
PRELIMINARY ANALYSIS OF A HOST SHIFT: REVISION OF THE NEOTROPICAL SPECIES OF *APOCEPHALUS*, SUBGENUS *MESOPHORA* (DIPTERA: PHORIDAE)

BRIAN V. BROWN¹

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1. Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California, 90007. E-mail: brianb@mizar.usc.edu.

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ABSTRACT. Twelve new species of *Apocephalus*, subgenus *Mesophora*, are described and named; an additional six unassociated males and females are described but not named. The 12 new species are *A. apivorus*, *atavus*, *emphysemus*, *lemniscus*, *lizanoi*, *megalops*, and *niveus* from Costa Rica and *A. crassus*, *echinatus*, *pilatus*, *prolixus*, and *secundus* from the Dominican Republic. *A. leptotarsus* Brown is synonymized with *A. antennatus* Malloch **new synonymy**. The previously unknown male of *A. absentis* Brown is described, as are the previously unrecognized females of *A. adustus* and *A. curtus*. A new key to species of the Neotropical Region is given. The relatively most primitive species, *A. apivorus* and *adustus*, are parasitoids of stingless bees, whereas *A. tritarsus* is a parasitoid of lampyrid beetles, like most other *Mesophora*. The host shift within the subgenus *Mesophora* from ants to lampyrid beetles appears to have been via parasitism of stingless bees.

INTRODUCTION

In a group of flies that are remarkably similar in their life histories, species of the genus *Apocephalus*, subgenus *Mesophora*, represent a major enigma. Whereas all other species of this genus are parasitoids of ants (Hymenoptera: Formicidae), species of *Mesophora* attack beetles, wasps, bees, and spiders (Brown, 1993). The reasons for this host shift are unknown; other genera hypothesized to be related to *Apocephalus* also are ant-parasitoids (Brown, 1992), so attacking the new hosts seems to represent a newly derived behavioral character (Brown, 1993). Study of this phenomenon is an important reason for this revision.

Although only a short period of time has passed since the first revision of *Mesophora* (Brown, 1993), already a significant amount of new material has accumulated. Previously, I dealt with one small subgroup (Brown, 1994b) and some new life history information (Brown, 1994a), but in general there still seems to be an almost unlimited number of new species to discover. Large collections still are available from only two countries, Costa Rica and the Dominican Republic, so it seems likely that as other sites are surveyed still more species and remarkable life histories will be uncovered.

In this paper, I describe newly discovered species and life histories, reviewing previously described taxa only when significant new information is available. The key to species, however, includes all species described previously (Brown, 1993, 1994b).

METHODS

Methods and terms are similar to those used in my previous revisions of this group (Brown, 1993, 1994b). One important difference is that I no longer report on costal sector ratios. The point that these measurements are of little use in identification, because they vary so much, has been adequately made (Disney, 1980). An overwhelming reliance on them by previous workers is a thing of the past.

Another change is that I no longer use potassium hydroxide to clear specimens. Following other dipterists (Cumming, 1992), I now use lactic acid as an alternative that is much safer for specimens.

For brevity, species names are cited as follows: *Apocephalus mortifer* or *A. mortifer*, rather than *Apocephalus (Mesophora) mortifer* and *A. (M.) mortifer*.

Geographical coordinates are quoted as decimal degrees, rather than degrees, minutes, and seconds.

In addition to the usual insect labels recording locality information, specimens were labelled with barcoded insect labels (Thompson, 1994) and data were recorded in a database. All barcoded labels begin with the abbreviation "LACM ENT," indicating that the Natural History Museum of Los Angeles County is the institution where the data are stored. To make later recognition of holotypes easier, I list their individual barcode number in square brackets.

Specimens were deposited in the following collections:

- CMNH Section of Invertebrate Zoology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213-4080, U.S.A. (C.W. Young)
- INBIO Instituto Nacional de Biodiversidad, A.P. 22-3100, Santo Domingo, Heredia, Costa Rica (M. Zumbado)

- LACM Entomology Section, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007, U.S.A. (B.V. Brown)
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, U.S.A. (on indefinite loan to B.V. Brown)
- MICR Museo de Insectos, Universidad de Costa Rica, San Pedro, San José, Costa Rica (P.S. Hanson)
- USNM United States National Museum, Smithsonian Institution, Washington, DC 20560, U.S.A. (on indefinite loan to B.V. Brown)

As previously, I name species only based on male specimens; an exception is the *Apocephalus anfractus*-subgroup, which was based on females. Unfortunately, this means that many forms known from one sex or another only cannot be formally dealt with at this time, especially the now known, but unassigned, males of *A. anfractus*-subgroup taxa. Unnamed Costa Rican species are described herein to facilitate their recognition in Costa Rica's ongoing biodiversity inventories; they are referred to by their Phorid Species Number in my phorid names database (e.g., Phorid species 3143). To make later recognition of these specimens easier, I list their individual barcode number in square brackets in the Material Examined sections.

SYSTEMATICS

PHYLOGENETIC RECONSTRUCTION

There are numerous species known from a single sex only. The lack of phylogenetic information from the missing sexes makes phylogenetic analysis using a computer program impossible; huge numbers of alternative trees are generated as the program attempts to analyze all possibilities of the missing character states. For that reason, the following analysis is based only on taxa known from both sexes, including those from the Nearctic Region. Also excluded is the new species *A. atavus*, for reasons stated in the discussion of the *A. borealis*-group.

Monophyly of Subgenus *Mesophora*

The monophyly of subgenus *Mesophora* is no longer supported by all of the same character states I proposed earlier (Brown, 1993). The discovery of *A. apivorus* reduces the number of possible synapomorphies of the group to the two listed below. The larval synapomorphies I proposed earlier are still speculative. The larva of *A. apivorus* is similar to that of other *Mesophora*, and divergent from the only described larva of an *Apocephalus* (*Apocephalus*) species (Brown and Feener, 1991), but our lack of knowledge about the larvae of outgroup taxa makes proposing larval synapomorphies of *Mesophora* premature.

