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# ANT-DECAPITATING FLIES, *APOCEPHALUS*, SUBGENUS *APOCEPHALUS* COQUILLETT (INSECTA: DIPTERA: PHORIDAE), OF ARIZONA

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**ABSTRACT.** Ant-parasitoid phorid flies are poorly known in North America but species rich, especially in the Southwest and particularly in Arizona. The eight known species of the ant parasitoid phorid fly subgenus *Apocephalus* (*Apocephalus*) from Arizona are reviewed and the following 20 new species are described: in the *Apocephalus feeneri* group (of Brown, 1997) are *A. brunneiventris*, *A. cochisei*, *A. mcfarlandi*, *A. orthocladus*, *A. reflexus*, *A. spantoni*, *A. titanis*, *A. uncinus*, and *A. wilki*; not assigned to species groups are *A. albipetrensis*, *A. anapastus*, *A. arizonensis*, *A. brevipennis*, *A. cernuus*, *A. fulleri*, *A. mesacanthus*, *A. nocturnus*, *A. pollocki*, *A. portalensis*, and *A. pugilis*. Host information and behavioral observations are given for many species. Seven of the new species are parasitoids of ants of the genus *Pheidole* Westwood, including *P. bicarinata* Mayr, *P. crassicornis* Emery, *P. diversipilosa* Wheeler, *P. hyatti* Emery, *P. obtusospinosa* Pergande, *P. perpilosa* Wilson, *P. rhea* Wheeler, *P. tetra* Creighton, and *P. vallicola* Wheeler, and one (*A. portalensis*) is a parasitoid of *Aphaenogaster texana* Wheeler.

## INTRODUCTION

The genus *Apocephalus* Coquillett, 1901, is the largest group of ant-parasitizing flies in the family Phoridae. All species of *Apocephalus*, subgenus *Apocephalus*, are parasitoids of adult ants, and because many species develop in the ant's head, they have acquired the common name "ant-decapitating flies." Species of the other subgenus, *Mesophora* Borgmeier, are parasitoids of other hosts, such as bees, wasps, and cantharoid beetles (Brown, 1996).

Like most phorids, ant-decapitating flies are poorly known, probably because they are small, inconspicuous flies (1–4 mm in body length). Their activities, however, are believed to have profound effects on the ants that they parasitize, and behavioral ecologists have a growing interest in studying phorid flies for both basic ecological and evolutionary science (e.g., LeBrun, 2005; LeBrun and Feener, 2007; Morehead et al., 2001; Philpott et al., 2004; Wilkinson and Feener, 2007) and for their potential to control pest ants (e.g., Morrison, 2000, and many other recent papers).

The *Apocephalus* fauna of Arizona, especially southern Arizona (south of Tucson), is extremely rich, with many undescribed species, some of which are beginning to be studied and referred to

in publications as numbered species: "*Apocephalus* sp. 25," for example. In order to make the research of ant ecologists working in Arizona (e.g., LeBrun, 2005; LeBrun and Feener, 2007; Wilkinson and Feener, 2007) more meaningful as well as to advance our knowledge of the genus in general, we decided to revise the species known from this state. Probably none of these species are restricted to Arizona, and our key will likely be equally useful for adjacent northern Mexico and southern New Mexico. Adjacent California has a more divergent fauna, although some species are shared with Arizona.

## METHODS AND MATERIALS

Seven species of *Apocephalus* from Arizona have already been treated in Brown's (1997, 2002) revisions; both papers are available as PDF files on the Internet at <http://www.phorid.net/phoridae/phorpub.html>. The rest of this material has been collected by the authors over many years, using Malaise and blacklight traps or by collecting over baited ants. Almost all are from the southern part of the state, which is biologically the most diverse area. Specimens were collected into alcohol and dried using hexamethyldisilazane (Brown, 1993).

Host records are given for Arizona *Apocephalus* are given in Table 1. Questionable records are discussed in the text.

The taxonomy of *Apocephalus*, subgenus *Apocephalus*, is based on females, specimens of which are the more distinctive than males. Male specimens are extremely similar to each other and are not easily associated with their respective females. We describe male specimens herein only if we have compelling evidence (such as collection in copula with a female) that they are conspecific.

Terms are those used in the *Manual of Central American Diptera* (Cumming and Wood, 2009). What

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Table 1 Host list for Arizona *Apocephalus* species (? = questionable or unverified records).

Ant host	<i>Apocephalus</i> species
<i>Aphaenogaster texana</i>	<i>A. portalensis</i>
<i>Camponotus sansabeanus</i>	<i>A. similis</i>
<i>Camponotus vicinus</i>	<i>A. horridus</i>
<i>Neivamyrmex</i> spp.	<i>A. platypalpis</i> ?
<i>Pheidole bicarinata</i>	<i>A. pugilis</i>
<i>Pheidole crassicornis</i>	<i>A. arizonensis</i>
<i>Pheidole diversipilosa</i>	<i>A. orthocladus</i>
<i>Pheidole hyatti</i>	<i>A. brunneiventris</i>
	<i>A. orthocladus</i>
<i>Pheidole obtusospinosa</i>	<i>A. anapastus</i>
	<i>A. mesacanthus</i> ?
	<i>A. uncinus</i>
<i>Pheidole perpilosa</i> Wilson	<i>A. brunneiventris</i>
<i>Pheidole rhea</i>	<i>A. titanus</i>
<i>Pheidole tetra</i>	<i>A. orthocladus</i>
<i>Pheidole vallicola</i>	<i>A. orthocladus</i>

Brown previously referred to as the ovipositor, a heavily sclerotized segment 7, is now called the oviscape.

We have not referred to the key to species of North American *Apocephalus* in Borgmeier (1963). This key is extremely outdated and of limited use to modern workers. The inclusion of *Apocephalus aridus* Malloch in Borgmeier's key, in particular, is highly questionable. This species is known only from males and is probably not distinguishable from many other Neotropical species that occur at the type locality in Veracruz, Mexico. It should not have been included in the key to North American species, as, biogeographically, Veracruz is part of the Neotropical Region. Furthermore, the specimens from Texas referred to this name by Borgmeier (1963) are of a different species than the holotype of *A. aridus*. LaBerge (1953) also erroneously used this name.

Borgmeier (1963) also included *Apocephalus grandipalpis* Borgmeier in his key. This is a species described from male specimens only from Pernambuco, Brazil. For this name to be usable, it would be necessary to establish which females of the hundreds of similar Neotropical species were conspecific with these males, and then compare them with North American species. In spite of this, Borgmeier assigned a large number of Texan specimens, male and female, to this taxon. It is unlikely that we will ever know with certainty which females should be associated with this name, so we do not recognize it in our work.

Some specimens were borrowed from the following institutions (codens from Arnett et al., 1993).

CASC	California Academy of Sciences, San Francisco, California
DEBU	University of Guelph, Ontario, Canada
EMUS	Utah State University, Logan, Utah
LACM	Natural History Museum of Los Angeles County, Los Angeles, California
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
SEMC	University of Kansas, Lawrence, Kansas
UCRC	University of California, Riverside, California
USNM	Smithsonian Institution, Washington, D.C.

In addition to the usual insect labels recording locality information, bar-coded insect labels were affixed to specimens (Thompson, 1994), and data were recorded in a database. All data are served to DiscoverLife (<http://www.discoverlife.org>), where range maps can easily be created.

SYSTEMATICS

*Apocephalus* Coquillett

*Apocephalus* Coquillett, 1901:501. Type species *A. pergandei* Coquillett, by original designation. Gender masculine (Ride et al., 1985: Article 30a iii).

*Pseudoplastophora* Schmitz, 1915:327, figs. 6, 7. Type species: *P. caudataria* Schmitz, by monotypy. Synonymized by Borgmeier, 1968.

*Anaclinusa* Borgmeier, 1969:63–64, figs. 35–37. Type species: *Anaclinusa lopesi* Borgmeier, by original designation. Synonymized by Brown, 2000.

*Pleurophorina* Borgmeier, 1969:66, figs. 40–42. Type species: *P. turgida* Borgmeier, by original designation. Synonymized by Brown, 1997.

*Zyziphora* Peterson and Robinson, 1976:119, figs. 1–5. Type species: *Z. hirtifrons* Peterson and Robinson, by original designation. Synonymized by Brown, 1992.

*Borgmeieria* Prado, 1976:582, figs. 52–53. Type species: *B. arnaudi* (Borgmeier) (= *Apocephalus horridus* Borgmeier), by original designation. Synonymized by Brown, 1997:4. (Note: Brown neglected to list this genus as a synonym in his 1997, 2000, and 2002 papers on *Apocephalus*.)

TAXONOMIC NOTE. The species groups used below were proposed by Brown (1997).

*Apocephalus attophilus* group

DIAGNOSIS. Oviscape with separate, apical sclerite (Figs. 3–5).

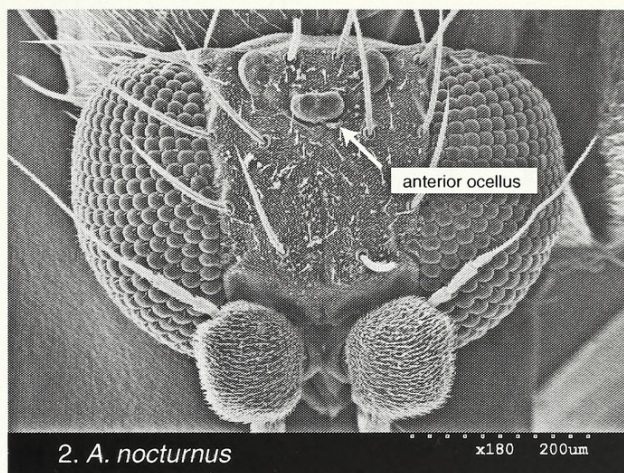
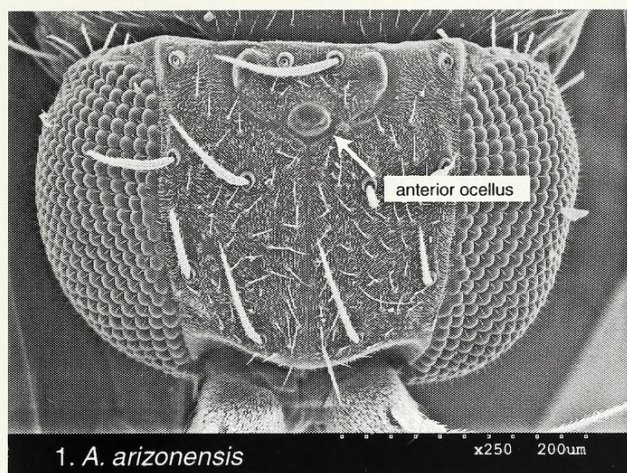
REMARKS. This group was revised by Brown (1997); since then, a few additional Neotropical species have been described (Corona and Brown, 2004; Disney and Bragança, 2000). Hosts are species of attine ants (Formicidae: Attinae), but no hosts are known for the Nearctic Region species.

*Apocephalus concavus* Brown (Fig. 3)

*Apocephalus concavus* Brown, 1997:53–54, fig. 77.

RECOGNITION. This species is extremely similar to *A. paulus* Borgmeier, 1963, but can be recognized by the thicker lateral margins and the lack of a medial, rounded sclerotization on the apical sclerite.





Figures 1, 2 Head, anterior

**HOST.** Unknown. Other species in the *A. attophilus* group attack attine ants.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona and New Mexico. See Brown (1997) for a list of localities.

*Apocephalus nigricauda* Brown  
(Fig. 4)

*Apocephalus nigricauda* Brown, 1997:39, fig. 54.

**RECOGNITION.** This species is easily recognized by the solid black apical sclerite.

**HOST.** Unknown. Other species in the *A. attophilus* group attack attine ants.

**GEOGRAPHICAL DISTRIBUTION.** Known from only the holotype specimen: **Arizona:** Upper White Rock Campground, Peña Blanca Lake, 31.38°N, 111.08°W, 1♀, 12–16.viii.1993, B. Brown, pan traps (LACM).

*Apocephalus paulus* Borgmeier  
(Fig. 5)

*Apocephalus paulus* Borgmeier, 1963:183, fig. 170; Brown, 1997:44, figs. 53, 83, 84.

**RECOGNITION.** The apical sclerite of this species is diagnostic, with its rounded medial sclerite and the thin lateral margins.

**HOST.** Unknown. Earlier, Brown (1997) speculated that based on this fly's distribution, the host is probably *Trachymyrmex septentrionalis* (McCook).

**GEOGRAPHICAL DISTRIBUTION.** USA, east of the western mountains. See Brown (1997) for a list of localities.

**NEW MATERIAL EXAMINED.** USA: **Arizona:** Cochise Co., 8.4 km W Portal, 31.88°N, 109.20°W, 1♀, 8.vii.1995, S. Gaimari, Malaise trap, 1520 m (LACM).

*Apocephalus pergandei* group

**DIAGNOSIS.** Tergite 6 broader than tergite 5, extending laterally on segment.

**REMARKS.** This group was revised by Brown (2002). Most hosts are ants of the genus *Camponotus* Mayr.

*Apocephalus aquilonius* Brown  
(Figs. 6, 10)

*Apocephalus aquilonius* Brown, 2002:27, figs. 57, 86.

**RECOGNITION.** This species is most similar to *A. horridus* and *A. wirthi*. Unlike *A. wirthi*, both *A. aquilonius* and *A. horridus* have supra-antennal setae; however, in *A. aquilonius*, these setae are farther apart than in *A. horridus*. The oviscapes of the three species also differ, with *A. wirthi* having a pair of stout dorsal, subapical setae (Fig. 9) and *A. horridus* having two longer lateral setae (Fig. 7) that are lacking in *A. aquilonius*.

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona and southern California. See Brown (2002) for a list of localities.

*Apocephalus horridus* Borgmeier  
(Figs. 7, 11)

*Apocephalus horridus* Borgmeier 1963:181–182, fig. 171; Brown, 2002:32–33, figs. 69–71, 87.

