

Review of the *Apanteles* Species (Hymenoptera: Braconidae) Attacking Lepidoptera in *Bombus* (*Fervidobombus*) (Hymenoptera: Apidae) Colonies in the New World, with Description of a New Species from South America

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ABSTRACT Field investigations of the nest architecture of the Amazonian bumble bee, *Bombus transversalis* (Olivier), revealed the presence of a new species of parasitoid wasp belonging to the microgastrine braconid genus *Apanteles* Foerster, reared from case-bearing tineid moth caterpillars feeding within the nests. The only other two species of *Apanteles* Foerster known to attack moth larvae within bumble bee colonies in the New World are here reviewed and compared taxonomically and biologically. An illustrated key to the three species recognized in this paper [*Apanteles galleriae* Wilkinson, *A. nephopteris* (Packard) and *A. nidophilus* Whitfield & Cameron, n. sp.] is presented, and the latter two species are fully described and illustrated for the first time.

DURING BEHAVIORAL STUDIES of two Neotropical species of bumble bees, *Bombus* (*Fervidobombus*) *atratus* Franklin (Cameron and Jost 1998) and *Bombus* (*Fervidobombus*) *transversalis* (Olivier) (Cameron and Whitfield 1996; Cameron and Jost 1998; Cameron et al. 1999), small casebearing moth caterpillars (Fig. 1) and adults of the family Tineidae were observed in some of the nests. This neotropical tineid appears to be a scavenger, the larva of which destroys the cells of the host nest while foraging. The moth belongs to a heretofore undescribed species, which is currently being described and characterized biologically by Donald R. Davis (Smithsonian Institution). These moths were frequently found to be parasitized by a small braconid wasp in the genus *Apanteles*, which differs from those described previously from *Bombus* nests (Whitfield and Cameron 1993), and appears to be new to science. Most of the *Apanteles* were collected from field-excavated surface colonies of *B. transversalis*. We have also obtained specimens from more typical underground *B. atratus* colonies in subtropical southern Brazil, so it is likely that this new *Apanteles* may be able to locate host caterpillars in colonies of several South American *Fervidobombus* species. It is interesting that both the

moths and the *Apanteles* parasitoids inhabiting *Bombus* colonies must enter the nest through a single entrance hole, suggesting that the bees guarding the nest either do not notice them or do not attempt to expel them.

Here, we review the three *Apanteles* species known from *Bombus* colonies in the New World, describe the new South American species, and provide an identification key with illustrations for the three species.

Materials and Methods

Colonies of *B. transversalis* were excavated in Colombia (three colonies at Amacayacu National Park, Amazonas, 8–10 June 2000), Ecuador (three colonies ≈6 km from the Yasuní Scientific Research Station, near the Pirana River, Yasuní National Park, Orellana, 1–2 July 2000) and Peru (two colonies along the Rio Tambopata, Baltimore Community, Tambopata-Candamo Reserve, Madre de Dios, 21–22 August 2000) during the rainy season (Colombia and Ecuador) or early dry season (Peru). All colonies were located in shallow depressions on the surface of the ground, under a dense nest canopy constructed of small pieces of leaf matter and rootlets (described in Cameron et al. 1999). Larval and adult lepidopteran nest associates and hymenopteran parasitoids were collected from the brood comb with forceps during the course of surveying the comb and counting the brood of each colony. A portion of the Lepidoptera and all the parasitoids were placed into 95% ethanol for later identification. The remainder of the Lepidoptera were placed into pinning boxes between layers of tissue paper.

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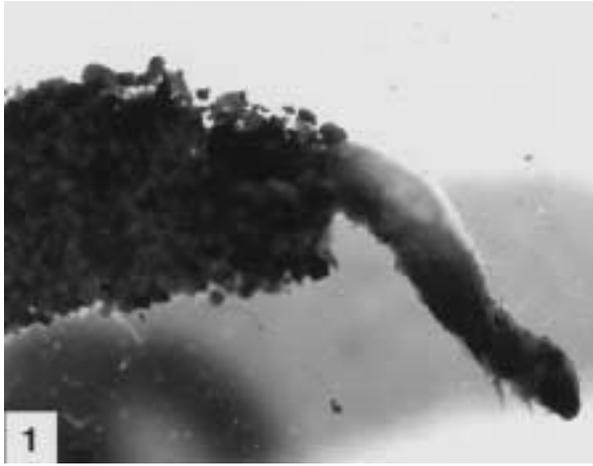


Fig. 1. Tineid larva (at $\approx 10\times$) protruding from its cryptic shelter made from silk and small particles of soil and nest materials. *Apanteles nidophilus* spins its own whitish silken cocoon within the shelter of the host.