- 1) Female with dark glands (plesiomorphic: abdominal glands white)
Because dark glands are absent from *A. atavus* and the next most primitive species, *A. adustus*, it is also equally parsimonious to propose that the dark glands arose separately in *A. apivorus* and the rest of *Mesophora* (excluding *A. atavus* and *adustus*).

- 2) Ovipositor notched (Brown, 1993, fig. 51, n) (plesiomorphic: ovipositor not notched)
This character reverses later in the subgenus.

Recognition of Subgenus *Mesophora*

Because of the reversals of characters in the subgenus, identification of an *Apocephalus* species as *Mesophora* is now complicated. The following key will allow recognition of all species:

- 1 Male 2
- Female 5
- 2 Flagellomere 1 greatly enlarged (Figs. 3–5); lower and usually upper fronto-orbital setae absent **subgenus *Mesophora***
- Flagellomere 1 small, round; fronto-orbital setae present (Fig. 1) 3
- 3 Wing vein CuA₁ short, not reaching wing margin
. ***A. (Mesophora) apivorus* new species**
- Wing vein CuA₁ reaching wing margin 4
- 4 Anteroventral row of setulae on hind basitarsus enlarged basally (similar to Fig. 63); flagellomere 1 pyriform; halter dark brown ***A. (Mesophora) atavus* new species**
- Anteroventral row of setulae on hind basitarsus not noticeably enlarged; other characters various **subgenus *Apocephalus***
- 5 Abdominal glands near segment 5 dark in color (Brown, 1993, fig. 45, g); if not, ovipositor with ventral notch apically (Brown, 1993, fig. 51, n) **subgenus *Mesophora***
- Abdominal glands white, invisible in cleared specimens; ovipositor lacking ventral notch 6
- 6 Lower fronto-orbital setae absent; in some species upper fronto-orbital setae also absent **subgenus *Mesophora***
- Fronto-orbital setae present
. **subgenus *Apocephalus***

Relationships within Subgenus *Mesophora*

Within *Mesophora*, I propose the following hypothesized synapomorphic characters:

- 3) Male flagellomere 1 enlarged, flattened (plesiomorphic: flagellomere 1 round)
- 4) Stylet with lateral barbs (plesiomorphic: barbs absent)
- 5) Lower fronto-orbital seta of male absent (plesiomorphic: present)
- 6) Upper fronto-orbital seta of male absent (plesiomorphic: present)
- 7) Lower fronto-orbital seta of female 1) slightly displaced medially, 2) in line with interfrontal setae (Fig. 10) (plesiomorphic: lower fronto-orbital seta close to eye)
- 8) Ovipositor cylindrical (plesiomorphic: ovipositor flat)

- 9) Dorsal apex of ovipositor rounded (plesiomorphic: apex pointed)
- 10) Ventral apex of ovipositor rounded (plesiomorphic: apex pointed)
- 11) Anteroventral row of setulae of hind tarsomere with at least basal setulae enlarged (Figs. 63–65) (plesiomorphic: setulae all short, subequal)
- 12) Anteroventral row of setulae of hind tarsomere sinuate (Fig. 65) (plesiomorphic: row straight)
- 13) Ventral setae of female abdominal segment 6 1) reduced (thin, but still long), 2) greatly reduced (short, thin), 3) absent (plesiomorphic: ventral setae large, thick, prominent)
- 14) Venter of mid tarsomere 2 with at least one extra setula (plesiomorphic: with only one setula)
- 15) Flagellomere 1 of male abruptly narrowed at base (Fig. 9) (plesiomorphic: flagellomere 1 more gradually narrowed)
- 16) Anterior margin of ovipositor narrowly produced in an anterior strip (Brown, 1994b, fig. 5A) (plesiomorphic: ovipositor anteriorly rounded)
- 17) Apex of male cercus truncate (plesiomorphic: apex of cercus elongate)
- 18) Ovipositor darkly sclerotized over entire surface (plesiomorphic: dark sclerotization confined to margin of ovipositor)
- 19) Surstylus with three or fewer setulae (plesiomorphic: surstylus with many setulae)
- 20) Palpus of male enlarged, with few short, stubby setulae (plesiomorphic: palpus small, with normal, pointed setulae)
- 21) Venter of female abdomen with distinctive combs of setulae (Figs. 66–67) (plesiomorphic: abdomen without combs of setulae)
- 22) Female stylet distinctive, with medial sclerite on venter (Figs. 60–61)
- 23) Male abdominal segment 6 with dark ventral setae (Fig. 70) (plesiomorphic: setae absent)
- 24) Epandrium extremely short (Figs. 20–22) (plesiomorphic: epandrium longer)
- 25) Surstylus with 1) single carina, 2) short multiple carinae, 3) long, complete carina (plesiomorphic: carinae absent)
- 26) Mid tarsomere 1 of male enlarged (plesiomorphic: tarsomeres slender)
- 27) Left side of epandrium with distinct ventral ridge (plesiomorphic: ridge absent)
- 28) Right surstylus elongate (plesiomorphic: surstylus short)

A number of hypothesized synapomorphies from my previous analysis (Brown, 1993) had to be disregarded. A list of them, and the reasons for no longer considering them as phylogenetically useful, is given below:

- a) Lower fronto-orbital seta absent from female.
Fronto-orbital setae are extremely variable throughout *Mesophora*. For instance, in the *A. borealis*-group, all frontal setae are present in females of species 3246 (Fig. 13), the lower fron-

to-orbital seta is absent from females of species 3223 (Fig. 12), and both the upper and lower fronto-orbital setae are absent from females of species 3251 (Fig. 11).

- b) Series of long, thick ventral setae on left side of epandrium.

Study of additional species has shown that “thick” and “thin” epandrial setae grade into each other. The distinction can no longer be maintained.

- c) Right side of epandrium with prominent, darkly sclerotized longitudinal ridge.

