spoon-shaped, spatulate, or narrowly spatulate hairs.

MODIFIED VERSION OF KEY IN BOLTON (2000)

In Bolton's (2000) key, *Strumigenys waiwai* keys out to *S. perdita*. The key for the species of *Strumigenys* of the Neotropics can be modified as below to properly include *S. waiwai*. Numbering of couplets follows Bolton (2000).

47. In full-face view upper scrobe margin with a row of 4–5 broadly spatulate to spoon-shaped hairs that are curved posteriorly ..... ***perparva***
– In full-face view upper scrobe margin with row of simple or spatulate to spoon-shaped hairs that are all curved anteriorly ..... couplet 48 in Bolton (2000)
48. Cephalic dorsum with two pairs of short erect hairs, one pair close to occipital margin, the other close to highest point of vertex. Ventral surface of petiole with curtain or fringe of spongiform tissue, or at least with spongiform lobes linked by carina. If spongiform tissue reduced to angular anteroventral process present, then dorsolateral margin of head with two freely laterally projecting short flagellate hairs, one at level of the vestigial eye, the other the apicoscrobal **49**
– Cephalic dorsum without or with one pair of short erect hairs, when one is present it is close to occipital margin. Ventral surface of petiole without spongiform tissue, sometimes with rounded or angular anteroventral cuticular process. Dorsolateral margin of head without projecting flagellate hairs or with single hair, in apicoscrobal position ..... couplet 52 in Bolton (2000)
49. Distal preapical tooth conspicuous and obviously spiniform, located markedly proximal of the apicodorsal tooth and at about right angle to long axis of the mandible. Distal preapical teeth of opposing mandibles so long that their apices meet or even slightly overlap when mandibles fully closed. Mandibles always with small denticle just proximal of the inner midlength **50**
– Distal preapical tooth small, thorn-like and not obviously spiniform, located very close to the apicodorsal tooth and inclined toward it. Distal preapical teeth of opposing mandibles so short that their apices are widely separated when mandibles fully closed. Mandible usually without trace of denticle proximal to inner midlength but rarely vestigial denticle visible ..... ***timicala***
50. Leading edge of scape at subbasal bend with projecting convex cuticular lamella; lamella originates close to scape base and terminates just distal of the bend. Distal preapical tooth about same distance from proximal preapical denticle as it is from apicodorsal tooth ..... ***nastata***
– Leading edge of the scape at subbasal bend without projecting convex cuticular lamella. Distal preapical tooth closer to apicodorsal tooth than it is to proximal preapical denticle **51a**
51a. Leading edge of antennal scape with spoon-shaped or narrowly spatulate hairs. In full-face view upper scrobe margin with row of spatulate to spoon-shaped hairs. Cephalic ground-pilosity spoon-shaped or spatulate .... couplet 51 of Bolton (2000)
– Leading edge of antennal scape with simple or filiform hairs. In full-face view, upper scrobe margin with a row of simple or filiform hairs. Cephalic ground-pilosity multifurcated ..... ***waiwai* new species**

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LITERATURE CITED

Alonso, L. E., and J. H. Mol eds. 2007, A Rapid Biological Assessment of the Lely and Nassau Plateaus, Suriname (with additional information on the Brownsberg Plateau). *RAP Bulletin of Biological Assessment* 43. Conservation International, VA, USA.

Alonso, L. E., J. McCullough, P. Naskrecki, E. Alexander, and H. E. Wright eds. 2008, A Rapid Biological Assessment of the Konashen Community Owned Conservation Area, Southern Guyana. *RAP Bulletin of Biological Assessment* 51. Conservation International, Arlington, VA, USA.

Azorsa, F. and J. Sosa-Calvo. 2008. Description of a remarkable new species of ant in the genus *Daceton* Perty (Formicidae: Dacetini) from South America. *Zootaxa* 1749: 27–38.

Baroni-Urbani, C. and M. L. de Andrade. 2007. The ant tribe Dacetini: Limits and constituent genera, with descriptions of new species. *Annali del Museo Civico di Storia Naturale Giacomo Doria (Genova)* 99: 1–191.

Bolton, B. 1994. *Identification guide to the ant genera of the World*. Harvard University Press, Cambridge, Massachusetts. 222 pp.

———. 1998. Monophyly of the dacetonine tribe-group and its component tribes. *Bulletin of the Natural History Museum (Entomology Series)* 67: 65–78.

———. 2000. The ant tribe Dacetini, with a revision of the *Strumigenys* species of the Malagasy Region by Brian L. Fisher, and a revision of the Austral epopostrumiform genera by Steven O. Shattuck. *Memoirs of the American Entomological Institute* 65: 1–1028.

———, J. Sosa-Calvo, F. Fernandez, and J. E. Lattke. 2008. New synonyms in neotropical Myrmicine ants (Hymenoptera: Formicidae). *Zootaxa* 1732: 61–64.

Brown, W. L., Jr. and W. W. Kempf. 1969. A revision of the Neotropical dacetine ant genus *Acanthognathus* (Hymenoptera: Formicidae). *Psyche* 76: 87–109.

——— and E. O. Wilson. 1959. The evolution of the dacetine ants. *Quarterly Review of Biology* 34: 278–294.

Dejean, A. 1985a. Etude éco-éthologique de la prédation chez les fourmis du genre *Smithistruma* (Formicidae: Myrmicinae: Dacetini) II. Attraction des proies principales (collemboles). *Insectes Sociaux* 32: 158–172.

———. 1985b. Etude éco-éthologique de la prédation chez les fourmis du genre *Smithistruma* (Formicidae: Myrmicinae: Dacetini) III. La capture des proies chez *S. emarginata*. *Insectes Sociaux* 32: 241–256.

———. 1987(1986). Etude du comportement de prédation dans le genre *Strumigenys*. *Insectes Sociaux* 33: 388–405.

Deyrup, M. 2006. *Pyramica boltoni*, a new species of leaf-litter inhabiting ant from Florida (Hymenoptera: Formicidae: Dacetini). *Florida Entomologist* 89: 1–5.

Dietz, B. H. and C. R. F. Brandão. 1993. Comportamento de caça e dieta de *Acanthognathus rudis* Brown & Kempf, com comentarios sobre a evolucão da predacão em Dacetini (Hymenoptera, Formicidae, Myrmicinae). *Revista Brasileira de Entomologia* 37: 683–692.

Feitosa, R. M. and C. R. F. Brandão. 2008. A taxonomic revision of the Neotropical myrmicine ant genus *Lachnomyrmex* Wheeler (Hymenoptera: Formicidae). *Zootaxa* 1890: 1–49.

Fernandez, F. and S. Sendoya. 2004. List of Neotropical ants (Hymenoptera: Formicidae). *Biota Colombiana* 5: 3–93.

Funk, V. A. and K. S. Richardson. 2002. Systematic data in biodiversity studies: use it or lose it. *Systematic Biology* 51: 303–316.

———, A. Sakai, and K. S. Richardson. 2002. Biodiversity: the interface between systematics and conservation. *Systematic Biology* 51: 235–237.

Gibbs, A. K. and C. N. Barron. 1993. The geology of the Guiana Shield. *Oxford Monographs on Geology and Geophysics* 22: 1–246.

Gronenberg, W. 1996. The trap-jaw mechanism in the dacetine ants *Daceton armigerum* and *Strumigenys* sp. *The Journal of Experimental Biology* 199: 2021–2033.

Harris, R. A. 1979. A Glossary of Surface Sculpturing. *Occasional Papers in Entomology*, No. 28. California State Department of Food and Agriculture, Sacramento, California. 31 pp.

Hölldobler, B. and E. O. Wilson. 1990. *The Ants*. Belknap Press, Cambridge, Massachusetts. 732 pp.

Kantarovich, S., J. Nardi, and A. Suarez. 2006. Exploring the form and function of the "sponge body" gland in the Dacetini. Poster. *Memoirs of the XV meeting of the International Union for the Study of Social Insects (IUSSI)*.

Kempf, W. W. 1972. Catalogo abreviado das formigas da região Neotropical (Hymenoptera: Formicidae). *Studia Entomologica* 15: 3–344.

LaPolla, J. S. 2004. *Acropyga* (Hymenoptera: Formicidae) of the World. *Contributions of the American Entomological Institute* 33: 1–130.

——— and S. P. Cover. 2005. New species of *Pheidole* (Hymenoptera: Formicidae) from Guyana, with a list of species known from the country. *Transactions of the American Entomological Society* 131: 1–11.

——— and J. Sosa-Calvo. 2006. Review of the Ant Genus *Rogeria* (Hymenoptera: Formicidae) in Guyana. *Zootaxa* 1330: 59–68.

———, T. Suman, J. Sosa-Calvo, and T. R. Schultz. 2007. Leaf Litter Diversity in Guyana. *Biodiversity and Conservation* 16: 491–510.

Longino, J. T., J. Coddington, and R. K. Colwell. 2002. The ant fauna of a tropical rain forest: Estimating species richness three different ways. *Ecology* 83: 689–702.

———. 2006. New species and nomenclatural changes for the Costa Rican ant fauna (Hymenoptera: Formicidae). *Myrmecologische Nachrichten* 8: 131–143.

Masuko, K. 1984. Studies on the predatory biology of oriental dacetine ants (Hymenoptera: Formicidae) I. Some Japanese species of *Strumigenys*, *Pentastruma*, and *Epitritus*, and a Malaysian *Labidogenys*, with special reference to hunting tactics in short-mandibulate forms. *Insectes Sociaux* 31: 429–451.

———. 2009. Studies on the predatory biology of Oriental dacetine ants (Hymenoptera: Formicidae) II. Novel prey specialization in *Pyramica benten*. *Journal of Natural History* 43: 825–841.

Sosa-Calvo, J., S. O. Shattuck, and T. R. Schultz. 2006. Dacetine ants of Panama: New records and description of a new species (Hymenoptera: Formicidae: Myrmicinae: Dacetini). *Proceedings of the Entomological Society of Washington* 108: 814–821.

———. 2007. Ants of the leaf litter of two plateaus in Eastern Suriname. *In*: Alonso, L. E., and J. H. Mol eds. *A Rapid Biological Assessment of the Lely and Nassau Plateaus, Suriname (with additional information on the Brownsberg Plateau)*. RAP Bulletin of Biological Assessment 43. Conservation International, VA, USA.

Theunis, L., M. Gilbert, Y. Roisin, and M. Leponce. 2005. Spatial structure of litter-dwelling ant distribution in a subtropical dry forest. *Insectes Sociaux* 52: 366–377.

Weber, N. A. 1946. The biology of the fungus-growing ants. Part IX. The British Guiana species. *Revista Entomologia* (Rio de Janeiro) 17: 114–172.

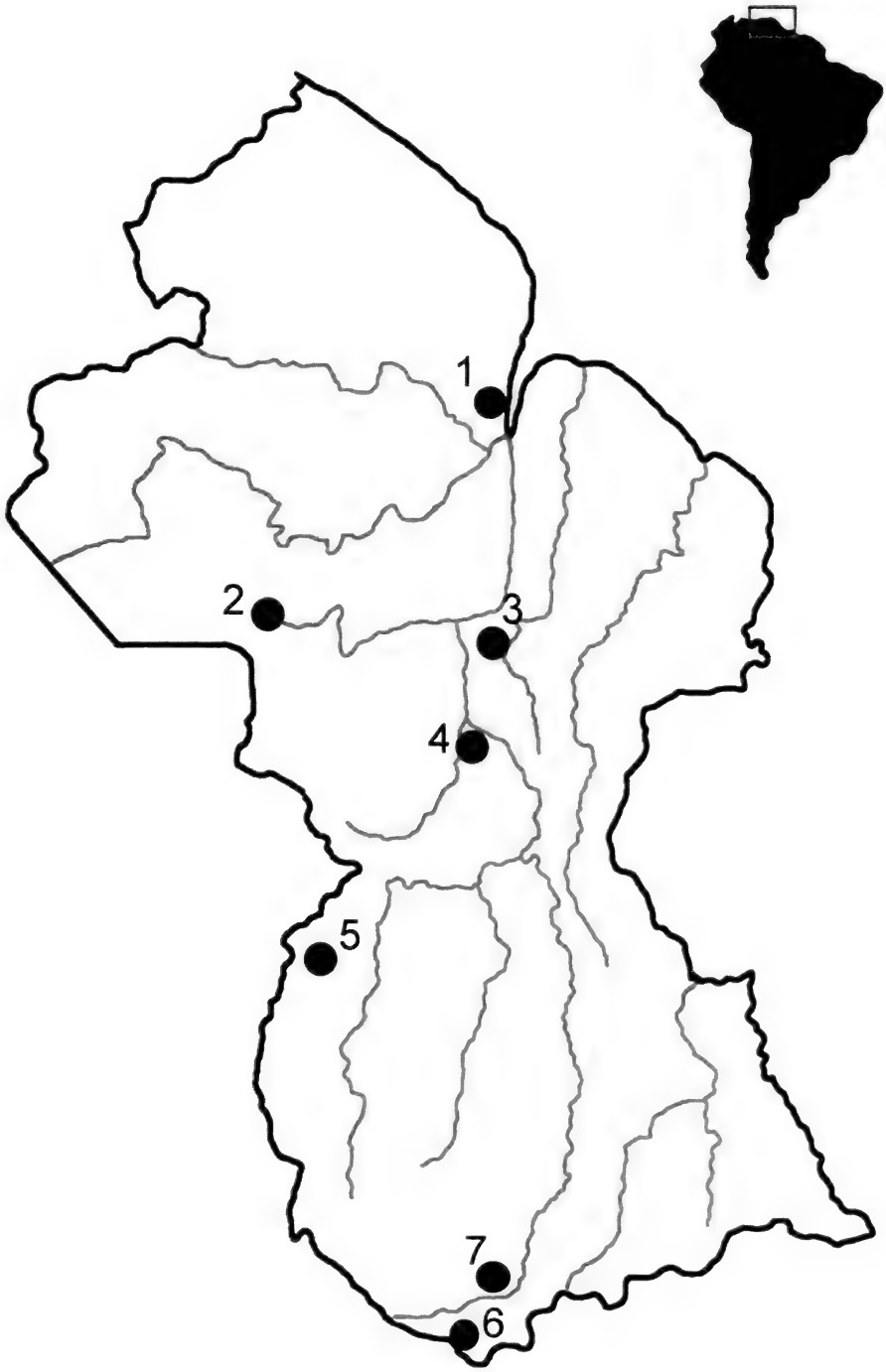
Wheeler, W. M. 1916. Ants collected in British Guiana by the expedition of the American Museum of Natural History during 1911. *Bulletin of the American Museum of Natural History* 35: 1–14.

———. 1918. Ants collected in British Guiana by Mr. C. William Beebe. *Journal of the New York Entomological Society* 26: 23–28.

Wilson, E. O. 1953. The ecology of some North American Dacetine ants. *Annals of the Entomological Society of America* 46: 479–495.

Appendix 1

Map of Guyana with locations of places sampled, modified from LaPolla et al. (2007). Legend (Abbreviations follow those of Appendix 1): (1) CWC; (2) MAB, MAD, MAF, MAU; (3) MHC; (4) IFR; (5) KMM; (6) ARC, ANR[1], ANR[2]; (7) KRC.



Appendix 2. Dacetine ant species currently known from Guyana.

Taxon	Locality	Notes/Reference
Acanthognathus brevicornis M.R. Smith	ARC, ANR[2], CWC, KRT, MAB	New record
A. lentus Mann	ANR[2], IFR, KRT	New record
A. ocellatus Mayr	ARC, KRT	New record
A. stipulosus? Brown & Kempf	ANR[1]	New record
Daceton armigerum (Latreille)	IFR, Essequibo River, Rupununi Savannah, Tukeit	Bolton 2000; Fernandez & Sendoya 2004; Wheeler 1916; this study
Pyramica alberti (Forel)	ANR[2], Kartabo, KRC, KRT	Bolton 2000; Fernandez & Sendoya 2004; this study
P. auctidens Bolton	ANR[1], KMM, KRC, KRT	New record
P. beebei (Wheeler)	ARC, ANR[1], IFR, KRC, KRT, MAB	New record
P. cincinnata (Kempf)	ANR[1], ANR[2], MAB	New record
P. crassicornis (Mayr)	ANR[1], ANR[2], Guyanas, KRC, KRT	Kempf 1972; Bolton 2000; Fernandez & Sendoya 2004; this study
P. dahlanae n. sp.	CWC, MHC	New species
P. denticulata (Mayr)	ARC, ANR[1], ANR[2], Berbice Dubulay Ranch, CWC, IFR, KMM, KRC, KRT, MAB, MHC, Morabukea, R. Mazaruni Forest	Bolton 2000; Fernandez & Sendoya 2004; this study
P. depressiceps (Weber)	Kartabo	Bolton 2000; Fernandez & Sendoya 2004
P. glenognatha Bolton	IFR, KMM, MAF, MAU	New record
P. inusitata (Lattke)	KRT	New record
P. mariae n. sp.	MAU	New species
P. metopia (Brown)	ARC, KRT	New record
P. metrix Bolton	ANR[1], ANR[2]	New record
P. mirabilis (Mann)	ARC	New record
P. stenotes Bolton	MHC	New record
P. subedentata (Mayr)	ARC, ANR[1], ANR[2], IFR, KMM, KRC, KRT, MAB, MHC	New record
P. thaxteri (Wheeler)	MAB	New record
P. urrhobia Bolton	ARC	New record
P. villiersi (Perrault)	ANR[1], IFR, KMM, KRC, KRT, MHC	New record
Strumigenys acarai	ANR[1]	New species
S. cordovensis Mayr	ARC, ANR[2]	New record
S. cosmostela Kempf	ANR[2], MAB	New record
S. dolichognatha Weber	IFR, Kartabo, MAB, MHC	Bolton 2000; Fernandez & Sendoya 2004; this study
S. dyseides Bolton	CWC, KRC, MHC	New record
S. elongata Roger	ANR[1], ANR[2], CWC, IFR, KMM, KRT, MAB, MHC, Morabukea,	Bolton 2000; Fernandez & Sendoya 2004; this study
S. godmani Forel	Kartabo	Bolton 2000; Fernandez & Sendoya 2004
S. pariensis Lattke & Goitía	ARC, ANR[1], ANR[2], KRC, KRT	New record
S. perparva Brown	ARC, ANR[1], ANR[2], Berbice Dubulay Ranch, CWC, IFR, KMM, KRC, KRT, MAB, MHC	Bolton 2000; Fernandez & Sendoya 2004; this study
S. precava Brown	ANR[2], Between R. Cuyuni & R. Mazaruni, Kamakusa, KRC, MHC, MAD	Bolton 2000; Fernandez & Sendoya 2004; this study
S. royi n. sp.	KRC, KRT	New species
S. ruta Bolton	KMN	New record

Appendix 2 Continued.

Taxon	Locality	Notes/Reference
S. silvestrii Emery	ANR[2]	New record
S. smilax Bolton	ARC	New record
S. smithii Forel	ANR[2]	New record
S. trinidadensis Wheeler	ANR[2], KRC, MHC	New record
S. trudifera Kempf & Brown	ANR[2], KRC, KRT	New record
S. waiwai n. sp.	KRC, KRT	New species

Abbreviations for localities: **ARC**: Upper Takutu-Upper Essequibo, Acarai Mountains, Romeo Camp, 58°56.789'W, 1°23.147'N, elev. 290 m; **ANR[1]**: Upper Takutu-Upper Essequibo, Acarai Mountains, New Romeo Camp, 58°57.828'W, 1°19.938'N, elev. 1069 m; **ANR[2]**: Upper Takutu-Upper Essequibo, Acarai Mountains, New Romeo Camp, 58°57.49'W, 1°20.854'N, elev. 750 m; **CWC**: Calm Water Creek, 58°37.16'W, 6°28.06'N, elev. 20 m; **IFR**: Iwokrama Forest Reserve Whitewater Camp, 58°50.992'W, 4°43.890'N, elev. 60 m; **KMM**: Kanuku Mountains near Moco-Moco Falls, 59°38.376'W, 3°17.297'N, elev. 224 m; **KMN**: Kanuku Mountains near Nappi Creek Camp, 59°33.963'W, 3°21.018'N, elev. 128 m; **KRC**: Upper Takutu-Upper Essequibo, Kamoa River Camp, 58°49.929'W, 1°32.786'N, elev. 530 m; **KRT**: Upper Takutu-Upper Essequibo, Kamoa River top mountain, 58°50.299' W, 1°33.046'N, elev. 717 m; **MAB**: Base Camp Mount. Ayanganna, 59°55.486'W, 5°20.063'N, elev. 732 m; **MAD**: *Dicymbe* Camp Mount Ayanganna, 59°54.632'W, 5°17.760'N, elev. 717 m; **MAF**: Falls Camp Mount Ayanganna, 59°57.563'W, 5°22.332'N, elev. 1134; **MAU**: Upper Forest Mount Ayanganna, 59°57.969'W, 5°22.483'N, elev. 1300 m; **MHC**: Mabura Hill, 58°41.982'W, 5°09.313'N, elev. 64 m. "**New record**" refers to a new record for Guyana.

Appendix 3

KEY TO DACETINI KNOWN FROM GUYANA

(NOTE: This key is an adaptation of that of Bolton [2000] to include only the species that occur in Guyana. This key also includes modifications from Brown and Kempf [1969]; Bolton [1994])

1. Antenna 11–segmented **2**
– Antenna 4 to 6–segmented **6**
2(1). In lateral view, antennal scape passes below eye when in resting position. Propodeal node bidentate. Palpal formula 5,3 ..... ***Daceton armigerum***
– In lateral view, antennal scape passes above eye when in resting position. Propodeal node unarmed. Palpal formula 0,1 ..... **3**
3(2). Preapical area of masticatory margin of mandibles with irregular denticles ..... ***Acanthognathus brevicornis***
– Preapical area of masticatory margin of mandibles lacking denticles **4**
4(3). Node of petiole with convex anterior face and flat, sloping posterior face, not evenly rounded ..... ***Acanthognathus stipulosus***
– Node of petiole low and evenly rounded when seen in profile **5**
5(4). Fossae on posterior half of dorsum of head smaller, mostly separated by flat, smooth spaces ..... ***Acanthognathus ocellatus***
– Fossae on posterior half of dorsum or head large, mostly contiguous or separated by single, simple longitudinal rugulae ..... ***Acanthognathus lentus***
6(1). Mandibles inserted on sides of anterior cephalic margin and converging towards apex when closed. Inner margin of mandibles generally with numerous teeth or denticles ..... **7 (*Pyramica*)**
– Mandibles inserted on median portion of anterior cephalic margin and diverging towards apex when closed. Inner margin of mandibles with 0–2 preapical teeth ..... **25 (*Strumigenys*)**

7(6). In full-face view, mandibles sublinear to linear, elongated and narrow; when closed, mandibles contacting each other only in apical halves or less of their lengths; either with an elongate space between mandibles or their inner margins convex so that margins touch, or nearly touch, near midlength **8**

– In full-face view, mandibles either short and trap-like, or triangular to elongate-triangular; when closed contacting through most or all of their exposed length, lacking an elongate space between mandibles or at most with diastema basally between basal lamella and basal tooth **15**

8(7). Disc of postpetiole smooth or with weak longitudinal costulae in parts, never densely reticulate-punctate ..... ***Pyramica dahlanae***

– Disc of postpetiole densely reticulate-punctate over most or all of its surface **9**

9(8). Inner margin of mandible with clearly defined submedian tooth or distinctly enlarged denticle at or just distal of midlength of mandible, this tooth or denticle obviously larger than any other preapical dentition that may be present distal to it, if two distinctive enlarged teeth present, distal located at about the apical third and proximal in basal third of mandible length. Labral lobes very long and slender, trigger hairs at apices of lobes short **10**

– Inner margin of mandible without a tooth or distinctly enlarged denticle at or near the midlength that is obviously larger than any other preapical dentition that may be present distal to it, if two distinctive enlarged teeth present, both of them closer to preapical dentition than to midlength of mandible. Labral lobes short, trigger hairs at apices of lobes long **13**

10(9). Pronotal humeral hair long and flagellate. Mesonotum with single pair of long flagellate hairs ..... ***Pyramica metopia***

– Pronotal humeral hair sometimes absent usually present, short-spatulate to filliform, never flagellate. Mesonotum without flagellate hairs **11**

11(10). Scape narrow basally; anterior margin of scape beyond base abruptly expanded and almost lobate at subbasal angle, scape distinctly widest at this point. Dorsolateral margin of head lacking apicoscrobal hair. Postpetiole, in profile, swollen or subglobular ..... ***Pyramica crassicornis***

– Scape gradually broadening from base to apex; anterior margin convex but not abruptly expanded at subbasal angle, scape widest at or near its midlength. Dorsolateral margin of head with an apicoscrobal hair of some form. Postpetiole, in profile, not swollen nor subglobular **12**

12(11). Inner margin of mandible with single enlarged preapical tooth, located near midlength; other minutely denticles present, but without a second equally sized tooth. Larger species (HL 0.61–0.63, HW 0.41–0.43, AL 0.58–0.60) ..... ***Pyramica stenotes***

– Inner margin of mandible with two enlarged preapical teeth of approximately equal size; in addition to other minutely denticles. Smaller species (HL 0.50–0.52, HW 0.34–0.36, AL 0.46–0.50) ..... ***Pyramica auctidens***

13(9). In lateral view, dorsum of mesosoma with 4–6 pair of stout remiform standing hairs (not including those at humeri). Mandibles short (MI 49–54). In full-face view, inner margins of mandibles convex and, when entirely closed, touching at about midlength ..... ***Pyramica subedentata***

– In lateral view, dorsum of mesosoma with single pair of standing hairs (not including those at humeri). Mandibles larger (MI 72–85). In full-face view inner margins of mandibles more or less straight to shallowly concave **14**

14(13). Inner margin of mandibles with 5–10 preapical denticles of similar size. Metapleuron entirely densely reticulate. Peduncle of petiole short, PI 38–42 ... ***Pyramica denticulata***

– Inner margin of mandibles with 3–4 preapical denticles, two of which are distinctly much larger than rest. Metapleuron in most of its surface smooth and shining. Peduncle of petiole elongate, PI 48–49 ..... ***Pyramica mariae***

15(7). With head in full-face view, anterior margin of scape with projecting curved hairs, of which one or more, distal to subbasal bend, distinctly curve toward base of scape. These hairs may be simple, spatulate, spoon-shaped, or wire-like **16**

– With head in full-face view, anterior margin of scape without projecting hairs that distinctly curve toward base of scape. Scape edge may have elongate simple straight or flagellate projecting hairs present; or may have entirely anteriorly or apically directed short hairs; or lacking hairs **21**

16(15). Pronotal humeral hair present, may be filiform, flagellate, remiform, or clavate; humeral hair always distinctly differentiated from any other pilosity that may be present on dorsal pronotum **17**

– Pronotal humeral hair absent; humerus without a hair that is distinctly differentiated from any other pilosity that may be present on dorsal pronotum **20**

17(16). Ventral surface of petiole in profile with spongiform tissue reduced to absent; discounting anterior subpetiolar process (if present) usually with narrow non-spongiform cuticular carina, but if weakly spongiform strip occurs then its maximum depth only fraction of depth of peduncle. Disc of postpetiole usually sculptured at least in part, only rarely mostly smooth **18**

– Ventral surface of petiole in profile with deep, conspicuous and very obviously spongiform curtain, its maximum depth at least half that of peduncle and usually more. Disc of postpetiole completely unsculptured and glassy smooth ..... ***Pyramica alberti***

18(17). Metapleuron and side of propodeum entirely reticulate-punctate **19**

– Metapleuron and side of propleuron mostly or entirely smooth and shinning .... ***Pyramica cincinnata***

19(18). Pronotal humeral hair elongate and freely projecting, slightly flattened apically and more or less straight. Scape in dorsal view slender, broadest point distinctly distal of midlenght. Anterior margin of clypeus very shallowly convex in full-face view. Disc of postpetiole not entirely densely reticulate-punctate ..... ***Pyramica urrhobia***

– Pronotal humeral hair very short, clavate. Scape in dorsal view broad and flattened, broadest point proximal of midlenght, at or just distal of subbasal bend. Anterior margin of clypeus transverse to very shallowly concave in full-face view. Disc of postpetiole entirely densely reticulate-punctate ..... ***Pyramica metrix***

20(16). Promesonotum, side of mesosoma, and disc of postpetiole finely reticulate-punctate. Head in profile incredible dorsoventrally flattened; at eye level depth of head capsule scarcely more than twice vertical diameter of the eye. Ventral margin of petiole lacking curtain of lamellate or spongiform tissue .... ***Pyramica depressiceps***

– Promesonotum and side of mesosoma smooth and shining, disco of pospetiole not reticulate-punctate. Head in profile not strongly dorsoventrally flattened; at eye level depth of head capsule distinctly more than twice vertical diameter of eye. Ventral margin of petiole with lamellate curtain that extends entire length of segment ..... ***Pyramica thaxteri***

21(15). With head in full-face view dorsolateral margin behind level of eye with laterally projecting hairs present; at least an apicoscrobal hair but often more along margin **22**

– With head in full-face view dorsolateral margin behind level of eye without laterally projecting hairs of any form; any hairs that do occur are minute and closely appressed, not at all projecting **24**

22(21). Midline of clypeal dorsum raised into a high-arched thick longitudinal crest that extends entire length of sclerite. With postpetiole in profile ventral spongiform lobe either completely absent or reduced to minute triangular vestige anteriorly on sternite ..... ***Pyramica inusitata***

– Midline of clypeal dorsum not raised into a high longitudinal crest that extends length of sclerite. With postpetiole in profile ventral spongiform lobe fully developed, basally extending length of sternite and conspicuously convex apically **23**

23(22). Dorsal surface of petiole without erect cuticular lamella on peduncle and anterior face of node. Dorsolateral margin of propodeum without an erect lamella on each side; lamella on propodeal declivity narrow to cariniform, in profile its maximum width much less than length of postpetiole disc ..... ***Pyramica villiersi***

– Dorsal surface of petiole with erect cuticular lamella that extends along peduncle and ascends anterior face of node, terminating just behind anterodorsal angle. Dorsolateral margin of propodeum with a tall erect cuticular lamella on each side that is continuous with extremely broad lamella on declivity; in profile maximum width of lamella on declivity equal to length of postpetiole disc ..... ***Pyramica mirabilis***

24(21). Dorsal outline of clypeus angled down at about 45 degrees to line of vertex. Ventral surface of petiole with well-developed curtain, of spongiform or translucent lamellar tissue, that runs most or all of the length of the segment. Head elongate (CI 68–70) ..... ***Pyramica beebei***

– Dorsal outline of clypeus not angled down from line of vertex. Ventral surface of petiole lacking curtain of spongiform or lamellar tissue. Head short and broad (CI 91–96) ..... ***Pyramica glenognatha***

25(6). Anterior margin of scape with all hairs curved or inclined toward apex of scape, without hairs that curve toward base of scape, and without a series of hairs at right-angles to long axis of scape shaft **26**

– Anterior margin of scape either with one to many hairs that distinctly curve toward base of scape, or rarely with hairs that are at right angles to long axis of scape shaft; never with all hairs obviously curved or inclined toward apex of scape **29**

26(25). Mandibles relatively short, MI < 75. Bulla of femoral gland located in apical quarter of dorsum of each leg; each bulla usually appears as pale oval patch, less commonly as short streak **27**

– Mandibles relatively long MI > 85. Bulla of femoral gland located close to midlength on dorsum of each leg; each bulla appears as pale elongate streak or as oval patch ... **28**

27(26). Mandibles short and stout (MI 41–48), broad and powerful, outer margins strongly bowed outwards. Declivity of propodeum in profile with tooth or spine above and triangular lobe or tooth below, two linked by lamella. First gastral tergite glassy smooth behind minute to vestigial basigastral costulae ..... ***Strumigenys godmani***

– Mandibles long and linear (MI 57–60), thick throughout most of their length and abruptly narrowing just before apex by sudden oblique divergence of inner margin, outer margins straight to slightly convex. Declivity of propodeum in profile with single tooth or spine, lacking second tooth or lobe below. First gastral tergite finely reticulate-substrigulate with some verrucose sculpture confined to basigastral area ..... ***Strumigenys royi***

28(26). In full-face view distal preapical tooth of mandible is closer to proximal preapical tooth than it is to apicodorsal tooth ..... ***Strumigenys dolichognatha***

– In full-face view distal preapical tooth of mandible is closer to apicodorsal tooth than it is to proximal preapical tooth ..... ***Strumigenys cordovensis***

29(25). Mandible without intercalary teeth or denticles that arise between apicodorsal and apicoventral teeth, nor that arise from dorsal base of apicoventral tooth **30**

– Mandible with 1 or 2 intercalary teeth or denticles that arise between apicodorsal and apicoventral teeth, or that arise from dorsal base of apicoventral tooth **40**

30(29). Mandible without preapical teeth or denticles **31**

– Mandible with 1 or 2 preapical teeth or denticles **32**

31(30). Hairs of first gastral tergite flagellate, not flattened and ribbon-like through most of their length ..... ***Strumigenys elongata***

– Hairs of first gastral tergite flattened and ribbon-like through most of their length, narrowly flagellate only in apical section ..... ***Strumigenys pariensis***

32(30). Mandibles very long, MI > 100 ..... ***Strumigenys trudifera***

– Mandibles much shorter, MI < 75 ..... **33**

33(32). With head in profile preocular carina extends back almost to apex of scrobe, well beyond level of minute eye. Bulla of femoral gland proximal of midlength on dorsum of middle leg, very conspicuous. Scape relatively long, SI 111-112 .... ***Strumigenys smilax***

– With head in profile preocular carina terminates at level of eye. Bulla of femoral gland distal of midlength on dorsum of middle leg or inconspicuous. Scape shorter, SI < 100 .... **34**

34(33). Large species (HL 0.86–1.02, ML 0.50–0.56, AL 0.80–1.00). Ventrolateral margin of head in front of eye, and side of head above it, deeply concave; margin and side appear excavated or constricted in oblique dorsal view .... ***Strumigenys precava***

– Smaller species (HL 0.39–0.45, ML 0.20–0.30, AL 0.36–0.47). Ventrolateral margin of head in front of eye, and side of head above it, not deeply concave; margin and side do not appear excavated or constricted in oblique dorsal view **35**

35(34). In full-face view upper scrobe margin with row of 4–5 broadly spatulate to spoon-shaped hairs that curve posteriorly .... ***Strumigenys perparva***

– In full-face view upper scrobe margin with row of simple, or narrowly spatulate to spoon-shaped hairs that all curve anteriorly **36**

36(35). Mandible with single spiniform preapicaltooth, in distal third, or with tooth in this position and denticle, that may be minute and difficult to see, close to midlength ... **37**

– Mandible with minute inconspicuous denticle close to midlength lacking second tooth of any form .... ***Strumigenys acarai***

37(36). Leading edge of antennal scape with spoon-shaped or spatulate hairs. In full-face view upper scrobe margin with row of spatulate to spoon-shaped hairs, and with apicoscrobal hair only. Cephalic ground-pilosity spoon-shaped or spatulate **38**

– Leading edge of antennal scape with narrowly spatulate or simple hairs. In full-face view upper scrobe margin with row of simple hairs and with two flagellate hairs, one of which is apicoscrobal hair. Cephalic ground-pilosity multi-furcate .... ***Strumigenys waiwai***

38(37). Hairs on first gastral tergite short and stout, broadly spatulate or remiform; elongate slender fine hairs absent or restricted to transverse row at extreme apex of sclerite .... ***Strumigenys silvestrii***

– Hairs on first gastral tergite elongate and slender, finely filiform to flagellate, or flexuous; short stout spatulate or remiform hairs entirely absent **39**

39(38). Mandibles relatively long, MI > 60. Disc of postpetiole smooth and shinning. Mesonotum without pair of erect flagellate hairs .... ***Strumigenys dyseides***

– Mandibles relatively short, MI < 60. Disc of postpetiole densely punctate to reticulate-punctate. Mesonotum with pair of erect flagellate hairs .... ***Strumigenys ruta***

40(29). Apical fork of mandible with single intercalary tooth or denticle that arises between apicodorsal and apicoventral teeth, or arises from dorsal surface of apicoventral tooth **41**

– Apical fork of mandible with two intercalary teeth or denticles that arise between apicodorsal and apicoventral teeth; frequently represented by distinct intercalary tooth accompanied by less conspicuous or minute denticle .... ***Strumigenys cosmostela***

41(40). First gastral tergite very finely and densely longitudinally striolate-costulate and opaque. Apicoscrobal hair, pronotal humeral hair and standing hairs on mesonotum all flagellate. Entire body dull yellow to brownish-yellow, gaster not contrasting with head and alitrunk .... ***Strumigenys trinidadensis***

– First gastral tergite glassy smooth. Apicoscrobal hair, pronotal humeral hair and standing hairs on mesonotum all stiff, simple to weakly remiform. Head and alitrunk reddish brown to brown, gaster blackish brown to black, both contrasting .... ***Strumigenys smithii***

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Two New Species of the *strigatus* Species Complex of the Ant Genus *Cyphomyrmex* (Hymenoptera: Formicidae) from Costa Rica and Panamá

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Abstract.—The *strigatus* species complex is defined as those workers and females of *Cyphomyrmex* in which the preocular carina extends back to the vertex, delimiting the lateral margin of a depressed concave scrobe. The mandibles have 6 or more teeth and there is a single medial pronotal tubercle. The complex was previously reported only in South America, especially southeastern Brasil and northern Argentina. Two **new species** were found in Central America: ***C. andersoni*** from Costa Rica, and ***C. snellingi*** from Panamá. *Cyphomyrmex andersoni* resembles *C. quebradae*, but can be separated as the hind femur is longer than the head capsule (shorter in *C. quebradae*). It can be differentiated from the similar *C. bruchi* as the mesosomal tubercles are distinct (indistinct in *C. bruchi*). *Cyphomyrmex snellingi* has the frontovertexal corners lobate and somewhat projecting posteriad. It is most similar to *C. faunulus*, but can be easily distinguished as the anterior mesonotal tubercle is not more developed than the other tubercles (much larger than the others in *C. faunulus*).

Resumen.—El complejo *strigatus* del género *Cyphomyrmex* se caracteriza porque las hembras y obreras presentan una carina preocular que se extiende posteriormente hasta el vertex y delimita la margen lateral de un escrobo antenal deprimido y cóncavo. Estas hormigas poseen mandíbulas con 6 o más dientes, y un sólo tubérculo pronotal mesial. El complejo *strigatus* se conocía solo de Suramérica, especialmente el sureste de Brasil y norte de Argentina. Dos **nuevas especies** fueron halladas en América Central: ***C. andersoni*** de Costa Rica, y ***C. snellingi*** de Panamá. *Cyphomyrmex andersoni* es similar a *C. quebradae*, pero se diferencia porque el fémur posterior es más largo que la cápsula cefálica (más corto en *C. quebradae*). A su vez, *C. andersoni* puede ser diferenciada de *C. bruchi* porque los tubérculos mesosomales son distinguibles (no distinguibles en *C. bruchi*). *Cyphomyrmex snellingi* tiene las esquinas frontovertexales lobosas y algo proyectadas posteriormente. Esta especie es más similar a *C. faunulus*, de la cual puede ser distinguida fácilmente por el tubérculo mesonotal anterior no tan desarrollado.

The ant genus *Cyphomyrmex* belongs to the New World fungus growing ants of the tribe Attini, and presently contains 40 species (Bolton et al. 2007). The genus is divided into two species complexes, the *strigatus* complex (Kempf 1964) and the *rimosus* complex (Kempf 1965; Snelling and Longino 1992). *Cyphomyrmex* workers and females are easily recognized, as the frontal carinae form a shield on the dorsum of the head, which covers most of the head. The mesosoma has a series of pairs of blunt tubercles in nearly all species. The first opisthogastral tergum* (see glossary in Serna and Mackay 2010) lacks tubercles. Most surfaces are dull and without sculpture; the hairs are mostly limited to appressed, often scale-like setae that are nearly always restricted to the gaster and the head.

Most species nest in the soil, in rotten logs and stumps, or in hollow dead twigs. This genus also nests under bark, under moss, and within epiphytic pseudobulbs (Snelling and Longino 1992). Colonies are small, probably not exceeding 500 workers (Snelling and Longino 1992). All *Cyphomyrmex* species cultivate badisiomycete fungi in the tribe Leucocoprineae. In the *C. rimosus* group, these fungi grow in a yeast form (small masses of unicellular fungal cells) rather than in the multicellular mycelial form typical for all other attine ant gardens (Schultz et al. 2002; Schultz and Brady 2008).

Workers of the *strigatus* complex can be recognized by the closed antennal scrobe (sometimes with poorly defined margins), mandibles with six or more teeth, and with a single medial pronotal tubercle (apparently a fusion of two tubercles). The species of the *strigatus* complex were previously considered to be primarily southern South American in distribution, although *C. faunulus* occurs as far north as Venezuela (Mayhé Nunes and Jaffé 1998). An unidentified species is found in Colombia (Fernández and Palacio 1995) and an apparently new species was found in Ecuador (Tiputini) by Kari Ryder Wilkie (http://people.bu.edu/karitr/genus/cyphomyrmex.html).

In comparison, the workers of the *rimosus* complex have an open antennal scrobe (anteriorly), with the preocular carina curved mesially in front of the eye, and not directed to the posterior corner of the head, the mandibles have five teeth, and the pronotum lacks medial tubercles, or has a pair of tubercles. The species of the *rimosus* complex are widely distributed from the United States to South America.

Two new species of the *strigatus* species complex were found in Costa Rica and Panamá. These new species will be included in a key to the species of *Cyphomyrmex* that can be found at http://www.utep.edu/leb/antgenera.htm.

METHODS AND MATERIALS

The specimens were examined with a Zeiss stereoscope, at 64X, and were measured with an ocular micrometer. The abbreviations are as follows:

HL	Head length, measured in full frontal view, from anterior margin of medial lobe of clypeus to medial posterior margin of frons
HW	Head width, measured in full frontal view, maximum width excluding eyes (Measured near posterior point of head)
SL	Scape length, excluding condyle
EL	Eye length, maximum diameter of eye
EW	Eye width, maximum width of eye, perpendicular to EL
WL	Weber's length, a diagonal line from the top of the anterior edge of the pronotum to the posterior edge of the posteropropodeal lobes.
CI	Cephalic index, HW/HL × 100
SI	Scape index, SL/HL × 100
OI	Ocular index, EW/EL × 100
MCZC	Museum of Comparative Zoology, Harvard University
CWEM	Collection of William and Emma Mackay, University of Texas at El Paso

Terms followed by an asterisk are defined at the end of this paper and explained in the glossary of Serna and Mackay (2010).

RESULTS

Cyphomyrmex andersoni new species
(Figs 1–6)

Diagnosis.—The worker is a small (total length about 2.5 mm, n=2) reddish-brown ant. The mandibles have six teeth, the frontal carinae do not reach the dorsad occular suture, the frontovertexal* corners

are barely extended into auricle-like structures; the pronotum has three angulate processes or teeth, including the medial process and two lateral processes, together with a pair of posterior swellings, and the mesonotum has a pair of conical processes; the propodeum has a pair of anterior, blunt processes and two well-developed angulate posterior processes; and the posterior 1/3 of the petiole is raised into a blunt process that appears bidentate when seen obliquely from above; the postpetiole has two parallel raised regions on the dorsal surface; and the gaster lacks longitudinal raised areas. The posterior femur has a distinctive ventral angulate process, followed distally by a poorly defined carina.

The female and male are unknown.

Distribution.—Known only from the states of Alajuela and Guanacaste, Costa Rica.

Worker measurements (mm).—HL 0.76–0.78, HW 0.64–0.66, SL 0.58–0.60, EL 0.13–0.14, EW 0.08–0.10 WL 0.90–0.93. Indices: CI 84–85, SI 74–79, OI 65–73. Mandible with 6 teeth; anteclypeus broadly rounded; paraclypeal teeth* spiniform, moderately developed; frontal lobes and frontal carinae relatively narrow, extending to frontovertexal corner*, forming carina that fuses with posterolateral margin of antennal scrobe, preocular carina continues posteriorly to form mesial margin of antennal scrobe; eyes relatively small, extending past sides of head; scape relatively short, barely reaches frontovertexal corner; pronotum with medial protuberance, 2 lateral, conical tubercles and 2 posterolateral lobate processes, anteroinfra angle of lateropronotum developed; 2 angulate conical tubercles on mesonotum (height approximately 0.05 mm); anterior margin of dorsopropodeum with 2 broad processes (height 0.03 mm), dorsopropodeum* relatively short (0.08 mm from notopropodeal groove to highest point of anterior tubercles) posteropropodeum* longer (0.25 mm, measured from anterior tubercles to metapleural lobe), propodeal spines small (length 0.04 mm) and rounded; petiole enlarged posteriorly, forming dorsal tubercles as seen in lateral view (length 0.1 mm, height 0.07 mm) that appears to have two lateral tiny bumps; postpetiole with longitudinal medial depression flanked by two longitudinal ridges; all femora swollen, fore femur with poorly developed longitudinal carina along posteroventral margin, middle femur similar, but carina poorly developed, posterior femur with well-developed longitudinal carina forming distinct angle distad about one third length from body.

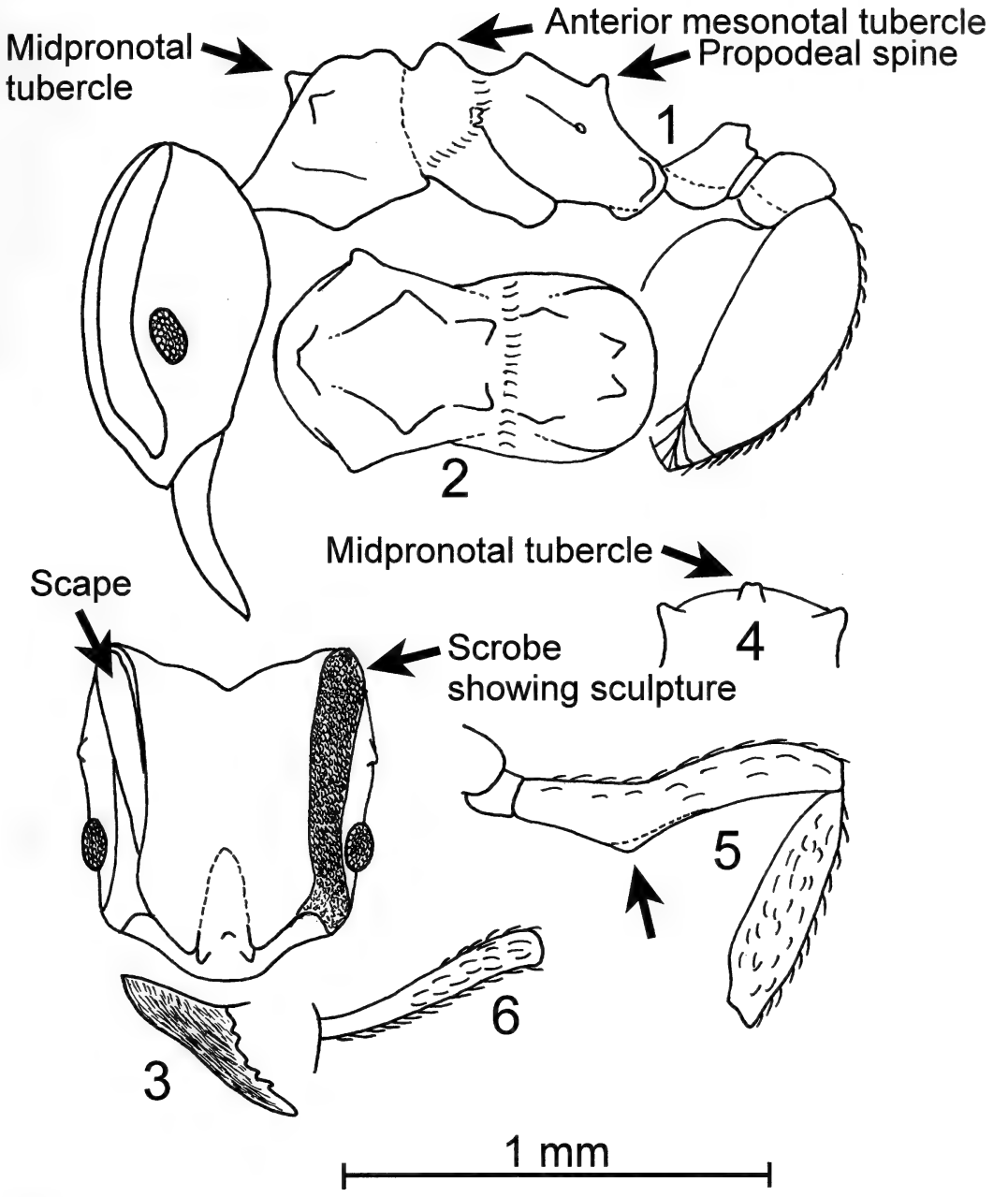
Erect hairs absent, except on mandible; hairs on scape and head appressed, hairs on ventral surface of head and anterior margin of procoxa subdecumbent, hairs on mesosoma, petiole, postpetiole, legs and gaster appressed.

Type series.—Holotype worker, Costa Rica, Alajuela, 27 k N and 8 k W west of San Ramón, 29-vi-6-vii-1999, R. Anderson # 19901, 99-109B, 10°13′30″N; 34°35′30″W (MCZC).

Additional material examined.—Costa Rica, Guanacaste, Cacao Field Station, 15-ii-1996, R. Anderson # 17682 (1 worker CWEM).

Etymology.—This new species is named in honor of Robert Anderson, who collected these specimens as well as thousands of other interesting specimens.

Discussion.—This species would key to *C. olitor* Forel in Kempf (1964), found in Brazil and Argentina. *Cyphomyrmex andersoni* is somewhat larger (HL of *C. olitor* 0.64, HW 0.56 from Kempf, 1964), has fewer mandibular teeth (7–8 in *C. olitor*), the midpronotal tubercle is approximately the same size as the lateral tubercles (midpronotal tubercle much smaller than lateral tubercles in *C. olitor*), and the propodeal spines are well developed (poorly developed in *C. olitor*). The mandibular teeth are worn and partially hidden by the clypeus in the holotype and badly worn in the mandible of the other specimen, but this species appears to be the only one of the *strigatus* species complex with six mandibular teeth (and as the members of the *rimosus* species complex



Figs 1–6. *Cyphomyrmex andersoni* holotype worker: 1, side view. 2, mesosoma as seen from above. 3, head and mandible, frontal views. 4, top of pronotum as seen from dorsoposterior view. 5, right posterior femur and tibia posterior aspect. 6, antennal scape.

all have five mandibular, it is apparently the only species in *Cyphomyrmex* with six teeth).

Biology.—The two specimens were collected in montane hardwood leaf litter at 1100–1200 m elevation and in wet montane forest litter.

Cyphomyrmex snellingi new species
(Figs 7–12)

Diagnosis.—The worker is a small (total length 2 mm) ferrugineous red specimen. The mandibles have seven teeth, the spini-

form paraclypeal teeth on the clypeus are markedly well developed; the frontal lobes do not reach the inner borders of the eyes (frontal view of head). The frontovertexal corners form auricle-like structures; the scape is short, and does not reach the posterior margin of the scrobe. The mid pronotal process is angulate, the lateral pronotal tubercles are poorly developed. The anterior mesonotal tubercles are conical and posterior mesonotal tubercles approximately the same size. The propodeum is rounded posteriorly and without angles or spines. The subpetiolar tooth is well-developed and sharp, dorsally the petiole extends over the base of the anterior part of the postpetiole, which has two longitudinal elevated regions, the posterior margin of the postpetiole is nearly straight; the first opisthogastral* tergum is without ridges or processes; all femora are swollen ventrally, with carinae, the posterior femur has a well-developed ventral lamina.

Erect hairs are sparse, present on the mandibles, apex of the scape, ventral surfaces of the legs, ventral and posterior surfaces of the gaster; appressed hairs are abundant on the dorsum of the first opisthogastral tergum.

All surfaces dull, except the region along base of mandibular teeth which is smooth and shiny.

Distribution.—Known only from the type locality in Panamá.

Description.—Worker measurements (mm): HL 0.71–0.74, HW 0.58, SL 0.48–0.50, EL 0.09–0.10, EW 0.08, WL 0.85–0.86. Indices: CI 78–81, SI 64–70, OI 82–86. Mandible with 7 teeth; spiniform paraclypeal teeth very well developed (length 0.07 mm), frontal carinae relatively narrowly spaced, not reaching preocular carina which forms mesiad margin of scrobe; eyes extending past sides of head, with about 20 ommatidia; scrobe greatly extending posteriorly, forming auricle-like structures; scapes not reaching posterior margin of scrobe; tubercles on pronotum poorly developed; anterior and posterior mesonotal tubercles moderately well developed and approximately same size, anterior tubercle with slighter broader base; dorsopropodeum shorter that posteropropodeum, propodeum without spines or angles; subpetiolar tooth sharp and well developed, petiole with two distinct, longitudinal lateral lobes, dorsum of posterior face extending over anterior part of postpetiole; postpetiole with longitudinal depressed region in dorsum of node, outlined by two elongated elevated areas; dorsal surface of gaster flat, bordered laterally by slightly elevated longitudinal areas; all femora with carinae along ventral posterior border, that on posterior femur more developed and forming lamina.

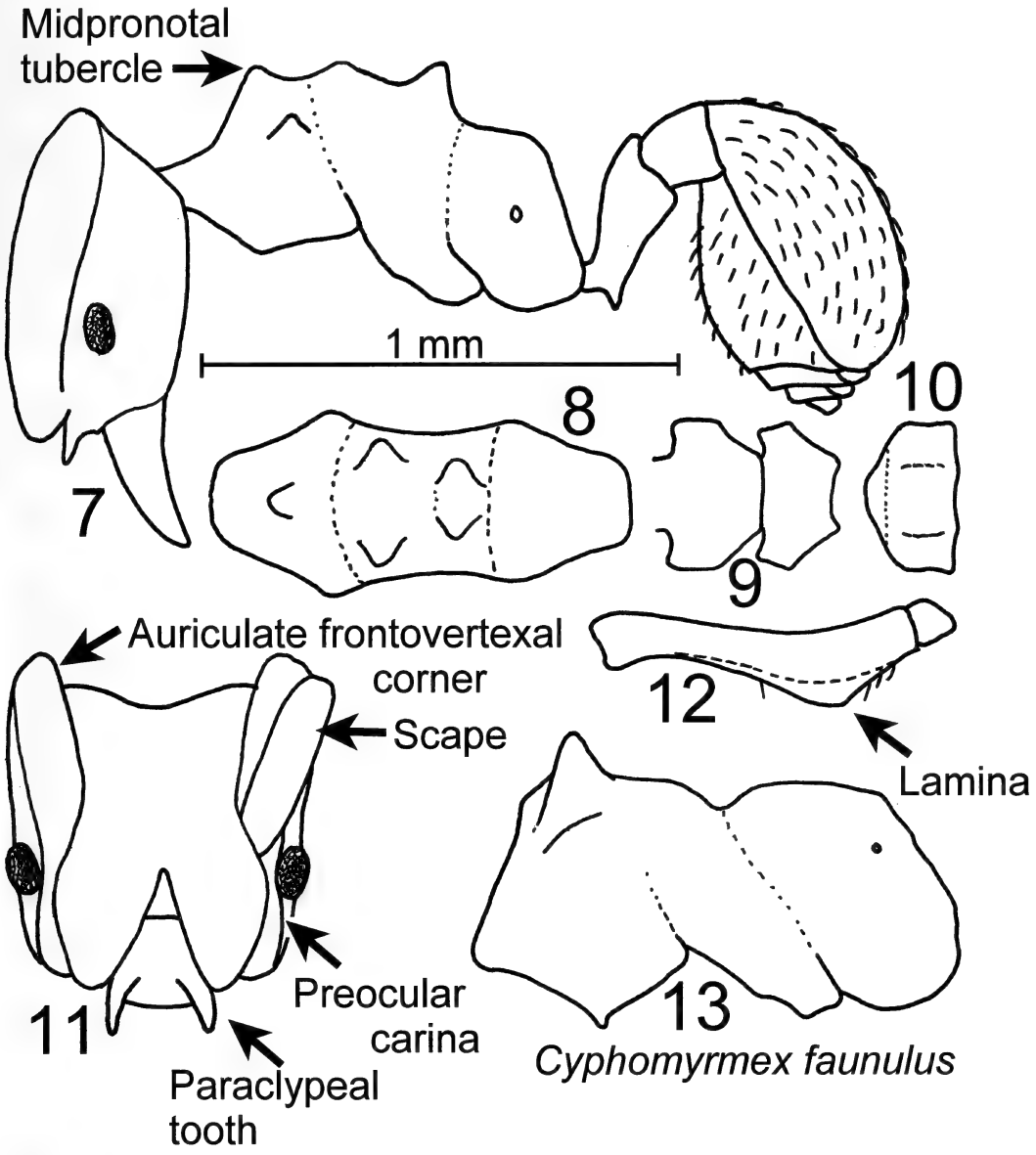
Few erect hairs on mandibles, anteclypeus and frontal lobes, remainder of hairs simple and appressed, located mostly on head and especially gaster.

All surfaces except mandiblular teeth and anterior edge of clypeus dull.

Type series.—Holotype worker (MCZC), 1 paratype worker (CWEM), Panamá, Cerro Campana, 950 m, 5-vi-1995, R. Anderson #17833.

Etymology.—Named in honor of the memory of Roy Snelling, recalling a pleasant visit to the Los Angeles County Museum of Natural History in May of 2007 where we spent time with Roy, Gordon Snelling, Brian Brown, and Weiping Xie.

Discussion.—*Cyphomyrmex snellingi* would key to *C. faunulus* in Kempf's key (1964). It can be easily distinguished as the anterior mesonotal tubercle is relatively small, as compared to the greatly enlarged anterior mesonotal tubercle of *C. faunulus* (Fig. 13). Additionally, the posterodorsal edge of the petiole of *C. faunulus* does not extend over the anterior face of the petiole as it does in *C. snellingi*. *Cyphomyrmex faunulus* also lacks the erect hairs on the frontal lobes. Although it would key to *C. faunulus*, the two species do not appear to be morphologically similar.



Figs 7–12. *Cyphomyrmex snellingi* holotype worker: 7, side view. 8, top view of mesosoma (based in part on the paratype). 9, petiole as seen from above, postpetiole as seen in anterior view. 10, postpetiole as seen from above. 11, Head. 12, left femur as seen from posterior view. Fig. 13, *Cyphomyrmex faunulus* mesosoma (Reserva Ducke, near Manaus, Amazonas, Brasil, LACM).

Biology.—The type series was collected in a leaf litter extraction from a wet montane habitat.

DISCUSSION

The genus *Cyphomyrmex* is divided into two species complexes, the *rimosus* complex and the *strigatus* species complex. The *strigatus* complex uses only mycelium cultivars and is probably plesiomorphic and paraphyletic to the *rimosus* complex (Schultz et al. 2002).

Cyphomyrmex has two centers of species richness: the *rimosus* group at about 10° north (Mayhé-Nunes and Jaffé 1998), whereas the majority of the species of the

strigatus group is restricted to 20°and 30° south (Sanhudo et al. 2007). The *strigatus* group also lacks species with wide distributions (Mayhé-Nunes and Jaffé 1998) as is found in the *rimosus* complex.

Apparently no new species of the *strigatus* group have been described since Kempf's revision (1964), although the recently described *C. muelleri* shows similarities to the *strigatus* species complex, and along with *C. longiscapus*, *C. costatus* and *C. wheeleri* may be related (Schultz et al. 2002). A similar new genus *Mycetagroicus*, with three new species has been recently described (Brandão and Mayhé-Nunes 2001).

GLOSSARY

Anteclypeus (="apron"): the anterior portion of the clypeus attached to the labrum. **Dorsopropodeum**: the dorsal surface of the propodeum.

Frontovertexal corner: the posterolateral angle between frons and vertex.

Notopropodeal groove: (= "metanotal groove") a transverse groove on the notopropodeal fusion.

Notopropodeal fusion: In workers, the tergal fusion of the thoracic notum and the propodeum.

Opisthogaster (adj. opisthogastral): (= "gaster") Abd IV to pygidium.

Paraclypeal teeth: (="parafrontal teeth" - Kempf 1964, 1965), referring to the anterior teeth-like processes on the clypeus.

ACKNOWLEDGMENTS

We would like to thank Roy Snelling and Weiping Xie for the loan of specimens of *Cyphomyrmex faunulus*. Two anonymous reviewers provided important comments. The research was supported by a grant from the National Geographic Society to Robert Anderson and the Ernst Mayr Fund of the Museum of Comparative Zoology.

LITERATURE CITED

Bolton, B., G. Alpert, P. Ward, and P. Naskrecki. 2007. *Bolton's Catalog of Ants of the World: 1758–2005.* Harvard University Press, available on CD.

Brandão, C. and A. Mayhé-Nunes. 2001. A new fungus-growing ant genus, *Mycetagroicus* gen. With the description of three new species and comments on the monophyly of the Attini (Hymenoptera: Formicidae). *Sociobiology* 38: 639–665.

Fernández, F. and E. Palacio. 1995. Hormigas de Colombia IV: Nuevos registros de géneros y especies. *Caldasia* 17: 587–596.

Kempf, W. W. 1964. A revision of the Neotropical ants of the genus *Cyphomyrmex* Mayr. Part I. Group of *strigatus* Mayr (Hym. Formicidae). *Studia Entomologica* 7: 1–44.

———. 1965. A revision of the Neotropical fungus-growing ants of the genus *Cyphomyrmex* Mayr. Part II: group of *rimosus* (Spinola) (Hym. Formicidae). *Studia Entomologica* 8: 161–200.

Mayhé-Nunes, A. and K. Jaffé. 1998. On the biogeography of Attini (Hymenoptera: Formicidae). *Ecotropicos* 11: 45–54.

Sanhudo, C., A. Mayhé-Nunes, and C. Brandão. 2007. Quem são as *Cyphomyrmex* (Myrmicinae: Attini). *Biológico* 69: 433–434.

Schultz, T. and S. Brady. 2008. Major evolutionary transitions in ant agriculture. *Proceedings of the National Academy of Sciences* 105: 5435–5440.

———, S. Solomon, U. Mueller, P. Villesen, J. Boomsma, R. Adams, and B. Norden. 2002. Cryptic speciation in the fungus-growing ants *Cyphomyrmex longiscapus* Weber and *Cyphomyrmex muelleri* Schultz and Solomon, new species (Formicidae, Attini). *Insectes Sociaux* 49: 331–343.

Serna, F. and W. Mackay. 2010. A descriptive morphology of the ant genus *Procryptocerus* (Hymenoptera: Formicidae). *Journal of Insect Science* (in press).

Snelling, R. R. and J. T. Longino. 1992. Revisionary notes on the fungus-growing ants of the genus *Cyphomyrmex, rimosus* group (Hymenoptera: Formicidae: Attini). Pp. 479–494 *in:* Quintero, D., and A. Aiello eds. *Insects of Panama and Mesoamerica: selected studies.* Oxford University Press, Oxford. 692 pp.

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Taxonomic Contribution to the *aurita* Group of the Ant Genus *Azteca* (Formicidae: Dolichoderinae)

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Abstract.—We describe five new species in the *aurita* group of the genus *Azteca*: ***Azteca andreae* sp. n.** (French Guiana), ***Azteca diabolica* sp. n.** (Panama), ***Azteca laurae* sp. n.** (Brazil), ***Azteca linamariae sp. n.*** *(Brazil and Colombia) and* ***Azteca snellingi* sp. n.** (Panama). Four of these new species are based on gynes, while the last is based only on the worker caste. All of them bear the *aurita* group characteristics. The second taxon is remarkable, as it differs from all of the other members of the group in the exaggerated, horn-like extensions of the posterolateral vertex margins. *Azteca snellingi* sp. n. is named in honor of our colleague, Roy Snelling, in tribute to his life-long contribution to knowledge of the world of Hymenoptera. A key to all known species of the *aurita* group, based on gynes, is provided. We report also for the first time an intercast case for the genus *Azteca*, based on an *Azteca schimperi* specimen.

Resumen.—Se describen cinco **nuevas especies** de hormigas del grupo *aurita* del género *Azteca*: ***Azteca andreae*** (Guyana Francesa), ***Azteca diabolica*** (Panamá), ***Azteca laurae*** (Brasil), ***Azteca linamariae*** y ***Azteca snellingi*** (Colombia y Brasil). Cuatro de las especies son descritas basadas en hembras, enguanto la última basada en la casta obrera. Todas poseen las características del grupo *aurita*. El segundo taxón es el más particular; es fácil diferenciar esta especie de las otras ya que presenta los márgenes posterolaterales del vértex exageradamente extendidos similares a unos cuernos. *Azteca snellingi* sp. n. es nombrada en honor a nuestro colega Roy Snelling quien consagró su vida al conocimiento de los himenópteros. Se presenta una clave actualizada basada en las hembras de las especies del grupo *aurita*. Reportamos también por primera vez un caso de intercasta para el género *Azteca*, con un espécimen en la especie *Azteca schimperi*.

Key words.—Ants, *Azteca*, identification keys, taxonomy

Palabras claves.—Hormigas, *Azteca*, claves para identificación, taxonomía

Azteca Forel is a genus of dolicoderine ant whose species-level taxonomy is still unclear. The only revision of the entire genus was conducted in the late nineteenth century (Emery 1893). Since then, no systematic review of the genus has been carried out and only isolated studies have allowed some species to be identified (Longino 1989, 1991a, 1991b, 1996). Recently, Longino (2007) reviewed the Costa Rican fauna and included a definition and global revision of the *aurita* group.

The *aurita* group of *Azteca* is monophyletic and characterized by: palpal formula 4,3; middle and hind tibia lacking an apical spur; an extremely convex anteromedial border of the clypeus that extends well beyond anterolateral clypeal lobes; HLB/HLA > 1.04 (Longino 2007, except latter trait discussed here; for further description of the measurements, see Materials and Methods). Gynes are generally small, similar in size to major workers. The integument is extremely smooth and shiny, glass-like, with an extremely dilute appressed pubescence (the pilosity, when present, is characterized by a stubble of short, stiff, fully erect setae). The petiole is bluntly subpyramidal to bilobed, never flat and scale-like (Longino 2007). Worker characters are provided in the group diagnosis by Longino (2007). The characteristics of gynes in this group suggest a syndrome of social parasitism (Hölldobler and Wilson 1990).

In this paper, we describe five new species of the *aurita* group: *Azteca andreae* (French Guiana), *Azteca diabolica* (Panama), *Azteca laurae* (Brazil), *Azteca linamariae* (Colombia and Brazil) and *Azteca snellingi* (Panama). The *A. diabolica* specimens (gynes only) were collected during the IBISCA international project through an intensive tridimensional sampling of arthropods in a Panamanian tropical rain forest (Basset et al. 2007), while the *A. snellingi* specimens were caught later in the same area. The other species were collected using Malaise traps (winged individuals) or manually from nests. An updated key derived from the one created by Longino (2007), based on the gynes of known species of the group, is provided.

MATERIALS AND METHODS

All measurements, indices and morphological characters are the same used by Longino (2007) and were made using a Nikon SMZ645 stereomicroscope with an ocular micrometer at 80× magnification.

Measurements (all in millimeters):

HLA: head length, full frontal view; perpendicular distance from the line tangent to the anterolateral clypeal lobes to the line tangent to the most extreme posterior of the vertex lobes. This measure was chosen because the anterolateral clypeal lobes are always visible, while the anteriormost extent of the medial lobe may be obscured by the closed mandibles.

HLB: medial head length; this is the same as HLA except that it is measured from the anteromedian rather than anterolateral lobe of clypeus. This measurement is important for the *A. aurita* group, where the lateral lobes are not well defined and the median lobe protrudes to a great extend. For most *Azteca*, HLA and HLB are very similar.

HW: head width; full frontal view, maximum width of head capsule above the eyes.

SL: scape length; length of the scape shaft from the apex to basal flange, not including the basal condyle and neck.

EL: eye length; maximum length of the eye.

OCW: width of the median ocellus.

Indices:

CI: cephalic index; 100*HW/HLA.

SI: scape index; 100*SL/HLA.

MTSC: number of metatibial setae; with the tibia seen from the anterior, such that the outer (dorsal) margin is in profile, and the number of erect to suberect setae (distinct from any underlying pubescence) are seen projecting from the outer margin.

Photographs were taken using a Nikon SMZ 1500 stereomicroscope at 40× and digital camera SIGHT DS - Fi 1. The images were fully-focused montage images created with the Combine version Z5 software package and edited using COREL PHOTO-PAINT ×3 version 13.

Types will be deposited in the follow collections: California Academy of Sciences, San Francisco, California, USA (CASC); Laboratório de Mirmecologia do

Centro de Pesquisas do Cacau (CPDC), Comissão do Plano da Lavoura Cacaueira, Ilhéus, Bahia, Brazil; Insect Collection, Instituto Humboldt, Claustro San Agustín, Villa de Leyva, Boyacá, Colombia (IAvH); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá D.C., Colombia (ICN-MHN); collection of John T. Longino, Evergreen State College, Olympia, Washington, USA (JTLC); Los Angeles County Museum of Natural History, Los Angeles, California, USA (LACM); Museu de Zoologia, Universidade de São Paulo (MZUSP), Brazil; and Royal Belgian Institute of Natural Sciences (RBINS).

TAXONOMIC SYNOPSIS OF THE *AZTECA AURITA* GROUP

Azteca andreae Guerrero, Delabie & Dejean. New species. French Guiana.

A. aurita Emery 1893. Panama to Amazonian Brazil.

= *silvae* Forel 1899. Synonymy, Longino (2007):55.

A. diabolica Guerrero, Delabie & Dejean. New species. Panama.

A. lallemandi Forel 1899. Panama, Colombia, eastern Brazil.

= *pruinosa* Mann 1916. Synonymy Longino (2007):56.

A. lanuginosa Emery 1893. Southern Brazil.

A. laurae Guerrero, Delabie & Dejean. New species. Western Amazonian Brazil.

Azteca linamariae Guerrero, Delabie & Dejean. New species. Amazonian Colombia and Western Amazonian Brazil.

A. nanogyna Longino 2007. Costa Rica.

A. pilosula Forel 1899. Costa Rica, Panama.

= *lacrymosa* Forel 1899. Synonymy, Longino (2007):57.

A. schimperi Emery 1893. Mexico to Argentina.

= *A. fiebrigi* Forel 1909. Synonymy, Longino (2007):58.

= *A. clariceps* Santschi 1933. Synonymy, Longino (2007):58.

= *A. pallida* Stitz 1937. Synonymy, Longino (2007):59.

A. snellingi Guerrero, Delabie & Dejean. New species. Panama

TAXONOMIC KEY TO SPECIES (GYNES) OF THE *AZTECA AURITA* GROUP [ADAPTED FROM LONGINO (2007)]

1.	Orange head and orange or light brown body; long scape, SI > 70	**2**
-	Uniform brown color; short scape, SI < 70	**7**
2.	Erect pilosity absent on dorsum of the head, lateral margins of the mesosoma, petiole, and gaster	**3**
-	Short, erect pilosity present on the dorsum of the head and mesosoma, petiole, and gaster	**6**
3.	Very pronounced vertex lobes appearing as elongate, horn-like projections (Fig. 6); a seemingly wide, U-shaped occipital margin	***diabolica* n. sp.**
-	Angulate vertex lobes never forming horn-like projections	**4**
4.	Head relatively broad CI > 99	***linamariae* n. sp.**
-	Head relatively narrow CI < 99	**5**
5.	Sides of the head flat and sub-parallel, only weakly diverging posteriorly; eyes more or less at mid-length of the head, HW < 1.30	***aurita***
-	Sides of the head flat and not sub-parallel, strongly diverging posteriorly; eyes anterior to the mid-length of the head, HW > 1.30	***laurae* n. sp.**
6.	Dense, short, erect pilosity on scape and tibiae; head relatively narrow (CI < 97)	***pilosula***
-	Scape and tibiae lacking erect pilosity; head relatively broad (CI > 97)	***lallemandi***
7.	Gastral dorsum lacking erect setae; HLA > 1.35	**8**
-	Gastral dorsum with erect setae; HLA < 1.35	**9**
8.	Head, scapes, mesosoma, legs and petiole with erect hairs; scapes relatively long, SL > 0.90	***schimperi***

- Head, scapes, mesosoma, legs and petiole devoid of any erect hairs; scapes relatively short, SL < 0.90 ..... ***andreae* n. sp.**
9. HLA about 1.3mm ..... ***lanuginosa***
- HLA about 0.86mm ..... ***nanogyna***

TAXONOMIC TREATMENT

Azteca andreae n. sp. Guerrero, Delabie & Dejean (Figs 1 & 2)

Holotype (gyne): FRENCH GUIANA, Sinnamary, 5°22'39"N 52°57'35"W, Carton nest in *Cecropia* sp tree, 24 Jul 2008, (A. Dejean, P-J Malé, S. Groc and J.H.C. Delabie) [CPDC]; **paratypes**: 7 gynes, same locality, [CASC,CPDC, ICN, JTLC, LACM, MZSP, RBINS].

Measurements of holotype: HLA 1.42, HLB 1.48, HW 1.08, AHW 0.72, SL 0.82, EL 0.34, OCW 0.08, CI 76, SI 58, MTSC 0.

Measurements of paratypes (N= 7): HLA 1.38–1.42, HLB 1.46–1.52, HW 1.06–1.10, AHW 0.70–0.76, SL 0.80–0.86, EL 0.32–0.36, OCW 0.06–0.08, CI 75–80, SI 57–61, MTSC 0.

Diagnosis.—*Azteca andreae* is a member of the *A. aurita* group with the body completely covered with small, widely scattered pits (foveate surface) bearing a very short white hair; scapes short, SI 57–61.

Gyne characters.—**Head**: Palpal formula 4,3. Dorsal surface of mandibles smooth and shiny; from an oblique angle from above, weak longitudinal waves can be observed that are not visible in full dorsal view, and with scattered small and widely-spaced holes, each with a short hair on the basal surface, with long hairs behind masticatory margin and anterior half of the outer margin of the mandibles; masticatory margin armed with strong apical and blunt tooth, sub-apical tooth, followed by very rounded teeth extending to the basal margin. Clypeal plate without conspicuous pilosity; medial clypeal lobe strongly convex and protruding, extending well beyond the lateral clypeal lobes. Head sub-rectangular, longer than wide; cephalic capsule in lateral view strongly convex in the front; posterior margin with blunt angulations, deeply excavated in the middle of the V-shape. Scape not reaching posterior margin of cephalic corner; funiculus covered with dense, long and appressed pilosity.

Mesosoma: Smooth and shiny, without conspicuous pilosity. Dorsal surface of propodeum much longer than posterior surface, the latter with a short projection at the base, tube-shaped and facing posteriorly. Edge of metapleural gland orifice bears long, golden hairs. Middle and hind tibiae lacking apical spur.

Metasoma: Petiolar node strongly subtriangular with rounded apex; anterior face of petiole excavated, posterior face nearly twice the length of anterior face; petiolar posteroventral lobe weakly convex behind, straight in the anterior half. Tergites and sternites of the gaster shiny.