Shelters formed by the tineid larvae were dissected to confirm that the cocoons of the new *Apanteles* species are actually spun inside them. The shelter and host larva were photographed at $25\times$ using a Contax 167 MT camera mounted on a Zeiss DRC stereomicroscope with fiber optic lighting. Fore wings, anterior metasomal tergites and hypopygium/ovipositor mechanisms were slide mounted in Euparal medium, projected using a microprojector, and drawn directly from the projected image. Morphological terminology, including wing vein nomenclature, follows that of Whitfield (1997).

Descriptive Taxonomy

Apanteles galleriae Wilkinson (Figs. 2–5)

Apanteles galleriae Wilkinson, 1932. *Stylops* 1: 139. Holotype female, Natural History Museum, London, examined.

Wilkinson (1932) provided an excellently detailed and illustrated original description of the species. Here, we provide a series of illustrations (Figs. 2–5) of critical features for its identification to supplement the key presented below and outline some important aspects of its biology.

This species has been reared throughout much of the world from the greater wax moth, *Galleria mellonella* (L.), in honey bee colonies. The species has obviously been introduced into many countries inadvertently with the transport of honey bees. It is a solitary parasitoid of early-instar larvae of wax moths and emerges to spin its cocoon and pupate well before the host larvae reach full size, usually before the final instar. Whitfield and Cameron (1993) also reported *A. galleriae* to be a parasitoid of *Vitula edmandsae* (Packard), the common wax moth in North American *Bombus* colonies. The parasitism in this case was observed

when bumble bee colonies were reared in close proximity to honey bee colonies. It is not surprising that *A. galleriae* can attack both moth species, because they are both in the same family (Pyralidae), and *V. edmandsae* was reported by Frison (1926) to be found occasionally within *Apis* colonies. In the cases where *Vitula* is the host, emergence is generally from fully-grown larvae, which are still much smaller than mature *Galleria* larvae. *A. galleriae* spins a white silken cocoon, often firmly attached by silk threads to some part of the nest substrate or surrounding structure. If the parasitoid is numerous, the cocoons may be spun together, giving the impression of a gregarious habit.

In wild colonies of *Bombus*, this species will probably be encountered only infrequently. However, Janzen (1971) reported larvae of *G. mellonella* from an arboreal nest of *Bombus pullatus* Franklin in Costa Rica, so it is possible that *A. galleriae* could also be found in neotropical *Bombus* colonies.

Apanteles nephopteris (Packard) (Figs. 6–9)

Microgaster nephopteris Packard, 1864, Proceedings of the Essex Institute 4: 122. Holotype male, Museum of Comparative Zoology, Harvard University, examined (in fragmentary condition).