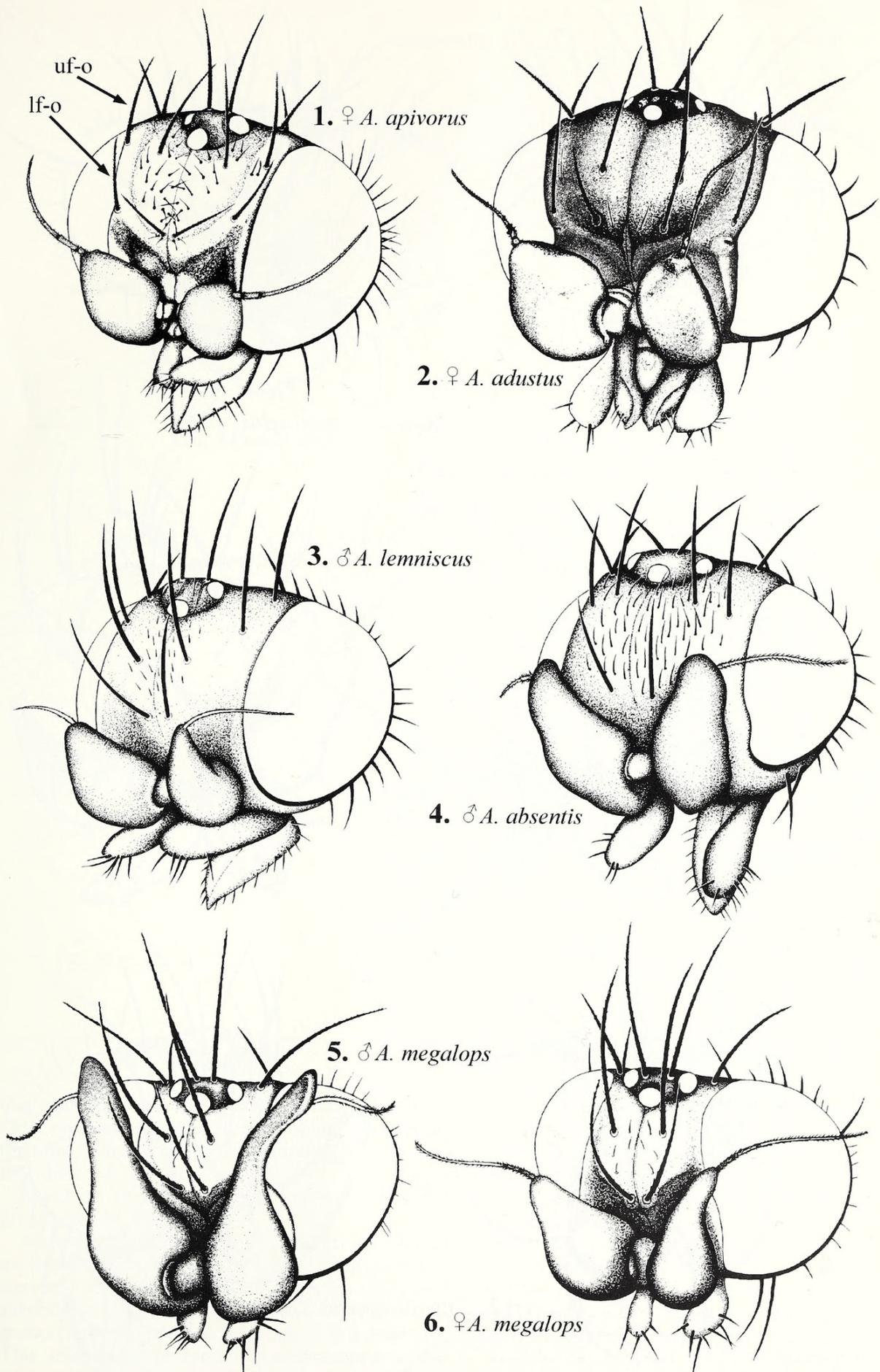
This character is found widely, including in the newly described, relatively primitive *A. apivorus*.

Based on characters 1–28 listed above, I analyzed a character matrix (Table 1) using HENNIG86. Characters were polarized with reference to the outgroup taxa *Pseudacteon* Coquillett and *Neodohrniphora* Malloch; species of these genera have the synapomorphic character of pointed horns on the larval spiracle in common with *Apocephalus* species (as in Brown, 1993, fig. 99s). All characters were equally weighted, and multistate characters unordered. This produced six equally parsimonious trees (length 49, ci 67, ri 81). The number of trees was unaffected by successive approximation weighting.