*Neodohrniphora arnaudi* Borgmeier, 1966:140–141, figs. 107–109; Brown, 1988:313–314, fig. 131. Synonymized by Brown, 1997:4.

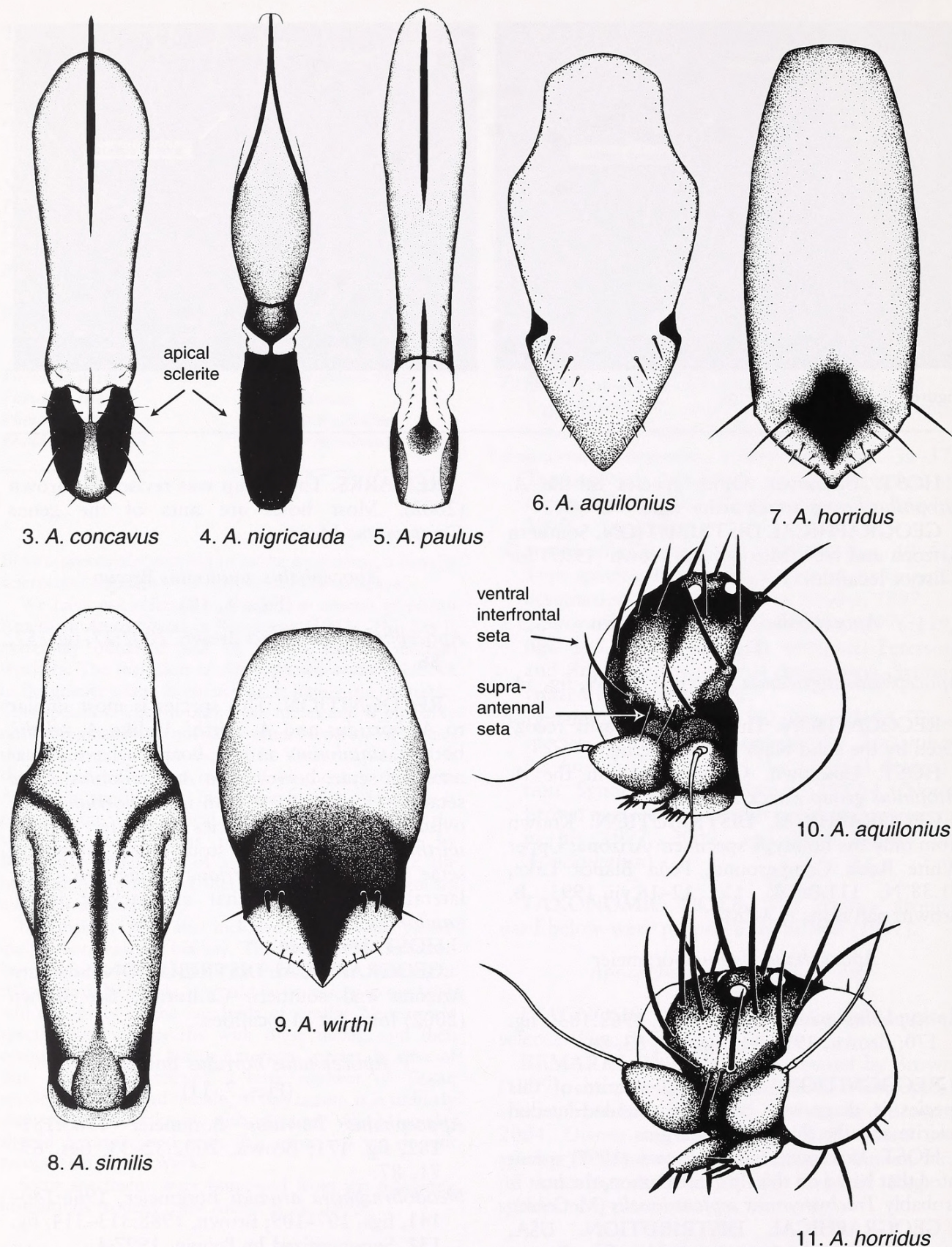
*Borgmeieria arnaudi*: Prado, 1976:582, figs. 52, 53.

**RECOGNITION.** See Recognition for *A. aquilonius*.

**HOST.** *Camponotus vicinus* Mayr (Mankowski and Morrell, 2003).

**GEOGRAPHICAL DISTRIBUTION.** Western North America. See Brown (2002) for a list of localities.





Figures 3–11 3–9. Oviscap (abdominal segment 7), dorsal; 10–11. head, anterolateral

*Apocephalus similis* Malloch  
(Fig. 8)

*Apocephalus similis* Malloch, 1912:444, pl. 38, figs. 7, 12, 13; Borgmeier, 1963:174–176, fig. 173; Brown, 2002:20–21, fig. 43.

**RECOGNITION.** This species differs from the other *A. pergandei*-group species in southern Arizona by its elongate, apically narrowed oviscape.

**HOST.** *Camponotus sansabeanus* Buckley.



**GEOGRAPHICAL DISTRIBUTION.** Arizona and Texas. See Brown (2002) for a list of localities. This fly was particularly common at Cochise Stronghold and was attracted in large numbers to colonies of *Camponotus sansabeanus* disturbed by turning over rocks along a dry streambed.

*Apocephalus wirthi* Borgmeier  
(Fig. 9)

*Apocephalus wirthi* Borgmeier, 1963:170–171, fig. 177; Brown, 2002:37, figs. 82–84, 88.

**RECOGNITION.** Lacking supra-antennal setae and possessing a narrow frons and a short, broad ov scape, this species is easily recognized. See also *A. aquilonius*.

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Eastern USA to Arizona (one record from Ramsey Canyon). For a full list of localities, see Brown (2002).

*Apocephalus feeneri* group

**DIAGNOSIS.** Intersegmental membrane 7–8, posterior to the ov scape (segment 7) with distinctive dorsal darkening (most *Apocephalus* have only clear, whitish membrane posterior to segment 7).

**NATURAL HISTORY.** All species within this group utilize species of the ant genus *Pheidole* Westwood as hosts. All the species known from this region for which the host is known parasitize the major worker caste only. Adult females oviposit into the gaster of the ant, typically injecting an egg through the membrane connecting terminal gastral tergites. Larvae migrate internally through the host and complete development in the head capsule. Pupariation has been observed in only one species: *A. orthocladus* new species. In this species, mature larvae crawl out of the head capsule and form a complete puparium nearby. This contrasts with some other groups of phorid parasitoids, such as species of *Pseudacteon* Coquillett, that pupariate inside the host head capsule.

**REMARKS.** This group and its structure are being studied more closely by the senior author (in preparation). Many species have a basal process on the venter of the ov scape (Fig. 12), formed from a pair of closely appressed, sometimes highly modified setae; they also have a more apical hook, which should not be confused with the basal process. All have long, thick setae and sclerites ventrally on the posterior margin of segment 6.

*Apocephalus brunneiventris* new species  
(Fig. 13)

**RECOGNITION.** This species is recognized by the shape of the basal process, whose setae are

flattened but anteriorly pointed, as well as the dark venter of the abdomen.

**DESCRIPTION. Female.** Body length 1.6–1.7 mm. Frons dark brown; mean frontal width 0.58 head width, range 0.56–0.61. Median furrow present. One pair of small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Flagellomere 1 round, brown. Palpus yellow, small, with normal-sized black setulae. Thorax brown. Scutellum with anterior seta small, subequal to posterior setulae of scutum. Anepisternum bare. Legs light brown. Tarsomeres unmodified. Hind femur darkened at apex. Wing of normal size. Mean costal length 0.37 wing length, range 0.36–0.39. Halter yellow. Abdominal tergites dark grayish-brown. Tergite 6 brown anteriorly to grayish-brown posteriorly, undivided; posterior margin of tergite with few elongate, thick setae. Venter of abdomen dark gray, segment 6 with large sclerite and row of long, thick setae that diminish in thickness medially except enlarged, well-separated medial pair.

**Female terminalia.** Ov scape with large lateral seta and few smaller apical setae. Venter of ov scape with basal process anteriorly directed, greatly thickened at midlength (Fig. 13).

**HOST.** *Pheidole hyatti* Emery and *P. perpilosa* Wilson.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona and New Mexico.

**DERIVATION OF SPECIFIC EPITHET.** Latin for “dark-ventered,” referring to the dark color of the abdomen.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Basin Trail, 31.88°N, 109.23°W, 20–24.viii.1993, B. Brown, Malaise trap [LACM ENT 012645] (LACM).

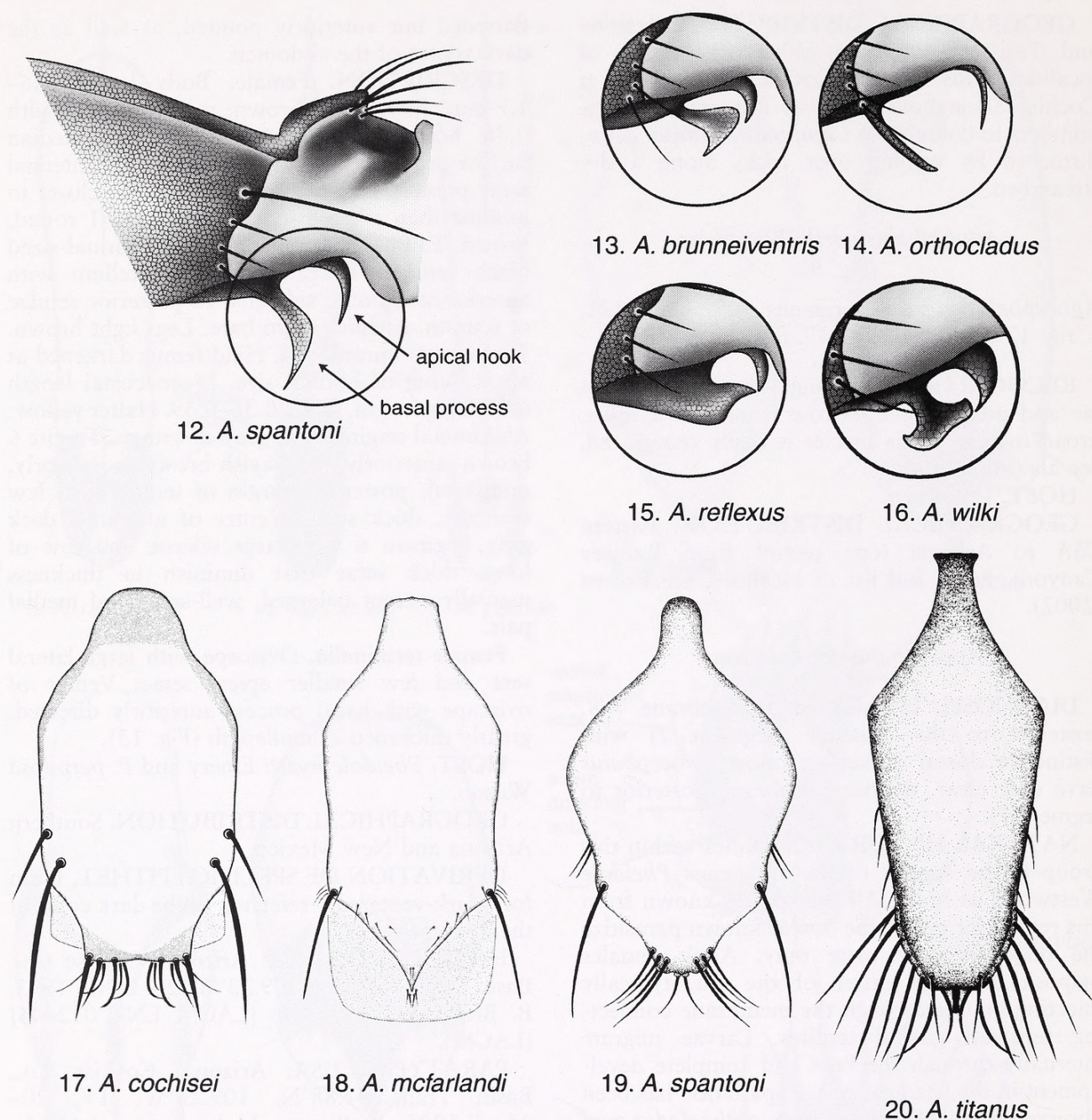
**PARATYPES.** USA: Arizona: Cochise Co., Basin Trail, 31.88°N, 109.23°W, 1♀, 20–24.viii.1993, B. Brown, Malaise trap (LACM), Chiricahua Mountains, 1♀, viii.2004, E. G. LeBrun, hovering over *Pheidole perpilosa*, pinel/juniper woodland (LACM). New Mexico: Catron Co., Pueblo Park, 33.59°N, 108.96°W, 1♀, 26.viii.1993, B. V. Brown, over *Pheidole* F29 [*P. hyatti*] (LACM).

*Apocephalus cochisei* new species  
(Figs. 17, 22, 45)

**RECOGNITION.** This species is recognized by the broad, truncate dorsal apex of the ov scape as well as the small, rounded setae that make up the basal process.

**DESCRIPTION. Female.** Body length 1.7 mm (no variation). Frons dark brown, 0.49 head width (no variation). Median furrow present. One pair of supra-antennal setae present. Ventral interfrontal seta closer to midline than eye margin. Ocelli and ommatidia not enlarged. Flagellomere 1 brown, rounded oval. Palpus yellow, with normal-





Figures 12–20 Oviscapes: 12–16. lateral; 13–16, inset of ventral details; 17–20. dorsal

sized black setulae. Thorax brown. Scutellum with anterior seta about same length as scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Tarsal claws modified, with basal lobe. Apex of hind femur darkened. Wing of normal size. Mean costal length 0.38 wing length, range 0.37–0.38. Halter yellow. Abdominal tergites dark brown; tergite 6 entire. Venter of abdomen dark gray; posterior margin of segment 6 with pair of triangular sclerites bearing posterior row of long, thick setae; largest setae most lateral in position (Fig. 45).