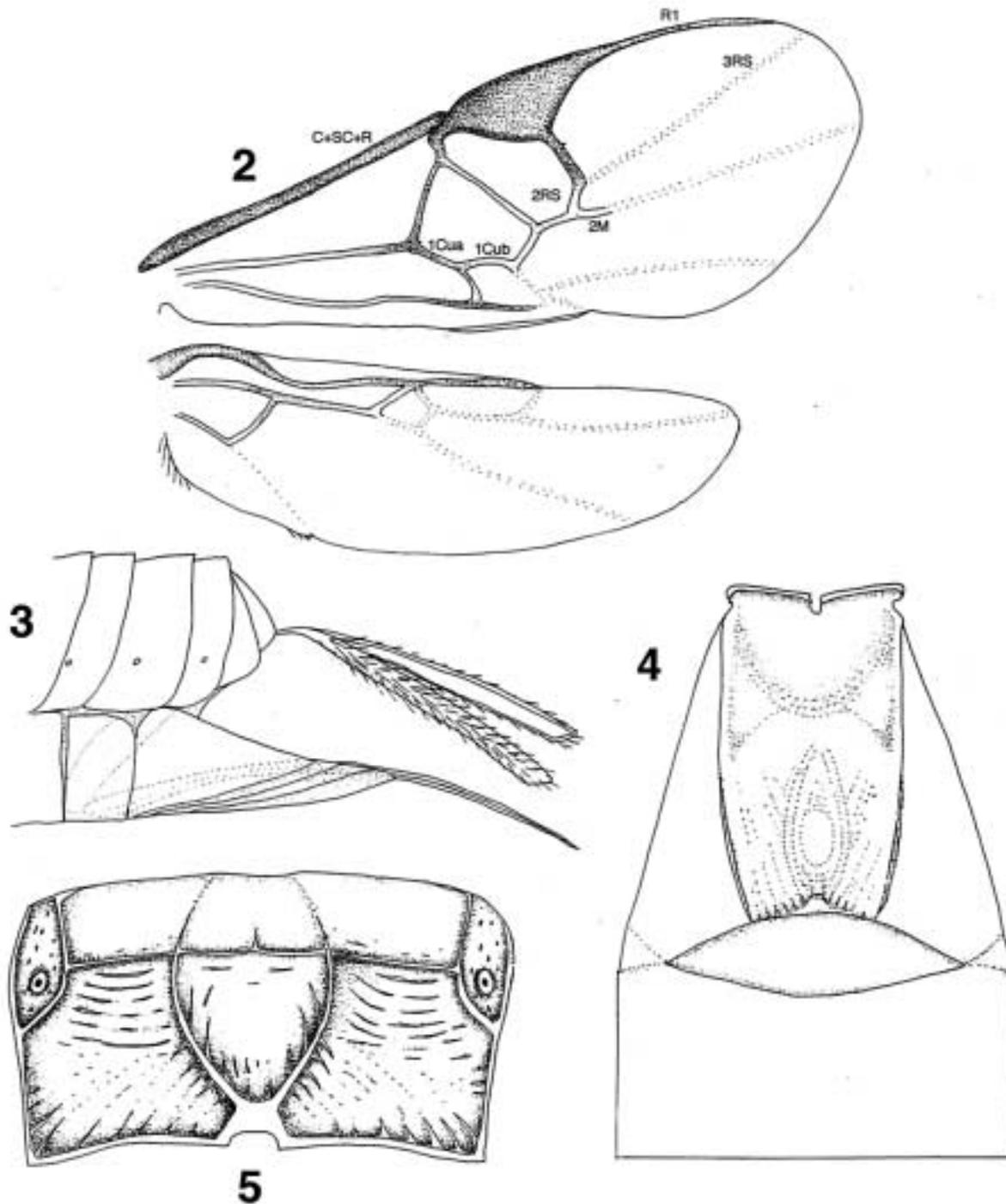
Apanteles ephestiae Baker, 1895, Entomological News 6: 201. Holotype female, U.S. National Museum, Washington, DC, examined.

This species of *Apanteles* has been reported frequently from temperate-zone colonies of *Bombus*. Neither the original describer of this species, Packard (1864), nor the first true reviser of the Nearctic species of its genus, Muesebeck (1920), provided a detailed description comparable to that of Wilkinson's (1932) description of *A. galleriae* or to that provided below for the new species. Thus, we redescribe this species here to allow detailed morphological comparison.

Female. Body length (excluding ovipositor and sheaths) 2.6–3.2 mm. Fore wing length 2.9–3.3 mm.

Color. General body color black, except lighter brown palpi, fore leg beyond coxa, mid leg beyond proximal 0.8 of femur, proximal 0.7 of hind tibia, and hind tarsus. Laterotergites of anterior metasomal tergites deep brown. Tegulae paler yellow-brown. Wings hyaline, most veins nearly colorless except C+Sc+R, stigma, R₁, r, 2RS, 2M, 1Cua + b, which are tinted deep brownish to varying degrees (Fig. 6). Stigma deep brown with pale translucent spot in proximal 0.3.