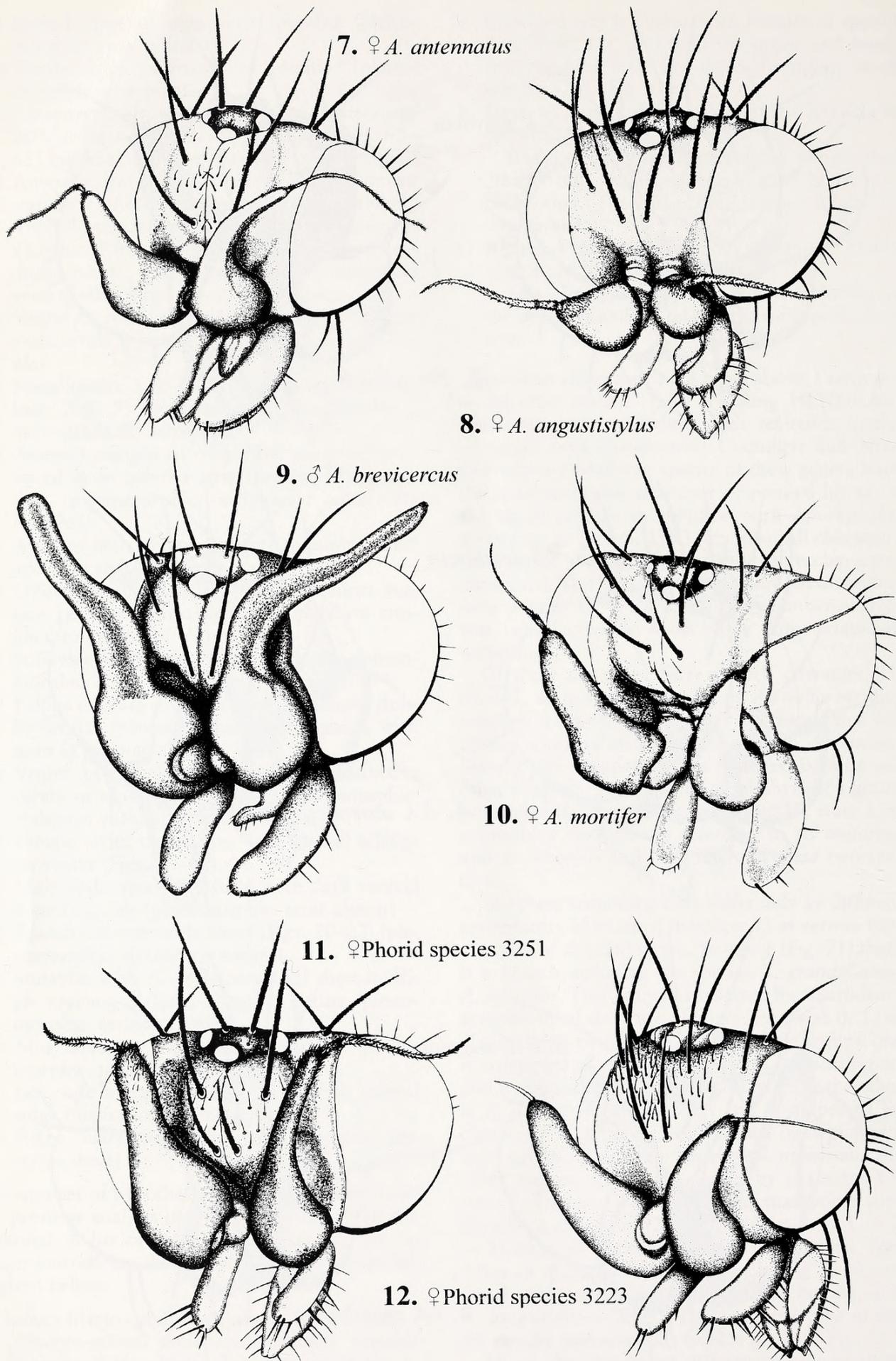
Of these six trees, three treated character 25, state 2, as a synapomorphy of *A. unitarsus* and *wheeleri*. However, this state is also found in a relatively primitive member of this group, *A. hansonii* Brown, not included in this analysis. Because another character supports the monophyly of a group not including *A. hansonii*, character 25, state 2, is a primitive character in reference to *A. unitarsus* and *A. wheeleri* and cannot group these two species.

The three remaining trees differ only by different assignments of states of character 13 at various basal nodes of the cladogram. In tree 1 (Fig. 71) there is a branch including the species *A. grandiflavus*–*A. wheeleri*. This branch is resolved by an arbitrary assignment of the state of character 13 as 0, 1, or 3 and allows two further monophyletic groups: one is composed of *A. grandiflavus*–*A. truncaticercus* and is supported by character 13, state 3; the other is *A. longistylus*–*A. wheeleri* and is supported by character 13, state 1. Tree 2 differs by depicting a sister-group relationship between *A. niveus* and the other species, which are united by character 13, state 1. This tree is similar to one that would stipulate that character 13 is ordered (as 0 → 1 → 2 → 3), an assumption not made in this analysis. Tree 3 has an unresolved polytomy including *A. niveus*, the *A. truncaticercus* infragroup (see below), and *A. longistylus*–*wheeleri*. The consensus tree of the six equally parsimonious trees is given in Fig. 71.

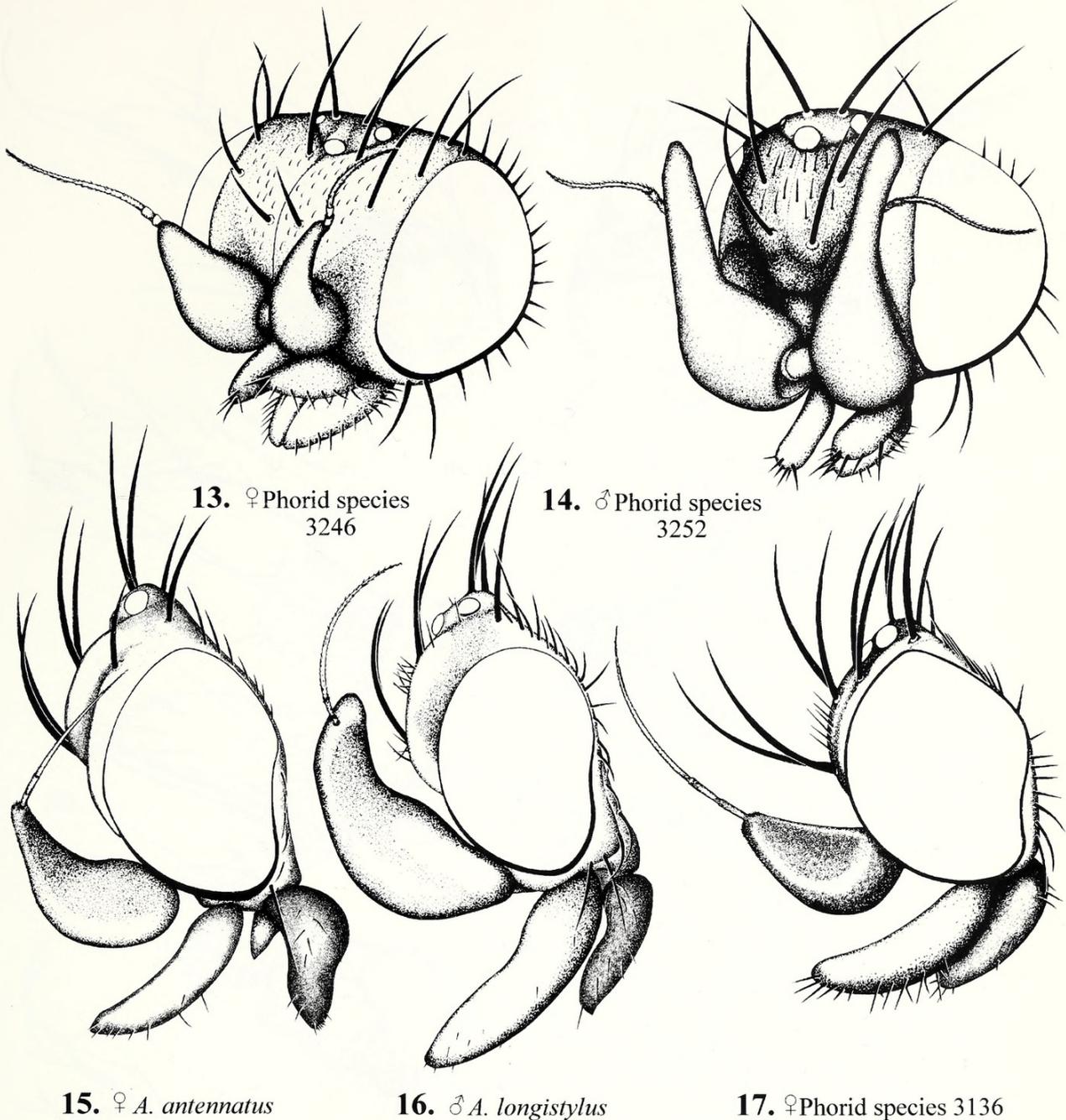
All of the significant differences among these trees are because of character 13. I prefer tree 2 because it has the most modest assumption about