**Female terminalia.** Oviscape broadly truncate dorsoapically, with curved-tipped apical setae, with two long lateral seta, posterior larger

(Fig. 17). Venter of oviscape darkened near apex, with rounded, paired, flattened apical setae near apical hook (Fig. 22).

**HOST.** Unknown.

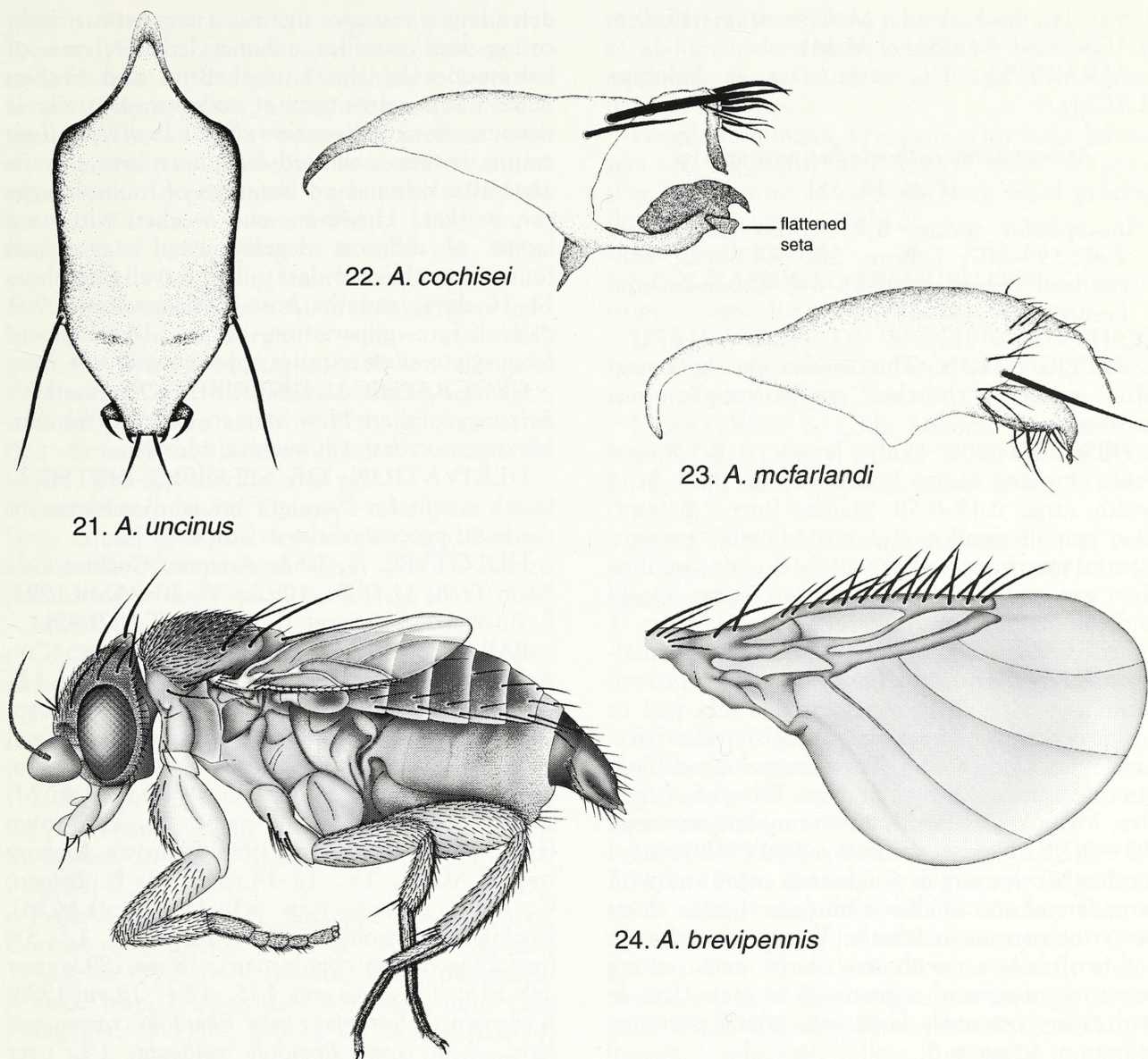
**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Named for the county in which the specimens were collected.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 24.ix–5-x.1993, N. McFarland, Malaise trap, 1550 m [LACM ENT 136758] (LACM).

**PARATYPES.** 1♀, same data as holotype (LACM).





Figures 21-24 21-23. Oviscapes: 21, dorsal; 22-23, lateral; 24. left, habitus, left side, right; wing, dorsal

*Apocephalus mcfarlandi* new species  
(Figs. 18, 23, 46)

**RECOGNITION.** The oviscap of this species differs from most others in the *A. feeneri* group by the lack of a basal process and the presence of thin ventral setae only.

**DESCRIPTION.** Female. Body length 1.8-2.0 mm. Frons dark brown; mean frontal width 0.54 head width, range 0.51-0.56. Median furrow present. One pair of supra-antennal setae present. Ventral interfrontal seta closer to midline than eye margin. Ocelli and ommatidia not enlarged. Flagellomere 1 brown, rounded oval. Palpus yellow, with short black setulae. Thorax brown. Scutellum with anterior seta about twice length of scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Tarsal claws modified, with basal

lobe. Apex of hind femur darkened. Wing of normal size. Mean costal length 0.45 wing length, range 0.44-0.45. Halter brown. Abdominal tergites dark brown; tergite 6 entire. Venter of abdomen dark gray; posterior margin of segment 6 with rectangular sclerite and row of long, thick setae (Fig. 46).

**Female terminalia.** Oviscap with long lateral seta (Fig. 18); lateral membrane of intersegment 7-8 heavily sclerotized. Venter of oviscap with long, thin setae only, without basal process (Fig. 23).

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Named for the collector of this and many other *Apocephalus* species.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 13-22.ix.



1993, N. McFarland, Malaise trap, 1550 m [LACM ENT 082381] (LACM).

**PARATYPES.** 1♀, same data as holotype (LACM).

*Apocephalus orthocladus* new species

(Figs. 14, 55)

"*Apocephalus* species 8," LeBrun and Feener 2002:599–607; LeBrun, 2005:643–652; LeBrun and Feener, 2007:58–64; Wilkinson and Feener, 2007:151–161.

**RECOGNITION.** This species can be recognized easily by the thin, nearly straight basal process.

**DESCRIPTION.** Body length 1.3–1.8 mm. Frons brown; mean frontal width 0.53 head width, range 0.49–0.58. Median furrow present. One pair of small supra-antennal setae present. Ventral interfrontal setae slightly closer to midline than eye margin, not strongly divergent. Ocelli and ommatidia not enlarged. Flagellomere 1 spherical, brown. Palpus yellow, with normal-sized black setulae. Thorax yellowish-brown. Scutellum with anterior seta small, subequal to scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur dark brown at apex. Wing of normal size. Mean costal length 0.36 wing length, range 0.34–0.38. Halter whitish-yellow. Abdominal tergites brown; tergite 6 lighter in color and with large lateral and smaller mediolateral setae along posterior margin in female. Venter of abdomen yellowish-brown, with few large setae along posterior margin of segment 6 in male, female with many extremely large setae along posterior margin of segment 6.

**Male terminalia.** Epandrium with long setae on both sides. Right surstylus short, deep, with large ventrally pointed seta and smaller dorsal setae (Fig. 55). Cercus nearly straight, light brown.

**Female terminalia.** Oviscape with large lateral seta at midlength and several setae at apex. Venter of oviscape with basal process nearly straight, thin (Fig. 14).

**NATURAL HISTORY.** With host records for *Pheidole diversipilosa* Wheeler, *P. hyatti*, *P. tetra* Creighton, and *P. vallicola* Wheeler, this species has the broadest host range known for any species in this group. Its collection over *Dorymyrmex insanus* (Buckley) was probably due to an unobserved competitive conflict between *D. insanus* and one of its *Pheidole* hosts at a bait. Both male and female flies are attracted to host ants recruiting to food items. At least for *P. diversipilosa* colonies, they are not attracted to disturbed nests. These flies mate at the host and are able to fly in copula; in fact, males and females commonly arrive at recruitment trails in copula, suggesting mate-guarding behavior by males. The flies' ability to discover recruitment trails of host ants is enhanced when the host is

defending a resource against a competitor, indicating that conflict enhances the release of kairomones by the host (LeBrun and Feener, 2002). Superparasitism at recruitment trails is uncommon, and dissection of 231 *P. diversipilosa* major workers collected from recruitment trails after attack found no instances of multiple eggs per worker. However, one worker with two larvae of different developmental stages was found (unpublished data). The larval stage lasts 11–16 days, and the host is incapacitated 2–3 days before pupariation occurs. Development from egg to adult requires approximately 34 days.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona; southern New Mexico; northern Sonora, Mexico; northern Chihuahua, Mexico.

**DERIVATION OF SPECIFIC EPITHET.** Greek words for "straight branch," referring to the basal process of the oviscape.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Basin Trail, 31.88°N, 109.23°W, 20–24.viii.1993, B. Brown, Malaise trap [LACM ENT 012649].

**PARATYPES.** USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 2♀, 13–22.ix.1993, N. McFarland, Malaise trap, 1550 m (LACM), 18.5 km W Portal, Basin Trail head, 3♀, 8–10.vii.1987, B. Brown, T. Spanton, yellow pans, oak/pine/juniper, 1950 m (LACM) 2♀, 26.vii.1988, yellow pans, B. V. Brown (LACM), 11♀, 20–24.viii.1993, B. Brown, Malaise trap (LACM), 1♀, 13–14.viii.1999, B. Brown, G. Kung, Malaise trap #3, 1950 m (LACM), Cochise Stronghold, 31.92°N, 109.97°W, 1♂, 5♀ (including one in copula pair), 18.viii.1993, over ant F16, 1♀, over ant F15, 12♀, 19.viii.1993, B. Brown, J. Stireman, over *Pheidole crassicornis* tetra, 7♀, over *Pheidole vallicola*, 1♀, over *Pheidole hyatti*, 2♀, over *Dorymyrmex insanus*, 2♀, over ant F26 (EMUS, SEMC, LACM, MCZC, USNM), 2♀, 16–20.viii.1993, B. V. Brown, Malaise trap, 1525 m (LACM), Greenhouse Trail, 31.88°N, 109.27°W, 3♀, 25–26.ix.1998, E. LeBrun, Malaise trap, 2000 m (LACM); Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 5♀, 24.vi.1994, 1♀, 1.viii.1994, 1♀, 4.ix.1994, 2♀, 7.x.1994, 1♀, 19.xi.1994, 1♀, 9.vii.1995, 3♀, 15.vii.1995, 1♀, 23.vii.1995, 1♀, 30.vii.1995, 4♀, 5.viii.1995, 3♀, 13.viii.1995, B. Brown, E. Wilk, Malaise trap (LACM). New Mexico: Guadalupe Co., Santa Rosa Lake State Park, 10♂, 1♀, 3–4.viii.1984, B. V. Brown, L. B. Carlson, dung traps, desert (LACM).

*Apocephalus reflexus* new species

(Fig. 15)

**RECOGNITION.** This species can be recognized by the shape of the basal process, which has a small, posteriorly directed point.

**DESCRIPTION.** Female. Body length 1.2–1.4 mm. Frons brown; mean frontal width 0.58 head width, range 0.56–0.59. Median furrow



present. One pair of small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Flagellomere 1 round, brown. Palpus yellow, small, with normal black setulae. Thorax light brown. Scutellum with anterior seta small, subequal to scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur darkened at apex. Wing of normal size. Mean costal length 0.35 wing length, range 0.33–0.37. Halter yellowish-brown. Abdominal tergites light brown to brown. Tergite 6 yellow, undivided; posterior margin of tergite with few elongate, thick setae. Venter of abdomen yellow, segment 6 with large sclerite and row of long, thick setae that diminish in thickness medially except enlarged, well-separated medial pair.

**Female terminalia.** Oviscape triangular, with large lateral seta and few smaller apical setae. Venter of oviscape with basal process curved posteriorly to meet apical hook (Fig. 15).

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Latin for “bent backwards,” referring to the antero-ventral process of the oviscape.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 9.vii.1995, B. Brown, E. Wilk, Malaise trap [LACM ENT 052285] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., Cochise Stronghold, 31.92°N, 109.97°W, 2♀, 16–20.viii.1993, B. V. Brown, white pan traps, Malaise trap, 1525 m (LACM); Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 2♀, 16.vi.1994, 1♀, 24.vi.1994, 1♀, 1.viii.1994, B. Brown, E. Wilk, Malaise trap (LACM).

*Apocephalus spantoni* new species  
(Figs. 12, 19)

**RECOGNITION.** This species is recognized by the anteriorly curved basal process.

**DESCRIPTION.** **Female.** Body length 1.25–1.50 mm. Frons dark brown; mean frontal width 0.52 head width, range 0.51–0.53. Median furrow present. One pair small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin, not strongly divergent. Ocelli and ommatidia not enlarged. Flagellomere 1 small, spherical, dark brown. Palpus yellow, small, with normal-sized black setulae. Scutum and scutellum reddish-brown. Scutellum with anterior seta extremely small, approximately equal in size to scattered setulae of scutum. Pleuron brown. Anepisternum bare. Legs yellowish-brown, except apex of hind femur darker. Wing of normal size. Mean costal length 0.38 wing length, range 0.36–0.40. Halter whitish-yellow. Abdominal tergites brown; tergite 6 lighter in color and with large lateral and smaller

mediolateral setae along posterior margin. Venter of abdomen dark gray, segment 6 with row of extremely large, thick setae (especially medial pair) posteriorly.

**Female terminalia.** Oviscape with large lateral seta at midlength and several setae at apex (Fig. 19). Venter of oviscape with basal process flattened, recurved (Fig. 12).