Head. Face distinctly but very shallowly punctate, wider than high, ventrally merging (on nearly same plane) with clypeus across nearly entire width. Malar space as short as or shorter than width of base of mandible, with distinct malar suture. Vertex coarsely but indistinctly punctate, surface smoother and shinier between ocelli. Ocelli orangish yellow, in a strongly obtuse angle, lateral ocelli more than two times as far from one another as either is from anterior ocellus. Antennae clearly shorter than body; distal 8–9 flag-



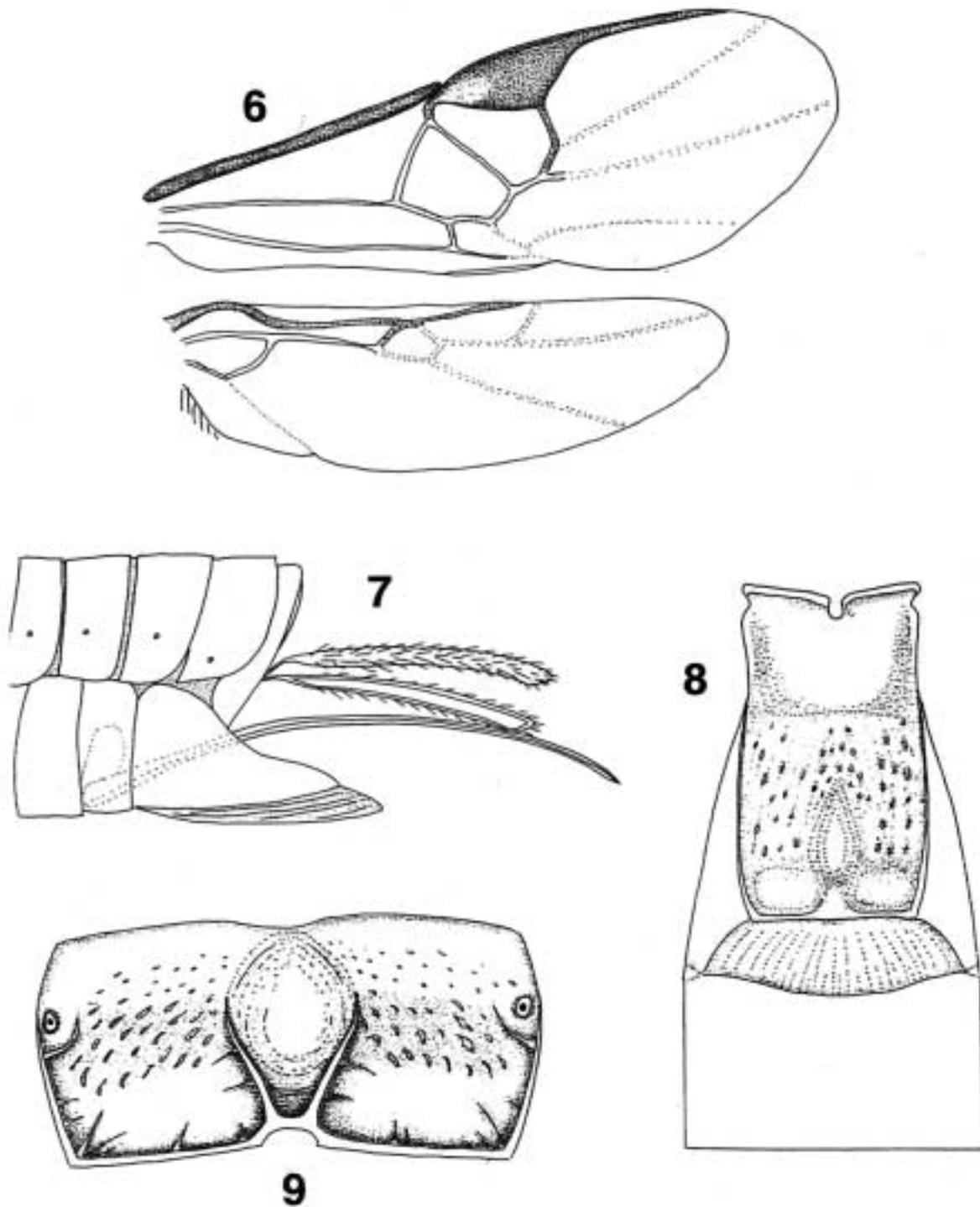
Figs. 2–5. *Apanteles galleriae* Wilkinson. (2) Wings. (3) Posterior end of female metasoma, lateral view. (4) Anterior metasomal tergites, dorsal view. (5) Propodeum, dorsal view.

ellomeres <1.5 times as long as broad and with only a single rank of placodes.