Figures 1-6. Heads. Abbreviations: l f-o—lower fronto-orbital seta; u f-o—upper fronto-orbital seta.



Figures 7-12. Heads. Abbreviation: l f-o—lower fronto-orbital seta.



Figures 13-17. Heads.

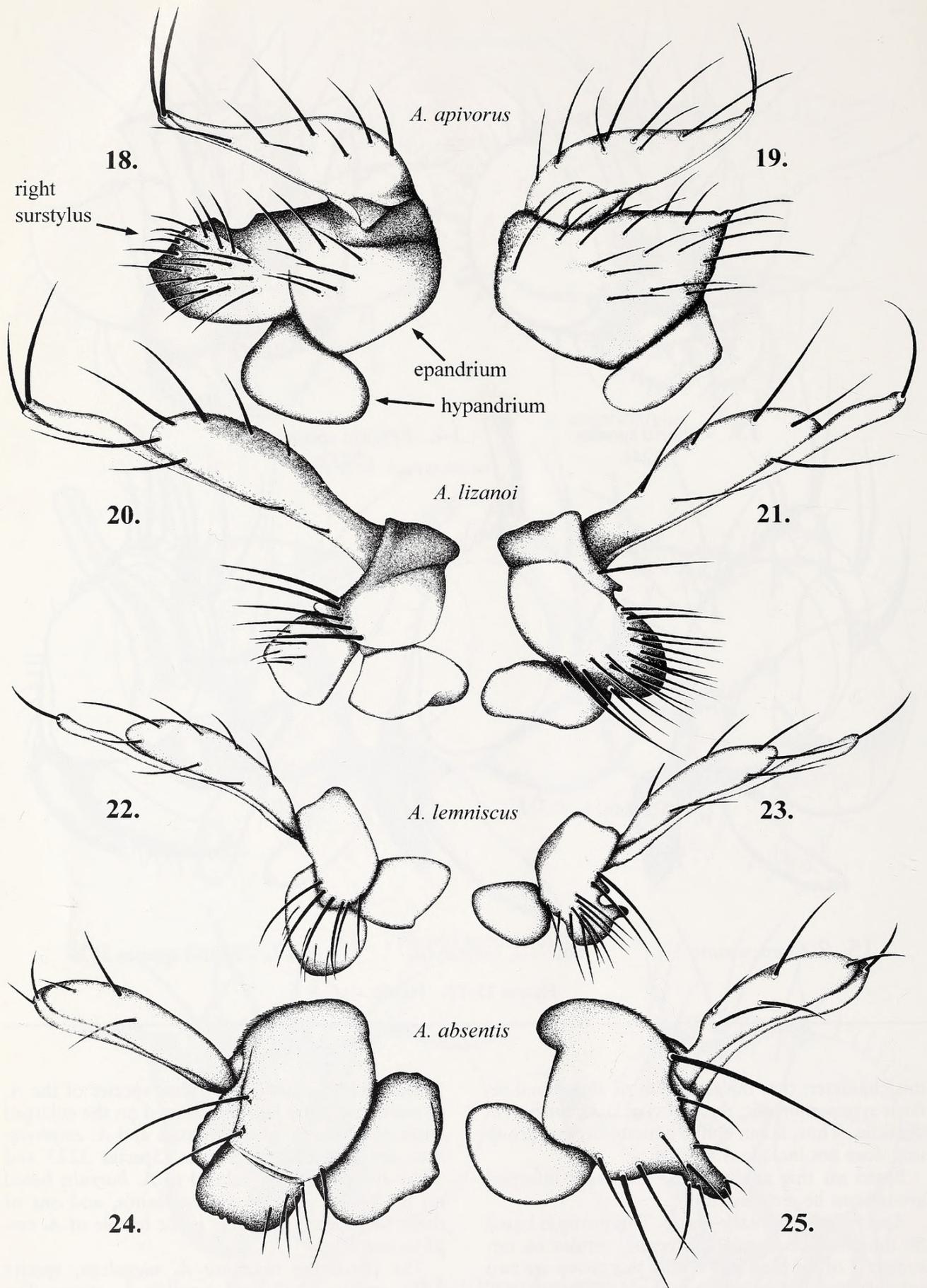
this character: that the reduction of abdominal setae is synapomorphic, regardless of later, further reductions. Thus, it can define a monophyletic group that does not include *A. niveus*.

Based on this analysis, the following informal groups can be recognized.