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Known from a single site in southeastern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Named for the senior author’s friend and fellow entomologist, the late Timothy G. Spanton.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Basin Trail, 31.88°N, 109.23°W, 20–24.viii.1993, B. Brown, pan traps [LACM ENT 012680] (LACM).

**PARATYPES.** USA: Arizona: 18.5 km W Portal, Basin Trail head, 2♀, 8–10.vii.1987, T. G. Spanton, FIT, oak/pine/juniper (LACM).

*Apocephalus titanus* new species  
(Fig. 20)

**RECOGNITION.** This species is easily recognized by its large size, the extremely thick ventral setal bundles on segment 6, and the series of long posterior setae on the oviscape.

**DESCRIPTION.** **Female.** Body length 2.2–2.7 mm. Frons brown; mean frontal width 0.53 head width, range 0.49–0.55. Median furrow present. One pair of small supra-antennal setae present. Ventral interfrontal setae slightly closer to midline than eye margin, not strongly divergent. Ocelli and ommatidia not enlarged. Flagellomere 1 spherical, yellow, but darker laterally. Palpus yellow, with normal-sized black setulae. Thorax yellow. Scutellum with anterior seta about one-half length of posterior seta, but much thinner. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur darkened at apex. Wing of normal size. Mean costal length 0.45 wing length, range 0.43–0.46. Halter yellow. Abdominal tergites yellowish-brown, with darker brown markings posteriorly, especially on tergite 6; tergite 6 entire. Venter of abdomen yellow. Venter of segment 6 with large sclerite, each side with extraordinarily thick process formed of bundle of several long setae bundled together, with line of relatively short setae between them, more laterally with two long setae on each side.

**Female terminalia.** Oviscape triangular, with series of long, posterior setae (Fig. 20). Venter of oviscape with long, thin setae; basal process absent.

**NATURAL HISTORY.** The host of this species is *Pheidole rhea* Wheeler, a granivore that utilizes a trunk-trail foraging system. This fly attacks its host along these trunk trails. It is most abundant in open oak woodlands and drainages containing



host colonies. Attack by this fly induces defensive posturing in host workers. Females attack both major and media worker castes in this trimorphic ant (host caste size distribution: Wilson, 1953).

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** From Titan, a giant in Greek mythology, referring to the large size of this species.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., 11 km W Peña Blanca Lake [Yank's Canyon, 31.43°N, 111.16°W], 28.vii.1988, B. Brown, D. Feener, over *Pheidole rhea* [LACM ENT 010890] (LACM).

**PARATYPES.** 9♀, same data as holotype, 8♀, same data except 15.viii.1993 (LACM, MCZC, USNM).

*Apocephalus uncinus* new species

(Figs. 21, 57)

**RECOGNITION.** This species can be recognized by the single apical pair of setae on the dorsum of the ov scape, as well as the two pairs of curved, apical hooks.

**DESCRIPTION.** Body length 1.7–2.1 mm. Frons brown; mean frontal width 0.52 head width, range 0.50–0.53. Median furrow present. One pair of small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Flagellomere 1 round, brown. Palpus yellow, of normal size, with normal-sized black setulae. Thorax yellowish-brown. Scutellum with anterior seta small, subequal to scattered setulae of scutum. Anepisternum bare. Legs mostly yellowish-brown. Tarsomeres unmodified. Hind femur darkened at apex. Wing of normal size. Mean costal length 0.40 wing length, range 0.40–0.41. Halter yellow. Abdominal tergites yellow anteriorly, darker posteriorly (darker and more extensively dark in males); tergite 6 yellow; female tergite 6 yellow. Venter of abdomen yellow; bare except with few scattered setulae on segment 6 in male; female segment 6 with large sclerite with row of long, thick setae that diminish in thickness medially.

**Male terminalia.** Epandrium with long setae, especially on left side. Right surstylus short, tall, with long setae. Cercus yellowish brown, relatively straight (Fig. 57).

**Female terminalia.** Oviscape triangular, with one large seta laterally (Fig. 21); apex with two pairs of flattened, hooklike setae; first pair smaller, attached apically and curving downward; second pair larger more ventral in attachment and curving upwards. Venter of oviscape without basal process or apical hook.

**NATURAL HISTORY.** The host of this species is *Pheidole obtusospinosa* Pergande (formerly known as *P. subdentata* Pergande). The fly attacks its host along recruitment trails, and is most abundant in open oak woodlands and

drainages containing host colonies. Attack by this fly induces defensive posturing in host workers of all castes, effectively shutting down all activity on recruitment trails for prolonged periods. Females attack both major and media worker castes in this trimorphic ant (host caste size distribution: Wheeler, 1991).

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona, northern Mexico.

**DERIVATION OF SPECIFIC EPITHET.** Latin for “hooked” or “barbed,” referring to the two pairs of hooks at the apex of the ov scape.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., Patagonia, 15.vii.1995, B. Brown, E. Wilk, Malaise trap [LACM ENT 052270] (LACM).

**PARATYPES.** MEXICO: Sonora: Alamos, 3♀, 23.ii.1963, P. H. Arnaud, Jr. (CASC). USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 2♀, 13–22.ix.1993, 3♀, 1–11.xi.1993, N. McFarland, Malaise trap, 1550 m (LACM), Sunnyside Canyon, 3♀, 29.viii.1981, 4♀, 30.viii.1981, D.H. Feener, over *Pheidole subdentata* (LACM), 1♀, 9.viii.1989, D. Pollock, black-light trap (LACM) 3♀, 8–11.viii.1989, E. Fuller, Malaise trap (LACM); Pima Co., General Hitchcock Campground, 32.38°N, 110.68°W, 3♀, 27.viii.1993, J. Stireman, 12♂, 26♀, 28.viii.1993, B. Brown, over *Pheidole subdentata* (EMUS, LACM, MCZC, SEMC, USNM); Pinal Co., Oracle, 1♀, vi.1991, J. O'Hara, Malaise trap, 4700 feet (LACM); Santa Cruz Co., 16 km N Nogales, 11 km W Peña Blanca Lake, 9♂, 7♀, 28.vii.1988, 1♂, 29.vii.1988, B. Brown, D. Feener, over *Pheidole subdentata* (LACM), Patagonia, 31.53°N, 110.77°W, 1♀, 10.ix.1995, B. Brown, E. Wilk, Malaise trap (LACM), Peña Blanca Canyon, 31.38°N, 111.09°W, 3♂, 4♀ (including two in copula pairs), 14.viii.1993, 1♂, 12♀, 15.viii.1993, B. Brown, over *Pheidole subdentata* (LACM), Upper White Rock Campground [Peña Blanca Lake], 31.39°N, 111.08°W, 22♀, 12.viii.1993, B. Brown, *Neivamyrmex* raid [on *Pheidole subdentata*] (LACM), 1♀, hovering over *Pheidole subdentata* (LACM), 3♀, 12–16.viii.1993 (LACM), 1♀, 18–20.ix.1997, B. Brown, G. Kung, J. Paldi, white pans (LACM).

*Apocephalus wilki* new species

(Fig. 16)

**RECOGNITION.** This species is distinguished by the flattened setae of the basal process, which extend both anteriorly and posteriorly.

**DESCRIPTION.** Female. Body length 1.6–1.9 mm. Frons dark brown; mean frontal width 0.56 head width, range 0.54–0.57. Median furrow present. One pair of small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Flagellomere 1 round, brown. Palpus yellow, small, with slightly reduced black setulae. Thorax light brown. Scutellum with anterior seta small, subequal to scat-



tered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur darkened at apex. Wing of normal size. Mean costal length 0.36 wing length, range 0.35–0.38. Halter yellow. Abdominal tergites light brown to brown. Tergite 6 yellow, undivided; posterior margin of tergite with few elongate, thick setae. Venter of abdomen yellow, segment 6 with large sclerite and row of long, thick setae that diminish in thickness medially except enlarged medial pair, which are often close together and appear as one.

**Female terminalia.** Oviscape triangular, with large lateral seta and few smaller apical setae. Venter of oviscape with basal process expanded apically in both anterior and posterior directions (Fig. 16).

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Known only from southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Named for Mr. Ed Wilk, staff member of the Patagonia-Sonoita Nature Conservancy Reserve, who kindly operated a Malaise trap for us on Conservancy land.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 13.viii.1995, B. Brown, E. Wilk, Malaise trap [LACM ENT 050806] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 1♀, 13–22.ix.1993, N. McFarland, Malaise trap, 1550 m (LACM); Santa Cruz Co., 1♀, same data as holotype, 2♀, same data except 15.vii.1995, 6♀, 30.vii.1995 (LACM, MCZC, USNM).

#### Other *Apocephalus*

#### *Apocephalus albipetrensis* new species

(Figs. 25, 40, 42, 49)

**RECOGNITION.** This species has a non-descript oviscape similar to that of *A. pollocki* new species. The stylet of *A. albipetrensis*, however, has subparallel basal apices (Fig. 49), whereas those of *A. pollocki* are roundly convergent (Fig. 52). Also, the ventral setae of segment 6 are slightly different, with the medial two pairs enlarged in *A. albipetrensis* but only one medial pair enlarged in *A. pollocki*. Finally, tergite 6 is fully separated into two sclerites (similar to Fig. 41) in *A. pollocki* but still joined by a narrow bridge in *A. albipetrensis* (Fig. 40).

**DESCRIPTION. Female.** Body length 1.2 mm. Frons dark brown, 0.58 head width. Median furrow present. One pair of supra-antennal setae present. Ventral interfrontal seta closer to midline than eye margin. Ocelli enlarged, ommatidia not enlarged. Flagellomere 1 brown, oval. Palpus yellow, not enlarged, with normal-sized black setulae. Thorax brown, pleuron lighter. Scutellum with anterior seta small, slightly longer than scattered setulae of scutum. Anepisternum bare.

Legs yellowish-brown. Tarsomeres unmodified. Apex of hind femur not darkened. Wing of normal size. Costa 0.45 wing length. Halter brown. Abdominal tergites brown; tergite 6 separated into two smaller tergites joined by medial bridge of sclerotization (Fig. 40). Venter of abdomen whitish-gray, segment 6 with thin sclerite and four long, thick setae flanked by few thinner setae (Fig. 42).

**Female terminalia.** Oviscape short, without apical sclerite, dorsoapically merging into heavily sclerotized lateral membrane (Fig. 25). Stylet with anterior arms parallel (Fig. 49).

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Latin *albus* and *petra* for “white rock,” referring to the name of the type locality, which has yielded many new species of Phoridae.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., Upper White Rock Campground, 31.39°N, 111.08°W, 18–20.ix.1997, B. Brown, G. Kung, J. Paldi, pan traps [LACM ENT 082434] (LACM).

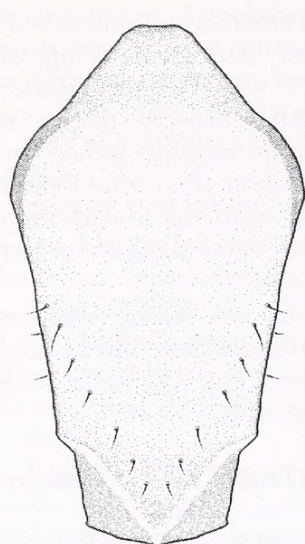
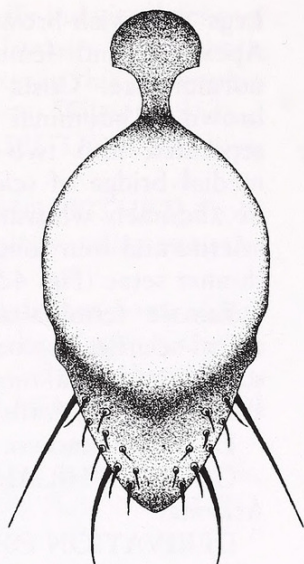
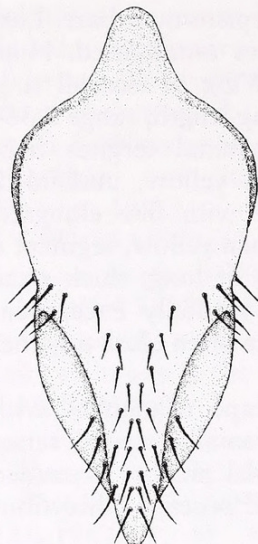
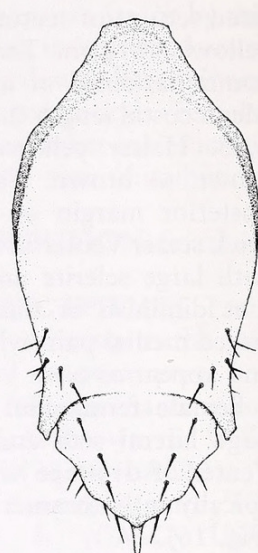
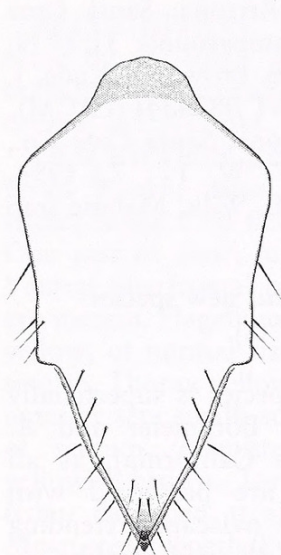
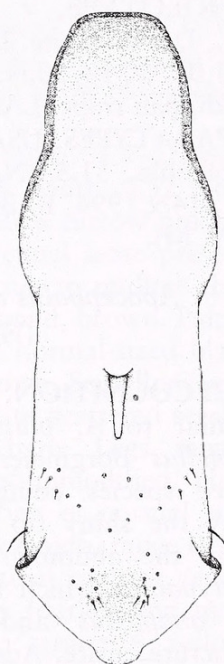
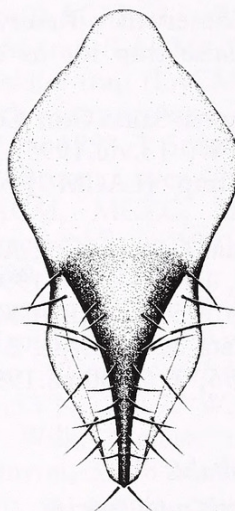
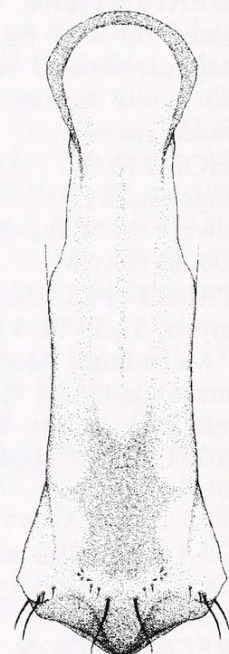
**PARATYPES.** USA: Arizona: Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 1♀, 7.x.1994, 1♀, 14.x.1994, B. Brown, E. Wilk, Malaise trap (LACM).