Mesosoma. Pronotum virtually smooth and polished over most of lateral surface except extreme dorsal and ventral corners, but bearing deep crenulate furrow dividing into clear posterodorsal and posteroventral arms. Mesonotum densely and distinctly punctate throughout, with punctations becoming rougher, denser and more confluent in posterior courses of

notauli. Scutoscutellar scrobe formed by ≈14 sometimes partially confluent fine pits. Scutellum subtriangular, less densely and coarsely punctate than mesoscutum; lunules subsemicircular (broader anteriorly), set off by strongly transcostate broad curving furrows.

Propodeum (Fig. 9) weakly sculptured anteriorly and posteriorly, more obliquely and roughly sculptured over middle 0.4 of length; areola well indicated



Figs. 6-9 *Apanteles nephopteris* (Packard). (6) Wings. (7) Posterior end of female metasoma, lateral view. (8) Anterior metasomal tergites, dorsal view. (9) Propodeum, dorsal view.

posteriorly by nearly V-shaped carinae, anteriorly open but shape indicated by distinct depression and weak concentric sculpturing. Costulae incomplete anteriorly and medially.

Metasoma. Tergite I (Fig. 8) approximately two times as long as broad, almost equally broad anteriorly as posteriorly but slightly bulging subapically, more strongly sculptured over posterior 0.6; narrow pos-

teromedial depression confined to posterior 0.5 of tergite, bordered laterally by two small posterior weakly sunken areas. Tergite II very weakly and longitudinally sculptured, ≈ 3.2 times as broad as long and with weakly convex posterior margin (slightly sinuate laterally).

Hypopygium (Fig. 7) $\approx 3/4$ as long as ovipositor sheaths, strongly acuminate apically, medially desce-

rotized into a series of expandible folds over entire length. Ovipositor sheaths (Fig. 7) nearly as long as hind tibia, weakly decurved, hairy over most of length, moderately slender with dorsally bluntly pointed tips.

Legs. Hind tibiae on outer faces with scattered spines of two thicknesses. Inner hind tibial spurs $\approx 10\%$ longer than outer and ≈ 0.35 as long as hind basitarsus.

Wings. Fore wing (Fig. 6). R1 extending ≈ 0.7 of distance beyond stigma to distal tip to end of 3RS fold. Vein r longer than 2Rs and weakly curved, but meeting 2RS at a distinct obtuse angle. Stigma of normal proportions, with pale spot in proximal 0.3.

Male. Similar to female except apical antennal segments longer, and first metasomal tergite tending to be more strongly narrowing posteriorly.

Material Examined for Redescription. ARKANSAS: Washington County, 3 miles NE Fayetteville, 8 females, 31 males, 1-7-X-1993, J. B. Whitfield, JBW no. 28-J-93, ex nest of *Bombus pennsylvanicus* infested with moth larvae. KANSAS: Douglas County, Lawrence, 2 males, September 1982, D. B. Wahl, emerged ex pyralid (?) in nest of *Bombus griseocollis* (DeGeer). OHIO: Franklin County, Columbus, 1 female, 2 males, 29-VII-1987, J. B. Whitfield and S. A. Cameron, JBW no. 7-G-87, emerged VII-VII-87, ex *Vitula edmandsae* larvae in old nest of *Bombus bimaculatus*.

Comments. Among the species from *Bombus* colonies, the shape of the propodeal areola and the pale spot at the base of the fore wing stigma are diagnostic.

Apanteles nidophilus Whitfield and Cameron, n. sp.
(Figs. 10-13)

Female. Body length (excluding ovipositor) 2.4-2.7 mm. Fore wing length 2.5-2.8 mm.

Color. General body color black, except deep yellow-brown palpi, fore leg beyond coxa, mid leg trochanter, distal 0.6 of femur, all of mid tibia and tarsus, and hind leg beyond femur. Fore and mid coxae often lighter ventrally. Tegulae nearly black. Laterotergites of anterior metasomal segments dark brown. Wings with all veins nearly colorless except darker gray-brown-tinted C+Sc+R, R1, periphery of stigma, r and 2RS. Stigma centrally whitish, somewhat more transparent.