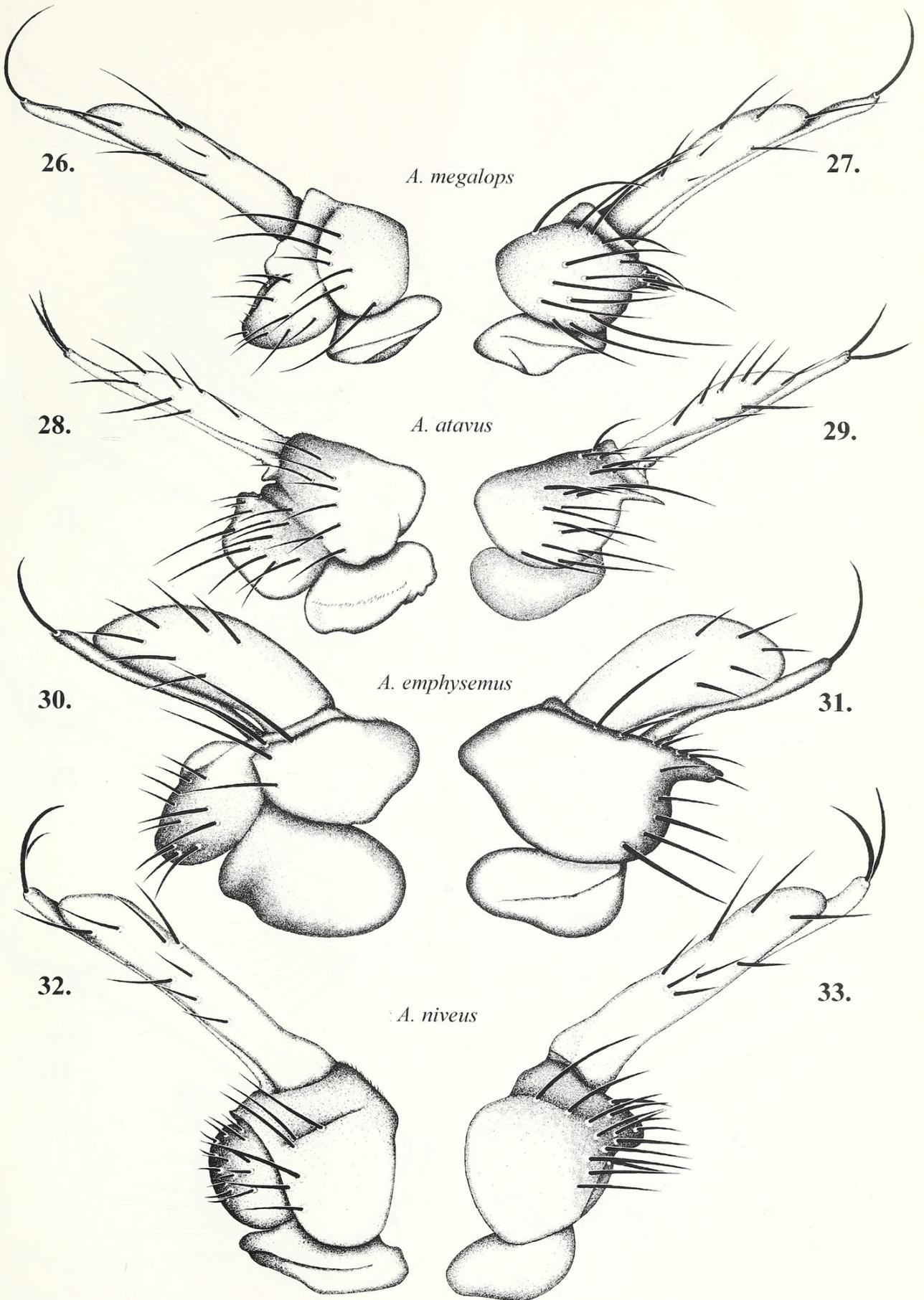
***Apocephalus borealis*-group.** This group is based on the presence of enlarged ventral setulae on tarsomere 1 of the hind leg. Within this group are two subdivisions, one of which is the *A. anfractus*-subgroup (represented by *A. absentis* in this analysis). This assemblage of species is well defined by the presence of a sinuate line of setulae on hind tarsomere 1. The relationships of the *A. anfractus*-subgroup were discussed previously (Brown, 1993).

The relationships of the other species of the *A. borealis* group are less clear. Based on the enlarged costa of males, *A. borealis* Brues and *A. emphysemus* are probably sister taxa. Species 3223 and 3246 are also clearly related to *A. borealis* based on the broad apex of the ovipositor, and one of these two species probably is the female of *A. emphysemus*.