Head, mesosoma, petiole and legs dark, reddish brown, gaster yellowish brown with some darker areas. Body shiny.

Worker characters.—**Measurements** (N= 5): HLA 1.18–1.36, HLB 1.20–1.46, HW 1.20–1.36, SL 0.84–0.96, EL 0.20–0.26, CI 100–102, SI 67–75.

Palpal formula 4,3. Middle and hind tibiae lacking apical spur. Same combination of characters as *Azteca schimperi* in Longino (2007). Minor workers with tube-like propodeal spiracles projecting outwards, unlike those of *A. schimperi*.

Male characters.—**Measurements** (N= 4): HLA 0.70–0.72, HW 0.67–0.68, SL 0.11–0.12, EL 0.30, CI 94–97, SI 16–17.

Head: Mandibles sub-triangular, outer edge twice as long as inner edge, masticatory margin unarmed, with only a small projection in the middle of margins and a sharp apical tooth; a basal tooth differenti-

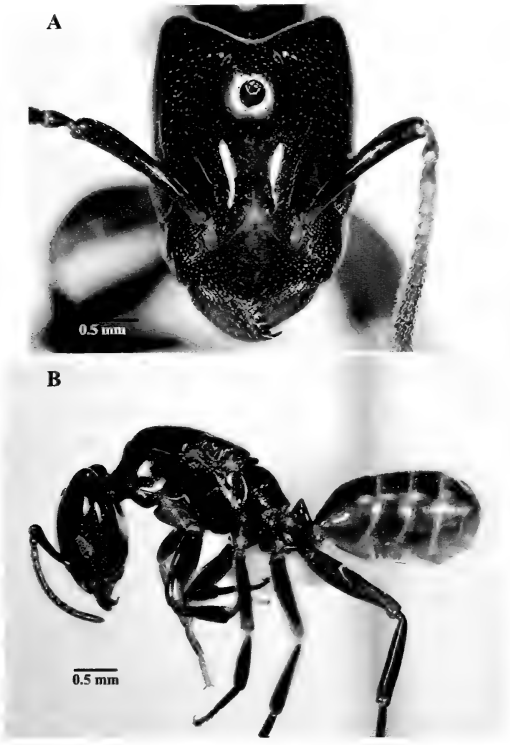

Fig. 1. Paratype female of *Azteca andreae* (French Guiana; CASENT 0179545). A). Full frontal view of the head of *A. andreae*. B). Lateral view of the body of *A. andreae*.

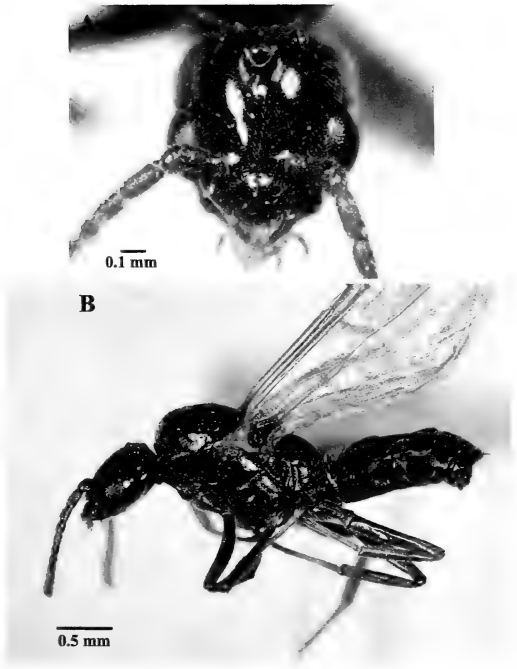

Fig. 2. *Azteca andreae* male from French Guiana (CASENT 0179546). A). Full frontal view of the head of *A. andrea*. B). Lateral view of the body of *A. andreae*.

ates masticatory and basal margins. Clypeal plate strongly convex, as medial clypeal lobe extends well beyond small, lateral clypeal lobes; surface smooth with small foveae near anterior ridge of clypeal plate. Scapes small, trapezoidal, thin at base and wider distally; pedicel small, nearly equal to maximum scape width; second funicular segment roughly twice as long as scape; remaining funiculus little longer than scape; scape with smooth surface and a few scattered hairs; funicular segments 3–11 with long, dense and appressed pilosity, surface densely punctate and dull. Eyes large, located near anterior half of the cephalic capsule, separated from mandible insertion by less than 0.1 mm; eyes break the plane on side of head. Lateral ocelli protruding slightly above vertex in dorsal view. Margins of the cephalic capsule, above the eyes, slightly convex; posterolateral corners rounded.

Mesosoma: Parapsidal furrows weakly developed. Anepisternum and katepisternum divided by a deep mesopleural groove. Anterior and posterior surfaces of propodeum undifferentiated. Propodeal spiracles visibly protruding.

Metasoma: Petiolar node rectangular with rounded corners and straight dorsal face; anterior surface much longer than posterior surface; petiolar node partly fused to gaster. Tergites and sternites smooth and shiny. Pygostyle thin and long, with distal half curved downwards and squared at the tip, smooth and shiny.

Body dark brown, shiny, slightly punctate in some areas, covered with very sparse decumbent, long white hairs.

Etymology.—Azteca andreae is named in honor of Andrea Dejean, the third author's wife, in acknowledgment of her considerable editorial help with myrmecology papers in English.

Range.—French Guiana.

Natural History.—This species constructs large, conspicuous globular carton nests at the base of the stem or near the crown of *Cecropia* trees (Fig. 4). Alain Dejean has observed and collected several *A. andreae* nests from trees in French Guiana, the vast majority of which were *Cecropia obtusa* Trecul. *A. andreae* can also nest on *C. palmata* Willd, which also often shelters *Azteca alfari* or *A. ovaticeps*. The nests observed by A. Dejean always were in pioneer vegetation highly-altered through human activity.

All nests collected contained colonies with many workers, dozens of winged females and few males; for example, type series of this species came from a colony with hundreds of workers, hundreds of winged females (only 55 were collected), five male, several brood and pupae, although no queen was observed. Other collections made by A. Dejean produced colonies with some physogastric females (Fig 5).

Comments.—*A. andreae* is close to *A. schimperi* but can be distinguished by morphological characters of gynes and males; the major workers of the two species are indistinguishable. *A. andreae* gynes conspicuously lack pilosity over the entire body, while *A. schimperi* gynes are densely covered with erect hairs on the head and mesosoma. The anteromedial portion of the clypeus protrudes more in *A. andreae* than in *A. schimperi*; the masticatory margin of the mandibles of *A. andreae* is armed with blunt teeth, while *A. schimperi* has sharp teeth. The scapes of *A. andreae* are significantly shorter than those of *A. schimperi* (0.80–0.86 vs. 0.94–1.01 mm, respectively); the posterior margin of the head is much more excavated in *A. andreae* than in *A. schimperi*, and the posterolateral corners are also more angular in the first species; another important character amongst the females of both species is the color: *A. andreae* females are a dark reddish brown, while *A. schimperi* females are uniformly brown.

The males of both species are very similar in color, type and distribution of hairs, and wing venation; however, when we examined the male *genitalia* of both species, we found that there are conspicuous differences. The pygostyle on *A. andreae* is smooth and shiny, thin, long, and with the distal half curved downwards and squared at the tip, while those on *A. schimperi* are short, thick and with a rounded tip (Fig. 3).

The major workers of both species are indistinguishable, although the workers of *A. andreae* have a relatively smaller head; however, the ranges of both species overlap. The minor workers are also undifferentiated, but *A. andreae* have thin, protruding tube-shaped propodeal spiracles, whereas *A. schimperi* are open at the propodeum.

The females of *A. lanuginosa*, *A. schimperi* and *A. andreae* are related to each other and show a clear gradation in the quantity, distribution and type of body hair. The first species is the only one of them with an abundant, erect pilosity all over the body, including the gaster (Longino 2007); it becomes sparse in *A. schimperi* and disappears altogether in *A. andreae* (in the latter two species, the gaster is devoid of any hair).

Azteca diabolica n. sp. Guerrero, Delabie & Dejean (Fig. 6)

Holotype (gyne): PANAMA, San Lorenzo Forest, IBISCA project, 9°16′47.58″N, 79°58′29.94′W, Flight-interception trap in the canopy, 3–13 Ago 2004 (M. Rapp) [CPDC]; **paratypes:** 1 gyne, same location, Fogging #FO-C3-6C, 13 Oct. 2004 (J. Bail) [RBINS]; 1 gyne, same location, Fogging FOG-R1-5, 20 Oct. 2003 (J. Schmidl) [ICN]. 2 gynes, same location, Fogging #J-2, 17 Oct. 2003 (J. Schmidl) [CPDC, MZUSP].

Measurements of Holotype: HLA 1.48, HLB 1.56, HW 1.12, AHW 0.72, SL 1.24, EL 0.30, OCW 0.06, CI 76, SI 84, MTSC 0.

Measurements of Paratypes (N= 2): HLA 1.60–1.62, HLB 1.64–1.74, HW 1.20–1.24, AHW 0.78–0.80, SL 1.34–1.36, EL 0.30–0.32, OCW 0.06, CI 75–77, SI 84–85, MTSC 0.

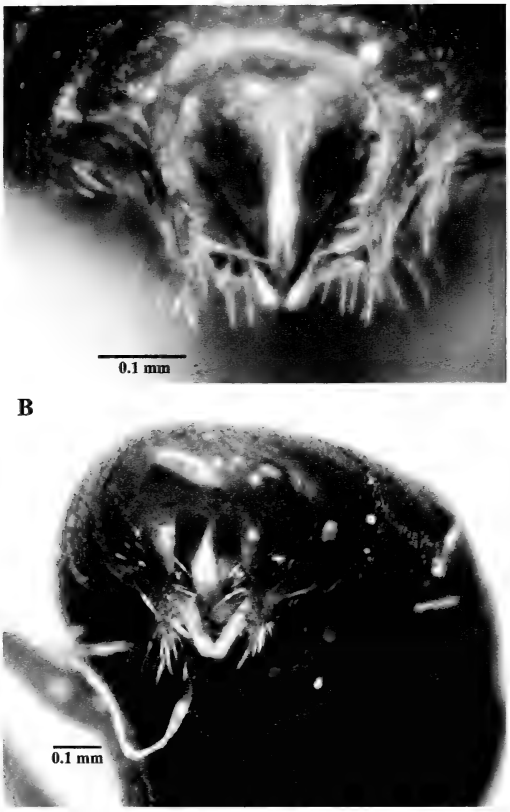

Fig. 3. Genitalia of male *A. andreae* and *A. schimperi*. The arrow indicates the pygostyle.

Fig. 4. *A. andreae* nests built in *Cecropia* spp. trees.

Diagnosis.—*Azteca diabolica* is a member of the *A. aurita* group with a deep and smoothly rounded excavation at the posterior vertex margin extending to the corners that form posteriorly-projecting rounded horns. Mesosoma smooth, shiny and hairless. Propodeal spiracles protruding. Gastral tergum and sternum with hairless, polished surface.

Gyne characters.—**Head**: Palpal formula is 4,3. Dorsal and ventral surfaces of head hairless. Dorsal surface of mandibles mostly smooth and shiny, with fine longitudinal striae near masticatory margin; masticatory margin armed with five teeth and two denticles, with no angle or tooth separating it from basal margin; basal margin slightly serrated; surface of mandibles with scattered, sub-decumbent long hairs. Clypeal plate with sub-decumbent, sparse pilosity; medial clypeal lobe strongly convex and protruding, extending well beyond lateral clypeal lobes. Head almost rectangular, somewhat swollen between ocellar region and compound eye; posterior margin highly angular, horn-like laterally, deeply excavate medially. When laid back, scape reaches prolongations of vertex at apex of posterolateral projection; scape and funiculus provided with abundant, nearly erect pilosity.

Mesosoma: Smooth and shiny, without appressed hairs. Middle and hind tibiae lacking apical spur. Dorsal surface of propodeum shorter than posterior surface; propodeal spiracles protruding.

Metasoma: Petiolar node bluntly triangular, posterior surface straight, twice as long as anterior surface; posteroventral petiolar lobe very low, very shallowly convex, ending posteriorly in a somewhat

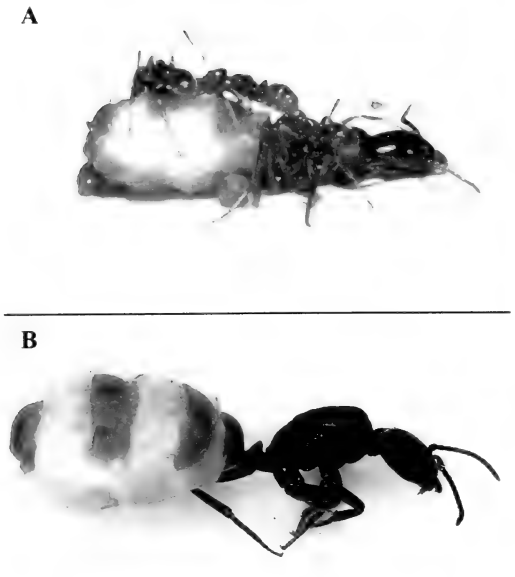

Fig. 5. Physogastric *A. andreae* queens from French Guiana. A. Physogastric *A. andreae* queen attended by workers. B. Preserved physogastric *A. andreae* queen.

abrupt shelf. Tergites and sternites hairless, smooth and shiny.

Body reddish brown, surface smooth and reflective.

Worker and male.—Unknown

Etymology.—The name refers to the form of the head of the gyne which suggests popular representations of the Devil.

Range.—Panama.

Natural History.—The five specimens were collected from the rain forest canopy, first with a flight-intercept trap, later by applying a chemical treatment to vegetation. Three gynes were collected by fogging; one from a tree where both *Azteca* sp.2 *chartifex* group and *Azteca instabilis* (Fr. Smith) occurred, the two others from a tree with *Azteca* sp.2 *chartifex* group. This suggests that *A. diabolica* may be a social parasite, in particular of carton-nesting species of the *chartifex* group.

Comments.—The gyne differs from those of other species in the *A. aurita* group in being almost hairless, having only sparse, short and decumbent hairs on the clypeus,

Fig. 6. Head of *Azteca diabolica* (Paratype female, Panama; ICN-022611), full frontal view.

mandibles and legs. Some species in the *aurita* group have a strongly pronounced lateral vertex margin, but none is as pronounced as in *Azteca diabolica*.

Azteca laurae n. sp. Guerrero, Delabie & Dejean (Fig. 7)

Holotype (gyne): BRAZIL, Rondônia, Parque Estadual Guajará Mirim, 10°19′17″S, 64°33′47″W, #5256, Malaise trap, 02 Mar. 1998 (J.R.M. Santos) [CPDC].

Measurements of Holotype: HLA 1.56, HLB 1.62, HW 1.46, AHW 0.90, SL 1.24, EL 0.36, OCW 0.06, CI 94, SI 79, MTSC 0.

Diagnosis.—*Azteca laurae* is a member of the *A. aurita* group with an inverted, cone-like (cuneiform) head whose sides strongly diverge from the lateral region; surface of head smooth and shiny, with very thin and weak punctations visible laterally by tilting the specimen (dorsal-oblique view), although these one more noticeably visible in the ocellar region (full frontal view).

Gyne characters.—**Head**: Palpal formula 4,3. Dorsal and ventral surface devoid of any type of hair, although very short and sparse hair covers a small portion of the genae. Dorsal surface of mandibles completely smooth and shiny, clearly seen in spaces between the sparse, long hairs. Masticatory margin of mandibles armed with four teeth and two denticles.

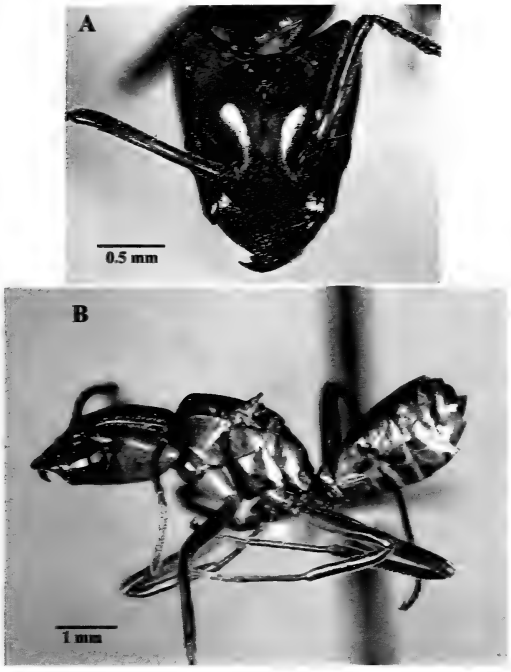

Fig. 7. Holotype female of *Azteca laurae* (Brazil; CPDC-5256). A). Full frontal view of the head of *A. laurae*. B). Lateral view of the body of *A. laurae*.

Clypeal plate covered with abundant short, nearly erect pilosity; medial clypeal lobe strongly convex, projecting outwards, with hairless anterior ridge extending well beyond lateral clypeal lobes. Vertex with prominent, rounded corners deeply excavated in middle in U-shape with gently-rounded tips. Ocelli in a loose clump, forming a dark stain in dorsoposterior region. Scapes barely reaching extensions of vertex; scapes and funiculus covered with abundant, short, sub-decumbent pilosity, shorter than maximum width of scape.

Mesosoma: Smooth and shiny, with no conspicuous hairs, only a few very short, appressed hairs becoming sparser towards katepisternal and propodeal region. Dorsal side of propodeum almost equal in length to posterior surface, nearly undifferentiated due to absence of a defined boundary; propodeal spiracles weakly protruding. Middle and hind tibiae lacking spurs.

Metasoma: Petiolar node triangular, sloping gently posteriorly; posterior margin almost twice as long as anterior; petiolar lobe weakly convex behind; ventral surface roughly parallel to dorsal surface. Gaster hairless, surface polished and very shiny.

Body reddish brown, surface smooth and reflective.

Worker and male.—Unknown

Etymology.—The name is in honor of Laura Mariano Delabie, the second author's daughter.

Range.—Western Amazonian Brazil.

Natural History.—The holotype was collected in the mature forest of the Parque Estadual Guajará Mirim, Rondônia, Brazil, using a Malaise trap.

Comments.—The gyne of this species is closely similar to *A. aurita*, differing in the amount and distribution of the hairs on the dorsum of the head and the scapes. *A. laurae* has very few short hairs on the genae, while the anterior part of the head of *A. aurita* is covered with a uniform vestiture of short, dense, white pilosity. The scapes of *A. laurae* are sparsely covered with short hairs, while those of *A. aurita* are densely covered by the same type of pilosity present in the dorsal region of the head. Another notable trait is the shape of the head, the sides of which are almost parallel in *A. aurita* (Fig. 8), while in *A. laurae* they diverge posteriorly, resulting in a cuneiform-shaped head (Fig. 7); the vertexal margin in *A. laurae* is wider and slightly more concave than in *A. aurita*.

Azteca linamariae n. sp. Guerrero, Delabie & Dejean (Fig. 9)

Holotype (gyne): COLOMBIA, Vaupés, Estación Biológica Mosiro-Itajura (Caparú), Antigua Cabaña, 1° 4'S, 69° 3'W, 60 m, Malaise trap, 18–27 mar 2003 (J. Pinzón), M.3610 – Insects of Colombia project [IAvH]; **paratype (gyne)**: BRAZIL, Rondônia, Parque Estadual Guajará Mirim, 10°19'17"S, 64°33'47"W, #5248, Malaise trap, 28 Jan. 1998 (J.R.M. Santos) [CPDC].

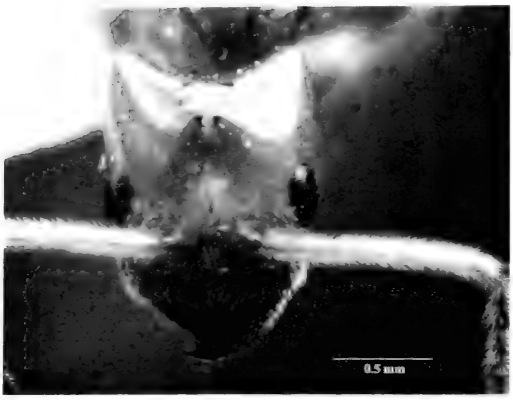

Fig. 8. Head of an *Azteca aurita* female from Panama, full frontal view.

Measurements of Holotype: HLA 1.86, HLB 2.0, HW 1.84, AHW 1.18, SL 1.48, EL 0.40, OCW 0.14, CI 99, SI 80, MTSC 8.

Measurements of Paratype: HLA 1.82, HLB 1.86, HW 1.82, AHW 1.16, SL 1.46, EL 0.44, OCW 0.14, CI 100, SI 80, MTSC 8.

Diagnosis.—Azteca linamariae is a member of the *A. aurita* group with the dorsal and ventral surfaces of the head, mesonotal dorsal region and gastral tergum and sternum covered with abundant, very thin, short, white, scale-like setae. It is the largest queen of any known species in the *aurita* group.

Gyne characters.—**Head**: Palpal formula 4,3. Ventral surface with abundant pilosity, as well as long, very closely spaced, erect hairs covering all head margins and back of foramen magnum. Mandibles smooth and shiny, with abundant decumbent pilosity, longer hairs toward masticatory margin. Clypeal plate covered with short, abundant pilosity; medial clypeal lobe strongly convex, but projected slightly toward the front, extending well beyond lateral clypeal lobes. Head nearly rectangular, slightly diverging laterally, flat in the ventral region; posterior margin deeply excavated, sharply angled with rounded corners. Scapes a significant distance from corners of vertex with nearly erect, short hairs approximately equal to half maximum width of scapes; funiculus cov-

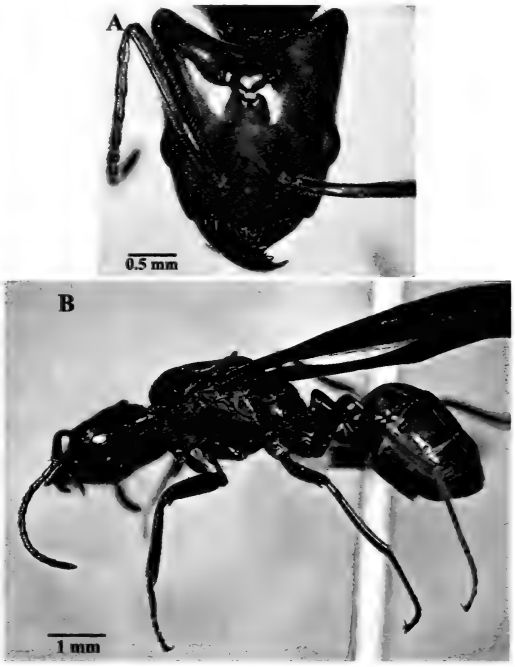

Fig. 9. *Azteca linamariae* (Holotype female, Colombia; IAvH- M 3610). A). Full frontal view of the head of *A. linamariae*. B). Lateral view of the body of *A. linamariae*.

ered with abundant, appressed, sub-decumbent pilosity much shorter than that of scapes.

Mesosoma: Smooth and opaque, with some sparse and scattered long hairs, mainly on promesonotal dorsum, mostly appressed below propodeal spiracle. Sides of propodeum shorter than posterior region; propodeal spiracles projecting slightly outward. Middle and hind tibiae lack spurs.

Metasoma: Petiolar node triangular, with front straight and nearly as long as posterior surface; posteroventral lobe often convex, inverted, and hump-like. Gaster smooth and polished, without long hairs.

Head reddish brown, mesosoma brown, gaster yellowish-brown with a highly polished and reflective surface.

Worker and male.—Unknown

Etymology.—This name is in honor of Lina María Ramos, the first author's wife, busy and active like an ant.

Range.—Amazonian Colombia and Brazil.

Natural History.—The holotype was collected in the upland Amazonian forest at the Mosiro-Itajura (Caparú) biological station in Vaupés, Colombia. This area is mainly covered by primary forest. The paratype was collected in a Malaise trap in the Parque Estadual Guajará Mirim, Rondônia state, Brazil.

Comments.—The gynes of this species are similar to those of *A. pilosula*, from which it is distinguished by hair characters. *A. pilosula* has long, dense, white hairs on all sides of the head and on other regions of the body, while *A. linamariae* has very thin, short, white, scale-like setae, as well as some emerging long hairs (like those of *A. pilosula*) covering the head margins and the back of the foramen magnum and promesonotal dorsum, but not the dorsum of the head, lateral margins of the mesosoma, petiole or gaster. *A. linamariae* is the largest known species in the group, and the gyne is much darker in color than that of *A. pilosula*.

The holotype and paratype differ only in the venation of the forewings. The forewings of both specimens have an r-rs cross-vein starting in the anteroinferior portion of the stigma; however, this cross-vein in the paratype is attached to Rs1 and Rs2 base veins. The holotype r-rs cross-vein, on the other hand, is attached to the Rs short vein. The latter diverges in Rs1 and Rs, posteriorly; moreover the paratype has two crossveins, 1 cu-a and 2cu-a, forming a small cell, while in the holotype there is only a crossvein, 1 cu-a, and no small cell. Despite this difference in the pattern of venation of the forewing and the great distance (around 1.350 km) between the two capture sites, these two specimens undoubtedly belong to the same species described above. Further material collection should confirm this identification and elucidate the small differences presented here.

Azteca snellingi n. sp. Guerrero, Delabie & Dejean (Fig. 10)

Holotype (major worker): PANAMA, Colón, San Lorenzo Forest (SLPA), área metropolitana, IBISCA project, 9°16.793'N, 79° 58.499'W, manual collection in the canopy, 26 Feb 2008 (N. B. Espirito Santo & S. P. Ribeiro) [CPDC]; **paratypes:** 6 major workers, same data as for holotype [1, CASC; 1, ICN; 1, JTLC; 1, LACM; 1, MZSP; 1, RBINS].

Measurements of Holotype: HLA 1.56, HLB 1.66, HW 1.60, SL 1.30, EL 0.30, CI 103, SI 83.

Measurements of Paratype (N=6): HLA 1.44–1.58, HLB 1.52–1.66, HW 1.44–1.60, SL 1.18–1.32, EL 0.24–0.30, CI 99–101, SI 81–88.

Diagnosis.—Azteca snellingi is a member of the *A. aurita* group with a large head, slightly wider than long, with margins strongly convex; metanotal groove wide and deep; workers have reddish brown head and dark brown body.

Worker characters.—**Head**: Palpal formula 4,3. Mandibles completely flat, apical tooth much larger than anterior; dorsal surface with dense longitudinal sculpture; surface rough and opaque. Median clypeal lobe strongly convex, extending well beyond lateral clypeal lobes. Sides of head strongly curved, corners of posterolateral margins angled; posterior margin (vertex) strongly concave. Scapes curved, not reaching posterolateral corners of head.

Mesosoma: In lateral view, pronotum weakly convex or straight toward anterior, without a posterior face. Mesonotum strongly convex, rising well above pronotum like a hump; globular in front, gently flattened posteriorly. Metanotal sulcus large and deep. In lateral view, propodeum roughly flat, dorsal face much larger that the posterior face. Middle and hind tibiae lacking spurs.

Metasoma: Petiolar node large, with rounded end, sloped at front; posterior face nearly twice as large as the anterior face. Ventral lobe conspicuously uniformly convex.

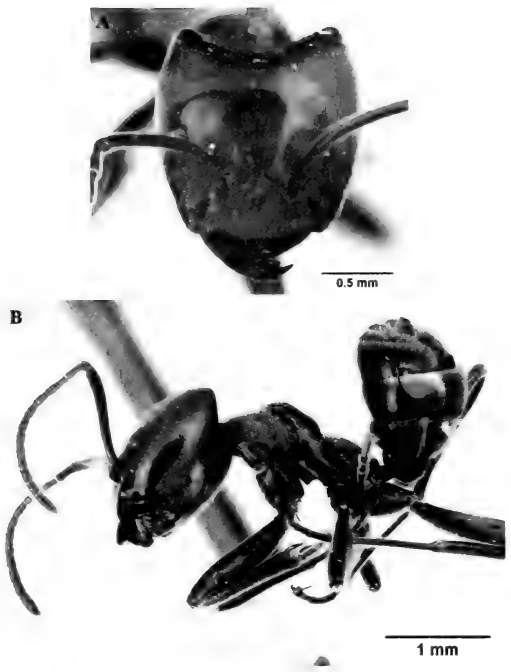

Fig. 10. *Azteca snellingi* (Paratype, worker major, Panama; CASENT 0179543). A). Full frontal view of the head of *A. snellingi*. B). Lateral view of the body of *A. snellingi*.

Body entirely covered with fine, dense punctations. Pubescence thin and whitish, appressed, covering each tagma; some setae conspicuous near base of ventral lobe of petiole and sternites 2–4. Body with shiny, weakly reflective surface. Part of head, scape and mandibles dark reddish-brown. Posterior third of the head dark brown. Mesosoma, legs, petiole and gaster dark brown.

Gyne and male.—Unknown

Etymology.—This ant is named in honor of Roy Snelling, our colleague and friend, who contributed notably to the knowledge of Hymenoptera.

Range.—Panama.

Natural History.—Specimens of the type series were collected at different heights on the canopy in the San Lorenzo forest, Panama. Two were collected at 21m from a *Pouteria caimito* (Ruiz & Pav.) Radlk. (Sapotaceae) tree. Others were collected at 20m and 23.7m height from *Luehea seemannii* Planch. & Triana. (Tiliaceae).

Comments.—This species is close to *A. aurita* and *A. pilosula*. While workers of *A. aurita* and *A. pilosula* are undistinguishable (Longino 2007), those of *A. snellingi* have a distinctly larger head, as long as it is wide. Posterior margin of the head with a deep concavity and continuous while the other two species has a V-shaped concavity. In general *A. snellingi* is a species with workers (reproductive castes unknown) larger than *A. aurita* and *A. pilosula* workers (CI 99–101 vs. *A. aurita*: CI 85–88, *A. pilosula*: CI 89–90). Sides of head strongly convex in *A. snellingi*, however, some *A. pilosula* workers (*A. lacrimosa* syntype and lectotype, synonymized by Longino 2007) have curved margins but not become as convex as in *A. snellingi*. *Azteca snellingi* mandibles, with the dorsal surface as those of *Azteca aurita*, but those of *A. snellingi* are more opaque. Furthermore, the anterior region of the mesonotum is higher and more globular in *A. snellingi*. Metanotal groove is wide and deep in *A. snellingi* whereas other two species is absent or inconspicuous.

Azteca snellingi also differs from *A. aurita* and *A. pilosula* in the distribution and kind of the hairs on the body. *A. snellingi* workers have no erect hairs in the petiolar node in contrast *A. pilosula* workers have erect hairs on the anterior face and apex of the petiole. Lateral margins of petiole lacking of any pilosity whereas *A. pilosula* has erect, conspicuous and scattered setae. *A. snellingi* workers have no erect hairs on the posterior margin of the head whereas *A. pilosula* workers posterior margin of head with sparse, very short erect setae grading into white pubescence (Longino 2007). *A. snellingi* is reddish-brown and the body is entirely dark brown, which is notable in this species as no other known worker in the *aurita* group presents this coloration pattern.

This species will key to couplet 2 in Longino's (2007) key to *A. aurita* group workers. The following modifications to the key will accommodate the new species:

2. Head relatively broad (CI > 105); posterolateral margins of the vertex rounded and cordate, not bluntly angulate ..... *A. lallemandi*
- Head relatively narrow (CI < 106); posterolateral margins of the vertex bluntly angulate 3
3. Head light orange brown; mesosoma, legs, and gaster darker reddish-brown .... *A. aurita, A. pilosula*
- Scape, mandibles and a part of the head dark reddish-brown; posterior third of the head is dark brown. Mesosoma, legs, petiole and gaster dark brown .... *A. snellingi* n. sp.
4. Pubescence dilute and tightly appressed; color usually brown with an orange head ... . *A. schimperi*
- Pubescence more abundant, giving a somewhat wooly appearance; color all brown ..... *A. lanuginosa*

Other relevant material relative to this group was also studied:

Azteca aurita Emery (Fig. 8): COLOMBIA, Putumayo, PNN La Paya, riparian forest, 0°7'S, 74°56'W 320m, Malaise trap (M.2440), 19 Sep-1 Oct 2001 (R. Cobete) – 1 gyne [IAvH]. BRAZIL, Amazonas, Manaus, 12 sep 1962, # 3414, (K. Lenko) – 1 male, 3 minor workers [MZSP]; Mato Grosso, Sinop, 12°31'S, 55°32'W, Oct 1974, #12458, (M. Alvarenga) – 3 major workers [MZSP]; Mato Grosso, Vila Vera, Oct 1973, #10348 (M. Alvarenga) – 1 gyne [MZSP]; Para, Belém, 12–19 Aug 1962 (K. Lenko) – 1 dealate gyne [MZSP]. PANAMA, Colon, San Lorenzo Forest, IBISCA project, 9°16.793'N, 79°58.499'W, flight-interception trap in the canopy, 3–13 Ago 2004 (M. Rapp) – 2 gynes [CPDC]; same location, fogging (FO-R3-05c), 13 Oct 2004 (J. Bail) – gyne [CPDC]; same location, fogging (FOG-R1–4), 20 Oct 2003 (J. Schmid) – 1 gyne [CPDC]. PERU, Cusco, Pillcopata, 7 Dec 1974, #15, (J.A. Escalante) – 1 minor worker, 2 major workers [MZSP].

Azteca lallemandi Forel: BRAZIL, Bahia, Ilhéus, Praia do Norte, 27 Jun 2004 (J.H.C. Delabie) – 1 gyne [CPDC]; same location, 04 Dec 2004 (J.H.C. Delabie) – 3 gynes [CPDC]; same location, 27 Dec 1994 (I.C. Nascimento; J.H.C. Delabie) – 5 gynes [CPDC]. PANAMA, San Lorenzo Forest, IBISCA project, 9°16'47"N, 79°58'W, mosaic, Oct 2003 (A. Dejean, J. Orivel, B. Corbara, H.-P. Aberlenc & M. Leponce) – 1 gyne [CPDC]; same location, fogging (FO-R3-05re, FO-R3-01), 18 May 2004 (J. Schmidl & J. Bail) – 2 gynes [CPDC]; same location, light trap, (LC3-C3-3), 20 May 2004 (A. Cornejo *et al.*) – queen [CPDC].

Azteca lanuginosa Emery: BRAZIL, Rio de Janeiro, Cascadura,1 Jan 1906, # 2317 – 2 minor workers [MZSP].

Azteca pilosula Forel: BRAZIL, Bahia, Ilhéus, Ilhéus - Para, (J.H.C. Delabie) – 1 gyne [CPDC].

Azteca schimperi Emery: BRAZIL, Amazonas, Manaus, 14 Apr 1981, Carton nest in *Cecropia concolor*, (INPA #428F) – 1 alated gyne, 1 male (measured), 2 minor workers [MZSP]; measurements of *Azteca schimperi* male: HLA 0.74, HW 0.66, SL 0.10, EL 0.28, CI 89, SI 14. COSTA RICA, San Jose de Costa Rica, (H. Schmidt) – 1 major worker [MZSP].

DISCUSSION

Longino (2007) proposed four features that distinguish the species in the *aurita* group from other species of ants of the genus *Azteca* (see introductory section), but one of those, the proportion HLB/HLA > 1.04, is not a consistent and stable feature within some of the females studied here (*e.g.*, *A. linamariae* paratype). This trait, therefore, should not continue to be used as diagnostic tool for the *aurita* group while all the other traits are strongly consistent: the palpal formula is 4,3; the middle and hind tibia lack an apical spur; the anteromedial border of the clypeus is strongly convex and extends well beyond the anterolateral clypeal lobes. These traits can, however, still be of great taxonomic value for separing the *aurita* group from other groups of species in the genus *Azteca*.

Fig. 11. *Azteca schimperi* major worker with vestigial wings, Costa Rica.

Until now, *Tapinoma nigerrimum* (Nylander) is the only species in the Dolichoderinae subfamily for which winged or stumped workers have been reported (Scupola 2008), something that is always considered to be a characteristic of gynes. Unexpectedly, the examination of the *Azteca aurita* group material coming from MZSP allowed us to observe a major worker of *A. schimperi* coming from Costa Rica with all of the morphological characters of a worker except for its vestigial wings (Fig. 11). This worker presents some characteristics that differentiate it from normal workers: the head is a little larger than the normal major workers from the same species (HLA: 1.56 vs. 1.16–1.51 mm), the median ocellus a little more developed and similar to that of the gynes of *A. schimperi*, and there is the presence of wing rudiments on the mesosoma. The elements that determine these kinds of morphological anomalies are generally considered to be environmental factors, as these are essential for the determination and development of the casts (Scupola 2008); these environmental factors, which have a decisive function in the formation of a hybrid phenotype, are poor nutrition and different chemicals (Heinze 1998). Nevertheless, simple genetic accidents, viruses or parasites can also provoke the development of abnormalities. This is the first report of the intercast syndrome in the genus *Azteca* and the second for the Dolichoderinae subfamily, after the results reported by Scupola (2008) for *Tapinoma nigerrimum*.

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LITERATURE CITED

Basset, Y., B. Corbara, H. Barrios, P. Cuénoud, M. Leponce, H.-P. Aberlenc, J. Bail, D. Bito, J. R. Bridle, G. Castañomeneses, L. Cizek, A. Cornejo, G. Curletti, J. H. C. Delabie, A. Dejean, R. K. Didham, M. Dufrêne, L. L. Fagan, A. Floren, D. M. Frame, F. Hallé, O. J. Hardy, A. Hernandez, R. L. Kitching, T. M. Lewinsohn, O. T. Lewis, M. Manumbor, E. Medianero, O. Missa, A. W. Mitchell, M. Mogia, V. Novotny, F. Ødegaard, E. Gama de Oliveira, J. Orivel, C. M. P. Ozanne, O. Pascal, S. Pinzón, M. Rapp, S. P. Ribeiro, Y. Roisin, T. Roslin, D. W. Roubik, M. Samaniego, J. Schmidl, L. L. Sørensen, A. Tishechkin, C. van Osselaer, and N. N. Winchester. 2007. IBISCA-Panama, a large-scale study of arthropod beta-diversity and vertical stratification in a lowland rainforest: rationale, description of study sites and field methodology. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* 77: 39–69.

Emery, C. 1893. Studio monografico sul genere *Azteca* Forel. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna* 5: 119–152.

Forel, A. 1899. Formicidae. *Biologia Centrali-Americana* 3: 1–160.

Hölldobler, B. and E. O. Wilson. 1990. *The Ants*. Harvard University Press, Cambridge, MA. 732 pp.

Heinze, J. 1998. Intercastes, intermorph, and ergatoid queens: who is who in ant reproduction? *Insect Sociaux* 45: 113–124.

Longino, J. T. 1989. Taxonomy of the *Cecropia*-inhabiting ants in the *Azteca alfari* species group: evidence for two broadly sympatric species. *Contributions in Science (Natural History Museum of Los Angeles County)* 412: 1–16.

———. 1991a. *Azteca* ants in *Cecropia* trees: taxonomy, colony structure, and behavior. Pp. 271–288 *in*: *Ant-Plant Interactions*, Huxley, C., and D. Cutler eds., Oxford University Press, Oxford.

———. 1991b. Taxonomy of the *Cecropia*-inhabiting *Azteca* ants. *Journal of Natural History* 25: 1571–1602.

———. 1996. Taxonomic characterization of some live-stem inhabiting *Azteca* (Hymenoptera: Formicidae) in Costa Rica, with special reference to the ants of *Cordia* (Boraginaceae) and *Triplaris* (Polygonaceae). *Journal of Hymenoptera Research* 5: 131–156.

———. 2007. A taxonomic review of the genus *Azteca* (Hymenoptera: Formicidae) in Costa Rica and a global revision of the *aurita* group. *Zootaxa* 1491: 1–63.

Scupola, A. 2008. Presence of brachypterous intercastes in *Tapinoma nigerrimum* (Nylander, 1856) (Hymenoptera, Formicidae). *Bollettino del Museo Civico di Storia Naturale di Verona, Botanica e Zoologia* 32: 157–160.

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Social Behaviours in Solitary Bees: Interactions Among Individuals in *Xeralictus bicuspidariae* Snelling (Hymenoptera: Halictidae: Rophitinae)

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Abstract.—Understanding behavioural interactions among ancestrally solitary species is key to understanding the evolutionary origins of group living and cooperation. Previously, Packer (2006) showed that circle tube arenas can be used to evaluate the social status of species for which nesting data are unavailable. We used circle tube arenas to study the behaviour among 30 female dyads of the solitary halictid bee, *Xeralictus bicuspidariae* Snelling, a member of the subfamily Rophitinae, all members of which are ancestrally solitary. Overall, 75.2% of frontal encounters resulted in avoidance, 20.7% in aggression, and 4.1% in a successful pass, values which are similar to those previously observed in solitary halictids. Although passing events, which are interpreted as cooperative behaviour, were rare, they were significantly correlated with bees' rates of approach and avoidance, and also with differences between dyad members in rates of ovarian development. Rates of aggression were not correlated with physical traits of females or with other behaviours. We compare the circle tube behaviour of *X. bicuspidariae* to previously studied solitary and social halictids, and provide statistical support for this method of assessing social status.

The origin of eusociality is one of the major events in the evolutionary history of life (Szathmáry and Maynard Smith 1995), yet our understanding of what transpires during transitions to sociality remains poor. One reason is the great age at which most solitary to eusocial transitions took place – over 100 million years ago for termites, ants, and vespid wasps (Wenzel 1990; Martinez-Delclos and Martinell 1995), perhaps somewhat less in the bees (Michener and Grimaldi 1988), and around 20 million years ago in the three main lineages of eusocial Halictinae (Brady et al. 2006). The great age of these social lineages means that to investigate the evolutionary origins of sociality, we must often use comparative methods based on detailed knowledge of the behaviour of extant species. However, a second reason for our incomplete understanding of the origins of eusociality stems from our poor knowledge of solitary species, whose behaviour is most likely to represent the ancestral forms from which sociality evolved.

Sweat bees (Halictidae: Halictini and Augochlorini) are the most socially variable group of animals on earth, including species that run the gamut from obligately solitary to obligately social, with sociality varying from communal to semisocial and eusocial forms (Schwarz et al. 2007). There are even examples of intraspecific social polymorphism, in which solitary or social behaviour is expressed within or among populations, often in response to variability in environmental conditions (Schwarz et al. 2007). The ecological processes that shape the social behaviour of modern halictines are often considered to be analogous to those that shaped the evolution of major social transitions in the subfamily as a whole, including at least three origins of eusociality and multiple reversions to

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solitary behaviour (Danforth et al. 2003; Danforth et al. 2008).

Recent behavioural studies provide intriguing evidence that behavioural transitions from solitary to social behaviour may occur easily and rapidly. Jeanson et al. (2005) observed that in forced associations of solitary *L. (Chilalictus)* NDA-1 or of communal *L. hemichalceum*, both dominance interactions and division of labour arose as natural outcomes of normal solitary behavioural patterns expressed in the context of novel, social environments, the effect being stronger in the solitary than in the communal species. A similar phenomenon occurred in experiments on solitary *Ceratina* carpenter bees (Apidae, Xylocopinae) when females were forced to nest in social associations (Sakagami and Maeta 1977). This suggests that at the very beginning of evolutionary transitions to caste-based sociality, 'emergent' social behaviour by solitary bees could provide the behavioural substrate upon which natural selection acts, before the evolution of caste-based sociality. This fascinating possibility makes understanding the behaviour of obligately solitary bees all the more critical.

Although behavioural interactions among individuals of social and socially polymorphic sweat bees have been studied in detail on numerous occasions (Breed et al. 1978; Buckle 1984; McConnell-Garner and Kukuk 1997; Wcislo 1997; Soucy 2002), solitary species have received less attention. Consequently, we know little about the potential for social interactions among individuals of solitarily nesting species, and how naturally occurring variation in individual behaviour might impinge upon the development of sociality remains obscure. Of course, one problem with studying the behaviour of solitary bees is a dearth of opportunities for observing known individuals under natural conditions at sufficient frequency to permit detailed analysis. Fortunately, a recent comparative study suggests that the circle tube arena, a circle of clear plastic tubing in which bees are forced to interact (Breed et al. 1978), is one route to obtain sufficient behavioural data on interactions among individuals of solitary species (Packer 2006).

In this paper we analyse the results of a detailed study of interactions among individuals in a solitary species of the bee family Halictidae. *Xeralictus bicuspidariae* Snelling is a member of the halictid subfamily Rophitinae with several advantages as a study organism. First, the phylogenetic position of rophitine bees suggests that their solitary behaviour is ancestral, i.e. there is no evidence that there has been any sociality in the evolutionary history of the entire subfamily (Danforth et al. 2008; Patiny et al. 2008), so any potential for social interactions that might be induced experimentally, is part of its solitary ground plan. Second, this bee exhibits considerable variation in colour of the metasoma of females (Snelling and Stage 1995) such that pairs can easily be chosen to permit individual recognition without the intervention of artificially marking the bees (marking has been shown to influence interactions among individuals; Packer 2005). Third, it is a large bee, facilitating observations of behaviours.

METHODS

Xeralictus bicuspidariae was studied at Dome Rock Road, La Paz County, Arizona, USA, in April 2005. Female bees were collected from flowers of *Mentzelia* (Loasaceae) and retained in microcentrifuge tubes for no more than 30 minutes before behavioural observations commenced. This duration between capture and observation was maintained to reduce the effect of captivity-induced physiological changes upon behaviour (Pabalan et al. 2000). Two bees were then placed simultaneously in a clean, plastic circle tube of internal diameter 7 mm and length 20 cm. Simultaneous entry precludes ownership effects (Wcislo 1997), and this tube diameter was sufficient for the two individuals to pass one another and to turn around (Packer 2005), but

narrow enough that one bee could block an attempted pass by the other. Observations lasted for fifteen minutes, a time period sufficient for differences in behaviour between individuals within a pair to be detected, and took place outdoors in the shade. The metasomal colour of females varied from entirely brick red to entirely dark brown (Snelling and Stage 1995); pairs were set up with one red and one dark female that could be easily differentiated by the observer without being artificially marked. Several experiments were terminated when discrimination between the individuals was found to be more difficult than expected.

An approach was taken to have occurred when individuals came within a distance of one body length of each other (Kukuk 1992; Packer 2005). Both frontal (head to head) and front-to-back (head to tail) encounters were assessed and their outcomes classified into categories: approaches, aggression, avoidance and passes. Aggressive interactions included nudges, lunges and C-postures. Interactions that resulted in avoidance arose when one individual moved away from a stationary individual or they both moved away from each other. A pass was scored when the two bees manoeuvred to permit one to move past the other, or they both moved past one another simultaneously. All behavioural observations were carried out by LP, and are therefore directly comparable to the data presented in Packer (2006). For more detailed descriptions of individual behaviours, see Batra (1966).

All bees were measured and assessed for relative age and reproductive condition as follows. Head width was measured as the greatest distance across the compound eyes; this was the greatest diameter of the head in dorsal view. Relative wear was assessed from mandibles, scored from 0 (unworn) to 6 (worn to the base of the subapical mandibular tooth), and from wings (the total number of nicks along the margin of the left forewing).

Reproductive status was estimated based upon dissection of the metasoma. The spermatheca was inspected for the presence of sperm and ovarian development was assessed by estimating the size of oocytes in each ovariole relative to the size of a fully developed oocyte, and summing the resulting proportions across all six ovarioles. As expected for a solitary bee during nest provisioning, all females had mated and so matedness was not considered further.

Statistical analysis.—In circle tubes, the behaviour of each member of a pair is affected by the behaviour of the second member of the pair. This creates a problem of statistical non-independence between members of each dyad. A second problem is variation in behavioural rates among pairs – some pairs are very active and some do almost nothing. A common approach has been to standardize focal behaviors by the encounter rate, which in effect means all the behaviours are analyzed as ratios, so information related to absolute frequency is lost and the statistical problems of analysing ratios are gained. To address these issues, we present an approach somewhat different than in previous circle tube studies. First, when behavioural patterns of individuals are considered, we analyse only one individual per dyad (red bees or dark bees), which avoids inflating the number of degrees of freedom in each measurement. Second, when properties of dyads are considered, we analyse both behavioural frequencies and physical traits in terms of differences between each bee in a pair. Correlations between trait differences can be interpreted in the same way as correlations between the traits themselves. For instance, a negative correlation between head width difference and wear difference would indicate that larger bees tended to be less worn. All differences between pair members were calculated as (value for red bee) – (value for dark bee), except for head width (HW) difference, which was calculated as (red HW – dark HW) / average HW.

Table 1. Physical characteristics of adult female *Xeralictus bicuspidariae* used in circle tube experiments. Signed rank tests were used to compare the physical characteristics of red and dark females in each dyad; non-significant (n.s.) results indicate that overall, red and dark females were equivalent.

Variable	Mean	SD	Range	Signed rank test
Head width (mm) (n=56)	7.4	0.24	7.0–8.0	S = −22.5, n.s.
Mandibular wear (n=56)	2.1	1.2	0–5	S = 31.5, n.s.
Wing wear (n=48)	8.0	5.1	0–20	S = 4.0, n.s.
Total ovarian score (n=55)	1.7	0.4	0.5–2.6	S = 8.0, n.s.

All variables, including differences, were checked for normality using the array of tests in SAS 9.1 (PROC UNIVARIATE); since several variables were non-normally distributed, we mainly used non-parametric statistical methods. Additionally we used principal components analysis (PCA) to further explore and confirm relationships among physical and behavioural variables in *X. bicuspidariae*. Initially, the PCA was based on eight variables (entered as untransformed differences between females in mandibular wear, wing wear, head width, total ovarian score, approach frequency, aggressive frequency, avoidance frequency, and pass frequency). However, since Kaiser's Measure of Sampling Adequacy (MSA) with all eight variables had a value of only 0.467, the variable with the lowest communality measure (head width) was dropped from the PCA. With the remaining seven variables, MSA=0.63, which exceeds the 0.6 criterion. We present both factor loading scores (the degree to which each variable influences the inferred factors) and communality estimates (a reliability score which estimates the proportion of variance in each variable that is jointly explained by all three factors).

Packer (2006) argued that the social status of halictine bees can be accurately assessed using circle tube assays of females, even in the absence of nesting data. Solitary bees should be characterized by high levels of avoidance behaviour, communal bees by high levels of cooperative behaviour (passing) and low levels of aggression, and semisocial and eusocial bees by low levels of cooperation and high levels of both aggression and avoidance. We used discriminant functions analysis (DFA) to assess how accurately *X. bicuspidariae* and 21 other species (references in Packer 2006) can be categorized as solitary, communal, or semi and eusocial, based on the percentages of avoidance, aggression, and passing behaviours in circle tubes.

RESULTS

Circle tube assays.—Physical traits of the 60 females used in 30 circle tube trials are presented in Table 1. There were no significant correlations among body size, degree of wear, and degree of ovarian development within individuals used in the behavioural tests, although degree of mandibular wear was positively correlated with degree of wing wear (Pearson correlation coefficient, $r=0.55$, $n=48$, $p<0.0001$). All females had at least one ¼-size, developing oocyte, and 25 of 52 (48%) dissected females contained a full-size oocyte, ready to lay. The mean difference between red and dark females in each dyad for each of these characteristics, was zero (Table 1), so bee colouration had no significance other than providing a convenient identification tool for the observer.

The frequencies of each of the four classes of behaviour per dyad and per female are given in Table 2. The most frequent behaviours were approaches (32.5 per dyad) and avoidance (25.1 per dyad), followed by aggressive behaviours (6.7 per dyad) and passing (1.2 per dyad).

Table 2. Behavioural frequencies for approach, avoid, pass, and aggressive behaviours. Note that 'aggression' includes C-postures, biting, and pushing. Since the behavioural rates of each member of a dyad are non-independent, only one bee per dyad is used to provide an estimate of behavioural frequencies per individual. Measurements of mutual behaviour refer to simultaneous performance of that behaviour by both members of a dyad. Sample size N=30 dyads, except where otherwise noted.

Behaviour	Rate	Mean	SD	Range
Frontal encounters	Dyad total	33.0	8.3	13–46
Approach	Dyad total [1]	32.5	9.1	11–52
	Red female [1]	4.6	4.8	0–22
	Dark female	7.6	7.4	0–35
	Mutual	20.3	10.6	0–44
Avoid	Dyad total	25.1	7.5	10–37
	Red female	9.3	4.3	3–19
	Dark female	9.7	4.3	0–20
	Mutual	6.1	4.0	0–13
Pass	Dyad total	1.2	1.1	0–4
	Red female	0.3	0.5	0–2
	Dark female	0.2	0.6	0–3
	Mutual	0.7	0.9	0–3
Aggression	Dyad total	6.7	5.0	1–19
	Red female	3.8	3.8	0–16
	Dark female	2.9	3.0	0–11

[1] N=29

Overall, 75.2% of frontal encounters resulted in avoidance, 20.7% in aggression, and 4.1% in a successful pass.

Aggressive acts were observed in all 30 pairs, and by 52 of the 60 (87%) individuals assayed. Withdrawals were also observed in all 30 pairs; only 1 bee of 60 (2%) did not display a unilateral withdrawal, but she did take part in a mutual (bilateral) withdrawal. Passing or cooperative acts were rare, being observed in only 22 of 30 (73%) pairs. Of a total of 35 passes, 20 (57%) were bilateral (both bees moved past each other) and 15 (43%) were unilateral (1 bee moved past the other bee).

Based on behavioural frequency differences (red bee – dark bee), three behaviours, approach, avoid, and pass were found to be mutually positively correlated (i.e. the bee that did one behaviour more frequently also did the other behaviour more frequently; Spearman rank correlations: approach vs. avoid, $r=0.798$, $n=29$, $p<0.0001$, approach vs. pass: $r=0.577$, $n=29$, $p=0.001$; avoid vs. pass: $r=0.460$, $n=30$, $p=0.010$), but none was correlated with the frequency of aggression (aggress vs. approach: $r=-0.224$, $n=29$, n.s.; aggress vs. pass: $r=-0.106$, $n=30$, n.s.; aggress vs. avoid: $r=-0.193$, $n=30$, n.s.).

Differences between bees with respect to head width, wing wear, and mandibular wear were not significantly correlated with differences in behavioural frequency for any of the behaviours. Differences in total ovarian score did correlate positively with the rates of approach and pass, although not with either avoidance or aggressive frequencies (Table 3, Fig. 1). In other words, the female with greater ovarian development was almost significantly likely to approach and was significantly more likely to pass than the female with lesser ovarian development.

A principal components analysis (PCA) further describes behavioural and physical variation among female interactants in circle tubes. As outlined in the Methods, the PCA (Table 4) included all variables except head width, which contributed little to understanding variation among the dyads. Three factors had eigenvalues > 1.0 and were retained, explaining 77.9% of the variation among dyads. Factor 1 was

Table 3. Influence of female physical status on behaviour. Spearman rank correlations were based on differences in both female traits and differences in behaviour frequencies (red bee – dark bee). Positive correlations indicate that the bee with the greater trait value exhibited the behaviour more frequently.

	Behaviour (N=number of dyads)			
Physical trait of females	Approach	Avoid	Cooperate	Aggression
Head width	0.197 (27)	0.018 (28)	−0.054 (28)	0.292 (28)
Wing wear	0.020 (20)	−0.123 (21)	−0.092 (21)	0.077 (21)
Mandibular wear	−0.007 (27)	−0.100 (28)	−0.068 (28)	0.215 (28)
Total ovarian score	0.451 (26), p=0.062	0.250 (27)	0.435 (27), p=0.023	−0.132 (27)

most influenced by non-aggressive behaviour and ovarian development, reflecting the previously noted positive association between ovarian development and approach and passing frequencies. Factor 2 was influenced mainly by mandibular and wing wear; thus Factor 2 describes variability in wear differences among dyads, and so does not reflect behavioural variation. Factor 3 was influenced mainly by aggression. PCA based only on the four behavioural frequency differences, resulted in two factors that together explained 79.7% of the variation among

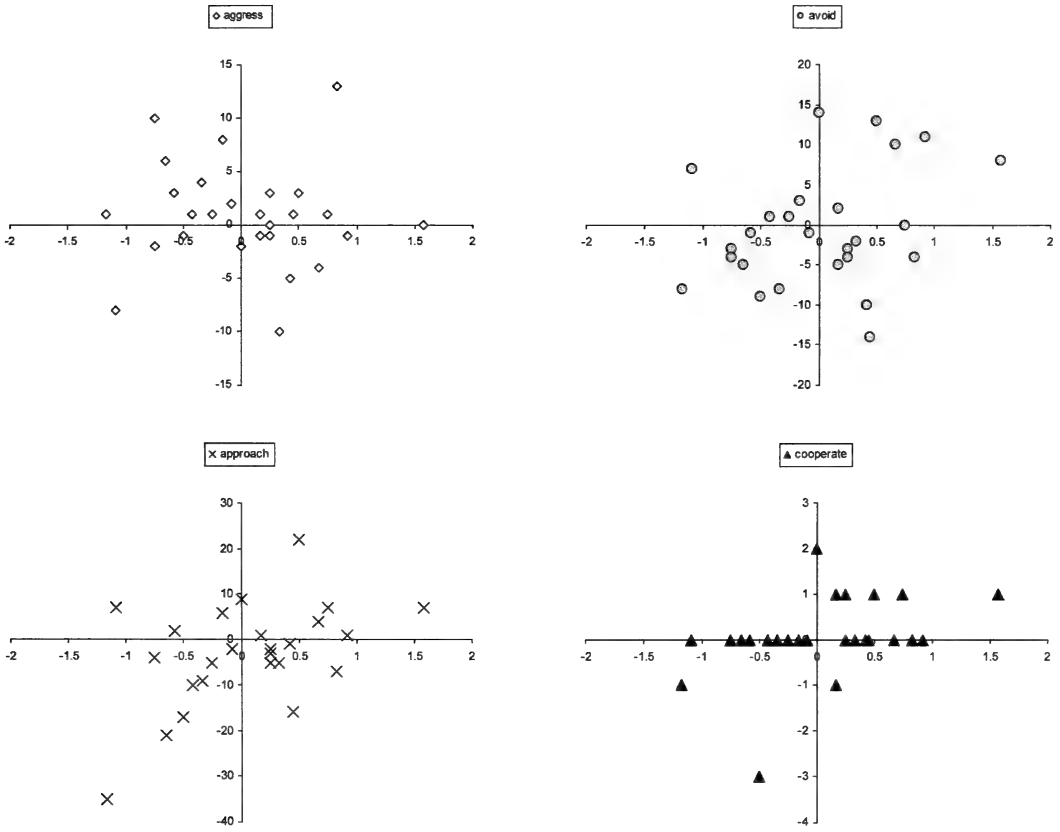

Fig. 1. Influence of ovarian development (OD, horizontal axes) on different behaviours (vertical axes), scored in terms of the differences between individuals (red-dark). Positive values on the horizontal and vertical axes indicate a greater value for the red bee, whereas negative values indicate a greater value for the dark bee. Top left: OD vs. aggression. Top right: OD vs. avoidance. Bottom left: OD vs. approach frequency. Bottom right: OD vs. cooperation (pass).

Table 4. Principal components analysis describing variation among dyads based on differences between interactants in both physical and behavioural traits. Three factors were retained with eigenvalues > 1, explaining a cumulative total of 77.9% of the variation among dyads. Relatively strong factor loading scores (>0.6) are indicated in boldface. Communality estimates describe the proportion of variance in each trait that is jointly explained by Factors 1, 2 and 3. Kaiser's overall Measure of Sampling Adequacy (MSA) was 0.6312.

Trait (difference between females)	Factor 1	Factor 2	Factor 3	Communality estimate
Mandibular wear	0.0124	**0.9064**	−0.0567	0.4962
Wing wear	−0.1391	**0.7738**	−0.5193	0.4465
Ovarian score	**0.6217**	0.3534	0.2441	0.7520
Approaches	**0.9017**	0.0752	−0.1593	0.6582
Avoidance	**0.8311**	−0.0742	−0.2158	0.7008
Pass	**0.8116**	−0.0438	0.2910	0.7450
Aggression	−0.1848	0.5085	**0.7388**	0.5381
Eigenvalue	2.602	1.817	1.035	
Variance explained	37.2%	26.0%	14.8%	

dyads. Factor 1, which explained 55.0% of the behavioural variation among dyads, was strongly influenced by approaches (loading score 0.910), avoidance (0.866), and passes (0.752). Factor 2, which explained 24.6% of the variation, was strongly influenced by aggression (loading score 0.959).

Comparison of X. bicuspidariae *with other halictines.*—Fig. 2 compares *X. bicuspidariae* to 21 other species, in terms of the proportion of avoidance, aggressive, and cooperative (passing) behaviours observed in circle tube assays. It most closely resembles *Penapis toroi*, another solitary rophitine. Discriminant functions analysis (DFA) based on four putative categories (solitary, communal, semisocial, and eusocial) perfectly assigned solitary and communal species, but failed to distinguish between the latter two, assigning 1 eusocial species to the semisocial category and 1 semisocial species to the eusocial category. DFA based on three putative categories (solitary, communal, and caste-based social) reassigned each species into the category presented in Fig. 2. Moreover, when *Caenohalictus pygosinuatum* was categorized as communal (Michener et al. 1979), then DFA assigned it to the solitary group (as suggested by Packer 2006). The success of the DFA approach is based on significant differences among solitary, communal, and caste-based social bees in the proportions of aggressive behaviour (ANOVA, $F=50.32$, $df=2,19$, $p<0.0001$) and avoidance behaviour (ANOVA, $F=15.15$, $df=2,19$, $p<0.0001$), as well as significantly more frequent passing behaviour in communal species, as compared to both solitary and social species (ANOVA, $F=62.55$, $df=2,19$, $p<0.0001$).

DISCUSSION

Solitary behaviour of X. bicuspidariae.—In *X. bicuspidariae*, differences between circle tube interactants in head width, wing wear, and mandibular wear were not associated with differences in behaviour, suggesting that neither body size nor wear (and possibly age) structured interactions among adult females. Differences in ovarian development (OD) also did not predict differences in either aggression or avoidance, but were associated with rates of approach and pass behaviours, these being exhibited more frequently by the bee with greater ovarian development. Why would high OD females be more likely to approach and especially, to pass? One possibility is that the closer a female is to laying an egg, the more active she is likely to be. Under natural circumstances, a female halictine getting ready to lay an egg should be spending considerable time readying a brood cell and provisioning it. In a circle

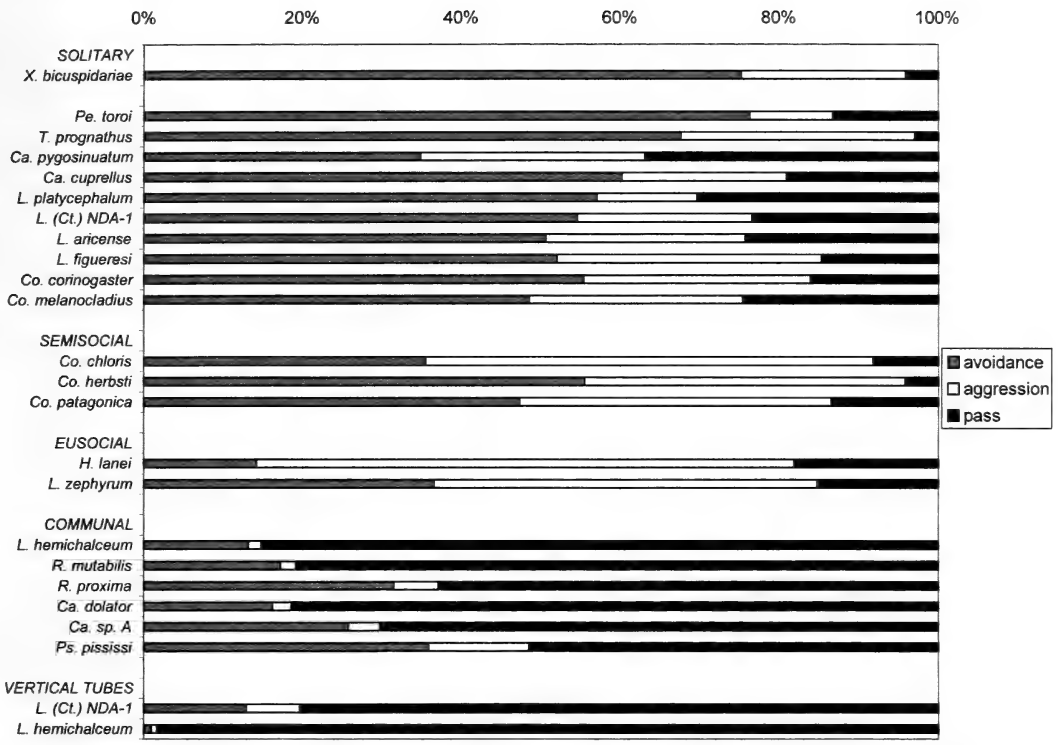

Fig. 2. Comparison of circle tube behaviour of *X. bicuspidariae* with literature values (partially redrawn from Packer 2006, which also contains a complete list of references). Solitary bee species are characterized by high rates of avoidance (withdrawals), communal bees by high rates of cooperation or tolerance (passing), and semisocial and eusocial species by high rates of aggression, coupled with very low rates of passing. Differences in behavioural profiles of bees tested in circle tubes versus vertical tubes (Jeanson et al. 2005) are evident. Genera represented (top to bottom) are *Xeralictus (X.), Penapis (Pe.), Thrincohalictus (T.), Caenohalictus (Ca.), Lasioglossum (L.), Corynura (Co.), Halictus (H.), Ruizantheda (R.),* and *Pseudagapostemon (Ps.).*

tube, heightened activity rates make it more likely that a bee will approach the second bee, and then perhaps continue right past her. In other words, bees with higher ovarian development may be more motivated to remain active, which in a circle tube would result in higher rates of approaching and passing.

The lack of correlation between ovarian status and aggression might seem surprising, but is consistent with observations in other species, including the solitary halictine, *L. (Ctenonomia)* NDA-1, and the communal species, *L. (Chilalictus) platycephalum*, in which ovarian status was not associated with aggression (McConnell-Garner and Kukuk 1997). In contrast, in *Lasioglossum figueresi* the female with larger ovaries was often first to be aggressive, and the bee with smaller ovaries was often first to withdraw (Wcislo 1997). Even in obligately eusocial species like *Halictus ligatus*, dominance, aggression, and defensive behaviours are most likely and most severe when the two members of a dyad both have relatively high ovarian development, for example, when a queen is paired with a worker with highly developed ovaries (Pabalan et al., 2000). This suggests that correlations between OD and aggression might have more to do with reactions to the threat of egg replacement than with dominance behaviour *per se*. In solitary bees, we should not then expect to see a correlation between ovarian development and aggressive behaviour (or withdrawal behaviour) except perhaps in species with high rates of intraspecific egg parasitism.

Our experiments uncovered considerable variability among individuals. Random pairings of individuals with different behavioural tendencies (personalities) must then have contributed to variation among dyads, creating behavioural scenarios that bear a marked resemblance to those expressed by social bees. Indeed, this would seem to be the basis of the phenomenon of 'emergent' sociality as described by Jeanson et al. (2005). However, the use of the term 'emergent' to describe forced social interactions among solitary bees is somewhat problematic, even in those which like *X. bicuspidariae* are ancestrally and monomorphically solitary. This is because solitary bees may also experience social interactions that insect sociobiologists do not usually categorize as 'social', such as interactions between foragers on flowers, between nest residents in dense nesting aggregations, between nest residents and would-be nest usurpers, or between residents and egg kleptoparasites. Moreover, group living may occur at very low frequencies in some solitary species without extensive nest observations, as has recently been found for several species of the apid genus, *Ceratina* (Rehan et al. 2009). In other words, many solitary bees, both ancestrally solitary and ancestrally social, may have considerable scope for intraspecific social behaviour, even if they rarely or never nest in multifemale groups. The variability in behavioural syndromes of solitary halictines (Fig. 2) suggests that eventually it may be possible to detect differences among obligately solitary, socially polymorphic, and reversed solitary species, especially based on the frequency of avoidance and aggession.

Behavioural changes in social transitions.— One caveat to the use of artificial arenas for observing bee behaviour is that the frequencies of circle tube behaviours may or may not represent the frequencies of same or similar behaviours in natural settings. Indeed, there are obvious differences in behavioural frequencies assessed using horizontal circle tubes versus vertical linear tubes (Fig. 2), implying that major differences in behavioural frequencies are produced by different experimental methodologies. Nevertheless, the interspecific consistency of behavioural syndromes observed in circle tube assays of solitary, communal, and caste-based social species is striking and statistically supportable, suggesting that when circle tube assays are used consistently, they uncover fundamental differences in behaviour among solitary, communal, and semisocial and eusocial species. These differences, if not the behavioural frequencies themselves, can be used to infer general behavioural tendencies in bees of different social levels.

In halictids, the ancestral trait of intolerance is suggested by high rates of avoidance in solitary bees such as *X. bicuspidariae* and another solitary rophitine species, *Penapis toroi*, in which avoidance behaviours comprise about 75% of encounters (Fig. 2). Transitions to communal versus caste-based social behaviour may be quite different. Circle tube assays imply that solitary-communal transitions involve significant decreases in both aggression and avoidance, whereas transitions to caste-based eusociality involve a significant increase in aggression, coupled with a decrease in avoidance. To the extent that passes represent cooperative interactions, solitary-communal transitions would appear to involve huge increases in cooperation whereas transitions to caste-based eusociality involve little change or perhaps even a decrease in cooperative behaviour. It will be important in future studies of both solitary and social halictines, to assess the degree of behavioural concordance between natural versus artificial contexts whenever possible, so that we can actually understand how representative circle tube behaviour is for those species for which nesting data are unobtainable.

Given that one of the most outstanding features of the eusocial insects is their frequent and sophisticated cooperative

behaviour, the hypothesis that transitions to caste-based sociality should involve decreases in cooperation coupled with increases in aggression seems contradictory. However, semisocial and eusocial halictines not only interact with many more individuals than solitary bees do, but they must also cope with dominance-subordinance relationships, many of which are regulated by aggressive behaviour (Kukuk and May 1991; Pabalan et al. 2000). Semisocial and eusocial bees must be able to exercise both tolerance and aggression with the same individuals. Although aggressive behaviours by solitary and caste-based social bees in circle tubes may appear to be similar, a major difference in natural settings is that aggressive behaviour by the latter is likely modulated by nest-mate recognition, such that encounters with non-nestmates will likely provoke aggression, whereas encounters with nestmates may engender aggression, tolerance, or cooperation (Peso and Richards 2010), depending on the immediate behavioural context.

Transitions to social behaviour, especially to caste-based sociality, are rarer in halictines than reversals to solitary behaviour (Danforth et al. 2003). Recent evidence suggests that reversals to solitary behaviour do not necessarily retrace the original evolutionary steps that led to sociality. For instance, reversed-solitary *Lasioglossum* have retained the social nesting characteristic of constructing brood cells close to the main burrow, facilitating both maternal inspection and care of the cells (Plateaux-Quénu 2008), and the potential for social interactions among newly emerged, adult brood. Thus reversed solitary bees may have lost caste-based sociality, but may have retained the context-dependent ability to discriminate nestmates from non-nestmates. Circle tube comparisons of ancestrally solitary species like *X. bicuspidariae*, and reversed-solitary species like *L. figueresi*, may help to illuminate and distinguish the evolutionary sequences involved in forward and reverse social transitions, especially where these involve the expression of context-dependent behaviour.

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LITERATURE CITED

Batra, S. W. 1966. The life cycle and social behavior of the primitively social bee *Lasioglossum zephyrum* (Hymenoptera: Halictidae). *University of Kansas Science Bulletin* 46: 359–423.

Brady, S. G., S. Sipes, A. Pearson, and B. N. Danforth. 2006. Recent and simultaneous origins of eusociality in halictid bees. *Proceedings of the Royal Society B-Biological Sciences* 273: 1643–1649.

Breed, M. D., J. M. Silverman, and W. J. Bell. 1978. Agonistic behavior, social interactions, and behavioral specialization in a primitively eusocial bee. *Insectes Sociaux* 25: 351–364.

Buckle, G. R. 1984. A second look at queen-forager interactions in the primitively eusocial halictid, *Lasioglossum zephyrum*. *Journal of the Kansas Entomological Society* 57: 1–6.

Danforth, B. N., L. Conway, and S. Ji. 2003. Phylogeny of eusocial *Lasioglossum* reveals multiple losses of eusociality within a primitively eusocial clade of bees (Hymenoptera: Halictidae). *Systematic Biology* 52: 23–36.

———, C. Eardley, L. Packer, K. Walker, A. Pauly, and F. J. Randrianambinintsoa. 2008. Phylogeny of Halictidae with an emphasis on endemic African Halictinae. *Apidologie* 39: 86–101.

Jeanson, R., P. F. Kukuk, and J. H. Fewell JH. 2005. Emergence of division of labour in halictine bees: contributions of social interactions and behavioural variance. *Animal Behaviour* 70: 1183–1193.

Kukuk, P. F. and B. May. 1991. Colony dynamics in a primitively eusocial halictine bee *Lasioglossum (Dialictus) zephyrum* (Hymenoptera: Halictidae). *Insectes Sociaux* 38: 171–189.

———. 1992. Social interactions and familiarity in a communal halictine bee *Lasioglossum (Chilalictus) hemichalceum*. *Ethology* 91: 291–300.

Martinez-Delclos, X. and J. Martinell. 1995. The oldest known record of social insects. *Journal of Paleontology* 69: 595–599.

McConnell-Garner, J. and P. F. Kukuk. 1997. Behavioral interactions of two solitary, halictine bees with comparisons among solitary, communal and eusocial species. *Ethology* 103: 19–32.

Michener, C. D., M. D. Breed, and W. J. Bell. 1979. Seasonal cycles, nests, and social behavior of some Colombian halictine bees (Hymenoptera, Apoidea). *Revista de Biología Tropical* 27: 13–34.

——— and D. Grimaldi. 1988. The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. *Proceedings of the National Academy of Sciences of the USA* 85: 6424–6426.

Pabalan, N., K. G. Davey, and L. Packer. 2000. Escalation of aggressive interactions during staged encounters in *Halictus ligatus* Say (Hymenoptera: Halictidae), with a comparison of circle tube behaviors with other halictine species. *Journal of Insect Behavior* 13: 627–650.

Packer, L. 2005. The influence of marking upon bee behaviour in circle tube experiments with a methodological comparison among studies. *Insectes Sociaux* 52: 139–146.

———. 2006. Use of artificial arenas to predict the social organisation of halictine bees: Data for fourteen species from Chile. *Insectes Sociaux* 53: 307–315.

Patiny, S., D. Michez, and B. N. Danforth. 2008. Phylogenetic relationships and host-plant evolution within the basal clade of Halictidae (Hymenoptera, Apoidea). *Cladistics* 24: 255–269.

Peso, M. and M. H. Richards. 2010. Knowing who's who: Nestmate recognition in the facultatively social carpenter bee, *Xylocopa virginica*. *Animal Behaviour* in press.