Head. Face distinctly but shallowly punctate, wider than high, medially with incompletely demarcated border with clypeus. Malar space slightly longer than width of base of mandible, with obvious but not crisp malar suture. Vertex somewhat coarsely but indistinctly punctate, dull. Ocelli yellowish, in a strongly obtuse angle, lateral ocelli more than two times as far from one another as either is from anterior ocellus. Antennae slightly shorter than body, with distal 7-8 flagellomeres less than two times as long as broad, and with only a single rank of placodes.

Mesosoma. Pronotum very weakly sculptured and shiny throughout, with clearly defined furrow forking posteriorly into a deeper dorsal and thinner, more shallow ventral furrow. Mesonotum densely and distinctly punctate over most of surface, with more lon-

gitudinal confluent sculpturing along posterior courses of notauli; bearing a smoother, somewhat sunken transverse band just anterior to scutoscuteellar scrobe. Scrobe formed of ≈ 12 small, partially confluent pits. Scutellum elongate-triangular, very weakly and indistinctly punctate, with lunules rounded but nearly triangular in overall form, set off by narrow furrows from central triangle of scutellum. Propodeum (Fig. 13) more strongly sculptured anteriorly than posteriorly, with clearly carinated pentagonal areola that is open at anterior end in a sculptured depression. Transverse carinae laterally complete as are costulae.

Metasoma. Tergite I (Fig. 12) slightly barrel-shaped, 1.7 times longer than broad, about as broad posteriorly as anteriorly or up to 10% broader. Anterior depression broad and truncate posteriorly; posterior 0.7 of tergite weakly sculptured and mostly convex, with a shallow, weakly sculptured medial depression over middle half of tergite. Tergite II virtually smooth, 3.5-4.0 times as broad as long down middle, with strongly convex hind margin. Hypopygium (Fig. 11) approximately two-thirds as long as ovipositor sheaths, medially desclerotized and folded, apically weakly acuminate. Ovipositor sheaths (Fig. 11) about same length as hind tibiae, slender, weakly decurved and evenly hairy over most of length, apically pointed dorsally.

Legs. Hind tibiae with fairly evenly distributed larger spines on outer faces, all of one kind. Inner hind tibial spurs $\approx 30\%$ longer than outer and ≈ 0.4 as long as hind basitarsus.

Wings. Fore wing (Fig. 10) with R1 extending essentially to distal tip to end of 3RS fold or nearly so. Stigma of normal proportions but translucent whitish centrally. Vein r longer than 2RS, angle between them distinct.