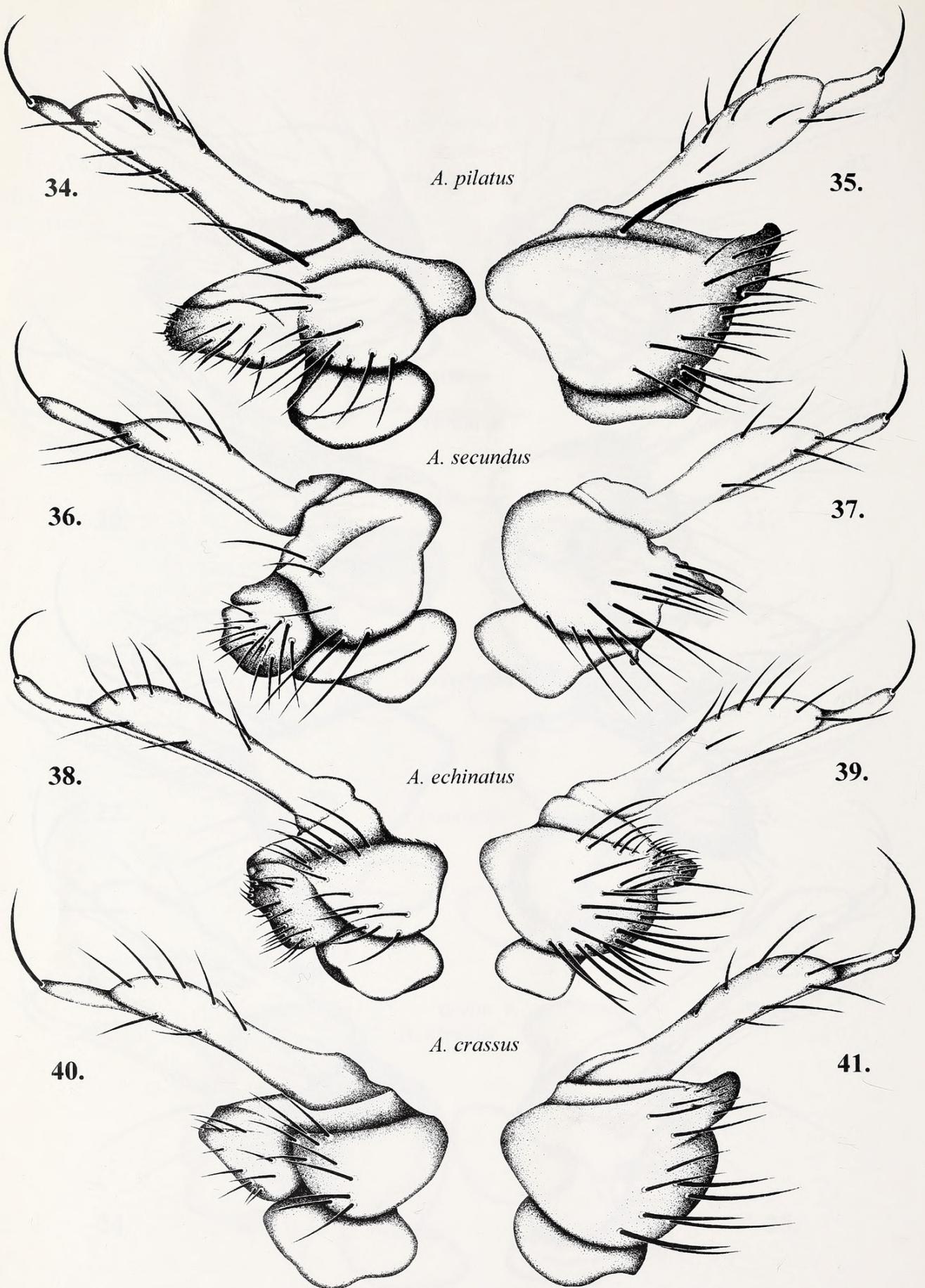
The remaining taxa are *A. megalops*, species 3251, species 3247, and possibly *A. atavus*. The first three species are relatively similar, although *A. megalops* and species 3247 have barbed stylets and might be part of a group including *A. borealis* and relatives. This character, however, has occurred more than once in the subgenus *Mesophora*, and



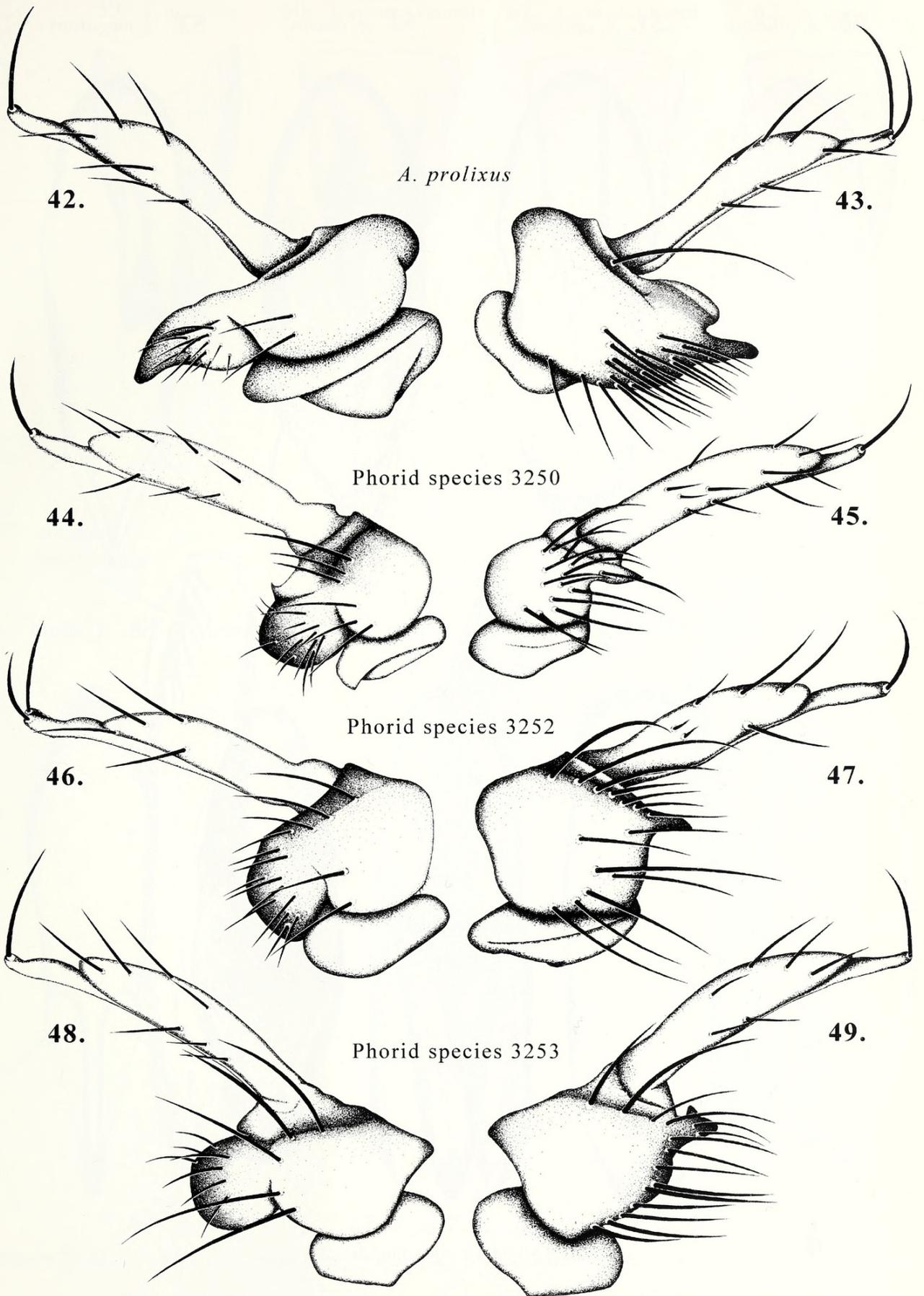
Figures 18–25. Male terminalia, right lateral and left lateral.



Figures 26–33. Male terminalia, right lateral and left lateral.



