

**Night-flying Sweat Bees *Megalopta genalis* and *Me. ecuadoria*  
(Hymenoptera: Halictidae) as Hosts of the Parasitoid Beetle  
*Macrosiagon gracilis* (Coleoptera: Rhipiphoridae)**

ZACHARY H. FALIN,<sup>1</sup> LAURA C. ARNESON,<sup>2</sup> AND WILLIAM T. WCISLO<sup>2,3</sup>

**ABSTRACT:** The nocturnal bees *Megalopta genalis* Meade-Waldo and *Me. ecuadoria* Friese are reported as hosts of *Macrosiagon gracilis* Brewer, a member of a genus more commonly parasitic on solitary wasps. These associations represent the first halictid hosts for *Macrosiagon* as well as the first examples of a rhipiphorid parasitizing night-flying Hymenoptera.

Only about 10% of species in the genus *Macrosiagon* (Coleoptera: Rhipiphoridae) have confirmed host associations (Z.H.F., pers. obs.). While these beetles have long been known as parasitoids of solitary wasps in the Scoliidae, Tiphiidae and Eumeninae (Vespidae) (Clausen, 1940), only relatively recently has a bee host been identified. Raw (1977) discovered individuals of an as yet undetermined species of *Macrosiagon* (probably *Ma. mutilatum* (Gerstaecker) based on locality and the following host association) in the cells of *Exomalopsis globosa* (Fabricius) and *E. similis* Cresson (Hymenoptera: Apidae) in Jamaica. Twenty years later, Rozen (1997) discovered what have since been confirmed by Z.H.F. as individuals of *Ma. vittatum* (Erichson), the likely sister-taxon to *Ma. mutilatum* (Falín, in prep.), in the nests of *Exomalopsis brusei* Cockerell in Lima Department, Peru.

This paper reports confirmed host associations between *Macrosiagon gracilis* Brewer, a species described from northwestern Argentina, and two species of nocturnal bees, *Megalopta genalis* Meade-Waldo and *Me. ecuadoria* Friese (Hymenoptera: Halictidae), in central Panamá. These parasite-host associations are noteworthy for two reasons: they extend the host range of *Macrosiagon* to a second bee family and they represent the first records of a rhipiphorid species being reared from nests of nocturnal Hymenoptera.

Nests of *Me. genalis* were first discovered by W.T.W. on Barro Colorado Island (BCI), Panamá, and in the forest along Pipeline Road (Camino de Oleoducto) in Soberanía National Park (Panamá Province) in June, 1997. Since then, *Me. genalis* has been the subject of on-going studies in central Panamá (Wcislo et al., in prep.). Females live as solitary bees or in small social groups and nest in undisturbed primary and secondary forests in dead or soft wood that is at least partially raised above the forest floor (e.g., dead, hanging branches or lianas) up to approximately 2 m in height or more. Females forage at night and gather pollen from more than 20 plant species, though *Pseudobombax* and *Ceiba* (both Bombacaceae) predominate (Wcislo et al., loc. cit.). *Ceiba* flowers from December through February while *Pseudobombax* flowers from January through March (Croat, 1978), suggesting that adult beetles are active during the dry season in Panamá.

<sup>1</sup> Snow Entomological Collection, Division of Entomology, KU Natural History Museum, 1460 Jayhawk Blvd., Lawrence, KS 66045-7523 U.S.A.; email: zack@falcon.cc.ukans.edu

<sup>2</sup> Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancon, Republic of Panamá. US address: Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948 U.S.A. email: WcisloW@tivoli.si.edu<sup>1</sup>

In an on-going study of the social behavior and natural history of nocturnal bees by W.T.W. and colleagues, we made regular collections of nests in the field and transported them to the laboratory. Nests were opened by splitting them lengthwise with a sharp knife. Cells were opened and the contents of each were transferred to an individual well of a plastic tissue-culture tray.

No immature or adult rhipiphorids were observed in any nests collected in 1997 and 1998 ( $N = 45$ ). From December 1998 through September 1999 approximately 700 cells of *Me. genalis* were reared out under laboratory conditions. Six *Ma. gracilis* individuals emerged from cells in nests collected near the end of the dry season (mid-April) on BCI. Two individuals eclosed within 3 days of collection while one eclosed 14 days after collection. Four of the reared rhipiphorids (three females and a male) were examined by Z.H.F. and deposited as vouchers in the Snow Entomological Collection of the Division of Entomology, Natural History Museum, University of Kansas; another male is deposited in the Museo de Insectos "Graham Fairchild", Universidad de Panamá. Voucher specimens of the bees and their nests are in these same collections and in the Dry Reference Collection, Smithsonian Tropical Research Institute.

In 1998–1999 no beetles emerged from over 350 cells of *Me. ecuadoria*, a congener slightly smaller than *Me. genalis* but otherwise similar in nesting biology and distribution in Panamá. Out of an additional 200 cells reared in 2000, a single parasite was discovered on 4-II-2000 as a post-defecating larva without visible appendages. It was a white-eyed pupa 5 days later, a black-eyed pupa 11 days following discovery and an eclosed adult 14 days following discovery.