#### *Apocephalus anapastus* new species (Figs. 26, 38)

**RECOGNITION.** This species is superficially similar to *A. platypalpis* Borgmeier and *A. gemellus* Borgmeier (from California), as all three species commonly are preserved with only the shiny tip of the oviscape extending from the abdomen (Figs. 38, 39). Unlike *A. platypalpis*, which has tergite 6 fully divided, *A. anapastus* and *A. gemellus* have this structure entire. Additionally, there are numerous differences in the form of the oviscape. The oviscape of *A. anapastus* differs from that of *A. gemellus* by having an elongate, narrowed anterior process (much broader in *A. gemellus*), and a long medial pair of ventral setae of segment 6 are also more differentiated than in *A. gemellus*.

**DESCRIPTION. Female.** Body length 1.5–1.7 mm. Frons brown; mean frontal width 0.60 head width, range 0.59–0.60. Median furrow present. One pair large supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Ocelli enlarged, ommatidia not enlarged. Flagellomere 1 brown, round. Palpus yellow, with normal-sized black setulae. Scutum brown; pleuron in some specimens lighter. Scutellum with anterior seta small, slightly longer than scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Apex of hind femur not darkened. Wing of normal size. Mean costal length 0.43



25. *A. albipetrensis*26. *A. anapastus*27. *A. arizonensis*28. *A. cernuus*29. *A. fulleri*30. *A. mesacanthus*31. *A. nocturnus*32. *A. platypalpis*

Figures 25–32 Oviscapes, dorsal

wing length, range 0.41–0.44. Halter brown. Abdominal tergites light brown; tergite 6 entire, narrow, elongate, apically rounded. Venter of abdomen gray; posterior margin of segment 6 with row of six long setae, with medial pair longest (Fig. 38).

**Female terminalia.** Oviscape (Fig. 26) rounded, with mushroom-shaped anterior process; two long ventrolateral setae present; apical one-third of oviscape strongly ventrally deflected.

**HOST.** Unknown, although one specimen was collected over a disturbed colony of *Pheidole* sp.

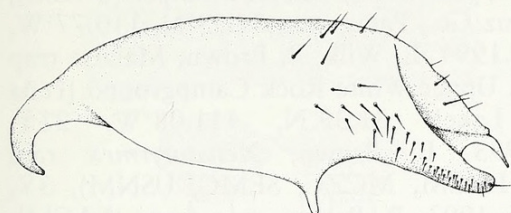
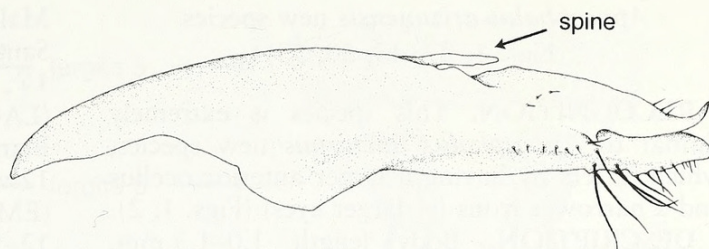
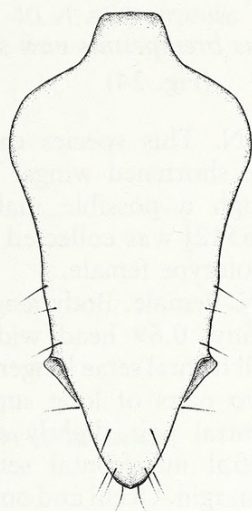
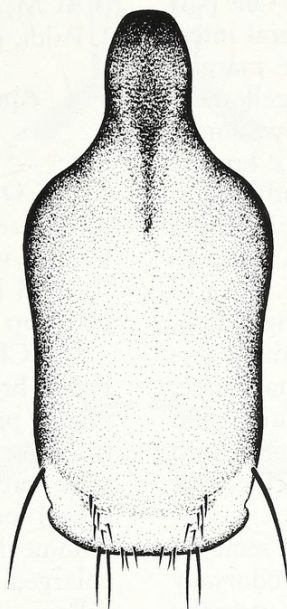
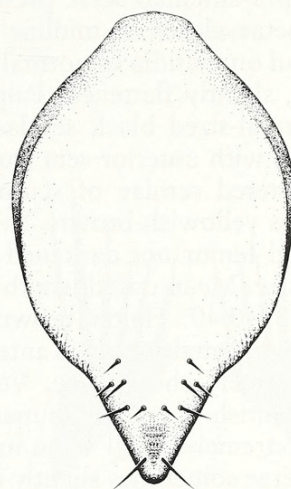
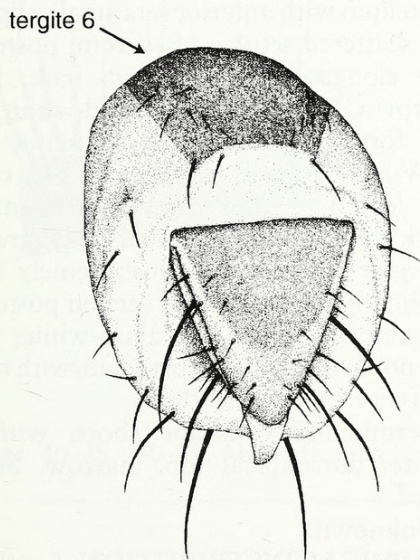
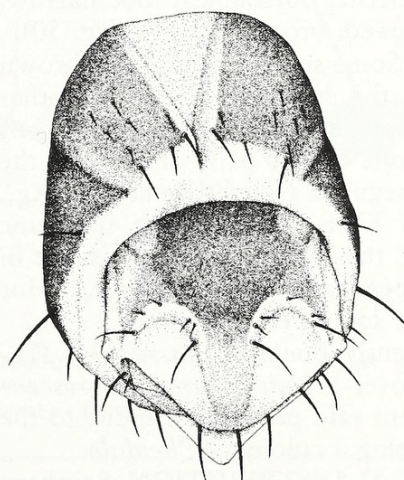
**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Greek *anapastos* for “drawn up,” referring to the oviscape, which is usually withdrawn into the abdomen.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 1–11.xi.1993, N. McFarland, Malaise trap, 1550 m [LACM ENT 050576] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., Greenhouse Trail, 31.88°N, 109.27°W, 1♀,



33. *A. cernuus*34. *A. mesacanthus*35. *A. pollocki*36. *A. portalensis*37. *A. pugilis*38. *A. anapastus*39. *A. platypalpis*

Figures 33–39 33–37. Oviscapes: 33–34, lateral; 35–37, dorsal; 38–39. abdomen, posterolateral, showing apical portion of oviscap

10.viii–11.ix.1999, E. LeBrun, Malaise trap (LACM); 12.5 km S Sierra Vista, Ramsey Canyon, 22.vi.1987, B. V. Brown, Malaise trap, 1700 m, oak/pine/juniper (LACM); Pima Co., General Hitchcock Campground, 32.38°N, 110.68°W, 1♀, 27.viii.1993, J. Stireman, over

*Pheidole* F30 (LACM), 16 km W Tucson, SASI, 32.24°N, 111.13°W, 1♀, 7–14.vi.1995, S. Prchal, Malaise trap (LACM); Santa Cruz Co., Peña Blanca Lake [Upper White Rock Campground], 31.39°N, 111.08°W, 1♀, 12.viii.1993, B. Brown, blacklight trap (LACM).



*Apocephalus arizonensis* new species

(Figs. 1, 27, 43, 50, 53)

**RECOGNITION.** This species is extremely similar to *Apocephalus nocturnus* new species, which differs by having a larger anterior ocellus and a narrower frons (= larger eyes) (Figs. 1, 2).

**DESCRIPTION.** Body length 1.0–1.3 mm. Frons brown; mean frontal width 0.54 head width, range 0.49–0.58. Median furrow present. One pair small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Ocelli and ommatidia of normal size. Flagellomere 1 round, slightly flattened. Palpus yellow, small, with normal-sized black setulae. Thorax brown. Scutellum with anterior seta small, slightly larger than scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur not darkened at apex. Wing of normal size. Mean costal length 0.37 wing length, range 0.35–0.40. Halter brown. Abdominal tergites brown; female tergite 6 anteriorly emarginate, with extremely short setae. Venter of abdomen gray to whitish-gray, bare in male, segment 6 with line of extremely small setae in female (Fig. 43); medial setae sometimes slightly enlarged.

**Male terminalia.** Epandrium with long setae on both sides. Right surstylus elongate, posterodorsally emarginate, with divergent dorsally and ventrally pointed setae (Fig. 53). Cercus yellow, curved.

**Female terminalia.** Oviscape (Fig. 27) short, without apical sclerite, dorsoapical lobe narrow. Stylet strongly curved, broad medially (Fig. 50).

**VARIATION.** Some specimens are light brown in color, unlike the holotype and most other specimens described above. Also, some specimens have the medial one or two pairs of setae on the venter of female segment 6 slightly enlarged (e.g., specimen LACM ENT 008975, with the same collection data as the holotype). The oviscape in all specimens appears the same, however, so for now only a single species is recognized.

**HOST.** Apparently *Pheidole crassicornis* Emery. Collections over a *Neivamyrmex nigrescens* (Cresson) army ant raid probably are due to the army ants disturbing a colony of *Pheidole*.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Named for the state of Arizona.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., Upper White Rock Campground, 31.39°N, 111.08°W, 12.viii.1993, B. Brown, *Neivamyrmex* raid [LACM ENT 008957] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 1♀, viii.1993, 1♀, 13–22.ix.1993, 4♂, 4♀, 1–11.xi.1993, N. McFarland, Malaise trap, 1550 m (LACM), Cochise Stronghold, 31.92°N, 109.97°W, 2♀, 18.viii.1993, J. Stireman, disturbed *Pheidole crassicornis* (LACM), 12.5 km S Sierra Vista, Ramsey Canyon, 1♀, 9.vii.1987, B. V. Brown,

Malaise trap, 1700 m, oak/pine/juniper (LACM); Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 1♀, 25.v.1994, E. Wilk, B. Brown, Malaise trap (LACM), Upper White Rock Campground [Peña Blanca Lake], 31.39°N, 111.08°W, 21♀, 12.viii.1993, B. Brown, *Neivamyrmex* raid (EMUS, LACM, MCZC, SEMC, USNM), 3♀, 12–16.viii.1993, B. Brown, pan traps (LACM), 1♀, 14.viii.1993, B. Brown, blacklight trap (LACM), 1♀, 18–20.ix.1997, B. Brown, G. Kung, J. Paldi, pan traps, 1220 m (LACM).

*Apocephalus brevipennis* new species

(Fig. 24)

**RECOGNITION.** This species can be easily recognized by the shortened wings. The male is unknown, although a possible male specimen [LACM ENT 138512] was collected in the same pan trap as the holotype female.

**DESCRIPTION. Female.** Body length 0.9 mm. Frons brown, shiny, 0.69 head width. Median furrow present. All frontal setae longer and thinner than normal. Two pairs of long supra-antennal setae present; ventral pair slightly shorter than dorsal pair. Ventral interfrontal seta closer to midline than eye margin. Ocelli and ommatidia not enlarged. Flagellomere 1 oval, yellow. Palpus yellow, with normal-sized black setulae. Thorax light brown. Major setae of scutum longer than normal. Scutellum with anterior seta small, slightly longer than scattered setulae of scutum; posterior seta greatly elongate. Anepisternum bare. Legs yellowish-brown. Tarsomeres rounded, short, especially in foreleg. Apex of hind femur not darkened. Wing extremely short (Fig. 24), costa 0.65 wing length. Halter brown. Abdominal tergites dark brown, with lateral seta greatly elongate; tergite 6 divided, with extremely long lateral and slightly shorter medial seta on posterior margin. Venter of abdomen grayish-white; segment 6 with posterior row of short setae, with most medial seta twice as long as others.

**Female terminalia.** Oviscape short, without apical sclerite, dorsoapical lobe narrow. Stylet not examined.

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Latin for “short-winged,” referring to the brachypterous female.