Plateaux-Quénu, C. 2008. Subsociality in halictine bees. *Insectes Sociaux* 55: 335–346.

Rehan, S., M. H. Richards, and M. P. Schwarz. 2009. Evidence of social nesting in the *Ceratina* of Borneo. *Journal of the Kansas Entomological Society* 82: 194–209.

Sakagami, S. F. and Y. Maeta. 1977. Some presumably presocial habits of Japanese *Ceratina* bees, with notes on various social types in Hymenoptera. *Insectes Sociaux* 24: 319–343.

Schwarz, M. P., M. H. Richards, and B. N. Danforth. 2007. Changing paradigms in insect social evolution: Insights from halictine and allodapine bees. *Annual Review of Entomology* 52: 127–150.

Snelling, R. R. and G. I. Stage. 1995. Systematics and biology of the bee genus *Xeralictus* (Hymenoptera: Halictidae, Rophitinae). *Contributions in Science, Natural History Museum of Los Angeles County* (451): 1–17.

Soucy, S. L. 2002. Nesting biology and socially polymorphic behavior of the sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Annals of the Entomological Society of America* 95: 57–65.

Szathmáry, E. and J. Maynard Smith. 1995. The major evolutionary transitions. *Nature* 374: 227–232.

Wcislo, W. T. 1997. Social interactions and behavioral context in a largely solitary bee, *Lasioglossum (Dialictus) figueresi* (Hymenoptera, Halictidae). *Insectes Sociaux* 44: 199–208.

Wenzel, J. W. 1990. A social wasp's nest from the Cretaceous period, Utah, USA, and its biogeographical significance. *Psyche* 97: 21–29.

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Plega hagenella (Neuroptera: Mantispidae) Parasitism of *Hylaeus (Hylaeopsis)* sp. (Hymenoptera: Colletidae) Reusing Nests of *Trypoxylon manni* (Hymenoptera: Crabronidae) in Trinidad

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Abstract.—Two adult specimens of *Plega hagenella* were reared from a nest of the crabronid wasp *Trypoxylon manni* collected in Trinidad in 2008. The mantispids developed by feeding on the immature stages of a colletid bee, *Hylaeus (Hylaeopsis)* sp., which had secondarily occupied the cells of the aerial mud nest of *T. manni*. Two dead *Hylaeus* pupae were found within the nest, one of which had six dead mantispid larvae attached. Numerous insect egg chorions, interpreted as belonging to *P. hagenella*, were found in clusters inserted into small cavities in the mud of the outer surface of the nest. Five additional adult *P. hagenella* were collected in microhabitats where other *T. manni* nests were collected. These new observations confirm the presence of *P. hagenella* in Trinidad, establish the presence of the subgenus *Hylaeopsis* in Trinidad, and document *Plega hagenella* as a new parasite of bees in the genus *Hylaeus*.

The insect order Neuroptera – lacewings, antlions and their relatives – currently comprises approximately 5,730 valid extant species placed in about 17 families. The family Mantispidae – mantispids or mantis-flies – form a distinctive clade of about 395 species that is well known for the raptorial forelegs of its predatory adults, and the larval life history strategy of species in the subfamily Mantispinae as spider egg parasites. Less well known are the larval strategies of species in the three other extant mantispid subfamilies – the Symphrasinae, Drepanicinae and Calomantispinae – none of which are known to be associated with spiders.

Of particular interest are larval associations of species belonging to the subfamily Symphrasinae, which is generally considered to be the sister-group to all other mantispid subfamilies collectively (Penny and da Costa 1983; Lambkin 1986). The biologies of symphrasine species are poorly known and, consequently, new host records are of considerable interest. The Symphrasinae contains three extant genera – *Anchieta*, *Trichoscelia* and *Plega* – all of which are currently restricted to the New World (Penny 1982), and for each of which few larval host/feeding records are available. *Anchieta* includes five species known from Brazil and French Guiana, only one of which has a reported host: *A. fumosella* (Westwood), which has recently been reared from cocoons of *Trypoxylon* (*Trypargilum*) *aestival* Richards in southeastern Brazil (Buys 2008). *Trichoscelia* contains 13 species distributed from southern Mexico south to Uruguay, Argentina and southern Brazil (Penny 1982; Ohl 2004). *Trichoscelia varia* (Walker) has been reared from nests of the vespid wasps, *Polybia ruficeps* Schrottky and *P. scutellaris* (White) (Penny 1982); and Dejean and Canard (1990) provide an interesting account of *Trichoscelia santareni* (Navás) invading a colony of *Polybia diguetana* Buysson on the Yucatan Peninsula.

Table 1. *Plega melitomae* species-group host records.

Plega sp.	Host record	Location	Reference
beardi(?)	*Trypoxylon albitarse* (Crabronidae)	Trinidad	Penny 1982
hagenella	*Hylaeus (Hylaeopsis)* sp. (Colletidae), in *Trypoxylon manni* nest	Trinidad	(this work)
melitomae	*Melitoma segmentaria* (as *M. euglossoides*) (Apidae)	Mexico (Chiapas)	Linsley and MacSwain 1955
sp. near *melitomae*	*Trypoxylon* sp.	Mexico (Veracruz)	Parker and Stange 1965
yucatanae	*Megachile exaltata* (Megachilidae)	Mexico (Yucatan)	Parker and Stange 1965

Plega includes 14 species distributed from the southwestern United States, south to Bolivia and Brazil (Penny 1982). Two species groups are generally recognized – the *melitomae* and *signata* groups. Members of the *P. melitomae* group (*P. beardi, hagenella, melitomae, paraense* and *yucatanae*; see Penny 1982) have been reported as parasites of several bees and aculeate wasps (Table 1). In contrast to the hymenopteran feeding records of the *melitomae* group, members of the *signata* group have been reared from subterranean insects (Parker and Stange 1965). *Plega signata* Hagen cocoons have been found inside subterranean cocoons of the noctuid moth *Egira curialis* (Grote) (Woglum 1935; as *Xylomyges curialis*). Werner and Butler (1965) presented circumstantial evidence of *Plega banksi* Rehn devouring a scarab pupa as well as an asilid pupa associated with a scarab pupa in Arizona. They suggested that the larvae live in soil as predators.

The global crabronid genus *Trypoxylon*, which figures prominently in several host records for the *P. melitomae* group, contains more than 600 species and is well represented in the New World. *Trypoxylon manni* Richards is known from Brazil and Trinidad and commonly attaches its nests to rootlets under dirt banks next to road cuts in the Northern Range, Trinidad, West Indies (Vesey-FitzGerald 1936). Nests of *T. manni* are often communal and may contain up to six females and 64 cells (Hook and Starr unpubl.). *Trypoxylon manni* is a member of the *T. fabricator* group, in which nest sharing by females is known in at least three species: *T. fabricator* Smith (Sakagami et al. 1990), *T. maidli* Richards and *T. manni* (Hook and Starr pers. obs.).

MATERIALS

Between 2003 and 2008 the senior author field collected five specimens of *Plega hagenella* in several places on the island of Trinidad. Three of the specimens were collected in 2008 under dirt banks harboring *Trypoxylon manni* nests. One female was taken on 18 July along the Paria Trail, another female was collected on 23 July up the Maracas Valley in the Northern Range and a male was taken on 25 July in the Arena Forest Reserve. A fourth specimen (male) was collected on 26 July 2003 up the Caura Valley (Northern Range) and a fifth specimen (female) was collected on 25 August 2005 at U.W.I. Flats (apartments) in St. Augustine (*Trypoxylon* spp. were observed nesting around the apartments).

In July of 2008 AWH collected 10 nests of *Trypoxylon manni* – seven from along the upper reaches of the Paria Trail (10.746°N 61.285°W; connecting the village of Brasso Seco to Paria Bay on the north coast) on 18 July, two in the Maracas Valley (10.705°N 61.368°W) on 23 July and one on 25 July along a road entering the Arena Forest Reserve (10.562°N 61.256°W). All nests were collected into and maintained isolated in separate plastic bags in order to rear their contents. Two adults of *Plega*

hagenella, and numerous presumed eggs and larvae of the same species, were later found to be associated with one of the nests collected along the Paria Trail (AWH field note 36-2008). Most of the cells of this nest were subsequently dissected and examined for evidence of insect occupation and usage. Observations made during the examination of this nest are summarized below.

RESULTS

Observations on Trypoxylon and Hylaeus.—The mantispid-parasitized nest had 14 cells, of which nine were open when collected, two were closed with mud and three were closed with a tough, transparent, membrane indicative of cell reutilization by a colletid bee, subsequently identified as *Hylaeus (Hylaeopsis)* sp. Of nine cells opened by dissection, *Hylaeus* had reutilized eight, as evidenced by typical *Hylaeus*-type transparent cell linings and partitions found within the original mud cells of the *Trypoxylon manni* nest. *Hylaeus* reused 11 of the 14 cells this nest contained. *Trypoxylon* species do not line their nest cells with secretions, but this is a characteristic feature of colletid bee cells (Almeida 2008). Two dead *Hylaeus* pupae were found in these lined exterior cells. Of these, one pupa was unparasitized but the other had six dead mantispid larvae attached to its thorax and abdomen (the head was missing).

Identification of the bee species as *Hylaeus (Hylaeopsis)* sp. is based on the dead pupae found in the nest and on bee rearings from 46 additional *Trypoxylon manni* nests collected previously in 1996 and 1999 (primarily along the Blanchisseuse Road in the Northern Range of Trinidad). Interestingly, a diversity of cleptoparasites was reared from 19 of the earlier 46 nests, but no mantispids. Six (13%) of the 46 nests collected during this earlier period had some level of *Hylaeus* cell reutilization. Those six nests contained a total of 93 cells, of which 16 (17%) were reused by *Hylaeus*, with one to two or possibly three *Hylaeus* cells per *T. manni* cell.

Observations on Plega.—Two adult *Plega hagenella*, one male and one female, were subsequently found in the plastic bag containing the parasitized *Trypoxylon* nest, which had been maintained indoors, dry, and at ambient room temperatures since its collection. The male was discovered nearly dead on 26 July 2008. The nest was subsequently checked irregularly until 18 August. The next inspection was not until 9 October, when a dead female was discovered. The adult *Plega hagenella* specimens were identified using the keys and descriptions of Penny (1982), who noted the existence of previously-collected females resembling, but not conclusively identifiable as, *P. hagenella* from Trinidad. The present material confirms the presence *P. hagenella* in Trinidad based on definitively identifiable male specimens and associated females.

Subsequent examination of the nest revealed two mantispid pupal exuviae, one protruding from each of two nest cells, both of which were marked by the characteristic cellophane-like lining of *Hylaeus*. A loose double-walled cocoon of typical neuropteran form was extracted from one of these cells. In another cell, six neuropteran larvae of at least two sizes were found attached to a dead *Hylaeus* pupa.

Further inspection of the partially dissected nest revealed the existence of numerous, small, whitish, insect egg chorions associated with its outer layers. While some of the eggs may have been deposited on the exposed outer surface of the nest, most appear to have been inserted into small cavities in the nest's irregular mud surface, often in small groups of 3–6 per cavity. The small cavities are natural features of the original mud nest, the result of incomplete joining or smoothing of adjacent, rounded, mud boluses used in its construction. At least 29 empty egg chorions were found in or on the nest, but

it seems likely that additional eggs were lost during the dissection of the nest, or were inserted so deeply into crevices that they were hidden from view. The eggs were narrowly lacrimiform in shape (with the micropylar process terminating the narrowed end), ca. 0.7 mm long, simple (i.e., stalkless), and marked externally with a network of raised polygonal ridges. All of the eggs appeared to be empty, their larvae having emerged through longitudinal slits located near the micropylar ends of each egg.

DISCUSSION

Hylaeus (Hylaeopsis).—This Neotropical subgenus of 15 species has been reported from Mexico south to Paraguay and southern Brazil, but it has not previously been reported from Trinidad, the neighboring Guyanas, or Venezuela (Urban and Moure 2007). Ten or more undescribed *Hylaeopsis* species are suspected to be present in the Neotropical fauna (Michener 2007). Adults of the Trinidad *Hylaeopsis* are much smaller than adult *Plega hagenella*, suggesting that *Plega* larvae must consume multiple bee larvae and/or pupae to reach adulthood. If this is true, the pattern of multiple bee cells per wasp cell and gregarious nesting (also reported in *H. (Hylaeopsis) tricolor* (Schrottky) by Sakagami and Zucchi 1978) may contribute to making this bee species a suitable host for *Plega hagenella*. Not all *Hylaeopsis* species nest gregariously, however, and the hyperdispersed, single-celled nests of *H. (Hylaeopsis) grossus* (Cresson) (Michener and Brooks 2003) may be adaptive in helping to avoid attacks by larger nest parasites like *Plega*.

Plega.—Although definitive, reared, larvae and eggs of *P. hagenella* have yet to be described, detailed observations derived from the parasitized *Trypoxylon* nest reported here, together with existing knowledge of mantispid immatures, present a strong circumstantial case that the eggs and larvae noted above are those of *P. hagenella*. The rearing of definitively identified *P. hagenella* adults from the *Trypoxylon* nest renders plausible the discovery of immature *P. hagenella* stages in the same nest. The general morphology of the recovered larvae is consistent with their determination as first-instar mantispid larvae. The larvae are morphologically similar to the first-instar larvae of both *Plega yucatanae* (described by Parker and Stange 1965) and other described first-instar mantispids (e.g., *Climaciella brunnea* [as *Mantispa brunnea*], *Dicromantispa interrupta* [as *Mantispa interrupta*], *Dicromantispa sayi* [as *Mantispa sayi*], *Leptomantispa pulchella* [as *Mantispa pulchella*] and *Zeugomantispa virescens* [as *Mantispa viridis*], see Hoffman and Brushwein 1992; *Tuberonotha strenua* [as *Climaciella magna*] and *Mantispa japonica*, see Kuroko 1961).

The eggs noted above, in addition to being physically associated with the mantispid-parasitized nest, are also consistent both morphologically and behaviorally with a mantispid identification. Their size is appropriate to that of the smaller mantispid larvae observed in the nest. The deep insertion of many of the eggs into fine crevices in the mud surface of the nest is consistent with oviposition via a slender, elongate, ovipositor, the presence of which is, within the order Neuroptera, a synapomorphy of the mantispid subfamily Symphrasinae, to which *Plega hagenella* belongs. Although at least two *Plega* species have been reared from egg to adult (*P. dactylota* and *P. signata*; see MacLeod and Redborg 1982), no published descriptions or illustrations of Symphrasine mantispid eggs exist. Interestingly, however, the eggs noted here bear a strong resemblance to, though are somewhat more slender and elongate than, those illustrated by Minter (1990, fig. 1) for *Mucroberotha vesicaria* – a species belonging to a group of several genera of uncertain phylogenetic placement that have in recent years been placed in either the family Mantispidae or Berothidae (as Rhachiberothinae), or as a separate family (as Rhachiberothidae). The

presence of sessile eggs in both rhachiberothines/ids and symphrasine mantispids has potentially interesting implications for the interpretation of the stalked eggs found in both mantispine mantispids and berothine berothids (both of which are relatively derived subfamilies within their families). If sessile eggs are found to be symplesiomorphic in rhachiberothines/ids and symphrasine mantispids, the stalked eggs found in berothines and mantispines are likely to be independent, derived innovations.

Parasite Biology.—Because the *Plega hagenella* adults emerged from the mud nest of *Trypoxylon manni*, it was initially assumed that *P. hagenella* was a parasite of *T. manni*. However, several observations and lines of evidence suggest that, at least in this case, *P. hagenella* was parasitizing the *Hylaeus* (*Hylaeopsis*) sp., not *T. manni*. First, no remnants of *Trypoxylon* immatures were found in the nest, suggesting that the original nest builders had vacated the nest prior to its occupation by *Hylaeus* and *Plega*. Second, all evidence of *P. hagenella* cell occupation (i.e., pupal exuviae, cocoon, presumed larvae) was found in nest cells with membranous linings, indicating an association with the cells reused by *Hylaeus*, rather than the uncoated cells of *Trypoxylon*. Third, the presumed larvae of *P. hagenella* were clearly found in association with a *Hylaeus* pupa in the nest. Several of the larvae appeared to have their jaws successfully inserted into the cuticle of the bee pupa, and differences in the sizes of some of the larvae suggest that at least some had fed successfully. What actually killed the discovered bee pupae and mantispid larvae is unknown. Finally, a bee host for *P. hagenella* is consistent with the known bee hosts of at least two other members of the *Plega melitomae* species group (*P. melitomae* and *yucatanae*; see Table 1). In fact, the three-species interaction documented here – *Plega hagenella* parasitizing a *Hylaeus (Hylaeopsis)* species reutilizing a *Trypoxylon manni* nest – calls into question the accuracy of previous host records of *Trypoxylon* species for other *P. melitomae* group species (Table 1). The discovery of a mantispid-parasitized bee in a reutilized aculeate wasp nest makes it apparent that accurate host records for *P. melitomae* group mantispids cannot be inferred from published associations unless the possibility of nest reuse is explicitly addressed.

The observation that *P. hagenella* adults can be collected in sheltered, exposed-soil, situations favorable for *Trypoxylon* nesting provides a new focal point for field collecting *Plega* adults, which are rather rarely collected in tropical regions. It remains to be determined, however, whether these *Plega* individuals are preferentially targeting bees reusing *Trypoxylon* nests in such microhabitats, or whether they are attracted to such areas for general shelter and/or for access to a potentially larger array of subterranean-, surface- and aerial-nesting aculeate Hymenoptera that would likely be attracted to the same sites because of their suitability for nest-building.

Because of the paucity of available host records, the degree of host-specificity of individual *Plega* species is currently unclear, though the possible division of wild hosts proposed by Parker & Stange (1965) – i.e., *P. melitomae* group species on aculeate Hymenoptera and *P. signata* group species on a larger array of subterranean insects (e.g., larvae and/or pupae of Coleoptera, Lepidoptera and Diptera) – still appears as a broad generalization. It should be noted, however, that this generalization may not apply to captive individuals reared under artificial conditions (MacLeod and Redborg 1982).

All Mantispinae with known biologies have spider-associated larvae, and adults with highly r-selected reproductive strategies, each female producing hundreds to thousands of minute, stalked, eggs that are deposited in the environment with apparently little or no attempt to oviposit in sites

that might increase the probability of emerging larvae encountering suitable hosts. The finding of *Plega hagenella* eggs directly deposited on a nest containing the immature stages of its host suggests that *P. hagenella*, and possibly other symphrasine mantispids, employs a different, more targeted, oviposition strategy that actively places eggs in closer proximity to potential hosts. Strategies such as this suggest the existence of more complex adult behaviors, particularly higher levels of host-searching ability in females. Within the Mantispidae, extraordinary intraspecific and oviposition behaviors are also found in the symphrasine species *Trichoscelia santareni*, whose males and females engage in lekking behavior, followed by the females flying to, entering and ovipositing within active vespid nests (Dejean and Canard 1990).

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LITERATURE CITED

Almeida, E. A. B. 2008. Colletidae nesting biology (Hymenoptera: Apoidea). *Apidologie* 39: 16–29.

Buys, S. C. 2008. Observations on the biology of *Anchieta fumosella* (Westwood 1867) (Neuroptera: Mantispidae) from Brazil. *Tropical Zoology* 21: 91–95.

Dejean, A. and M. Canard. 1990. Reproductive behavior of *Trichoscelia santareni* (Navás) (Neuroptera: Mantispidae) and parasitism of the colonies of *Polybia diguetana* R. du Buysson (Hymenoptera: Vespidae). *Neuroptera International* 6: 19–26.

Hoffman, K. M. and J. R. Brushwein. 1992. Descriptions of the larvae and pupae of some North American Mantispinae (Neuroptera: Mantispidae) and development of a system of larval chaetotaxy for Neuroptera. *Transactions of the American Entomological Society* 118: 159–196.

Kuroko, H. 1961. On the eggs and first-instar larvae of two species of Mantispidae. *Esakia. Occasional Papers of the Hikosan Biological Laboratory* 3: 25–32.

Lambkin, K. J. 1986. A revision of the Australian Mantispidae (Insecta: Neuroptera) with a contribution to the classification of the family. I. General and Drepanicinae. *Australian Journal of Zoology, Supplementary Series* 116: 1–142.

Linsley, E. G. and J. W. MacSwain. 1955. Two new species of *Plega* from Mexico. *Pan-Pacific Entomologist* 31: 15–19.

MacLeod, E. G. and K. E. Redborg. 1982. Larval Platymantispine mantispids (Neuroptera: Planipennia): possibly a subfamily of generalist predators. *Neuroptera International* 2: 37–41.

Michener, C. D. 2007. *Bees of the World*. Johns Hopkins University Press, Baltimore. xvi + 557 pp.

——— and R. W. Brooks. 2003. Dispersal of brood cells in a Mesoamerican hylaeine bee: a probable risk-spreading behavior (Hymenoptera, Colletidae). Pp. 151–152 *in:* Melo, G. A. R., and I. A. dos Santos eds. *Apoidea Neotropica: homenagem aos 90 anos de Jesus Santiago Moure*. Editora UNESC, Criucuma, Brazil.

Minter, L. R. 1990. A comparison of the eggs and first-instar larvae of *Mucroberotha vesicaria* Tjeder with those of other species in the families Berothidae and Mantispidae (Insecta: Neuroptera). Pp. 115–129 *in:* Mansell, M. W. and H. Aspöck eds. *Advances in Neuropterology. Proceedings of the Third International Symposium on Neuropterology* (3–4 February 1988, Berg en Dal, Kruger National Park, South Africa). South African Department of Agricultural Development, Pretoria. 298 pp.

Ohl, M. 2004. Annotated catalog of the Mantispidae of the World (Neuroptera). *Contributions on Entomology, International*. 5: 131–262.

Parker, F. D. and L. A. Stange. 1965. Systematics and biological notes on the tribe Platymantispini (Neuroptera: Mantispidae) and the description of a new species of *Plega* from Mexico. *Canadian Entomologist* 97: 604–612.

Penny, N. D. 1982. Neuroptera of the Amazon Basin. Part 6. Mantispidae. *Acta Amazonica* 12: 415–463.

——— and C. A. da Costa. 1983. Mantispídeos do Brasil (Neuroptera: Mantispidae). *Acta Amazonica* 13: 601–687.

Sakagami, S. F., N. Gobbi, and R. Zucchi. 1990. Nesting biology of a quasisocial sphecid wasp *Trypoxylon fabricator*. *Japanese Journal of Entomology* 58: 846–862.

——— and R. Zucchi. 1978. Nests of *Hylaeus* (*Hylaeopsis*) *tricolor*: the first record of non-solitary life in colletid bees, with notes on communal and quasisocial colonies (Hymenoptera: Colletidae). *Journal of the Kansas Entomological Society* 51: 597–614.

Vesey-FitzGerald, D. F. 1936. Nesting habits of *Trypoxylon* (Hym. Sphec.) from Trinidad. *Proceedings of the Royal Entomological Society of London. Series A* 11: 111–115.

Urban, D. and J. S. Moure. 2007. *Hylaeini* Viereck, 1916. Pp. 710–722 *in:* Moure, J. S., D. Urban, and G. A. R. Melo eds. *Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region*. Sociedade Brasileira de Entomologia, Curitiba. xiv + 1058 pp.

Werner, F. G. and G. D. Butler, Jr. 1965. Some notes on the life history of *Plega banksi* (Neuroptera: Mantispidae). *Annals of the Entomological Society of America* 58: 66–68.

Woglum, R. S. 1935. *Symphrasis signata* Hagen. *Pan-Pacific Entomologist* 11: 119.

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Chartergellus golfitensis West-Eberhard: a new species of Neotropical swarm-founding wasp (Hymenoptera: Vespidae, Polistinae) with notes on the taxonomy of *Chartergellus zonatus* Spinola

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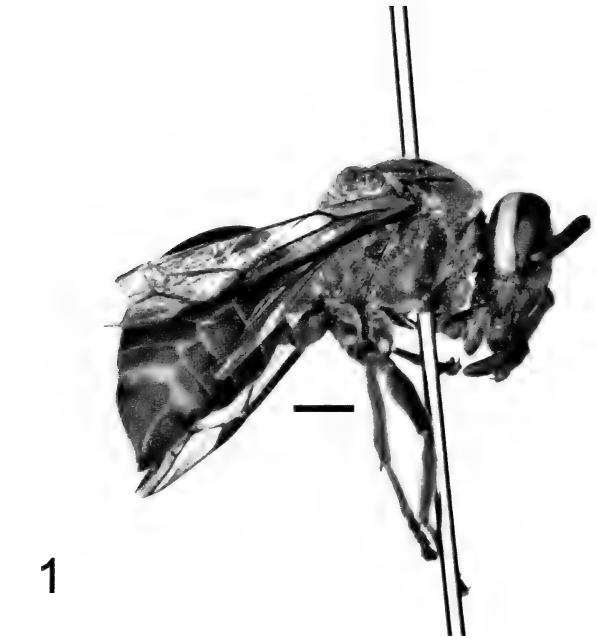
Abstract.—***Chartergellus golfitensis* West-Eberhard new species**, is described from Central America and compared with *C. zonatus* Spinola, a species heretofore inadequately described.

Chartergellus is a genus of Epiponini (Hymenoptera, Vespidae, Polistinae) ranging from southeastern Brazil to Costa Rica (West-Eberhard et al. 2006). The taxonomic background of *Chartergellus* is somewhat troublesome. It was described by Bequaert (1938) as a subgenus of *Chartergus sensu* Bequaert. The use of the name *Chartergus* was due to overlooking the type designation for that genus, and Bequaert (1943) pointed out that the name *Parachartergus* von Ihering, 1904 was correct. Bequaert (1938) designated as type species *Vespa frontalis* Fabricius, 1804, the only species included in *Chartergellus*. Richards (1978) raised *Chartergellus* to genus, and pointed out that *Vespa frontalis* Fabricius was preoccupied by *Vespa frontalis* Latreille 1802. He proposed *C. amazonicus* as a replacement name, and described five new species: *C. atectus* Richards 1978, *C. communis* Richards 1978, *C. nigerrimus* Richards 1978, *C. punctatior* Richards 1978, and *C. sanctus* Richards 1978. He treated *Chartergus zonatus* Spinola 1851, as an unrecognized species and did not include it in his key, because the description "does not agree fully with any specimens I have seen of *Chartergellus*" (Richards 1978: 217). Most recently an eighth species has been added, *C. afoveatus* Cooper 1993.

With the exception of *C. atectus* (see Richards 1978, and below), the species of *Chartergellus* build nests consisting of multiple combs attached laterally to the substrate by pedicels and covered by an envelope of a single sheet, with the entrance a short spout (Wenzel 1998). The envelope may be irregular, with the lines of construction evident and contributing to camouflaging of the nest. *Chartergellus* is characterized by having a prominent curved bristle on the third labial palpomere, the maxillary palpi five-segmented and labial palpi three-segmented, lacking



Figs 1–8. *Chartergellus golfitensis* West-Eberhard **new species**. Holotype. 1. Habitus. Lateral view. 2. Dorsal view. 3. Head, frontal view. 4. Head, lateral view. 5. Head, dorsal view. 6. Mesosoma, dorsal view. 7. Mesosoma, lateral view. 8. Scutellum, metanotum and propodeum, dorsal view. Scale bars = 1 mm.

an occipital carina, the mesepisternum lacking a dorsal groove, and the metanotum rounded (Carpenter 2004).

Previously, only *Chartergellus atectus* was recorded for the Costa Rican fauna (Richards 1978). We describe here *Chartergellus golfitensis*, a new species from Costa Rica.

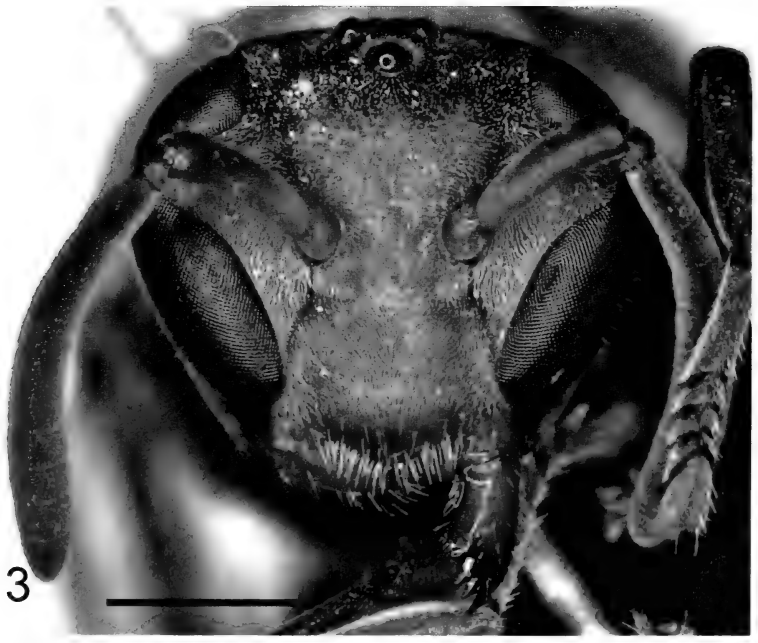
Chartergellus golfitensis West-Eberhard, new species
(Figs 1–9)

Diagnosis.—Chartergellus golfitensis is distinguished by the presence of a raised black-lipped arc at the base of the mandible; clypeus in short contact with eye; pale markings on the scutellum; frons with three-pointed reddish brown mark with the central point nearly reaching the median ocellus and in the intraocular space to the center of the ocular sinus; and a broad pale stripe along the entire length of the gena, usually without red or black region below, which when present is no wider than the diameter of the median ocellus.

Description.—*Female*. Holotype fore wing length 6.72 mm.

Color. Black. Reddish brown: clypeus, first antennal segment and flagellum beneath, malar space, lower 3/4 of the head, mandibles except teeth, fore tibia, tips of tarsi. Whitish anterior stripes on metanotum curved at margin of propodeum, pronotal carina, and broadly along entire length of gena. Wings hyaline, venation brownish. *Head*. Eyes with short sparse hairs, touching clypeus for short distance. Clypeus wider than long (median length x width at middle = 0.74). Entire surface of head pubescent except for malar space and gena posterior to it, and clypeus below level of eyes, where there are long bristles. Frons with sparse and shallow punctures. Malar space present, about as wide as length of fourth antennomere. Gena with width equal to width of compound eye. Widest part of eye seen from front only half length of first antennomere. Vertex

Figs 1–8. Continued.

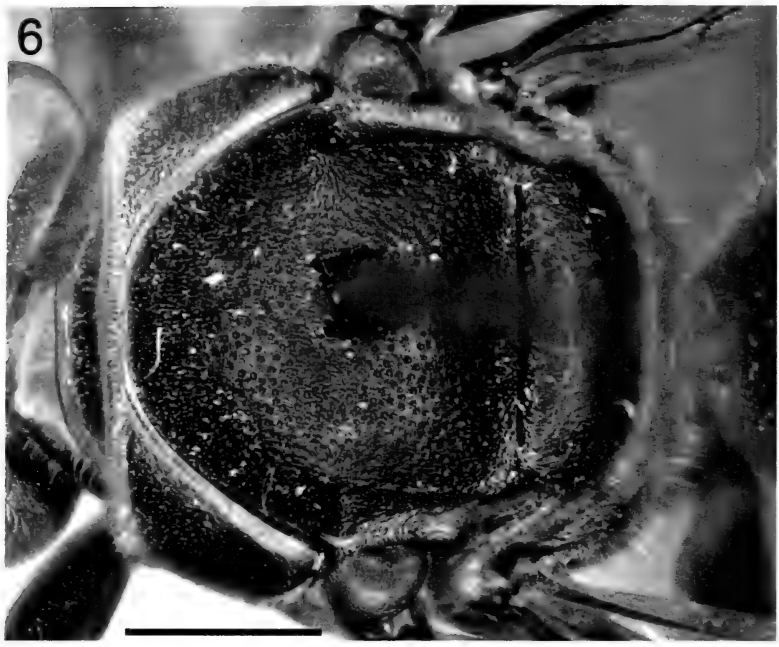


Figs 1–8. Continued.

Figs 1–8. Continued.

hairs present, sparser and shorter than those of frons which are nearly as long as bristles of clypeus below level of eyes. Base of mandible with raised rim, forming an arc with a black basal lip, dorsal third covered by lateral clypeal lobe. Mandible smooth, outer surface with a few long bristles. *Mesosoma*. Pronotum, scutum and

Figs 1–8. Continued.



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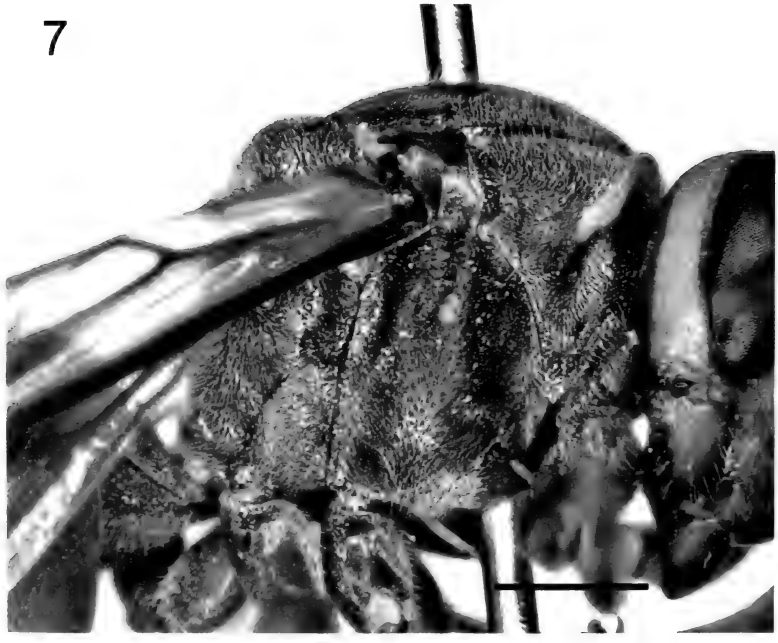

Figs 1–8. Continued.

Figs 1–8. Continued.

scutellum with fine, dense punctation and covered with straight hairs. Mesepisternum with scrobal furrow beginning at margin beneath tegula and curving posteriorly to form a gentle arc about half as long as the mesepisternum, which is rounded anterior to the furrow. Dorsal pronotal carina well developed, ending close to the posterior margin. Pronotal fovea present. Propodeum without posterior concavity, with hairs on entire surface, propodeal valve narrow throughout.

Male.

Color. As in female but metasoma (gaster) and legs dark brown. Reddish-brown of face fills entire ocular sinus and lacks three medial peaks on frons. Whitish genal stripe touching eye. Additional white:

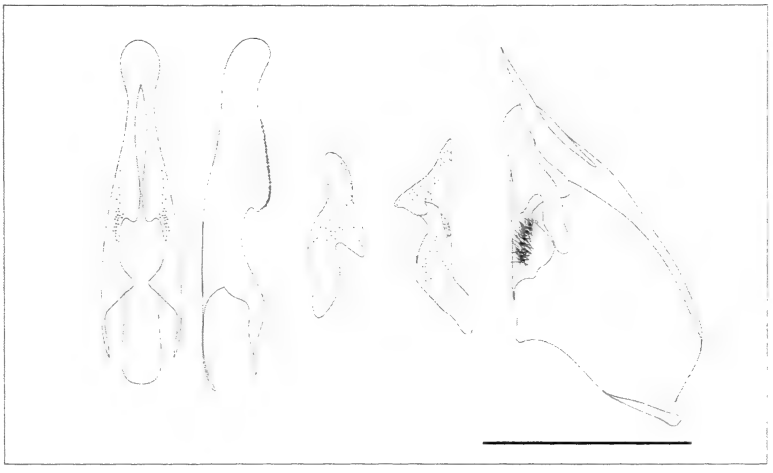

Fig. 9. Male genitalia of *Chartergellus golfitensis*. From left to right, aedeagus in ventral view, aedeagus in lateral view, digitus, cuspis and paramere. Scale bar = 1 mm.

stripe anterior to scrobal furrow, and coxae. *Head.* Mandibles with silvery appressed hairs on basal half of outer surface, apical half with a few long bristles, undersurface covered with long hairs. Clypeus as long as wide (L:W = 1.06), in extensive contact with eyes except for a short distance dorsally, and covered with silvery pubescence, ventrally forming a dense band of long appressed bristles which gleam in direct light as do similar hairs on lateral portions of frons, white portions of coxae, and a thin line on curved distal margin of last metasomal sternum. Malar space about half as wide as length of fourth antennomere. Gena only about half width of eye. Widest part of eye seen from front as long as first antennomere; saber-like ventral mandibular tooth longer and sharper-edged than in female.

Male genitalia (Fig. 9). Aedeagus serrate beneath. Ventral process (at base of serrate portions of aedeagus) forming a "U" with outer end sharply pointed, as in *C. communis* (Richards 1978, fig.88b). Serrations: proximal nine very fine and triangular (pointed), more distal 25 broader, curved on the posterior edge and pointing forward. Serrate edge slightly longer than distance from end of serrations to tip of aedeagus. Parameral spine hairless, slightly curved laterad, with elongate lateral opening near tip. Inner surface of digitus with long fine hairs, longer than width of digitus seen in profile, and shorter toward tip, which is bare.

Distribution.—Known only from Pacific lowlands of Costa Rica.

Habitat.—The two observed living colonies of *C. golfitensis* (the colony of the holotype and another from the same locality), and all other collected specimens, were found in areas of lowland humid forest. Nests were built on a vertical tree trunk and the wall of a building.

Types.—**Holotype**, ♀, COSTA RICA, **Puntarenas Prov.**, Refugio de Vida Silvestre Golfito, 83°11'55"W, 8°39'25"N, 500m from the sea level. 2.i.2006 (L. Chavarría), deposited in the Museum of Zoology of the University of Sao Paulo, Sao Paulo, Brazil. **Paratypes**. In Museo de Zoología, Escuela de Biología, University of Costa Rica: **Puntarenas Prov.** 40 females, 17 males, all with the same locality and collector as the holotype. Golfo Dulce, 24 km W. Piedras Blancas, alt. 200m, iii 1992, 1♀ (Paul Hanson); 3 km SW Rincón, VI 1991, 2 ♀♀ (Paul Hanson); III–IV 1992, 1♀ (Paul Hanson). In Instituto Nacional de Biodiversidad (INBio), Costa Rica: **Puntarenas Prov.** Est. Agujas, Sendero Zamia, 300m. 22–30 AGO 1996. L_S_276750_526550 #8318, 1♀ (E. Fletes, A. Azofeifa, M. Lobo); Albergue Cerro de Oro, 200m., 5–9 MAY 1995, L N 279650 #4745, 1♀ (B. Gamboa); 4–14 May 1995, L_S_280450_517500 #5919, 1♀ (E. Alfaro); Rancho Quemado, 200m., Dic 1992, L-S 292500_511000, 1♀ (F. Quesada); Abr 1992, 1♀ (K. Flores); 2♀♀ (D. Brenes); Jun 1992, 1♀ (F. Quesada); Est. Esquinas, Peninsula de Osa, 200m. Abr 1993, L S 301400_542200 #2076, 1♀ (J.F. Quesada); Est. Sirena, 0–100m, P.N. Corcovado, Jun 1991, L-S270500_508300, 1♀ (G. Fonseca); P.N. Manuel Antonio, Quepos, 80m. Abr 1993, L S 370900_448800 #2140, 1♂ (G. Varela); Oct 1992, L-S 370900_448800, 1♀ (G. Varela).

Etymology.—The name is given after the type locality, the Golfito region in Costa Rica, Central America.

Remarks.—INBio collecting stations Est. (Estacion) Agujas, Est. (Estacion) Esquinas, Albergue Cerro de Oro, and Rancho Quemado are all in the Osa Peninsula of southwestern Costa Rica.

The holotype and paratypes were compared with paratypes of three other species of *Chartergellus*: *C. punctatior* Richards, *C. communis*, and *C. zonatus* Spinola. The paratype of *C punctatior* Richards, labeled as such by Richards, is from the same nest as a specimen (COLOMBIA: Valle, Anchicayá, 27.vii.73, M.J.W. Eberhard) mistakenly listed by Richards (1978: 222) as a paratype of *C. nigerrimus*. Richards (1978) listed no specimens of *C. punctatior* from Colombia in the description, but included Colombia in the distribution of this species in his key, further indicating his intention to consider the Colombian specimen (which fits the description of *punctatior*) a

paratype of this species. Besides this specimen, two other Colombian (Anchicayá) specimens of *C. punctatior* (28.ix.76, M. J. West-Eberhard) were examined by Richards in London. One was retained in the Natural History Museum, London, and the other, from the same colony, is in West-Eberhard's collection, labeled by Richards as a paratype of *C. atectus*. But it is clearly a specimen of *C. punctatior* that conforms in structure (mandibles with strong basal rim, and first metasomal tergum with broad yellow apical band) and nest type (unexceptional for the genus: combs on a rock rather than leaves, covered by a full envelope) to the published description of *punctatior*, not to those of the holotype of *C. atectus* collected at the same locality and described as having a nest unusual for the genus in being constructed between leaves and lacking a full envelope (Richards 1978). The paratype of *C. communis* examined here (BRAZIL: MT, Ilha de Bananal, Santa Isabella [*recte*: do Bananal, Santa Isabel], 25.viii.68, W. D. Hamilton) was deposited in the West-Eberhard collection by Richards. Along with other West-Eberhard voucher specimens, these paratypes will eventually be deposited in the US National Museum, Smithsonian Institution, Washington DC. We also compared a paratype female of *C. golfitensis* with three female syntypes of the Spinola type series of *C. zonatus* in the collection of the Museo di Zoologia Sistematica dell'Università di Torino, now housed in the Museo Regionale di Scienze Naturali in Turin.

Richards (1978) described three *Chartergellus* species (*amazonicus*, *punctatior*, and *communis*) as having a "raised rim" at the base of the manidible. In the *communis* paratype this is a rim-like ridge that rises abruptly forming a dark-brown-edged arc near the inner margin of the mandible, continued as a straight black line to the overlapping corner of the clypeus. In the *punctatior* paratypes and in *C. golfitensis* the arc arises less abruptly and is not continued as a line.

Color variation.—The colony of the type specimen contained three queens and two readily distinguished age cohorts: young individuals (16 females and 17 males), distinguished by wide clear metasomal apodeme margins with only a very thin black marginal line, as is characteristic of recently emerged vespid adults (West-Eberhard 1975), and 22 older females (including the holotype), with wide black apodeme margins. The young females resembled the queens in being lighter in color: meso- and metasoma and some parts of legs that are black in the older females are dark to light brown in the young females and queens, suggesting that the recently emerged females, although lacking sperm in the spermatheca and with undeveloped ovaries, are young queens. Queens have light brown first antennomere and nearly white mandibles. White lines at the posterior margin of the pronotum and the scrobal furrow are present in some females, absent in some (including the holotype), and a brownish spot in some, variation not correlated with age or caste. A white stripe on the distal margin of the first metasomal tergum is complete or absent in some, or at the lateral margins only in most females. A detailed morphometric analysis of both sexes and castes will be published elsewhere.

The Sendero Zamia, Rancho Quemado, and Manuel Antonio specimens have dark brown rather than reddish brown facial markings, and light markings are brown or yellowish brown rather than whitish.

NOTES ON *CHARTERGELLUS ZONATUS* SPINOLA

Spinola (1851) referred to four female specimens collected by M. Ghiliani in Pará, with the male unknown, but only three specimens are present in the Turin collection and there is no record of the location of the missing female. Examination of the remaining specimens indicate that Richards' (1978: 218) doubts regarding the Spinola (1851) description of *C. zonatus*,

resulting in its status as *incertae sedis* (Carpenter and van der Vecht 1991; Cooper 1993), are largely unjustified, though a few inaccuracies were evident (see below). Richards stated that "the description of ...*Chartergus zonatus* does not agree fully with any specimens I have seen of *Chartergellus*" but the Spinola specimens accord with Richards' (1978) generic description for *Chartergellus* in having the propodeal valve linear rather than in-curving, pronotal fovea present, widely separated from carina; hind-wing vein cu-a much longer than 1 Cu_1; labial palpi with three segments (the maxillary palpi could not be seen); scrobal furrow strong; margin of mesoscutum opposite tegula strong; scutellum rounded in profile; metanotum not vertical; and occipital carina lacking.

Species level characters are as follows:

Color. Black. Dark brown: antennae (lighter brown at tip and beneath), legs and wing venation. Reddish- brown: clypeus and three-pointed area of frons to 1/3 distance from antennal insertions to median ocellus. Yellow: intraocular space to ocular sinus; broad genal stripe (about half width of gena) from mandible nearly to dorsal margin of eye; propodeal carina; stripe anterior to scrobal furrow and about ¾ its length; anterior margins of scutellum, metanotum; thin stripes on margins of all sclerites bordering mesoscutum; posterior margins of terga 1, 2 (one female) or terga 1, 2, 3 (two females). Other variation: one female, labeled with a small green tag marked "♀," is darker in color than the other two: all of the markings that are yellow in the other two specimens and in the Spinola description, are brown, and all brown markings are darker brown in this specimen, which is one of those with three metasomal stripes. A female labeled "Pungono fortemente" (stung strongly) was affected by mold, so the remaining specimen, with no special label, and having yellow coloration like that described by Spinola, was used for the description reported here.

Other characters: eyes with sparse short hairs; mandible with four teeth, base with raised basal arc, scutal punctures separated by one diameter or more, scrobal furrow rises to gentle ridge at anterior side, coarsely and irregularly punctuate, with appressed hairs on posterior part and striate anterior ridge.

As suspected by Richards regarding a strongly yellow-marked species, the mandibles are not black; they are brown, with only the teeth dark brown or black, including in the darkest of the three specimens seen. The scutal margins are not yellow, as stated by Spinola; instead, it is the margin of the adjacent sclerites that are yellow; and only about half of the metanotum is yellow, not the entire metanotum.

Spinola (1851) cited Ghiliani's notes as stating that the nest of this species, in contrast to that of *Chartergus nitidulans* Fabricius, is found on the trunks of trees, and that the sting is very painful. Spinola was sent a sample of the nest carton, which he described as "terne et grisatre," (dull and grayish) but this has evidently been lost. There is no holotype labeled, hence all three specimens examined are syntypes.

ACKNOWLEDGMENTS

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LITERATURE CITED

Bequaert, J. C. 1938. A new *Charterginus* from Costa Rica, with notes on *Charterginus*, *Pseudochartergus*, *Pseudopolybia*, *Epipona*, and *Tatua* (Hymenoptera, Vespidae). *Revista Entomologia Rio de Janeiro* 9: 99–117, 1 pl., 1fig.

———. 1943. The generic names *Chartergus, Parachartergus, Epipona* and *Tatua*. A correction (Vespidae, Hymenoptera). *Bulletin Brooklyn Entomological Society* 38: 4.

Carpenter, J. M. 2004. Synonymy of the genus *Marimbonda* Richards, 1978, with *Leipomeles* Möbius, 1856 (Hymenoptera: Vespidae; Polistinae), and a new key to the genera of paper wasps of the New World. *American Museum Novitates* 3465: 1–16.

——— and J. van der Vecht. 1991. A study of the Vespidae described by William J. Fox (Insecta: Hymenoptera), with assessment of taxonomic implications. *Annals of the Carnegie Museum* 60: 211–241.

Cooper, M. 1993. A new species of *Chartergellus* (Hym., Vespidae, Polistinae, Polybiini) from Bolivia. *Entomologist's Monthly Magazine* 129: 165–166.

Fabricius, J. C. F. 1804. *Systema Piezatorum*. 439 pp. Brunsvigae.

Ihering, H. von. 1904. As vespas sociaes do Brasil. *Revista do Museu Paulista* 6: 97–309, 5pls, 3 figs.

Latreille, P. A. 1802. *Historie naturalle, générale et particulère des Crustacées es des Insectes*. (Sonnini's suites à Buffon), Paris. 3 xxi + 468 pp.

Richards, O. W. 1978. *The Social Wasps of the Americas, Excluding the Vespinae*. British Museum (Natural History), London. 580 pp + 4 pp plates.

Spinola, M. 1851. Compte rendu des Hyménoptères inédits provenant du voyage entomologique de Ghiliani dans le Para en 1846, 3–78. [Preprint of *Memorie della Reale Accademia della Scienze di Torino* (2)13: 19–94,1853 [Spinola (1853) is available at http://ripley.si.edu/ent/nmnhtypedb/images/pdfs/2746.pdf]

Wenzel, J. W. 1998. A generic key to the nests of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). *American Museum Novitates* 3224: 1–39.

West-Eberhard, M. J. 1975. Estudios de las avispas sociales (Himenóptera, Vespidae) del Valle del Cauca. I. Objetivos, métodos y notas para facilitar la identificación de especies comunes. *Cespedesia* 4 (16): 245–267.

———, J. M. Carpenter, and P. E. Hanson. 2006. Familia Vespidae. 617–644 *in*: Hanson, P. E., and I. D. Gauld eds., Hymenoptera de la Región Neotropical. *Memoirs of the American Entomological Institute* 77: 1–994.

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The Description of *Banacuniculus* Buffington, New Genus (Hymenoptera: Figitidae: Eucoilinae)

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Abstract.—The **new eucoiline genus *Banacuniculus*** is described to accommodate several species previously placed in *Ganaspidium*: ***Banacuniculus hunteri* (Crawford), new combination**; ***B. merickeli* (Miller), new combination**; ***B. nigrimanus* (Kieffer), new combination**; ***B. utilis* (Beardsley), new combination**; these species are all redescribed. The following **new species** are described: ***Banacuniculus brautigani***, ***B. beardsleyi***, ***B. dis***, and ***B. strykeri***. As is the case with *Ganaspidium*, species of *Banacuniculus* are parasitoids of some of the most pestiferous species of leafmining Agromyzidae (Diptera) and have been investigated for use as biological control agents of *Liriomyza trifolii* (Burgess). Additional phylogenetic, host range, and distributional data, and a key to all species are provided.

Key words.—*Liriomyza*, Agromyzidae, new species, new genus, species revision, parasitoid.

While revising *Ganaspidium* Weld (Hymenoptera: Figitidae: Eucoilinae), Buffington (2010) determined that some species of eucoiline wasps that had been historically included within *Ganaspidium* would render that genus polyphyletic if they remained within the genus. Buffington et al. (2007) supported this observation, where *Ganaspidium pussillae* Weld was recovered as a separate clade from *G. hunteri* (Crawford) and *G. utilis* Beardsley. Buffington (2010) further examined the characters of the mesosoma in both *G. hunteri* and *G. utilis*, revealing additional data supporting the removal of these two species from *Ganaspidium*. Buffington (2010) placed these two species, as well as *G. merickeli* (Miller) and *G. nigrimanus* (Kieffer), as *incertae sedis* pending the erection of a new genus to accommodate them. This paper provides the description of *Banacuniculus* Buffington, new genus, to accommodate these species. Included in this description is a redescription of the previously named species *Banacuniculus hunteri* (Crawford), new combination; *B. merickeli* (Miller), new combination; *B. nigrimanus* (Kieffer), new combination; and *B. utilis* (Beardsley), new combination. Four new species are also described: *Banacuniculus brautigani* Buffington, *B. beardsleyi* Buffington, *B. dis* Buffington, and *B. strykeri* Buffington.

Species of *Banacuniculus* are koinobiont endoparasitoids of agromyzid fly larvae (Diptera: Agromyzidae). Beardsley (1986, 1988) provided the first taxonomic work on eucoiline parasitoids of agromyzids in Hawai'i, and associated host remains with several species that he considered *Ganaspidium*, chiefly *G. hunteri* and *G. utilis*. The latter was described in Beardsley (1988) and has been shown to be an instrumental species in controlling pestiferous *Liriomyza* (Johnson 1987; Lynch and Johnson 1987; Mason and Johnson 1988; Rathman et al. 1991, 1995).

Banacuniculus is nested within the *Gronotoma* genus group (Buffington et al. 2007) and shares several synapomorphies with

those genera, including a complete parascutal impression, a large scutellar plate with a centrally placed midpit, protuberance on the clypeal and malar spaces, and remnants of notauli on the mesoscutum. Only the clypeal and malar protuberances are shared with *Ganaspidium*; all the other features are shared with other *Gronotoma* group genera (further discussed below).

MATERIALS AND METHODS

List of depositories

BPBM -Bernice B. Bishop Museum, Honolulu, HI, USA (N. Evenhuis).

CASC -California Academy of Sciences, San Francisco, CA, USA (R. Zuparko).

CNCI -Canadian National Collection of Insects, Ottawa, Canada (J. Read).

KSCU -Kansas State University, Manhattan, KS (G. Zolnerowich).

TAMU -Texas A&M University Insect Collection, College Station, TX, USA (E. Riley).

UCDC -Bohart Museum, University of California at Davis, Davis, CA, USA (L. Kimsey).

UCRC -University of California at Riverside, Riverside, CA, USA (S. Triapytsin).

USNM -National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (M. Buffington).

Additional sources of specimens.—Extensive collections from Texas were made available for my examination by Ricardo Hernandez (Department of Entomology, TAMU) and from Kansas by Robert Kula (Systematic Entomology Laboratory, Washington, DC) and Gregory Zolnerowich (Kansas State University, Manhattan, KS).

Specimen illustration and observation.—Methods for the imaging of specimens using light microscopy follow those of Buffington and van Noort (2007, 2009). For specimens too small for light microscopy, an environmental scanning electron microscope (ESEM) was used to image characters; specimens were shot uncoated in a Philips XL-30 ESEM machine, with lanthanum hexaboride electron source (LaB6). The instrument was operated in low vacuum mode with water vapor as the imaging gas and backscatter imaging with one-half of the diode active. Specimen mounting and lighting techniques follow Buffington and Gates (2009). Slide mounts were prepared with PVA mounting medium, cured for 72 hours at 43°C, and photographed with a JVC KW-75C camera on a Leica DMRB compound microscope. Specimens were examined with a Leica M10 stereomicroscope, illuminated with a pair of florescent desk lights.

Descriptive format.—Diagnoses focus on features that are easily recognizable by other observers, and closely related species that may have similar gross morphologies are distinguished. Terminology for all descriptive characters as well as phylogenetic characters are defined in Buffington (2009) and are not repeated here; surface sculpture terminology follows that of Harris (1979). Following the descriptions are summaries of general distribution, biology and comments on nomenclatural issues (when applicable). The species descriptions are generated by a database application, vSysLab (Johnson 2008), designed to facilitate the generation of taxon by character data matrices and to export the data both as text and as input files for other applications. A link to a distribution map is included in each species description. New species are designated are accompanied by a ZooBank registration number.

SYSTEMATIC TREATMENT

Banacuniculus Buffington, new genus

urn:lsid:zoobank.org:act:CD614635-1C08-459E-8E28-8B2EBE9972A5

Type species: *Banacuniculus hunteri* (Crawford), by present designation.

Diagnosis.—Malar space and ventral clypeal margin with distinct conical protuberances. Notauli lacking, setal tracks present where notauli are located in related taxa. Parascutal impression complete, terminating anteriorly at the point of origin of the notaular setal tracks. Scutellar plate nearly circular with midpit located in center of plate; plate lacking tubercles; setae-bearing pits present, encircling midpit. Setal band at base of syntergum of metasoma complete. Similar to *Ganaspidium* but easily separated based on the morphology of the scutellar plate: *Ganaspidium* always has a pair of tubercles on the anterior half of the plate, and the plate is not circular but oblong. *Banacuniculus* is also similar to *Microstilba, Nordlanderia,* and *Disorygma,* but distinguished based on notauli being absent and the hairy ring of syntergum present (notauli present and hairy ring of metasoma absent in *Microstilba, Nordlanderia,* and *Disorygma*); similar to *Agrostocynips,* but with pronotol plate less than one-half the width of the head (nearly as wide as head in *Agrostocynips*) and genal carina absent (present ventrally in *Agrostocynips*).

Description.—Head. Nearly glabrous with a few scattered setae on lower face, clypeus, inner margins of compound eyes and gena; ocellar hair patches absent. Ventral 1/4 of lower face with admedial clypeal furrows converging towards the clypeus; point of convergence resulting in the formation of distinct conical protuberance protruding from anterior margin of clypeus. Orbital furrows absent. Malar sulcus ranging from simple to compound. Malar space smooth to distinctly strigose, with large conical protuberance present. Genal carina absent.

Antennae: Female: 13 segments, moniliform, clavate; segments 3–13 sub-equal in length; rhinaria present only on the last 7 segments. Male: 15 segments; segments 3–15 sub-equal in length; rhinaria present on segments 3–15. Segment 3 modified, curved outwardly, excavated laterally.

Pronotum: Pronotal plate narrow, with setae present along dorsal margin; dorsal margin rounded; pronotal fovea open. Lateral pronotal carina absent. Pronotal triangle absent. Pronotal impression absent. Lateral aspect of pronotum smooth, glabrous in most species.

Mesoscutum: Smooth and glabrous; no sculpture present. Parascutal impression complete, lined with setae, extending from the tegula to point along anterior margin of mesoscutum where notaular setal line originates. Notauli, mesoscutal keel, parapsidal ridges and parapsidal hair lines absent; notaular setal line present.

Mesopectus: Upper and lower part of mesopleuron completely smooth and glabrous. Mesopleural triangle present, faintly indicated (often only visible in the space immediately anterior to the mesopleural spiracle). Mesopleural carina simple. Precoxal carina of lower part of mesopleuron present anteriorly and posteriorly, absent ventrally. Surcoxal depression reduced, smooth.

Scutellum: Scutellar plate ranging from small to large; midpit centrally placed; rim of plate translucent; dorsal surface of plate smooth in most species; setae-bearing pits present around midpit. Dorsal surface of the scutellum reticulate to smooth; rounded posteriorly and laterally; posterior carina present or absent. Laterodorsal and posterior projections absent. Lateral bars as long as wide; ventral lobe absent. Scutellar fovea oval, smooth and deep.

Metapectal-propodeal complex: Posterior 1/3-1/4 of metapectus setose. Spiracular groove with a well-defined dorsal margin, reduced ventral margin. Posterior margin of metapectus smooth, not ridged. Metapleural ridge and submetapleural ridge absent. Anterior impression of metepimeron absent; anterior impression of metepisternum present, reduced. Anteroventral cavity rounded, setose. Propodeum

covered in dense, appressed setae. Lateral propodeal carinae semi-parallel, bowed at junction with auxiliary propodeal carinae; auxiliary propodeal carinae distinct. Nucha glabrous, reticulate.

Wings: Hyaline; setose. R_1 complete, pigmented along anterior margin of wing; marginal cell not truncate, as deep as long. Apical fringe present, short (Fig. 3C).

Legs: Fore and mid coxa subequal in size, hind coxa twice the size of either fore or mid coxa. Fore coxa variously setose; mid and hind coxa with distinct anterior and posterior dorsoventral setal bands. Femora with sparse setal lines; tibiae and tarsomeres with dense, appressed setae. Length of hind tarsomere 1 equal to 0.5× the combined length of remaining hind tarsomeres.

Metasoma: Female: Subequal in size to mesosoma. Base of syntergum with hairy ring present, comprised of dense, appressed setae and a ring of thin, erect setae; remainder of metasoma glabrous. Micropunctures present on posterior 1/3 of the syntergum, and on remaining terga. Terga posterior to syntergum gradually directed ventrally, resulting in a 70 degree angle between syntergum and remaining terga. Ovipositor with series of sub-apical serrations (seen only in large specimens). Male: as in female with the terga posterior to syntergum abruptly angled ventrally, resulting in a 90 degree angle between syntergum and remaining terga.

Distribution.—Neotropical Region: Chile, Argentina, Panama, Costa Rica, Southern Mexico; Nearctic Region: Northern Mexico, continental United States, southern Canada; Hawaiian Islands.

Biology.—Several species of *Liriomyza* have been recorded as hosts (Beardsley 1986; Johnson 1987; Hara and Matayoshi 1990; Acosta and Cave 1994; present study). *Banacuniculus hunteri* and *B. utilis* have been evaluated for their usefulness in biological control of pestiferous leafmining flies (Johnson 1987; Lynch and Johnson 1987; Mason and Johnson 1988; Rathman et al. 1991; Rathman et al. 1995). Petcharat and Johnson (1988) studied the larval stages of *Banacuniculus utilis*.

Etymology.—The name translates in Latin to 'miner hunter': *bana*, hunter; *cuniculus*, miner. The name refers to the host preference of species of *Banacuniculus*, which putatively all attack leaf mining agromyzid flies. The gender is masculine.

Included species.—

Banacuniculus beardsleyi Buffington, new species.

B. brautigani Buffington, new species.

B. dis Buffington, new species.

B. hunteri (Crawford), Beardsley (1986). *Eucoila hunteri* Crawford, 1913: 310, holotype in USNM. *Ganaspidium hunteri* (Crawford): Beardsley (1986, 1988), Buffington (2004, 2010).

B. merickeli (Miller), new combination. *Nordlanderia merickeli* Miller, 1989: 158–159, 162, holotype lost.

B. nigrimanus (Kieffer). *Eucoela nigrimanus* Kieffer, 1907:138, holotype in CASC. *Ganaspidium nigrimanus* (Kieffer): Buffington (2004).

B. strykeri Buffington, new species.

B. utilis (Beardsley). *Ganaspidium utilis Beardsley*, 1988: 44–46, holotype in BPBM.

KEY TO SPECIES OF *BANACUNICULUS*

1. Dorsal surface of scutellum completely smooth and glabrous (Figs 2F and 3B); posterior margin of scutellum lacking a carina (Fig. 2F) 2
- Dorsal surface of scutellum distinctly sculptured, ranging from rugulose to striate (Fig. 1D); posterior margin of scutellum with (Fig. 1E) or without (Fig. 1D) a distinct carina 4
2. In lateral view, scutellar plate extending to posterior margin of scutellum (Fig. 3B); in dorsal view, the scutellar plate completely obscures the dorsal surface of the scutellum 3

- In lateral view, scutellar plate not extending to the posterior margin of scutellum (Fig. 2E); in dorsal view, much of the dorsal surface of the scutellum visible ... ***B. nigrimanus* (Kieffer)**

3. Dorsal surface of the scutellar plate horizontally strigose anterior of scutellar midpit ... ***B. beardsleyi*, n. sp.**
- Dorsal surface of scutellar plate entirely smooth anterior to the scutellar midpit ... ***B. utilis* (Beardsley)**

4. Posterior margin of the scutellum without a well-developed and distinct posterior carina, resulting in a broadly rounded posterior margin of the scutellum, lacking a distinct transition from the dorsal surface to the latero-postero surface (Fig. 1D) ... **5**
- Posterior margin of the scutellum with a well-developed and distinct posterior carina, separating the dorsal surface of the scutellum from the latero-postero surface (PC, Fig. 1E) ... **6**

5. Lateral aspect of pronotum and ventral half of mesopleuron covered with long, thin, white setae (PHP, Fig. 1B); metasoma at least twice as long as mesosoma .... ***B. brautigani* n. sp.**
- Lateral aspect of pronotum and ventral half of mesopleuron largely glabrous (in some specimens, there may be short setae present along the anterior margin of the pronotum) (Fig. 1C) ... ***B. dis*, n. sp.**

6. Dorsal surface of scutellum distinctly rugulose to coriaceous over its entirety (Fig. 2A) **7**
- Dorsal surface of scutellum longitudinally striate, frequently smooth and glabrous anteriorly just posterior to the scutellar fovea ... ***B. merickeli* (Miller)**

7. Scutellar plate flat to slightly convex surrounding the midpit (Fig. 2A) ... ***B. hunteri* (Crawford)**
- Scutellar plate distinctly concave surrounding the midpit (Fig. 2C) .. ***B. strykeri*, n. sp.**

Banacuniculus beardsleyi Buffington, new species

urn:lsid:zoobank.org:act:649F3AB4-DC91-4CFE-880B-07B5A6A76F1D

urn:lsid:biosci.ohio-state.edu:osuc_concepts:253198

Fig. 1F.

Description.—Malar sulcus simple. Malar space smooth. Malar protuberance smooth, short, not extending beyond length of ventral margin of malar space. Clypeal protuberance short, not overhanging anterior margin of clypeus. Tubercles of scutellar plate absent. Dorsal surface of scutellar plate flat, horizontally striate, setal bearing pits present surrounding midpit. Carina along posterior margin of scutellum absent. Dorsal surface of scutellum entirely smooth. Midpit of scutellar plate in center of plate; plate large, obscuring dorsal surface of scutellum when viewed dorsally. Mesopopleural setal patch absent. Mesopleuron entirely smooth. Lateral aspect of pronotum with some short setae anteriorly, remainder glabrous. Marginal cell of forewing as deep as long.

Metasoma sub-equal in size to mesosoma (in lateral view).

Diagnosis.—This species resembles both *B. nigrimanus* and *B. utilis* in the morphology of the dorsal surface of the scutellum, but is easily separated from these species by the presence of the horizontally striate scutellar plate

Etymology.—Named in honor of my late mentor Jack Beardsley.

Link to Distribution Map.—http//hol.osu.edu/map-full.html?id=253198

Biology.—Unknown.

Type Material.—Holotype, female: **MEXICO**: Mexico, SIN, Mazatlán, 27.III.1979, L. D. French, USNM ENT 00655548 (deposited in UCDC).

Banacuniculus brautigani Buffington, new species

urn:lsid:zoobank.org:act:662617B2-0DCB-4643-AD80-2CCD8E1BE83F

urn:lsid:biosci.ohio-state.edu:osuc_concepts:253199

Figs 1 A and B.

Description.—Malar sulcus compound. Malar space partially striate, striations extending 1/2 to 2/3 distance from ventral margin of malar space to base of compound eye. Malar protuberance smooth, elongate, extending beyond length of ventral margin of malar space. Clypeal protuberance elongate, overhanging anterior margin of clypeus. Tubercles of scutellar plate absent. Dorsal surface of scutellar plate gently convex, smooth; setal bearing pits surrounding midpit. Carina along posterior margin of scutellum absent. Dorsal surface of scutellum entirely rugulose/wrinkled. Midpit of scutellar plate in center of plate; plate small, revealing dorsal surface of scutellum when viewed dorsally. Mesopopleural setal patch present. Mesopleuron entirely smooth. Lateral aspect of pronotum covered in long, thin, white setae. Marginal cell of forewing as deep as long. Metasoma distinctly larger than mesosoma (longer and deeper) when viewed laterally.

Diagnosis.—This species differs from all other *Banacuniculus* by the presence of an entirely setose lateral aspect of the pronotum and the presence of a metasoma that is roughly two times the size of the mesosoma (PHP, Fig. 1B).

Etymology.—Named in honor of the author Richard Brautigan who wrote many poems and short stories on the nature and culture of California.

Link to Distribution Map.—http://hol.osu.edu/map-full.html?id=253199

Biology.—Unknown.

Type Material.—Holotype, female: **UNITED STATES**: CA, Riverside Co., 3.5mi S Palm Desert, Nance (Coyote) Canyon, alluvial soil, Philip L. Boyd Deep Canyon Research Center, 12.IV.1975, J. D. Pinto, USNM ENT 00655348 (deposited in UCRC).

Banacuniculus dis Buffington, new species

urn:lsid:zoobank.org:act:504C0C75-864F-40C0-AEB5-2B0162591D51

urn:lsid:biosci.ohio-state.edu:osuc_concepts:253201

Figs 1 C–D and 3 E–F.

Description.—Malar sulcus compound. Malar space partially striate, striations extending 1/2 to 2/3 distance from ventral margin of malar space to base of compound eye. Malar protuberance smooth, elongate, extending beyond length of ventral margin of malar space. Clypeal protuberance elongate, overhanging anterior margin of clypeus. Tubercles of scutellar plate absent. Dorsal surface of scutellar plate gently convex, smooth; setal bearing pits surrounding midpit. Carina along posterior margin of scutellum absent. Dorsal surface of scutellum entirely rugulose/wrinkled. Midpit of scutellar plate in center of plate; plate small, revealing dorsal surface of scutellum when viewed dorsally. Mesopopleural setal patch absent. Mesopleuron entirely smooth. Lateral aspect of pronotum with some short setae anteriorly, remainder glabrous. Marginal cell of forewing as deep as long. Metasoma sub-equal in size to mesosoma in lateral view.

Diagnosis.—This species can be confused with *Banacuniculus hunteri*, but can be separated by the lack of a posterior carina of the dorsal surface of the scutellum.

Etymology.—Named after *Dis*, Dante Alighieri's name for the City of Hell in *The Inferno*. As used here, the name refers to the hell-like conditions this species seems to thrive in the desert Southwest.

Link to Distribution Map.—http://hol.osu.edu/map-full.html?id=253201

Biology.—Unknown.

Type Material.—Holotype, female: **UNITED STATES**: CA, Imperial Co., 5km from Gordons Well exit at I-8, Sand Highway, Algodones

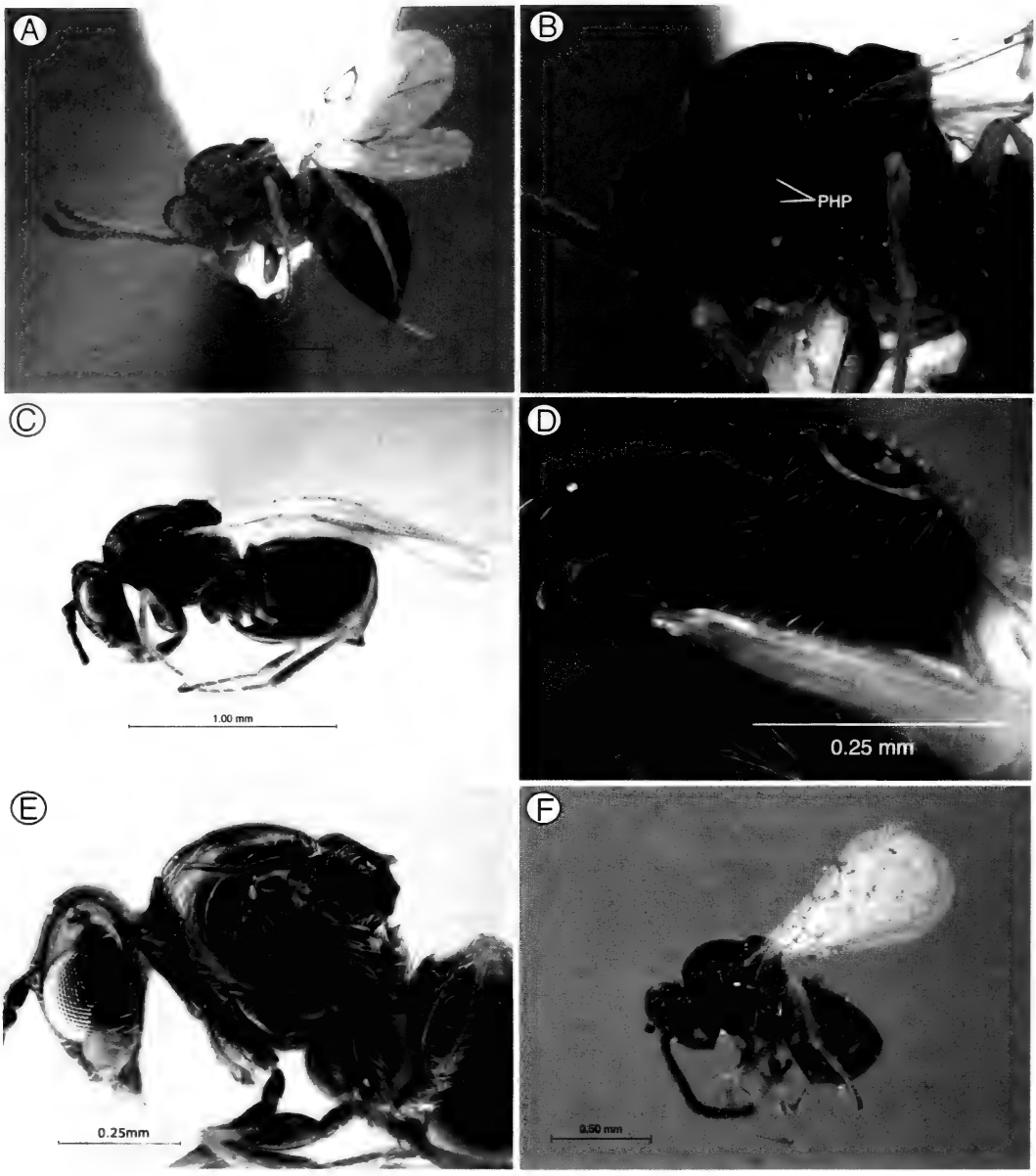

Fig. 1. A, *Banacuniculus brautigani*, n. sp., lateral habitus of holotype; B, *B. brautigani* n. sp., closeup of head and mesosoma; C, *B. dis* n. sp., lateral habitus; D, *B. dis* n. sp., poster-dorsal view of scutellum and scutellar plate; E, *B. merickeli* (Miller), closeup of head and mesosoma; F, *B. beardselyi* n. sp., lateral habitus of holotype. Abbreviations: PHP, pronotal hair patch; PC, posterior carina of the scutellum.

Dunes, 32°45.5'N 114°57'W, 24.VII.2008, S. L. Heydon, USNM ENT 00655716 (deposited in UCDC). *Paratypes*: (2 females, 3 males) **UNITED STATES**: *CALIFORNIA*. Inyo Co., 6km E Big Pine, 24.V.1994, S. L. Heydon (1 female, USNM ENT 00655523 (UCDC)); Inyo Co., Eureka Valley, Joshua Flat, 24.V.1994, S. L. Heydon (1 male, USNM ENT 00655522 (UCDC)); Riverside Co., 2mi NW Oasis, 15.V.1974, N. J. Smith (1 female, USNM ENT 00655486 (UCDC)); Solano Co., 6km SE Suisun City, Suisun Marsh, 14.VI.1993, S. L. Heydon & L. Guo (1 male, USNM ENT 00655454 (UCDC)). *MONTANA*. Silver Bow Co., Butte, 23.VII.1983, J. D. Pinto (1 male, UCRC ENT 196933 (UCRC)).

Banacuniculus hunteri (Crawford), new combination.

urn:lsid:biosci.ohio-state.edu:osuc_concepts:253431

Eucoila hunteri Crawford, 1913: 310. Holotype in USNM.

Ganaspidium hunteri (Crawford): Beardsley (1986), Buffington (2010).

Figs 2 A and B.

Description.—Malar sulcus compound. Malar space partially striate, striations extending 1/2 to 2/3 distance from ventral margin of malar space to base of compound eye. Malar protuberance striate, elongate, extending beyond length of ventral margin of malar space. Clypeal protuberance elongate, overhanging anterior margin of clypeus. Tubercles of scutellar plate absent. Dorsal surface of scutellar plate flat, smooth; setal bearing pits present surrounding midpit. Carina along posterior margin of scutellum delicate, defining transition from dorsal surface of scutellum from posterior surface. Dorsal surface of scutellum entirely rugulose/wrinkled. Midpit of scutellar plate in center of plate; plate small, revealing dorsal surface of scutellum when viewed dorsally. Mesopopleural setal patch absent. Mesopleuron entirely smooth. Lateral aspect of pronotum with some short setae anteriorly, remainder glabrous. Marginal cell of forewing as deep as long. Metasoma subequal in size to mesosoma in lateral view.