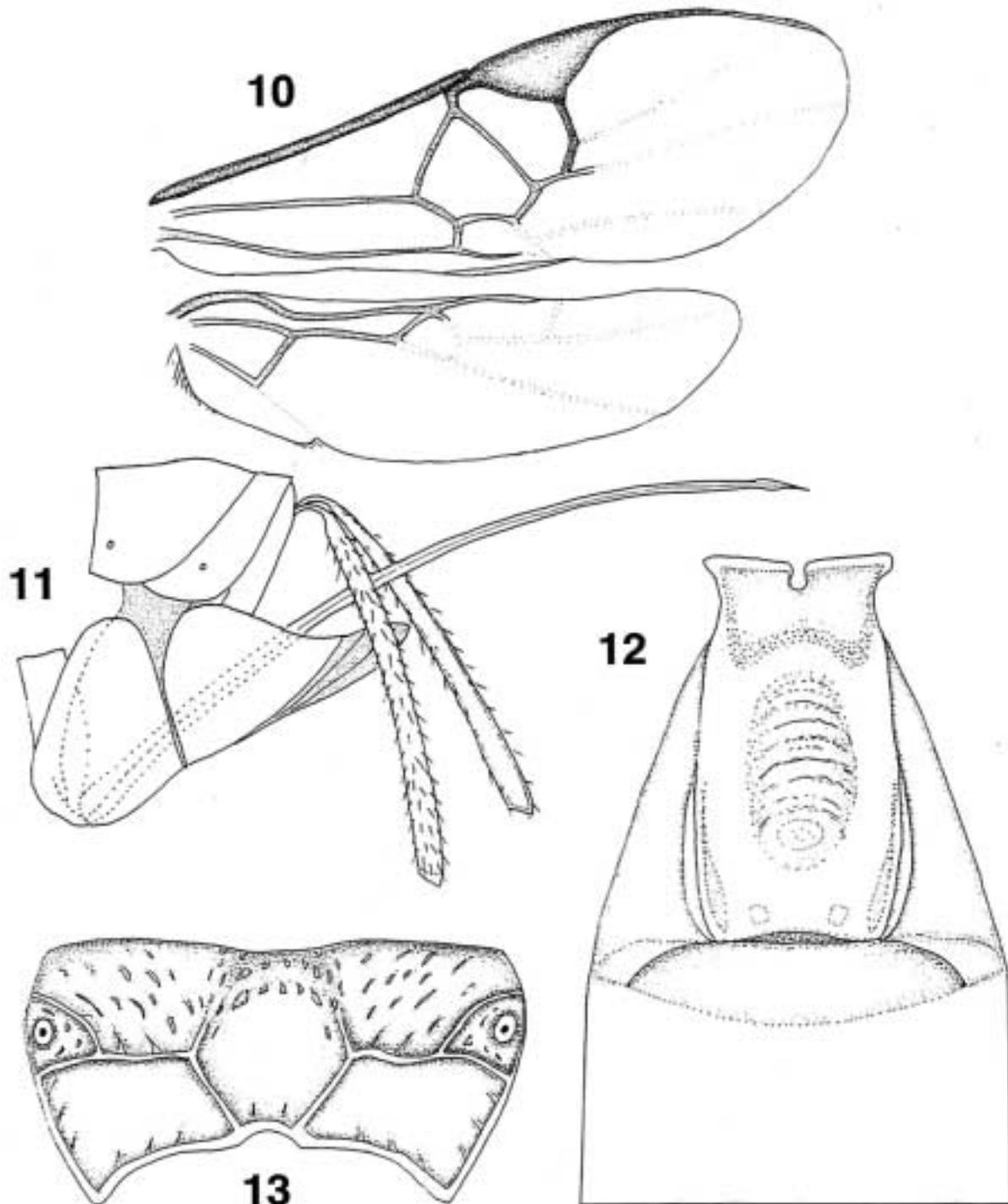
Male. Similar to female except apical antennal segments longer, anterior metasomal tergites slightly narrower.

Material Examined. Holotype female: ECUADOR: Orellana, Yasuní Scientific Station, 3-7-VII-2000, S. Cameron, S. Ramirez, J. Whitfield, S. Messinger, M. Taylor, ex excavated nest *Bombus transversalis*, host wax moths in old combs. Deposited in the U.S. National Museum, Washington, DC.

Paratypes: 5 males, same data as above, plus BRAZIL: São Paulo, Ribeirão Preto, 5 females, 6 males, 14-20-X-1993, S. A. Cameron, excavated wax moths in nest of *Bombus atratus*, emerged XI-1993. Deposited in the U.S. National Museum, Washington, DC, the Illinois Natural History Survey, Champaign, IL, and in the Humboldt Institute, Villa de Leyva, Boyacá, Colombia.

We have also collected material of this species from *Bombus transversalis* colonies near Palmari, Amazonas, Brazil, in Amacayacu National Park, Amazonas, Colombia, and in the Tambopata-Candamo Reserve Zone, Madre de Dios, Peru, as well as from a *B. atratus* colony at Subachoque (2,660 m), Cundinamarca, Colombia. This additional material was not used for the description (much of it is in poor condition).

Etymology. The name refers to the nest-inhabiting biology of this species, and is based loosely on the



Figs. 10-13 (13) *Apanteles nidophilus* Whitfield and Cameron, n. sp. (10) Wings. (11) Posterior end of female metasoma, lateral view. (12) Anterior metasomal tergites, dorsal view. (13) Propodeum, dorsal view.

Latin *nidus* for nest (*nido* in Spanish, which we refer to here) and the Greek -*philos* for loving (Latin *philus*).

Comments. The conspicuous centrally pale whitish stigma serves to clearly distinguish this species from the other two recovered from bumble bee colonies. This feature is, however, shared with a number of other neotropical *Apanteles* species, including the

aptly named *A. leucostigmus* (Ashmead), which attacks hesperiid larvae, and *A. balthazari* (Ashmead), which is known to attack oecophorid larvae attacking tropical fruit trees. None of these other species is, to our knowledge, associated with hymenopteran nests, nor do any of them share the same propodeal and anterior metasomal tergite features.