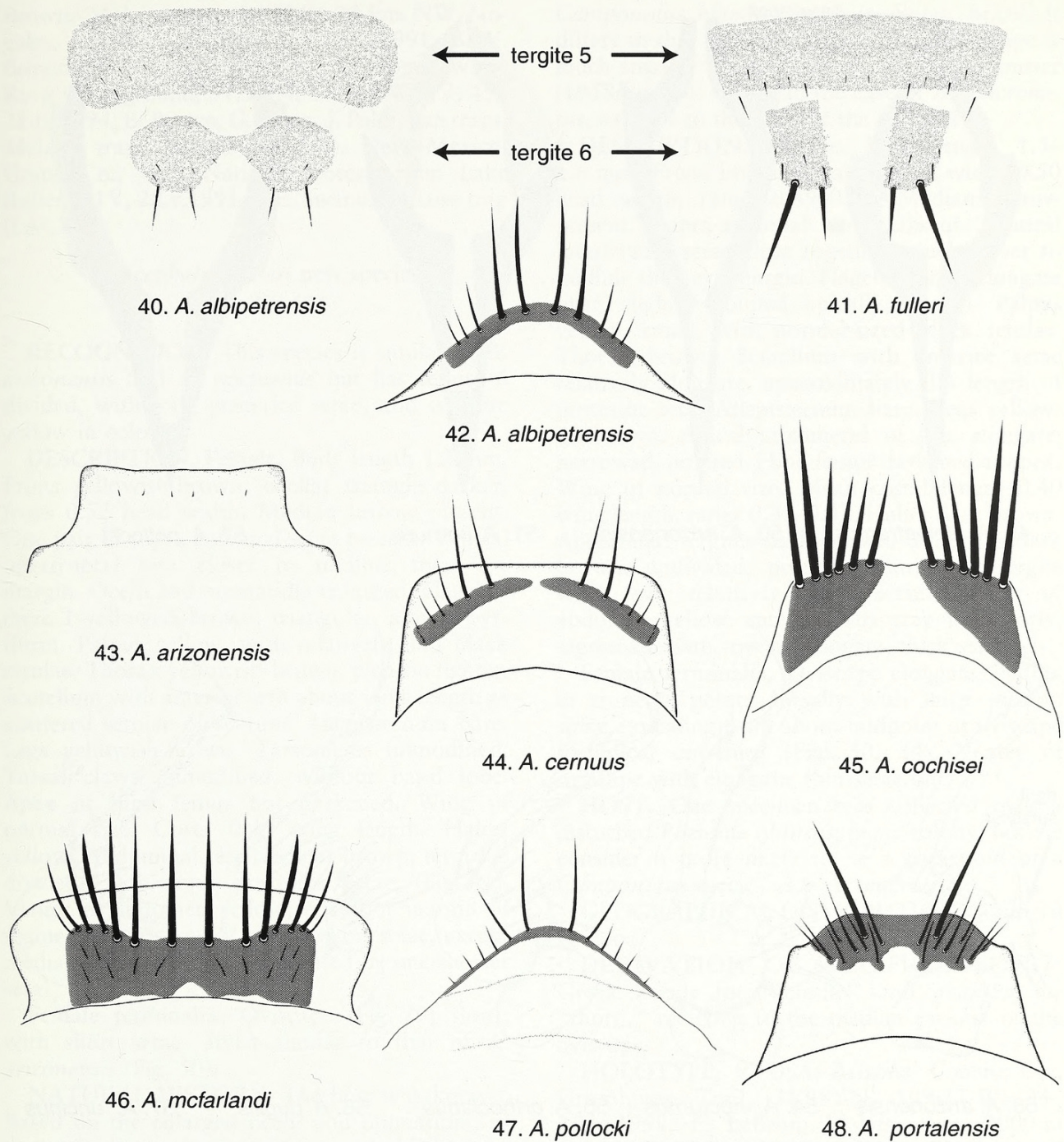
**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Basin Trail, 31.89°N, 109.23°W, 12–14.viii.1999, B. Brown, G. Kung, pan trap #8, 1950 m [LACM ENT 137501] (LACM).

*Apocephalus cernuus* new species

(Figs. 28, 33, 44, 51)

**RECOGNITION.** This species has an apically downturned oviscape but is more reliably distin-





Figures 40-48 40-41. Abdominal tergites, dorsal; 42-48. venter of segment 6

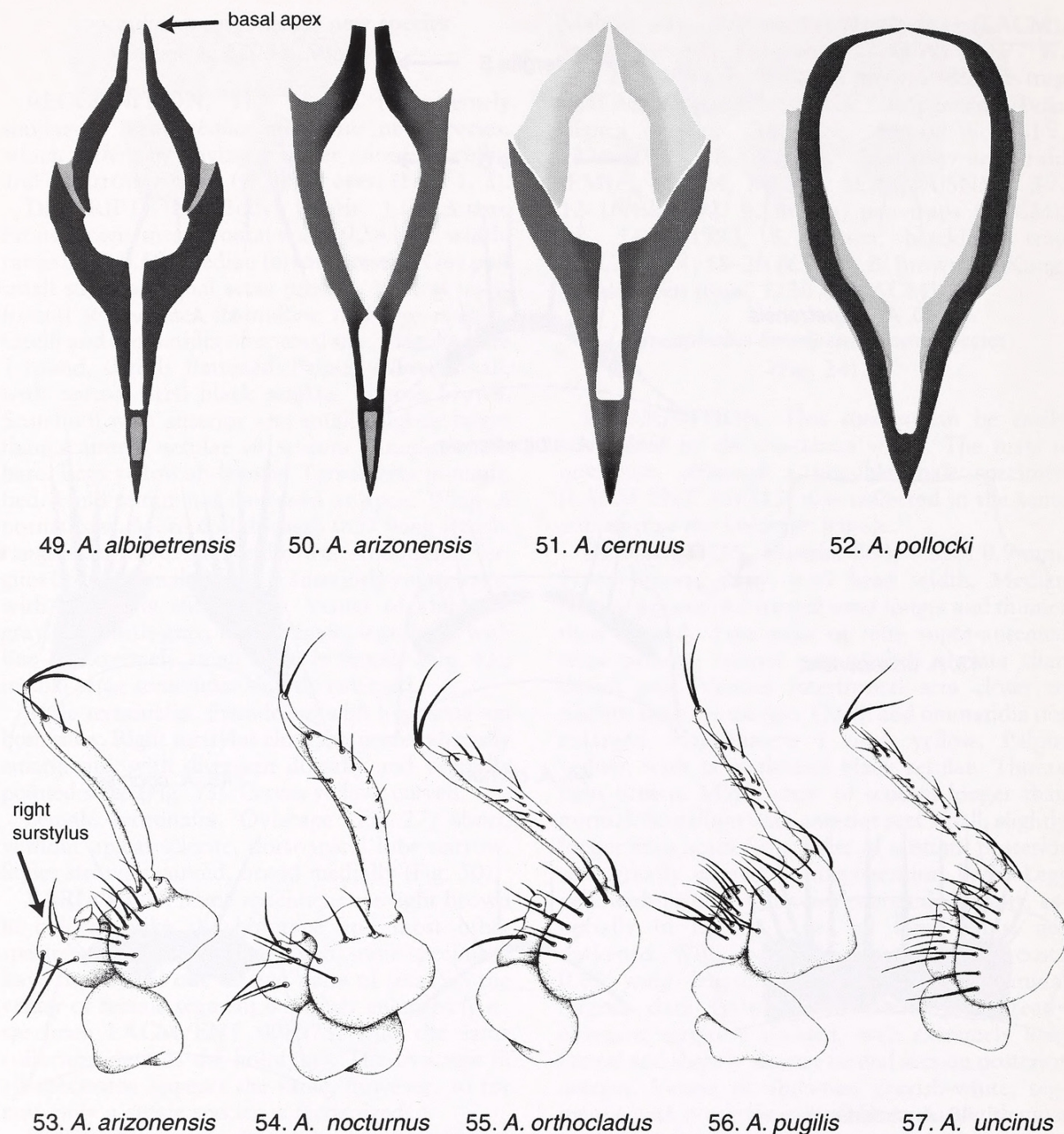
guished from similar species by the separated sclerites and medial setae on the venter of abdominal segment 6 (Fig. 44) and by the light-colored anterior arms of the stylet (Fig. 51).

**DESCRIPTION. Female.** Body length 1.2-1.4 mm. Frons dark brown, mean frontal width 0.57 head width, range 0.50-0.62. Median furrow present. One pair small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Ocelli and ommatidia of normal size. Flagellomere 1 round, brown. Palpus yellow, small, with normal-sized black setulae. Thorax brown. Scutellum with anterior setae small,

slightly longer than scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur not darkened at apex. Wing of normal size. Mean costal length 0.41 wing length, range 0.40-0.42. Halter brown. Abdominal tergites brown; female tergite 6 nearly divided by large posterior emargination. Venter of abdomen light brown, segment 6 with narrow, medially interrupted sternite and row of setae increasing in size medially, with medial gap between largest two setae (Fig. 44).

**Female terminalia.** Oviscape (Fig. 28) short, without apical sclerite, dorsoapical lobe broad,





Figures 49–57 49–52. Stylets, dorsal; 53–57. male terminalia, right lateral

oviscape deflected ventrally at apical one-third (Fig. 33). Stylet with anterior arms lightly sclerotized, convergent (Fig. 51).

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona and New Mexico.

**DERIVATION OF SPECIFIC EPITHET.** Latin for “drooping,” referring to the ventrally bent oviscape.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 25.v.1994, E. Wilk, B. Brown, Malaise trap [LACM ENT 040376] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 2♀, viii.1993, 6♀, 13–22.ix.1993, 1♀, 1–11.xi.1993, N. McFarland, Malaise trap, 1550 m (LACM), 18.5 km W Portal, Basin Trail head, 1♀, 7–10.vi.1986, B. V. Brown, Malaise trap, 1950 m, oak/pine/juniper (LACM); Pima Co., Florida Canyon, 1♀, 15–17.viii.1989, E. Fuller, Malaise trap (LACM); Pinal Co., Oracle, 2♀, vi.1991, J. O’Hara, Malaise trap, 4700 feet (LACM); Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 1♀, 25.v.1994, 2♀, 16.vi.1994, 3♀, 24.vi.1994, 1♀, 14.x.1994, 1♀, 19.xi.1994, 1♀, 30.vii.1995, E. Wilk, B.



Brown, Malaise trap (LACM), 20 km NW Nogales, Sycamore Canyon, 1♀, 27.v.1991, B. V. Brown, white pan trap (LACM), Upper White Rock Campground, 31.39°N, 111.08°W, 1♀, 19–21.ix.1994, B. Brown, G. Kung, J. Paldi, pan traps, Malaise trap, 1220 m (LACM). New Mexico: Grant Co., Gila National Forest, near Lake Roberts, 1♀, 28.v.1991, J. E. Swann, Malaise trap (LACM).

*Apocephalus fulleri* new species

(Figs. 29, 41)

**RECOGNITION.** This species is similar to *A. arizonensis* and *A. nocturnus* but has tergite 6 divided, with long posterior setae, and is more yellow in color.

**DESCRIPTION.** Female. Body length 1.3 mm. Frons yellowish-brown, ocellar triangle darker; frons 0.52 head width. Median furrow present. One pair of supra-antennal setae present. Ventral interfrontal seta closer to midline than eye margin. Ocelli and ommatidia enlarged. Flagellomere 1 yellowish-brown, triangular, almost pyriform. Palpus yellow, with relatively thin black setulae. Thorax yellowish-brown, pleuron lighter. Scutellum with anterior seta about same length as scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Tarsal claws unmodified, without basal lobe. Apex of hind femur not darkened. Wing of normal size. Costa 0.45 wing length. Halter yellow. Abdominal tergites light brown; tergite 6 divided, with long posterior setae (Fig. 41). Venter of abdomen yellow; posterior margin of segment 6 with row of mostly short setae, except medial pair longer (pair separated by one shorter seta).

**Female terminalia.** Oviscape (Fig. 29) short, with short setae. Stylet similar to that of *A. arizonensis* (Fig. 50).

**NATURAL HISTORY.** The host is unknown. Based on the enlarged ocelli and ommatidia, as well as its having been caught in a blacklight trap, this fly is probably crepuscular or nocturnal.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Named for the senior author's friend and colleague, Dr. Ed Fuller, who has collected many interesting phorids.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., Upper White Rock Campground, 31.39°N, 111.08°W, 18–20.ix.1997, B. Brown, G. Kung, J. Paldi, blacklight trap [LACM ENT 092005] (LACM).

*Apocephalus mesacanthus* new species

(Figs. 30, 34)

**RECOGNITION.** This species is similar to *A. mucronatus* Borgmeier, 1958, a parasite of

*Camponotus blandus* Smith in Goias, Brazil. It differs in that the dorsal spine of the oviscape is much smaller than that illustrated by Borgmeier (1958:fig. 43), which, in the case of *A. mucronatus*, extends to the apex of the oviscape.

**DESCRIPTION.** Female. Body length 1.5–1.6 mm. Frons brown; mean frontal width 0.50 head width, range 0.49–0.50. Median furrow present. Supra-antennal setae absent. Ventral interfrontal setae close together, much closer to midline than eye margin. Flagellomere 1 elongate oval, slightly pointed apically, brown. Palpus yellow, small, with normal-sized black setulae. Thorax brown. Scutellum with anterior setae relatively elongate, approximately 0.4 length of posterior seta. Anepisternum bare. Legs yellowish-brown. Apical tarsomeres of legs elongate, narrowed, pointed. Hind femur darkened at apex. Wing of normal size. Mean costal length 0.40 wing length, range 0.39–0.42. Halter dark brown. Abdominal tergites dark brown. Tergite 6 dark brown, undivided; posterior margin of tergite with few, relatively short setae. Venter of abdomen yellow anteriorly to gray posteriorly, segment 6 with row of elongate, thick setae.

**Female terminalia.** Oviscape elongate, ending in truncate point; dorsally with large median spine extending from about midpoint of oviscape to apical one-third (Figs. 30, 34). Venter of oviscape with elongate, thin setae only.

**HOST.** One specimen was collected over a disturbed *Pheidole obtusospinosa* colony, but we consider it more likely to be a parasitoid of a *Camponotus* species as is *A. mucronatus*.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Greek *mesos* for “middle” and *akantha* for “thorn,” referring to the median process of the oviscape.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Greenhouse Trail, 31.88°N, 109.27°W, 24–25.ix.1998, E. LeBrun, Malaise trap, 2000 m [LACM ENT 055140] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., 12.5 km S Sierra Vista, Ramsey Canyon, 1♀, 6.vi.1987, B. V. Brown, Malaise trap, 1700 m, oak/pine/juniper (LACM); Santa Cruz Co., Peña Blanca Canyon, 31.38°N, 111.09°W, 1♀, 15.viii.1993, B. Brown, over *Pheidole subdentata* (LACM).