Diagnosis.—This species is separated from all other *Banacuniculus* by simultaneously possessing a densely crenulate dorsal surface of the scutellum and a distinct posterior carina of the scutellum.

Link to Distribution Map.—http://hol.osu.edu/map-full.html?id=253204

Biology.—Recorded parasitizing *Liriomyza trifolii* (Burgess) and *L. sativae* Blanchard (Lynch and Johnson 1987).

Material Examined.—Holotype, female: **UNITED STATES**: TX, Dallas Co., cotton, Dallas, 19.V.1912, Hunter, USNM ENT 00655719 (deposited in USNM). *Paratype*: **UNITED STATES**: TX, Dallas Co., cotton, Dallas, 19.V.1912, Hunter (1 female, USNM ENT 00653537 (USNM)). *Other material*: (23 females, 12 males) **CANADA**: 2-25Y BRI-91, no date (1 female, USNM ENT 00652564 (CNCI)). *ALBERTA*. Calgary, 1. VII.1956, O. Peck (1 female, USNM ENT 00655545 (CNCI)); Lethbridge, Oldman River, 22.VI.1956, O. Peck (8 females, 2 males, USNM ENT 00652563, 00653555, 00653558, 00653559, 00653560-00653562, 00653566, 00653568, 00653569 (CNCI)); Lethbridge, Oldman River, 22.VI.1956, sweeping, O. Peck (1 female, USNM ENT 00653570 (CNCI)); grass, Elkwater Lake, 21.VII.1956, O. Peck (2 males, USNM ENT 00653567, 00653578 (CNCI)); montaine prairie, Waterton Lakes National Park of Canada, 5.VII-16.VII.1991, H. Goulet (1 male, USNM ENT 00653585 (CNCI)); montaine prairie, Waterton Lakes National Park of Canada, 5.VIII.1991, H. Goulet (1 female, 1 male, USNM ENT 00653581, 00653582 (CNCI)); montaine prairie, Waterton Lakes National Park of Canada, 8.VII.1991, H. Goulet (1 male, USNM ENT 00653565 (CNCI)); nr. mouth of Blakiston Creek, flowery prairie, Waterton Lakes National Park of Canada, 8.VII.1991, H. Goulet (2 females, 3 males, USNM ENT 00653572-00653576 (CNCI)); nr. mouth of Blakiston Creek, flowery prairie, Waterton Lakes National Park of Canada, no date, H. Goulet (1 female, USNM ENT 00653580 (CNCI)). *BRITISH COLUMBIA*. 57km N Princeton, hwy. 5, pine/grass, Kentucky-Alleyne Park, 10.VII.1986, H. Goulet (1 female, USNM ENT 00653571 (CNCI)). *NEW BRUNSWICK*. Kouchibouguac National Park of Canada, 7.VII.1977, M. Ivanochko (1 female, USNM ENT 00653579 (CNCI)). *NOVA SCOTIA*. sandbar, South Harbour, 28.VI.1983 (1 male, USNM ENT 00653577 (CNCI)). **UNITED STATES**: *COLORADO*. Boulder Co., University of Colorado Mountain Research Station (Science Lodge), 5.VII-6.VII.1961, W. R. M. Mason (1 female, USNM ENT 00653556 (CNCI)); Clear Creek Co., Mt. Evans, Doolittle Ranch, 8.VII.1961, S. M. Clark (1 female, USNM ENT 00653557 (CNCI)); Grand Co., 7km E Winter Park, Rollins Pass Road, 3.VIII.1999, S. L. Heydon & S. M. L. Heydon (1 male, USNM ENT 00655515 (UCDC)). *IDAHO*. Cassia Co., #8, Burley, 27.VI.1932, D. E. Fox (1 female, USNM ENT 00653510 (USNM)). *NEW MEXICO*. Valencia Co., 20mi W Los Lunas, along

streambed, Carrizo Creek, 1.VIII-23.VIII.1977, Malaise trap, S. Peck & J. Peck (1 female, USNM ENT 00653584 (CNCI)). *OREGON*. Lake Co., 15km N Lakeview, Bull Creek Campground, 20.VII.1994, S. L. Heydon (1 female, USNM ENT 00655445 (UCDC)). *UTAH*. Uintah Co., Vernal, 1912, C. N. Ainslie (1 female, USNM ENT 00653538 (USNM)).

Banacuniculus merickeli (Miller), new combination.

urn:lsid:biosci.ohio-state.edu:osuc_concepts: 253432

Nordlanderia merickeli Miller, 1989: 158–159, 162. Holotype lost.

Figs 1E and 3D.

Description.—Malar sulcus compound. Malar space partially striate, striations extending 1/2 to 2/3 distance from ventral margin of malar space to base of compound eye. Malar protuberance smooth, elongate, extending beyond length of ventral margin of malar space. Clypeal protuberance elongate, overhanging anterior margin of clypeus. Tubercles of scutellar plate absent. Dorsal surface of scutellar plate gently convex, smooth; setal bearing pits surrounding midpit. Carina along posterior margin of scutellum delicate, defining transition from dorsal surface of scutellum from posterior surface. Dorsal surface of scutellum smooth anteriorly, longitudinally striate posteriorly. Midpit of scutellar plate in center of plate; plate small, revealing dorsal surface of scutellum when viewed dorsally. Mesopopleural setal patch absent. Mesopleuron entirely smooth. Lateral aspect of pronotum with some short setae anteriorly, remainder glabrous. Marginal cell of forewing as deep as long. Metasoma subequal in size to mesosoma in lateral view.

Diagnosis.—This species is separated from all other *Banacuniculus* by having a longitudinally striate dorsal surface of the scutellum; in all other species in the genus, the dorsal surface of the scutellum is either entirely smooth, or variously crenulate-rugose.

Link to Distribution Map.—http://hol.osu.edu/map-full.html?id=253207

Biology.—Unknown.

Material Examined.—*Other material*: (13 females, 9 males) **CANADA**: *ALBERTA*. grass, Writing-On-Stone Provincial Park, 24.VIII.1990, McCorquodale (1 female, USNM ENT 00653589 (CNCI)); montaine prairie, Waterton Lakes National Park of Canada, 14.VII.1991, H. Goulet (2 males, USNM ENT 00653587, 00653588 (CNCI)); montaine prairie, Waterton Lakes National Park of Canada, 5.VII-16.VII.1991, H. Goulet (1 female, USNM ENT 00653583 (CNCI)); montaine prairie, Waterton Lakes National Park of Canada, 5.VII.1991, H. Goulet (1 female, 1 male, USNM ENT 00653586, 00655612 (CNCI)); nr. mouth of Blakiston Creek, flowery prairie, Waterton Lakes National Park of Canada, 8.VII.1991, H. Goulet (1 female, USNM ENT 00655580 (CNCI)). **MEXICO**: DF, 12mi W Texcoco de Mora, 2300m, 28.X.1982, screen sweeping, A. Gonzalez (1 female, UCRC ENT 196943 (UCRC)). MOR, El Zarco, 1.VI.1954 (1 unknown, USNM ENT 00653532 (USNM)). **NICARAGUA**: Rivas Dept., San Juan del Sur, 11°15'N 85°52'W, 21.VII.1994, L. J. Clark (1 female, USNM ENT 00655504 (UCDC)). **UNITED STATES**: *CALIFORNIA*. San Bernardino Co., S of Barton Flats, 2090m, 19.VI-26.VI.2007, Malaise trap, F. Reuter (1 male, USNM ENT 00655317 (USNM)); Stanislaus Co., romaine lettuce, Modesto, 8.XI.1944, C. Weber (1 female, USNM ENT 00655437 (UCDC)). *COLORADO*. Larimer Co., Fort Collins, 25.V.1995, C. F. Baker (1 female, USNM ENT 00655344 (USNM)); Larimer Co., Fort Collins, VI-1895, C. F. Baker (1 female, USNM ENT 00653528 (USNM)). *NORTH DAKOTA*. Hettinger, Mott, no date, sweeping, C. N. Ainslie (1 female, USNM ENT 00653519 (USNM)). *NEW MEXICO*. Quay Co., along rt. 66, within city limits, Tucumcari, 4.IV.2003, sweeping, M. Buffington (1 male, USNM ENT 00655334 (USNM)); Quay Co., along rt. 66, within city limits, general vegetation, Tucumcari, 4.VI.2003, sweeping, M. Buffington (1 male, USNM ENT 00655331 (USNM)). *NEVADA*. Lander Co., summit above Austin, 2430m, 8.VIII.1999, S. L. Heydon & S. M. L. Heydon (1 female, USNM ENT 00655440 (UCDC)). *TEXAS*. Val Verde Co., Seminole Canyon State Historical Park, 1400ft, 15.IV.1999, J. M. Heraty (1 female, UCRC

ENT 196938 (UCRC)). *WYOMING.* Big Horn Co., northern Big Horn Mts., alpine meadow, Sheep Mountain, 22.VII.1988, H. Goulet (1 male, USNM ENT 00655581 (CNCI)); Platte Co., Chugwater Creek, Chugwater, 16.VIII.1986, J. D. Pinto (1 male, USNM ENT 00655614 (USNM)); Platte Co., town center, Chugwater, 16.VIII.1986, J. D. Pinto (1 male, UCRC ENT 196936 (UCRC)); Platte Co., town center, Chugwater, 16.VIII.1996, J. D. Pinto (1 male, UCRC ENT 196935 (UCRC)); Sheridan Co., Bighorn Mountains, 24mi W Dayton, 20.VIII.1983, G. Gordh (1 male, UCRC ENT 196934 (UCRC)); Teton Co., Granite Canyon, 1987/060, Teton National Forest, 3.VII.1987, J. A. Jackson (1 female, USNM ENT 00655347 (USNM)).

Comments.—Miller (1989) described two species of eucoiline wasps that he placed in *Nordlanderia* Quinlan. Though the location of the type specimens for these two species is unknown (Miller, pers. comm.), it is clear from the scanning electron micrographs accompanying the descriptions that one species, *B. merickeli* (Miller) possesses the diagnostic features of *Banacuniculus* but not all of the defining features of *Nordlanderia*; therefore, this species is transferred to *Banacuniculus*. Communication with the original describer of the species suggests the holotype may yet surface; I am reticent to designate a neotype at the present time until it can be fully verified that the holotype is lost.

Banacuniculus nigrimanus (Kieffer), new combination.

urn:lsid:biosci.ohio-state.edu:osuc_concepts:253433

Eucoela nigrimanus Kieffer, 1907: 138. Holotype in CASC.

Ganaspidium nigrimanus (Kieffer): Buffington (2004, submitted).

Figs 2 D–F.

Description.—Malar sulcus simple. Malar space smooth; partially striate, striations extending to 1/4 distance from ventral margin of malar space to base of compound eye. Malar protuberance smooth, short, not extending beyond length of ventral margin of malar space. Clypeal protuberance short, not overhanging anterior margin of clypeus. Tubercles of scutellar plate absent. Dorsal surface of scutellar plate flat, smooth; setal bearing pits present surrounding midpit. Carina along posterior margin of scutellum absent. Dorsal surface of scutellum entirely smooth. Midpit of scutellar plate in center of plate; plate small, revealing dorsal surface of scutellum when viewed dorsally. Mesopopleural setal patch absent. Mesopleuron entirely smooth. Lateral aspect of pronotum with some short setae anteriorly, remainder glabrous. Marginal cell of forewing as deep as long. Metasoma subequal in size to mesosoma in lateral view.

Diagnosis.—This species is very similar to *B. utilis* but can be easily separated by the small relative size of the scutellar plate; in *B. utilis* the plate is enormous, covering the entire dorsal surface of the scutellum when viewed dorsally. In *B. nigrimanus*, the plate is much smaller, revealing the majority of the dorsal surface of the scutellum.

Link to Distribution Map.—http://hol.osu.edu/map-full.html?id=251126

Biology.—Recorded parasitizing *Liriomyza huidobrensis* (Blanchard) (based on label data).

Material Examined.—Holotype, male: [first label] Claremont Cal. Baker, [second label] 5695, [third label] *Eucoela nigrimanus* Kieffer (in Kieffer's hand), [fourth label] California Academy of Science Type No. 10573. [Note: this 'Baker number' could not be located in the Baker notes housed at the USNM]. *Other material*: (60 females, 14 males) **CANADA**: *ALBERTA*. Medicine Hat, 14.VII.1956, O. Peck (1 female, USNM ENT 00655592 (CNCI)); Waterton Park, 18.VI.1956, O. Peck (1 male, USNM ENT 00655579 (CNCI)); montaine prairie, Waterton Lakes National Park of Canada, 5.VIII-16.VIII.1991, Malaise trap, H. Goulet (1 female, USNM ENT 00655620 (USNM)); montaine prairie, Waterton Lakes National Park of Canada, 8.VII.1991, H. Goulet (1 male, USNM ENT 00655613 (CNCI)); nr. Mt. Galway, montaine prairie, Waterton Lakes National Park of

Canada, 5.VIII-16.VIII.1991, Malaise trap, H. Goulet (1 female, USNM ENT 00655622 (CNCI)); nr. Mt. Galway, subalpine prairie, Waterton Lakes National Park of Canada, 9.VII.1991, Malaise trap, H. Goulet (1 female, USNM ENT 00655621 (CNCI)). **MEXICO**: BCS, road, vicinity of La Ventana, 8.III.1963, P. H. Arnaud (1 male, USNM ENT 00655424 (CASC)). SON, tomatoes, Heroica Nogales, 23.III.1943 (1 female, USNM ENT 00653520 (USNM)). **UNITED STATES**: *ARIZONA*. Graham Co., desert, 2.4km W on hwy 366 from hwy 191 (666), 1160m, 27.VI-28.VI.1991, Malaise trap, J. E. O'Hara (2 females, USNM ENT 00655596, 00655597 (CNCI)). *CALIFORNIA*. Amador Co., 3km N Silver Lake, Martin Meadow, 22.VII.1993, L. S. Kimsey & R. B. Kimsey (1 female, USNM ENT 00655488 (UCDC)); Imperial Co., 11.3km NW hwy 78, Coachella Canal Road, Algodones Dunes, 25.III.2008, sweeping, S. L. Heydon (1 female, USNM ENT 00655525 (UCDC)); Inyo Co., 31km ENE Big Pine, 25.V.1994, S. L. Heydon (6 females, 2 males, USNM ENT 00655498, 00655499, 00655506-00655507, 00655508, 00655509, 00655510-00655511 (UCDC)); Inyo Co., Grays Meadow Campground, 6000ft, 17.VII.1985, A. S. Menke (1 female, USNM ENT 00655343 (USNM)); Nevada Co., 6km NW Hobart Mills, Sagehen Creek Field Station, 29.VII.2002, sweeping, S. L. Heydon (2 females, USNM ENT 00655434-00655435 (UCDC)); Nevada Co., Hobart Mills, 10.VII.1978, R. M. Bohart (1 female, USNM ENT 00655449 (UCDC)); Riverside Co., vegetation/wash, Wiley Well Campground, 176m, 1.V.2008, sweeping, M. Gates (1 female, USNM ENT 00653530 (USNM)); San Bernardino Co., 1mi N of crossing of 2N93 Service Road and hwy 38, H97-20, San Bernardino Mountains, 2350m, 24.VI.1997, J. M. Heraty (1 male, UCRC ENT 197000 (UCRC)); Solano Co., 6km SE Suisun City, Suisun Marsh, 14.VI.1993, S. L. Heydon & L. Guo (3 females, 1 male, USNM ENT 00655453, 00655455-00655456, 00655469 (UCDC)). *COLORADO*. Grand Co., 22km NNW Kremmling, Chimney Rock, 4.VIII.1999, S. L. Heydon & S. M. L. Heydon (3 females, USNM ENT 00655436, 00655441, 00655501 (UCDC)); Grand Co., 22km NNW Kremmling, hwy 40 & road 27, 4.VIII.1999, S. L. Heydon & S. M. L. Heydon (2 females, USNM ENT 00655439, 00655539 (UCDC)); Larimer Co., Fort Collins, 18.VIII.1893, Baker (1 female, USNM ENT 00653512 (USNM)); Park Co., 6km S Lake George, along Fish Creek, 7.VII.1992, S. L. Heydon (1 female, 1 male, USNM ENT 00655470, 00655475 (UCDC)). *FLORIDA*. Charlotte Co., Placida, 11.IV.1952, O. Peck (1 female, USNM ENT 00655594 (CNCI)). *KANSAS*. Geary Co., watershed 2D, Konza Prairie Biological Station, 5.V-12.V.2005, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655711 (USNM)); Geary Co., watershed C, Konza Prairie Biological Station, 26.VIII-2.IX.2005, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655712 (USNM)). *NEW MEXICO*. Doña Ana Co., Mesilla, no date (1 female, USNM ENT 00653536 (USNM)); Quay Co., along rt. 66, within city limits, general vegetation, Tucumcari, 4.VI.2003, sweeping, M. Buffington (2 females, USNM ENT 00655332-00655333 (USNM)); Valencia Co., 20mi W Los Lunas, along streambed, Carrizo Creek, 23.VIII.1977, Malaise trap, S. Peck & J. Peck (3 females, USNM ENT 00655573-00655574, 00655583 (CNCI)). *NEVADA*. White Pine Co., 45km SSE Eureka, 19.VII.1995, S. L. Heydon & R. M. Bohart (1 female, USNM ENT 00655513 (UCDC)). *OREGON*. Lake Co., 15km N Lakeview, Bull Creek Campground, 20.VII.1994, S. L. Heydon (10 females, 2 males, USNM ENT 00655442-00655444, 00655446-00655447, 00655448, 00655457, 00655458, 00655459, 00655460-00655461, 00655465 (UCDC)); Lake Co., Alkali Lake, 21.VII.1994, S. L. Heydon (1 female, 1 male, USNM ENT 00655477, 00655492 (UCDC)). *TEXAS*. Brewster Co., lowland desert springs, Big Bend National Park, 21.VII.1977, L. Masner (1 male, USNM ENT 00655600 (CNCI)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 30.IV.2008, Hernandez (1 unknown, USNM ENT 00655029 (USNM)); Presidio Co., Big Bend Ranch State Park, 27.X-1.IV.1989, Malaise trap, D. Judd (1 female, USNM ENT 00655571 (CNCI)). *UTAH*. Emery Co., nr. Goblin Valley State Park, Wild Horse Creek, 2.VIII-7.VIII.1997, Malaise trap, M. Wasbauer & J. Wasbauer (1 male, USNM ENT 00655450 (UCDC)); Emery Co., nr. Goblin Valley State Park, Wild Horse Creek, 2.VIII-7.VIII.1997, M. Wasbauer & J. Wasbauer (1 female, USNM ENT 00655524 (UCDC)); Washington Co., Pinto, no date, C. N. Ainslie (1 female, USNM ENT 00653531 (USNM)); Wayne Co., 6mi W Caineville, along Fremont River, 4700ft, 29.VI.1993, J. D. Pinto (1 female, UCRC ENT 196937 (UCRC)); Wayne

Co., vegetation, 11 km E Torrey, 7.VIII.1996, L. A. Baptiste (1 female, USNM ENT 00655438 (UCDC)). *WYOMING*. Big Horn Co., northern Big Horn Mts., alpine meadow, Sheep Mountain, 22.VII.1988, H. Goulet (4 females, USNM ENT 00655575-00655577, 00655578 (CNCI)).

Banacuniculus strykeri Buffington, new species

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urn:lsid:biosci.ohio-state.edu:osuc_concepts:253208

Fig. 2C.

Description.—Malar sulcus compound. Malar space partially striate, striations extending 1/2 to 2/3 distance from ventral margin of malar space to base of compound eye. Malar protuberance striate, short, not extending beyond length of ventral margin of malar space. Clypeal protuberance short, not overhanging anterior margin of clypeus. Midpit of scutellar plate in center of plate; plate large, obscuring dorsal surface of scutellum when viewed dorsally. Tubercles of scutellar plate absent. Dorsal surface of scutellar plate concave, radially striate; setal bearing pits surrounding midpit. Carina along posterior margin of scutellum present, distinctly cleft, defining transition from dorsal surface of scutellum from posterior surface. Dorsal surface of scutellum entirely rugulose/wrinkled. Mesopopleura setal patch absent. Mesopleuron striate within confines of mesopleural triangle, remainder of sclerite smooth. Lateral aspect of pronotum with some short setae anteriorly, remainder glabrous. Marginal cell of forewing as deep as long. Metasoma sub-equal size to mesosoma in lateral
view.

Diagnosis.—Differs from other species by the large scutellar plate, the presence of the radial striations on the surface of the scutellar plate, and by the reduced malar and clypeal protuberances.

Biology.—Reared from an isolated puparium of *Liriomyza lathyri* Seghal in Marquette, MI (holotype specimen).

Etymology.—Named in honor of my son, Stryker Buffington.

Link to Distribution Map.—http://hol.osu.edu/map-full.html?id=253208

Type Material.—Holotype, female: United States, MI, Marquette Co. 46°50.627'N 87°51.300'W, 16 August 2006, R. Priest. Lot # RJP1755.2.1, USNM ENT 00655717. Deposited in USNM. *Paratypes*: **UNITED STATES**: 1 female, 2 males: *COLORADO*. Fremont Co., Phantom Canyon, 29-31/5/1987, G. Hevel, 1 female USNM ENT 00653511 (USNM). *MICHIGAN*. Washtenaw Co., Ann Arbor, 7/12-21/1982, R. Wharton, 2 males USNM ENT 00655520-00655521 (TAMU).

Comments.—The scutellar morphology and the distribution patterns of this species are striking features. More *Banacuniculus* species are likely to occur in the Midwestern United States.

Banacuniculus utilis (Beardsley), new combination.

urn:lsid:biosci.ohio-state.edu:osuc_concepts:253430

Ganaspidium utilis Beardsley, 1988: 44–46, holotype in BPBM.

Synonymized with *Ganaspidium nigrimanus* (Kieffer) by Buffington (2004); revised status: Buffington (2010).

Figs 3 A–C.

Redescription.—Malar sulcus simple. Malar space smooth; partially striate, striations extending 1/2 to 2/3 distance from ventral margin of malar space to base of compound eye. Malar protuberance smooth, short, not extending beyond length of ventral margin of malar space. Clypeal protuberance short, not overhanging anterior margin of clypeus. Midpit of scutellar plate in center of plate; plate large, obscuring dorsal surface of scutellum when viewed dorsally. Tubercles of scutellar plate absent. Dorsal surface of scutellar plate flat, smooth, setal bearing pits present surrounding midpit. Carina along posterior margin of scutellum absent. Dorsal surface of scutellum entirely smooth. Mesopopleural setal patch absent.

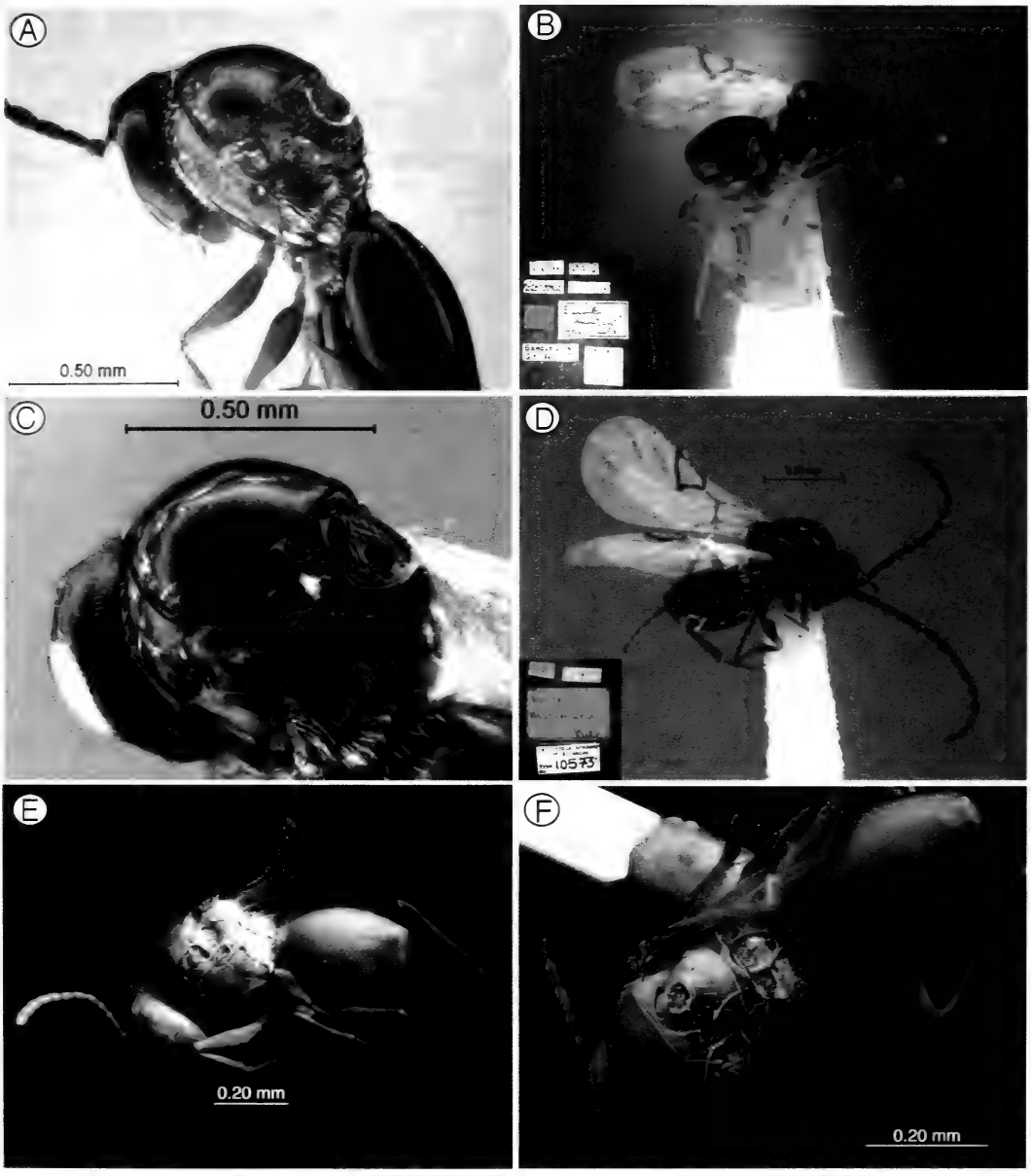

Fig. 2. A, *Banacuniculus hunteri* (Crawford), postero-dorsal view of mesosoma; B, *B. hunteri*, lateral habitus of holotype with inset of specimen labels; C, *B. strykeri*, n. sp., postero-dorsal view of scutellum and scutellar plate; D, *B. nigrimanus* (Kieffer), lateral habitus of holotype with inset of specimen labels; E, *B. nigrimanus*, lateral habitus of non-type specimen; F, *B. nigrimanus*, postero-dorsal view of scutellum, scutellar plate, and propodeum.

Mesopleuron entirely smooth. Lateral aspect of pronotum with some short setae anteriorly, remainder glabrous. Marginal cell of forewing as deep as long. Metasoma sub-equal size to mesosoma in lateral view.

Diagnosis.—Differs from *Banacuniculus nigrimanus* by having a large scutellar plate, and from *B. beardsleyi* by having a smooth dorsal surface of the scutellar plate; from the other species of *Banacuniculus* by characters in the beginning of the key.

Distribution.—Canada: Alberta; Guam; Guatemala: Esquintia; Mexico: Baja California, Chiapas, Morelos, Oaxaca, Sonora, and Zacatecas; Nicaragua: Rivas; United States: Arizona, California, Kansas, New Mexico, Oregon, Texas and Utah.

Link to Distribution Map.—http://hol.osu.edu/map-full.html?id=251127

Biology.—Recorded parasitizing *Liriomyza trifolii* (Hara and Matayoshi 1990; Johnson 1987; Beardsley 1986; this study), *L. sativae* (Johnson 1987) and *L. huidobrensis* (Blanchard) (Johnson 1987). This species has also been evaluated for its usefulness in biological control of pestiferous leafmining flies (Johnson 1987; Lynch and Johnson 1987; Mason and Johnson 1988; Rathman et al. 1991; Rathman et al. 1995). Petcharat and Johnson (1988) studied the larval stages.

Material Examined.—Holotype, female: [first label] USA. HI, Oahu. Nanakuli, X.3.1977, [second label] P.D. Mothershead, reared ex *Liriomyza* pupae from cucumber leaves. Deposited in BPBM. *Other material*: (176 females, 41 males) *Other material*: (176 females, 40 males, 1 unknown) **CANADA**: *ALBERTA*. Waterton Park, 18.VI.1956, O. Peck (1 female, USNM ENT 00655599 (CNCI)). **GUAM**: watermelon field, II-1989, pan trap, L. Yudin (3 females, UCRC ENT 196967-196969 (UCRC)). watermelon field, IX-1989, pan trap, L. Yudin (2 females, UCRC ENT 196970-196971 (UCRC)). **GUATEMALA**: Escuintla Dept., Escuintla, 20.VIII.1975, N. L. H. Krauss (1 male, USNM ENT 00653533 (USNM)). **MEXICO**: BC, 57km S Bahía de los Ángeles, 22.VII.1994, S. L. Heydon (1 male, USNM ENT 00655487 (UCDC)). BCS, 10km W San Ignacio, 24.III.1980, E. Fisher & J. Pinto (1 female, UCRC ENT 196944 (UCRC)). BCS, Barracas, 18.V.1985, pan trap, P. DeBach (1 female, UCRC ENT 196940 (UCRC)). BCS, Barracas, 20.V.1985, pan trap, P. DeBach (1 female, UCRC ENT 196939 (UCRC)). BCS, La Paz, 20.X.1983, J. D. Pinto (1 female, 1 male, UCRC ENT 196941-196942 (UCRC)). Chiapas, 14.VII.1983, A. Gonzalez (1 female, UCRC ENT 196951 (UCRC)). MEX, Naucalpan de Juárez, 18.V.1984, G. Gordh (1 female, UCRC ENT 196950 (UCRC)). MOR, Cuernavaca, III-1965 - V-1965, N. L. H. Krauss (1 female, 1 male, USNM ENT 00653515, 00653522 (USNM)). NL, Ciénega de Flores, 10.VII.1983, A. Gonzalez (1 female, 1 male, UCRC ENT 196952-196953 (UCRC)). OAX, Puerto Escondido, 29.V.1963, E. R. Oatman (1 female, UCRC ENT 196954 (UCRC)). OAX, Yagul, 13.VII.1984, G. Gordh (1 female, 1 male, UCRC ENT 196948-196949 (UCRC)). SON, 1.XI.1947 (1 unknown, USNM ENT 00653534 (USNM)). SON, San José de Guaymas, 4.X.1900, L. O. Howard (1 female, USNM ENT 00653535 (USNM)). ZAC, Monte Escobedo, 12.VII.1983, G. Gordh (3 females, UCRC ENT 196945-196947 (UCRC)). **NICARAGUA**: Rivas Dept., San Juan del Sur, 11°15'N 85°52'W, 15.IV.1998, L. J. Clark (1 female, USNM ENT 00655502 (UCDC)). Rivas Dept., San Juan del Sur, 11°15'N 85°52'W, 2.II.1998, Malaise trap, J. Clark (1 female, 1 male, USNM ENT 00655534, 00655537 (UCDC)). Rivas Dept., San Juan del Sur, 11°15'N 85°52'W, 25.VI.1998, L. J. Clark (1 female, USNM ENT 00655503 (UCDC)). **UNITED STATES**: *ARIZONA*. Cochise Co., Huachuca Mts., Ash Canyon Road, 15.III-30.IV.1994, Malaise trap, McFarland (1 female, USNM ENT 00655595 (CNCI)); Graham Co., desert, 2.4km W on hwy 366 from hwy 191 (666), 1160m, 27.VI-28.VI.1991, Malaise trap, J. E. O'Hara (1 female, USNM ENT 00655585 (CNCI)); Pima Co., Tucson, 11.IV.1896, Baker (2 females, USNM ENT 00653526, 00653539 (USNM)); Santa Cruz Co., Patagonia, 4.VI.1995, E. Wilk & B. Brown (1 female, USNM ENT 00655586 (CNCI)); Santa Cruz Co., juniper/oak/grassland, Sonoita, 29.IX-13.X.2006, Malaise trap, E. E. Grissell (1 female, USNM ENT 00655316 (USNM)). *CALIFORNIA*. Imperial Co., 14.4km WNW Glamis, 6.4km NW hwy 78, 2008Al126, Algodones Dunes, 22.IX-15.XI.2008, Malaise trap, E. Dreyfus (1 female, USNM ENT 00655519 (UCDC)); Los Angeles Co., Eaton Canyon, oak/scrub, Pasadena, 1000ft, 26.VI. 2002, A. Owens & J. George (1 female, UCRC ENT 56868 (UCRC)); Los Angeles Co., Forrestal Nature Preserve, coastal sage scrub, Rancho Palos Verdes, 20.IV-24.V.2003, Malaise trap, J. George (6 females, 4 males, USNM ENT 00655318, 00655319, 00655320-00655325, 00655329, 00655330 (USNM)); Los Angeles Co., Forrestal Nature Preserve, coastal sage scrub, Rancho Palos Verdes, 5.IV-20.IV.2003, Malaise trap, J. George (1 female, USNM ENT 00655339 (USNM)); Orange Co., T6S R10W S17, Huntington Beach, 3.IV.1969, lab reared, R. D. Gbeden &

D. W. Ricker (1 female, 1 male, UCRC ENT 196959-196960 (UCRC)); Riverside Co., Moreno Valley, University of California Experiment Station, 5.IX.1978, J. LaSalle (1 female, UCRC ENT 196963 (UCRC)); Riverside Co., N of Oasis, G95/155, Thousand Palms Canyon, 17.IX.1995, M. Gates (1 male, UCRC ENT 196962 (UCRC)); Riverside Co., PEET 001-08-14-01/MT3, Santa Rosa Plateau Ecological Reserve, 500m, 30.VII-14.VIII.2001, Malaise trap (4 females, USNM ENT 00655335-00655336, 00655338, 00655342 (USNM)); Riverside Co., Santa Rosa Mts., Santa Rosa Spring Campground, 6400ft, 10.IX.1964, E. I. Schlinger (1 female, UCRC ENT 196958 (UCRC)); San Bernardino Co., N of Silverwood Lake, Summit Valley, 27.VII.1996, M. Gates (1 female, UCRC ENT 196961 (UCRC)); San Diego Co., Rancho Santa Fe, 8.VIII.1979, C. Melton (2 females, UCRC ENT 196965-196966 (UCRC)); San Diego Co., Torrey Pines Park, 60m, 19.VI.1996, D. C. Hawks (1 female, UCRC ENT 196999 (UCRC)); San Diego Co., melon, Escondido, 4.VI.1964, E. R. Oatman (1 female, UCRC ENT 196957 (UCRC)); San Diego Co., pole beans, Escondido, 5.IX.1963, E. R. Oatman (1 female, UCRC ENT 196955 (UCRC)); San Diego Co., pole beans, Escondido, 9.VII.1964, E. R. Oatman (1 female, UCRC ENT 196956 (UCRC)); Santa Barbara Co., 45km NW Santa Barbara, Sedgwick Reserve, 308m, 24.VI-8.VII.1997, Malaise trap, E. S. Schlinger (2 females, USNM ENT 00655541, 00655549 (UCDC)); Santa Barbara Co., Santa Barbara, 11.VI.1997, E. Schlinger (1 female, USNM ENT 00655538 (UCDC)). *HAWAII*. Honolulu Co., tomato field, O'ahu (Oahu) Isl., 28.X.1976, R. Buckhart (8 females, 3 males, USNM ENT 00655601-00655607, 00655608, 00655609, 00655610-00655611 (USNM)). *KANSAS*. Geary Co., watershed 20B, Konza Prairie Biological Station, 12.IX-21.IX.2005, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655701 (USNM)); Geary Co., watershed 20B, Konza Prairie Biological Station, 16.VIII-26.VIII.2005, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655702 (USNM)); Geary Co., watershed 20B, Konza Prairie Biological Station, 2.IX-12.IX.2005, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655703 (USNM)); Geary Co., watershed 20B, Konza Prairie Biological Station, 20.VII-30.VII.2005, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655705 (USNM)); Geary Co., watershed 20B, Konza Prairie Biological Station, 27.V-6.VI.2005, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655706 (USNM)); Geary Co., watershed 20B, Konza Prairie Biological Station, 30.IX-11.X.2005, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655700 (USNM)); Geary Co., watershed 20B, Konza Prairie Biological Station, 30.VII-9.VIII.2005, Malaise trap, Zolnerowich & Metlevski (2 females, USNM ENT 00655707, 00655708 (USNM)); Geary Co., watershed 20C, Konza Prairie Biological Station, 18.V-22.V.2006, Malaise trap, Zolnerowich & Metlevski (1 female, USNM ENT 00655704 (USNM)). *NEW MEXICO*. Valencia Co., 20mi W Los Lunas, along streambed, Carrizo Creek, 23.VIII.1977, Malaise trap, S. Peck & J. Peck (6 females, 2 males, USNM ENT 00655582, 00655584, 00655587, 00655588, 00655589, 00655590, 00655593, 00655598 (CNCI)). *OREGON*. Lake Co., nr. pond, 22km N Lakeview, 20.VII.1994, S. L. Heydon (1 female, USNM ENT 00655433 (UCDC)). *TEXAS*. no date, Hernandez (8 females, 2 males, USNM ENT 00655227, 00655228, 00655229, 00655230-00655236 (USNM)); Cameron Co., Brownsville, no date, R. A. Vickery (1 female, USNM ENT 00653521 (USNM)); Cameron Co., TAM Veracruz hot pepper, Brownsville, 17.X.2007, Hernandez (1 female, USNM ENT 00655184 (USNM)); Hidalgo Co., Cuban Hots hot pepper, Edinburg, 12.XI.2007, Hernandez (1 female, USNM ENT 00655281 (USNM)); Hidalgo Co., Cuban Hots hot pepper, Edinburg, 27.XI.2007, Hernandez (1 female, USNM ENT 00655271 (USNM)); Hidalgo Co., Cuban Hots hot pepper, Edinburg, 30.X.2007, Hernandez (1 male, USNM ENT 00655262 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 1.IV.2008, Hernandez (1female, USNM ENT 00655116 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 10.I.2008, Hernandez (3 females, USNM ENT 00655259, 00655265, 00655268 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 12.XI.2007, Hernandez (9 females, 2 males, USNM ENT 00655243-00655247, 00655276, 00655280, 00655282, 00655283, 00655284, 00655287 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 13.XII.2007, Hernandez (3 females, 1 male, USNM ENT 00655239, 00655266, 00655270, 00655272 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 14.V.2008, Hernandez (2 females, USNM ENT 00655043, 00655057

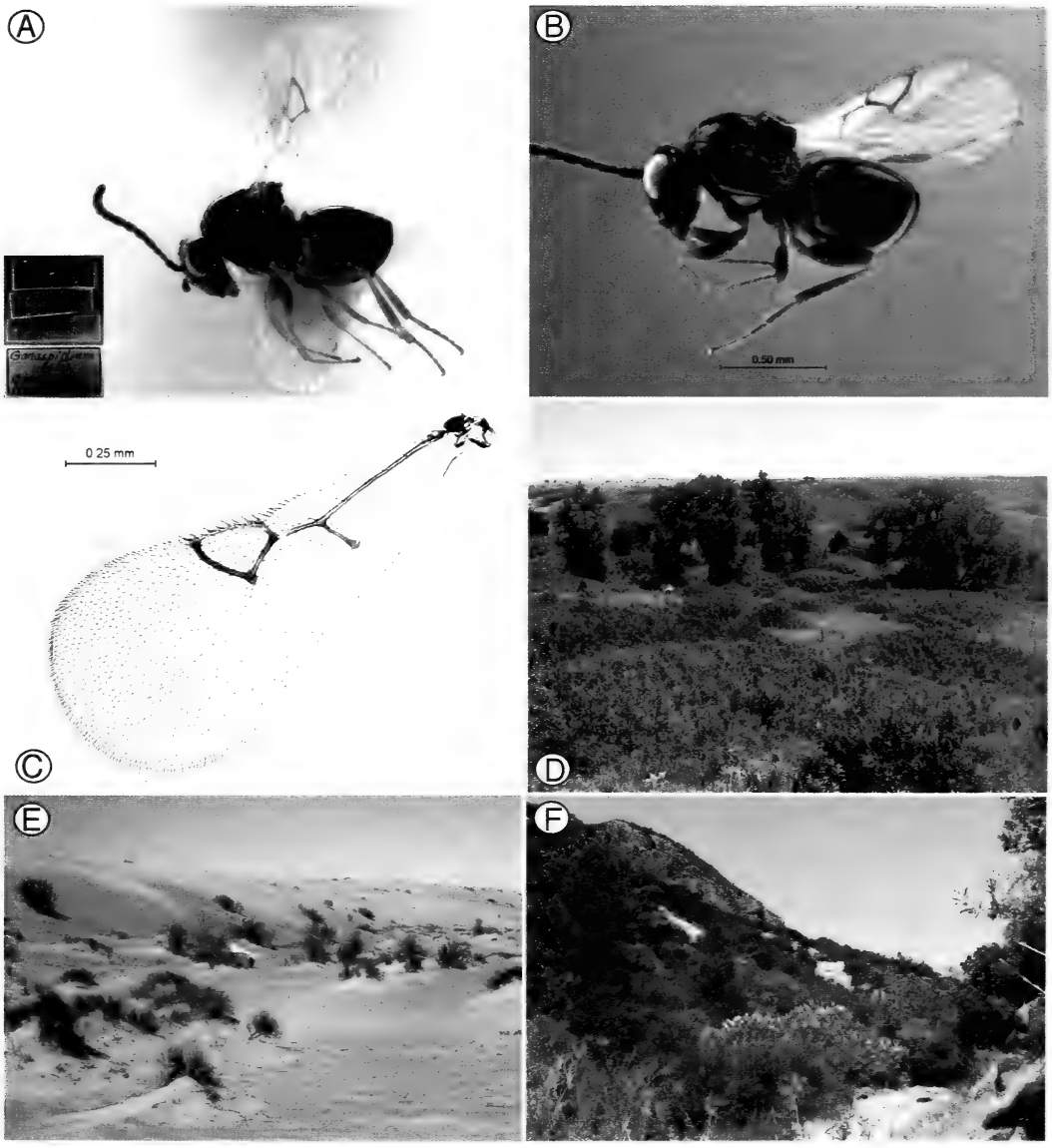

Fig. 3. A. *Banacuniculus utilis* (Beardsley), lateral habitus of holotype with inset of specimen labels; B, *B. utilis*, lateral habitus of non-type specimen; C, *B. utilis* forewing, non-type specimen; D, habitat photo of the Konza Prairie Preserve, Kansas; E, habitat photo of Algodone Dunes, California; F, habitat photo of Cold Canyon Preserve, California.

(USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 16.X.2007, Hernandez (2 females, 1 male, USNM ENT 00655251, 00655286, 00655296 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 19.IX.2007, Hernandez (14 females, 4 males, USNM ENT 00655196, 00655197, 00655198, 00655199, 00655202-00655207, 00655208, 00655209, 00655215, 00655255-00655257, 00655258, 00655263 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 19.X.2007, Hernandez (3 females, 1 male, USNM ENT 00655185, 00655186, 00655250, 00655285 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 2.XI.2007, Hernandez (3 females, USNM ENT 00655248, 00655290, 00655291 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 20.XII.2007, Hernandez (5 females, USNM ENT 00655238, 00655264, 00655267, 00655269, 00655273

(USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 25.X.2007, Hernandez (1 female, USNM ENT 00655249 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 26.VI.2008, Hernandez (1 female, 1 male, USNM ENT 00655058, 00655072 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 28.XI.2007, Hernandez (1 female, USNM ENT 00655279 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 29.V.2008, Hernandez (1 female, USNM ENT 00655070 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 30.X.2007, Hernandez (4 females, 1 male, USNM ENT 00655288, 00655289, 00655292, 00655293, 00655294 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 30.XI.2007, Hernandez (2 females, 2 males, USNM ENT 00655240-00655242, 00655275 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 6.IX.2007, Hernandez (4 females, USNM ENT 00655210-00655212, 00655254 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 8.X.2007, Hernandez (9 females, 2 males, USNM ENT 00655187, 00655188, 00655189, 00655190, 00655191, 00655192, 00655194, 00655195, 00655252-00655253, 00655295 (USNM)); Hidalgo Co., Jalapeño M hot peppers, Weslaco, 9.VI.2008, Hernandez (2 females, USNM ENT 00655059, 00655071 (USNM)); Hidalgo Co., Weslaco, 17.XII.1968, F. F. Smith (1 female, USNM ENT 00653518 (USNM)); Hidalgo Co., serrano hot pepper, San Juan, 12.XI.2007, Hernandez (1 male, USNM ENT 00655260 (USNM)); Hidalgo Co., serrano hot pepper, San Juan, 18.X.2007, Hernandez (1 female, 1 male, USNM ENT 00655140-00655141 (USNM)); Hidalgo Co., serrano hot pepper, San Juan, 3.X.2007, Hernandez (2 females, USNM ENT 00655200-00655201 (USNM)); Jim Wells Co., 8mi W Ben Bolt, area 4, N end of La Copita Ranch, 29.IX.1990, J. B. Woolley (2 females, USNM ENT 00655340, 00665341 (USNM)); Jim Wells Co., Ben Bolt, La Copita Ranch, 26.IX-30.IX.1990, Malaise trap, Wharton & Woolley (1 female, USNM ENT 00655591 (CNCI)). *UTAH*. Emery Co., nr. Goblin Valley State Park, Wild Horse Creek, 2.VIII-7.VIII.1997, Malaise trap, M. Wasbauer & J. Wasbauer (4 females, USNM ENT 00655533, 00655536, 00655540, 00655542 (UCDC)); Emery Co., nr. Goblin Valley State Park, Wild Horse Creek, 4.VII-7.VII.1997, Malaise trap, M. Wasbauer & J. Wasbauer (1 male, USNM ENT 00655535 (UCDC)); Emery Co., nr. Goblin Valley State Park, Wild Horse Creek, 4.VII-7.VII.1997, M. Wasbauer & J. Wasbauer (2 females, 1 male, USNM ENT 00655531-00655532, 00655543 (UCDC)); Wayne Co., vegetation, 11 km E Torrey, 7.VII.1996, sweeping, L. A. Baptiste (1 female, USNM ENT 00655544 (UCDC)); train, 3.VI.1924, Timberlake (1 female, UCRC ENT 196964 (UCRC)).

Comments.—After reconsideration of the holotypes of both *Banacuniculus nigrimanus* (Kieffer) and *B. utilis* Beardsley, it is clear that these are two distinct and readily diagnosed species. The morphology of the scutellum in *B. utilis* is unique within the Eucoilinae.

CONCLUSIONS

The species diversity of *Banacuniculus* is likely to be much higher than is presently recognized. Key locations in North America needing further fieldwork to collect and/or rear additional species include the upper Midwest and the Great Basin. Host habitat for *Banacuniculus* species appears to be rather variable; this is epitomized by the distribution of *B. dis*, whose hosts range from extremely dry conditions of the High Desert of California to moister, interior scrub oak habitats of Central California (Fig. 3 E–F). The distribution *B. utilis* demonstrates the ability of this species to be a New World tramp, ranging from the Konza Prairie in Kansas (Fig. 3D) and Algodone Dunes of California (Fig. 3E), to cultivated crops in southern Texas and Hawai'i. One of the preferred hosts for this species is *Liriomyza trifolii*, itself a tramp species of considerable agricultural importance in commodities such as tomato, cucumber and melon (Johnson 1987).

The phylogenetics of *Banacuniculus* species are not quantitatively analyzed here, but there are some morphological features that allow for a cautious suggestion of relatedness among species. The entirely smooth dorsal and lateral surface of the scutellum (Fig. 2F) in *B. beardsleyi*, *B. nigrimanus*, and *B. utilis* is not only rare within Eucoilinae, but unites these species. Based on the relative size of the scutellar

plate to the scutellum, the following relationship is suggested: (*B. nigrimanus* (*B. beardsleyi* + *B. utilis*)), and for convenience, this clade is referred to as the *utilis* species group. *Banacuniculus merickeli* is unique within the genus for having a striate dorsal surface of the scutellum, but the species does possess a distinct posterior carina of the scutellum. *Banacuniculus dis* and *B. brautigani* both lack the posterior scutellar carina, a character state also shared with the *utilis* group; but unlike the *utilis* group, the scutellum is not smooth. Hence, *B. dis* and *B. brautigani* form their own clade, referred to here as the *dis* species group. *Banacuniculus hunteri* and *B. strykeri* are morphologically very similar, differing only in the morphology of the scutellar plate and, possibly, their host geographic distribution (the latter may be a collection artifact); these species are referred to here as the *hunteri* species group. Given these observations, the following relationships are proposed: (*hunteri* group (*B. merickeli* (*dis* group + *utilis* group))). In this scenario, a complete posterior carina of the scutellum and rugose/crenulate dorsal surface of the scutellum is pleisiomorphic; *B. merickeli* retains the carina, but possesses the striate state for the dorsal surface of the scutellum; the clade *dis* group + *utilis* group all lack the posterior carina of the scutellum, and the *utilis* group possesses the entirely smooth state for the dorsal surface of the scutellum. This scenario of relationships is merely meant to summarize what appears to be a parsimonious summary of character evolution within *Banacuniculus*; a more thorough survey and analysis of characters is required to corroborate and confirm these relationships.

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LITERATURE CITED

Acosta, N. M. and R. D. Cave. 1994. Survey of parasitoids attacking *Liriomyza* spp. (Diptera: Agromyzidae) in southern Honduras. *Revista de Biologia Tropical* 42: 203–218.

Beardsley, J. W. 1986. Taxonomic notes on the genus *Ganaspidium* Weld (Hymenoptera: Cynipoidea: Eucoilidae). *Proceedings of the Hawaiian Entomological Society* 26: 35–39.

———. 1988. Eucoilid parasites of agromyzid leafminers in Hawaii (Hymenoptera: Cynipoidea). *Proceedings of the Hawaiian Entomological Society* 28: 33–49.

Buffington, M. L. 2004. The description of *Nordlandiella semirufa* (Kieffer), new combination, with notes on the status of *Ganaspidium* Weld (Hymenoptera: Figitidae: Eucoilinae). *Proceedings of the Entomological Society of Washington* 106: 192–198.

———. 2009. Description, circumscription and phylogenetics of the new tribe Zaeucoilini (Hymenoptera: Figitidae: Eucoilinae), including a description of a new genus. *Systematic Entomology* 34: 162–187.

———. 2010. A revision of *Ganaspidium* Weld, 1952 (Hymenoptera: Figitidae): new species, bionomics and distribution. *ZooKeys* 37: 81–101.

———, J. A. A. Nylander, and J. Heraty. 2007. The phylogeny and evolution of Figitidae (Hymenoptera: Cynipoidea). *Cladistics* 23: 1–29.

——— and M. Gates. 2009. Advanced imaging techniques II: using a compound microscope for photographing point-mount specimens. *American Entomologist* 54: 222–224.

——— and S. van Noort. 2007. A world revision of the Pycnostigminae (Cynipoidea: Figitidae) with descriptions of seven new species. *Zootaxa* 1392: 1–30.

——— and S. van Noort. 2009. A revision of *Anacharoides* Cameron, 1904 (Hymenoptera: Figitidae) with a description of a new species. *ZooKeys* 20: 245–274.

Crawford, J. C. 1913. Descriptions of new Hymenoptera, No. 7. *Proceedings of the United States National Museum* 45: 309–317.

Hara, A. H. and S. Matayoshi. 1990. Parasitoids and predators of insect pests on *Chrysanthemums* in Hawaii. *Proceedings of the Hawaiian Entomological Society* 30: 53–58.

Harris, R. 1979. A glossary of surface sculpturing. *California Department of Food and Agriculture, Occasional Papers in Entomology* 28: 1–31.

Johnson, M. W. 1987. Parasitization of *Liriomyza* spp. (Diptera: Agromyzidae) infesting commercial watermelon plantings in Hawaii. *Journal of Economic Entomology* 80: 56–61.

Johnson, N. 2008. vSysLab, http://vsyslab.osu.edu/index.html. Accessed 14 September 2009.

Kieffer, J. J. 1907. Beschreibung neuer parasitischer Cynipiden aus Zentral- und Nord-Amerika. *Entomologische Zeitschift* 21: 70–162.

Lynch, J. A. and M. W. Johnson. 1987. Stratified sampling of *Liriomyza* spp. (Diptera: Agromyzidae) and associated hymenopterous parasites on watermelon. *Journal of Economic Entomology* 80: 1254–1261.

Mason, G. A. and M. W. Johnson. 1988. Tolerance to permethrin and fenvalerate in hymenopterous parasitoids associated with *Liriomyza* spp. (Diptera: Agromyzidae). *Journal of Economic Entomology* 81: 123–126.

Miller, T. D. 1989. First Nearctic record of the genus *Nordlanderia* (Hymenoptera: Eucoilidae) with descriptions of two new species. *Proceedings of the Entomological Society of Washington* 91: 158–163.

Petcharat, J. and M. W. Johnson. 1988. Biology of the leafminer parasitoid *Ganaspidium utilis* Beardsley (Hymenoptera. Eucoilidae). *Annals of the Entomological Society of America* 81: 477–480.

Rathman, R. J., M. W. Johnson, and B. E. Tabashnik. 1991. Production of *Ganaspidium utilis* (Hymenoptera: Eucoilidae) for biological control of *Liriomyza* spp. (Diptera: Agromyzidae). *Biological Control* 1: 256–260.

———, M. W. Johnson, B. E. Tabashnik, and K. H. Spollen. 1995. Variation in susceptibility to insecticides in the leafminer parasitoid *Ganaspidium utilis* (Hymenoptera, Eucoilidae). *Journal of Economic Entomology* 88: 475–479.

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Phylogenetic Relationships of *Pluroides porteri*, a New Genus and Species of Plumariidae from Argentina (Hymenoptera: Chrysidoidea)

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Abstract.—***Pluroides porteri***, a **new genus and species** of plumariid wasp from the provinces of Catamarca, La Rioja and San Juan in western Argentina, is described. The new genus *Pluroides* together with *Mapluroides*, *Maplurius* and *Plumaroides*, belong in a strongly supported South American clade, which is the sister-group to the African *Myrmecopterinella*.

Key words.—Plumariidae, taxonomy, phylogeny, Argentina

The Plumariidae are a group of wasps with apterous females of subterranean habits and winged males strongly attracted to lights at night. This family is of particular interest, since it represents one of the basalmost lineages within the Hymenoptera Aculeata. These wasps inhabit desertic and semidesertic areas in southern Africa and South America. Although they are conspicuous faunal elements in some areas, their biology is still unknown.

The family is represented by two genera in Africa (*Myrmecopterina* Bischoff and *Myrmecopterinella* Day) and by four genera in South America (*Plumarius* Philippi, *Plumaroides* Brothers, *Maplurius* Roig-Alsina and *Mapluroides* Diez, Fidalgo and Roig-Alsina) (Brues 1924; Bradley 1972; Brothers 1974; Day 1977; Roig-Alsina 1994; Diez *et al.* 2007).

Among South American plumariids, the genus *Plumarius* is the most speciose and has the broadest distribution. Species of *Plumarius* range from Ecuador to southern Argentina (Evans 1966; Nagy 1973; Brothers 1974) with one species recently described from northeastern Brazil (Penteado-Dias and Scatolini 2003). The other three genera are restricted to western Argentina, from the province of Salta in the north to northern Patagonia in the south (Brothers 1974; Roig-Alsina 1994; Diez et al. 2007; Diez 2008). *Plumaroides* has three described, as well as several undescribed species (Diez 2008), while the other two genera are monotypic. Females of only two genera have been discovered to date, those of *Plumarius* (Evans 1966), and *Plumaroides* (Diez 2008).

The purpose of the present contribution is to describe a new genus and species from the provinces of Catamarca, La Rioja, and San Juan in Argentina. Both the generic and specific descriptions are based on the male sex. The relationships of the new genus are studied, taking into account previous contributions and recently described taxa.

METHODS

The specimens studied were collected at night with a camping lantern provided with a fluorescent tube, 360 degrees bright light. The lantern was placed on a white cloth extended on the ground. A few specimens were obtained with a trap designed to collect myrmecophilous insects.

Specimens are deposited at: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN); Instituto Fundación Miguel Lillo, Tucumán, Argentina (IFML); Museo de La Plata, La Plata, Argentina (MLP); Florida State Collection of Arthropods, USA (FSCA); University of California, Riverside, USA (UCRC).

Terminology follows Brothers (1975).

Pluroides new genus

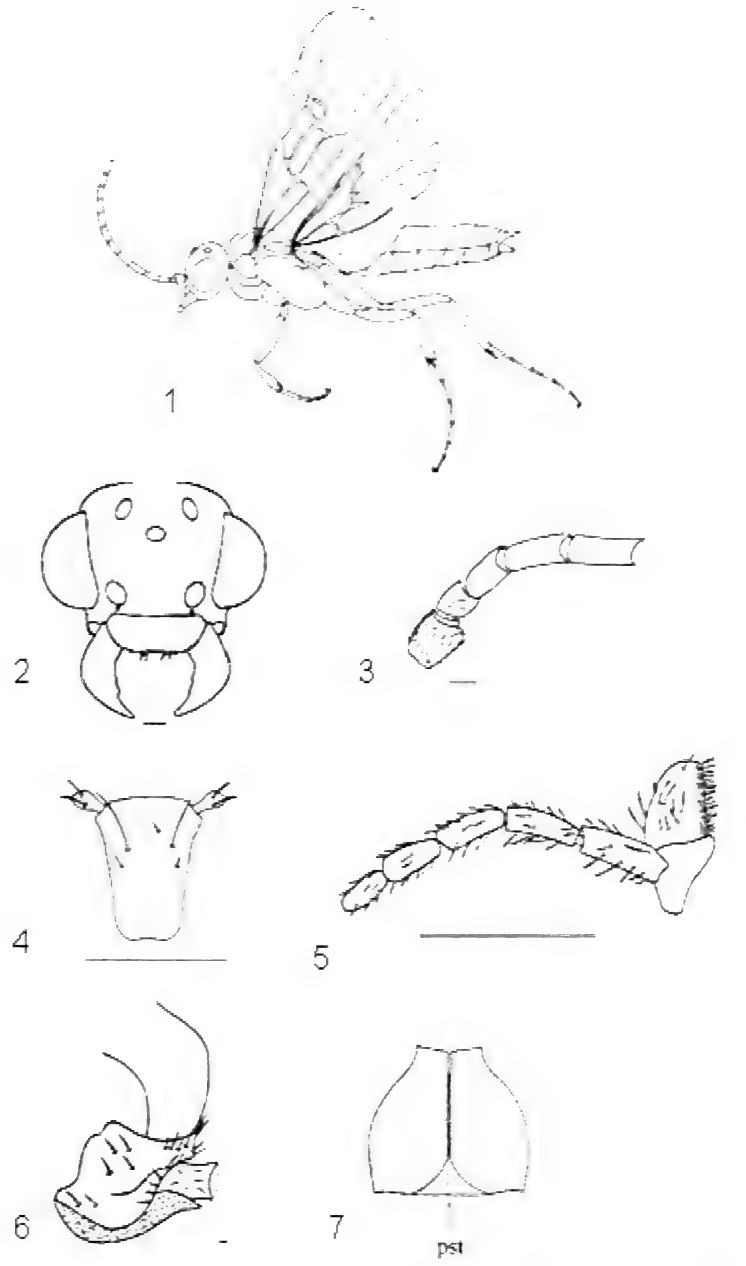
Type species: *Pluroides porteri* **sp. nov.**

Description.—Preoccipital carina absent. Antenna with 11 flagellomeres; scape as long as wide, with short radicle, ventrally with tuberculiform swelling (Fig. 3); flagellomeres with decumbent, short setae, the longest 0.25× as long as diameter of flagellum. Mandible with three teeth, preapical ones small, blunt, of similar size. Palpal formula: 5:1. Clypeus with epistomal suture distinct; apical margin with weak emargination medially, curved at sides; apical margin bent backwards. Prosternum visible in ventral view, subtriangular (Fig. 7). Forewing with first nebulous vein arising from marginal cell one third below middle of apical margin (Fig. 8). Hind wing with vannal (anal) lobe 3.3× as long as submedian cell (Fig. 9). Claws simple, arolium present only on foretarsus. First metasomal tergum with distinct anterior vertical surface, dorsal surface as long and wide as second tergum. First metasomal sternum with a longitudinal median keel on anterior two thirds, longer than second sternum. Seventh tergum subtriangular, apically rounded; posterior margin forming flat, sclerotized, polished flange, one third as long as tergum (Fig. 10). Seventh sternum broad, with apex weakly bilobed (Fig. 11).

Pluroides porteri new species
(Figs 1–13)

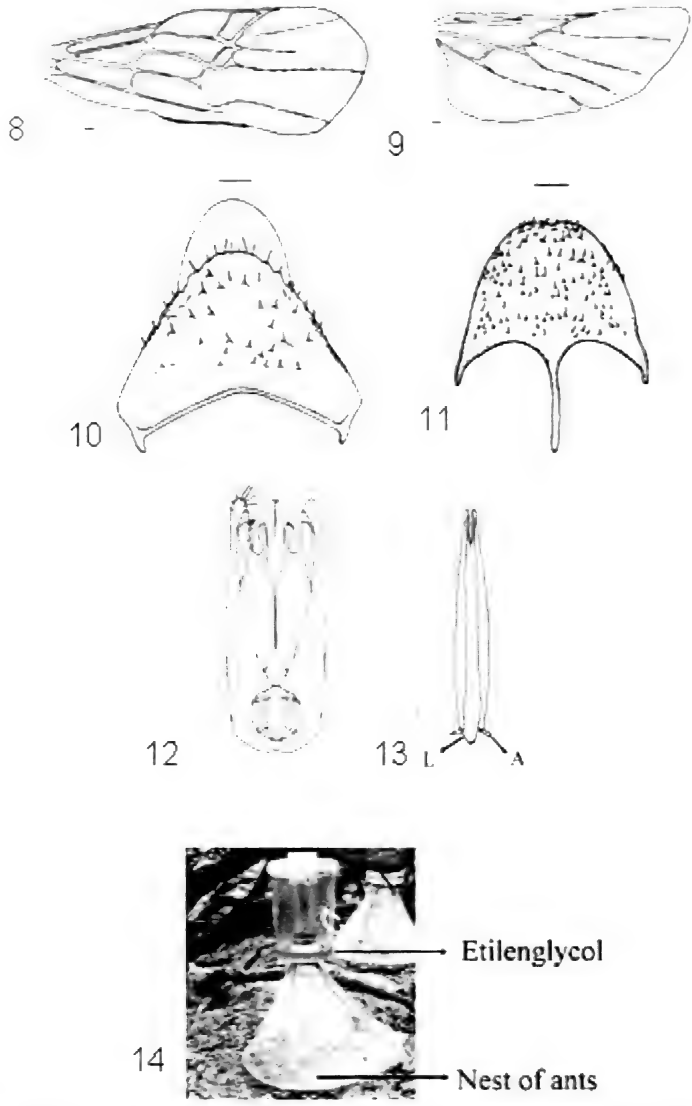
Description.—Holotype male. **Colour:** pale brown, head darker. Total length 3.5 mm (paratypes, 2.7 to 4.5 mm). Habitus as in figure 1. **Head:** hypognathous; in frontal view 1.3× as wide as high (Fig. 2), vertex rounded. Eye hemispherical, protruding, glabrous, without pre- or postorbital carinae. Ocellocular distance 3.8× diameter of lateral ocellus; postocellar distance 1.7× ocellocular distance. Antennal socket with lower rim elevated. Antennocular distance 0.3× diameter of antennal socket; interantennal distance 6.7× antennocular distance. Gena without furrows or carinae. Area between and below sockets weakly convex. Antenna tapering to apex. Pedicel with narrow base, as long as wide. Proportions of flagellomeres (length:width): 11:7,5; 13:7; 15:7; 14:6; 14:6; 12:5; 13:5; 13:5; 12:5; 11:5; 15:5. Sensory plates sub-oval, scarcely visible, present on flagellomeres 1–6; plates more numerous on basal flagellomeres. Clypeus with several setae of variable size. Labrum with concave apical margin, with two setae at each side. Mandible with broad base and setae of variable size. Labium subrectangular, wider basally than apically, with rounded apex; palp unsegmented (Fig. 4). Maxillary palp with five segments, proportions of segments (length:width): 67:22; 40:21; 33:20; 30:20; 31:20 (Fig. 5).

Mesosoma: 1.5× longer than maximum width. Proportions of lengths of mesoscutum, mesoscutellum, metanotum, metapostnotum and propodeum in dorsal view, along median axis: 25: 21: 12: 2: 10. Pronotum not visible dorsally, except for small part of pronotal lobe in front of tegula; in frontal view (head removed) medially forming narrow transverse band which broadens laterally to four times median height. Pronotal lobe flattened, truncate; posteroventral angle of pronotum narrowly rounded (Fig. 6). Propleuron extended anteriorly beyond pronotum. Prosternum visible ventrally as reduced triangular area; most of prosternal surface vertical, hidden by coxae (Fig. 7). Tegula semicircular. Mesoscutum with parapsidal line and notaulus distinct. Mesal area of axillae and scutellum forming nearly hor-



Figs 1–7. *Pluroides porteri* sp. nov.1, habitus of male; 2, head, frontal view; 3, scape, pedicel and first three flagellomeres; 4, labium, ventral view; 5, right maxilla, ventral view; 6, pronotum and mesoscutum, anterolateral view; 7, propleura and prosternum (pst), ventral view. Scale bars = 0.1 mm.

izontal, posteriorly directed triangular surface which steeply slants postero-laterally; axillar sutures indicated by conspicuous dark, continuous line. Prepectus much reduced, hidden by pronotum. Hypoepimeral area of mesopleuron limited inferiorly by dark line running from mesopleural scrobe to meso–metapleural suture; mesepisternal groove present, as short dark line running anteroventrally from mesopleural scrobe. Metanotum subrectangular. Metapostnotum broader medially and narrow-



Figs 8–14. *Pluroides porteri* sp. nov. 8, forewing; 9, hind wing; 10, seventh metasomal tergum, dorsal view; 11, hypopygium, ventral view; 12, genital capsule, ventral view, setae depicted on left side only; 13, aedeagus, dorsal view, apophysis (A), lamina (L); 14, trap for myrmecophilous insects. Scale bars = 0.1 mm.

ing at sides, narrowest at level of propodeal spiracles. Propodeum convex, transverse; propodeal spiracle narrow, removed from anterior margin of propodeum by less than its length. *Wings:* forewing 2.5× as long as maximum width. Pterostigma swollen apically. Marginal cell with anterior margin 2.1× longer than posterior margin; anterior and posterior margins diverging apically; apical margin 1.6× as long as basal margin, latter slightly curved (Fig. 8). Hind wing with vannal (anal) lobe 3.3× as long as submedian cell; with four hamuli (Fig. 9). *Legs*: slender; tibiae and tarsi with weak, sparse setae. Foretibia with about 13 spiniform setae on outer surface, mainly on apex; spiniform setae fewer on mid tibia and absent on hind tibia. Tibial spurs 1-2-2; anterior tibial spur with approximately 21–22 spines.

Metasoma: in dorsal view 2.1× longer than maximum width, tapering apically. Cercus well developed. Genital capsule as in figure 12; aedeagus with lamina surpassing apophyses basally (Fig. 13).

Etymology.—The species is named after Charles C. Porter, distinguished hymenopterist, who has greatly contributed to the knowledge of neotropical wasps, and who has participated in the collection of Plumariidae in the field.

Type material.—Holotype male: ARGENTINA: province of La Rioja, Ruta 7, 25 Km East of Anillaco, 850 m a.s.l., at light, 22-II-2006, col. P. Fidalgo & G. Fidalgo (MACN). The following are paratypes. **La Rioja**: 1 male, same data as holotype (MACN); 1 male, Ruta 7, 7 Km East of Anillaco, 1200 m a.s.l., at light, 17-II-2006, col. J. Torréns & P. Fidalgo (IFML); 2 males, 5 Km South of Udpinango, 1000 m a.s.l., at light, 21-II-2006, col. P. Diez, J. Torréns & P. Fidalgo (MACN, slide); 1 male, Santa Teresita, 736 m a.s.l., at light, 18-II-2006, coll. P. Fidalgo & G. Fidalgo (IFML); 1 male, Ruta 40, Km 395 (between San Blas de Los Sauces and Pituil), 1230 m a.s.l., at ligth, 9-XII-06, col. P. Fidalgo (MLP). **San Juan**: 1 male, Ruta 141, Km 173 near Caucete, 580 m a.s.l., at light, 14-I-2006, col. P. Fidalgo (MLP). **Catamarca**: 33 males, Ruta 46, km 64, entre Belén y Andalgalá, 965 m a.s.l., at light, 1/2-XI-06, col P. Fidalgo & P. Diez, (MACN); 3 males, Ruta 46, Km 204, East of Belén, 965 m a.s.l., at light, 6-XII-06, col. C. Nieto, G. Fidalgo & P. Fidalgo (MACN); 3 males, Ruta 46, Km 64/66 (between Andalgalá and Belén), 965 m a.s.l., pit-fall traps and trap for myrmecophiles, 2-XI-06 / 6-XII-06 (MACN).

Distribution.—ARGENTINA: Catamarca, La Rioja and San Juan provinces.

Comments.—This new species has been collected in moderate quantities (15 specimens per night) between the localities of Belén and Andalgalá in Catamarca province and in minor quantities (one or two specimens per night) in different localities of San Juan and La Rioja provinces. Three specimens of *P. porteri*, together with two of *Plumarius* sp. and two of *Plumaroides andalgalensis*, were obtained in a trap specially designed to catch emerging myrmecophilous insects from the nest (Fig. 14) of an undetermined species of ant of the genus *Acromyrmex* Mayr (Formicidae, Attini). It is not clear yet whether the life cycle of plumariids may be related to ant nests, or if they use these nests merely as emerging routes.

PHYLOGENETIC RELATIONSHIPS

The relationships among genera of Plumariidae were studied by Roig-Alsina (1994), based on 13 morphological characters. His study found that *Plumarius* and *Myrmecopterina* form a clade which is the sister-group to other plumariids (*Myrmecopterinella* (*Plumaroides Maplurius*)). Carpenter (1999) reanalyzed the data presented by Roig-Alsina, adding four new characters taken from Brothers (1974) and Day (1977), supporting the relationships previously found. We present here a more comprehensive analysis, including the new genus *Pluroides*, as well as the recently described genus *Mapluroides*. The analysis is based on 32 morphological characters, and considers species as terminal taxa for the ingroup, not genera as in previous studies. Other families of Chrysidoidea have been used for outgroup comparison, since the Plumariidae is the sister group to all other chrysidoids. For this purpose the phylogeny of the superfamily presented by Carpenter (1999) was taken into account, and the ground-plan states established for the superfamily were used to polarize characters within the Plumariidae. Characters not studied by Carpenter (1999) were polarized in a similar way, through comparison with other families of Chrysidoidea (Table 1).

Species examined for this study are *Plumarius hirticornis* (André), *Plumarius striaticeps* (André), *Plumarius* spp. (several unidentified species from xeric western Argentina), *Myrmecopterina filicornis* Bischoff, *Myrmecopterina* sp. from Northern Cape Province, South Africa, *Maplurius spatulifer* Roig-Alsina, *Plumaroides andalgalensis* Brothers, *Plumaroides brothersi* Diez and Roig-

Table 1. Data matrix for the 32 characters used in the phylogenetic analysis.

									1 0										2 0										3 0		
other Chrysidoidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plumarius hirticornis	1	0	0	1	1	1	2	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Plumarius striaticeps	1	0	0	1	1	1	2	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Myrmecopterina filicornis	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0
Myrmecopterina sp.	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	0
Myrmecopterinella okahandja	4	2	0	0	0	0	0	1	1	1	0	0	1	0	0	?	1	1	0	2	0	0	0	0	1	1	0	0	0	0	1	0
Maplurius spatulifer	3	1	0	0	1	1	1	0	1	1	0	0	1	1	0	1	2	0	0	0	0	1	1	1	1	0	1	0	1	1	0	1
Pluroides porteri	3	1	1	0	0	0	1	0	1	1	0	0	1	1	0	1	2	0	0	0	0	1	2	1	1	0	0	0	1	1	2	1
Mapluroides ogloblini	2	1	1	0	0	0	1	0	1	1	0	0	1	1	1	2	2	0	0	0	0	1	1	1	1	0	0	0	1	1	0	1
Plumaroides andalgalensis	2	1	1	0	0	0	1	0	1	1	0	0	1	1	1	1	2	0	0	0	1	1	1	1	1	0	0	0	1	1	1	0
Plumaroides brothersi	2	1	1	0	0	0	1	0	1	1	0	0	1	1	1	1	2	0	0	0	1	1	1	1	1	0	0	0	1	1	1	0

Alsina, *Plumaroides typhlus* Diez, *Mapluroides ogloblini* Diez, Fidalgo and Roig-Alsina, and *Pluroides porteri* n. sp. Character states for *Myrmecopterinella okahandja* Day were taken from the literature, because specimens were not available for study.

List of characters (based on the male sex)

1. Labial palpus. Four segments (0). Three segments (1). Two segments (2). One segment (3). Absent (4).
2. Maxillary palpus. Six segments (0). Five segments (1). Three segments (2).
3. Clypeus, apical margin. Straight or projecting, not bent backwards (0). Weakly emarginate, bent backwards (1).
4. Antennal socket. Removed from epistomal suture by one socket diameter or less (0). Removed from epistomal suture by 1.5 socket diametes, or more (1).
5. Antennal pedicel and flagellomeres 1–10, vestiture. Clothed with short setae, at most 0.25 times thickness of flagellomeres (0). Clothed with long setae, as long as or longer than thickness of flagellomeres (1).
6. Antennal pedicel and flagellomeres 1–10, transverse rows of setae. Absent (0). Present (1).
7. Antennal scape. Simple, without swellings or projections (0). With apico-ventral projection, varying from a distinct swelling to a digitiform projection (1). With a basiventral enlargement (2).
8. Number of flagellomeres. Eleven (0). Ten (1).
9. Occipital carina. Present (0). Absent (1).
10. Pronotal collar. Present (0). Absent (1).
11. Ventral angle of pronotum. Rounded (0). Pointed (1).
12. Dorsal area between propleural sclerites. Membranous (0). Anterior portions of propleura expanded dorsally forming tubular neck (1).
13. Epimeral area of propleuron. Present, set off by sulcus above forecoxa (0). Absent (1).
14. Pronotal lobe. Globose, posteriorly rounded (0). Flattened, posteriorly truncate (1).
15. Pronotal lobe. Posterior margin of pronotum continued laterally around pronotal lobe (0). Posterior margin of pronotum laterally forming carina superimposed on pronotal lobe, giving to it bilobate aspect (Fig. 6 in Diez *et al.* 2007) (1).
16. Prosternum, ventral view. Well developed, with distinct apophyseal pit (0). Visible as triangular sclerite, without apophyseal pit (1). Reduced, scarcely visible (2).
17. Prepectus. Well developed, broadest medially and with carinate margins (0). Reduced, as slender bar (1). Reduced, upper half narrow, widest at top, and lower half filiform (2).