Z.H.F. examined specimens of *Megalopta* in the Snow Entomological Collection ( $N = 457$ , 313 of which were collected on BCI). *Megalopta genalis* was the most numerous of seven determined species, though the majority (393) were undetermined. Four *Megalopta* specimens had one or more *Macrosiagon* triangulin larvae (putatively *Ma. gracilis*) attached to the wings; three were collected on BCI (on 15-IV-1952, 21-IV-1963, and 21-IX-1990), the fourth in eastern Ecuador (on 14-VIII-1970). All four are female specimens of *Me. genalis* (det. by C. D. Michener), the most abundant *Megalopta* species in central Panamá, reinforcing the idea that *Ma. gracilis* uses the more common bee as its principal host here.

Adult specimens of *Ma. gracilis* have been collected in Guanacaste Province, Costa Rica; on BCI, Panamá; in Cochabama, Bolivia; Santa Catarina State and "Capta", Brazil; and the Provinces of Catamarca and Jujuy, Argentina (Brewer, 1966; Falin, loc. cit.). The distribution of the beetle greatly exceeds the admittedly poorly understood distribution of *Me. genalis* (currently known from northern South America and Panamá) though is roughly sympatric with that of *Me. ecuadoria* (Moure and Hurd, 1987).

The adult beetles exhibit no morphological adaptations for nocturnal activity and Z.H.F. considers it unlikely that they are active during this period. The characteristically minute and necessarily poorly-sighted putative triangulin larvae of *Ma. gracilis* likewise appear to exhibit no nocturnal adaptations although they must find and cling to nocturnally foraging bees (see Clausen, 1976, for a review of phoresy in Rhipiphoridae). This suggests visual cues are of lesser import than tactile or chemical cues in host location and recognition for the larvae of this and likely all species in *Macrosiagon*. The actual sensory mechanisms for host location and recognition and the larvae's relative ability to determine among potential host species remains unknown.

The evolutionary significance of the patterns of host associations in *Macrosiagon* remains obscure due to the lack of a comprehensive review of the various recorded hosts, species-level revisionary work, and a rigorous phylogenetic analysis of the beetles. However, these new host associations are significant in that *Ma. gracilis*, along with the two other previously mentioned bee-parasitoids, differs in several morphological characters from the rest of the solitary wasp-parasitoid species in *Macrosiagon*. It possesses two protibial apical spurs instead of one and resembles, to a degree, the closely related social wasp-parasitoid genus *Metoecus* (Rhipiphoridae: Macrosiagonini) (Falin, loc. cit.). While the phylogenetic position of the bee-parasitoid species of *Macrosiagon* within the Macrosiagonini is uncertain, it is clear that this group of beetles has a complex history of host-shifting and fascinating variations in life histories remain to be discovered.

#### Acknowledgments

First, we thank C. D. Michener (Natural History Museum, University of Kansas) for his time and knowledge in discussing bees, for making the determinations of museum specimens presented in this study, and for providing many helpful comments on the manuscript as well as J. S. Ashe (Natural History Museum, University of Kansas) for help in reviewing this manuscript. The following people and institutions have loaned material used in this study: M. Brendell, The Natural History Museum, London; D. G. Furth, National Museum of Natural History; D. H. Kavanaugh, California Academy of Sciences; A. Newton, Field Museum of Natural History; J. G. Rozen, American Museum of Natural History; and A. Terán, Fundación Miguel Lillo. This work was supported in part by general research funds of the Smithsonian Tropical Research Institute to W. T. Wcislo. We are also grateful to the Autoridad Nacional del Ambiente de la República de Panamá for permits to work in Parque Nacional Soberanía. This paper is contribution no. 3248 from the Snow Entomological Collection, Division of Entomology, Natural History Museum, University of Kansas.

#### Literature Cited

- Brewer, M. M. 1966. Subfamily Ripiphorinae (Col., Ripiphoridae), revisión de las especies Argentinas del genero *Macrosiagon* Hentz. Rev. Fac. Ciencias Exact., Fis., Nat. 27(1, 2):5-47.
- Clausen, C. P. 1940. Entomophagus Insects. McGraw Hill, Inc., New York. 688 pp.
- Clausen, C. P. 1976. Phoresy among entomophagous insects. Ann. Rev. Entomol. 21:343-368.
- Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford Univeristy Press. 943 pp.
- Moure, J. S., and P. D. Hurd. 1987. An Annotated Catalog of the Halictid Bees of the Western Hemisphere (Hymenoptera: Halictidae). Smithsonian Institution Press, Washington, DC. 405 pp.
- Raw, A. 1977. The biology of two *Exomalopsis* species (Hymenoptera: Anthophoridae) with remarks on sociality in bees. Rev. Biol. Trop. 25(1):1-11.
- Rozen, J. G. 1997. New taxa of brachynomadine bees (Apidae: Nomadinae). Amer. Mus. Nov. 3200. 26 pp.