Key to Species

All three species keyed here can be referred to the diverse *ater-* group of *Apanteles* as recognized by Nixon (1965, 1976). Each of the diagnostic characteristics mentioned below in the key is found in other *ater-*group species, but not exactly in combination with the other features illustrated for these species in Figs. 2-13. It is beyond the scope of this paper to produce a new key to the entire species group, which contains several hundred species worldwide, but the three species treated here should be recognizable from the sets of figures, the geographical distributions and the habitats.

- (1) Stigma of fore wing entirely dark brown throughout (Fig. 2); propodeal areola anteriorly appearing truncated, closed by a transverse carina (sometimes weakly formed) (Fig. 5), first metasomal tergite usually clearly narrowing posteriorly (Fig. 4) . . . (essentially worldwide in distribution)
 *Apanteles galleriae* Wilkinson
- Stigma of forewing with paler area at base (Fig. 6), or with whitish/translucent wash centrally (Fig. 10); Propodeal areola appearing open anteriorly, although its anterior shape may be suggested by the edges of the central depression (figs. 10, 14); first metasomal tergite usually relatively equal in width anteriorly and posteriorly at least in females, sometimes broader posteriorly (Figs. 8 and 12) . . . 2
- (2) Stigma of fore wing with paler area at extreme base (Fig. 6); propodeum with well-marked areola but missing (or with only poorly formed) lateral portions of transverse carina (Fig. 9); (North America)
 *Apanteles nephopteris* (Packard)
- Stigma of fore wing whiter or more translucent centrally (Fig. 10); propodeum with well-formed lateral portions of transverse carina (Fig. 13) (South America)
 *Apanteles nidophilus* n. sp.
 Whitfield & Cameron

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References Cited

Cameron, S. A., and J. B. Whitfield. 1996. Use of walking trails by bees. *Nature* (Lond.) 379: 125.

Cameron, S. A., and M. C. Jost. 1998. Mediators of dominance and reproductive success among queens in the cyclically polygynous Neotropical bumble bee *Bombus atratus* Franklin. *Insectes Soc.* 45: 135-149.

Cameron, S. A., J. B. Whitfield, M. Cohen, and N. Thorp. 1999. Novel use of walking trails by the Amazonian bumble bee, *Bombus transversalis* (Hymenoptera: Apidae), pp. 187-193. *In* G. W. Byers, R. H. Hagen, and R. W. Brooks (eds.), *Entomological contributions in memory of Byron A. Alexander*. Univ. Kans. Nat. Hist. Mus. Spec. Publ. 24.

Frison, T. H. 1926. Contributions to the knowledge of the interrelationships of the bumblebees of Illinois with their animate environment. *Ann. Entomol. Soc. Am.* 19: 203-235.

Janzen, D. H. 1971. The ecological significance of an arboreal nest of *Bombus pullatus* in Costa Rica. *J. Kans. Entomol. Soc.* 44: 210-216.

Muesebeck, C.F.W. 1920. A revision of the North American species of ichneumonflies belonging to the genus *Apanteles*. *Proc. U.S. Nat. Mus.* 483-576.

Nixon, G.E.J. 1965. A reclassification of the tribe Microgasterini (Hymenoptera: Braconidae). *Bull. Br. Mus. (Nat. Hist.) Entomol. Suppl* 2: 1-284.

Nixon, G.E.J. 1976. A revision of the northwestern European species of the *merula*, *lacteus*, *vipio*, *ultor*, *ater*, *butalidis*, *popularis*, *carbonarius* and *validus*-groups of *Apanteles* Först. (Hymenoptera: Braconidae). *Bull. Entomol. Res.* 65: 687-735.

Whitfield, J. B. 1997. Subfamily Microgastrinae, pp. 333-364. *In* R. A. Wharton and P. M. Marsh, and M. J. Sharkey, [eds.], *Identification Manual to the New World Genera of the Family Braconidae* (Hymenoptera). *Int. Soc. Hymenopt. Spec. Publ.* 1.

Whitfield, J. B., and S. A. Cameron. 1993. Comparative notes on hymenopteran parasitoids in bumble bee and honey bee colonies (Hymenoptera: Apidae) reared adjacently. *Entomol. News* 104: 240-248.

Wilkinson, D. S. 1932. Four new *Apanteles* (Hymenoptera: Braconidae). *Stylops* 1: 139-144.

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