18. Scutellum. Normal, flat (0). Produced postero-dorsally as a sharp edged flange (1) (Day 1977).
19. Metapostnotum. Longest medially and narrowing towards propodeal spiracles; posterior margin distinct (0). Widening towards propodeal spiracles; posterior margin distinct medially, but limit between metapostnotum and propodeum indistinct laterally (1).
20. Forewing, second submarginal cell. Present, moderate (0). Present, but reduced (1). Absent (2).
21. Marginal cell of forewing. Anterior margin as long as, or longer than maximum width of pterostigma (0). Cell very short, anterior margin one third to half as long as maximum width of pterostigma (1).
22. Prestigma (first abscisa of R1). Linear, parallel sided except sometimes widened at tip (0). Wide, considerably widened on apical third (1).
23. Vannal lobe of hind wing. Moderate, less than twice (1.3–1.6) as long as submedian cell (0). Large, more than twice (2.1–2.3) as long as submedian cell (1). Exceedingly large (3.3 times as long as submedian cell) (2). The last state is autapomorphic for *Pluroides*.
24. Arolia of mid and hind tarsi. Present (0). Absent (1).
25. Claws. Dentate (0). Simple (1).
26. Mid-tibial spurs. Present (0). Absent (1).
27. Hind femur. Simple, without apical projection at each side of tibial articulation (0). Projected at each side of tibial articulation (1).
28. Ventral surface of hind coxa, specialized area of setae. Absent (0). Present (1).
29. First and second metasomal terga. First tergum in dorsal view narrower than second (0). First tergum in dorsal view as wide as second (1).
30. First metasomal sternum, median longitudinal keel. Absent (0). Present (1).
31. Seventh metasomal tergum. Simple, without carinae (0). Longitudinally carinate (1). With large, flat, sclerotized apical flange as large as 1/3 of tergum (2).
32. Seventh metasomal tergum. Simple, without carinae nor expanded apically (0). Longitudinally carinate (1). With large, flat, sclerotized apical flange as large as 1/3 of tergum (2).

An exact analysis was conducted with the program TNT (Goloboff et al. 2007) using implicit enumeration. Multistate characters were run as unordered. A single most-parsimonious tree resulted (Fig. 15), depicted with the aid of the program Clados (Nixon 1992). The length is 49 steps, with consistency index 0.85, and retention index 0.92. Autapomorphies are included in the tree to show distinctiveness of the taxa (Fig. 15, black squares). When autapomorphies are excluded from the analysis the statistics are: length 39 steps, consistency index 0.82, and retention index 0.92. Five characters (1, 2, 16, 17, and 25) have states with ambiguous optimizations; these are plotted in the figure using the accelerated transformation optimization.

The results of our analysis reinforce the support for the recognition of two major lineages within the Plumariidae, as suggested by previous analyses (Roig-Alsina 1994; Carpenter 1999). One of the lineages is formed by the American *Plumarius* and the African *Myrmecopterina*, both genera clearly monophyletic.

The new genus *Pluroides* and the recently described genus *Mapluroides*, together with *Maplurius* and *Plumaroides*, belong in a strongly supported South American clade, which is the sister-group to the African *Myrmecopterinella*. The genus *Plumaroides* has three described species, but current surveys have revealed that it is a speciose group, with several undescribed species. In the tree it appears as supported by three homoplasious states, but at least two of them are clearly convergences, and repre-

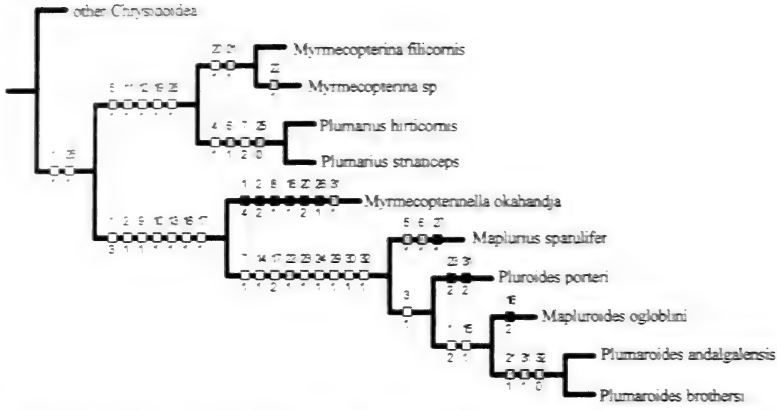


Fig. 15. Cladogram for genera and species of Plumariidae. Character numbers are above the hashmarks, and states are shown below. White squares indicate nonhomoplasious states, gray squares indicate homoplasious states, and black squares indicate autapomorphies.

sent independent derivations: the presence of carinae on the seventh tergum, and the very small marginal cell. The other three genera in this South American clade are monotypic, supported by their own autapomorphies. The new genus *Pluroides* is distinguished by the extremely large vannal (anal) lobe of the hind wing, and the large, flat, polished flange of the seventh tergum, one third as long as the tergum.

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LITERATURE CITED

Bradley, J. C. 1972. Notes on the distribution of the genus *Plumarius* (Hymenoptera, Plumariidae). *Entomological News* 83: 135–139.

Brothers, D. J. 1974. The genera of Plumariidae, with description of a new genus and species from Argentina (Hymenoptera: Bethyloidea). *Journal of the entomological Society of southern Africa* 37: 351–356.

———. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *The University of Kansas Science Bulletin* 50: 483–648.

Brues, C. T. 1924. Some South African parasitic Hymenoptera of the families Evaniidae, Braconidae, Alysiidae and Plumariidae in the South African Museum, with a catalogue of the known species. *Annals of the South African Museum* 19: 1–50.

Carpenter, J. M. 1999. What do we know about chrysidoid (Hymenoptera) relationships? *Zoologica Scripta* 28: 215–231.

Day, M. C. 1977. A new genus of Plumariidae from Southern Africa, with notes on Scolebythidae (Hymenoptera: Chrysidoidea). *Cimbebasia*, A 4: 171–177.

Diez, P. 2008. A new species of the genus *Plumaroides* Brothers (Hymenoptera, Chrysidoidea, Plumariidae) from Santiago del Estero, Argentina: male and female descriptions. *Zootaxa* 1891: 25–30.

———, P. Fidalgo, and A. Roig-Alsina. 2007. A new genus and species of Plumariidae (Hymenoptera, Chrysidoidea) from western xeric Argentina. *Zootaxa* 1467: 35–41.

Evans, H. E. 1966. Discovery of the female *Plumarius* (Hymenoptera, Plumariidae). *Psyche* 73: 229–237.

Goloboff, P., J. Farris, and K. Nixon. 2007. TNT, Tree analysis using new technology. Program and documentation. Version 1.1.

Nagy, C. G. 1973. Revisionary Studies on the Family Plumariidae Bischoff (Hymenoptera, Heterogynoidea). *Folia Entomológica Hungárica* 26 Suppl.: 255–267.

Nixon, K. C. 1992. Clados, version 1.21.

Penteado-Dias, A. M. and D. Scatolini. 2003. A new species of the genus *Plumarius* Philippi (Hymenoptera: Plumariidae) from Brasil. *Zoologische Mededelingen*, Leiden 77: 545–550.

Perez D'Angelo, V. 1974. *Plumarius coquimbo* n. sp. y primer registro de la hembra de *Plumarius* para Chile (Hymenoptera: Plumariidae). *Revista chilena de entomología* 8: 139.

Roig-Alsina, A. 1994. A new genus of Plumariidae, with notes on the relationships among the genera of the family. *Mitteilungen der Münchener entomologisches Gesellschaft* 84: 91–96.

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The Transcaucasian Species of *Coccobius* Ratzeburg 1852 (Chalcidoidea: Aphelinidae), with the Description of Three New Species from Georgia

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Abstract.—The species of *Coccobius* Ratzeburg from Transcaucasia are listed and ***Coccobius kato***, ***C. nunu*** and ***C. omari*** are described as **new**. Information on distribution, synonyms and hosts for eleven species is given. A key to the females of the *Coccobius* species from the Transcaucasus region is provided.

Key words.—*Coccobius*, Transcaucasia, Georgia, new species, Parasitoids, Biocontrol

The genus *Coccobius* Ratzeburg contains 81 species worldwide (Noyes 2009). They are parasitoids of Diaspididae (Hemiptera: Coccoidea) and some of them have been used in the biocontrol of harmful pests. For example, *Coccobius testaceus* (Masi) has been used as a control agent against *Lepidosaphes ulmi* (Linnaeus) and other armoured scale insects in the former USSR and Western Europe (Yasnosh 1968). This species was introduced into the USA for the control of *Lepidosaphes beckii* (Newman) (Flanders 1942; Myartseva 1995). *Coccobius varicornis* (Howard) was used against *Diaspidiotus perniciosus* (Comstock), *Aspidiotus destructor* Cockerell and other armoured scales in California. *Coccobius odonaspidis* (Tachikawa) is a host-specific parasitoid of *Odonaspis secreta* (Cockerell) in Japan (Yasnosh 1968).

The genus *Coccobius* is rather distinctive and is not likely to be confused with any other aphelinid genus. All known species show a high degree of structural similarity (Hayat 1985). Prior to our studies on *Coccobius* from the Transcaucasus, the following species were known from the region: *C. contigaspidis* (Yasnosh), *C. ephedraspidis* (Yasnosh), *C. granati* Yasnosh & Mustafaeva, *C. indefinitus* (Yasnosh & Myartseva), *C. mesasiaticus* (Yasnosh & Myartseva), *C. noaeae* (Yasnosh), *C. pistacicolus* (Yasnosh), *C. subterraneus* (Nikol'skaya) and *C. testaceus* (Masi). The genus is almost cosmopolitan in distribution and recent additions of species from the Palaearctic, Nearctic, Neotropical, Afrotropical and Oriental regions indicate that there should be more undescribed species.

The generic names *Physcus* Howard, *Encyrtophyscus* Blanchard and *Physculus* Yasnosh were placed in synonymy with *Coccobius* by Hayat (1983), but all the species known in these genera were not then specifically transferred to *Coccobius* until Hayat's new publication (Hayat 1985), where he transferred all the species to the present genus as new combinations.

MATERIAL AND METHODS

This work is based upon specimens deposited in the following collections, with abbreviations used in text: St. Petersburg Museum of Zoology (ZIN); personal collection of V. Yasnosh housed in the L. Kanchaveli Plant Protection Institute of the Georgian Academy of Agriculture (VYC); personal collection of the first author, housed in the Institute of Zoology of Ilia Chavchavadze state University, former Institute of Zoology, Georgian Academy of Sciences, Tbilisi, Georgia (IZGAS) and the Natural History Museum, London,

U.K. (BMNH). Descriptions and terminology follow Hayat (1998).

RESULTS

Coccobius Ratzeburg

Coccobius Ratzeburg, 1852: 195. Type: *Coccobius annulicornis* Ratzeburg, designated by Gahan and Fagan 1923: 37.

Physcus Howard, 1895: 43. Type: *Coccophagus varicornis* Howard, by monotypy.

Encyrtophyscus Blanchard, in De Santis, 1948: 192. Type: *Physcus flavoflagellatus* De Santis, by original designation.

Physculus Yasnosh, 1977: 1115. Type: *Physculus danzigae* Yasnosh, by original designation.

Diagnosis.—Female: antenna with one anellus between pedicel and F1 and with 7 segments; mandible with two teeth and truncation; maxillary palpi two-segmented, labial palpi unsegmented; pronotum narrow in dorsal view; median lobe of mesoscutum large, with numerous setae; axilla small with one seta; scutellum large, posterior margin widely rounded; fore wing without linea calva; disc usually setose to base; submarginal vein with 4 or more setae; tarsal formula 5-5-5; mid tibial spur large (compared to other aphelinid genera, except *Marietta* Motschulsky); gaster at least as long as thorax; hypopygium not reaching apex of gaster.

Male: similar to female, except antenna with 8 segments (1.1.6) and genitalia, which is elongate, phallobase almost truncate, narrowed in basal third and with apex bifid (Hayat 1985).

KEY TO THE FEMALES OF TRANSCAUCASIAN SPECIES OF *COCCOBIUS*

1.	Brachypterous	***subterraneus* (Nikol'skaya)**
-	Macropterous	**2**
2.	Antenna uniformly coloured	**3**
-	Antenna differently coloured	**4**
3.	Clypeus margin with brown band, mesoscutum with medial vertical line	***omari* Japoshvili sp. n.**
-	Clypeus margin without brown band, mesoscutum entirely fulvous	***ephedraspidis* (Yasnosh)**
4.	Antennae with F1 and clava very slightly dusky	***nunu* Japoshvili sp. n.**
-	Antennae with F1 and clava dark brown	**5**
5.	Thorax and usually the head, mostly yellow to brownish-yellow, with minimum of dark markings	**6**
-	Thorax and usually the head, mostly dark brown to black	**9**
6.	F1 slightly shorter than than pedicel, clava longer than funicle	**7**
-	F1 usually somewhat longer than pedicel or subequal, clava usually shorter than funicle	*testaceus* (Masi)
7.	F1 subquadrate or very slightly longer than wide	***granati* Yasnosh et Mustafaeva**
-	F1 almost 1.5× as long as wide	**8**
8.	F3 1.25× as long as wide. Clava length equal to all funicle length together	***indefinites* (Yasnosh & Myartseva)**
-	F3 1.56× as long as wide. Clava slightly longer than funicle	***kato* Japoshvili sp. n.**
9.	Submarginal vein at most with 6 and marginal vein with 9 setae	**10**
	Submarginal vein with at least 7 and marginal vein with 10 setae	*contigaspidis* (Yasnosh)
10.	Marginal fringe at the apex of fore wing almost 0.25× as long as width of forewings, mesoscutum and scutellum with small cellular sculpture	***pistacicolus* (Yasnosh)**
-	Marginal fringe at the apex of forewings shorter than 0.25× as long as width of forewings, mesoscutum and scutellum with bigger cellular sculpture	***noaeae* (Yasnosh)**

***Coccobius contigaspidis* (Yasnosh 1968)**

Distribution.—Armenia (Yasnosh 1968).

Host.—*Contigaspis kochiae* Borchsenius (Diaspididae) (Yasnosh 1968; Ben-Dov et al. 2008).

***Coccobius ephedraspidis* (Yasnosh 1968)**

Distribution.—Georgia, Turkmenistan (Yasnosh 1968).

Host.—*Dynaspidiotus ephedrarum* (Lindinger) (Diaspididae) (Yasnosh 1968; Ben-Dov et al. 2008).

***Coccobius granati* Yasnosh & Mustafaeva 1992**

Distribution.—Azerbaijan (Yasnosh and Mustafaeva 1992).

Host.—*Lepidosaphes granati* Koroneos (Diaspididae) (Yasnosh and Mustafaeva 1992).

***Coccobius indefinitus* (Yasnosh & Myartseva 1972).**

Distribution.—Armenia, Tajikistan, Turkmenistan (Yasnosh and Myartseva 1972).

Host.—*Chlidaspis asiatica* (Archangelskaya) (Diaspididae) (Yasnosh and Myartseva 1972).

***Coccobius noaeae* (Yasnosh 1968)**

Distribution.—Azerbaijan, Georgia (Yasnosh 1978).

Host.—*Duplachionaspis noaeae* (Hall) (Diaspididae) (Yasnosh 1978; Ben-Dov et al. 2008).

***Coccobius pistacicolus* (Yasnosh 1968)**

Distribution.—Azerbaijan, Georgia (Yasnosh 1978).

Host.—*Lepidosaphes pistaciae* Archangelskaya (Diaspididae) (Yasnosh 1978).

Comments.—Dr V. Yasnosh recorded 3 females (Yasnosh 1968), which we have not been able to find, unfortunately, in St. Petersburg (ZIN) or in her personal collection. There has also been no record of this species since then. We suppose that this species could be a synonym of *C. testaceus*. However, further study is needed to verify whether this species is a junior synonym of *C. testaceus*.

***Coccobius subterraneus* (Nikol'skaya 1966)**

Distribution.—Armenia (Nikol'skaya and Yasnosh 1966).

Host.—*Chortinaspis subterranea* (Lindinger) (Diaspididae) (Nikol'skaya and Yasnosh 1966; Ben-Dov et al. 2008).

***Coccobius testaceus* (Masi, 1909)**

Distribution.—Azerbaijan, Croatia, Czech Republic, Egypt, France, Georgia, Germany, Hungary, Iran, Italy, Lebanon, Moldova, Montenegro, China, Poland, Romania, Spain, Turkey, Ukraine, UK, USA, Uzbekistan (Noyes 2009).

Hosts.—*Chionaspis salicis* (L.), *Chlidaspis asiatica* (Archangelskaya), *Contigaspis kochiae* Borchsenius, *Diaspidiotus prunorum* (Laing), *D. transcaspiensis* (Marlatt), *D. gigas* (Thiem & Gerneck), *D. jaapi* (Leonardi), *D. perniciosus* (Comstock), *D. slavonicus* (Green), *Furchadaspis zamiae* (Morgan) (Noyes 2009; Ben-Dov et al. 2008), *Lepidosaphes beckii* (Newman) (Myartseva 1995), *L. conchiformis* (Gmelin), *L. malicola* Borchsenius, *L.ulmi* (L.), *Lineaspis striata* (Newstead), *Parlatoria oleae* (Colvée), *Eriococcus spurious* (Modeer) (Noyes 2009; Ben-Dov et al. 2008).

***Coccobius kato* Japoshvili sp. n.**

Material Examined.—*Holotype*, ♀, GEORGIA: Vashlovani, ex *Lineaspis striata* (Newstead) on *Thuja* sp. 2.VI. – 15.VII.2003, G. Japoshvili (IZGAS). *Paratypes*, 3 ♀♀, same data as holotype (IZGAS). *Homoeotype*: ♀ with label: *Physcus* sp. *aff. pistacicolus* Jasnosh ex *Lineaspis striata* collected on *Juniperus foetidissima*, 20.V.1968.

Female.—Length, 0.44–0.70 mm (Holotype: 0.56 mm).

Entire body yellow, legs and antenna slightly paler. F1 slightly brownish and clava brown. Head 1.8× as wide as FV. Head in front view almost as wide as high. Ocelli with apical angle obtuse. Eyes long, 2× as long as malar space. Toruli with upper margins level with lower eye margins. Antenna as Fig. 1A. Pedicel 1.8×, F1 – 1.56×, F2 – 1.4×, F3 – 1.45×, C1 – 1.2×, C2

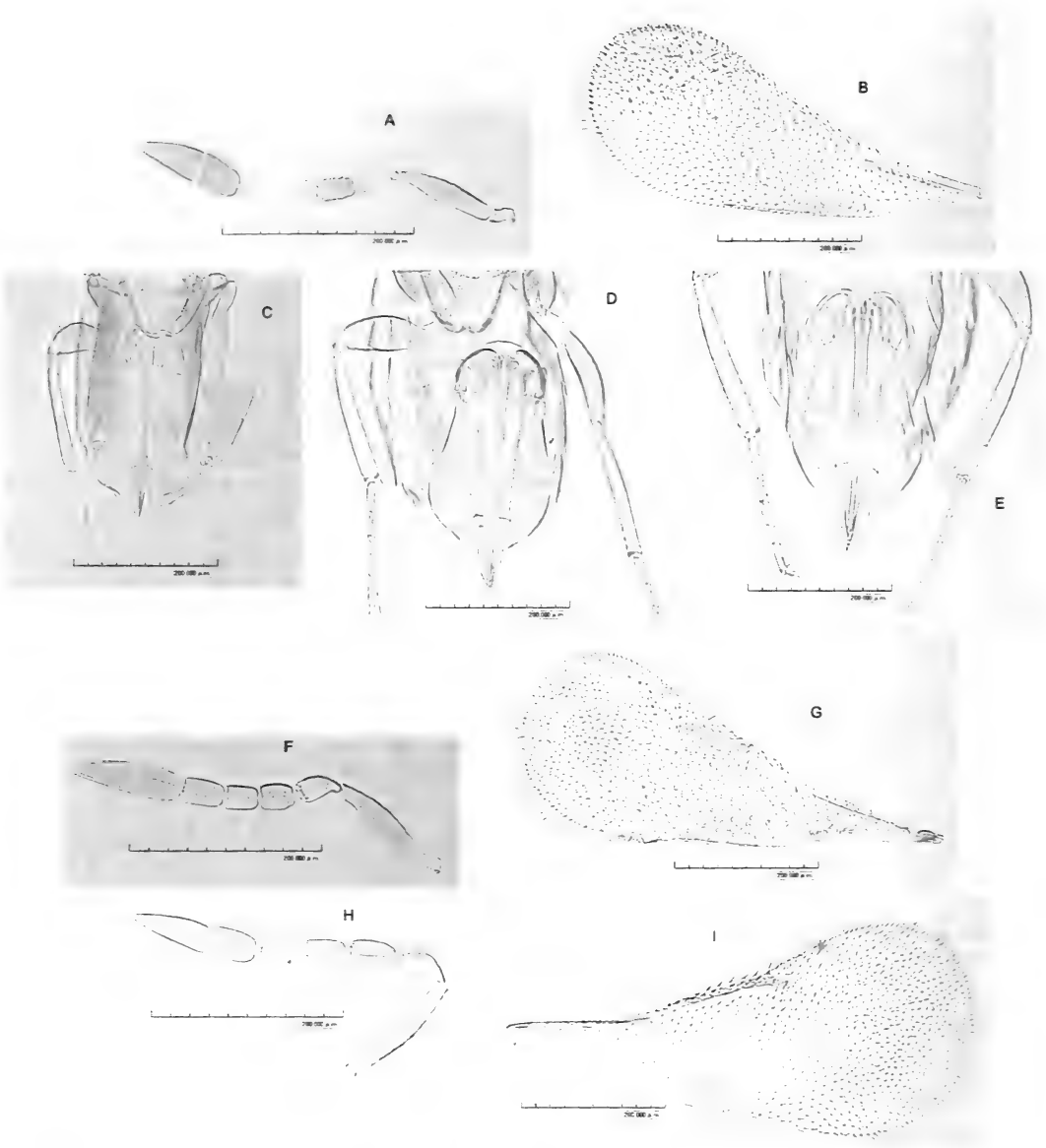

Fig. 1. *Coccobius kato* Japoshvili, sp.n. antenna (A), left fore wing (B), ovipositor (C); *C. omari* Japoshvili, sp.n. ovipositor (D), antenna (F), left fore wing (G); *C. nunu* Japoshvili sp.n. ovipositor (E), antenna (H), right fore wing (I).

– 2× as long as wide. Scape slightly more than 4× as long as wide. Mesoscutum (26) longer than scutellum (22). Scutellum 1.3× as wide as long.

Fore wings 2.6× as long as wide (Fig. 1B). Marginal fringe about 0.25× as long as wing width. Submarginal: marginal: stigmal veins as following 37:27:7. Hind wing slightly more than 5.5× as long as wide. Marginal fringe almost equal to that of wing width. Gaster slightly shorter (11:14) than head plus thorax. Pygostyles inserted at the 0.6 distance from base. Ovipositor (Figure 1C) second valvifer 0.7× as long as ovipositor and third valvula 0.4× as long as second valvifer. Ovipositor 1.5× longer than midtibia.

Male.—Unknown.

Comments.—The new species is close to *C. indefinitus* Yasnosh & Myartseva, but differs by the characters given in Table 1. The species mentioned as *Physcus* sp. *aff. pistacicolus* by Yasnosh (1972), is probably conspecific with this new species.

Coccobius omari Japoshvili, sp.n.

Material Examined.—Holotype, ♀, GEORGIA: Tbilisi, Gldanula, ex *Prodiaspis tamaricicola* (Malenotti) on *Tamarix* sp. 28.VI. – 20.VII.1998, G. Japoshvili (IZGAS). *Paratypes*, 10♀♀, same data as holotype (IZGAS).

Female.—Length, 0.62–0.89 mm. (Holotype: 0.67 mm).

Head with metallic lustre infuscated yellow or testaceous-brownish yellow. Anterior part of pronotum, mesoscutum in the middle vertically, and tergites, with hardly noticeable brownish lines. All body yellow. Femora and tibia brownish. Face above clypeus with dark brown band joining to eyes on margin. Antennae uniformly coloured.

Head 2.1× as wide as FV. Head in front view almost 1.13× as wide as high. Ocelli with apical angle obtuse. Eyes 1.2× as long as malar space. Toruli with upper margins below lower lower eye margins. Antennae as Figure 1F. Pedicel 2×, F1 – 1.27×, F2 – 1.4×, F3 – 1.33×, C1 – 1.29×, C2 – 2.33× as long as wide. Scape slightly more than 4× as long as wide. Mesoscutum (25) longer than scutellum (20). Scutellum 1.5× as wide as long. Fore wings 2.3× as long as wide (Figure 1G). Marginal fringe about 0.2× the length of wing width. Submarginal: marginal: stigmal veins as follows: 38:24:5. Hind wing slightly more than 5.16× as long as wide. Marginal fringe almost 0.6× as long as wing width. Gaster slightly longer (15:13) than head plus thorax. Pygostyles inserted at the 0.74 distance from base. Ovipositor (Figure 1D) second valvifer 0.7× as long as ovipositor and third valvula 0.41× as long as second valvifer. Ovipositor 1.76× longer than midtibia.

Male: Unknown.

Comments: The species is close to *C. sumbarensis* Myartseva but differs by the morphological characters given in Table 1., also *C. sumbarensis* is entirely brown, F1 and clava also brown. The new species when it has some brownish coloration, then it is hardly noticeable.

Etymology: This species is named in honour of the Georgian ichthyologist and zoologist, Dr Omar Japoshvili.

Coccobius nunu Japoshvili, sp.n.

Material Examined. *Holotype*, ♀, GEORGIA: Tbilisi, Gldanula, ex *Prodiaspis tamaricicola* (Malenotti) on *Tamarix* sp. 28.VI. – 20.VII.1998, G. Japoshvili (IZGAS). *Paratypes*, 30♀♀, same data as holotype (IZGAS).

Female: Length, 0.67–0.84 mm. (Holotype: 0.76 mm).

Coloration of body similar to that of *Coccobius omari* sp.n., the only difference being that this species has some brownish areas on the body. Head 1.85× as wide as FV. Head in front view almost 1.15× as wide as high. Ocelli with apical angle obtuse. Eyes slightly more than 2× as long as malar space. Toruli with upper margins level with lower eye margins or slightly lower. Antennae as Figure 1H. Pedicel 2×, F1 – 1.67×, F2 – 1.45×, F3 – 1.36×, C1 – 1.54×, C2 – 2.9× as long as wide. Scape 3.4× as long as wide. Mesoscutum (29) longer than scutellum (25). Scutellum 1.36× as wide as long. Forewings 2.3× as long as wide. Marginal fringe about 0.14× of wing width. Setation and venation as Figure 1I. Submarginal: marginal: stigmal veins as follows: 44:29:6. Hind wing 5.2× as long as wide. Marginal fringe almost 0.57× as long as wing width. Gaster longer (18:15) than head plus thorax. Pygostyles inserted at the 0.67 distance from base. Ovipositor second valvifer 0.75× as long as ovipositor and third valvula 0.37× as long as second valvifer. Ovipositor (Figure 1E) 1.67× longer than midtibia.

Male.—Unknown.

Comments.—The new species is close to *C. kurbani* Myartseva, but differs by the characters given in Table 1. This species is also

Table 1. Morphological differences between six *Coccobius* species.

C. kato sp.n.	*C. nunu* sp.n.	*C. omari* sp.n.	*C. kurbani*	*C. sumbarensis*	*C. indefinitus*	*C. ephedraspidis*
Scape 4× as long as wide	Scape 3.4× as long as wide	Scape 4× as long as wide	Scape more than 3× as long as wide	Scape slightly less than 5× as long as wide	Scape 4× as long as wide	Scape 3.875× as long as wide
F3 slightly longer than F2 and F1 separately	F2 shorter than F1 and F3	F3 slightly longer than F2 and F1	All funicular segments are equal in length	F3 slightly longer than F2 and F1	All funicular segments are equal in length	All funicular segments are equal in length
F1 1.56× as long as wide, F2 –1.4, F3 – 1.5	F1 1.7× as long as wide, F2 – 1.5, F3 – 1.4	F1 1.3× as long as wide, F2 – 1.4, F3 – 1.3	F1 1.6× as long as wide, F2 – 1.4, F3 – 1.5	F1 –2 1.5× as long as wide and F3 slightly longer than wide	F1-2 1.5× as long as wide and F3 1.25× as long as wide	F1, F2, F3 – 1.,5× as long as wide
Clava 3.2× as long as wide	Clava 3.7× as long as wide	Clava 3.3× as long as wide	Clava 5× as long as wide	Clava 3.5× as long as wide	Clava 3.55× as long as wide	Clava 3.5× as long as wide
Fore wing 2.6× as long as wide	Fore wing 1.7× as long as wide	Fore wing 2.3× as long as wide	Fore wing 2.5× as long as wide	Fore wing slightly more than 2.5× as long as wide	Fore wing 2.8× as long as wide	Fore wing 2.8× as long as wide
Submarginal with 7 Marginal with 8 setae	Submarginal with 10 Marginal with 11 setae	Submarginal with 8 Marginal with 9 setae	Submarginal with 10 Marginal with 11 setae	Submarginal with 7 Marginal with 7 setae	Submarginal with 7 Marginal with 8 setae	Submarginal with 8–10 Marginal with 8–10 setae
Third valvulae 0.4× as long as outer plates	Third valvulae 0.37× as long as outer plates	Third valvulae 0.42× as long as outer plates	Third valvulae 0.4× as long as outer plates	Third valvulae 0.33× as long as outer plates	Third valvulae 0.33× as long as outer plates	Third valvulae 0.39× as long as outer plates
Sensilla in same plane as follows F1-2- 0-2, F3 – 1-2, C1 -1-2, C2- 2-3	Sensilla as follows F1-2- 0-2, F3 – 1-2, C1 – 2, C2 - 2-4	Sensilla as follows F1 -0, F2 -0-1, F3 – 1, C1- 2-3, C2 – 1-4	Sensilla as follows F1 -3 and C1 with 2, C2 - 3	Sensilla as followsF1 -3 with 1, C1-2 - 2	Sensilla as follows F1 -3 with 1, C1-2 – 3-4	Sensilla as follows F1 -3 and C1 with 2-3, C2 – 4

close to *C. viggianii* Yasnosh (Yasnosh 1974) and *C. furvus* Huang (Huang 1994), but differs from both by the sculpture on mesoscutum and scutellum. The sculpture in *C. viggianii* is with elongated cells in the middle on both mesoscutum and scutellum and *C. furvus* with polygonal cells on both mesoscutum and scutellum, but in *C. nunu* sp.n. the sculpture on the mesoscutum is polygonal and on the scutellum a little elongated. Also, there are less than 10 setae on the submarginal vein in *C. viggianii* and *C. furvus*, while there are at least setae on *C. nunu* is at least 10.

DISCUSSION

We did not include *Coccobius mesasiaticus* (Yasnosh and Myartseva 1971) in the key and list of species of *Coccobius* of the Transcaucasian region. *Coccobius mesasiaticus* was described from Turkmenistan, and mentioned as also being distributed in Azerbaijan (Yasnosh 2000), however it was impossible to find any material from Azerbaijan to confirm its distribution there. Yasnosh (2000) cited distributional data based on Mustafaeva's doctoral thesis, but later Rzaeva (2002), in her monographic work on chalcidoids of Azerbaijan, did not mention this species. Also, G. Japoshvili could not find any information about the material from Azerbaijan (Mustafaeva pers. comm.). We would like to note that distributional data concerning Afganistan and Iran (Hayat 1985) is also doubtful, in as much as Hayat did not mention the examined material and sources of data.

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LITERATURE CITED

Ben-Dov, Y. D. R. Miller, and G. A. P. Gibson. 2008. ScaleNet. http://www.sel.barc.usda.gov/scalenet/scalenet.htm

Flanders, S. E. 1942. The introduction of *Physcus testaceus* Masi into California. *Journal of Economical Entomology* 35: 290–291.

Hayat, M. 1983. The genera of Aphelinidae (Hymenoptera) of the World. *Systematic Entomology* 8: 63–102.

———. 1985. Notes on some species of *Coccobius* and *Prophyscus* (Hymenoptera: Aphelinidae), with special reference to Girault and Howard types. *Oriental Insects* 18: 289–334.

———. 1998. Aphelinidae of India (Hymenoptera: Chalcidoidea): a taxonomic Revision. *Memoirs on Entomology, International* 13: 1–416.

Huang, J. 1994. *Systematic studies on Aphelinidae of China*. Chonqing publishing house, China.

Myartseva, S. N. 1995. New species of Aphelinids (Hymenoptera, Aphelinidae) – parasites of scale insects on *Tamarix* in Turkmenia. *Entomological Review* 74: 432–440 (In Russian).

Nikol'skaya, M. and V. Yasnosh. 1966. *Aphelinids of European part of USSR and Caucasus*. Nauka, Leningrad. 295 pp.

Noyes, J. 2009. Universal Chalcidoidea Database (online). http://www.nhm.ac.uk/research-curation/research/projects/chalcidoids/.

Rzaeva, L. 2002. *Chalcids of eastern Azerbaijan and their economic importance*. ELM, Baku. 354 pp.

Yasnosh, V. A. 1968. Species of the genus *Physcus* Howard (Hymenoptera, Chalcidoidea), parasites of scale insects in the USSR. *Entomologicheskoe Obozrenie* 47: 205.

———. 1972. Chalcidoid parasites (Hymenoptera, Chalcidoidea) of scale insects (Homoptera, Coccoidea) from Georgian arid light forests. *Proceedings of All-union Entomological society*. Nauka, Leningrad. 55: Pp. 217–247.

———. 1974. A new species of Physcus Howard (Hymenoptera, Aphelinidae) from Italy. *Bolletino del laboratorio di Entomologia Agraria "di Portici"* 31: 105–108.

———. 1978. Aphelinids. Pp. 469–501 *in*: Medvedev, G. S. ed. *Keys to the Insects of the European part of USSR. Hymenoptera Vol. III. Part 2*. Nauka, Leningrad.

———. 2000. Aphelinid parasitoids (Hymenoptera, Aphelinidae) of armored scale insects (Coccinea, Diaspididae) in the Caucasus. *Proceedings of the Institute of Zoology*, Academy of Sciences of Georgia 20: 159.

——— and G. A. Mustafaeva. 1992. New parasitoid of *Lepidosaphes granati, Coccobius granati* sp. n. (Hymenoptera, Aphelinidae). *Zoologicheskiy Zhurnal* 71: 142–143.

——— and S. N. Myartseva. 1971. Two New aphelinid species (Chalcidoidea, Aphelinidae) – parasites of armoured scales (Coccoidea, Diaspididae) from middle Asia. *Bulletin of Academy of Sciences of Turkmenistan SSR* 6: 35–41 (In Russian).

——— and S. N. Myartseva. 1972. New parasite of Asiatic scale – *Physcus indefinites*, sp. n. (Chalcidoidea, Aphelinidae). *Bulletin of Academy of Sciences of Turkmenistan SSR* 5: 51–55 (In Russian).

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Host Range and Offspring Quantities in Natural Populations of *Nasonia vitripennis* (Walker, 1836) (Hymenoptera: Chalcidoidea: Pteromalidae)

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Abstract.—The gregarious ectoparasitic wasp *Nasonia vitripennis* is a well-established model organism in various aspects of genetics. In the field it is the dominant species in the parasitoid community found in birds' nests. In these nests *N. vitripennis* parasitizes the puparia of cyclorrhaphous flies. The most frequently recorded natural field host species are two ornithoparasitic bird blow flies *Protocalliphora azurea* and *P. falcozi*, the necrophagous *Calliphora vicina* (all: Calliphoridae) and the sapro-necrophagous *Potamia littoralis* (Muscidae). These field host records along with additional laboratory rearings allowed us to define the host range of *N. vitripennis*: It is restricted to Cyclorrhapha with further restrictions in size, shape and surface structure of the host species. The host acceptance excludes Hippoboscidae, Fanniidae and small species like heleomyzids and drosophilids, but includes parasitism of tachinids and sarcophagids or facultative hyperparasitism of Alysiinae (Hymenoptera: Braconidae) in calliphorid primary host puparia. The mean number of parasitoids emerging from field-collected specimens of the four regular host species ranged from 9.3 to 25.7 and the sex ratio was female-biased with proportions of males ranging from 0.13 to 0.34. This study shows that there are significant differences between host species in the number of individuals that emerged and the proportion of males. A correlation between the number of individuals and host size was indicated, but not between host size and sex ratio.

Nasonia vitripennis (Walker, 1836) (Hymenoptera: Pteromalidae) is a gregarious cosmopolitan idiobiontic parasitoid species and one of the most prominent model organisms in speciation and developmental genetics (e.g. Gadau et al. 1999; Perfectti and Werren 2001; Werren et al. 2004), but little is known about its natural life history. The most comprehensive work on this species is still the review by Whiting (1967), focused on behaviour and laboratory tests. In Europe *Nasonia vitripennis* is the only species of the genus *Nasonia*, in Northern America two additional species are present: *Nasonia giraulti* Darling, 1990 and *Nasonia longicornis* Darling, 1990 (Darling and Werren 1990).

Nasonia vitripennis has been frequently recorded from birds' nests (e.g. Abraham 1985; Darling and Werren 1990; Molbo and Parker 1996; Peters and Abraham 2004) and repeatedly recorded from carrion (e.g. Blanchot 1995; Grassberger and Frank 2004; Marchiori 2005). Carrion, as a habitat, overlaps with birds' nests as dead birds can be regularly found in nests. Within both habitats, *N. vitripennis* parasitizes numerous species of cyclorrhaphous flies such as Calliphoridae and Sarcophagidae. Records from dung show that *N. vitripennis* is not a dominant species in this habitat (Floate et al. 1999; Skovgard and Jespersen 2000; Kaufman et al. 2001; Birkemoe et al. 2008) and cannot be considered an economically important antagonist of synanthropic flies (Legner 1967; McKay and Galloway 1999).

Abraham (1985) and Abraham and Peters (2008) hypothesized that birds' nests are the primary habitat of *N. vitripennis*.

Peters (2007) corroborated that the habitat specialist *N. vitripennis* is the key species in the birds' nest parasitoid web. First field studies on *N. vitripennis* in birds' nests (Abraham 1985; Schlein 2002) were mostly made with sentinel replacement host puparia, which helped to reconstruct the parasitoids' phenology but gave little evidence regarding the natural hosts appearing in the nests. Subsequent studies (Peters and Abraham 2004; Abraham et al. 2005) reported field host records and defined a preliminary host range of *N. vitripennis* but left differences in life history patterns concerning number of offspring and sex ratio in relation to host species unclarified.

Theoretical considerations predict a correlation between host size and the number of offspring produced (Waage 1986; Godfray 1994). The correlation between host size and number of parasitoids has already been described for *N. vitripennis* under laboratory conditions by Wylie (1967) and Rivers and Denlinger (1995). In parasitoids it is generally advantageous if the sex ratio is shifted in favour of the females (Godfray 1994). However, parasitoid sex ratio is influenced by various variables and has been subject of numerous studies in the past and present. Host-quality (or host-size) model predicts that in smaller, less suitable hosts, more males are produced as the males' fitness is less dependent on host quality (Charnov et al. 1981; Waage 1986; Ueno 1999). Werren (1983), Molbo and Parker (1996) and Grillenberger et al. (2008) observed that other factors such as the parasitoid population size and the number of ovipositing females exert a strong influence on sex ratio which might suppress the predicted correlation between sex ratio and host size. These results are connected to local mate competition (LMC) theory (Hamilton 1967). LMC describes that male-male competition for mates is restricted to the natal patch. *N. vitripennis* exhibits typical characteristics predicted for a species with LMC: Sex ratio is highly female-biased if females oviposit alone, more males are produced by superparasitizing females to maximize the opportunities of their offspring to be able to mate (Werren 1980). To a lower extent asymmetric larval competition between sexes (Sykes et al. 2007) and characteristics of mating males (Shuker et al. 2006) have been demonstrated in laboratory studies to influence sex ratio in *N. vitripennis*. Sex ratio in relation to field host species of different size might give further insight into sex ratio mechanisms in *N. vitripennis*.

In contrast to previous studies, this study presents field data on offspring quantities of *N. vitripennis* reared from different natural host species collected as puparia from birds' nests. Data are examined for any differences between host species in number of individuals per host and proportion of males and for any correlations between the size of host puparia and the number of parasitoids reared and between host size and sex ratio. Furthermore, this study utilized field collection of host puparia and additional laboratory rearings to define the host range of *N. vitripennis*. These results can circumscribe host acceptance and rejection cues of *N. vitripennis* such as shape and size of the host which are known to be used by parasitoids (Wylie 1967; Cooperband and Vinson 2000).

MATERIAL AND METHODS

Nests of *Parus* spp. (tits) were examined for the presence of puparia of cyclorrhaphous flies parasitized by *Nasonia vitripennis*. The nine collection sites were located in Germany and included: Hamburg (5 sites), (1) Hamburg-Eissendorf, "Staatsforst Haake" forest N53.4548 E09.9207, (2) Hamburg-Eissendorf, garden N53.4540 E09.9391, (3) Hamburg-Rotherbaum, "Sternschanzenpark" N53.5655 E09.9709, (4) Hamburg-Bramfeld, "Umweltzentrum Karlshöhe" park N53.6295 E10.1092, (5) Hamburg-Poppenbüttel (garden in the district of Poppenbüttel without exact locality); Schleswig-Holstein (3 sites), (6) "Linauer

Forst" forest N53.6734 E10.4897, (7) Elmshorn, garden N53.7656 E09.6725, (8) Haseldorf, garden N53.6352 E09.5986; Baden-Württemberg (1 site), (9) Bad Mergentheim, "Stadtwald" forest N49.5083 E09.7722 (reference system WGS84).

Puparia were stored in Petri dishes at room temperature until the emergence of parasitoids. These were preserved in 70% EtOH in pools of multiple puparia or in single puparium tubes. The latter will be referred to as "separately stored puparia" within this paper. The corresponding host puparia were taped to the EtOH tubes. The parasitoids that emerged were counted and sex was determined. Maximum length and maximum width of host puparia were measured. For puparia species identification voucher specimens of puparia and corresponding identified imagines were used that were collected during our studies on birds' nest fly fauna (Peters and Abraham 2004; Peters 2007). Voucher specimens are deposited at Zoologisches Museum Hamburg (ZMH).

A laboratory stock of *N. vitripennis* was maintained on *Calliphora vomitoria* (Linnaeus, 1758) puparia in Petri dishes at room temperature. The stock was originally reared from *Protocalliphora azurea* (Fallén, 1816) puparia collected from a nest of *Parus* sp. in Hamburg-Rotherbaum. For laboratory rearing tests on host range parasitoid females were put on puparia or pupae of a variety of Diptera and Lepidoptera species. Parasitoids were taken from the laboratory stock. They were 3–6 days old, mated and fed on moistened raisins. 10 females were put on 30 to 50 puparia or pupae until they died. Hosts included puparia of *Triarthria setipennis* (Fallén, 1810) (Diptera: Tachinidae) reared from *Forficula auricularia* Linnaeus, 1758 collected in Hamburg-Rotherbaum, puparia of *Protophormia terranovae* (Robineau-Desvoidy, 1830), *Calliphora vomitoria*, *Lucilia sericata* (Meigen, 1826) (all: Diptera: Calliphoridae; obtained as larvae from bait shops) and *Drosophila melanogaster* Meigen, 1830 (Diptera: Drosophilidae) and pupae of *Galleria mellonella* (Linnaeus, 1758) (Lepidoptera: Pyralidae) presented with their cocoons. *G. mellonella* larvae were reared on artificial medium containing cereals, glycerin, milk powder and honey. All hosts were 4–6 days old. In 2 of the 4 tests with *D. melanogaster* >100 puparia of different ages from a laboratory mass-rearing were presented.

Additionally, parasitoids were reared on freeze-killed *C. vomitoria* puparia, which were stored in −28°C 4–6 days after pupation and thawed before a new rearing. All rearings were made in Petri dishes at 24–26°C. If the rearing resulted in a viable F1, it was considered successful, regardless of the number of parasitoid specimens reared. If it did not result in any offspring after four attempts, it was considered unsuccessful.

All data analyses were performed with SPSS 16.0 for Windows. Tests on normal distribution of data were made with Kolmogorov-Smirnov-tests. All significance levels of comparisons were Bonferroni corrected.

RESULTS

Host records.—Nasonia vitripennis was reared from six host species that were collected from birds' nests in the field. These included two species of dipteran bird parasites *Protocalliphora* spp., the necrophagous *Calliphora vicina* (all: Diptera: Calliphoridae) and *Sarcophaga* sp. (Sarcophagidae) and the polyphagous muscid *Potamia littoralis*. Furthermore, intraordinal hyperparasitism of the dipterophagous braconid *Alysia manducator* was recorded. In the laboratory, rearing was possible on three additional calliphorid host species and on *Triarthria setipennis* (Tachinidae). *Calliphora vomitoria* puparia that were freeze-killed before and then thawed for rearing tests are also suitable hosts for *N. vitripennis*. *Drosophila melanogaster* was the only presented Diptera species on which no rearing of *N. vitripen-*

Table 1. Host records for *Nasonia vitripennis* from field collections and laboratory rearings; * hyperparasitism in *Calliphora vicina*.

Field host records	Laboratory rearings
Protocalliphora azurea (Fallén, 1816) (Calliphoridae)	**Successful**
Protocalliphora falcozi Séguy, 1928 (Calliphoridae)	*Protophormia terranovae* (Calliphoridae)
Calliphora vicina Robineau-Desvoidy, 1830 (Calliphoridae)	*Calliphora vomitoria* (Calliphoridae)
Potamia littoralis Robineau-Desvoidy, 1830 (Muscidae)	*Lucilia sericata* (Calliphoridae)
Sarcophaga sp. (Sarcophagidae)	*Triarthria setipennis* (Tachinidae)
Alysia manducator (Panzer, 1799) (Hym.: Braconidae) *	*Calliphora vomitoria* (freeze-killed puparia)
	Unsuccessful
	Drosophila melanogaster (Drosophilidae)
	Galleria mellonella (Lepidoptera: Pyralidae)

nis was possible. Also, rearing was unsuccessful on the pupae of the greater wax moth *Galleria mellonella* (Lepidoptera: Pyralidae).

The recorded field hosts of *N. vitripennis* in birds' nests, potential hosts that were confirmed in successful laboratory rearings and examples of species outside the parasitoids' host range are listed in Table 1.

Offspring numbers and sex ratio.—Specimens of *N. vitripennis* emerging from the host species *Calliphora vicina, Protocalliphora azurea, P. falcozi* and *Potamia littoralis* were counted. In total 5333 individuals from 490 puparia from 17 *Parus* spp. nests were examined (Table 2). All puparia and emerging parasitoids were used for calculation of overall mean of individuals per host and an overall sex ratio (Table 2). 140 puparia were separately stored and were used for comparisons of number of parasitoids per host and proportion of males. These puparia included *Protocalliphora azurea* (N = 16), *P. falcozi* (N = 15), *C. vicina* (N = 72) and *P. littoralis* (N = 37). From these puparia 1897 parasitoids emerged.

Mean comparisons made of the parasitoids of separately stored puparia showed that there are significant interspecific differences in numbers of individuals per puparium. The number was higher in *Protocalliphora azurea* (median 23.0) and *P. falcozi* (median 22.0) than in *C. vicina* (median 10.0) and *P. littoralis* (median 8.0) (U-test, $p < 0.001$). The difference between neither the two *Protocalliphora*-species (U-test, $p > 0.7$) nor between *C. vicina* and *P. littoralis* (U-test, $p > 0.1$) was significant.

For mean comparison of proportion of males, puparia from which only males

Table 2. The total number, the number per puparium and the proportion of males of *Nasonia vitripennis* in field host species; * = puparia with emergence of only males excluded; ** = recorded from separately stored puparia with reduced sample size.

host species	*Calliphora vicina*	*Calliphora vicina* *	*Protocalliphora azurea*	*Protocalliphora falcozi*	*Potamia littoralis*
total no. of host puparia	389	378	47	17	37
total no. of *N. vitripennis*	3614	3530	929	436	354
total no. of ♀	2334	2334	699	379	303
total no. of ♂	1280	1196	230	57	51
overall mean no. per host	9.3	9.3	19.8	25.7	9.6
overall mean ♀	6.0	6.2	14.9	22.3	8.2
overall mean ♂	3.3	3.2	4.9	3.4	1.4
median no. per host **	10.0		23.0	22.0	8.0
maximum no. per host **	28		53	46	25
overall sex ratio ♂:♀	1:1.8	1:1.9	1:3.0	1:6.6	1:5.9
overall proportion of ♂	0.35	0.34	0.25	0.13	0.14
median proportion of ♂ **		0.222	0.155	0.079	0.125

Table 3. Size of puparia of four field host species of *N. vitripennis*.

	Calliphora vicina	*Protocalliphora azurea*	*Protocalliphora falcozi*	*Potamia littoralis*
puparium length (mm)				
median	7.5	7.6	8.4	6.7
interquartile range	2.1	0.8	0.5	0.8
minimum; maximum	4.6; 9.5	6.3; 8.4	7.7; 9.1	6.0; 7.5
length/width				
median	2.34	2.08	2.13	2.78
mean ± std	2.37 ± 0.14	2.1 ± 0.11	2.14 ± 0.08	2.82 ± 0.14

emerged (possibly due to unmated females in the arrhenotokous hymenopterans) were excluded (only in *C. vicina*). The only significant difference after Bonferroni correction is found between *C. vicina* (N = 61) and *P. littoralis* (U-test, p = 0.001). *C. vicina* puparia exhibit a higher proportion of male parasitoids (Table 2). The proportions of males in *P. falcozi* and *P. littoralis* are lower than in *P. azurea*, but these differences are not significant (U-test, p = 0.04, p = 0.047). There is no difference between *P. falcozi* and *P. littoralis* (U-test, $p > 0.6$). The difference between *C. vicina* and *P. azurea* is also not significant (U-test, $p > 0.2$). The overall sex ratio measured as the number of females per male was higher in *P. falcozi* and *Potamia littoralis* than in all other species (Table 2; χ^2, $p < 0.001$). The lowest value compared to all other species was found in the *C. vicina* puparia ($p < 0.001$). There was no difference if the puparia from which only males emerged, were excluded ($p > 0.1$).

The host puparia were of different size depending on species (Table 3). The puparia of the *Protocalliphora* species were particularly big, wide and massive. *P. falcozi* puparia are significantly longer than *P. azurea* puparia (U-test, $p < 0.001$). Puparia size was remarkably variable in *C. vicina*. The smallest and the largest puparia in the study belong to this species. The mean length of *C. vicina* puparia was significantly greater than *P. littoralis* (U-test, $p < 0.001$), but smaller than *Protocalliphora* spp., although the length difference with *P. azurea* is not significant (U-test, $p > 0.1$). On average the puparia of *P. littoralis* are the smallest. Their shape is rather slim which is shown in the high length to width ratio (Table 3).

DISCUSSION

Host range.—Dominant field host species of *N. vitripennis* from the specific primary habitat (birds' nests) were bird blowflies (*Protocalliphora azurea* and *P. falcozi*), the necrophagous blowfly *Calliphora vicina* and the polyphagous muscid *Potamia littoralis*. The puparia of the parasitic and the necrophagous blowflies appear in the nests when either live or dead nestlings are available. The activity of *N. vitripennis* is linked to the birds' breeding season and largely restricted to the summer months (Schlein 2002). During this time the parasitoid can use the blowfly hosts, the predominantly necrophagous summer generation of *P. littoralis* and, additionally, other necrophagous taxa occurring less frequently like *Sarcophaga* spp. (Table 1). There is no evidence of parasitism of other nidicolous taxa, such as lepidopterans, in this study nor in Noyes (2007).

Successful rearing on the tachinid *Triarthria setipennis*, a parasitoid of earwigs, and on other calliphorid species like *Calliphora vomitoria, Lucilia sericata* and *Protophormia terranovae* supports the general use of cyclorrhaphous hosts (Table 1). It demonstrated that *N. vitripennis* can parasitize taxonomically related hosts, with which the species will not have contact under natural conditions. Further examples of suitable cyclorrhaphous hosts of *N. vitri-*

pennis that have been recorded in various studies are *Musca domestica* Linnaeus, 1758, *Muscina stabulans* (Fallén, 1817) and *Stomoxys calcitrans* (Linnaeus, 1758) (all: Muscidae) (e.g. Rivers and Denlinger 1995; Blanchot 1995; Gibson and Floate 2004). Rearing on the pupae of the wax moth *Galleria mellonella* was not possible. All results imply that Lepidoptera are outside the host range of *N. vitripennis*. The very few records of lepidopteran hosts (Noyes 2007) should be seen as misinterpretations or accidental events.

The first limitation of host range within the Cyclorrhapha is host size. Puparia are not parasitized if they are too small, even if they appear in suitable habitats, like the frequent birds' nest species *Tephroclamys tarsalis* (Zetterstedt, 1847) (Heleomyzidae) (Noyes 2007; Peters 2007). It was not possible to rear *N. vitripennis* on *Drosophila melanogaster* in the laboratory, which corroborates the observations of Rivers and Denlinger (1995). A threshold in host suitability regarding puparium size might be represented by the cheese-fly *Piophila casei* (Noyes 2007) (puparia length 4–5 mm). The smallest parasitized puparium in this study was 4.6 mm (Table 3).

A second limiting factor of host range is the shape of puparia: Aberrant forms like the puparia of fanniids, with their conspicuous appendages, are not or not regularly parasitized (only two records: Legner et al. 1967; Blanchot 1995); the almost circular louse fly puparia (Hippoboscidae) are not suitable hosts either (only one record from *Pseudolynchia canariensis* (De Santis 1967)). Like in *N. vitripennis*, host shape as an important host acceptance cue is known from e.g. *Melittobia digitata* (Eulophidae) (Cooperband and Vinson 2000).

A third decisive factor is the host surface structure: *N. vitripennis* hyperparasitizes *Alysia manducator* (Hymenoptera: Braconidae: Alysiinae) inside *Calliphora vicina* puparia as the surface structure indicates a suitable and intact host. The same can be found to explain the parasitism of freeze-killed hosts (Table 1). Although the content of the puparium is completely different from a live pupa in shape and consistency, the host is accepted. An examination of the host pupae with the ovipositor, as described for *N. vitripennis* by Edwards (1954), is therefore unlikely, at least for its impact on host acceptance. The discrimination of hosts using cues of puparia and not cues of their content was recorded for *N. vitripennis* by Smith (1969). In a more general statement Rivers (1996) concluded from his studies that host acceptance in *N. vitripennis* is related to exterior cues of the puparia. These cues are now specified as size, shape and surface structure.

In summary the host range of *Nasonia vitripennis* is defined as:

Polyphagous; Cyclorrhaphous Diptera, especially Calliphoridae, Muscidae and Sarcophagidae at least 4–5 mm in size, excluding puparia with appendages (Fanniidae) and aberrant shapes (Hippoboscidae), including hyperparasitism of Alysiinae in suitable host puparia.

Offspring numbers and sex ratio.—The *Protocalliphora* puparia showed the highest parasitoid numbers while the puparia of *Calliphora vicina* and *Potamia littoralis* had on average significantly fewer (Table 2). Puparia of *Protocalliphora* spp. are larger, which indicates a correlation between host size and number of individuals in the field, although it appears nonlinear: The *C. vicina* puparia are often smaller than the *Protocalliphora* puparia (Table 3), but the size difference is not as big as the difference in parasitoid numbers. Furthermore, *C. vicina* puparia are larger than the *P. littoralis* puparia (Table 3), but the number of parasitoids does not differ. Taken together, *C. vicina* individuals seem to be a less suitable host, independent of host size. The reasons for this are unclear. One possible influential factor is that puparia of *C. vicina* show high variation of puparia size (Table 3), explained by limited food resources (carrion) during the larval development, which results in small specimens and

maybe lower host quality while the parasitic *Protocalliphora* spp. and the small *P. littoralis* have distinctly less variation of puparia size (Table 3).

The correlation between host size and number of parasitoids was also recorded by Wylie (1967) and Rivers and Denlinger (1995) under laboratory conditions. Consequently there is a preference of *N. vitripennis* for larger hosts if choice is possible, recorded by Wylie (1967) and corroborated in field studies, whereas the parasitism rate of the smaller *P. littoralis* increases if the larger calliphorids are missing from a birds' nest (Peters and Abraham 2004).

Field records of parasitoid numbers of *N. vitripennis* in the literature correspond quite well with the average parasitoid number from this study (16.1 parasitoids per host) but are rather rare and restricted to few larger hosts. Gold and Dahlsten (1989) recorded between 15 and 20 parasitoids from *Protocalliphora* spp., Draber-Monko (1995) collected *P. azurea* puparia from tree sparrow nests and recorded a mean number of 20 *N. vitripennis*, but the sample size was small. Marchiori (2005) collected puparia of *Peckia chrysostoma* (Sarcophagidae) and noted a mean number of 15.2 *N. vitripennis* specimens. Molbo and Parker (1996) did not differ between *Protocalliphora* and *Calliphora* hosts and recorded a mean of 26 *N. vitripennis* from both species in the field. The results of Schlein (1998, 2001) using *Calliphora vomitoria* as host species indicate a significant difference between field and laboratory conditions: An average of 33 *N. vitripennis* specimens were reared from *Calliphora vomitoria* in the laboratory (Schlein 2001). In the field numbers were distinctly lower with a mean of 15.7 specimens from the same host species (sentinel puparia placed inside the nest boxes) (Schlein 1998).

The results show that there are interspecific differences between host species and indicate that a correlation of parasitoid numbers and host size is present under natural conditions, but taxonomically restricted exceptions exist. Identifying the factors that underlie the differences in parasitoid numbers per host needs further experiments with different host species and values like parasitoid individual body size, developmental time and mortality rate to be included.

Some differences in proportion of males emerging from puparia were recorded between host species, but no consistent correlation was indicated between sex ratio and host size (Table 2 and 3). Host quality model predictions (larger hosts exhibit more parasitoid females) cannot be found in our field data. The field recorded proportion of males especially in the abundant *C. vicina* and *P. azurea* are higher than expected assuming host-quality control. The sex ratio in the smallest host, *P. littoralis*, is more female-biased than expected. Other factors than host size must be considered for sex ratio determination. Accordant with the predictions for a species that shows local mate competition (LMC), Werren (1984) recorded a higher proportion of males in previously parasitized hosts (superparasitism) for *N. vitripennis*. A further factor affecting sex ratio, which is also related to LMC theory, is the number of ovipositing females in the host patch, with increasing proportion of males if more females are present (Charnov et al. 1981; King and Skinner 1991; Grillenberger et al. 2008). However, Burton-Chellew et al. (2008) showed that offspring sex ratio in natural populations was not directly influenced by number of females in the patch but only by relative clutch size. Besides LMC theory there are other demonstrated influences on sex ratio in *N. vitripennis*: Asymmetric larval competition between sexes is shown to favour less female-biased sex ratios as under larval competition females are smaller when a higher proportion of females was competing within a host (Sykes et al. 2007). Smaller females then produce less offspring (Charnov and Skinner 1984; Sykes et al. 2007). Shuker et

al. (2006) showed that not only females but also males can have an effect on sex ratio, although underlying reasons for this effect are still unclear. The effect might be due to differences in sperm quality between male strains or due to active male influence in order to increase female offspring, i.e. to increase fertilisation and therefore increase contribution to next generation. However, both influencial factors are considered weak when compared to LMC (Shuker et al. 2006; Sykes et al. 2007). Constrained females which can produce only males obviously have effect on sex ratio. In this study hosts from which only males emerged were excluded from comparisons, but in superparasitized hosts we could not control the effect. An indirect effect of constrained females was shown to be absent in *N. vitripennis* by King and D'Souza (2004): The presence of a constrained female did not influence offspring sex ratios of non-constrained females. Abraham and König (1977) studied the influence of temperature during oviposition on sex ratio in *N. vitripennis*. At lower temperatures less eggs are laid per host with a more female-biased sex ratio. They explain these results with differential mortality: less females and more of the smaller males are able to finish development the more larvae are developing within one host.

Recently, Grillenberger et al. (2009) studied the influence of multiparasitism on sex ratio in *N. vitripennis* and the closely related *N. giraulti*. They showed that multiparasitim in this case has no effect on sex ratio. In our studies we recorded no multiparasitism although multiparasitism with *Pachycrepiodeus vindemmiae* (Rondani, 1875) is known to occur in the Central European study area (Peters 2007). Another factor that might indeed influence sex ratio is host age which was recorded as influencial for the solitary *Spalangia* sp. (King 2000) and might also have an impact on sex ratio in the gregarious *N. vitripennis*. In this study the only known factor among all these reported influences is host species and size. Number of females, degree of superparasitism, differences between mating males, oviposition temperature etc. are unknown.

Other known data on the sex ratio of *N. vitripennis* show a tendency towards lower proportions of males than in this study (especially when compared to the overall proportion of males, Table 2) but also display a wide range depending on various factors. In Schlein's (2001) laboratory rearings of *N. vitripennis* on *C. vomitoria*, the proportion of males was 0.17. In the studies of Abraham and König (1977) on another calliphorid host, *Phormia regina*, the ratio ranges from 0.125 to 0.2 depending on the temperature. Comparable ratios were found by Rivers and Denlinger (1995) for three larger sarcophagid host species in the laboratory. The exception in their studies was a proportion of males of 0.41 within the smaller *Musca domestica*. Two studies on the sex ratio of *N. vitripennis* in natural populations and natural host species recorded a mean proportion of males of 0.19 in unidentified *Calliphora* sp. and *Protocalliphora* sp. (Molbo and Parker 1996) or report a wide range dependant on wasp population size (Werren 1983; host species: various necrophagous Cyclorrhapha). The recent studies of Grillenberger et al. (2008) and Burton-Chellew et al. (2008) on natural populations of *N. vitripennis* were done with a mixture of bait hosts and unidentified natural hosts and thus provide no additional information on the role of host species.

As discussed above, factors affecting parasitoid sex ratios are complex and cannot be solved here. However, our results indicate that host species should be considered when studying the influences on proportion of males in host patches and parasitoid populations. This study initially shows data of *N. vitripennis* under field conditions and in identified field hosts which have been very rarely studied before.

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LITERATURE CITED

Abraham, R. 1985. *Nasonia vitripennis* an insect from birds' nests (Hymenoptera: Chalcidoidea: Pteromalidae). *Entomologia Generalis* 10: 121–124.

——— and H. König. 1977. Der Einfluss der Temperatur auf die Anstichaktivität bei *Nasonia vitripennis* und *Spalangia nigra*. *Entomophaga* 22: 299–308.

——— and R. S. Peters. 2008. Nestboxes as habitat for insects, especially for flies and their parasitoids. *Vogelwarte* 46: 195–205 (German with English summary).

———, L. Krogmann, and R. Peters. 2005. Ecological and systematic studies on Pteromalidae (Hymenoptera: Chalcidoidea). *Faunistisch-Ökologische Mitteilungen* 8: 353–361 (German with English summary).

Birkemoe, T., A. Soleng, and A. Aak. 2008. Biological control of *Musca domestica* and *Stomoxys calcitrans* by mass releases of the parasitoid *Spalangia cameroni* on two Norwegian pig farms. *BioControl*. published online 15 August 2008.

Blanchot, P. 1995. Inventaire des parasitoides de mouches synanthropes recensés en France. *EPHE, Biologie et Évolution des Insectes* 7–8: 111–119.

Burton-Chellew, M. N., T. Koevoets, B. K. Grillenberger, E. M. Sykes, S. L. Underwood, K. Bijlsma, J. Gadau, L. van de Zande, L. W. Beukeboom, S. A. West, and D. M. Shuker. 2008. Facultative sex ratio adjustment in natural populations of wasps: cues of local mate competition and the precision of adaptation. *The American Naturalist* 172: 393–404.

Charnov, E. L. and S. W. Skinner. 1984. Evolution of host selection and clutch size in parasitoid wasps. *The Florida Entomologist* 67: 5–21.

———, R. L. Los-den Hartogh, W. T. Jones, and J. van den Assem. 1981. Sex ratio evolution in a variable environment. *Nature* 289: 27–33.

Cooperband, M. F. and S. B. Vinson. 2000. Host-acceptance requirements of *Melittobia digitata* (Hymenoptera: Eulophidae), a parasitoid of mud dauber wasps. *Biological Control* 17: 23–28.

Darling, D. C. and J. H. Werren. 1990. Biosystematics of *Nasonia* (Hymenoptera: Pteromalidae): Two new species reared from bird's nests in North America. *Annals of the Entomological Society of America* 83: 352–370.

De Santis, L. 1967. *Catálogo de los Himenópteros Argentinos de la Serie Parasitica, incluyendo Bethyloidea*. Comision de Investigacion Cientifica, La Plata.

Draber-Monko, A. 1995. *Protocalliphora azurea* (Fall.) (Diptera, Calliphoridae) and other insects found in nests of sparrows, *Passer domesticus* (L.) and *Passer montanus* (L.) in the vicinity of Warsaw. *International Studies on Sparrows* 22: 3–10.

Edwards, R. L. 1954. The host-finding and oviposition behaviour of *Mormoniella vitripennis* (Walker) (Hym., Pteromalidae), a parasite of muscoid flies. *Behaviour* 7: 88–112.

Floate, K. D., B. Khan, and G. Gibson. 1999. Hymenopterous parasitoids of filth fly (Diptera: Muscidae) pupae in cattle feedlots. *The Canadian Entomologist* 131: 347–362.

Gadau, J., R. E. Page Jr, and J. H. Werren. 1999. Mapping of hybrid incompatibility loci in *Nasonia*. *Genetics* 153: 1731–1741.

Gibson, G. A. P. and K. D. Floate. 2004. Filth fly parasitoids on dairy farms in Ontario and Quebec, Canada. *The Canadian Entomologist* 136: 407–417.

Godfray, H. C. J. 1994. *Parasitoids. Behavioural and evolutionary ecology*. Princeton University Press, Princeton, New Jersey.

Gold, C. S. and D. L. Dahlsten. 1989. Prevalence, habitat selection, and biology of *Protocalliphora* (Diptera: Calliphoridae) found in nests of mountain and chestnut-backed chickadees in California. *Hilgardia* 57: 1–19.

Grassberger, M. and C. Frank. 2004. Initial study of arthropod succession on pig carrion in a Central European urban habitat. *Journal of Medical Entomology* 41: 511–523.

Grillenberger, B. K., T. Koevoets, M. N. Burton-Chellew, E. M. Sykes, D. M. Shuker, L. van de Zande, R. Bijlsma, J. Gadau, and L. W. Beukeboom. 2008. Genetic structure of natural *Nasonia vitripennis* populations: validating assumptions of sex-ratio theory. *Molecular Ecology* 17: 2854–2864.

———, L. van de Zande, R. Bijlsma, J. Gadau, and L. W. Beukeboom. 2009. Reproductive strategies under multiparasitism in natural populations of the parasitoid wasp *Nasonia* (Hymenoptera). *Journal of Evolutionary Biology* 22: 460–470.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156: 477–488.

Kaufman, P. E., S. J. Long, and D. A. Rutz. 2001. Impact of exposure length and pupal source on *Muscidifurax raptorellus* and *Nasonia vitripennis* (Hymenoptera: Pteromalidae) parasitism in a New York poultry facility. *Journal of Economic Entomology* 94: 998–1003.

King, B. H. 2000. Sex ratio and oviposition responses to host age and the fitness consequences to mother and offspring in the parasitoid wasp

Spalangia endius. *Behavioral Ecology and Sociobiology* 48: 316–320.

——— and S. W. Skinner. 1991. Sex ratio in a new species of *Nasonia* with fully-winged males. *Evolution* 45: 225–228.

——— and J. A. D'Souza. 2004. Effects of constrained females on offspring sex ratios of *Nasonia vitripennis* in relation to local mate competition theory. *Canadian Journal of Zoology* 82: 1969–1974.

Legner, E. F. 1967. The status of *Nasonia vitripennis* as a natural parasite of the house fly, *Musca domestica*. *The Canadian Entomologist* 99: 308–309.

———, E. C. Bay, and E. B. White. 1967. Activity of parasites from Diptera: *Musca domestica*, *Stomoxys calcitrans*, *Fannia canicularis*, and *F. femoralis*, at sites in the Western hemisphere. *Annals of the Entomological Society of America* 60: 462–468.

Marchiori, C. H. 2005. *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae) gregarious parasitoid in pupae of *Peckia chrysostoma* (Wiedemann) (Diptera: Sarcophagidae) in Brazil. *Arquivos de Instituto Biologico* 72: 269–270.

McKay, T. and T. D. Galloway. 1999. Survey and release of parasitoids (Hymenoptera) attacking house and stable flies (Diptera: Muscidae) in dairy operations. *The Canadian Entomologist* 131: 743–756.

Molbo, D. and E. D. Parker Jr. 1996. Mating structure and sex ratio variation in a natural population of *Nasonia vitripennis*. *Proceedings of the Royal Society of London B* 263: 1703–1709.

Noyes, J. S. 2007. *Universal Chalcidoidea Database*. World Wide Web electronic publication. www.nhm.ac.uk/research-curation/projects/chalcidoids/index [accessed 10-October-2008]

Perfectti, F. and J. H. Werren. 2001. The interspecific origin of B chromosomes: experimental evidence. *Evolution* 55: 1069–1073.

Peters, R. 2007. Interaktionen zwischen Wirten und Parasitoiden: Nahrungsnetzstruktur, Wirtsspektren und Wirtsfindung am Beispiel der Arten aus Vogelnestern. Ph.D. thesis. University of Hamburg, Germany. http://www.sub.uni-hamburg.de/opus/volltexte/2007/3234/pdf/DissertationPeters.pdf

——— and R. Abraham. 2004. Interactions between parasitoid Hymenoptera (Chalcidoidea: Pteromalidae) and Diptera: Cyclorrhapha in nests of cavity-nesting birds. *Entomologia Generalis* 27: 133–141.

Rivers, D. B. 1996. Changes in the oviposition behavior of the ectoparasitoids *Nasonia vitripennis* and *Muscidifurax zaraptor* (Hymenoptera: Pteromalidae) when using different species of fly hosts, prior oviposition experience, and allospecific competition. *Annals of the Entomological Society of America* 89: 466–474.

——— and D. L. Denlinger. 1995. Fecundity and development of the ectoparasitic wasp *Nasonia vitripennis* are dependent on host quality. *Entomologia Experimentalis et Applicata* 76: 15–24.

Schlein, O. 1998. Das Auftreten von den Pteromalidae *Nasonia vitripennis* und *Dibrachys* cf. *cavus* in Vogelnestern (Chalcidoidea, Hymenoptera). Diploma thesis. University of Hamburg (unpublished).

———. 2001. Interspecific competition between two dipterophagous parasitoids, *Nasonia vitripennis* and *Dibrachys cavus* (Hymenoptera: Pteromalidae), in birds' nests. Pp. 374–381 *in*: Melika, G., and C. Thuroczy eds. *Parasitic wasps: Evolution, systematics, biodiversity and biological control*. Agroinform, Budapest.

———. 2002. Nischendifferenzierung und Reduktion von interspezifischer Konkurrenz zwischen den Parasitoiden *Nasonia vitripennis* (Walker 1836) und *Dibrachys cavus* (Walker 1835) (Hymenoptera: Pteromalidae) bei der Wirtssuche in Vogelnestern. Ph.D. thesis. University of Hamburg, Germany. http://www.sub.uni-hamburg.de/opus/volltexte/2002/860/pdf/dissertation.pdf

Shuker, D. M., E. M. Sykes, L. E. Browning, L. W. Beukeboom, and S. A. West. 2006. Male influence on sex allocation in the parasitoid wasp *Nasonia vitripennis*. *Behavioral Ecology and Sociobiology* 59: 829–835.

Skovgard, H. and J. B. Jespersen. 2000. Seasonal and spatial activity of hymenopterous pupal parasitoids (Pteromalidae and Ichneumonidae) on the house fly (Diptera: Muscidae) on Danish pig and cattle farms. *Environmental Entomology* 29: 630–637.

Smith, G. J. C. 1969. Host selection and oviposition behavior of *Nasonia vitripennis* (Hymenoptera: Pteromalidae) on two host species. *The Canadian Entomologist* 101: 533–538.

Sykes, E. M., T. M. Innocent, I. Pen, D. M. Shuker, and S. T. West. 2007. Asymmetric larval competition in the parasitoid wasp *Nasonia vitripennis*: a role in sex allocation? *Behavioral Ecology and Sociobiology* 61: 1751–1758.

Ueno, T. 1999. Host-size-dependent sex ratio in a parasitoid wasp. *Researches on Population Ecology* 41: 47–57.

Waage, J. K. 1986. Family planning in parasitoids: adaptive pattern of progeny and sex allocation. Pp. 63–95 *in*: Waage, J., and D. Greathead eds. *Insect Parasitoids*. Academic Press, London.

Werren, J. H. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. *Science* 208: 1157–1159.

———. 1983. Sex ratio evolution under local mate competition in a parasitic wasp. *Evolution* 37: 116–124.

———. 1984. Brood size and sex ratio regulation in the parasitic wasp *Nasonia vitripennis* (Walker) (Hy-

menoptera: Pteromalidae). *Netherlands Journal of Zoology* 34: 123–143.

———, J. Gadau, L. Beukeboom, C. Desplan, J. Lynch, R. Rivers, S. Richards, and L. van de Zande. 2004. Proposal to sequence the *Nasonia* genome. http://www.genome.gov/Pages/Research/Sequencing/SeqProposals/NasoniaSeq.pdf

Whiting, A. R. 1967. The biology of the parasitic wasp *Mormoniella vitripennis* (*Nasonia brevicornis*) (Walker). *The Quarterly Review of Biology* 42: 333–406.

Wylie, H. G. 1967. Some effects of host size on *Nasonia vitripennis* and *Muscidifurax raptor* (Hymenoptera: Pteromalidae). *The Canadian Entomologist* 99: 742–748.

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Rhopalum nasale, a New Species from Australia (Hymenoptera: Crabronidae)

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Abstract.—The **new species *Rhopalum nasale*** from Southern Australia is mainly characterized by its unique clypeal process, the expanded occipital carina, and the pronotal and propodeal structures.

Of the 278 currently recognized species of *Rhopalum*, 98 occur in Australia (Leclercq, 1997). This number, however, if far from complete. I have recently seen in the Australian National Insect Collection, Canberra, a dozen species that cannot be identified using Leclercq's key and that are apparently undescribed. They are represented mostly by one or a few specimens each. One of them, represented by a series of 10 females, is so unusual that I cannot stand the temptation of describing it.