*Apocephalus nocturnus* new species

(Figs. 2, 31, 54)

**RECOGNITION.** This species is extremely similar to *A. arizonensis* but has larger ocelli and eyes.

**DESCRIPTION.** Body length 1.25–1.75 mm. Frons brown, ocellar triangle darker; mean frontal width 0.44 head width, range 0.41–0.49. Median furrow present. One pair small supra-antennal setae present. Ventral interfrontal setae



closer to midline than eye margin. Ocelli and ommatidia enlarged (Fig. 2). Flagellomere 1 oval, enlarged (especially in male), laterally flattened, light brown, but darker laterally. Palpus yellow, small, with normal-sized black setulae. Thorax light brown. Scutellum with anterior seta small, slightly longer than scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur unusually thin, extremely faintly darkened at apex. Wing of normal size. Mean costal length 0.40 wing length, range 0.37–0.43. Halter yellowish-brown. Abdominal tergites brown; female tergite 6 entire, although with small anterior emargination. Venter of abdomen whitish, bare in male, segment 6 with row of short setae posteriorly in female.

**Male terminalia.** Epandrium with long setae on both sides. Right surstylus elongate, apically truncate, with divergent dorsally and ventrally pointed setae (Fig. 54). Cercus curved, yellow.

**Female terminalia.** Oviscape (Fig. 31) short, without apical sclerite, dorsoapical lobe narrow. Stylet strongly curved, broad medially.

**NATURAL HISTORY.** The host is unknown. The large ommatidia and ocelli, as well as the collection records at light, indicate that this species has a nocturnal or crepuscular host.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Latin for “of the night,” referring to the nocturnal activity of this species.

**HOLOTYPE.** ♀, USA: Arizona: Santa Cruz Co., 20 km NW Nogales, Sycamore Canyon, 27.v.1991, B. V. Brown, blacklight trap [LACM ENT 011017] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., Coronado National Monument, 7♂, 2♀, 11.viii.1984, 2♀, 27.vii.1988, B. V. Brown, blacklight trap (LACM), Sunnyside Canyon, 1♀, 8.viii.1989, D. Pollock, blacklight trap, oak/juniper (LACM); Pima Co., Florida Canyon, 1♀, 15.viii.1989, D. Pollock, blacklight trap, desert scrub (LACM); Santa Cruz Co., 16 km N Nogales, Peña Blanca Lake, Upper White Rock Campground, 10♂, 1♀, 28.vii.1988, B. Brown, D. Feener, blacklight trap, 5♂, 12.viii.1993, B. V. Brown, blacklight trap, 2♀, 18.ix.1997, B. Brown, G. Kung, J. Paldi, blacklight trap (LACM), 20 km NW Nogales, Sycamore Canyon, 5♀, 26.v.1991, 4♂, 27.v.1991, B. V. Brown, blacklight trap (LACM, MCZC, USNM), Walker Canyon, 1♀, 11.viii.1989, D. Pollock, blacklight trap (LACM).

*Apocephalus platypalpis* (Borgmeier)  
(Figs. 32, 39)

*Aphiochaeta platypalpis* Borgmeier, 1925:164–165, pl. VI, fig. 26 (♂, Petrópolis, Brazil).

*Apocephalus platypalis*: Borgmeier, 1958:315, 1963:179–180 (♂, ♀, Texas, Arizona).

**RECOGNITION.** This species was originally described from male specimens from southeastern Brazil, but the specimens from the USA are similar and possibly conspecific. Males are recognized by the enlarged brown palpus with short, thin setae.

Females have the oviscape (Fig. 32) usually withdrawn deeply into the abdomen, such that only the dark, shiny apex is seen flush with the end of segment 6 (Fig. 39). They are extremely similar to *A. anapastus* and *A. gemellus* (which also have the oviscape largely withdrawn) but are easily separated by tergite 6, which is divided longitudinally in *A. platypalpis* but is entire in the other two species (see also Recognition for *A. anapastus*).

**HOST.** Borgmeier (1963) noted that some males were collected over the army ant *Labidus praedator* (Smith) in Brazil. Many collections in Arizona are from blacklight traps, consistent with this fly attacking a largely nocturnal army ant host such as a species of *Neivamyrmex* Borgmeier in Arizona, although no such association has been established yet. No species of the genus *Labidus* Jurine are known from Arizona (Cover and Johnson, 2002–2009).

**GEOGRAPHICAL DISTRIBUTION.** Brazil and southwestern USA.

**MATERIAL EXAMINED.** BRAZIL: Rio de Janeiro: Petrópolis, 1♂, 12.ii.1923, Ronchi (USNM). USA: Arizona: Cochise Co., Ash Canyon, 31.39°N, 110.24°W, 2♂, 1–11.xi.1993, N. McFarland, Malaise trap, 1550 m (LACM), Cochise Stronghold, 31.92°N, 109.97°W, 3♀, 17.viii.1993, B. V. Brown, blacklight trap (LACM), Coronado National Memorial, 1♂, 3♀, 11.viii.1984, 2♀, 27.vii.1988, B. V. Brown, blacklight trap (LACM); Santa Cruz Co., 20 km NW Nogales, Sycamore Canyon, 3♂, 27.v.1991, B. Brown, blacklight trap (LACM), Upper White Rock Campground [Peña Blanca Lake], 31.39°N, 111.08°W, 1♂, 12.viii.1993, B. V. Brown, blacklight trap (LACM). California: Los Angeles Co., Topanga Canyon, 34.08°N, 118.59°W, 1♂, 1.xi–17.xii.1994, B. Brown, G. Hendler, Malaise trap (LACM), Walker Ranch, Placerita Canyon, 34.38°N, 118.44°W, 1♂, 8–17.ix.1998, 1♂, 29.ix.1998, B. Brown, I. Swift, Malaise trap (LACM); Riverside Co., Deep Canyon, 1♀, 19.xi.1963, E. Schlinger, M. Irwin, at light (UCRC), Menifee Valley, 33.65°N, 117.22°W, 1♀, 12.viii.1995, J. Pinto, Malaise trap (LACM), P. L. Boyd Desert Research Center, 3.5 miles S Palm Desert, Marker #57, 2♀, 18–20.x.1969, S. Frommer, R. Worley, Malaise trap (UCRC). Texas: Kerrville, 1♀, vii.1953, 1♀, 18.viii.1953, 1♀, viii.1953, 1♀, 4.ix.1953, 1♀, 25.ix.1953, 3♀, ix.1953, 1♀, 2.x.1953, 2♀, 9.x.1953, 1♀, x.1953, 3♀, 27.i.1954, 1♀, 29.iv.1954, 1♀, v.1954, 1♀, vi.1954, 2♀, vii.1954, 1♀, viii.1954, L.J. Bottimer (USNM).



*Apocephalus pollocki* new species

(Figs. 35, 47, 52)

**RECOGNITION.** See *A. albigutrensis* for discussion of differences between these two species.

**DESCRIPTION.** Female. Body length 0.9–1.1 mm. Frons brown, ocellar triangle darker; mean frontal width 0.56 head width, range 0.54–0.58. Median furrow present. Two pairs of supra-antennal setae present; ventral pair three-quarters length of dorsal pair. Ventral interfrontal seta closer to midline than eye margin. Ocelli and ommatidia not enlarged. Flagellomere 1 brown, oval. Palpus yellow, not enlarged, with normal-sized black setulae. Thorax light brown. Scutellum with anterior seta small, slightly longer than scattered setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Apex of hind femur not darkened. Wing of normal size. Mean costal length 0.43 wing length, range 0.42–0.44. Halter light brown. Abdominal tergites brown; tergite 6 divided (similar to Fig. 41). Venter of abdomen gray; posterior margin of segment 6 with thin sclerite and four long setae; medial pair of setae largest, next most lateral setae shorter (about three-quarters length of medial pair), and more lateral setae much smaller (Fig. 47).

**Female terminalia.** Oviscape (Fig. 35) short, without apical sclerite, dorsoapical lobe moderately narrow. Stylet with anterior arms rounded, convergent (Fig. 52).

**HOST.** Unknown.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Named for the senior author's friend and colleague, Dr. Darren Pollock, who collected the holotype specimen.

**HOLOTYPE.** ♀, USA: Arizona: Pima Co., Florida Canyon, 15.viii.1989, D. Pollock, black-light trap, desert scrub [LACM ENT 113341] (LACM).

**PARATYPES.** USA: Arizona: Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 1♀, 7.x.1994, 1♀, 14.x.1994, B. Brown, E. Wilk, Malaise trap (LACM).

*Apocephalus portalensis* new species

(Figs. 36, 48)

**RECOGNITION.** This species can be most easily recognized by the setation of the ventral sclerite of segment 6, with one long pair of setae and several shorter ones.

**DESCRIPTION.** Female. Body length 1.7–2.1 mm. Frons dark brown; mean frontal width 0.53 head width, range 0.51–0.55. Median furrow present. One pair of small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Flagellomere 1 round,

light brown. Palpus yellowish-brown, with slightly reduced black setulae. Thorax brown. Scutellum with anterior seta about twice size of posterior setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur only slightly darkened at apex. Wing of normal size. Mean costal length 0.43 wing length, range 0.41–0.45. Halter dark brown. Abdominal tergites dark grayish-brown. Tergite 6 same color as other tergites, undivided; posterior margin of tergite with relatively short posterior setae. Venter of abdomen yellow, except gray laterally and on entire segment 6; venter of segment 6 with rounded sclerite and two large plus several smaller setae (Fig. 48).

**Female terminalia.** Oviscape (Fig. 36) broadly truncate, with large lateral seta. Venter of oviscape with apical hook but lacking more basal enlarged setae. Anterior arms of stylet rounded, convergent.

**NATURAL HISTORY.** The host is *Aphaenogaster texana* Wheeler. Female flies are attracted primarily to disturbed host colonies that commonly nest under rocks. They are apparently highly motivated by olfactory cues: you can crush ants on your hands, and the flies will dart at your fingers, apparently trying to oviposit or to assess a potential host.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona.

**DERIVATION OF SPECIFIC EPITHET.** Named for some of the collecting localities that are near the town of Portal.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., 5 km W Portal, Cave Creek Campground, 25.vii.1988, B. Brown, D. Feener, on *Aphaenogaster* [LACM ENT 010846] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., 5 km W Portal, Cave Creek Campground, 25♀, 25.vii.1988, B. Brown, D. Feener, on *Aphaenogaster* (EMUS, LACM, MCZC, SEMC, USNM), W of Portal, South Fork, 6♀, 18.viii.1982, D. Feener, *Aphaenogaster*, #470 (LACM), 5 km W Portal, Sunny Flats Campground, 11♀, 26.vii.1988, B. Brown, D. Feener, on *Aphaenogaster* (LACM), 27♀, 21.viii.1993, B. Brown, over *Aphaenogaster texana* (LACM), 12.5 km S. Sierra Vista, Ramsey Canyon, 2♀, 6–13.vii.1986, B. Brown, Malaise trap, 1700 m, oak/pine/juniper (LACM); Santa Cruz Co., Patagonia, 31.53°N, 110.77°W, 1♀, 18.ix.1994, B. Brown, E. Wilk, Malaise trap (LACM).

*Apocephalus pugilis* new species

(Figs. 37, 56)

“*Apocephalus* sp. 25,” LeBrun, 2005:643–652; LeBrun and Feener, 2007:58–64; Wilkinson and Feener, 2007:151–161.

**RECOGNITION.** This might be an unusual species of the *A. feeneri* group. It can be recognized by the short oviscape with short setae,



coupled with the long ventral setae and sclerite on segment 6.

**DESCRIPTION.** Body length 1.2–1.5 mm. Frons brown; mean frontal width 0.61 head width, range 0.60–0.61. Median furrow present. One pair of extremely small supra-antennal setae present. Ventral interfrontal setae closer to midline than eye margin. Flagellomere 1 brown, round. Palpus yellow, small, with normal-sized black setulae. Thorax light brown. Scutellum with anterior seta small, subequal to posterior setulae of scutum. Anepisternum bare. Legs yellowish-brown. Tarsomeres unmodified. Hind femur slightly darkened at apex. Wing of normal size. Mean costal length 0.35 wing length, range 0.32–0.38. Halter yellow. Abdominal tergites dark brown, yellowish-brown medially. Tergite 6 light brown, medially divided in female; posterior margin of each division with two to three enlarged setae. Venter of abdomen yellow, without setae in male; in female with gray markings laterally, segment 6 with narrow sternite with row of moderately large setae that increase in size medially.

**Male terminalia.** Epandrium with long setae on both sides. Right surstylus short, deep, with long setae (Fig. 56). Cercus nearly straight, light brown.

**Female terminalia.** Oviscape (Fig. 37) short, triangular, with short setae. Venter of oviscape with apical hook, but lacking basal process.

**NATURAL HISTORY.** The host is *Pheidole bicarinata* Mayr. Both male and female flies are attracted to host ants recruiting to food items. They are not common at disturbed nests. These flies mate at the host, are able to fly in copula, and occasionally arrive at recruitment trails in copula. Superparasitism of major workers is common; dissection of 53 major workers immediately following attack revealed 30 percent of parasitized workers containing multiple eggs and up to four eggs being found in the gaster of a single worker (unpublished data). Females exhibit a remarkable attack behavior, in which they perch on a piece of leaf-litter near or over a recruitment trail. When a major worker passes beneath, they drop into the trail and attack the worker on foot from behind.

**GEOGRAPHICAL DISTRIBUTION.** Southern Arizona and Utah.

**DERIVATION OF SPECIFIC EPITHET.** Latin for fighter or boxer, referring to the attack of the female on host ants.

**HOLOTYPE.** ♀, USA: Arizona: Cochise Co., Basin Trail, 31.89°N, 109.23°W, 12–14.viii.1999, B. Brown, G. Kung, pan trap #8, 1950 m [LACM ENT 138513] (LACM).