The following are the abbreviations used in the text:

ANIC: Australian National Insect Collection, Canberra, A.C.T., Australia.

CAS: California Academy of Sciences, San Francisco, California, USA.

Rhopalum nasale Pulawski, sp. n.

Name derivation.—The Latin adjective *nasalis* (neuter: *nasale*) means "referring to the nose", or "with a big nose"; with reference to the clypeal process of the female.

Diagnosis.—The new species can be easily recognized by the unique, narrow, conspicuous process emerging from the upper part of the clypeus (Fig. 1c, d), and the conspicuously expanded dorsolaterally occipital carina (Fig. 1a, b). The unusual pronotum and the propodeal side (see description below) are also diagnostic.

Description.—Head as seen from above transverse (Fig. 1a); vertex thick (distance between hindocellus and occipital carina twice as long as ocellocular distance), its lateral margins nearly parallel. Midocellus slightly smaller than hindocellus; distance between hindocelli 2.6 × distance between midocellus and hindocellus; ocellocular distance 1.4 × hindocellar width. Orbital fovea well defined. Interantennal area flat, without specialized structures; interantennal distance about 1.1 × antennal socket width; distance between antennal socket and orbit about 1.5 antennal socket width. Clypeus with median process emerging from its dorsal area (Fig. 1c, d); process narrow, asetose, slightly broadening toward apex, emarginate apically; area between process and clypeal ventral margin concave, asetose, delimited dorsally by carina that extends from each side of process. Mandibular apex unidentate. Occipital carina joining hypostomal carina, conspicuously enlarged subdorsally but not enlarged dorsally (Fig. 1a, b). Upper frons and postocellar area finely punctate, punctures less than one diameter apart. Ventral portion of gena (on each side of hypostomal carina) without tubercle, un-

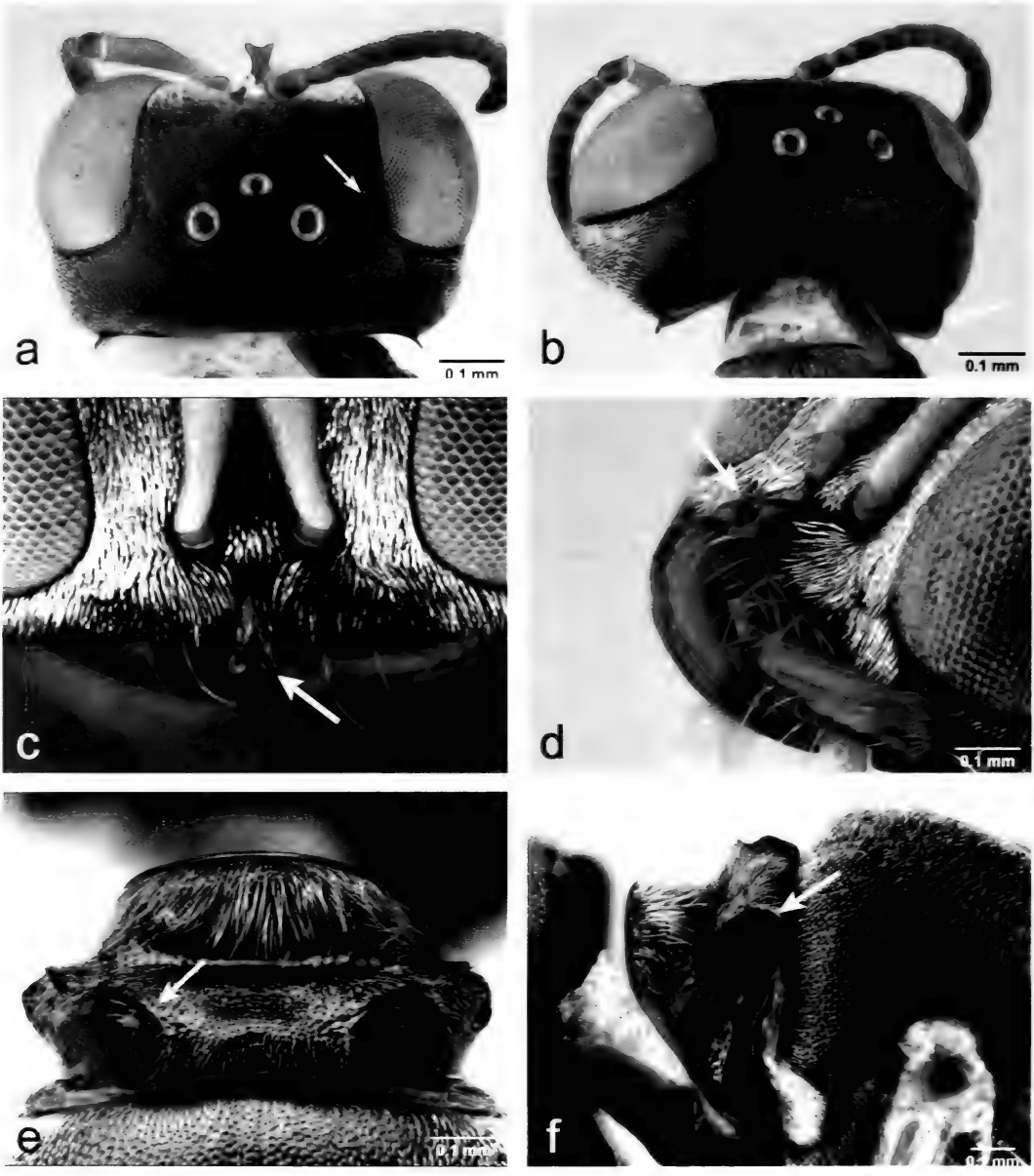

Fig. 1. *Rhopalum nasale* sp. n., ♀: a – head in dorsal view (arrow indicates orbital fovea); b – head in oblique view (arrow indicates occipital carina); c – clypeus in frontal view (arrow indicates projection); d – clypeus in lateral oblique view (arrow indicates projection); e – pronotum dorsally (arrow indicates sublateral carina); f – pronotum laterally (arrow indicates sublateral carina).

sculptured except for a few sparse punctures; posterior part of gena (behind eye) minutely punctate, punctures almost contiguous. Pronotum with pair of sublateral carinae (Fig. 1e) that diverge both anterad and posterad, nearest to each other at top of collar; anterior portion of each carina convex dorsally, concave subdorsally, and irregularly convex ventrally; pronotal side with deep, narrow sulcus anterad of lobe, with glabrous, unsculptured area dorsally that is delimited by carina anteriorly and dorsally, and by sulcus posteriorly (Fig. 1f). Scutum finely punctate, punctures

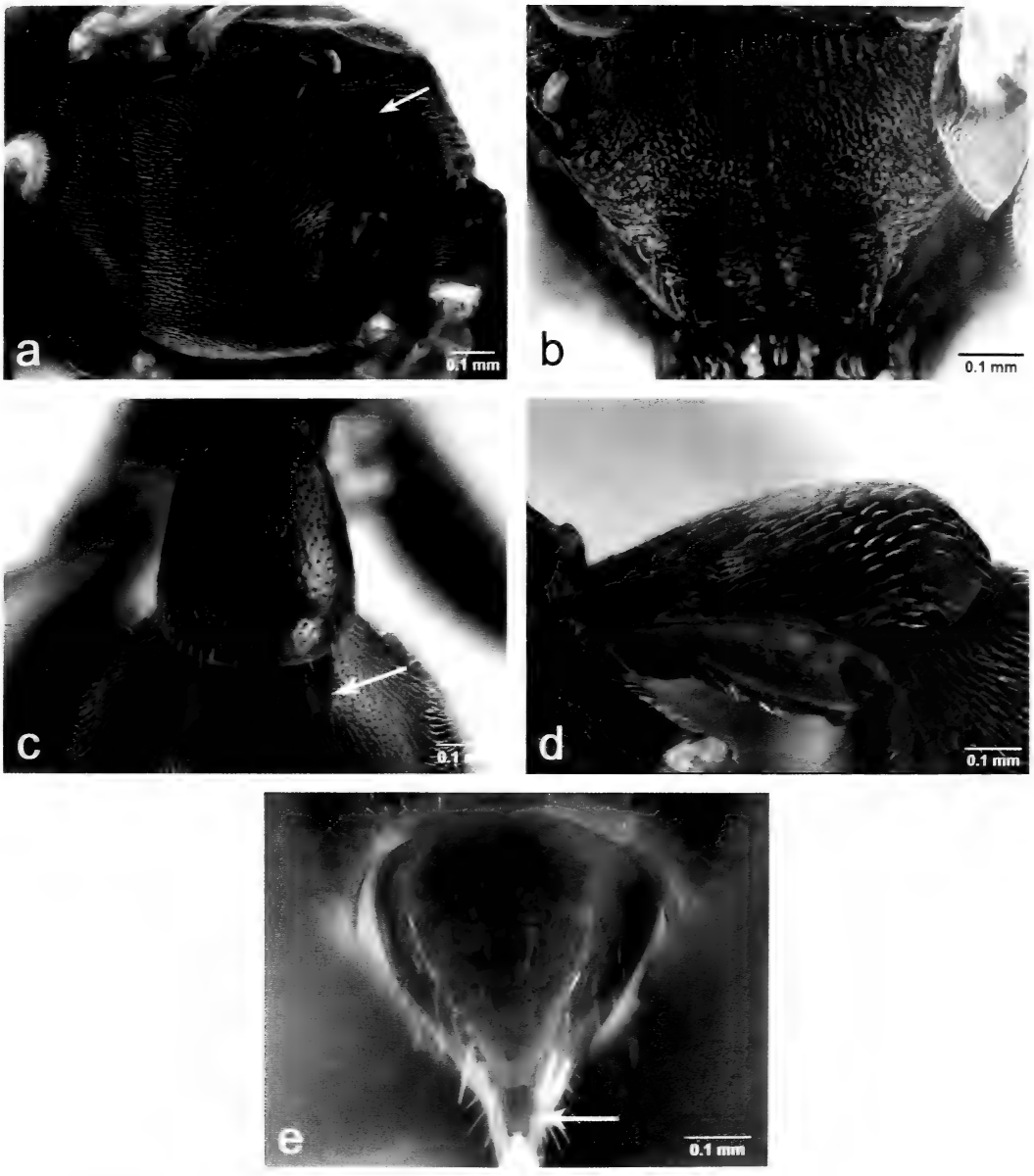

Fig. 2. *Rhopalum nasale* sp. n., ♀: a – thorax and propodeum in lateral view (arrow indicates longitudinal carina on propodeal side); b – propodeal dorsum; c – tergum I and base of tergum II in dorsal vies (arrow indicates reddish brown basal spot on tergum II); d – tergum I laterally; e – pygidial plate in dorsal view (arrow indicates bifid apical process).

averaging about one diameter apart except more than one diameter apart at center; interspaces unsculptured. Mesopleural punctures larger than those on scutum, averaging less than one diameter apart except vertical subdorsal area adjacent to metapleuron unsculptured (Fig. 2a); episternal sulcus crenulate; prepectus rounded. Propodeal enclosure not delimited, microareolate, dull, longitudinally ridged basally, without median sulcus (Fig. 2b); propodeal side with longitudinal

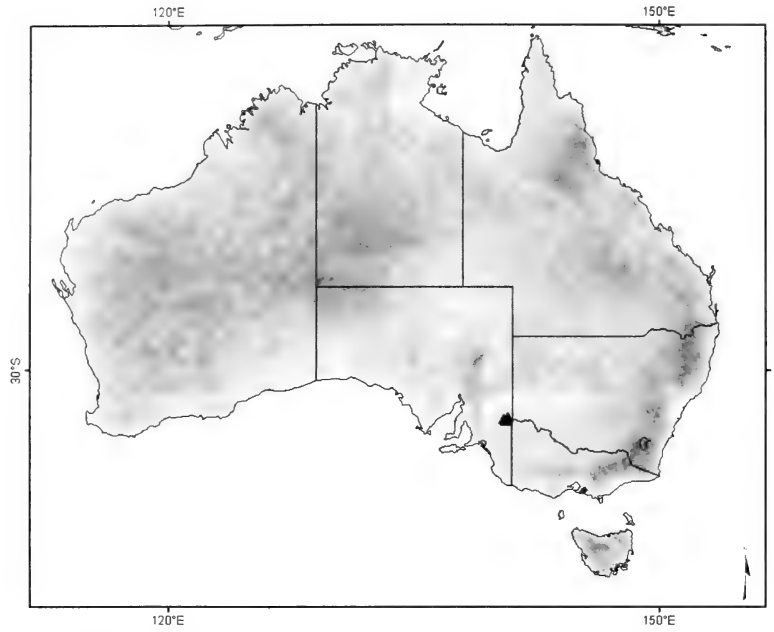

Fig. 3. Collecting localities of *Rhopalum nasale*, sp. n.

carina that joins metapleural flange anteriorly and ends just in front of hindcoxal base (Fig. 2a); area beneath carina unsculptured, shiny, area above carina with traces of longitudinal ridges. Recurrent vein joining submarginal cell at about two thirds of its length. Submarginal cell obliquely truncate. Forebasitarsus with two preapical rake spines that are about as long as basitarsus width. Hindtibia and basitarsi not swollen, hindtibia with well-defined spines. Tergum I relatively short, constricted apically (Fig. 2c), distance between basal tendon and imaginary line connecting spiracles half that of distance between line and apex; posterior half convex in profile (Fig. 2d); tergum length about 1.2 × maximum width, its maximum width 0.4–0.5 × that of tergum II. Tergum II with pair of dark reddish brown, asetose, elongate spots basally (Fig. 2c). Pygidial plate broad basally, gradually narrowing posterad, apically elongate as narrow, bifid process; with well-defined, sparse punctures basally, and conspicuous setae next to process (Fig. 2e).

Head, thorax, propodeum, and gaster black except the following: scape pale yellow, flagellum brown dorsally, light brown ventrally, mandible yellowish brown, dark apically, pronotal lobe pale yellow, tegula pale yellow (partly translucent), humeral plate dark brown mesally, pale yellow along margin. Femora black, forefemur pale yellow apically, largely yellowish brown in some specimens. Foretibia yellow; midtibia brown or yellowish brown, pale yellow basally and apically; hindtibia brown, pale yellow basally and apically. Tarsi yellow.

Male.—Unknown.

Geographic distribution (Fig, 3).—Southeastern South Australia.

Records.—HOLOTYPE: ♀, **AUSTRALIA**: **South Australia**: 32 km N Renmark at 33°53′S 140°44′E, 2–29 Mar 1995, K.R. Pullen (ANIC). PARATYPES (all collected by K.R. Pullen): **AUSTRALIA**: **South Australia**: 32 km N Renmark at 33°53′S 140°44′E, 2–29 Mar 1995 (2 ♀, ANIC; 1 ♀, CAS); 31 km NW Renmark at 33°59′S 140°30′E, 1–30 Mar 1995 (1 ♀, ANIC; 1 ♀,

CAS) and 30 Mar – 2 May 1995 (1 ♀, ANIC; 2 ♀, CAS); 14 km WNW Renmark at 34°07′S 140°37, 28 Feb – 28 Mar 1995, (1 ♀, ANIC).

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I sincerely thank Robert L. Zuparko for his critical comments on the manuscript. Helen K. Court confirmed that the species is undescribed. Erin Prado generated the illustrations using Auto-Montage software package by Syncroscopy, and Lindsay Irving produced the distribution map.

LITERATURE CITED

Leclercq, J. 1997. Hyménoptères Sphécides d'Australie du genre *Rhopalum* Stephens, 1829. *Notes Fauniques de Gembloux* 32: 3–101.

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Colony Social Organisation of *Halictus confusus* in Southern Ontario, with Comments on Sociality in the Subgenus *H. (Seladonia)*

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Abstract.—*Halictus (Seladonia) confusus* Smith is one of the most common bees in North America. Classified as eusocial, its colony social organization is known only from qualitative descriptions of a population in Indiana. We studied the phenology and social behaviour of this bee in the Niagara Region of southern Ontario, using nest excavations, dissections and measurements of adult females, and pan trap samples of foraging bees to elucidate key elements of colony social organisation. The colony cycle in Niagara is typical of temperate-zone halictines, with overwintered foundresses producing a first brood of worker-sized females and a few males, followed by production of Brood 2, consisting of gynes and more males. Many Brood 1 females become reproductive: about one-quarter of Brood 1 females dissected exhibited levels of ovarian development rivalling queens. In contrast, only about one-quarter of Brood 1 females become classically altruistic, sterile workers. High rates of worker reproductivity may result from early queen mortality and supersedure or from the inability of viable queens to control worker behaviour – the average queen-worker size difference was only 5.6%, and queens were not always larger than the workers in their own nests. Comparisons with the Indiana population suggest a geographic component to variation in colony social organisation. Comparisons with other members of the subgenus for which detailed information is available, suggest that in *Seladonia*, as in other eusocial halictines, queen control of worker behaviour depends on the ability of queens to dominate small numbers of small-bodied workers.

Key words.—Halictidae, eusociality, pan traps, sweat bee

In halictine bees, evolutionary transitions from solitary to eusocial behaviour involve two components, a demographic change from univoltine to multivoltine colony phenology, and a behavioural change from maternal care by a lone foundress, to associations between mothers and daughters that raise brood cooperatively (Schwarz et al. 2007). Likewise, evolutionary transitions from eusociality to solitary behaviour, involve the reverse changes in demography and behaviour. Therefore, to understand evolutionary transitions between solitary and social behaviour, it may be particularly fruitful to examine species that exhibit intraspecific variability in either or both of these traits. If the adaptive significance of intraspecific demographic and social variability can be understood, this in turn may help to illuminate patterns observed at higher taxonomic levels, such as differences among subgenera or genera. For instance, socially polymorphic sweat bees such as *Lasioglossum calceatum* and *Halictus rubicundus*, exhibit solitary, univoltine colony cycles in regions with short breeding seasons, and eusocial, bivoltine (actually, double-brooded) colony cycles in regions with long breeding seasons (Sakagami and Munakata 1972; Eickwort et al. 1996). There are also obligately eusocial species, such as *H. ligatus* and *L. malachurum* that exhibit considerable demographic variation, with colonies growing to larger sizes in areas with longer breeding seasons (Michener and Bennett 1977; Knerer 1992). These intraspecific patterns suggest that one

cause of the phylogenetic lability of social behaviour observed in several halictine genera, might be geographic or temporal variability in the harshness of local environmental conditions. Indeed, this prediction is borne out by recent evidence that halictine sociality may have first evolved during a period of global climate warming (Brady et al. 2006), when it would have been possible for univoltine halictine lineages to adopt bivoltine or multivoltine nesting phenologies.

One of the most common eusocial halictines in North America is *Halictus (Seladonia) confusus* Smith, but detailed information on its nesting and social biology are distinctly lacking. Dolphin (1966) studied the nesting biology and social behaviour of this bee in Indiana, USA, from 1963–1965. Although many crucial details were never published, Dolphin suggested that *H. confusus* was demographically and socially polymorphic. His study population contained nests that produced one, two, or three broods, comprising both solitary and eusocial colonies. Eickwort et al. (1996) commented that *H. confusus*, presumed by Knerer and Atwood (1962) to be solitary in boreal Ontario, is social in New York. These tantalizing descriptions suggest that *H. confusus* may exhibit considerable demographic and social variability within and between populations. Understanding the ecological factors associated with such variation is key to investigating hypotheses about the origins and extinctions of sociality in bees.

In this paper, we describe the colony phenology and social organisation of *H. confusus* in southern Ontario. We studied a mixed nesting aggregation of halictine bees, including a small number of nests of *H. confusus*. We also used pan traps to collect adult females and males throughout the breeding season, in order to supplement the information from colony excavations. We show that while *H. confusus* is predominantly eusocial in southern Ontario, there is evidence that large numbers of Brood 1 females become reproductives, rather than sterile workers, suggesting that the population contains a mix of solitary and social strategies, as well as univoltine and bivoltine phenologies. We also compare *H. confusus* to other well studied members of the subgenus *Seladonia*, in order to assess the level of social variation in the subgenus as a whole.

METHODS

Study sites.—All study sites were on or within walking distance of the Brock University Campus in St. Catharines, Ontario (W 79 14′ 57″ N 43 07′11″). We excavated nests from a small nesting aggregation on the north shore of Lake Moodie that contained nests of *Halictus confusus* and *H. ligatus*, and hibernacula of *H. rubicundus*. The nests were on a gentle, south-facing slope. Nests were excavated using a standard technique in which baby powder was blown in at the nest entrances to coat the sides of the burrows, which were then carefully exposed using a kitchen knife. Nests were excavated in the morning before the entrances were open in or in the late afternoon after they were closed. All adult occupants were preserved in 95% ethanol, while brood were placed in wax-lined petri dishes indented with small chambers and brought back to the lab to be raised to adulthood. When these died or emerged as adults, they also were preserved in ethanol.

In addition to nest excavations, we used pan traps to capture flying bees at six sites on the Brock University campus and at the contiguous Glenridge Quarry Naturalization Site; pan trap sites were within 2 km of the nesting aggregation. At each site, 30 pan traps were laid out in an X or other space-filling pattern, alternating yellow, white, and blue pans at 10m intervals, according to standard protocols (Lebuhn et al. 2003). Pans were set out weekly from 1 May to 30 September 2006 at six locations. Bees caught in pan traps were used to determine the timing of important pheno-

logical events, including nest founding, the first and second brood-provisioning phases, and brood emergence from the nests. Since trapping effort was constant over the course of the summer, the numbers of bees caught per week should provide a consistent estimate of bee density and flight activity. Weeks were numbered starting with 1 May 2006 as the beginning of week 1.

Dissections.—Adult bees were measured, assessed for wear, and females were dissected. Body size was measured in terms of head width (HW, the distance across the widest part of the head, including the compound eyes) and length of the forewing costal vein (CVL, from the stigma to the end of the marginal cell); the head widths of pupae were also measured. Queen-worker size difference was calculated as (queen HW – worker HW) / (queen HW) * 100. Mandibular wear (MW) was assessed on a scale of 0–5, with 0 representing completely unworn mandibles with sharp teeth and 5 representing mandibles so worn as to be completely blunted. Wing wear (WW) was also assessed on a scale of 0–5, 0 representing wings with no damage to the margin and 5 representing wings with the margin completely obliterated by nicks and tears. A total wear (TW) score was obtained by summing mandibular and wing wear scores for each female. As wings can be nicked during handling and because unworn mandibles sometimes appear somewhat blunt, bees were categorized as worn if TW≥2.

Females were dissected to determine mating status (whether the spermatheca was opaque, indicating that it was filled with sperm, or transparent, indicating that it was empty) and ovarian development. For the latter, all developing oocytes were assigned fractional scores of ¼, ½, ¾, or 1, indicating their size relative to a fully developed oocyte. These scores were then summed to make a total ovarian development (OD) score. Females with undeveloped or only thickened ovaries but no visible oocytes, were assigned OD scores of 0 or 0.1, respectively.

Caste assignments for females were based primarily on seasonal activity patterns and secondarily on body size, based on the assumption that in Niagara, *Halictus confusus* would exhibit the bivoltine phenology typical of primitively eusocial halictines in the temperate zone (Schwarz et al. 2007). The term 'foundress' is used for overwintered females that excavate burrows and forage in spring. The term 'worker' is used for Brood 1 females. After workers emerge, a foundress may be referred to as a 'queen'. A gyne is a Brood 2 female that will overwinter and found a nest the following spring. A 'replacement queen' is a Brood 1 worker that takes over the role of queen from a dead or moribund foundress.

Caste designations were assigned to females caught in pan traps and nests based on the following criteria. When newly emerged from hibernation, foundresses are unworn, becoming progressively more worn as they excavate nests and provision brood cells. Thus in midsummer, we can use wear scores to distinguish worn, late-foraging foundresses from unworn, early workers. In late summer, we used wear scores to distinguish worn workers from unworn gynes. Ovarian development was not used to assign caste designations, thus avoiding teleological complications in comparisons of the reproductive status of queens and workers. All adult females caught in nest excavations, as well as the majority of pan-trapped females (all foundresses, all gynes, and 100 workers) were measured and dissected.

Interspecific comparisons.—To examine interspecific variation in the subgenus *Seladonia*, the best approach would be to map these data onto a phylogeny and then investigate evolutionary correlations among the various traits (Felsenstein 1988). However, in the absence of a phylogeny, several authors have used

principal components analysis (PCA) to quantify social variation among halictine bees and to construct hypotheses about how social traits co-evolve (Michener 1974; Breed 1976; Packer and Knerer 1985). Hypotheses constructed without a phylogenetic framework, can then be tested when an appropriate phylogeny becomes available. For comparisons among *Seladonia* populations, we used five variables commonly assessed in studies of halictine sociality: the proportion of males in Brood 1, the number of workers per nest (or the number of females produced in Brood 1), the proportion of workers with developing ovaries, the proportion of mated workers, and the queen-worker size difference based on head width. Values for each variable were either taken directly from the literature, recalculated from figures in the literature, or recalculated as midpoints of ranges. The initial PCA was based on all five variables, retaining factors with eigenvalues ≥ 1.0. However, since Kaiser's Measure of Sampling Adequacy (MSA) with all five variables had a value of only 0.55, the variable with the lowest communality measure (proportion of workers mated) was dropped from the PCA. With the remaining four variables, MSA=0.77, which exceeds the 0.6 criterion. We present both factor loading scores (the degree to which each variable influences the inferred factors) and communality estimates (a reliability score which estimates the proportion of variance in each variable that is jointly explained by all three factors). Note that the interspecific comparisons based on the PCA are presented in the last section of the Discussion, rather than in the Results.

RESULTS

Colony cycle.—In southern Ontario, *H. confusus* exhibits a foraging and nesting cycle typical of temperate zone, eusocial halictines (Fig. 1). The beginning of the foundress foraging period was marked by the capture on 1 May 2006 of an overwintered foundress. Since only two foundresses were captured in the first 3 weeks, they likely emerged from overwintering diapause in late April and early May, but mostly did not venture out of their nests until mid-May when the weather became more suitable. Foundresses continued to be caught in pan traps for about eight weeks, with the last foraging foundress caught on 28 June (week 9). Most foundress foraging and provisioning of Brood 1 probably occurred from weeks 4–8.

There was a sharp increase in the number of females caught beginning in week 8, many of them small and unworn. Large numbers of brood continued to be caught until week 11 after which pan trap catches declined. Weeks 8–11 thus represented the peak emergence period of Brood 1 and the peak worker foraging period. In the population as a whole, there was no quiescent period between the foundress and worker foraging periods, as the first Brood 1 females (which were small and unworn) were caught on 21 June (week 8) when clearly identifiable foundresses (large, worn females) were still flying. The first Brood 1 males were caught in week 9, so emergence of Brood 1 was slightly protogynous. Based on pan trap samples from weeks 8–11, the proportion of males in Brood 1 was about 1.9%.

The emergence of Brood 2 was marked by a small increase in trap numbers of both males and females beginning around week 15 (7–13 August), with the majority of Brood 2 emerging between weeks 18–20 (Fig. 1). Week 15 was marked not only by the appearance of large, unworn females from Brood 2, but also by the last capture of small, unworn females deemed to be from Brood 1, suggesting that the last of Brood 1 had emerged as adults by week 15. The worker foraging period was mostly finished by week 17, although one small, worn forager was captured in week 19. Based on pan trap samples from weeks 12–20, the proportion of males produced in Brood 2 was about 22%.

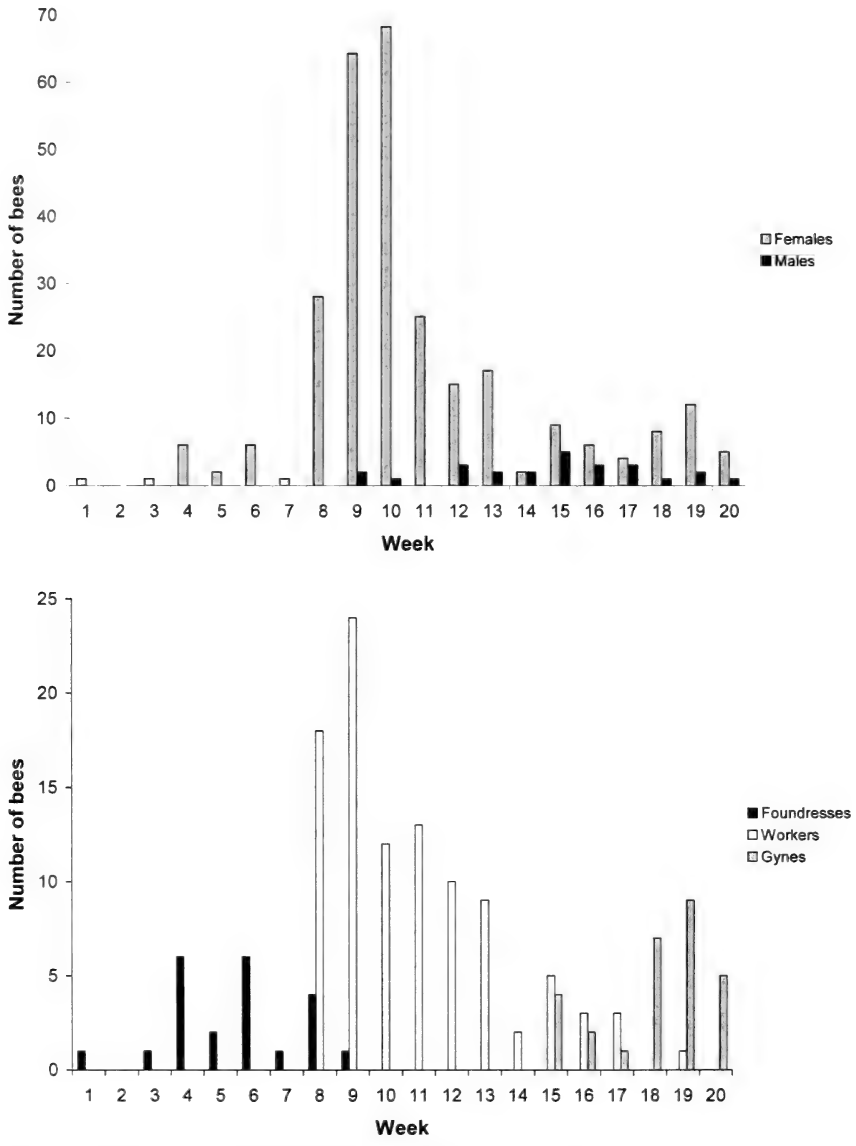

Fig. 1. Flight phenology of *H. confusus* based on 2006 pan trap samples. Top: Phenology of all adult bees collected in pan traps. The sharp rise in numbers of females caught in mid-summer (beginning with week 8) corresponds with the first appearance of males in week 9, suggesting that this mid-summer peak marks the emergence of Brood 1. Bottom: Timing of female caste emergence based on size and wear patterns. Foundresses emerge in early May and continue to forage until mid-summer, slightly overlapping with females of Brood 1 (workers). Gynes first begin to appear in week 15. Sample size differences between top and bottom graphs are because only 100 of the workers caught in pan traps was dissected.

Nest contents.—Fourteen nests were excavated in total, four prior to worker foraging and ten later in the summer. A single nest excavated during week 5 contained a foundress and three brood cells, comprising one provision mass with an egg, one medium larva, and one early stage pupa (damaged during excavation). In week 8, three nests were excavated. The first nest contained a queen and 3 worker pupae; the second nest contained a queen, one worker with worn mandibles, three worker pupae, and an unfinished provision mass; and the third nest contained a

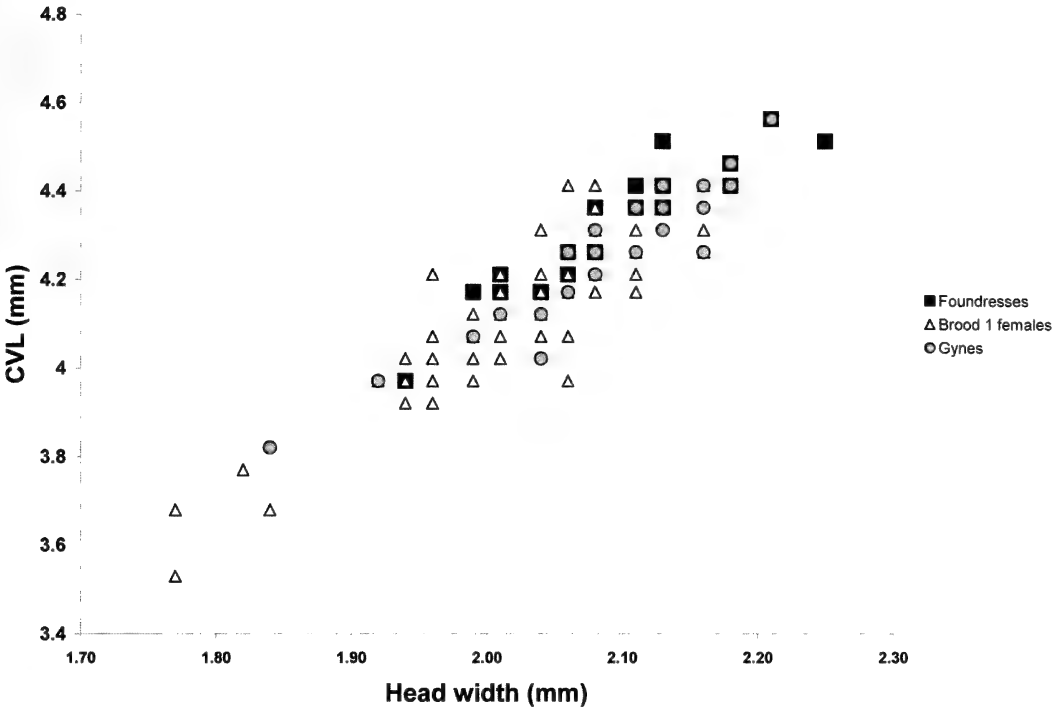

Fig. 2. Body size distributions of pan trapped *H. confusus* foundresses, Brood 1 females, and gynes based on head width and wing length (measured as costal vein length, CVL).

queen, two workers with worn mandibles, five female pupae, four male pupae, one larva that had completely consumed its provisions, one provision mass with an egg, and one unfinished provision mass. The average brood size of these three nests was 6.3, and 22% of the sexable brood were males. The latter figure is considerably higher than the estimate of 2% males based on pan traps and implies that males are under-represented in pan trap samples. The presence of workers in these nests, together with evident age gaps between younger (eggs and larvae) and older brood (pupae), indicates that the younger brood were from Brood 2 and that within individual nests there is a hiatus or quiescent period between Broods 1 and 2.

Ten nests were excavated during weeks 17 and 18. None contained a live foundress (queen). Four nests contained a total of six worn adult workers. Dissections showed that three of these had undeveloped ovaries but were mated (the other three were poorly preserved and could not be scored). The youngest brood were pigmented pupae, so it is likely that older adult brood had already dispersed from their natal nests. The average number of brood per nest had fallen to 3.4, and only 3% of sexable brood were males (as compared with 22% in pan trap samples). Of the 23 gynes in these nests, 21 had mated and 20 had noticeable fat deposits in their abdomens. There was no evidence that gynes had begun digging hibernacula below their natal nests.

Female body size.—Foundresses and gynes were very similar in size, and both were larger than Brood 1 females; there was no indication of a body shape difference between the gyne and worker castes (ANOVA, $F=8.56$, $df=2,147$, $p=0.0003$; Fig. 2 and Table 1). Queen and worker size measurements were available for two nests (both excavated in week 8). In Nest 166, the queen was larger than all four of her workers (adults and pupae), and the

Table 1. Caste characteristics of females caught in pan traps. Smaller sample sizes for ovarian and mating success reflect technical difficulties with dissections. Females were considered as worn if MW≥2 or WW ≥2, and ready to lay if they contained at least one, ¾-developed oocyte. Statistical comparisons of foundresses versus Brood 1 females were based on ANOVA (F statistics), Kruskal-Wallis tests (H statistics), and chi square tests.

Trait	Foundresses (n=22)	Brood 1 females (n=100)	Gynes (n=28)	Statistical comparison (foundresses vs. Brood 1 females)
HW (mm ± 1 sd)	2.09 ± 0.07	2.03 ± 0.08	2.09 ± 0.09	F=11.22, df=1, p=0.0011
CVL (mm ± 1 sd)	4.33 ± 0.16	4.15 ± 0.16	4.25 ± 0.17	F=21.91, df=1, p=0.0001
Proportion with worn mandibles	13/22 (60%)	32/100 (32%)	0/28 (0%)	χ^2=5.68, df=1, p<0.0171
Proportion with worn wings	1/22 (4%)	8/100 (8%)	0/28 (0%)	χ^2=0.32, df=1, n.s.
OD score (mean and range)	1.82 (0.5–2.75)	0.58 (0–2.25)	0.03 (0–0.1)	F=21.64, df=1, p=0.0001
Proportion ready to lay	16/22 (73%)	23/100 (23%)	0/28 (0%)	χ^2=20.50, df=1, p<0.0001
Proportion mated	18/18 (100%)	39/80 (49%)	17/28 (61%)	χ^2=15.86, df=1, p<0.0001

queen-worker size difference was 7.2% based on head width and 9.9% based on wing length. In Nest 168 the situation was very different. The small, worn queen was the same size as one worker, but smaller than four others (two worker pupae were not measured), resulting in a queen-worker size difference of negative 4.0% based on head width and negative 1.2% based on wing length. Since the above calculations were based on females from only two nests, we also calculated the average size differences for pan trapped foundresses and workers: these were 2.9% based on head width and 4.2% based on wing length.

Wear and reproductive status.—Based on females caught in pan traps, foundresses sustained higher levels of mandibular wear than Brood 1 females (Table 1). Few females had worn wings, but one notable exception was the queen of Nest 168 (excavated in week 8), with a total wear score of 10; this female was so much more worn than other bees examined that she might have been nesting for the second time, having overwintered twice.

Potential for reproduction by foundresses and Brood 1 females is compared in Table 1. All foundresses dissected (18 from pan traps and 4 from nest excavations) had sperm in their spermathecae, whereas only about half of the Brood 1 females examined had sperm in their spermathecae. Foundresses also had significantly higher OD scores than Brood 1 females, and were more likely to have at least one oocyte ready or almost ready to lay.

Four types of 'workers' could be distinguished based on wear and ovarian development, each category comprising about 25% of the total among Brood 1 females caught in pan traps (Table 2). The first group comprised unworn (TW ≤ 1) females with undeveloped ovaries (OD ≤ 0.1); these were evidently newly eclosed workers. The second group were worn (TW≥2) but exhibited no ovarian development, suggesting that they were engaged in nest maintenance or foraging activities, but were not laying eggs; these bees were categorized as sterile altruists. The third group were queen-like, at least in terms of their readiness to lay eggs: most of these (18.3% of all Brood 1 females) contained at least one fully developed oocyte ready to lay, while the remainder contained at least one ¾-developed oocyte. The remaining group of Brood 1 females can be categorized as potentially reproductive workers, exhibiting a distinct degree of wear and some ovarian development, but not sufficient to be ready to lay eggs. These workers likely provision both queen-laid and sometimes their own eggs, and could also be referred to as 'partial altruists'.

Table 2. Comparison of ovarian development and wear in Brood 1 females collected in pan traps. Unworn females had total wear (|TW = MW + WW) scores of 0 or 1, whereas worn females had TW ≥ 2. Percentages represent proportions of the total (n=93). Four categories of workers can be distinguished: 'newly eclosed' females that have not yet accumulated either wear or ovarian development; 'altruists', worn, working females with no ovarian development, 'queen-like' females with very high rates of ovarian development, and the remainder, with intermediate levels of wear and ovarian development, that can be referred to simply as 'workers'.

Size of largest oocyte	Unworn	Worn	Total
None	24 (25.8%) Newly eclosed	21 (22.6%) Altruists	45 (48.4%)
¼	6 (6.5%) Potentially reproductive workers	10 (10.8%) Potentially reproductive workers	16 (17.2%)
½	2 (2.2%) Potentially reproductive workers	7 (7.5%) Potentially reproductive workers	9 (9.7%)
¾	2 (2.2%) Queen-like	4 (4.3%) Queen-like	6 (6.5%)
Full	6 (6.5%) Queen-like	11 (11.8%) Queen-like	17 (18.3%)
Total	**40 (43.0%)**	**53 (57.0%)**	**93 (100%)**

Roughly half of Brood 1 females caught in pan traps were mated (this value underestimates the rate of worker mating as it includes newly eclosed individuals that might not yet have met males). Those with developed ovaries (OD scores ≥ 0.25) were more likely to have mated than females with no ovarian development (Likelihood ratio chi-square, G=14.46, df=1, p<0.0001; Table 3), and this was significant even when newly eclosed females are excluded from consideration (Likelihood ratio chi-square, G=4.978, df=1, p=<0.0257). Degree of ovarian development was not correlated with body size (head width: ρ=−0.01, n=95, n.s.; costal vein length: ρ=0.02, n=95, n.s.), even when females assumed to be newly eclosed were excluded.

Table 3. Association between mating status and ovarian development in 80 *H. confusus* Brood 1 females collected from pan traps. The minimum OD score for a female with at least one visibly developed oocyte is 0.25. Statistical analysis is given in the text.

	Mating status		
Ovarian score	Unmated	Mated	Total
OD ≤ 0.1	29 (36%)	11 (14%)	40 (50%)
OD ≥ 0.25	12 (15%)	28 (35%)	40 (50%)
Total	41 (51%)	39 (49%)	80 (100%)

Comparisons of queens to the workers in their own nests suggest that queens dominated but did not completely monopolize oviposition. Nest 166 was excavated on 22 June 2006 (week 8), and contained a queen, one adult worker, three worker pupae, and an unfinished provision mass. The queen (TW=6) had an OD score of 2.75, including three ¾-developed oocytes but no fully developed oocytes. The adult worker was slightly worn (TW=3) and had probably collected the pollen provisions. She was mated and her OD score was 0.75, comprising a single ¾-developed oocyte. Evidently, the queen or the worker could have had a mature oocyte to lay by the time the provision mass was completed. In nest 168, excavated on the same day, the queen, which was the most worn bee we found (TW=10) had an OD score of 1.75, comprising one fully developed and one ¾ developed oocyte. Of the two adult workers in the nest, the one smaller than the queen was worn (TW=3), was unmated and had only slightly thickened ovaries,

while the one larger than the queen was a bit less worn (TW=2), was mated and had an OD score of 1.0, including a ¾-developed oocyte. Since both workers were worn, they were probably both foragers, but only the former would be categorized as a 'sterile altruist'.

Dissections of pan-trapped bees revealed that 4/22 foundresses, 14/100 workers, and 0/28 gynes had been parasitized by conopid larvae, many of them large enough to fill their host's abdominal cavity. Perhaps noteworthy is the fact that two foundresses caught in pan traps in late May contained conopid parasites so large as to prevent any ovarian development. Two gynes from nests excavated in late August were also parasitized by conopids.

DISCUSSION

Phenology and colony social organization in southern Ontario.—In southern Ontario, *Halictus confusus* exhibits a colony cycle which in broad terms, is typical of eusocial, temperate zone halictines (Schwarz et al. 2007). In spring, large females excavate new burrows, then provision a first brood that is composed mainly of workers and a few males. Foundresses cease provisioning shortly after the summer solstice, and then are replaced as small Brood 1 females emerge from their nests, and begin to provision Brood 2. Most individuals of Brood 2 are provisioned by the end of July, emerging as adults until mid-September. Since many queens evidently survive until mid-summer when workers emerge and begin foraging, this suggests that many surviving colonies become eusocial. As in other halictine bees (Packer 1992; Richards et al. 1995; Paxton et al. 2003; Richards et al. 2005), foundress queens likely produce the majority of Brood 2 gynes and males. Dissections indicate that queens have higher reproductive potential on average, and that workers can have high rates of ovarian development even in queen-right nests. The relatively large numbers of unworn workers with highly developed ovaries caught in midsummer, suggest that when foundress queens die or become moribund, they are replaced by one of their Brood 1 daughters, and colonies become parasocial.

Halictus confusus nests are probably founded haplometrotically (singly), as the few (n=4) nests that we excavated in spring each contained a single foundress. Haplometrotic nest founding is more likely when gynes overwinter away from the summer nesting sites, while pleometrotic co-founding is more likely when gynes overwinter together near the nesting site (Packer 1993; Richards and Packer 1998). Atwood (1933) and Dolphin (1966) suggested that *H. confusus* gynes overwinter away from their natal nests, and nests that we excavated near the end of August contained newly eclosed gynes but no evidence that these were preparing hibernacula. Nevertheless, pleometrosis cannot be ruled out entirely, as we did excavate a nest in which the queen was smaller than most of her workers. In eusocial halictines, queens control worker body size by manipulating the size of larval provision masses (Richards and Packer 1994), making workers that are almost always smaller than themselves (Richards and Packer 1996), so the finding of a very worn queen smaller than some of her own workers suggests that she may have been a small subordinate co-foundress that outlived a larger dominant (Packer 1986; Richards and Packer 1996).

In *H. confusus*, it appears that females produced in Brood 1 may adopt one of three or four different reproductive options. Some Brood 1 females become classical, sterile, altruistic workers that provide provisions for eggs laid by the queen but produce no offspring of their own. Some Brood 1 females become reproductive workers, a category that comprises workers that collect provisions upon which a queen will lay eggs, but whose developing ovaries suggest that they also will lay eggs given the chance. For many,

perhaps most, of these 'reproductive workers', egg-laying opportunities may never present themselves, so observations that many workers have ovarian development do not necessarily translate into high rates of worker oviposition in queen-right nests (Packer 1992; Packer and Owen 1994). Nevertheless, worker maternity in queen-right nests does occur even in strongly eusocial halictines (Richards et al. 2005) so in *H. confusus*, it is likely that at least some reproductive workers, successfully produce brood, even in queen-right nests. The workers with queen-like ovaries would almost certainly be egg-layers, and most likely were replacement queens. We found no new *H. confusus* nests in midsummer after the first emergence of workers, so it is unlikely that workers with queen-like ovaries were Brood 1 females that leave their natal nests to found new nests in summer, either solitarily or communally (Sakagami and Hayashida 1968; Richards et al. 2003).

A curious feature of the flight phenology of *H. confusus* in Niagara was the small number of females captured in late summer, following emergence of Brood 2, compared to the far greater numbers captured in midsummer following emergence of Brood 1. Several explanations present themselves. First, gynes might have been under-represented in pan traps relative to workers, due to changes in flower and forage availability. Pan traps are known to capture relatively fewer foragers when flower availability increases (Roulston et al. 2007). Pan traps may therefore be less attractive to gynes (and males) because they are not active provisioners, and because flower availability may be higher after midsummer than before. It is also possible that the pattern of lower gyne than worker densities is real. If so, then one explanation would be high rates of colony failure prior to worker emergence (Richards and Packer 1995a). Another possibility is that some Brood 1 females leave their natal nests to enter diapause preparatory to becoming foundresses the following spring, a phenomenon known as differential diapause and well documented in *Halictus rubicundus* (Yanega 1988). It would be interesting to compare pan trap phenologies with detailed nesting data for several species with different colony cycles, in order to assess concordance in the patterns inferred using the two types of information.

Geographic variation in colony social organisation.—Demographic differences between Indiana (Dolphin 1966) and Ontario likely stem from differences in the timing of important colony events. In Indiana, foundresses emerge from hibernation as early as March or April and complete foraging by late May or early June, with first brood workers emerging from mid-May to early June, second brood workers emerging in mid to late July, and gynes emerging from mid-July to early September. In Ontario, foundresses emerge from hibernation in late April and forage until about the third week of June, with workers emerging from about June until the end of July, and gynes from mid-August to mid-September. This suggests that Dolphin's population experienced a breeding season about three weeks longer than we observed in Niagara in 2006. In Indiana, many colonies produced two worker broods. This seems unlikely for our Ontario population, as pan traps suggested that the majority of Brood 1 workers emerged between weeks 8 and 13, a six week period that is only slightly shorter than the period encompassing most foundress foraging activity between weeks 3 and 9. However, the intriguing, small peak in captures of females around weeks 14 and 15, might have signaled the emergence of a secondary worker brood. We did capture some small, unworn females at this time, which we categorized as gynes, but which were possibly workers. The ability to interpolate a second worker brood in areas with long enough breeding is well known in *Lasioglossum malachurum*, which produces a

single worker brood at the northerly edge of its range, but two or three worker broods in warmer environs and at the southerly extent of its range (Knerer 1992; Wyman and Richards 2003; Weissel et al. 2006). *Augochlorella striata* apparently has sufficient behavioural flexibility that it can respond to annual weather conditions by producing workers when conditions will create a long breeding season or omitting workers and producing gynes directly when conditions will create a short breeding season (Packer 1990).

Another phenological difference between Ontario and Indiana *H. confusus* was the absence in Ontario of a distinct quiescent period between the foundress and worker foraging periods. Not only was there no quiescent period, but there was at least a week of overlap in the foraging periods of foundresses and workers. This was somewhat unexpected as a quiescent period between the two flight periods is typical of many primitively eusocial halictines, even when multiple worker broods are produced. The overlap suggests an extended rather than a synchronized period of nest establishment in spring, with the result that some foundresses continued to provision brood as long as 2–3 weeks after the earliest foundresses had completed their first broods. However, lack of synchronicity may not be typical of Niagara *H. confusus*, if weather conditions in the spring of 2006 led to early nesting activity by some foundresses. In *H. ligatus* nesting near Victoria, Ontario, unusually warm conditions in spring 1991 led to an extended nest founding period that obliterated the usually predictable hiatus between the foundress and worker foraging periods (Richards and Packer 1995b).

Sociality in the subgenus Seladonia.—Table 4 compares *H. confusus* to other species of the subgenus *Seladonia* for which sufficiently detailed sociobiological data are available. All members of the subgenus are thought to be primarily social (Packer et al 2007), including *H. tumulorum* which originally was thought to be solitary (Sakagami 1974). For three species, *H. confusus*, *H. hesperus*, and *H. lucidipennis*, social data are available for intraspecific comparisons between populations. Variation between populations suggests considerable geographic variability in rates of worker mating and ovarian development. In *H. confusus*, there seems to be a link between breeding season length and colony size, as additional worker broods were interpolated before the gyne brood in Indiana. A similar pattern seems to occur in *H. lucidipennis*, which produces more workers in southern than in northern India (Batra 1966).

In the absence of a phylogeny for behaviourally known members of the subgenus *Halictus (Seladonia)*, we used principal components analysis (PCA) to quantitatively explore correlations among five sociobiologically important variables (Table 4). Only six populations (*H. confusus* from Ontario, *H. aerarius*, *H. hesperus* from Mexico, *H. lucidipennis* from northern and southern India, *H. tumulorum* from France, and *H. vicinus* from southern India) could be included as basic information was missing for the remainder. We did not attempt a hierarchical analysis to distinguish between inter and intraspecific variation, although it is possible that intra- and interspecific patterns might differ (this could eventually be tested phylogenetically). As noted in the methods, proportion of workers mated explained little of the variation among populations and was dropped from the analysis. Its lack of explanatory power could stem either from difficulties in data collection (Table 4 suggests considerable variability depending on when workers are captured for dissection) or could reflect a genuine lack of relevance to explaining behavioural variation among populations. The remaining four variables together explained 76% of variability among populations, ranked along a single eigenvector (principal component) with eigenvalue = 3.051. The

Table 4. Sociobiological comparison of *H. confusus* and other *Halictus (Seladonia)* species. Figures in boldface were used for the principal components analysis presented in Table 5. Where the figure '1+' is given for the number of worker broods, it is likely that worker brood production is extended such that early workers provision subsequent worker brood. Figures in parenthesis were inferred as noted.

Species	Location (reference)	No. worker broods	Males in Brood 1 (%)	No. workers (Brood 1)	Workers with developed ovaries (%)	Workers mated (%)	Queen-worker size difference based on head width (%)
confusus	Ontario (this study)	1	**22** (based on excavated nests)	**4.9**	**44.2** (18.3 with mature oocyte)	**51.3**	Nest bees: **5.6** Pans: 4.0
confusus	Indiana (Dolphin 1966)	1–2	13.8	2–3 foraging per day	-	-	Brood 1: 4.8 Brood 2: 1.9
aerarius	Japan (Sakagami and Fukushima 1961)	1	**(0)**[1]	**>10**	**0**	**0**	**17.1** (recalculated based on Fig. 2)
hesperus	Mexico (Packer 1985)	-	**0**	**6.5**	**9.3**	**5.6**	**23.4**
hesperus	Panama (Brooks and Roubik 1983)	1+	0	97–149 (probably not first brood)	4.7	10.7	19.7
hesperus	Costa Rica (Wille and Michener 1971)	1+	0	37.8	25	0.0	not available (10.6% based on wing length)
lucidipennis	southern India (Batra 1966)	1+	**61.7**	**21**	**51.1**	**12.8**	**>2.8**
lucidipennis	northern India (Batra 1966)	1+	**76.6**	**14.7**	**39.1**	**26.1**	**(2.8)**[2]
lutescens	Costa Rica (Wille and Michener 1971)	1+	>0	187.5	26	31	-
lutescens	Guatemala (Sakagami and Okazawa 1985)	1+	0	>600	18	-	-
tripartitus	California, USA (Packer et al. 2007)	1+	-	-	34–55	13.7–34.2	5.1 (early workers)
tumulorum	France (Plateaux-Quénu and Plateaux 1994)	1	**30**	**3** (1 nest)	**9** (5% with a mature oocyte)	**90**	8.8 (foragers) 15.0 (1 nest) **(11.9)**
tumulorum	Japan (Sakagami and Fukushima 1961, Sakagami 1974)	0–1	-	10–20 females per nest	-	-	-
vicinus	southern India (Batra 1966)	1+	**29.4**	**18**	**24.1**	**10.3**	**7.8**

[1] Since no workers were mated, it was inferred that no males were available.
[2] Used same value as for northern Indian population.

Table 5. Results of principal components analysis for 7 populations of *Seladonia* (*H. confusus* from Ontario, *H. aerarius*, *H. hesperus* from Mexico, *H. lucidipennis* from northern and southern India, *H. tumulorum* from France, and *H. vicinus*) compared in Table 4. Only the first principal component (eigenvalue = 3.051) was retained based on the criterion that eigenvalue ≥ 1.000.

Variable	Factor 1 loading score	Communality estimate
Proportion of males in worker brood	0.917	0.846
Number of workers per nest	0.723	0.994
Proportion of workers with developed ovaries	0.897	0.866
Queen-worker size difference	−0.940	0.932

results showed that about 76% of the variation among these populations and species was explained by this principal component (Table 5). The factor loading scores indicate strong negative correlations between queen size relative to workers versus number of workers produced in Brood 1 (which are usually provisioned by the queen herself), the proportion of males in this brood, and rates of worker ovarian development. Taken together, this suggests that in the subgenus *Seladonia*, that sociality, especially the degree of queen-worker reproductive skew, is related to the ability of queens to dominate workers. This is a well-known pattern in eusocial halictines, in which greater skew occurs when queens must contend with fewer and/or smaller workers (Schwarz et al. 2007).

Two species not included in the PCA, *H. hesperus* and *H. lutescens* (Wille and Michener 1971; Brooks and Roubik 1983; Sakagami and Okazawa 1985), can develop extraordinarily large colony sizes numbering in the many hundreds. It seems unlikely that such large colonies result from egg production by only one female (but see Plateaux-Quénu (1962) for an important exception), and more likely these colonies contain multiple egg-layers. This suggests that queens might dominate oviposition early in the colony cycle, but eventually are superseded or lose control of worker reproduction as colonies grow. This switch to 'worker' reproduction would allow colonies to grow even larger and would also blur the distinction between queens and reproductive workers. Interestingly, queen supersedure was suggested by Dolphin (1966) for *H. confusus* in areas with colony cycles longer than average queen lifespan. Another *Seladonia* species not included in our comparative analysis due to a lack of nesting data, is *H. lanei*. In this species, the degree of queen-worker size dimorphism is extraordinary, with queens being as much as eight times larger than their workers (Janjic and Packer 2001). This exceptional degree of size differentiation may allow queens to dominate oviposition and effectively control worker behaviour even with large colony sizes. Clearly, more behavioural data on more species in this interesting subgenus are required for us to better understand how queen control and reproductive skew co-evolve.

CONCLUSION

Across *Halictus (Seladonia)*, all species thus far studied exhibit sociality (Packer et al. 2007). However, the social behaviour of *H. confusus* suggests a high degree of intraspecific social variability. Moreover, specimens have been collected as far north as Alaska and Finland, where breeding seasons may be too short to allow foundresses to produce workers, so there is a high probability that at least some *Seladonia* populations or species are monomorphically solitary. Social polymorphism, co-occurrence of solitary and social nests within populations, might represent an ecological intermediate between solitary populations in areas with very short breeding seasons and social populations in areas with longer seasons (Packer 1990). Behaviourally, variation in the strength of dominance hierarchies and in queen-worker reproductive skew may also be

taken as evidence of intermediate stages in social evolution. The behavioural variability that we have observed in *H. confusus* and which others have observed in other members of the subgenus, make it likely that further study of *H. (Seladonia)* populations will shed considerable light on the ecological and evolutionary factors that promote social transitions in halictine bees. Species like *H. confusus*, with wide geographic ranges encompassing very short to relatively long breeding seasons, would be ideal candidates for studies of reproductive skew using microsatellite markers to specifically investigate the circumstances under which queens lose control of worker reproduction.

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LITERATURE CITED

Atwood, C. E. 1933. Studies on the Apoidea of western Nova Scotia with special reference to visitors to apple bloom. *Canadian Journal of Research* 9: 443–457.

Batra, S. W. T. 1966. Nests and social behavior of halictine bees of India (Hymenoptera: Halictidae). *Entomological Society of India* XXVIII, part III: 375–393.

Brady, S. G., S. Sipes, A. Pearson, and B. N. Danforth. 2006. Recent and simultaneous origins of eusociality in halictid bees. *Proceedings of the Royal Society B-Biological Sciences* 273: 1643–1649.

Breed, M. D. 1976. The evolution of social behavior in primitively social bees: A multivariate analysis. *Evolution* 30: 234–240.

Brooks, R. W. and D. W. Roubik. 1983. A halictine bee with distinct castes: *Halictus hesperus* (Hymenoptera, Halictidae) and its bionomics in central Panama. *Sociobiology* 7: 263–282.

Dolphin, R. E. 1966. *The Ecological Life History of Halictus (Seladonia) confusus Smith (Hymenoptera: Halictidae)*. PhD. Purdue University.

Eickwort, G. C., J. M. Eickwort, J. Gordon, and M. A. Eickwort. 1996. Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology* 38: 227–233.

Felsenstein, J. 1988. Phylogenies and quantitative characters. *Annual Review of Ecology and Systematics* 19: 445–471.

Janjic, J. and L. Packer. 2001. New descriptions of *Halictus (Seladonia)* from the New World (Hymenoptera: Halictidae). *Journal of Hymenoptera Research* 10: 55–75.

Knerer, G. 1992. The biology and social behaviour of *Evylaeus malachurus* (K.) (Hymenoptera; Halictidae) in different climatic regions of Europe. *Zoologische Jahrbuch Systematik* 119: 261–290.

——— and C. E. Atwood. 1962. An annotated check list of the non-parasitic Halictidae (Hymenoptera) of Ontario. *Proceedings of the Entomological Society of Ontario* 92 (1961): 160–176.

Lebuhn, G., T. L. Griswold, R. L. Minckley, S. Droege, T. H. Roulston, J. H. Cane, F. D. Parker, S. L. Buchmann, V. J. Tepedino, N. M. Williams, C. Kremen, and O. Messenger. 2003. A standardized method for monitoring bee populations - the bee inventory (BI) plot, draft 2003. http://online.sfsu.edu/~beeplot/pdfs/Bee%20Plot%202003.pdf.

Michener, C. D. 1974. *The Social Behavior of the Bees, A Comparative Study*. Harvard University Press, Cambridge, Massachusetts.

——— and F. D. Bennett. 1977. Geographical variation in nesting biology and social organization of *Halictus ligatus*. *University of Kansas Science Bulletin* 51: 233–260.

Packer, L. 1985. Two social halictine bees from southern Mexico with a note on two bee hunting philanthine wasps (Hymenoptera: Halictidae and Sphecidae). *Pan-Pacific Entomologist* 61: 291–298.

———. 1986. Multiple-foundress associations in a temperate population of *Halictus ligatus* (Hymenoptera; Halictidae). *Canadian Journal of Zoology* 64: 2325–2332.

———. 1990. Solitary and eusocial nests in a population of *Augochlorella striata* (Provancher) (Hymenoptera: Halictidae) at the northern edge of its range. *Behavioral Ecology and Sociobiology* 27: 339–344.

———. 1992. The social organisation of *Lasioglossum (Dialictus) laevissimum* (Smith) in southern Alberta. *Canadian Journal of Zoology* 70: 1767–1774.

———. 1993. Multiple-foundress associations in sweat bees. Pp. 215–233 *in:* Keller, L. ed. *Queen Number and Sociality in Insects*. Oxford University Press.

———, A. I. D. Gravel, and G. LeBuhn. 2007. Phenology and social organization of *Halictus (Seladonia) tripartitus* (Hymenoptera : Halictidae). *Journal of Hymenoptera Research* 16: 281–292.

——— and G. Knerer. 1985. Social evolution and its correlates in bees of the subgenus *Evylaeus* (Hymenoptera: Halictidae). *Behavioral Ecology and Sociobiology* 17: 143–149.

——— and R. E. Owen. 1994. Relatedness and sex ratio in a primitively eusocial halictine bee. *Behavioral Ecology and Sociobiology* 34: 1–10.

Paxton, R. J., E. Arevalo, and J. Field. 2003. Microsatellite loci for the eusocial *Lasioglossum malachurum* and other sweat bees (Hymenoptera, Halictidae). *Molecular Ecology Notes* 3: 82–84.

Plateaux-Quénu, C. 1962. Biology of *Halictus marginatus* Brullé. *Journal of Apicultural Research* 1: 41–51.

——— and L. Plateaux. 1994. Polyphenism of *Halictus (Seladonia) tumulorum* (L.) (Hymenoptera, Halictinae). *Insectes Sociaux* 41: 219–222.

Richards, M. H., D. French, and R. J. Paxton. 2005. It's good to be queen: classically eusocial colony structure and low worker fitness in an obligately social sweat bee. *Molecular Ecology* 14: 4123–4133.

——— and L. Packer. 1994. Trophic aspects of caste determination in *Halictus ligatus*, a primitively eusocial sweat bee. *Behavioral Ecology and Sociobiology* 34: 385–391.

——— and L. Packer. 1995a. Annual variation in survival and reproduction of the primitively eusocial sweat bee *Halictus-Ligatus* (Hymenoptera-Halictidae). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 73: 933–941.

——— and L. Packer. 1995b. Annual variation in survival and reproduction of the primitively eusocial sweat bee *Halictus ligatus* (Hymenoptera: Halictidae). *Canadian Journal of Zoology* 73: 933–941.

——— and L. Packer. 1996. The socioecology of body size variation in the primitively eusocial sweat bee, *Halictus ligatus* (Hymenoptera: Halictidae). *Oikos* 77: 68–76.

——— and L. Packer. 1998. Demography and relatedness in multiple-foundress nests of the social sweat bee, *Halictus ligatus*. *Insectes Sociaux* 45: 97–109.

———, L. Packer, and J. Seger. 1995. Unexpected patterns of parentage and relatedness in a primitively eusocial bee. *Nature* 373: 239–241.

———, E. J. von Wettberg, and A. C. Rutgers. 2003. A novel social polymorphism in a primitively eusocial bee. *Proceedings of the National Academy of Sciences, USA* 100: 7175–7180.

Roulston, T. H., S. A. Smith, and A. L. Brewster. 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *Journal of the Kansas Entomological Society* 80: 179–181.

Sakagami, S. F. 1974. Sozialstruktur und Polymorphismus bei Furchen- unds Schmalbienen (Halictinae). Pp. 257–293 *in:* Schmidt, G. H., ed. *Sozialpolymorphismus bei Insekten*. Wissensch. Verlagsgesellschaft mbH, Stuttgart.

——— and K. Fukushima. 1961. Female dimorphism in a social halictine bee, *Halictus (Seladonia) aerarius* Smith (Hymenoptera, Apoidea). *Japanese Journal of Ecology* 11: 118–124.

——— and K. Hayashida. 1968. Bionomics and sociology of the summer matrifilial phase in the social halictine bee, *Lasioglossum duplex*. *Journal of the Faculty of Science, Hokkaido University, Series 6 {Zoology}* 16: 413–513.

——— and M. Munakata. 1972. Distribution and bionomics of a transpalaeartic eusocial halictine bee, *Lasioglossum (Evylaeus) calceatum*, in northern Japan, with reference to its solitary life cycle at high altitude. *Journal of the Faculty of Science, Hokkaido University, Series 6 {Zoology}* 18: 411–439.

——— and T. Okazawa. 1985. A populous nest of the Halictine bee *Halictus (Seladonia) lutescens* from Guatemala (Hymenoptera, Halictidae). *Kontyu* 53: 645–651.

Schwarz, M. P., M. H. Richards, and B. N. Danforth. 2007. Changing paradigms in insect social evolution: Insights from halictine and allodapine bees. *Annual Review of Entomology* 52: 127–150.

Weissel, N., O. Mitesser, L. Liebig, H. J. Poethke, and E. Strohm. 2006. The influence of soil temperature on the nesting cycle of the halictid bee *Lasioglossum malachurum*. *Insectes Sociaux* 53: 390–398.

Wille, A. and C. D. Michener. 1971. Observations on the nests of Costa Rican *Halictus* with taxonomic notes on Neotropical species (Hymenoptera: Halictidae). *Revista de Biología Tropical* 18: 17–31.

Wyman, L. M. and M. H. Richards. 2003. Colony social organization of *Lasioglossum malachurum* Kirby (Hymenoptera, Halictidae) in southern Greece. *Insectes Sociaux* 50: 201–211.

Yanega, D. 1988. Social plasticity and early-diapausing females in a primitively social bee. *Proceedings of the National Academy of Sciences, USA* 85: 4374–4377.

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Ultrastructure of Scutellar Sensilla in *Aphytis melinus* (Hymenoptera: Aphelinidae) and Morphological Variation across Chalcidoidea

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Abstract.—Paired, disc-like campaniform sensilla occur on the scutellum of many minute parasitic wasps in the superfamily Chalcidoidea (Hymenoptera). The ultrastructure of the sensilla is examined in *Aphytis melinus* DeBach (Aphelinidae). Each sensillum consists of a bilayered cuticular cap directly covering a tubular body with microtubules extending at a right angle to the cuticle. A large electron-dense mass attached to the tubular body extends laterally beneath the cuticle. Other structures occupying the space between the scutellum and longitudinal flight muscles include the paired mesoscutello-metanotal muscles and a previously undescribed layer of oblong structures lining the cuticle throughout the thorax. Among 23 additional species examined, the sensilla range in diameter from 1.81μm to 5.79 μm, with no apparent relationship between diameter of the sensilla and size of the scutellum. The function of the sensilla is unknown, but the consistent presence of the sensilla in small chalcidoids and the frequent absence in the largest species suggests a possible association with specialized flight peculiar to small insects obliged to utilize the clap-and-fling flight mechanism.

Key words.—campaniform sensilla, morphology, sensory structures

Chalcidoidea is a diverse superfamily of parasitic Hymenoptera whose species range in length from the smallest known insect (0.11 mm) to relatively large wasps (45 mm), with most specimens averaging 2–4 mm in length (Heraty and Gates 2003). Over 22,000 species of Chalcidoidea are described, making it second to Ichneumonoidea in diversity, but with an estimated 100,000 to 400,000 undescribed species, it may well prove to be the largest superfamily of Hymenoptera (Gibson et al. 1999; Gordh 1975a; Heraty and Gates 2003; Noyes 2000, 2003). Despite over 200 years of taxonomic work, phylogenetic relationships at the family and subfamily levels remain unclear (LaSalle et al. 1997). Difficulties in understanding chalcidoid phylogenetics are due in part to the vast numbers of undescribed species and the poor preservation of many curated specimens (Heraty 2004; LaSalle 1993). Additionally, with the vast majority of chalcidoids measuring less than 4 mm, there is often a paucity of reliable phylogenetically informative morphological structures.

Sensillar structures have proven to be a rich source of morphological characters, and there have been numerous investigations into the structure and function of sensilla found within Chalcidoidea (Baaren et al. 1996; Barlin and Vinson 1981; Olson and Andow 1993; Schmidt and Smith 1985, 1987). The antenna has been the focal point of the majority of sensillar investigations in chalcidoids due to the high concentration and diversity of antennal sensilla (Barlin and Vinson 1981; Basibuyuk et al. 2000; Olson and Andow 1993; Walther 1983). These studies have focused largely on classifying types of antennal sensilla based on ultrastructural morphology (Amornsak et al. 1998; Baaren et al. 1996; Barlin and Vinson 1981; Basibuyuk and Quicke 1999; Cônsoli et al. 1999; Isidoro et al. 1996; Olson and Andow 1993). Other investiga-

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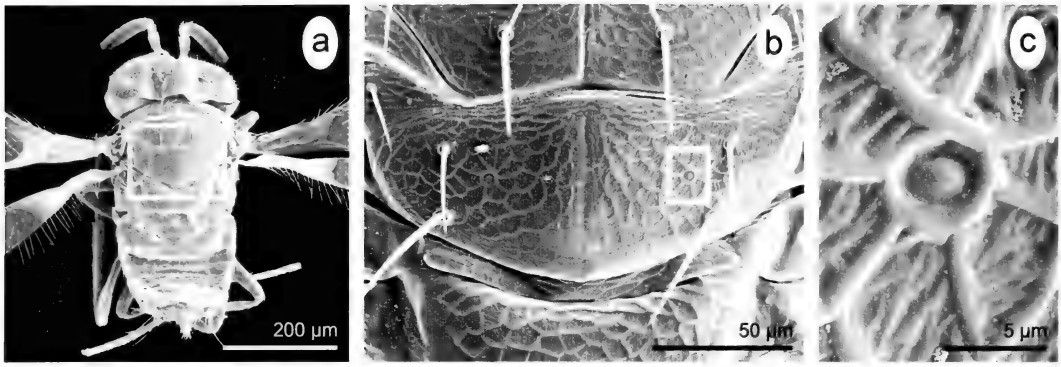

Fig. 1. Location and appearance of scutellar sensilla in *Aphytis melinus*. a: whole specimen, b: scutellum, c: right scutellar sensillum. White boxes in (a) and (b) indicate area magnified in following figure.

tions have examined sensory structures of the ovipositor (Cônsoli et al. 1999; Le Ralec et al. 1996; Le Ralec and Rabasse 1988; Veen and Wijk 1985), male genitalia (Chiappini and Mazzoni 2000) and wings (Schmidt and Smith 1985). The paired sensilla of the scutellum (Fig. 1a–c) have been identified as phylogenetically important (Hayat 1998; Heraty and Polaszek 2000; Kim 2003; Schauff et al. 1996), but there has been no investigation into their ultrastructure, possible function or distribution across Chalcidoidea.

The scutellar sensilla are a feature frequently overlooked in taxonomy and have received only sparse attention in the literature. Domenichini (1969) was one of the first morphologists working with Chalcidoidea to point out the scutellar sensilla, noting their occurrence in several different families and recommending that their function and taxonomic value be studied. Rosen and DeBach (1979) also noted the sensilla in their treatise on *Aphytis* Howard (Aphelinidae), mentioning in each of their species descriptions the location of the scutellar sensilla relative to the anterior and posterior scutellar setae. They observed that, in slide preparations, the sensilla can be mistaken for empty setal sockets due to the thinness of the cuticle over the sensilla. They also noted rare mutations involving the sensilla in which one or both sensilla are replaced by an extra seta, by a pair of setae, or where there appears to be one, three, or four sensilla in place of the normal pair of sensilla. Both Schauff et al. (1996) and Hayat (1998) incorporated the placement of the sensilla in their keys of *Encarsia* Förster (Aphelinidae). Heraty and Polaszek (2000) used the close placement of the sensilla on the scutellum as a defining characteristic of the *Encarsia strenua* group. Placement of the sensilla on the scutellum was also used by Schauff (1984) as a character in his phylogeny of Mymaridae. Other allusions to the sensilla in the literature are limited to inclusion in illustrations and an occasional mention in species descriptions.

Herein we demonstrate that these scutellar structures are campaniform sensilla, which are circular to oval in shape and innervated by just one sense cell, or neuron, that partially penetrates the thin-domed cuticle (Hicks 1857; Berlese 1909; Snodgrass 1935; McIver 1985). Campaniform sensilla have a mechanoreceptive function targeted at sensing tension or torsion in the associated cuticle (Pringle 1938a; McIver 1985; Zill and Moran 1981).

In chalcidoids, campaniform sensilla have been identified on the antenna (Amornsak et al. 1998; Olson and Andow 1993), ovipositor (Cônsoli et al. 1999; Le Ralec et al. 1996; Le Ralec and Wajnberg 1990), male genitalia (Chiappini and Mazzoni 2000), wing (Schmidt and Smith 1985;

Weis-Fogh 1973), pretarsus (Gladun and Gumovsky 2006) and legs (Schmidt and Smith 1987), but the internal ultrastructure of these sensilla in the superfamily has been examined only in male genitalia of Mymaridae (Chiappini and Mazzoni 2000).

In the current study, *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae: Aphelininae) was chosen to examine the ultrastructure of the scutellar sensilla. *Aphytis melinus* range in size from 0.78 mm to 1.21 mm (Rosen and DeBach 1979) and have been well studied because of their success as biological agents controlling the California Red Scale, *Aonidiella aurantii* (Maskell) (Lenteren 1994). Prior to this study, paired scutellar sensilla were recorded only in the smallest Chalcidoidea such as Aphelinidae (Hayat 1984, 1997; Huang 1994; Heraty and Polaszek 2000; Babcock et al. 2001; Kim 2003; Noyes and Valentine 1989; Schauff et al. 1996), Encyrtidae (Hayat 2003; Noyes 1988; Noyes et al. 1997; Prinsloo 1997), Mymaridae (Schauff 1984), Signiphoridae (Noyes and Valentine 1989) and Trichogrammatidae (Doutt and Viggiani 1968; Noyes and Valentine 1989), with most attention being given to scutellar sensilla in Aphelinidae (Heraty and Polaszek 2000; Kim 2003; Rosen and DeBach 1979).

No previous work has sought to examine the ultrastucture of the scutellar sensilla found in Chalcidoidea. This study seeks to survey variation in external appearance of the scutellar sensilla found in Chalcidoidea, examine the ultrastucture of the sensilla in *A. melinus*, and accurately determine the category of sensilla to which they belong.

MATERIALS AND METHODS

Terminology.—Terms and abbreviations follow Gibson (1997) and Kim (2003) for the structures of the mesonotum, Krogmann and Vilhelmsen (2006) and Vilhelmsen (2000) for muscles and internal morphology, and Harris (1979) for cuticular sculpturing. The paired campaniform sensilla on the scutellum have been termed campaniform sensilla (cs), and terminology specific to structures of the campaniform sensilla follows McIver (1985). Abbreviations are listed in Table 1.

Table 1. Abbreviations used in figures.

112	longitudinal flight muscles
114	mesoscutello-metanotal muscle
2ph	second phragma
ass	anterior scutellum setae
cs	campaniform sensilla
cut	cuticle
edm	electron dense mass
edr	electron dense ring
ela	electron lucent area
epd	epidermal cells
fb	fat body
fl	flange
L1	outer layer
L2	inner layer
m	mitochondria
ml	midline between left and right longitudinal flight muscles
ms	mesoscutum
pss	posterior scutellum setae
scl	scutellum
ssr	scutoscutellar ridge
sss	scutoscutellar suture
tb	tubular body
tsa	transscutal articulation

Specimens.—*Aphytis melinus* for scanning electron microscopy (SEM) and transmission electron microscopy (TEM) were obtained from a colony reared on *Aspidiotus nerii* Bouché (Diaspididae) at the University of California, Riverside. An additional 30 specimens representing 23 species from ten families of Chalcidoidea, and one specimen of Mymarommatoidea were imaged with SEM. A list of Chalcidoidea used for SEM imaging is given in Table 2; all material is represented by vouchers deposited at the University of California, Riverside Entomology Research Museum (UCRC). The external morphology of the sensilla in Chalcidoidea and outgroups were more broadly surveyed, but this will be treated separately (Romero and Heraty, *in prep.*). Scutellar sensillae have not been documented outside of Chalcidoidea and

Table 2. Sensillum diameters from SEM images. n indicates number of sensilla examined for that species.

Taxon	n	Shape of sensillum	Maximum diameter mean ± SD (range)	Average area of scutellum
Aphelinidae				
Aphytis melinus DeBach	7	circular	4.94 μm ± 0.40 (3.68–4.94 μm)	14.84 mm
Marietta sp.	4	circular	2.25 μm ± 0.27 (1.93–2.60 μm)	11.18 mm
Ablerus americanus Girault	2	circular	2.86 μm ± 0.37 (2.60–3.12 μm)	6.48 mm
Cales noacki Howard	3	circular	2.99 μm ± 0.58 (2.32–3.39 μm)	6.29 mm
Eretomocerus sp.	2	circular	4.11 μm ± 0.17 (3.99–4.23 μm)	9.58 mm
Eriaphytis sp.	1	circular	5.10 μm	26.83 mm
Encyrtidae				
Comperiella bifasciata Howard	4	circular	4.10 μm ± 0.38 (4.14–4.83 μm)	23.71 mm
Microterys nietneri (Motschulsky)	2	circular	5.35 μm ± 0.62 (4.92–5.79 μm)	42.66 mm
Eucharitidae				
Orasema minutissima (Howard)	2	circular	1.87 μm ± 0.08 (1.81–1.93 μm)	27.06 mm
Gollumiella antennata (Gahan)	2	circular	3.47 μm ± 0.45 (2.24–3.79 μm)	45.9 mm
Eulophidae				
Pnigalio sp.	3	subcircular	3.39 μm ± 0.82 (2.82–4.44 μm)	28.36 mm
Pnigalio agraules (Walker)	2	subcircular	3.93 μm ± 0.17 (3.80–4.05 μm)	34.43 mm
Mymaridae				
Gonatocerus ashmeadi Girault	1	circular	4.87 μm	48.76 mm
Pteromalidae				
Philotrypesis sp.	2	subcircular	3.70 μm ± 0.11 (3.78–3.62 μm)	52.76 mm
Asaphes sp.	1	subcircular	3.66 μm	30.07 mm
Nasonia vitripennis (Walker)	1	subcircular	4.34 μm	NA
Signiphoridae				
Signiphora sp.	2	circular	2.99 μm ± 0.20 (2.85–3.13 μm)	26.54 mm
Tanaostigmatidae				
Tanaostigma sp.	1	circular	3.82 μm	56.54 mm
Tetracampidae				
Epiclerus sp.	1	circular	4.86 μm	17.80 mm
Torymidae				
Megastigmus transvaalensis (Hussey)	1	circular	5.39 μm	101.49 mm
Trichogra mmatidae				
Aphelinoidea sp.	2	circular	5.07 μm ± 0.14 (4.97–5.17 μm)	7.99 mm
Haeckeliania sp.	2	circular	5.05 μm ± 0.12 (4.96–5.13 μm)	10.14 mm
Hayatia sp.	2	circular	3.82 μm ± 0.30 (3.60–4.03 μm)	5.34 mm
Total	50		3.89 μm ± 1.01 (1.81–5.79 μm)	27.91 mm

the majority of outgroup Hymenoptera examined had no trace of sensilla. However, sensilla were found in species from four outgroup families, Ceraphronidae (*Ceraphron* sp.), Diapriidae (*Trichopria* sp.), Mymarommatidae (*Mymaromma anomalum* (Blood & Kryger)) and Scelionidae (*Telenomus* sp.). These families represent three different superfamilies from the subdivision Proctotrupomorpha, which includes Chalcidoidea, and Ceraphronidae, representing the more distantly related subdivision Evaniomorpha.

SEM.—Specimens selected for SEM were collected in 70% ethanol then dried in hexamethyldisilazane (HMDS) (Heraty and Hawks 1998). Some specimens were gradually rehydrated through a series of

increasingly dilute ethanol baths, rinsed in two baths of deionized water, then digested in 10% KOH for 5–30 min according to the size of the specimen in order to clean the specimen of debris. Specimens were again rinsed in deionized water and dehydrated through a series of increasingly concentrated ethanol baths, then chemically dried in HMDS. Once dry, specimens were either dissected or placed whole onto SEM mounting stubs. Specimens were Au/Pd coated using a Cressington 108 Auto® sputter coater set for 60–90 seconds, then examined and digitally imaged under a XL30 FEG scanning electron microscope at 10 or 15 kV.

Measurements.—Scutellar and sensillar measurements were taken in ImageJ 1.38× using the digital SEM images. Width measurements of the scutellum were made across the broadest point of the scutellum, excluding the axillula, and length measurements along the longest medial part of the scutellum including the frenum. Area measurements were made using the freehand tool in ImageJ. Measurements of the differentiated area of the sensillum were taken along the longest axis and excluding the encircling ring, if present. To determine if there is a correlation between the size of the scutellum and the diameter of the sensilla, the length, width and area of the scutella of 50 specimens were measured (Table 2). A regression line was calculated for each of the three measurements of the scutellum that were graphed, and the coefficient of determination (R-squared) value calculated.

TEM.—Live *A. melinus* were decapitated while immersed in Karnovsky's fixative (Karnovsky 1965). After approximately two hours they were placed in sodium cacodylate buffer, dehydrated in ethanol and embedded in Spurr resin (Spurr 1969). Sections approximately 60–70 μm thick were cut using a diamond knife on a Leica Ultracut microtome. Sections were mounted on Electron Microscopy Sciences nickel slot grids coated with formvar/carbon. Sections were then post stained using the SynapTec GridStick™ system as follows. The uranyl acetate stain was diluted in methanol and the lead citrate stain mixed using 0.3 grams lead citrate, 0.3 grams lead nitrate, 0.3 grams lead acetate and 0.6 grams sodium citrate dissolved in 24.6 ml pre-boiled double distilled deionized water using a sonicator; after sonication 5.4 ml of 1N NaOH solution was added to the lead stain. Grids were initially stained for 5 minutes in uranyl acetate followed by two rinses in 100% methanol, one rinse each in 75%, 50% and 25% methanol, and four rinses in pre-boiled, double-distilled deionized water. The grids were then immediately stained for 10 minutes in the lead stain followed by a 30 second rinse in 0.02 N NaOH and 30 minutes of rinsing with water changed every 5 minutes. Sections were examined with a Philips Tecnai 12 transmission electron microscope and digitally imaged using a model 780 Gatan DualVision 300 camera.

Slide Mounts.—*Aphytis melinus* were collected in 70% ethanol and gradually hydrated through a series of increasingly dilute ethanol baths, rinsed in two baths of deionized water and then digested in 10% KOH for 10 minutes. Following digestion, specimens were rinsed in deionized water and dehydrated through a series of increasingly concentrated ethanol baths to 100% ethanol. They were then placed in a well plate with three drops of clove oil and the ethanol allowed to evaporate completely. The antennae, head, wings and body were separated from each specimen and arranged on the slide in 25% Canada Balsam and 75% clove oil (Noyes 2003). As the clove oil evaporated, the Canada Balsam was gradually built up until the structures were covered and four 5 mm coverslips applied.

RESULTS

In most Apocrita, the mesonotum is divided by the transscutal articulation

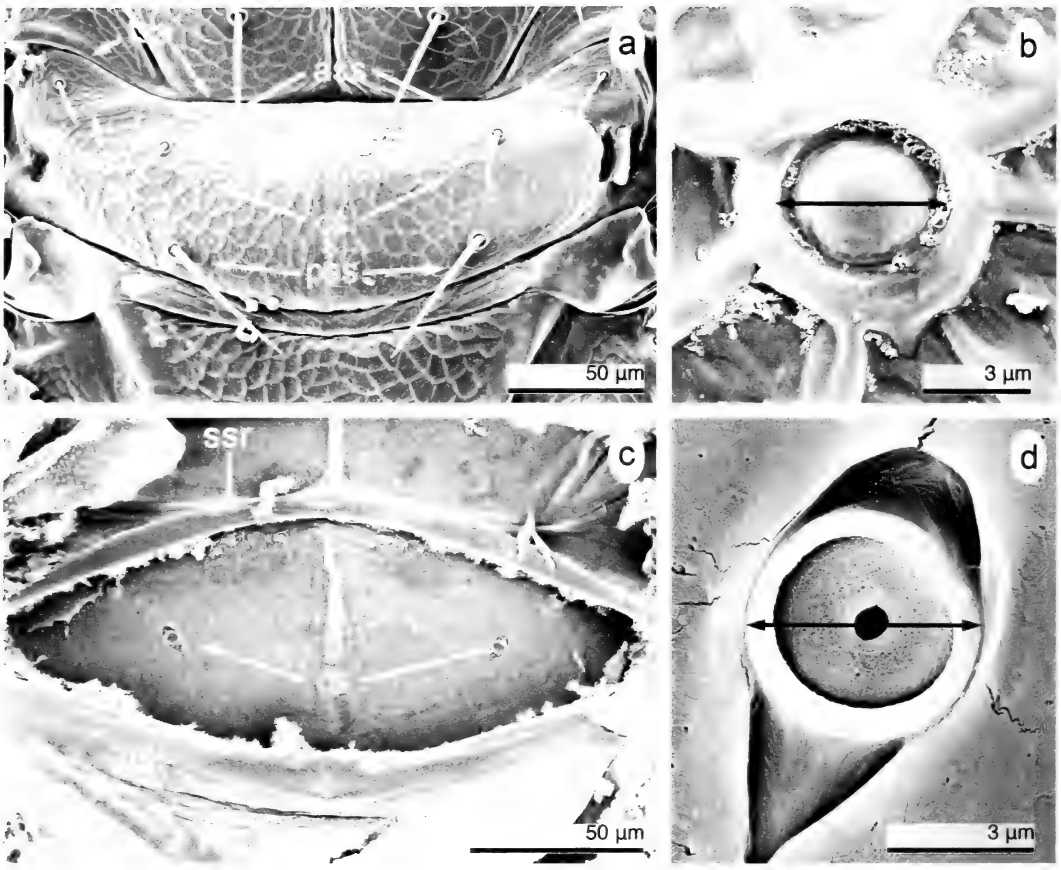

Fig. 2. Structure of scutellum and scutellar sensilla in *Aphytis melinus*. a: scutellum, b: scutellar sensillum, c: underside of scutellum with tissue removed and both sensilla visible, d: underside of sensillum with tissue removed. Black arrows = 4.84µm, indicate equal distance in both (b) and (d).

(Fig. 2a: tsa) into an anterior mesoscutum and a posterior scutellar-axillar complex (Gibson 1997). The medially located scutellum is separated from the anterolateral axilla by the scutoscutellar suture (Fig. 2a: sss). With the exception of Signiphoridae, in which the scutellum is reduced to a transverse band, all Chalcidoidea possess a scutellum that is a prominent plate of variable size and shape. The scutellum can be roughly circular, oval, shield or teardrop shaped and can also vary in topography. For example, some Encyrtidae have a rounded scutellum with sharply rising sides that form a dorsal hump, while some Mymaridae have a flat planar scutellum. Many chalcidoids (i.e. Eucharitidae, Mymaridae, Pteromalidae, Tetracampidae and Torymidae) have a transverse sulcus or change in sculpture differentiating a posterior region of the scutellum termed the frenum. In many taxa, lateral axillular grooves separate the axillula from the main portion of the scutellum, but this is often more apparent in lateral view. The scutellum of many smaller Chalcidoidea often has two pairs of prominent setae: the anterior scutellar setae (Fig. 2a: ass) and the posterior scutellar setae (Fig. 2a: pss). When present, these setae are used as reference points for the campaniform sensilla on the scutellum.

Structure of scutellum and sensilla in Aphytis.—A. melinus has a roughly oval scutellum with a pair of circular sensilla located medially to the four primary

scutellar setae (Fig. 2a). Each campaniform sensillum appears externally as a smooth dome in the cuticle surrounded by a raised ring that interrupts the imbricate sculpturing of the scutellum (Fig. 2b). Internally, the cuticle forms a raised ring around an area of reticulate cuticle with an elliptical central depression oriented diagonally to the longitudinal axis of the body (Fig. 2c–d). This ellipse-shaped thinning of the cuticle probably creates a weakness along the long axis of the ellipse and enhances movement along the short axis conferring directional sensitivity similar to that obtained through an elliptically shaped cuticular cap (Moran and Rowley 1975). Across all of the specimens surveyed, the elliptical depression, which is also visible in slide mounts, was found only in *Aphytis* and *Aphelinus* (Aphelininae).

Internally, the scutellum is bordered by several ridges forming a differentiated region directly above the longitudinal flight muscles. Along with the mesoscutello-metanotal muscles (Fig. 3a–e: 114) and randomly distributed fat body (Figs 3e: fb), this space also contains several unidentified structures. In certain dissections examined with SEM (Figs 3c, 4a–b), there appears to be membranous divisions that run through this area defining irregular sections as large as 20 μm in diameter, however these divisions were not apparent in TEM preparations. Just below the cuticle, and between these divisions, there is a single, or sometimes double, layer of elongate epidermal cells (Fig. 4a–i: epd). While tightly packed, these cells appear independent of each other in SEM preparations (Fig. 4a–c) and in TEM preparations appear hollow due to a lack of penetration by the resin. Similar impenetrable epidermal cells also appear in sections of the male antennae prepared by Romani et al. (1999) in their TEM investigation of the male antennae of *A. melinus*. It may be that in the adult wasp the epidermal cells have died leaving a thick waxy cell membrane that is impermeable to resin. These are not likely artifacts of dried haemolymph which is apparent in the layer of "tissue" surrounding muscle 114 and the sensillar stem (cs) in Fig. 3c. These cells line the entire internal surface of the cuticle, including ventral surfaces (Fig. 4i: epd) and internal apodemes (Fig. 4h: epd), but are absent where the scutellar sensilla attach to the cuticle (Fig. 4g).

Mesoscutello-metanotal muscles.—In *A. melinus*, a pair of muscles traverse the length of the scutellum between the longitudinal flight muscles and the dorsal surface of the scutellum (Fig. 3a–b and e), which are synonymous with Kelsey's (1957) muscle 114 and Vilhelmsen's (2000) mesoscutello-metanotal muscle. The muscles attach to the anterior portion of the scutellum just posterior to the scutoscutellar ridge (Fig. 3a–c: 114 and ssr). From this point of origin they narrow and are slightly angled medially to a posterior insertion to the anterior edge of the metanotum above the margin of the second phragma (2ph) to the anterior edge of the metanotum (Fig. 3a–b: 114). In cross section, the longitudinal flight muscles have clearly defined axon bundles interspersed with mitochondria (Fig. 3d–e: 112), whereas the mesoscutello-metanotal muscle has mitochondria restricted to the periphery. Consequently axon bundles are not as easily distinguished (Fig. 3d–e). These mucles may affect longitudinal tension of the scutellar disc and possibly deformation of shape in small soft-bodied chalcidoids.

Ultrastructure of the sensillar cuticular cap.—In *A. melinus*, there are several distinct features of the cuticular portion of the scutellar sensilla evident through electron microscopy. In cross sections there is a thin outer layer of solid cuticle. This layer (Fig. 5a–e: L1) sits external to a thicker layer of mesh-like cuticle (Fig. 5a–f: L2). These two layers of the cap are consistent with the cuticular structure found in campaniform sensilla observed in other studies where 2 or 3 layer-caps are reported (McIver 1985) and it is nearly

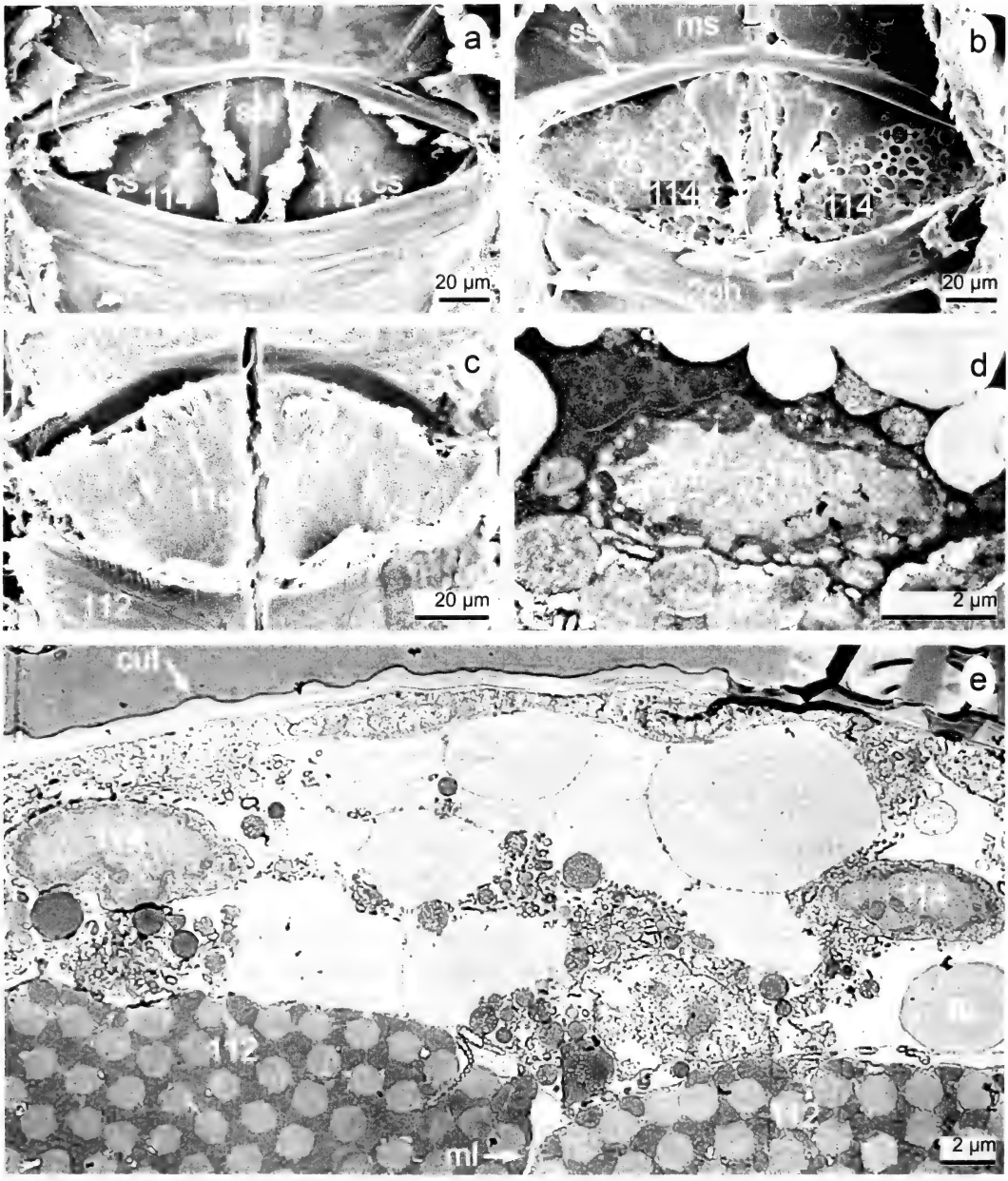

Fig. 3. Mesoscutello-metanotal muscles in *Aphytis melinus*. a: underside of scutellum with most tissue removed leaving mesoscutello-metanotal muscles (114), b: same view in (a) with slightly different results from the chemical drying process, c: dorsal tissue found just beneath scutellum, d: cross section through mesoscutello-metanotal muscle, e: cross section through dorsal portion of scutellum.

identical to the structure observed by Bromley et al. (1980) in aphid antennae. The bilayered cap is encircled by a flange that protrudes internally. This flange was observed by McIver and Siemicki (1975) in the mosquito, and in the cockroach by Moran and Rowley (1975), who called the structure a cuticular collar. Moran and Rowley also suggested that it provides structural support and rigidity for the cap of the sensilla and enables the cap to move as a unit in response to cuticular deforma-

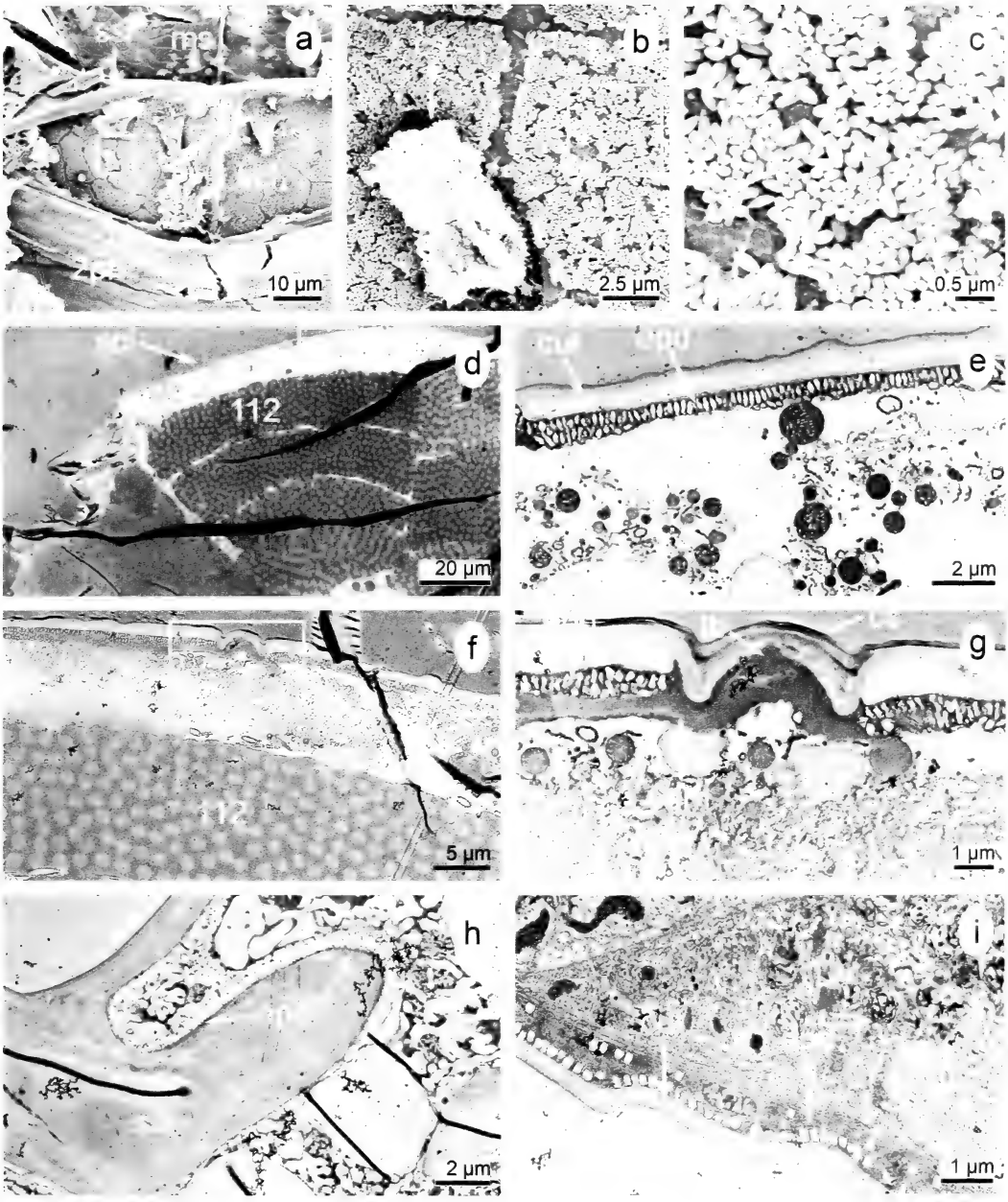

Fig. 4. Epidermal cells in *Aphytis melinus*. a: underside of scutellum with most tissue removed leaving epidermal cells, b: underside of scutellum with campaniform sensillum tissue and epidermal cells attached, c: underside of sensilla with epidermal cells attached, d–e: cross section through scutellum, f–g: cross section through scutellum with a campaniform sensillum, h: cross section through notal ridge, i: cross section through ventral portion of mesosoma. White boxes indicate area magnified in following figure.

tion. Just dorsal to the flange, layer 1 is attached to the cuticle by a ring of dark staining cuticle (Fig. 5a–c) that McIver and Siemicki (1975) called a hinge. This designation seems appropriate since it is at this junction point, at the base of the flange where the cap and cuticle meet, that the cuticle would presumably bend.

Tubular body and electron dense mass.— One of the most distinctive features of a campaniform sensilla is the tubular body at the distal end of the nerve cell (McIver 1985), which is a bundle of microtubules set in an electron dense material that functions as the site of transduction (Thurm 1964). In *A. melinus*, the tubular body is a striated cap that inserts into layer two of the cuticle, almost extending to layer one (Fig. 5d: tb). The tubular body consists of microtubules perpendicularly oriented to the surface of the cuticle and set in an electron-dense material. An electron-lucent area located at the proximal end separates the tubular body from the electron-dense mass beneath (Fig. 5c: ela and edm). In some preparations, the tubular body appears to have a slightly indented tip in the very center of its distal end (Fig. 5e). The proximal end of the cap-like tubular body is nested in an electron-dense mass (Fig. 5c: edm). This dense material surrounds the tubular body and is directly adjacent to the modified portions of the cuticular cap, completely filling the sunken areas below layer two and surrounding the flange (Fig. 5b–c). It also extends beyond the campaniform sensillum, particularly in the lateral direction, to form a large matt beneath the cuticle (Fig. 6a–d). The electron-dense mass appears to consist of microtubules or lamella similar to the tormogen cell associated with campaniform sensilla found on mosquito palps (McIver 1985), but appears to lack other cellular structures indicative of a tormogen cell such as a membrane bound nucleus (Thurm and Küppers 1980). No other dendritic cells were identified in association with the campaniform sensilla.

Distribution of sensilla across Chalcidoidea.—The paired scutellar sensilla are found in most families of Chalcidoidea and in exemplars of four outgroup families (Ceraphronidae, Mymarommatidae [single sensillum], Scelionidae and Diapriidae). In prepared slides, the sensilla appear as pale spots or thin areas in the cuticle and are readily identified in smaller taxa such as *Aphytis* (Rosen and DeBach 1979). In SEM preparations, they appear externally as differentiated areas of the cuticle that break the cuticular pattern and typically are ringed by raised or depressed cuticle (Figs 7a–h, 8a–h).The location and shape of the sensilla on the scutellum are highly variable across Chalcidoidea, but there is consistency within taxonomic groups at the family, tribe, genus and species levels (Romero and Heraty, in prep.). The location of the sensilla varies from medially abutting in some Aphelinidae, Encyrtidae and Mymaridae, to a lateral location within 5 μm of the edge of the scutellum in some Pteromalidae and Eulophidae. Sensillar location also varies along the longitudinal axis from an anterior location contiguous with the scutoscutellar suture (sss) in some Aphelinidae and Mymaridae to a posterior location within a few microns of the posterior margin in some Mymaridae. The sensilla are always found anterior to the frenal line when a frenum is present. The most common location is generally central and just medial of the anterior and posterior scutellar setae when present (Fig. 2a). The shape of the sensilla range from circular (Fig. 7a), to longitudinally oblong (Fig. 7d), to transversely oblong (Fig. 7c), with circular being the predominant shape. For the subset of representative specimens measured, the diameter of the sensilla ranges from 1.81μm in *Orasema* sp. (Eucharitidae) to 5.79 μm in *Microterys nietneri* (Motschulsky) (Encyrtidae) (Table 2).

Comparisons of sensillar diameter and scutellar length, width and area revealed that scutellar size accounts for very little variation in sensillar diameter (Fig. 9a–c). R-squared values were low with the highest value at 0.081 (Fig. 9a). Comparisons of scutellar length and sensillar diameter had an R-squared value of 0.024 (Fig. 9b), and scutellar area and sensillar diameter had an R-squared value of 0.057 (Fig. 9c). The low R-squared values for the regression lines indicate that the variation in the size

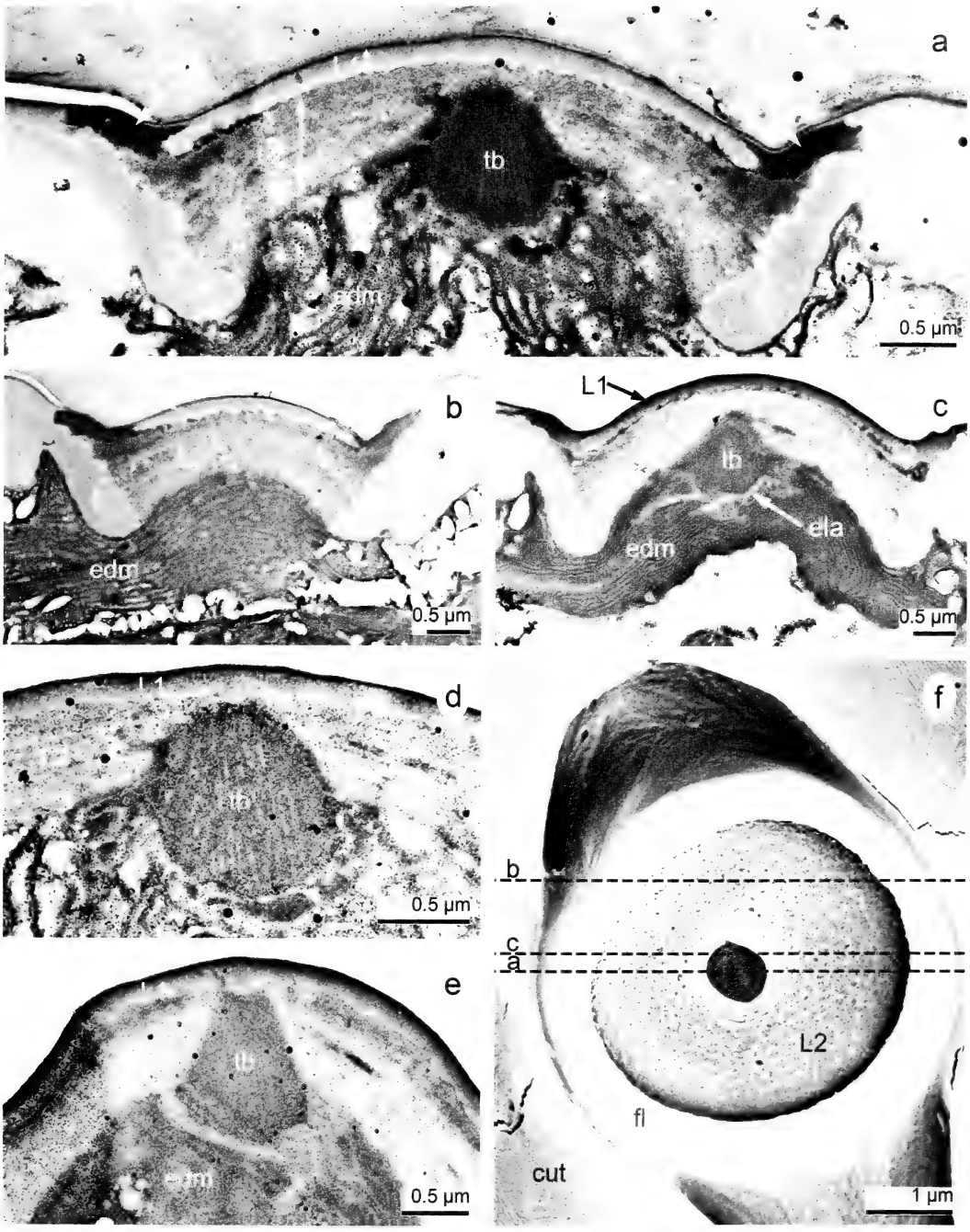

Fig. 5. *Aphytis melinus*, multiple specimens. a–c: cross sections through portions of campanifrom sensilla shown in (f), d: cross section through the tubular body, e: cross section through the tubular body showing divot at tip, f: the underside of a campaniform sensillum with tissue removed, dashed lines indicate the general location of cross sections in (a), (b) and (c).

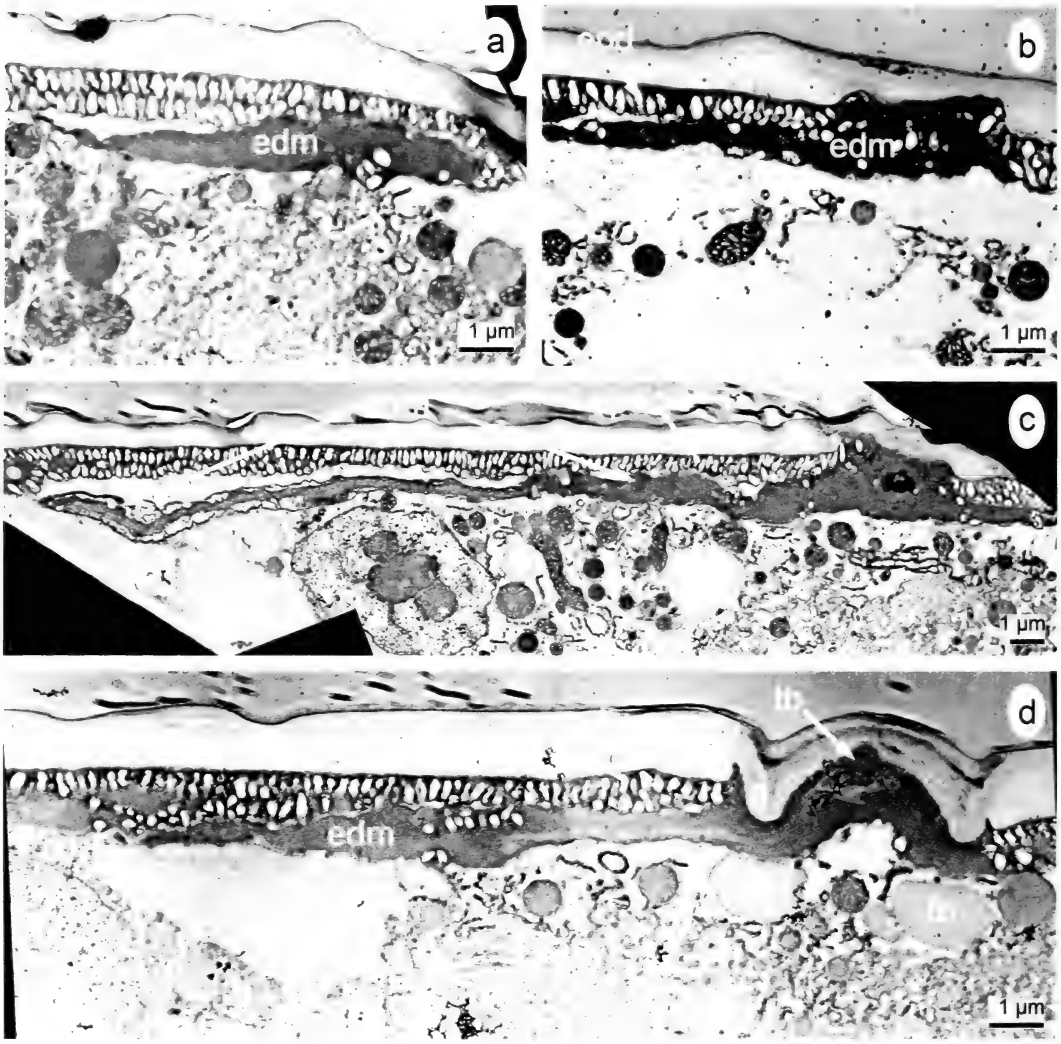

Fig. 6. Electron-dense mass associated with the campaniform sensillum to the left of the midline in *Aphytis melinus*. a: cross section anterior to campaniform sensillum, b–c: cross sections just anterior to the main structure of the campaniform sensillum, d: cross section through the center of the campaniform sensillum.

of the scutellum accounts for less than 9% of the variation in the diameter of the sensilla. While there does not appear to be a relationship between size of scutellum and size of sensilla, the sensilla are absent or undetectable in chalcidoid families with the largest species, which have a scutellar size far beyond that indicated in Fig. 9 (i.e. Chalcididae and Perilampidae, >2 mm) (Romero and Heraty, in prep.). Thus our correlations are based only on taxa that are normally small in size, not those taxa that are large. A similar situation occurs in the outgroups, and we failed to find evidence of the sensilla in the majority of species which are usually larger or more heavily sclerotized. Strong correlations do appear within species (i.e. *A. melinus*, Fig. 9), but these were not correlated across subfamily or family groups.

DISCUSSION

This is the first study to examine the morphology of scutellar sensilla of Chalcidoidea. The presence of sensilla has been noted sporadically in the literature, and

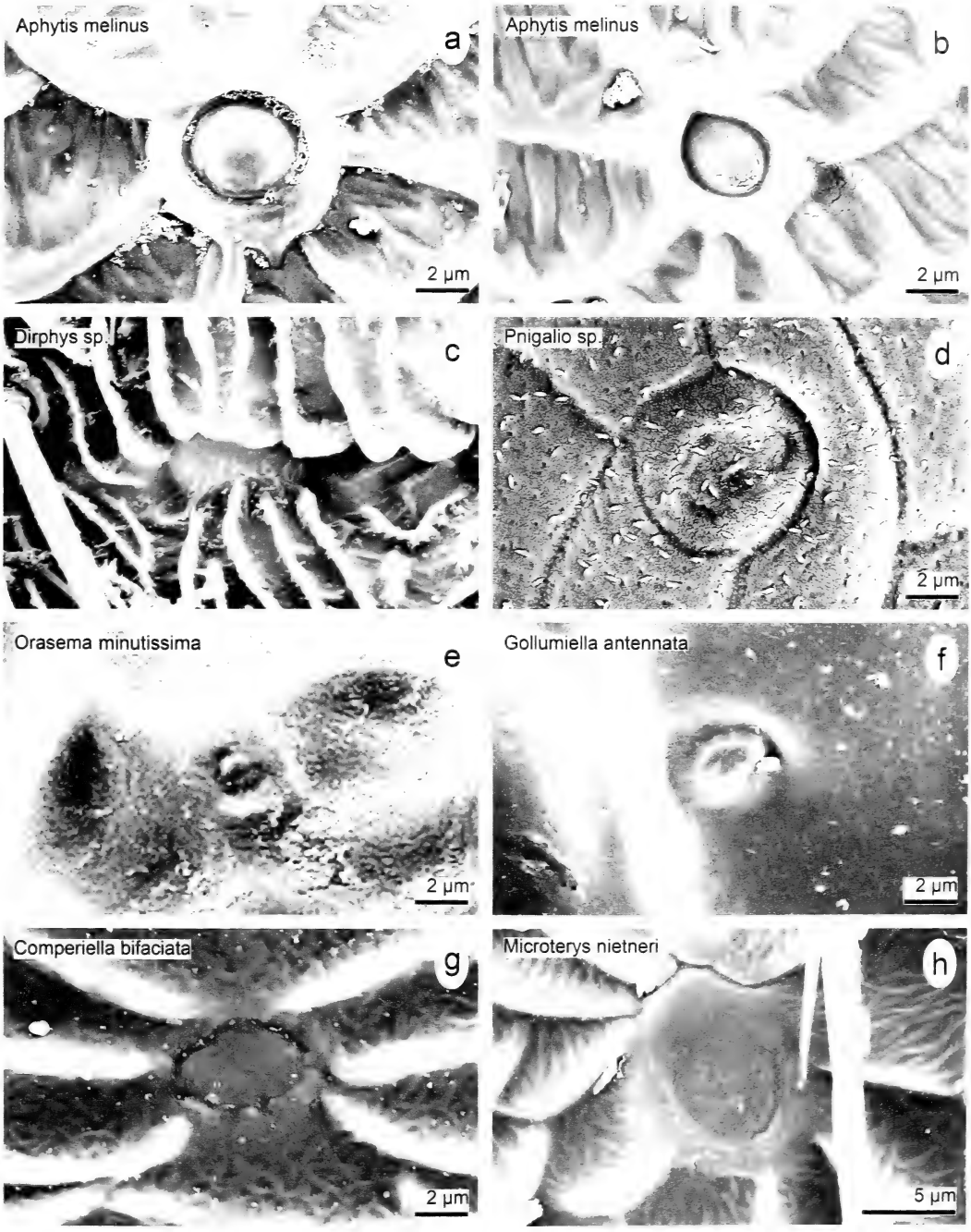

Fig. 7. Variations in external appearance of scutellar sensilla. a: *Aphytis melinus* ♀ (Aphelinidae), b: *A. melinus* ♂, c: *Dirphys* sp. (Aphelinidae), d: *Pnigalio* sp. (Eulophidae), e: *Orasema minutissima* (Eucharitidae), f: *Gollumiella antennata* (Eucharitidae), g: *Comperiella bifaciata* Howard (Encyrtidae), h: *Microterys nietneri* (Encyrtidae).

often included in illustrations without comment in the text. The most attention this feature has received is in *Encarsia* (Aphelinidae), where relative placement on the scutellum has been used in several keys to discriminate both individual species and species groups (Hayat 1998; Hernández-Suárez et al. 2003; Schauff et

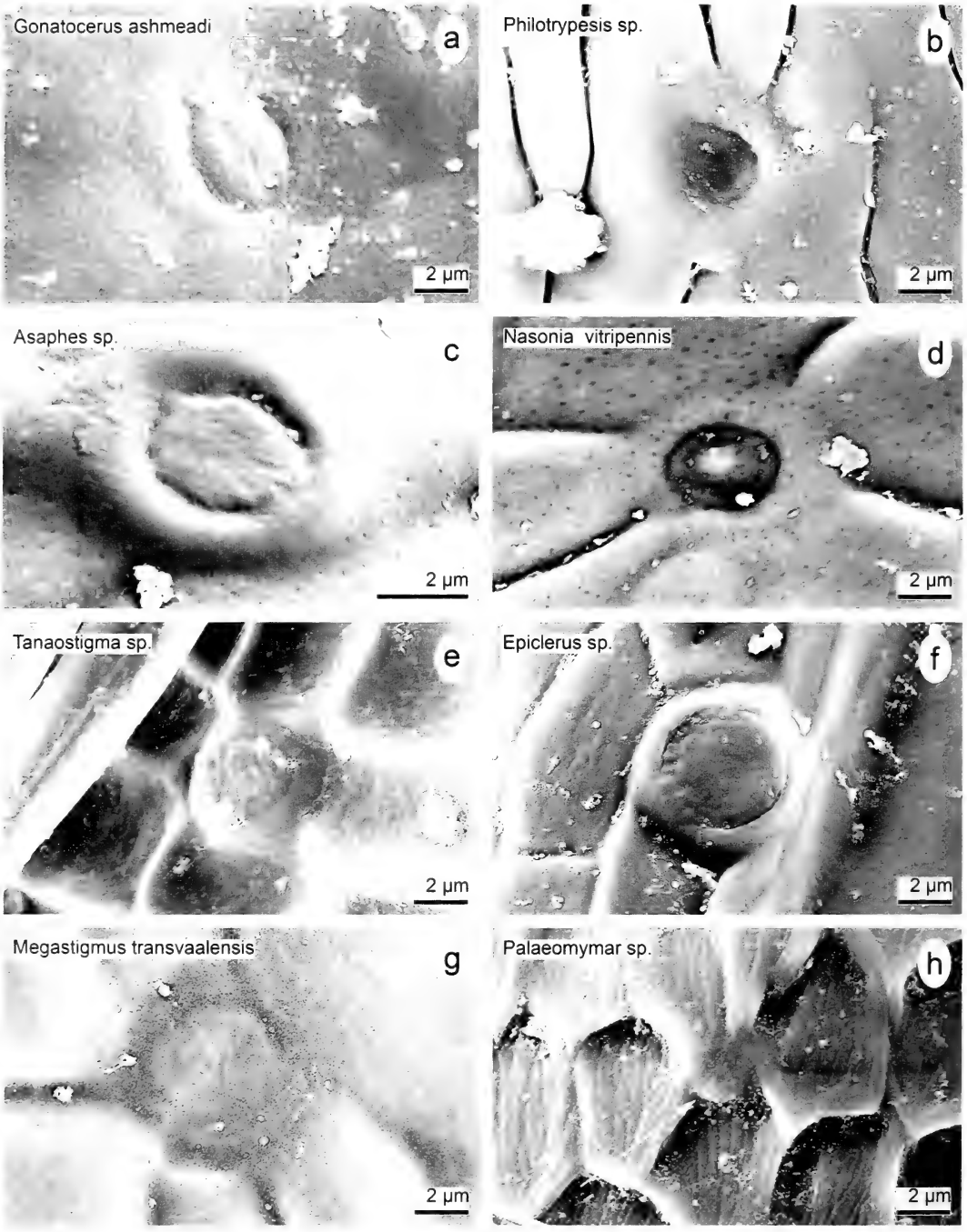

Fig. 8. Variations in external appearance of scutellar sensilla. a: *Gonatocerus ashmeadi* (Mymaridae), b: *Philotrypesis* sp. (Pteromalidae), c: *Asaphes* sp. (Pteromalidae), d: *Nasonia vitripennis* (Pteromalidae), e: *Tanaostigma* sp. (Tanaostigmatidae), f: *Epiclerus* sp. (Tetracampidae), g: *Megastigmus transvaalensis* (Torymidae), h: *Mymaromma anomalum* (Mymarommatidae). Arrow indicates location of sensillum.

al.1996). The sensilla have been referred to as scolopophorous sensilla (Gordh 1975b), and more recently as scutellar sensilla (Babcock et al. 2001; Hayat 1998; Heraty and Polaszek 2000), but most often as placoid sensilla (Annecke and Doutt 1961; Hayat 1998; Kim 2003; Rosen and DeBach 1979; Schauff 1984). Both scolopophorous and placoid refer to specific types of sensilla described by Snodgrass (1935). Scolopophorus sensilla, also known as chordotonal organs, are composed of bundles of sensory cells that attach to a specific point on the cuticle in order to detect vibration. Placoid sensilla are composed of multiple sense cells and function as olfactory sensilla, often with numerous pores through the cuticle. The sensilla found on the chalcidoid scutellum do not possess pores, and are innervated by a single nerve cell as indicated by the lone tubular body (Fig. 6a). They are best defined as campaniform sensilla, which function as mechanoreceptors (Pringle 1938a).

Scutellar sensilla are found in chalcidoid families with small-bodied species, but generally not in families with the largest-bodied species. There does not seem to be an absolute size at which the sensilla are consistently absent, but rather a trend where chalcidoid families with consistently small members such as Aphelinidae, Encyrtidae and Trichogrammatidae possess the sensilla, those with consistently large members such as Chalcididae and Perilampidae do not, and those with intermediate-sized members such as Eulophidae and Torymidae have members with and without the sensilla (Romero and Heraty, in prep.). Presence does not appear to be necessarily correlated with degree of body sclerotization, as sensilla are retained in both larger members of soft-bodied Eulophidae and small well-sclerotized members of some Pteromalidae and Eucharitidae. Scutellar sensilla were found in the outgroup families Ceraphronidae, Diapriidae, Scelionidae and Mymarommatidae. In these families the sensilla are only present in smaller species as is the case within Chalcidoidea. This would indicate that presence of scutellar sensilla is plesiomorphic for Chalcidoidea, and their subsequent loss derived.

In chalcidoids that possess scutellar sensilla, the sensilla vary in size, shape and location. The shape varies from circular to oval, with both shapes commonly observed in campaniform sensilla recorded from other studies (McIver 1985). The size of the sensilla in the subset of taxa measured ranges from 1.81 μm to 5.79 μm. While this is over a 3 fold difference, campaniform sensilla have been recorded as small as 1 μm (Hawke et al. 1973) and as large as 30 μm in other insects (Hustert et al. 1981). Chalcidoid scutellar sensilla generally fall in the 1.5–10 μm range as reported for most campaniform sensilla (Amornsak et al. 1998; Blaney and Chapman 1969; Chevalier 1969; McIver 1985; Moran and Rowley 1975; Schmidt and Smith 1985, 1987).

Variation in size of the sensilla does not seem to be closely tied to the size of the scutellum (Fig. 9a–c). The low R-squared values (≤ 0.081) indicate that size of the scutellum is a poor predictor of the size of the sensilla. In several specimens such as *Gollumiella antennata* (Gahan) (Eucharitidae) and *Microterys nietneri*, there is as much as a 0.87 μm difference between the left and right sensilla on the same specimen. In species represented by multiple specimens, such as *A. melinus*, there appears to be a relation between size of sensilla and size of scutellum with larger specimens possessing larger sensilla (Fig. 9a–c: *A. melinus*). This intraspecific trend between sensillar size and specimen size was also observed by Schmidt and Smith (1985) in their examination of wing sensilla in 18 specimens of *Trichogramma minutum* Riley (Trichogrammatidae).

The shape of the campaniform sensilla has been shown to confer directional sensitivity (Pringle 1961). Circular sensilla do not have directional sensitivity whereas

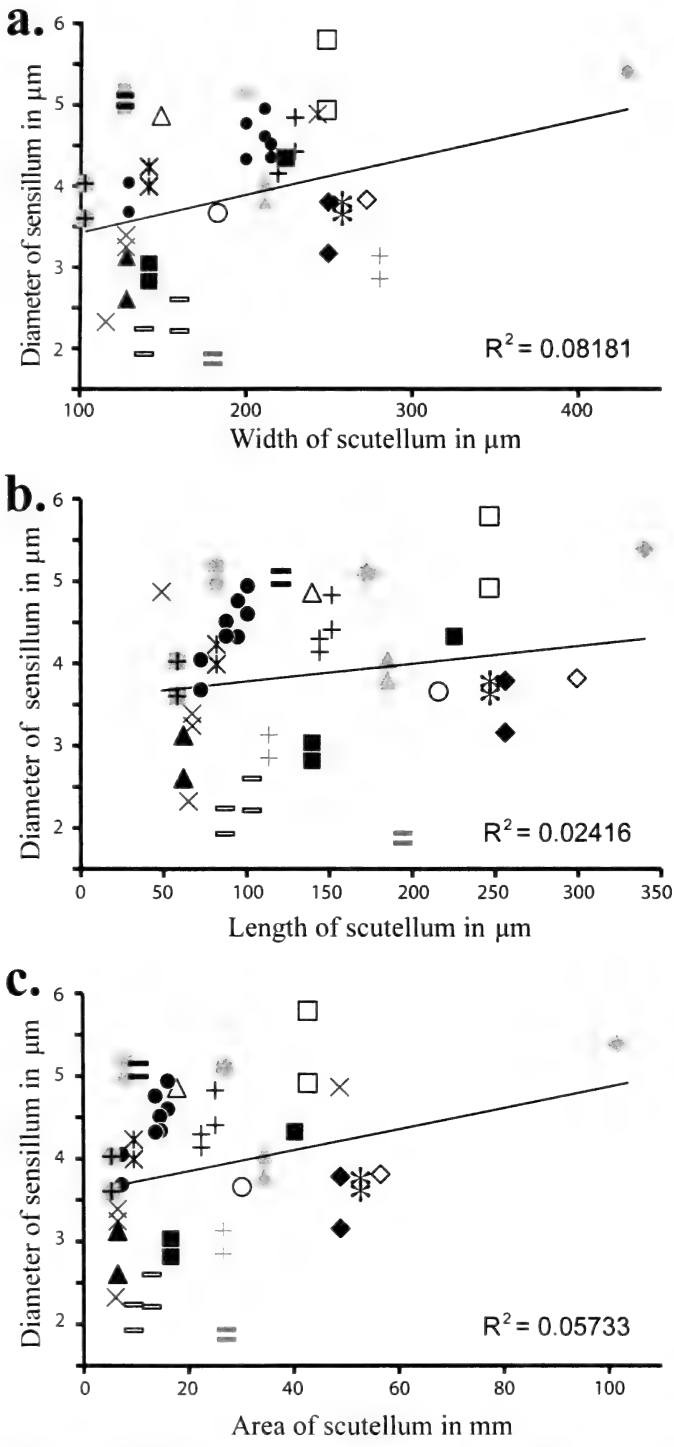

Fig. 9. Diameter of scutellar sensilla and size of scutellum for various chalcidoids. a: Scutellum width and sensillum diameter. b: Scutellum length and sensillum diameter. c: Scutellum area and sensillum diameter.

oval sensilla have more sensitivity to cuticular strain along the major axis (Moran and Rowley 1975). In chalcidoids, the scutellar sensilla can be circular or oval, with oval sensilla found oriented transversely in some Aphelinidae and longitudinally in some Eulophidae and Pteromalidae (Romero and Heraty, in prep.). The variability in the shape as well as in the location of the sensilla on the scutellum is most likely related to the variable morphology of the scutellum and the mesonotum as a whole. Different combinations of morphological features such as thickness and shape of the scutellum, placement of internal ridges, and relation of the scutellum to other sclerites could be associated with diverse complimentary positions of mechanoreceptors such as the scutellar sensilla. The consistent presence of the sensilla across entire families seems to indicate that there is strong selective pressure to maintain the sensilla. The symmetric variation in shape and position of the sensilla and consistency within phylogenetic lineages (Romero and Heraty, in prep.), further support the hypothesis that variation in the sensilla is tied to optimal functionality.

Scutellar sensilla are notably absent in taxa with larger members. One explanation for the exclusive presence of the sensilla in smaller chalcidoids is that these smaller insects employ unique flight techniques not often utilized by larger insects. In his paper on flight and lift production, Weis-Fogh (1973) observed a novel wing motion mechanism in small (1–2 mm) *Encarsia formosa* Gahan (Aphelinidae), later termed clap-and-fling. This mechanism involves the right and left wing meeting, or clapping, at the end of the up-stroke and beginning of the down-stroke and has been observed in other small insects with low Reynolds numbers such as the greenhouse whitefly (Weis-Fogh 1975) and thrips (Ellington 1984). Miller and Peskin (2005) have shown that clap-and-fling provides less of a lift enhancing effect for insects with intermediate Reynolds numbers, such as the fruit fly, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) (Re=64). While larger insects are known to use clap-and-fling when tethered (Vogel 1966; Götz 1987; Zanker 1990), when carrying large loads (Marden 1987), and when performing certain steering maneuvers (Cooter and Baker 1977; Ellington 1984), it seems very small insects are obliged to utilize clap-and-fling on a regular basis (Lehmann et al. 2005; Miller and Peskin 2005). The scutellum is uniquely placed between the junction of the wing base and the lateral anterior connection of the posterior attachment of the longitudinal flight muscles (2nd phragma) and thus could play an important role in monitoring flight activity. As mechanoreceptors, the campaniform sensilla are likely measuring changes in the torsion and tension of the scutellar cuticle. It specifically relates to a small insect flight specialization such as clap-and-fling, and consequently scutellar sensilla are consistently retained in the smallest of chalcidoids and other Hymenoptera.

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LITERATURE CITED

Amornsak, W., B. Cribb, and G. Gordh. 1998. External morphology of antenna sensillae of *Trichogramma australicum* Girault (Hymenoptera: Trichogrammatidae). *International Journal of Insect Morphology and Embryology* 27: 67–82.

Annecke, D. P. and R. L. Doutt. 1961. An interesting encyrtid parasitic in the larvae of carpenter-bees (Hymenoptera: Encyrtidae). *Pan-Pacific Entomologist* 37: 195–200.

Baaren, J. van, R. Barbier, and J. P. Nénon. 1996. Females antennal sensilla of *Epidinocarsis lopezi* and *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), parasitoids of pseudococcid mealybugs. *Canadian Journal of Zoology* 74: 710–720.

Babcock, C. S., J. M. Heraty, P. J. De Barro, F. Driver, and S. Schmidt. 2001. Preliminary phylogeny of *Encarsia* Forster (Hymenoptera: Aphelinidae) based on morphology and 28S rDNA. *Molecular Phylogenetics and Evolution* 18: 306–323.

Barlin, M. R. and S. B. Vinson. 1981. Multiporous plate sensilla in antennae of the Chalcidoidea (Hymenoptera). *International Journal of Insect Morphology and Embryology* 10: 29–42.

Basibuyuk, H. H. and D. L. J. Quicke. 1999. Gross morphology of multiporous plate sensilla in the Hymenoptera (Insecta). *Zoologica Scripta* 28: 51–67.

———, D. L. J. Quicke, A. P. Rasnitsyn, and M. G. Fitton. 2000. Morphology and sensilla of the orbicula, a sclerite between the tarsal claws, in the Hymenoptera. *Annals of the Entomological Society of America* 93: 625–636.

Berlese, A. 1909. *Gli Insetti.* Vol. 1. Societa Editrice Libraria, Milano. 1004 pp.

Blaney, W. M. and R. F. Chapman. 1969. The anatomy and histology of the maxillary palp of *Schistocerca gregaria* (Orthoptera, Acrididae). *Journal of Zoology* 157: 509–535.

Bromley, A. K., J. A. Dunn, and M. Anderson. 1980. Ultrastructure of the antennal sensilla of aphids II. Trichoid, chordotonal and campaniform sensilla. *Cell and Tissue Research* 205: 493–511.

Chevalier, R. L. 1969. The fine structure of campaniform sensilla on the halteres of *Drosophila melanogaster*. *Journal of Morphology* 128: 443–464.

Chiappini, E. and E. Mazzoni. 2000. Differing morphology and ultrastructure of the male copulatory apparatus in species-groups of *Anagrus* Haliday (Hymenoptera: Mymaridae). *Journal of Natural History* 34: 1661–1676.

Cônsoli, F. L., E. W. Kitajima, and J. R. P. Parra. 1999. Sensilla on the antenna and ovipositor of the parasitic wasps *Trichogramma galloi* Zucchi and *T. pretiosum* Riley (Hym., Trichogrammatidae). *Microscopy Research and Technique* 45: 313–324.

Cooter, R. J. and P. S. Baker. 1977. Weis-Fogh clap and fling mechanism in *Locusta*. *Nature* 269: 53–54.

Domenichini, G. 1969. Materiali per la morfologia comparata degli Hymenoptera Chalcidoidea. *Memorie della Società Entomologica Italiana* 48: 583–608.

Doutt, R. L. and G. Viggiani. 1968. The classification of the Trichogrammatidae (Hymenoptera: Chalcidoidea). *Proceedings of the California Academy of Sciences* 35: 477–586.

Ellington, C. P. 1984. The aerodynamics of insect flight. III. Kinematics. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 305: 41–78.

Gibson, G. A. P., J. M. Heraty, and J. B. Woolley. 1999. Phylogenetics and classification of Chalcidoidea and Mymarommatoidea - A review of current concepts (Hymenoptera, Apocrita). *Zoologica Scripta* 28: 87–124.

———, J. Read, and J. T. Huber. 2007. Diversity, classification and higher relationships of Mymarommatoidea (Hymenoptera). *Journal of Hymenoptera Research* 16: 51–146.

Gladun, D. and A. Gumovsky. 2006. The pretarsus in Chalcidoidea (Hymenoptera Parasitica): functional morphology and possible phylogenetic implications. *Zoologica Scripta* 35: 607–626.

Gordh, G. 1975a. Some evolutionary trends in the Chalcidoidea (Hymenoptera) with particular reference to host preference. *Journal of the New York Entomological Society* 83: 279–280.

———. 1975b. A new species of *Forcipestricis* Burks, 1968 (Hymenoptera: Encyrtidae) from Puerto Rico parasitic on *Forcipomyia* (Diptera: Ceratopogonidae). *Florida Entomologist* 58: 239–241.

Götz, K. G. 1987. Course-control, metabolism and wing interference during ultralong tethered flight in *Drosophila melanogaster*. *Journal of Experimental Biology* 128: 35–46.

Harris, R. A. 1979. A glossary of surface sculpturing. *Occasional Papers in Entomology, Sacramento California* 28: 31.

Hayat, M. 1984. Notes on some species of *Coccobius* and *Prophyscus* (Hymenoptera: Aphelinidae), with special reference to Girault and Howard types. *Oriental Insects* 18: 289–334.

———. 1997. 2.3.2. Aphelinidae. Pp. 111–145 *in*: Ben-Dov, Y., and C. J. Hodgson, eds. *Soft Scale Insects their Biology Natural Enemies and Control, Vol 7B.* Elsevier Science Publishers, New York. 442 pp.

———. 1998. Aphelinidae of India (Hymenoptera: Chalcidoidea): A taxonomic revision. *Memoirs of the American Entomological Society* 13: 416.

———. 2003. Records and descriptions of Indian Encyrtidae (Hymenoptera: Chalcidoidea). *Oriental Insects* 37: 187–260.

Hawke, S. D., R. D. Farley, and P. A. Greany. 1973. The fine structure of sense organs in the ovipositor of the parasitic wasp *Orgilus lepidus* Muesbeck. *Tissue and Cell* 5: 171–184.

Heraty, J. 2004. Molecular systematics, Chalcidoidea and biological control. Pp. 39–71 *in*: Ehler, L. E., R. Sforza, and T. Mateille, eds. *Genetics, Evolution and Biological Control.* CABI Publishing, Wallingford, UK. 260 pp.

——— and M. Gates. 2003. Diversity of Chalcidoidea (Hymenoptera) at El Edén Ecological Reserve, México. Pp. 277–292 *in*: Gomez-Pompa, A., M. F. Allen, S. L. Fedick, and J. J. Jimenez-Osornio, eds. *The Lowland Maya Area: Three Millenia at the Human-Wildland Interface. Proceedings of the 21st Symposium of Plant Biology, University of California at Riverside, USA, January 2001.* Food Products Press, Binghamton, USA. 659 pp.

——— and D. Hawks. 1998. Hexamethyldisilazane – A chemical alternative for drying insects. *Entomological News* 109: 369–374.

——— and A. Polaszek. 2000. Morphometric analysis and descriptions of selected species in the *Encarsia strenua* group (Hymenoptera: Aphelinidae). *Journal of Hymenoptera Research* 9: 142–169.

Hernández-Suárez, E., A. Carnero, A. Agular, G. Prinsloo, J. LaSalle, and A. Polaszek. 2003. Parasitoids of whiteflies (Hymenoptera: Aphelinidae, Eulophidae, Platygastridae; Hemiptera: Aleyrodidae) from the Macaronesian archipelagos of the Canary Islands, Madeira and the Azores. *Systematics and Biodiversity* 1: 55–108.

Hicks, J. B. 1857. On a new organ in insects. *The Journal of the Linnean Society, Zoology* 1: 136–140.

Hustert, R., H.-J. Pflüger, and P. Bräunig. 1981. Distribution and specific projections of mechanoreceptors in the thorax and proximal leg joints of locusts. III. The external mechanoreceptors: The campaniform sensilla. *Cell and Tissue Research* 216: 97–111.

Huang, J. 1994. *Systematic studies on Aphelinidae of China (Hymenoptera: Chalcidoidea).* Chongquing Publishing House, Chongquing. 348 pp.

Isidoro, N., F. Bin, S. Colazza, and S. B. Vinson. 1996. Morphology of antennal gustatory sensilla and glands in some parasitoid Hymenoptera with hypothesis on their role in sex and host recognition. *Journal of Hymenoptera Research* 5: 206–239.

Karnovsky, M. J. 1965. A formaldehyde-glutaraldehyde fixative of high osmolality for use in electron microscopy. *Journal of Cell Biology* 27: 137–138A.

Kelsey, L. P. 1957. The skeleto-motor mechanism of the Dobson Fly, *Corydalus cornutus*. Part II. Pterothorax. *Memoirs of the Cornell University Agricultural Experimental Station* 346: 31 pp. +55 Figs.

Kim, J.-W. 2003. *Classification and evolution of the Aphelininae (Hymenoptera: Aphelinidae).* PhD. Dissertation, University of California, Riverside. 287 pp.

Krogmann, L. and L. Vilhelmsen. 2006. Phylogenetic implications of the mesosomal skeleton in Chalcidoidea (Hymenoptera, Apocrita) – tree searches in a jungle of homoplasy. *Invertebrate Systematics* 20: 615–674.

LaSalle, J. 1993. Parasitic Hymenoptera, biological control and biodiversity (Chapter 8). Pp. 197–215 *in*: LaSalle, J., and I. D. Gauld eds. *Hymenoptera and Biodiversity*. CAB International, Wallingford, UK. 348 pp.

———, A. Polaszek, J. S. Noyes, and G. Zolnerowich. 1997. A new whitefly parasitoid (Hymenoptera: Pteromalidae: Eunotinae) with comments on its placement, and implications for classification of Chalcidoidea with particular reference to the Eriaporinae (Hymenoptera: Aphelinidae). *Systematic Entomology* 22: 131–150.

Le Ralec, A. and J. M. Rabasse. 1988. Structure, sensory receptors and operation of the ovipositor of three Aphidiidae. Pp. 83–88 *in*: Niemczyk, E., and A. F. G. Dixon eds. *Ecology and effectiveness of Aphidophaga*. SPB Academic Publishing, *The Hague*. 341 pp.

———, J. M. Rabasse, and E. Wajnberg. 1996. Comparative morphology of the ovipositor of some parasitic Hymenoptera in relation to characteristics of their host. *Canadian Entomologist* 128: 413–433.

——— and E. Wajnberg. 1990. Sensory receptors of the ovipositor of *Trichogramma maidis* (Hym: Trichogrammatidae). *Entomophaga* 35: 293–299.

Lehmann, F.-O., S. P. Sane, and M. Dickinson. 2005. The aerodynamic effects of wing–wing interaction in flapping insect wings. *The Journal of Experimental Biology* 208: 3075–3092.

Lenteren, C. J. van. 1994. Oviposition behavior of *Aphytis* (Hymenoptera, Chalcidoidea, Aphelinidae), parasitoids of armored scale insects (Homoptera, Coccoidea, Diaspididae). Pp. 13–39 *in*: Rosen, D. ed. *Advances in the Study of Aphytis (Hymenoptera: Aphelinidae).* Intercept Ltd., Andover. 362 pp.

Marden, J. 1987. Maximum lift production during takeoff in flying animals. *Journal of Experimental Biology* 130: 235–258.

McIver, S. B. 1985. Mechanoreception. Pp. 71–132 *in*: Kerkut, G. A., and L. I. Gilbert eds. *Comprehensive Insect Physiology, Biochemistry and Pharmacology, Volume 6: Nervous System: Sensory*. Pergamon Press, New York. 710 pp.

——— and R. Siemicki. 1975. Campaniform sensilla on the palps of *Anopheles stephensi* Liston (Diptera: Culicidae). *International Journal of Insect Morphology and Embryology* 4: 127–130.

Miller, L. A. and C. S. Peskin. 2005. A computational fluid dynamics of 'clap and fling' in the smallest insects. *Journal of Experimental Biology* 208: 195–212.

Moran, D. T. and J. C. RowleyIII 1975. High voltage and scanning electron microscopy of the site of stimulus reception of an insect mechanoreceptor. *Journal of Ultrastructure Research* 50: 38–46.

Noyes, J. S. 1988. Encyrtidae (Insecta: Hymenoptera). *Fauna of New Zealand* 13: 188.

———. 2000. Encyrtidae of Costa Rica (Hymenoptera: Chalcidoidea), 1. The subfamily Tetracneminae, parasitoids of mealybugs (Homoptera: Pseudococcidae). *Memoirs of the American Entomological Institute* 62: 355.

———. 2003. *Universal Chalcidoidea Database*. World Wide Web electronic publication. www.nhm.ac.uk/entomology/chalcidoids/index.html [accessed 28-July-2006].

——— and E. W. Valentine. 1989. Chalcidoidea (Insecta: Hymenoptera) – introduction, and review of genera in smaller families. *Fauna of New Zealand* 18: 91.

———, J. B. Woolley, and G. Zolnerowich. 1997. Encyrtidae. Pp. 170–320 *in*: Gibson, G. A. P., J. T. Huber, and J. B. Woolley eds. *Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera)*. NRC Research Press, Ottawa. 794 pp.

Olson, D. M. and D. A. Andow. 1993. Antennal sensilla of female *Trichogramma nubilale* (Ertle and Davis) (Hymenoptera: Trichogrammatidae) and comparisons with other parasitic Hymenoptera. *International Journal of Insect Morphology and Embryology* 22: 507–520.

Pringle, J. W. S. 1938a. Proprioception in insects: I. A new type of mechanical receptor from the palps of the cockroach. *The Journal of Experimental Biology* 15: 101–113.

———. 1938b. Proprioception in insects: II. The action of the campaniform sensilla on the legs. *The Journal of Experimental Biology* 15: 114–131.

———. 1961. Proprioception in arthropods. Pp. 256–282 *in*: Ramsay, J. A., and V. B. Wigglesworth, eds. *The Cell and the Organism*. Cambridge University Press, London. 349 pp.

Prinsloo, G. L. 1997. 2.3.1 Encyrtidae. Pp. 69–109 *in*: Ben-Dov, Y., and C. J. Hodgson, eds. *Soft Scale Insects their Biology Natural Enemies and Control, Vol 7B*. Elsevier Science Publishers, New York. 442 pp.

Romani, R., N. Isidoro, and F. Bin. 1999. Further evidence of male antennal glands in Aphelinidae: the case of *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae). *Journal of Hymenopteran Research* 8: 109–115.

Rosen, D. and P. DeBach. 1979. Species of *Aphytis* of the World (Hymenoptera: Aphelinidae). *Series Entomologica* 17: 801.

Schauff, M. E. 1984. The holarctic genera of Mymaridae (Hymenoptera: Chalcidoidea). *Memoirs of the Entomological Society of Washington* 12: 67.

———, G. A. Evans, and J. M. Heraty. 1996. A pictorial guide to the species of *Encarsia* (Hymenoptera: Aphelinidae) parasitic on whitefies (Homoptera: Aleyrodidae) in North America. *Proceedings of the Entomological Society of Washington* 98: 1–35.

Schmidt, J. M. and J. J. B. Smith. 1985. The ultrastructure of the wings and the external sensory morphology of the thorax in female *Trichogramma minutum* Riley (Hymenoptera: Chalcidoidea: Trichogrammatidae). *Proceedings of the Royal Society of London. Series B, Biological Sciences* 224: 287–313.

——— and J. J. B. Smith. 1987. The external sensory morphology of the legs and hairplate system of female *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae). *Proceedings of the Royal Society of London. Series B, Biological Sciences* 232: 287–313.

Snodgrass, R. E. 1935. The sense organs. Pp. 515–25 *in*: Snodgrass, R. E. ed. *Principles of Insect Morphology*. McGraw-Hill, New York. 667 pp.

Spurr, A. R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. *Journal of Ultrastructure Research* 26: 31–43.

Thurm, D. 1964. Mechanoreceptors in the cuticle of the honey bee: fine structure and stimulus mechanism. *Science* 145: 1063–1065.

——— and J. Küppers. 1980. Epithelial physiology of insect sensilla. Pp. 735–763 *in*: Locke, M., and D. S. Smith, eds. *Insect Biology in the Future "VBW 80"*. Academic Press, New York. 977 pp.

Veen, J. C. van. and M. L. E. van Wijk. 1985. The unique structure and functions of the ovipositor of the non-paralyzing ectoparasitoid *Colpoclypeus florus* Walk. (Hym., Eulophidae) with special reference to antennal sensilla and immature stages. *Zeitschrift fur Angewandte Entomologie* 99: 511–531.

Vilhelmsen, L. 2000. Before the wasp-waist: comparative anatomy and phylogenetic implications of the skeleto-musculature of the thoraco-abdominal boundary region in basal Hymenoptera (Insecta). *Zoomorphology* 119: 185–221.

Vogel, S. 1966. Flight in *Drosophila*. I. Flight performance of tethered flies. *Journal of Experimental Biology* 44: 567–578.

Walther, J. R. 1983. Antennal patterns of sensilla of the Hymenoptera - a complex character of phylogenetic reconstruction. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 26: 373–392.

Weis-Fogh, T. 1973. Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift production. *Journal of Experimental Biology* 59: 169–230.

———. 1975. Unusual mechanisms for the generation of lift in flying animals. *Scientific American* 233: 81–87.

Zanker, J. M. 1990. The wing beat of *Drosophila melanogaster*. I. Kinematics. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 327: 1–18.

Zill, S. N. and D. T. Moran. 1981. The exoskeleton and insect proprioception: I. Responses of tibial campaniform sensilla to external and muscle regenerated forces in the American cockroach, *Periplaneta americana*. *Journal of Experimental Biology* 91: 1–24.

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A New Species of *Lysiphlebus* Förster 1862 (Hymenoptera: Braconidae, Aphidiinae) Attacking Soybean Aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) from China

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Abstract.—***Lysiphlebus orientalis* sp. n.** is described from China. The new species was reared from *Aphis glycines* Matsumura/ *Glycine max* association. On the basis of the fore wing venation pattern (short R1 vein) and the number of maxillary and labial palpomeres, we can preliminarily classify *L. orientalis* sp.n. as a member of the "*testaceipes* Cresson" species-group. Laboratory populations of *L. orientalis* are thelytokous, the first record of this phenomenon in this species group.

Key words.—*Lysiphlebus orientalis sp.n.*, aphid parasitoids, *Glycine max*

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is native to northeast Asia (China, Korea and Japan) but was discovered infesting soybean fields in North America beginning in summer 2000 (Venette and Ragsdale 2004) and has become a serious pest throughout soybean-growing areas of the Midwest (Ragsdale et al. 2004, 2007). These aphids not only devastate soybean plants by direct feeding, but they also spread plant-pathogenic viruses (Halbert et al. 1986; van den Berg et al. 1997; Wang et al. 1994).

In Asia, the soybean aphid is attacked by braconid and aphelinid parasitoids (Chang et al. 1994; Wu et al. 2004b; Liu et al. 2004; Miao et al. 2007). The main natural enemies of soybean in North America are native and naturalized predators, including lady beetles, minute pirate bugs and predatory flies (Fox et al. 2004, 2005; Rutledge et al. 2004; Rutledge and O'Neil 2005; Costa-

magna and Landis 2006, 2007; Desneux et al. 2006; Donaldson et al. 2007; Gardiner and Landis 2007; Chacon et al. 2008; Costamagna et al. 2008; Gardiner et al. 2009). Parasitoids attacking soybean aphid in North America have been rare, on the other hand (Lin and Ives 2003; Kaiser et al. 2007; Noma and Brewer 2008; Pike et al. 2007), with the exception of relatively high parasitism by aphidiine braconids reported in New York state (Nielsen and Hajek 2005) and also by *Aphelinus certus*, an accidentally-introduced species, in eastern North America (Heraty et al. 2007; Heimpel et al. in press).