**PARATYPES.** USA: Arizona: Cochise Co., Basin Trail, 31.89°N, 109.23°W, 51♂, 15♀, 9.vii.1987, B. V. Brown, over *Pheidole bicarinata* (EMUS, SEMC, LACM, MCZC, USNM), 2♂, 4♀, 8–10.vii.1987, B. Brown, T. Spanton, yellow

pans, 1950 m, oak/pine/juniper (LACM), 1♀, 12–14.viii.1999, B. Brown, G. Kung, pan trap #1 (LACM), Pinery Canyon, 1♀, 5–8.viii.1989, E. Fuller, Malaise trap (LACM), 5 km E Portal, Sunny Flats Campground, 2♂, 12♀, 25.vii.1988, B. V. Brown, over *Pheidole bicarinata* (LACM). Utah: Grand Co., Castleton, 1♀, 20.vii.1968, Malaise trap (EMUS).

KEY TO SPECIES, FEMALES ONLY

- 1 Wing short, only reaching anterior margin of abdominal tergite 5 (Fig. 24); vein R<sub>2+3</sub> absent; costa 0.65 wing length; each abdominal tergite with enlarged lateral seta at least two segments long ..... *Apocephalus brevipennis* n. sp.
- Wing long, reaching or exceeding posterior margin of tergite 6; vein R<sub>2+3</sub> present; costa short, usually less than 0.50 wing length; lateral setae of tergites much shorter .... 2
- 2 Tergite 6 broader than tergite 4, extending laterally on segment ..... 3
- Tergite 6 equal to or narrower than tergite 4, restricted to dorsum of segment ..... 6
- 3 Supra-antennal setae absent ..... 4
- Supra-antennal setae present (see Fig. 10) ... 5
- 4 Oviscape about three times longer than broad, relatively parallel-sided with an expansion in proximal one-third (Fig. 8) ..... *Apocephalus similis* Malloch  
[Host: *Camponotus sansabeanus*]
- Oviscape short, at most twice as long as broad, without proximal expansion (Fig. 9) ..... *Apocephalus wirthi* Borgmeier
- 5 Supra-antennal setae closer to ventral interfrontal setae than to each other (Fig. 10); oviscape as in Fig. 6 ..... *Apocephalus aquilonius* Brown
- Supra-antennal setae close together, about as far from each other as from ventral interfrontal setae, which are themselves close together (Fig. 11); oviscape as in Fig. 7 ..... *Apocephalus horridus* Borgmeier  
[Host: *Camponotus vicinus*]
- 6 Oviscape with at least one pair of large, posterolateral to ventrolateral setae (Figs. 17–21, 26, 36) ..... 7
- Large lateral setae absent (Figs. 25, 27–35, 37) ..... 17
- 7 Oviscape with several long, lateral and posterolateral setae (Fig. 20); venter of segment 6 with setae concentrated in large bundles, resembling single pair of large thick setae ..... *Apocephalus titanus* sp.  
[Host: *Pheidole rhea*]
- Oviscape with only one or two pairs of lateral setae; setae of venter of segment 6 not concentrated in bundles ..... 8
- 8 Apex of oviscape with two pairs of flattened, hooklike setae; first pair smaller, attached apically and curving downward; second pair



- larger more ventral in attachment and curving upwards (Fig. 21); apically with only one pair of long setae . . . . . *Apocephalus uncinus* n. sp.  
[Host: *Pheidole obtusospinosa*]
- Oviscape without paired, ventroapical setae (but often with ventromedial hooklike processes, see Figs. 12–16); apically often with more than one pair of long setae . . . . . 9
- 9 Only one visible hook apically on venter of oviscape; halter brown, especially at apex. . . . . 10
- One apical hook and one more basal, enlarged structure present on venter of oviscape (Figs. 12–16); halter yellow . . . . . 12
- 10 Oviscape withdrawn into abdomen, so only triangular, shiny, ventrally turned apex visible (Fig. 38); venter of segment 6 with thin, hairlike setae only . . . . . *Apocephalus anapastus* n. sp.  
[Host: *Pheidole obtusospinosa*]
- Oviscape more fully extended, tip not so ventrally deflected; venter of segment 6 with at least some thick, black, bristlelike setae (Figs. 46, 48) . . . . . 11
- 11 Venter of segment 6 with row of long, thick setae (Fig. 46) . . . . . *Apocephalus mcfarlandi* n. sp.
- Venter of segment 6 with numerous small setae and two long, strong mediolateral setae (Fig. 48) . . . . . *Apocephalus portalensis* n. sp.  
[Host: *Aphaenogaster texana*]
- 12 Basal process (paired, closely appressed setae) thin, relatively straight (Fig. 14) . . . . . *Apocephalus orthocladus* n. sp.  
[Hosts: *Pheidole hyatti*, *diversipilosa*, *tetra*, *vallicola*]
- Basal process flattened, variously curved (Figs. 12, 13, 15, 16, 22) . . . . . 13
- 13 Basal process curved anteriorly, at least in part (Figs. 12, 13, 16) . . . . . 14
- Basal process curved posteriorly only (Figs. 15, 22) . . . . . 16
- 14 Basal hook curved both posteriorly and anteriorly (Fig. 16) . . . . . *Apocephalus wilki* n. sp.
- Basal hook curved anteriorly only (Figs. 12, 13) . . . . . 15
- 15 Basal hook thickest at midpoint; obtusely curved anteriorly, approximately 1.5 times as wide at midpoint as at attachment, and slightly reclinate in orientation (Fig. 12). . . . . *Apocephalus spantoni* n. sp.
- Basal hook thickest near apex; acutely curved anteriorly, approximately 2.5 times as wide at midpoint as at attachment, and strongly reclinate in orientation (Fig. 13) . . . . . *Apocephalus brunneiventris* n. sp.  
[Host: *Pheidole hyatti*, *P. perpilosa*]
- 16 Oviscape with only one pair of large lateral seta (as in Fig. 19); basal hook apically pointed (Fig. 15); dorsal apex of oviscape more pointed; venter of abdomen yellow . . . . . *Apocephalus reflexus* n. sp.
- Oviscape with two pairs of large lateral setae (Fig. 22); basal hook apically rounded (Fig. 17); venter of abdomen dark gray . . . . . *Apocephalus cochisei* n. sp.
- 17 Oviscape with distinct, separate, apical sclerite (Figs. 3–5) . . . . . 18
- Oviscape lacking apical sclerite . . . . . 20
- 18 Dorsal surface of apical sclerite entirely shining black (Fig. 4) . . . . . *Apocephalus nigricauda* Brown
- Apical sclerite with at least some white, membranous areas (Figs. 3, 5) . . . . . 19
- 19 Apical sclerite without sclerite in middle; lateral darkenings extremely thick (Fig. 3) . . . . . *Apocephalus concavus* Brown
- Apical sclerite with round, dark, shiny sclerite in middle; lateral darkenings relatively thin (Fig. 5) . . . . . *Apocephalus paulus* Borgmeier
- 20 Small fingerlike projection present in dorsocentral surface of oviscape, often projecting from beneath tergite 6 (Fig. 30, 34); numerous stout, equal length thick setae on venter of segment 6; apical tarsomeres of legs elongate, apically narrowed, pointed . . . . . *Apocephalus mesacanthus* n. sp.  
[one female collected over *Pheidole obtusospinosa*]
- Without fingerlike projection on dorsum of oviscape; ventral setation various; apical tarsomeres of legs not elongate and pointed . . . . . 21
- 21 Oviscape (Fig. 32) dorsoventrally flattened, not deep; often withdrawn deep into abdomen so that only broad, shiny apex is visible (Fig. 39); two pairs of well-developed super-antennal setae present; tergite 6 medially divided into two lateral sclerites, with widest part of division anterior (Fig. 39) . . . . . *Apocephalus platypalpis* Borgmeier  
[Host: *Neivamyrmex* sp.?] Note: The oviscape of *Apocephalus anapastus* n. sp. is similar in appearance to that of *A. platypalpis*, and some specimens of the former might key here if the lateral setae of the oviscape are not seen. It differs from *A. platypalpis* most clearly by the undivided tergite 6.
- Oviscape (Figs. 25, 27–29, 31, 33) deep; one pair of supra-antennal setae present, although sometimes setae small; tergite 6, if divided, with widest part of division various . . . . . 22
- 22 Segment 6 with sternite; sternite with enlarged ventral setae, with at least one pair as long as segment length (Figs. 42, 44–48) . . . . . 23
- Segment 6 without sternite, or if sternite slightly visible, then ventral setae of segment 6 not longer than segment length; at most one pair of ventral setae slightly enlarged (Fig. 43) . . . . . 26
- 23 Halter yellow; costa extremely short (0.35 wing length); venter of segment 6 with several long, strong setae distributed across entire segment (as in Fig. 46) . . . . . *Apocephalus pugilis* n. sp.  
[Host: *Pheidole bicarinata*]
- Halter brown; costa longer (0.40 or more); venter of segment 6 with one or two pairs of



- medial long, strong setae, with more lateral setae decreasing in size (Figs. 42, 44, 47) . . . . . 24
- 24 Venter of segment 6 with pronounced gap between to largest medial setae (Fig. 44); stylet with light-colored, convergent anterior arms (Fig. 51) . . . . . *Apocephalus cernuus* n. sp.
- Venter of segment 6 lacking medial gap between largest setae; stylet with dark, variously directed anterior arms . . . . . 25
- 25 Tergite 6 consists of two round patches joined by narrow bridge (Fig. 40); ventral setae of segment 6 consist of two large pairs flanked by few smaller ones (Fig. 42); basal apices of stylet subparallel (Fig. 49) . . . . . *Apocephalus albipetrensis* n. sp.
- Tergite 6 completely separated into two round sclerites; ventral setae of segment 6 consist of one large pair with more lateral setae gradually decreasing in size (Fig. 47); basal apices of stylet broadly rounded, convergent at tip (Fig. 52) . . . . . *Apocephalus pollocki* n. sp.
- 26 Tergite 6 clearly divided into two round sclerites (Fig. 41); yellow species . . . . . *Apocephalus fulleri* n. sp.
- Tergite 6 undivided, at most anteriorly emarginate; brown species . . . . . 25
- 25 Anterior ocellus enlarged, oval, about 0.22–0.25 width of frons at level of lowest ocellus (Fig. 2); ommatidia enlarged (Fig. 2); ventral setae of segment 6 all short (as in Fig. 43) . . . . . *Apocephalus nocturnus* n. sp.
- Anterior ocellus small, round, about 0.13–0.15 width of frons at level of lowest ocellus (Fig. 1); ommatidia smaller (Fig. 1); medial pair of ventral setae slightly enlarged in some specimens . . . *Apocephalus arizonensis* n. sp.
- [Host: *Pheidole crassicornis*]

DISCUSSION

The genus *Apocephalus* is found only in the New World, in spite of some purported species from other regions that probably belong in other genera. It is a mostly tropical group that shows a distinctive latitudinal gradient, as do its hosts. For example, for subgenus *A.* (*Apocephalus*) (hereafter simply “*Apocephalus*”), there is one species, *A. pergandei* Coquillett, 1901, known from Alaska, where 19 species of ants are found (Francoeur, 1997; Nielsen, 1987). Canada has four known ant-decapitating flies (*A. pergandei*; *A. coquilletti* Malloch, 1912; *A. rugosus* Brown, 2002; and *A. horridus*), probably all parasitoids of *Camponotus* species, and fewer than 200 species of ants (Francoeur, 1979). The *Apocephalus* fauna of all of North America has not been fully revised, but there were 25 described species before this review, coexisting with nearly 1,000 ant species (Fisher and Cover, 2007). This paper describes a further 20, all from Arizona. In contrast, at least 127 species of *Apocephalus* are known from La Selva Biological Station in Costa

Rica alone (Brown, 2004), a site with about 450 species of ants (J. Longino, The Evergreen State University, personal communication). Obviously, a greater diversity of ant hosts allows a larger community of parasitoids exist, and Arizona has the most diverse ant fauna in the USA (318 species; Cover and Johnson, 2002–2009), including 55 species (some undescribed) of *Pheidole*.

Species of *Apocephalus* associated with *Pheidole* are the last large, untreated section of the genus. We estimate that, based on the number of probable *Pheidole* parasitoids in the fauna of La Selva, there could be another 400 species of *Apocephalus* still to be collected, identified, and described (unpublished data). Even within North America, including Arizona, there are many potentially suitable *Pheidole* species (i.e., those with major workers having large enough heads to allow a fly larva to complete development) that might harbor *Apocephalus* species but that have not been studied. We expect that further fieldwork will reveal more *Apocephalus* species in Arizona, and this paper represents only a small step in documenting the overall diversity of New World *Pheidole* parasitoids.

Species of *Apocephalus* have profound effects on their *Pheidole* hosts, interrupting their foraging (Feener, 1988) and controlling the outcome of ant–ant competition (Feener, 1981; LeBrun, 2005; LeBrun and Feener, 2007). Other sympatric phorids are parasitoids of different ant species, including of other taxonomically and ecologically dominant ants in the genera *Camponotus*, *Solenopsis* Westwood, *Neivamyrmex*, and *Crematogaster* Lund. Their importance in modifying the behavior of their hosts is largely unstudied but potentially as great as those affecting *Pheidole* species. The number of potential interactions of competing ants and their parasitoids is extremely large and represents a fruitful area for future studies.

Ants are extremely important organisms in most terrestrial ecosystems, with their high density and dominant roles as predators, herbivores, scavenger, and seed feeders (Hölldobler and Wilson, 1990), they are major agents of energy flow. Parasitoid phorid flies have profound effects on ants that remain largely undiscovered. Our lack of knowledge, even of the identity of these parasitic flies, is readily apparent with the description of the 20 new species documented herein. Our ignorance of their interactions with their hosts, not to mention the effects of parasitoids on interactions of competing ant species, means that we have a long way to go towards understanding the ecology of these important elements of terrestrial ecosystems.

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