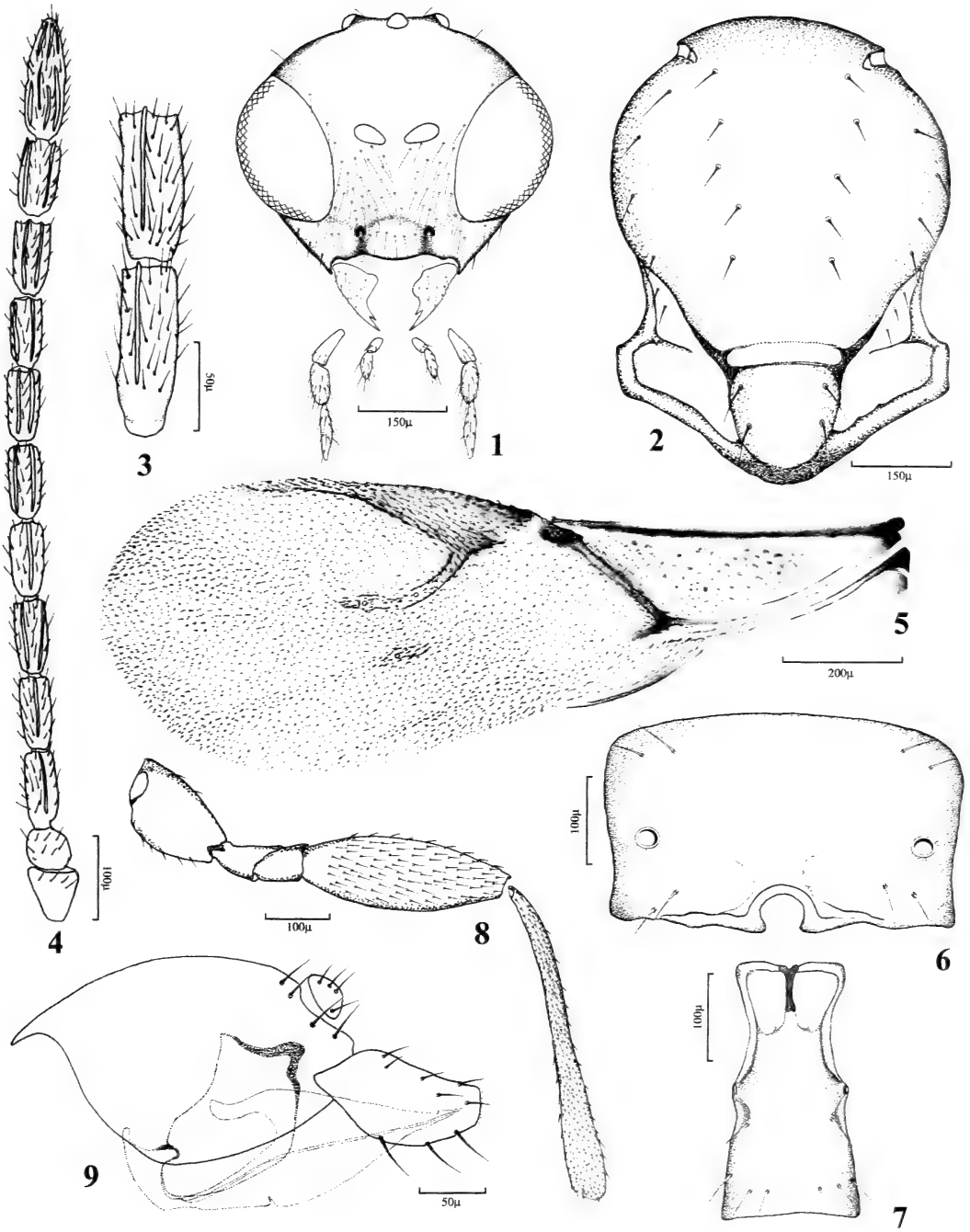
Initial biological control efforts directed at the soybean aphid have resulted in the importation of several aphid parasitoids and predators from China, Japan and South Korea into quarantine, including a strain of an aphelinid parasitoid from Japan in 2001 (Heimpel et al. 2004; Wu et al. 2004a) and at least two species of the aphidiine braconid genus *Binodoxys* (Wyckhuys et al. 2007; Desneux et al. 2009a; Desneux et al. 2009b). In addition to these species, recent ongoing research on the introduction of the braconid parasitoids of soybean aphid from China has yielded the discovery of a new species of *Lysiphlebus* Förster contributing to our current revisionary work on the subtribe Lysiphlebina Mackauer. Here we describe the new species and discuss its identity and possible distributional pattern.

MATERIAL AND METHODS

Parasitoids were obtained by collecting samples of *Glycine max* plants colonized by *A. glycines* in commercial and experimental fields in China. Collections at field sites in northeastern Chinese provinces were made by K. Hoelmer, J. Yu and M. Wang during June, July and August of 2006 in the vicinity of Harbin, Heilongjiang province, and Xiuyan, Liaoning province. Leaves and stems of plants with aphid colonies were cut, placed into plastic zip-lock bags and held in chilled picnic coolers while in the field, then transferred to the laboratory where they were kept in containers covered with nylon mesh at room temperature during sample processing. Emergent adults were collected in vials and mummified aphids containing developing parasitoids were placed individually in wells of plastic microtiter plates and sealed with corks for shipment. Vials with adults were streaked with honey, and each microtiter plate well was given a small droplet of honey to sustain adults that emerged during transit. Parasitoids were shipped to the USDA ARS biological control quarantine laboratory in Newark, Delaware, USA. Quarantine cultures of *A. glycines* parasitoids were initiated at Newark from these shipments and maintained on *A. glycines* on soybean. After establishment, a portion of the cultures were transferred to the University of Minnesota, USA to support host range evaluations. The new species of *Lysiphlebus* was discovered during these evaluations. Slides were made of dissected specimens using Hoyer's media. External morphology was studied using an Olympus SZX9 stereomicroscope. Illustrations were made based on slide-mounted specimens using an Olympus BH2 Phase-contrast microscope with a drawing tube. Morphological terminology follows Starý (1973) and Sharkey and Wharton (1997). Subdivisions of the flagellum are referred to as segments in order to maintain consistency with other taxonomic works on Aphidiinae. Measurements in the description were taken using an ocular micrometer. See Tomić et al. (2005) for more details regarding measurements.

RESULTS

Diagnosis.—On the basis of the fore wing venation pattern (short R1 vein, which is equally or slightly shorter than the stigma) (Fig. 5) and the number of maxillary and labial palpomeres (three maxillary and two labial palpomeres) (Fig. 1), we preliminarily classify *Lysiphlebus orientalis* sp.n. as a member of the "*testaceipes* Cresson" spe-



Figs 1–9. *Lysiphlebus orientalis* sp. n., female paratype. 1, head and mouthparts; 2, mesoscutum; 3, first and second flagellar segments; 4, antenna; 5, fore wing; 6, propodeum; 7, petiole; 8, hind leg; 9, genitalia.

cies-group. *Lysiphlebus orientalis* sp. n. differs from the nominate species *L. testaceipes* by having a smaller number of antennal segments (*L. orientalis* sp. n. has 12-segmented antennae vs. 13–14-segmented antennae of *L. testaceipes*). Also, flagellomeres 1 and 2 of *L. orientalis* sp. n. bear 1–2 and 2–3 longitudinal placodes, respec-

tively, but *L. testaceipes* has 4–6 longitudinal placodes on flagellomere 1 and 5–7 on flagellomere 2. *Lysiphlebus orientalis* sp. n. has an elongately triangular stigma (stigma length/width ratio of 2.9–3.2), but *L. testaceipes* has a widely triangular stigma (stigma length/width ratio of 2.4–2.6). In addition, *L. orientalis* sp. n. differs from all other species in having short marginal fore wing setae. All other species of the "*testaceipes* " species-group have long marginal fore wing setae.

***Lysiphlebus orientalis* Starý & Rakhshani sp. n.**

(Figs 1–12)

Description

Female: Head (Fig. 1) transverse, wider than mesosoma at tegulae, bearing sparse setae. Eyes medium sized, oval, laterally prominent. Face laterally pubescent. Tentorial index (tentoriocular line/intertentorial line) 0.49–0.50, Clypeus slightly protruding with 5–6 long setae. Labrum distinct, with 2 short setae on outer margin. Malar space equal to 0.28–0.30 of longitudinal eye diameter. Mandible bidentate, with 7–9 setae in outer surface. Maxillary palpi with 3 palpomeres, labial palpi with 2 palpomeres. Antenna 12-segmented (scape and pedicel as primary segments and 10 flagellomeres), filiform (Fig. 4). Pedicel subsphaerical. F_1 (Fig. 3) equal or slightly longer than F_2 and 2.2–2.6× as long as its maximum width. F_1 and F_2 bearing 1–2 and 2–3 longitudinal placodes respectively (Fig. 3). Flagellomeres covered uniformly with semi-erect setae.

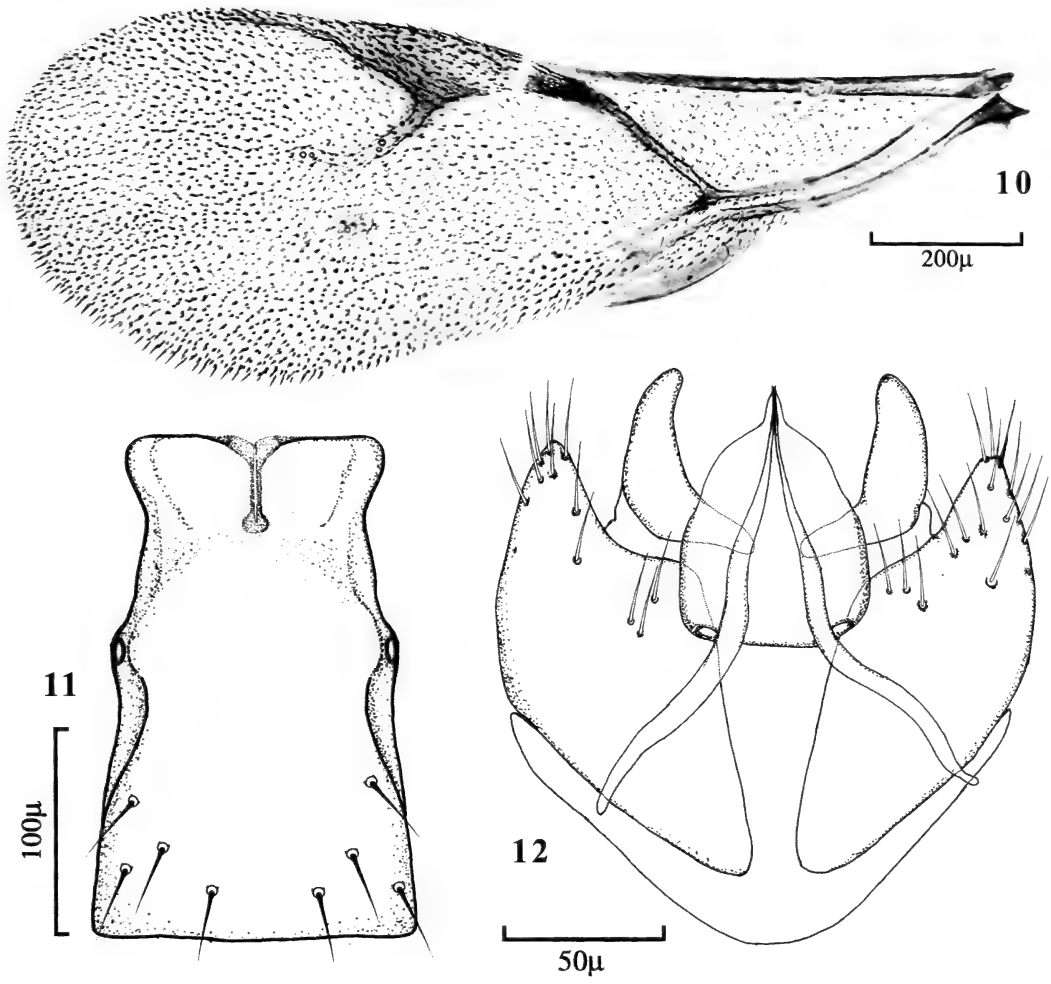
Mesosoma - Mesoscutum (Fig. 2) smooth, covering pronotum from above; notaulices distinct in ascedent portion of anterolateral margin, effaced dorsally, with 6–7 long setae along laterodorsal part of mesoscutum. Scutellum subquadrate, bearing 2 long setae at each lateral margin. Propodeum (Fig. 6) smooth, with two divergent carinae at base, (some specimens manifest indications of "pseudo-carination" or rugosities in upper part of propodeum, establishing incomplete central areola). Upper and lower parts of propodeum with 2–3 and 1–2 long setae on each side. Fore wing (Fig. 5) densely pubescent, lower marginal setae short, equal to those on surface; stigma, 2.9–3.2× as long as its width, 1.00–1.27 as long as R1 vein (=metacarpus). R_1 vein 1.35–1.40× as long as R_2 vein, 2.00–2.10× as long as rs-m vein. Hind femur with short adpressed setae (Fig. 8).

Metasoma - Petiole (Fig. 7) elongate, smooth, slightly convex dorsally, with lateral depression after prominent spiracular tubercles, positioned midsegment; its length 2.00–2.25× its width at spiracles, 1.50–1.70× its width at base; 4–5 setae positioned on posterior laterodorsal margin, one long seta posterior to spiracles. Ovipositor sheath (Fig. 9) short, wide at base, dorsally slightly convex, narrowed toward tip, apically truncated, bearing four long setae at tip and 4–5 shorter scattered setae on lateral and dorsal surface. Length of ovipositor sheath 1.8–2.0× its maximum width at base, 4.2–4.4× its minimum width at tip. Second valvula with smooth dorsal outline.

Body length: 1.5–1.7 mm

Coloration: General body color light brown, head and antenna light brown, mouthparts except tips of mandible yellowish. Pronotum brown; mesoscutum and mesopleuron dark brown. Propodeum brown. Legs yellow, hind leg with brown dorsal outlines. Wings hyaline, venation yellowish brown. Propodeum brown. Petiole yellow, other metasomal terga light brown, dorsally darker. Ovipositor sheath dark brown.

Male: Antenna 14-segmented. Maxillary palpi with 3 palpomeres, labial palpi with 2 palpomeres. Fore wing venation as in female (Fig. 10). Fore wing lower marginal setae distinctly longer than those on surface; stigma widely triangular, 2.8–3.1× as long as its width. Petiole (Fig. 11) elongately quadrangular, 1.75–1.85× its width



Figs 10–12. *Lysiphlebus orientalis* sp. n., male. 10, fore wing; 11, petiole; 12, genitalia.

at spiracles, with lateral depression after spiracular tubercles. Aedeagus subtriangular (Fig. 12) with subparallel posterolateral margins and short tip. Body darker than female, head and thorax black brown, antenna dark brown, mouthparts yellowish brown. Wings slightly translucent. Legs brown with light yellow patches at ventral and tip of segments. Petiole light brown, other metasomal segments greyish brown. Body length: 1.5–1.6 mm.

Material

Holotype: ♀ reared from *Aphis glycines* Matsumura on *Glycine max* (L.) Merrill, CHINA, Harbin, VIII 2006, Leg. K. Hoelmer, laboratory culture, reared on *Aphis glycines* on *Glycine max*, University of Minnesota, USA, 2008, G. E. Heimpel (Collection of United States National Museum of Natural History).

Paratypes (same sampling data as holotype): 3♀ and ♂ paratypes are deposited in the collection of United States National Museum of Natural History. 6♀ paratypes are deposited in the collection of P. Starý (České Budějovice). 3♀ paratypes are deposited in the collection of Institute of Zoology, Chinese Academy of Sciences, Beijing, China. 7♀ and 2♀ paratypes are deposited in the collection of Institute of Zoology, Faculty of Biology, University of Belgrade (Serbia) and in collection of University of Zabol (Iran), respectively.

Additional material: 20♀ and 2♂ with same sampling data as holotype deposited in the collection of Institute of Zoology, Faculty of Biology, University of Belgrade (Serbia).

DISCUSSION

Lysiphlebus orientalis n. sp. is a new member of the "*testaceipes*" species group, a tentative taxon which has previously been classified within subgenus *Phlebus* (Starý 1975). The group includes the species distributed within a specific geographic area of which only *L. testaceipes* Cresson has a wider distribution, assumed to be due to introduction and expansion of its range in combination with its opportunistic host range (Kavallieratos and Lykouressis 1999, 2004; Kavallieratos et al. 2001; Pons et al. 2004; Starý et al. 2004). Originally believed to be a North American species, *L. testaceipes* has also been recovered from the east Palaearctic (Starý et al. 2002). The known distribution of *L. orientalis* is northeast China, but further research may document a broader distribution. Other taxa which should be preliminarily included in the "*testaceipes*" group are: *L. fritzmuelleri* Mackauer (Europe), *L. desertorum* Starý (Central Asia), *L. ussuriensis* Kiriac (Far East) and *L. utahensis* (Smith) (Nearctic).

Examination of the field-collected specimens revealed a highly skewed female: male sex ratio. However, laboratory cultured material comprised a mostly or completely uniparental population, a phenomenon that has not been previously recorded in any member of the *testaceipes* group, although it occurs in other *Lysiphlebus* species, namely *L. fabarum* (Marshall), *L. cardui* (Marshall), and *L. confusus* Tremblay and Eady (Belshaw et al. 1999; Starý 1999; Starý et al. 2002), which belong to the subgenus *Phlebus* Starý. Further investigations are needed to elucidate the nature and distribution of thelytoky in the respective groups.

Our ongoing research on the subtribe Lysiphlebina Mackauer reveals several *Lysiphlebus* species in Europe that are putatively related to *L. orientalis* sp.n. on the basis of morphological characters. We shall resolve the taxonomic status of the aforementioned *Lysiphlebus* taxa and their possible relations with *L. orientalis* sp.n. using molecular markers in a future contribution.

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LITERATURE CITED

Belshaw, R., D. L. J. Quicke, W. Völkl, and H. C. J. Godfray. 1999. Molecular markers indicate rare sex in a predominantly asexual parasitoid wasp. *Evolution* 53: 1189–1199.

Chacon, J. M., D. A. Landis, and G. E. Heimpel. 2008. Potential for biotic interference of a classical biological control agent of the soybean aphid. *Biological Control* 46: 216–225.

Chang, Y. D., J. Y. Lee, and Y. N. Youn. 1994. Primary parasitoids and hyperparasitoids of the soybean aphid, *Aphis glycines* (Homoptera: Aphididae). *Korean Journal of Applied Entomology* 33: 51–55.

Costamagna, A. C. and D. A. Landis. 2006. Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. *Ecological Applications* 16: 1619–1628.

——— and D. A. Landis. 2007. Quantifying predation on soybean aphid through direct field observations. *Biological Control* 42: 16–24.

———, D. A. Landis, and M. J. Brewer. 2008. The role of natural enemy guilds in *Aphis glycines* suppression. *Biological Control* 45: 368–379.

Desneux, N., R. J. O'Neil, and H. J. S. Yoo. 2006. Suppression of population growth of the soybean

aphid, *Aphis glycines* Matsumura, by predators: the identification of a key predator and the effects of prey dispersion, predator abundance, and temperature. *Environmental Entomology* 35: 1342–1349.

———, R. J. Barta, K. A. Hoelmer, K. R. Hopper, and G. E. Heimpel. 2009a. Multifaceted determinants of host specificity in an aphid parasitoid. *Oecologia* 160: 387–398.

———, P. Starý, C. J. Delebeque, T. D. Gariepy, R. J. Barta, K. A. Hoelmer, and G. E. Heimpel. 2009b. Cryptic species of parasitoids attacking the soybean aphid (Hemiptera: Aphididae), in Asia: *Binodoxys communis* (Gahan) and *Binodoxys koreanus* (Hymenoptera: Braconidae: Aphidiinae). *Annals of the Entomological Society of America* 102: 925–936.

Donaldson, J. R., S. W. Myers, and C. Gratton. 2007. Density-dependent responses of soybean aphid (*Aphis glycines* Matsumura) populations to generalist predators in mid to late season soybean fields. *Biological Control* 43: 111–118.

Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2004. Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environmental Entomology* 33: 608–618.

———, D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2005. Impact of predation on establishment of the soybean aphid, *Aphis glycines* in soybean, *Glycine max*. *BioControl* 50: 545–563.

Gardiner, M. M. and D. A. Landis. 2007. Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera : Coccinellidae) on *Aphis glycines* (Hemiptera : Aphididae) biological control in cage studies. *Biological Control* 40: 386–395.

———, D. A. Landis, C. Gratton, C. D. Difonzo, M. E. O'Neal, J. Chacon, M. Wayo, N. Schmidt, and G. E. Heimpel. 2009. Landscape structure impacts biocontrol services in north-central U.S. soybean fields. *Ecological Applications* 19: 143–154.

Halbert, S. E., G. X. Zhang, and Z. Q. Pu. 1986. Comparison of sampling methods for alate aphids and observations on epidemiology of soybean mosaic virus in Nanjing, China. *Annals of Applied Biology* 109: 479–483.

Heimpel, G. E., D. W. Ragsdale, R. Venette, K. R. Hopper, R. J. O'Neil, C. Rutledge, and Z. Wu. 2004. Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits. *Annals of the Entomological Society of America* 97: 249–258.

———, L. E. Frelich, D. A. Landis, K. R. Hopper, K. A. Hoelmer, Z. Sezen, M. K. Asplen, and K. Wu. In press. European buckthorn and Asian soybean aphid as part of an extensive invasional meltdown in North America. *Biological Invasions*, in press.

Heraty, J. M., J. B. Woolley, K. R. Hopper, D. L. Hawks, J. W. Kim, and M. Buffington. 2007. Molecular phylogenetics and reproductive incompatibility in a complex of cryptic species of aphid parasitoids. *Molecular Phylogenetics and Evolution* 45: 480–493.

Kaiser, M. E., T. Noma, M. J. Brewer, K. S. Pike, J. R. Vockeroth, and S. D. Gaimari. 2007. Hymenopteran parasitoids and dipteran predators found using soybean aphid after its midwestern United States invasion. *Annals of the Entomological Society of America* 100: 196–205.

Kavallieratos, N. G. and D. P. Lykouressis. 1999. Parasitoids (Hymenoptera: Braconidae) emerged from aphids (Homoptera: Aphidoidea) on citrus and their frequency in Greece. *Bolletino del Laboratorio di Entomologia Agraria "Filippo Silvestri" di Portici* 55: 93–104.

——— and D. P. Lykouressis. 2004. The coloration of *Aphis gossypii* Glover mummies as a useful tool for Aphidiinae parasitoid identification (Hymenoptera: Braconidae). *Israel Journal of Entomology* 34: 75–82.

———, D. P. Lykouressis, G. P. Sarlis, G. J. Stathas, A. Sanchis Segovia, and C. G. Athanassiou. 2001. The Aphidiinae (Hymenoptera: Ichneumonoidea: Braconidae) of Greece. *Phytoparasitica* 29: 306–340.

Lin, L. A. and A. R. Ives. 2003. The effect of parasitoid host-size preference on host population growth rates: an example of *Aphidius colemani* and *Aphis glycines*. *Ecological Entomology* 28: 542–550.

Liu, J., K. Wu, K. R. Hopper, and K. Zhao. 2004. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in Northern China. *Annals of the Entomological Society of America* 97: 235–239.

Miao, J., K. Wu, K. R. Hopper, and G. Li. 2007. Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and impact of natural enemies in northern China. *Environmental Entomology* 36: 840–848.

Nielsen, C. and A. E. Hajek. 2005. Control of invasive soybean aphid, *Aphis glycines* (Hemiptera: Aphididae), populations by existing natural enemies in New York state, with emphasis on entomopathogenic fungi. *Environmental Entomology* 34: 1036–1047.

Noma, T. and M. J. Brewer, M.J. 2008. Seasonal abundance of resident parasitoids and predatory flies and corresponding soybean aphid densities, with comments on classical biological control of soybean aphid in the Midwest. *Journal of Economic Entomology* 101: 278–287.

Pike, K. S., P. Starý, M. I. Brewer, T. Noma, S. Langley, and M. Kaiser. 2007. A new species of *Binodoxys* (Hymenoptera: Braconidae, Aphidiinae), parasitoid of the soybean aphid, *Aphis glycines* Matsunmura, with comments on biocontrol. *Proceedings of the Entomological Society of Washington* 109: 359–365.

Pons, X., B. Lumbierres, and P. Starý. 2004. Expansion de *Lysiphlebus testaceipes* (Cresson) (Hym., Braconidae, Aphidiinae) en el Noreste de la Peninsula Iberica. *Boletin de sanidad vegetal. Plagas* 30: 547–552.

Ragsdale, D. W., B. P. McCornack, R. C. Venette, B. D. Potter, I. V. Macrae, E. W. Hodgson, M. E. O'Neal, K. D. Johnson, R. J. O'Neil, C. D. Difonzo, T. E. Hunt, P. A. Glogoza, and E. M. Cullen. 2007. Economic threshold for soybean aphid (Hemiptera : Aphididae). *Journal of Economic Entomology* 100: 1258–1267.

———, D. J. Voegtlin, and R. J. O'Neil. 2004. Soybean aphid biology in North America. *Annals of the Entomological Society of America* 97: 204–208.

Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. *Annals of the Entomological Society of America* 97: 240–248.

——— and R. J. O'Neil. 2005. *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumura. *Biological Control* 33: 56–64.

Sharkey, M. J. and R. A. Wharton. 1997. Morphology and terminology. Pp. 19–37 *in*: Wharton, R. A., P. M. Marsh, and M. J. Sharkey eds. *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*. Special Publication 1, International Society of Hymenopterists, Washington, DC.

Starý, P. 1973. A review of the *Aphidius* species (Hymenoptera: Aphidiidae) of Europe. *Annotationes Zoologicae et Botanicae* 84: 1–85.

———. 1975. The subgeneric classification of *Lysiphlebus* Foerster, 1862 (Hymenoptera, Aphidiidae). *Annotationes Zoologicae et Botanicae* 105: 1–9.

———. 1999. Biology and distribution of microbe-associated thelytokous population of aphid parasitoids (Hym., Braconidae, Aphidiinae). *Journal of Applied Entomology* 123: 231–235.

———, J. Havelka, and J. Y. Choi. 2002. New species and populations of *Lysiphlebus* Föerster - aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) in Korea. *Insecta Koreana* 19: 205–211.

———, B. Lumbierres, and X. Pons. 2004. Opportunistic changes in the host range of *Lysiphlebus testaceipes* (Cr.), an exotic aphid parasitoid expanding in the Iberian Peninsula. *Journal of Pest Science* 77: 139–144.

Tomić, M., Ž. Tomanović, N. G. Kavallieratos, P. Starý, C. G. Athanassiou, V. Tomić, and L. Lučić. 2005. Morphological variability of several biotypes of *Ephedrus plagiator* (Nees) (Hymenoptera: Braconidae: Aphidiinae) with the description of a new species. *Zoologischer Anzeiger* 244: 153–162.

van den Berg, H., D. Ankasah, A. Muhammad, R. Rusli, A. Widayanto, H. B. Wirasto, and I. Yully. 1997. Evaluating the role of predation in population fluctuations of the soybean aphid, *Aphis glycines* in farmers' fields in Indonesia. *Journal of Applied Entomology* 34: 971–984.

Venette, R. C. and D. W. Ragsdale. 2004. Assessing the invasion by soybean aphid (Hemiptera: Aphididae): where will it end? *Annals of the Entomological Society of America* 97: 219–228.

Wang, X. B., C. H. Fang, X. P. Zheng, Z. Z. Lin, L. R. Zhang, and H. D. Wang. 1994. A study on the damage and economic threshold of the soybean aphid at the seedling stage. *Plant Protection* 20: 12–13.

Wu, Z., K. R. Hopper, R. J. O'Neil, D. J. Voegtlin, D. R. Prokrym, and G. E. Heimpel. 2004a. Reproductive compatibility and genetic variation between two strains of *Aphelinus albipodus* (Hymenoptera: Aphelinidae), a parasitoid of the soybean aphid, *Aphis glycines* (Homoptera: Aphididae). *Biological Control* 31: 311–319.

———, D. Schenk-Hamlin, W. Zhan, D. W. Ragsdale, and G. E. Heimpel. 2004b. The soybean aphid in China-an historical review. *Annals of the Entomological Society of America* 97: 209–218.

Wyckhuys, K. A. G., K. R. Hopper, K.-M. Wu, C. Straub, C. Cratton, and G. E. Heimpel. 2007. Predicting potential ecological impact of soybean aphid biological control introductions. *Biocontrol News and Information* 28 (2): 30–34.

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Note
Chromosomes of *Blastophaga psenes* (Hymenoptera: Agaonidae)

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Parasitic wasps are one of the largest and most taxonomically complicated groups of insects (Rasnitsyn 1980). They play a very important role in food chains as parasitoids of many insect pests of agriculture and forestry. In addition, certain species of 'parasitic' Hymenoptera are associated with plants, either as pests or pollinators (Quicke 1997). Chromosomes of about 420 species of parasitic wasps have been studied (Gokhman 2009). However, chromosomes of the medium-sized family Agaonidae that is associated with fruits of the plant genus *Ficus*, were never examined before. We have managed to study the karyotype of *Blastophaga psenes* (Linnaeus), the sole pollinator of the edible fig, *Ficus carica* Linnaeus. The description of the karyotype is given below.

Syconia of the cultivated form of *F. carica* that contained immature stages of *B. psenes*, were collected by V.N. Fursov at Nikitsky Botanical Garden, Ukrainian Academy of Agrarian Sciences (about 5 km E Yalta, the Crimea, South Ukraine) on 2–10 October 2008, preserved at 10–12°C for three to four months and then incubated for a few days at room temperature. Cerebral ganglia of prepupae were used for karyotyping according to the technique developed by Imai et al. (1988). Chromosomes of a single male and five females were studied. Micrographs of chromosomes were obtained using Zeiss Axioskop 40 FL optic microscope fitted with Zeiss AxioCam MRc digital camera. Chromosomes of five diploid metaphase plates were measured on digital micrographs using Zeiss AxioVision; all chromosomes were then arranged according to the classification provided by Levan et al. (1964). Voucher adult specimens of *B. psenes* are deposited in the Zoological Museum, Moscow State University, Moscow, Russia.

RESULTS AND DISCUSSION

The chromosomal study of female individuals of *B. psenes* has revealed a chromosome set of 2n = 12 (Fig. 1). An analogous study of the male individual has yielded very few metaphases with n = 6 (not shown here). The haploid karyotype of this species comprises five large metacentric chromosomes and a smaller subtelocentric one (Fig. 2, Table 1).

The families Agaonidae (at least those belonging to Agaoninae; Rasplus et al. 1998), Torymidae and Ormyridae are usually believed to form a common clade (Noyes 1990, see also Bouček 1988 and Gibson et al. 1999). The karyotype structure similar to that found in *B. psenes* (five large metacentrics and a smaller subtelocentric/acrocentric) is also characteristic of many Torymidae (including most species of the less advanced subfamily Toryminae) and one of the two studied species of the Ormyridae that belong to the genus *Ormyrus* (see Gokhman 2009 for review).

Fig. 1. Karyogram of the diploid karyotype of *Blastophaga psenes*.

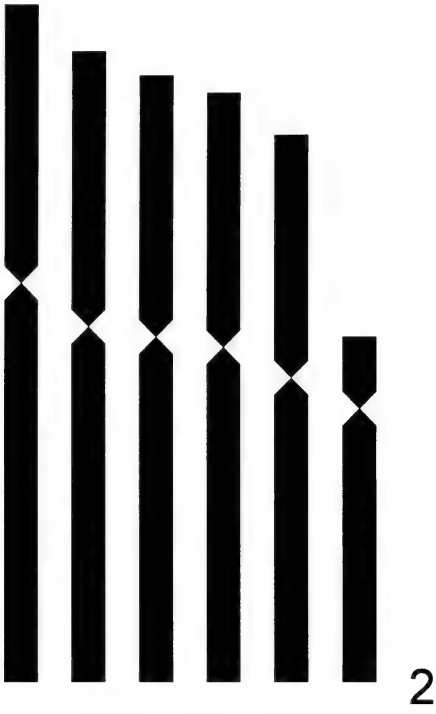

Fig. 2. Ideogram of the haploid karyotype of *Blastophaga psenes*.

Moreover, karyotypes of a few species of the Torymidae and Ormyridae that contain only five metacentric chromosomes are obviously derived from the preceding ones through tandem fusions, analogous, for example, to certain Eulophidae with similar chromosome sets (Gokhman 2009). The karyotype structure of *B. psenes* therefore represents the ground plan feature of the common clade of the Torymidae, Ormyridae and Agaonidae. On the other hand, karyotypes of many Pteromalidae (another group that is probably related to Agaonidae s.l.; Campbell et al. 2000) also comprise five biarmed chromosomes, and those chromosome sets could originate as well from a karyotype with an additional subtelocentric/acrocentric through chromosomal fusion (Gokhman 2009).

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The authors are grateful to the Director and staff of Nikitsky Botanical Garden (Dr. V.N. Ezhov and Drs. A.V. Smykov, E.L. Shishkina and A.N. Kazas respectively) for their kind permission to collect syconia of *F. carica* at the Garden. The present study was partly supported by the research grant no. 07-04-00326 from the Russian Foundation for Basic Research to VEG and APM.

Table 1. Parameters of chromosomes of *Blastophaga psenes*.

Chromosome no.	Relative length	Centromere index
1	19.97±0.84	41.04±2.86
2	18.58±0.37	43.73±2.69
3	17.87±0.32	43.17±3.96
4	17.34±0.38	43.20±3.96
5	16.08±0.66	44.39±4.00
6	10.16±0.72	22.48±3.27

LITERATURE CITED

Bouček, Z. 1988. *Australasian Chalcidoidea (Hymenoptera). A biosystematic revision of genera of fourteen families, with a reclassification of species.* CAB International, Wallingford. 832 pp.

Campbell, B., J. Heraty, J.-Y. Rasplus, K. Chan, J. Steffen-Campbell, and C. Babcock. 2000. Molecular systematics of the Chalcidoidea using 28S-D2 rDNA. Pp. 59–73 *in*: Austin, A. D., and M. Dowton, eds. *Hymenoptera: Evolution, Biodiversity and Biological Control.* CSIRO Publishing, Collingwood. XI + 468 pp.

Gibson, G. A. P., J. M. Heraty, and J. B. Woolley. 1999. Phylogenetics and classification of Chalcidoidea and Mymarommatoidea – a review of current concepts (Hymenoptera, Apocrita). *Zoologica Scripta* 28: 87–124.

Gokhman, V. E. 2009. *Karyotypes of Parasitic Hymenoptera.* Springer Science+Business Media B.V., Dordrecht. XIII + 183 pp.

Imai, H. T., R. W. Taylor, M. W. J. Crosland, and R. H. Crozier. 1988. Modes of spontaneous chromosomal mutation and karyotype evolution in ants with reference to the minimum interaction hypothesis. *Japanese Journal of Genetics* 63: 159–185.

Levan, A., K. Fredga, and A. A. Sandberg. 1964. Nomenclature for centromeric position on chromosomes. *Hereditas* 52: 201–220.

Noyes, J. S. 1990. A word on chalcidoid classification. *Chalcid Forum* 13: 6–7.

Quicke, D. L. J. 1997. *Parasitic Wasps.* Chapman and Hall, London. XVII + 470 pp.

Rasnitsyn, A. P. 1980. Origin and evolution of hymenopterous insects. *Trudy Paleontologicheskogo Instituta AN SSSR* 174: 1–191 (in Russian).

Rasplus, J.-Y., C. Kerdelhué, I. Le Clainche, and G. Mondor. 1998. Molecular phylogeny of fig wasps (Hymenoptera). Agaonidae are not monophyletic. *Comptes Rendus de l'Académie des Sciences de Paris* III 321: 517–527.

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OBITUARY

Ian David Gauld
25 May 1947–12 January 2009

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The generalities of Ian Gauld's life and career have been covered in Hanson et al. (2009a,b). He was a hymenopterist, from the beginning to the end, and examination of his 100 or so life publications (Appendix A) shows two major themes: overviews of the Hymenoptera and detailed studies of Ichneumonidae. The first theme is exemplified by Gauld and Bolton (1988), Hanson and Gauld (1995), and Hanson and Gauld (2006). Such detailed compendia had never before been gathered together for the order. Ichneumonids, however, were the focus of Gauld's life work, and there are three main interests: 1) selected subfamilies, 2) evolutionary biology of the family, and 3) faunal studies.

The Anomaloninae, Labeninae, Ophioninae, and Pimplinae were of great interest to Gauld. A revision of the genera of Anomaloninae was the topic of his Master's thesis (Gauld 1976), and he completed several faunal treatments of the group. Pimplinae, especially with regard to the subfamily's diverse biologies, fascinated him, and those who did not share his enthusiasm for the group were nevertheless subjected to long expositions. Labeninae and Ophioninae were the subject of his doctoral dissertation (*"A taxonomic study of the Ophioninae and Labeninae (Hymenoptera; Ichneumonidae)"*; submitted to the Council for National Academic Awards, Nov. 1983; The City of London Polytechnic and the British Museum (Natural History)). The labenine section was published as Gauld (1983) and the ophionine section as Gauld (1985a). His interest in Labeninae was continued through a series of faunal studies and culminated in Gauld and Wahl (2000).

Prior to his work on the Ophioninae, it is safe to say that species limits in this subfamily were not well understood. Perusal of the American Entomological Institute collection reveals that even Henry Townes did not understand morphological variation within the subfamily, nor even which characters were essential for species delimitation. Gauld's thousands of hours of ophionine study 'cracked the code', so to speak, and has allowed a much more accurate assessment of ophionine diversity. This is in addition to his work on ophionine genera (Gauld 1979; Gauld 1985b), which greatly changed the Townesian classification.

Gauld (1988) was the first discussion of ichneumonid biology from an evolutionary perspective. This topic captivated him, and

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Ian's place of burial is in Spratton, 52°19′39.09″N, 0°57′15.53″W [52.327521°N, −0.954318°W]

Table 1. Top ten most prolific ichneumonid taxonomists based on number of taxa described.

Author	Ichneumonid taxa described
Cameron	1796
Heinrich	1776
Townes	1752
Förster	1651
Gauld	**1602***
Dasch	1185
Gravenhorst	1143
Uchida	1120
Cresson	1114
Thomson	1079

*will increase to greater than 2150 names following posthumous publication.

it was a focal point of his studies. As cladistic methodology was incorporated into his research, biology was increasingly tied to explicit hypotheses of relationship (examples being: Gauld 1983; Gauld and Janzen 1994; Wahl and Gauld 1998; Gauld and Wahl 2000).

The regional comprehensive treatment of an ichneumonid fauna became an organizing principle of his research, starting with his study of the Australian genera (Gauld 1984). He became increasingly disillusioned with the monographic treatment of genera at the World level, seeing such studies as useful to only a small group of museum workers at major institutions (pers. comm. to DBW). The fortuitous combination of factors that led him to Costa Rica has been covered elsewhere; the last two decades of his life were mostly focused upon the Costa Rican fauna. The results of this work have been wonderfully stimulating to New World ichneumonid studies in and out of the tropics, both in terms of providing a baseline for other countries and encouraging local systematic endeavors.

In terms of Gauld's relative impact on our knowledge of Ichneumonidae, Table 1 lists the top ten most prolific ichneumonid taxonomists based on the number of taxa described. Currently, Gauld lies in fifth position with 1,602 (1,516 species, 82 genera and 4 tribes) (Yu et al. 2008). With the planned, posthumous publication of Gauld's last work (*The Ichneumonidae of Costa Rica, 5*) which treats the subfamily Campopleginae, this number will increase to over 2,150 making him the most prolific ichneumonid taxonomist in history. Whereas the number of taxa described does not always equate to the quality of the taxonomist, in the case of Ian Gauld, both quantity and quality were of the highest order. At the time of writing, only 10 species, 3 genera and 1 tribe of Gauld's have been synonymized (less than 1% of all Gauld names). Recent work using DNA barcoding on the ophionines of Guanacaste, Costa Rica have shown his keen sense of morphological species limits to be almost always correct (Janzen and collaborators, work in progress).

Certainly, part of the reason for Gauld's exceptionally high level of accuracy can be attributed to his encyclopaedic knowledge of the world fauna at a species level. Many were the times when we would present Ian with an enigmatic specimen or potential new character and, following the obligatory stroking of the beard and pensive stare into the distance, he would extract the relevant information from his prodigious memory, thereby allowing us to place the specimen or character in its correct context. But needless to say, he did not describe over 2,000 taxa with simply a good memory. Ian was an extremely efficient taxonomist and a hard worker. By "efficient", we do not mean to imply that his descriptions were cursory. On the contrary – they are generally model examples of the correct balance between brevity and completeness. For many taxa (not only ophionines), he introduced new character systems that either reinforced previous hypotheses of relationship or supported new ones. Note that it should not be suggested that Ian worked entirely by himself. Many people contributed to his research, and foremost among these were his late wife Pam Mitchell (Gauld and Mitchell 1978,

1981) and his long-time technician Sondra Ward (Ward and Gauld 1987; Gauld 1997, 2000). Perhaps the greatest legacy of Ian Gauld is that he empirically demonstrated that the estimate of Townes (1969) of 60,000 species of ichneumonids worldwide was likely much too low. Gauld's last estimate of total species of ichneumonids was 120,000 (www.amentinst.org). This number was reached by consideration of ichneumonid species richness in tropical regions which Townes clearly underestimated. In so doing, Gauld dispelled the hypothesis that ichneumonid species richness decreases with decreasing latitude (Owen and Owen 1974; Gauld 1986) and reinforced the fact that ichneumonids are a major constituent of biodiversity in all regions of the world.

DAVID B. WAHL
ANDREW M. R. BENNETT

As friends, colleagues and past students of Ian's (formally or very informally), we would like to take this opportunity to record a few words of appreciation for Ian, the old wasp taxonomist, as he used to sign his emails:

When Ian Gauld passed away we abruptly lost a huge stock of ichneumonid wisdom. Ian's enthusiasm and knowledge were even larger than his physical presence and we have written this obituary as students and colleagues who gained from this enthusiasm and knowledge, through formal and informal project supervision and very pleasant collaboration. The Ichneumonidae is a large and complex family and when starting from a very limited knowedge-base, to come under the wing of Ian was a tremendous help. Ian's achievements were immense in producing taxonomic monographs and in pushing forwards the theme of biodiversity in the neotropics. Suffice to say that Ian was the world authority and really opened up the study of Ichneumonidae to the next generation.

Ian was able to synthesise huge amounts of information and make it readily accessible, something he achieved through taxonomic monographs and through introductory texts. Every working day we reach for Gauld volumes from the shelf; there is no higher recommendation of his work than that it is essentially practical and useful. It is remarkable that for many subfamilies of Ichneumonidae it is now easier to identify species from Costa Rica than it is from northern Europe, despite centuries more effort in describing the European fauna. If it wasn't for the efforts of Ian and his fellow Costa Rican pioneers we would have very little idea of the potential species richness of ichneumonids in the neotropics, where they used to be thought of as a rather species-poor group compared to their north temperate riches.

We have all been out for many long, slightly alcohol-lubricated, dinners with Ian. He was always keen to give his time towards those he considered worth encouraging and was incredibly generous when it came to dinners and trips to the American Entomological Institute. Information on ichneumonids, geography, flora and fauna, cuisine, all sorts of topics, would flow forth and we learnt a lot. Ichneumonids were always foremost though.

GAVIN R. BROAD

We will always remember Ian as a good friend. He was a humble and warm-hearted man, always ready to encourage the research projects of his friends and colleagues. Ian was the world authority on Ichneumonidae but never tried to prove to others how good he actually was. In this respect, he was a perfect teacher and supervisor. He encouraged us to resolve taxonomic and systematic problems in our way and was always there when support was needed.

Ian was one of few ichneumonologists capable of dealing with some taxonomically

Fig. 1. Ian Gauld at the Natural History Museum in 1975 or 1976 and at his home in 2005 (R. Zuñiga).

extremely difficult subfamilies – a true star in the world of parasitoid Hymenoptera research. He, for example, supervised his younger colleagues with a smile in his face by saying that "nobody can escape from the Campopleginae for long!", and attacked this subfamily, avoided by most of us, with all his enthusiasm. Ian's positive attitude towards life and ichneumonid taxonomy and systematics is something that we will always remember and miss.

In taxonomy, new species are often named in honour of distinguished researchers of the field. For example, at least 13 species and one genus of ichneumonoid and one species of chalcidoid have been named after Ian. In contrast, Ian named a large number of species after people, whether they were academics or not, who had helped somehow, e.g. in the field inventories of Costa Rica. As a consequence, from Ian's books one can find species named after people who helped Ian with Spanish language tuition or joined the first biodiversity training course for the national parks of Costa Rica. It was Ian's way of thanking the people he had met during the years.

He loved to spend time with his friends and readily treated these nights to his younger colleagues. The dinners were always finished with sweet desserts, which were his favourite. We all learned to know, for examples, *creme brulé* and *suspiro limeña*, the latter being a very sweet and delicious Peruvian dessert. Ian took his friends and colleagues often to his home, in the beautiful village of Spratton in the English countryside close to the city of Northampton. It was always nice to stay with Ian and his wife Pam. They were a lovely and loving couple, always taking good care of their friends. Many of us have spent some truly nice days at their house studying ichneumonids in Ian's fully equipped home office, sharing lovely meals prepared by Pam and excellent wines which were appreciated by both of them. In their way, Ian and Pam were like Henry and Marjorie Townes – the founders of the American Entomological Institute. Pam often joined Ian in his research and they provided a lovely environment for visiting colleagues. Pam died less than one year before Ian. It was a hard time for Ian and he wrote us "Thank goodness I still have my work". Their marriage lasted 35 happy years and they leave behind Ian's son, Darren. We all remember Ian and Pam with love and affection, and with many shared years, we

will always have a treasure trove of good memories.

ILARI E. SÄÄKSJÄRVI

Ian Gauld was a person full of charisma in entomology, his passion and dedication to his work led him to make great discoveries. He was simple and humble, willing to listen to anyone who had an idea to tell. Ian was a great teacher, but more a great friend, often giving advice to improve as individuals and as professionals.

Ian's way of working is an example to follow, with enthusiasm and joy, a lover of good food, talks and desserts. In Costa Rica, he spent many years teaching and working in difficult places, but always with a tremendous joy for what he did. Pam, his wife, at his side helping him in his huge task of preparing the material, that Ian would later describe. He is remembered as the great teacher and great friend; our obligation is to follow in his footsteps and continue working the way he would have wanted to. Working day to day is the best way to remember him.

We can write hundreds of anecdotes about Ian, all filled with joy; his house was a university classroom, he was a man who never failed to surprise us, who lived as he wanted, enjoying all he did.

RONALD J. ZUÑIGA

LITERATURE CITED

Gauld, I. D. 1976. The classification of the Anomaloninae (Hymenoptera: Ichneumonidae). *Bulletin of the British Museum (Natural History) (Entomology)* 33: 1–135.

———. 1979 (1980). An analysis of the classification of the *Ophion* genus-group (Hymenoptera: Ichneumonidae). *Systematic Entomology* 5: 59–82.

———. 1983. The classification, evolution and distribution of the Labeninae, an ancient southern group of Ichneumonidae (Hymenoptera). *Systematic Entomology* 8: 167–178.

———. 1984. *An Introduction to the Ichneumonidae of Australia*. British Museum (Natural History): London. 413 pp.

———. 1985a. The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae). *Bulletin of the British Museum (Natural History) (Entomology)* 51: 61–185.

———. 1985b. A preliminary survey of the Ophioninae (Hymenoptera; Ichneumonidae) of Brunei. *Brunei Museum Journal* 6: 169–188.

———. 1986. Latitudinal gradients in ichneumonid species-richness in Australia. *Ecological Entomology* 11: 155–161.

———. 1988. Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). *Biological Journal of the Linnean Society* 35: 351–377.

———. 1997. The Ichneumonidae of Costa Rica, 2. *Memoirs of the American Entomological Institute* 57: 1–485.

———. 2000. The Ichneumonidae of Costa Rica, 3. *Memoirs of the American Entomological Institute* 63: 1–453.

Gauld, I. D., and B. Bolton, eds. 1988. *The Hymenoptera*. British Museum (Natural History)/Oxford University Press: London. 332 pp.

Gauld, I. D. and D. H. Janzen. 1994. The classification, evolution and biology of the Costa Rican species of *Cryptophion* (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society* 110: 297–324.

——— and P. A. Mitchell. 1978. *The taxonomy, distribution and host preferences of African parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae)*. Commonwealth Agricultural Bureaux: Slough, United Kingdom. 287 pp.

——— and P. A. Mitchell. 1981. *The taxonomy, distribution and host preferences of Indo-Papuan parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae)*. Commonwealth Agricultural Bureaux: Slough, United Kingdom. 611 pp.

——— and D. B. Wahl. 2000. The Labeninae (Hymenoptera: Ichneumonidae): a study in phylogenetic reconstruction and evolutionary biology. *Zoological Journal of the Linnean Society* 129: 271–347.

Hanson, P. E., and I. D. Gauld, eds. 1995. *The Hymenoptera of Costa Rica*. Oxford University Press: Oxford. 893 pp.

Hanson, P. E., and I. D. Gauld, eds. 2006. Hymenoptera de la región neotropical. *Memoirs of the American Entomological Institute* 77: 1–994.

Hanson, P., Coronado, J., Ugalde, J., Godoy, C., and Zuñiga, R. 2009a. Ian David Gauld (1947–2009). Su legado a la biodiversidad entomológica de Costa Rica y el mundo. *Revista de Biología Tropical* 57 (Suppl. 1): XXV–XXX.

———, Janzen, D., Knapp, S., Scoble, M., Wahl, D., and West-Eberhard, M. J. 2009b. Ian Gauld FLS (1947–2009). Master taxonomist and morphologist. *The Linnaean* 25 (2): 46–47.

Owen, D. F. and Owen, J. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature* 249: 583–584.

Townes, H. K. 1969. The genera of Ichneumonidae, Part 1. *Memoirs of the American Entomological Institute* 11: 1–300.

Wahl, D. B. and I. D. Gauld. 1998. The cladistics and higher classification of the Pimpliformes (Hymenoptera: Ichneumonidae). *Systematic Entomology* 23: 265–298.

Ward, S. and I. D. Gauld. 1987. The callajoppine parasitoids of sphingids in Central America (Hymenoptera: Ichneumonidae). *Systematic Entomology* 12: 503–508.

Yu, D., van Achterberg, K., and Horstmann, K. 2008. World Ichneumonoidea 2004. Taxonomy, biology, morphology and distribution. [CD/DVD]. Taxapad®, Vancouver, Canada. [Available for sale at: http://www.taxapad.com].

Appendix A: Complete Publication List of Ian D. Gauld

Bartlett, R., J. Pickering, I. Gauld, and D. Windsor. 1999. Estimating global biodiversity: tropical beetles and wasps send different signals. *Ecological Entomology* 24: 118–121.

Billany, D. J., T. J. Winter, and I. D. Gauld, 1985. *Olesicampe monticola* (Hedwig) (Hymenoptera: Ichneumonidae) redescribed together with notes on its biology as a parasite of *Cephalcia lariciphila* (Wachtl) (Hymenoptera: Pamphiliidae). *Bulletin of Entomological Research* 75: 267–274.

Coronado-Rivera, J., A. González-Herrera, I. D. Gauld, and P. Hanson, P. 2004. The enigmatic biology of the ichneumonid subfamily Lycorininae. *Journal of Hymenoptera Research* 13: 223–227.

Danthanarayana, W., D. Farrugia, and I. D. Gauld. 1977. Studies on the biology and systematic position of a new species of ichneumonid parasitising the light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), in Australia. *Bulletin of Entomological Research* 67: 607–617.

Fitton, M. G. and I. D. Gauld. 1976. The family-group names of Ichneumonidae (excluding the Ichneumoninae). *Systematic Entomology* 1: 247–258.

Fitton, M. G. and I. D. Gauld. 1978. Further notes on family-group names of Ichneumonidae (Hymenoptera). *Systematic Entomology* 3: 245–247.

Fitton, M. G. and I. D. Gauld. 1980. A review of the British Cremastinae (Hymenoptera: Ichneumonidae) with keys to the species. *Entomologist's Gazette* 31: 63–71.

Fitton, M. G. and I. D. Gauld. 1991. [Comments on the proposed conservation of *Cryptus* Fabricius, 1804 (Insecta, Hymenoptera)]. *Bulletin of Zoological Nomenclature* 48: 326–327.

Fitton, M. G., I. D. Gauld, L. I. N. Roberts, and A. K. Walker. 1983. An African ichneumonid (Hymenoptera) in Australasia. *Bulletin of Entomological Research* 73: 465–468.

Fitton, M. G., I. D. Gauld, and M. R. Shaw. 1982. The taxonomy and biology of the British Adelognathinae (Hymenoptera: Ichneumonidae). *Journal of Natural History* 16: 275–283.

Fitton, M. G., M. R. Shaw, and I. D. Gauld. 1988. Pimpline ichneumon-flies (Hymenoptera, Ichneumonidae, Pimplinae). *Handbook for the identification of British insects* 7(1): 1–110.

Gamez, R. L. and I. D. Gauld. 1993. Costa Rica: an innovative approach to the study of tropical biodiversity. *In:* LaSalle, J. and I. D. Gauld, eds. *Hymenoptera and Biodiversity*. CAB International: Wallingford, UK. 348 pp.

Gaston, K. J. and I. D. Gauld. 1993. How many species of pimplines (Hymenoptera: Ichneumonidae) are there in Costa Rica? *Journal of Tropical Ecology* 9: 491–499.

Gauld, I. D. 1970. Some records of Ichneumonoidea (Hymenoptera) collected at light, during autumn 1969 in Perthshire and southern Inverness-shire, including a species new to Britain. *Entomologist's Gazette* 21: 282–284.

Gauld, I. D. 1973a. Notes on the British Ophionini (Hymenoptera: Ichneumonidae) including a key to species. *Entomologist's Gazette* 24: 55–66.

Gauld, I. D. 1973b. Notes on some Anomaloninae (Hymenoptera: Ichneumonidae) on Cannock Chase during August 1973. *Entomologist's Gazette* 24: 304.

Gauld, I. D. 1974a. Further notes on the British Ophionini (Hymenoptera: Ichneumonidae). *Entomologist's Gazette* 25: 147–148.

Gauld, I. D. 1974b. Notes on the species of *Heteropelma* Wesmael (Hymenoptera: Ichneumonidae) occurring in Australia. *Bulletin of Entomological Research* 64: 541–544.

Gauld, I. D. 1976a. The classification of the Anomaloninae (Hymenoptera: Ichneumonidae). *Bulletin of the British Museum (Natural History) (Entomology)* 33: 1–135.

Gauld, I. D. 1976b. A revision of the Anomaloninae (Hymenoptera: Ichneumonidae) of Australia. *Australian Journal of Zoology* 24: 597–634.

Gauld, I. D. 1976c. Notes on the British Ophioninae (Hymenoptera: Ichneumonidae). Part 3. The identity of the species described by Morley, 1915 and Thomson, 1888 and a checklist of British species. *Entomologist's Gazette* 27: 113–117.

Gauld, I. D. 1976d. The taxonomy of the genus *Heteropelma* Wesmael (Hymenoptera: Ichneumonidae). *Bulletin of the British Museum (Natural History) (Entomology)* 34: 153–219.

Gauld, I. D. 1976e. Notes on the species of *Trichomma* Wesmael (Hymenoptera: Ichneumonidae) occurring in the Indian subcontinent. *Bulletin of Entomological Research* 65: 643–649.

Gauld, I. D. 1976f. Description of a new genus of Ichneumonidae (Hymenoptera) of economic importance from Sabah. *Bulletin of Entomological Research* 66: 1–4.

Gauld, I. D. 1977. A revision of the Ophioninae (Hymenoptera: Ichneumonidae) of Australia. *Australian Journal of Zoology (Supplementary Series)* 49: 1–112.

Gauld, I. D. 1978a. Notes on the British Ophioninae (Hymenoptera: Ichneumonidae). Part 4. A revised key to species of the genus *Ophion* Fabricius. *Entomologist's Gazette* 29: 145–149.

Gauld, I. D. 1978b. A revision of the Ethiopian species of *Agrypon* Foerster (Hymenoptera: Ichneumonidae). *Journal of Natural History* 12: 649–660.

Gauld, I. D. 1978c. A revision of the Anomaloninae (Hymenoptera: Ichneumonidae) of Melanesia I. The genera *Anomalon* Panzer to *Aphanistes* Foerster. *Bulletin of Entomological Research* 68: 501–519.

Gauld, I. D. 1978d. A revision of the Anomaloninae (Hymenoptera: Ichneumonidae) of of Melanesia II. The genera *Perisphincter* Townes and *Agrypon* Foerster. *Bulletin of Entomological* Research 68: 543–557.

Gauld, I. D. 1979 (1980). An analysis of the classification of the *Ophion* genus-group (Hymenoptera: Ichneumonidae). *Systematic Entomology* 5: 59–82.

Gauld, I. D. 1980a. A synopsis of the Anomaloninae (Hymenoptera: Ichneumonidae) of sub-Saharan Africa with special reference to species of potential economic importance. *Bulletin of Entomological Research* 70: 33–41.

Gauld, I. D. 1980b. Notes on an economically important species of *Temelucha* Foerster (Hymenoptera: Ichneumonidae) and a preliminary key to Australian species. *Bulletin of Entomological Research* 70: 43–47.

Gauld, I. D. 1980c. Notes on the New Zealand Anomaloninae (Hymenoptera: Ichneumonidae) with description of a new species of *Aphanistes* Foerster of possible economic importance in forestry. *New Zealand Entomologist* 7: 130–134.

Gauld, I. D. 1982. A revised key to the *Enicospilus antefurcalis* (Szepligeti) (Hymenoptera: Ichneumonidae) species-group of the Afrotropical region. *Bulletin of Entomological Research* 72: 33–38.

Gauld, I. D. 1983a (1982). *Netelia* species of the subgenera *Apatagium* Enderlein and *Monomacrodon* Cushman (Hymenoptera: Ichneumonidae) of Brunei with a re-assessment of the supraspecific classification. *Brunei Museum Journal* 5(2): 123–143.

Gauld, I. D. 1983b. The classification, evolution and distribution of the Labeninae, an ancient southern group of Ichneumonidae (Hymenoptera). *Systematic Entomology* 8: 167–178.

Gauld, I. D. 1984a. The Australian Ophioninae (Insecta; Hymenoptera): a historical biogeographic study. *Journal of Biogeography* 11: 269–288.

Gauld, I. D. 1984b. *An Introduction to the Ichneumonidae of Australia*. British Museum (Natural History): London. 413 pp.

Gauld, I. D. 1984c. The Pimplinae, Xoridinae, Acaenitinae and Lycorininae (Hymenoptera: Ichneumonidae) of Australia. *Bulletin of the British Museum (Natural History) (Entomology)* 49: 235–339.

Gauld, I. D. 1985a. The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae). *Bulletin of the British Museum (Natural History) (Entomology)* 51: 61–185.

Gauld, I. D. 1985b. A preliminary survey of the Ophioninae (Hymenoptera; Ichneumonidae) of Brunei. *Brunei Museum Journal* 6: 169–188.

Gauld, I. D. 1986a. Latitudinal gradients in ichneumonid species-richness in Australia. *Ecological Entomology* 11: 155–161.

Gauld, I. D. 1986b. Taxonomy, its limitations and its role in understanding parasitoid biology. *In:* Waage, J. and D. Greathead, eds. *Insect Parasitoids*. Academic Press: London. 389 pp.

Gauld, I. D. 1987a. Some factors affecting the composition of tropical ichneumonid faunas.

Biological Journal of the Linnean Society 30: 299–312.

Gauld, I. D. 1987b. Chapter 5: Ichneumonidae. The ichneumonid parasitoids associated with South-east Asian Limacodidae. *In:* Cock, M. J. W., H. C. J. Godfray, and J. D.Holloway, eds. *Slug and nettle caterpillars: the biology, taxonomy and control of the Limacodidae of economic importance on palms in South-east Asia.* Commonwealth Agricultural Bureaux: Wallingford, United Kingdom. 270 pp.

Gauld, I. D. 1988a. The species of the *Enicospilus americanus* (Hymenoptera: Ichneumonidae) complex in eastern North America. *Systematic Entomology* 13: 31–53.

Gauld, I. D. 1988b. A survey of the Ophioninae (Hymenoptera: Ichneumonidae) of tropical Mesoamerica with special reference to the fauna of Costa Rica. *Bulletin of the British Museum (Natural History)(Entomology)* 57: 1–309.

Gauld, I. D. 1988c. Evolutionary patterns of host utilization by ichneumonoid parasitoids (Hymenoptera: Ichneumonidae and Braconidae). *Biological Journal of the Linnean Society* 35: 351–377.

Gauld, I. 1991. The Ichneumonidae of Costa Rica, 1. *Memoirs of the American Entomological Institute* 47: 1–589.

Gauld, I. D. 1996. The cost of data repatriation versus the potential of biosystematic capacity building. *In:* McNeely, J. A. and Y. S. Soucherita, eds. *Biodiversity in Asia: Challenges and Opportunities for the Scientific Community.* Ministry of Science, Technology and Environment: Bangkok.

Gauld, I. D. 1997. The Ichneumonidae of Costa Rica, 2. *Memoirs of the American Entomological Institute* 57: 1–485.

Gauld, I. D. 2000a. The re-definition of pimpline genus *Hymenoepimecis* (Hymenoptera: Ichneumonidae) with a description of a plesiomorphic new Costa Rican species. *Journal of Hymenoptera Research* 9: 213–219.

Gauld, I. D. 2000b. The Ichneumonidae of Costa Rica, 3. *Memoirs of the American Entomological Institute* 63: 1–453.

Gauld, I. D., ed. 2002. The Ichneumonidae of Costa Rica, 4. *Memoirs of the American Entomological Institute* 66: 1–768.

Gauld, I. D. and B. Bolton, eds. 1988. *The Hymenoptera.* British Museum (Natural History)/Oxford University Press: London. 332 pp.

Gauld, I. D. and J.M. Carter. 1983. The Ophioninae of the Galapagos Islands (Hymenoptera: Ichneumonidae). *Journal of Natural History* 17: 145–155.

Gauld, I. D., N. M. Collins, and M. G. Fitton. 1990. The biological significance and conservation of Hymenoptera in Europe. *Nature and Environment Series* (Council of Europe) 44: 1–47.

Gauld, I. D. and J. Dubois. 2006. Phylogeny of the *Polysphincta* group of genera (Hymenoptera: Ichneumonidae; Pimplinae): a taxonomic revision of spider ectoparasitoids. *Systematic Entomology* 31: 529–564.

Gauld, I. D. and M. G. Fitton. 1980 (1979). The British species of Phrudinae (Hymenoptera: Ichneumonidae) *Entomologist's Monthly Magazine* 115: 197–199.

Gauld, I. D. and M. G. Fitton. 1981. Keys to the British xoridine parasitoids of wood-boring beetles (Hymenoptera: Ichneumonidae). *Entomologist's Gazette* 32: 259–267.

Gauld, I. D. and M. G. Fitton. 1987. Sexual dimorphism in Ichneumonidae: a response to Hurlbutt. *Biological Journal of the Linnean Society* 31: 291–300.

Gauld, I. D. and K. J. Gaston. 1994. The taste of enemy-free space: parasitoids and nasty hosts. *In:* Hawkins, B.A. and W. Sheehan, eds. *Parasitoid Community Ecology.* Oxford University Press: Oxford. 516 pp.

Gauld, I. D., K. J. Gaston, and D. H. Janzen. 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos* 65: 353–357.

Gauld, I. D. and G. A. Holloway. 1983. A new genus of endaseine Ichneumonidae from Australia (Hymenoptera). *Contributions of the American Entomological Institute* 20: 191–197.

Gauld, I. D. and G. A. Holloway. 1985. Australian ichneumonids of the tribes Labenini and Poecilocryptini. *Bulletin of the British Museum (Natural History) Entomology* 53: 107–149.

Gauld, I. D. and T. Huddleston. 1976. The Nocturnal Ichneumonoidea of the British Isles, including a key to genera. *Entomologist's Gazette* 27: 35–49.

Gauld, I. D. and D. H. Janzen. 1994. The classification, evolution and biology of the Costa Rican species of *Cryptophion* (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society* 110: 297–324.

Gauld, I. D. and D. H. Janzen. 2004. The systematic and biology of the Costa Rican species of parasitic wasps in the *Thyreodon* genus-group (Hymenoptera: Ichneumonidae). *Zoological Journal of the Linnean Society* 141: 297–351.

Gauld, I. D. and D. Lanfranco. 1988. Los generos de Ophioninae de Centro y Sudamerica. *Revista Biologia Tropical* 35: 257–267.

Gauld, I. D. and J. LaSalle. 1992. Parasitic Hymenoptera and the Biodiversity Crisis. *Redia* 74: 315–334.

Gauld, I. D., R. Menjívar, M. O. Gonzalez, and A. Monro. 2002. *Guía para la identificacíon de los Pimplinae de cafetales bajo sombra de El Salvador (Hymenoptera: Ichneumonidae).* Natural History Museum: London. 76 pp.

Gauld, I. D. & P. A. Mitchell. 1976. The ichneumonid genus *Pseudanomalon* (Hymenoptera). *Systematic Entomology* 1: 117–122.

Gauld, I. D. and P. A. Mitchell. 1977. Nocturnal Ichneumonidae of the British Isles: the genus *Alexeter* Foerster. *Entomologist's Gazette* 28: 51–55.

Gauld, I. D. and P. A. Mitchell. 1978. *The taxonomy, distribution and host preferences of African parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae).* Commonwealth Agricultural Bureaux: Slough, United Kingdom. 287 pp.

Gauld, I. D. and P. A. Mitchell. 1981. *The taxonomy, distribution and host preferences of Indo-Papuan parasitic wasps of the subfamily Ophioninae (Hymenoptera: Ichneumonidae).* Commonwealth Agricultural Bureaux: Slough, United Kingdom. 611 pp.

Gauld, I. D. and L. A. Mound. 1982. Homoplasy and the delineation of holophyletic groups. *Systematic Entomology* 7: 73–86.

Gauld, I. D., M. A. O'Neill, and K. J. Gaston. 2000. Driving Miss Daisy: the performance of an automated insect identification system. *In:* Austin, A. D. and M. Dowton. *Hymenoptera: Evolution, Biodiversity and Biological Control.* CSIRO: Collingwood, Australia. 468 pp.

Gauld, I. D., J. A. Ugalde, and P. Hanson. 1998. Guía de los Pimplinae de Costa Rica (Hymenoptera: Ichneumonidae). *Revisita de Biologia Tropical* 46 (Supplement 1): 1–189.

Gauld, I. D. & G. Underwood. 1986. Some applications of the LeQuesne compatibility test. *Biological Journal of the Linnean Society* 29: 91–222.

Gauld, I. D. and D. B. Wahl. 2000. The Labeninae (Hymenoptera: Ichneumonidae): a study in phylogenetic reconstruction and evolutionary biology. *Zoological Journal of the Linnean Society* 129: 271–347.

Gauld, I. D. and D. B. Wahl. 2001. The Townesioninae: a distinct subfamily of Ichneumonidae (Hymenoptera) or a clade of the Banchinae? *Transactions of the American Entomological Society* 126: 279–292.

Gauld, I. D. and D. B. Wahl. 2002. The Eucerotinae: a Gondwanan origin for a cosmopolitan group of Ichneumonidae? *Journal of Natural History* 36: 2229–2248.

Gauld, I. D. and D. B. Wahl. 2006. The relationship and taxonomic position of the genera *Apolophus* and *Scolomus* (Hymenoptera: Ichneumonidae). *Zootaxa* 1130: 35–61.

Gauld, I. D., D. B. Wahl, and G. R. Broad. 2002. The suprageneric groups of the Pimplinae (Hymenoptera: Ichneumonidae): a cladistic re-evaluation and evolutionary biological study. *Zoological Journal of the Linnean Society* 136: 421–485.

Gauld, I. D. and R. Zúñiga. 2003. *Apechoneura naturaeconservatio* Gauld & Zúñiga. INBio: San Jose, Costa Rica. [Note: a small card proposing a species without a formal description, hence a *nomen nudum*]

Hanson, P. E. and I.D. Gauld, eds. 1995. *The Hymenoptera of Costa Rica.* Oxford University Press: Oxford. 893 pp.

Hanson, P. E. and I. D. Gauld, eds. 2006. Hymenoptera de la región neotropical. *Memoirs of the American Entomological Institute* 77: 1–994.

Huddleston, T. and I. D. Gauld. 1988. Parasitic wasps (Ichneumonoidea) in British light-traps. *Entomologist* 107: 134–154.

Janzen, D. H., A. K. Walker, J. B. Whitfield, G. Delvare, and I. D. Gauld. 2003. Host-specificity and hyperparasitoids of three new Costa Rican species of *Microplitis* Foerster (Hymenoptera: Braconidae: Microgastrinae), parasitoids of sphingid caterpillars. *Journal of Hymenoptera Research* 12: 42–76.

Jerman, E. J. and I. D. Gauld. 1988. *Casinaria*, a paraphyletic ichneumonid genus (Hymenoptera), and a revision of the Australian species. *Journal of Natural History* 22: 589–609.

LaSalle, J. and I. D. Gauld, eds. 1993a. *Hymenoptera and Biodiversity.* CAB International: Wallingford, UK. 348 pp.

LaSalle, J. and I. D. Gauld. 1993b. Hymenoptera: their diversity and their impact on the diversity of other organisms. *In:* LaSalle, J. & I. D. Gauld, eds. *Hymenoptera and Biodiversity*. CAB International: Wallingford, UK. pp. 1–26.

Memmott, J., H. C. J. Godfray, and I. D. Gauld. 1994. The structure of a tropical host-parasitoid community. *Journal of Animal Ecology* 63: 521–540.

Sääksjärvi, I. E., S. Haataja, S. Neuvonen, I. D. Gauld, R. Jussila, J. Salo, and A. M. Burgos. 2004. High local species richness of parasitic wasps (Hymenoptera: Ichneumonidae; Pimplinae and Rhyssinae) from the lowland rainforests of Peruvian Amazonia. *Ecological Entomology* 29: 735–743

Sääksjärvi, I. E., E. Palacio, I. D. Gauld, R. Jussila, and J. Salo. 2003. A new genus and six new species of the tropical *Camptotypus* genus-group (Hymenoptera: Ichneumonidae; Pimplinae) from northern South America. *Zootaxa* 197:1–18.

Sääksjärvi, I. E., I. D. Gauld, and J. Salo. 2004: Phylogenetic evaluation of the tropical *Camptotypus* genus-group (Hymenoptera: Ichneumonidae), with a key to the world genera. *Journal of Natural History* 38: 2759–2778.

Wahl, D. B. and I. D. Gauld. 1998. The cladistics and higher classification of the Pimpliformes (Hymenoptera: Ichneumonidae). *Systematic Entomology* 23: 265–298.

Ward, S. and I. D. Gauld. 1987. The callajoppine parasitoids of sphingids in Central America (Hymenoptera: Ichneumonidae). *Systematic Entomology* 12: 503–508.

Weeks, P. J. D., I. D. Gauld, K. J. Gaston, and M. A. O'Neill. 1997. Automating the identification of insects: a new solution to an old problem. *Bulletin of Entomological Research* 87: 203–211

Weeks, P. J. D, M. A. O'Neill, K. J. Gaston, and I. D. Gauld. 1999a. Species-identification of wasps using principal component associative memories. *Image and Vision Computing* 17: 861–866.

Weeks, P. J. D., M. A. O'Neill, K. J. Gaston, and I. D. Gauld. 1999b. Automating insect identification: exploring the limitations of a prototype system. *Journal of Applied Entomology* 123: 1–8.

EDITOR'S NOTE

This is my final issue as editor of *Journal of Hymenoptera Research*. There has been much discussion within the society recently about the direction that *Journal of Hymenoptera Research* should take and we now have a good idea of how to adapt the journal. However, I think it is best that a fresh pair of hands guides our journal through these changes. We are still short of copy but we are confident that *Journal of Hymenoptera Research* has a bright future and I hope that, as we change our format, more members will submit their manuscripts here.

I would like to take this opportunity to record my thanks to everybody who made this job much easier than it could have been, and often even enjoyable. We depend on the many reviewers who almost always say 'yes' when approached and make the journal what it is. It is very pleasing that so many of you continue to devote some of your increasingly stretched time to reviewing. The subject editors, of course, have been unstintingly generous in devoting their time and efforts towards the journal, very frequently going out of their way to improve manuscripts that have merit but were not quite there yet, and I have relied upon them much more than I would normally care to admit.

One of the more gratifying aspects of editing *JHR* has been learning just how frequently hymenopterists are willing to devote considerable time and effort towards improving promising manuscripts and providing constructive criticism. Another boon of the job has been corresponding with so many hymenopterists around the world. I've also learned that almost nobody can format a manuscript precisely in accordance with the instructions. It has certainly made me a better proof-reader.

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INSTRUCTIONS FOR AUTHORS

General Policy. *The Journal of Hymenoptera Research* invites papers of high scientific quality reporting comprehensive research on all aspects of Hymenoptera, including biology, behavior, ecology, systematics, taxonomy, genetics, and morphology. Taxonomic papers describing single species are acceptable if the species has economic importance or provides new data on the biology or evolution of the genus or higher taxon. Manuscript length generally should not exceed 50 typed pages; however, no upper limit on length has been set for papers of exceptional quality and importance, including taxonomic monographs at generic or higher level. All papers will be reviewed by at least two referees. The referees will be chosen by the appropriate subject editor. However, it would be helpful if authors would submit the names of two persons who are competent to review the manuscript. The language of publication is English. Summaries in other languages are acceptable. This journal is ISI-listed.

The deadline for receipt of manuscripts is 1 September (for the April issue) and 1 March (for the October issue).

Format and Preparation. Authors are strongly encouraged to submit manuscripts electronically to the editor at the email address below, and in the format specified below. On the upper left of the title page give name, address, telephone and fax numbers, and email address of the author to whom all correspondence is to be sent. The paper should have a concise and informative title, followed by the names and addresses of all authors. The sequence of material should be: title, author(s), abstract, text, acknowledgments, literature cited, appendix, figure legends, figure copies (each numbered and identified), tables (each numbered and with heading). Each of the following should start a new page: (1) title page, (2) abstract, (3) text, (4) literature cited, (5) figure legends, (6) footnotes.

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