Figures 34-41. Male terminalia, right lateral and left lateral.



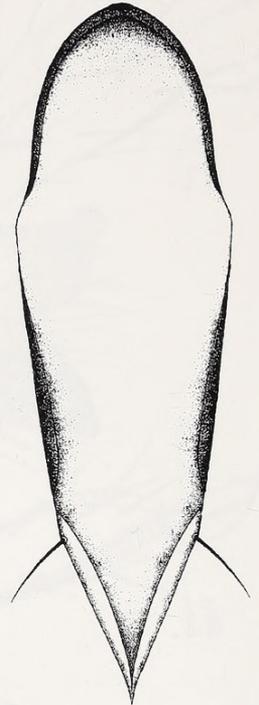
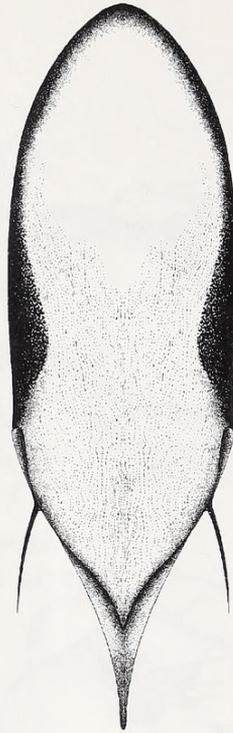
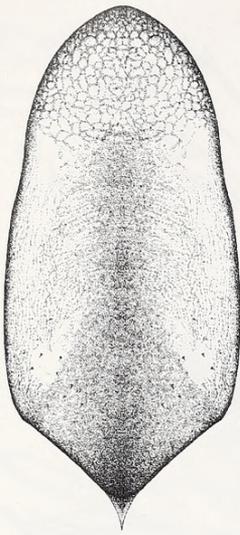
Figures 42-49. Male terminalia, right lateral and left lateral.

50. *A. adustus*

51. *A. apivorus*

52. *A. atavus*

53. *A. megalops*



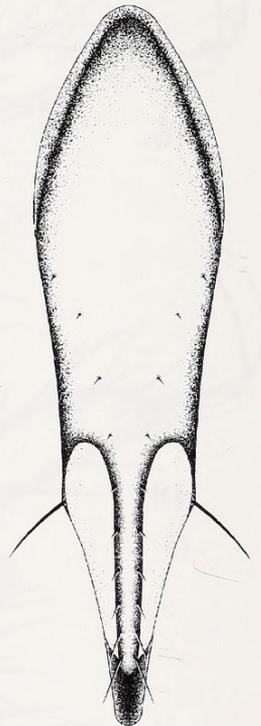
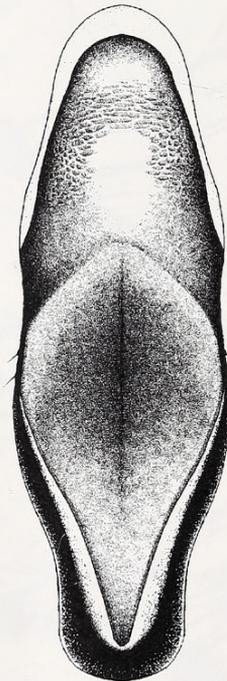
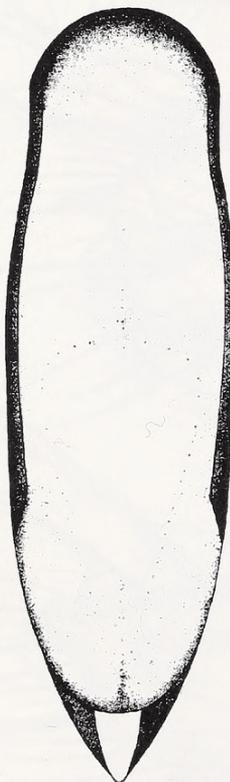
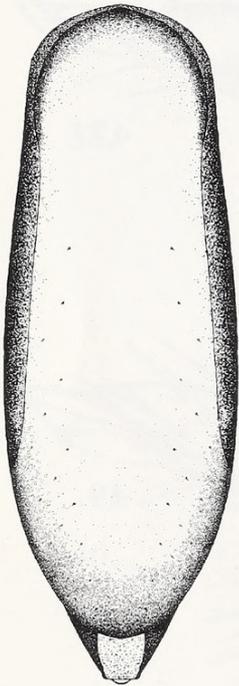
54. Phorid species
3223

55. Phorid species
3246

56. *A. curtus*

57. *A. lizanoi*

58. *A. niveus*



Figures 50-58. Ovipositors, dorsal.

its presence does not provide strong evidence for grouping.

Apocephalus atavus is an extraordinarily difficult species to place. On one hand, it lacks nearly all of

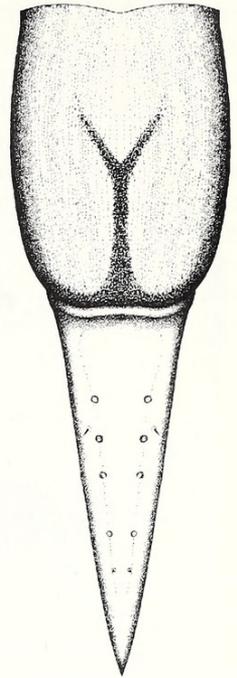
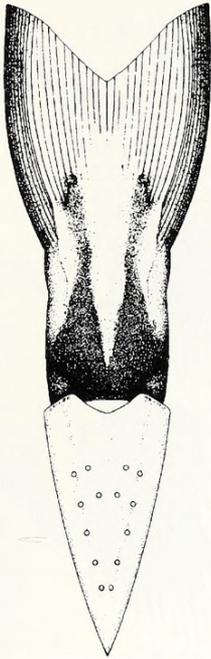
the apomorphies of *Mesophora* and is barely recognizable as a member of this subgenus with only the anteroventral notch of the ovipositor indicating its affinities. If we accept it as part of the *A. bo-*

59. *A. apivorus*

60. *A. curtus* (ventral)

61. *A. curtus* (dorsal)

62. *A. atavus*



enlarged
basal setulae

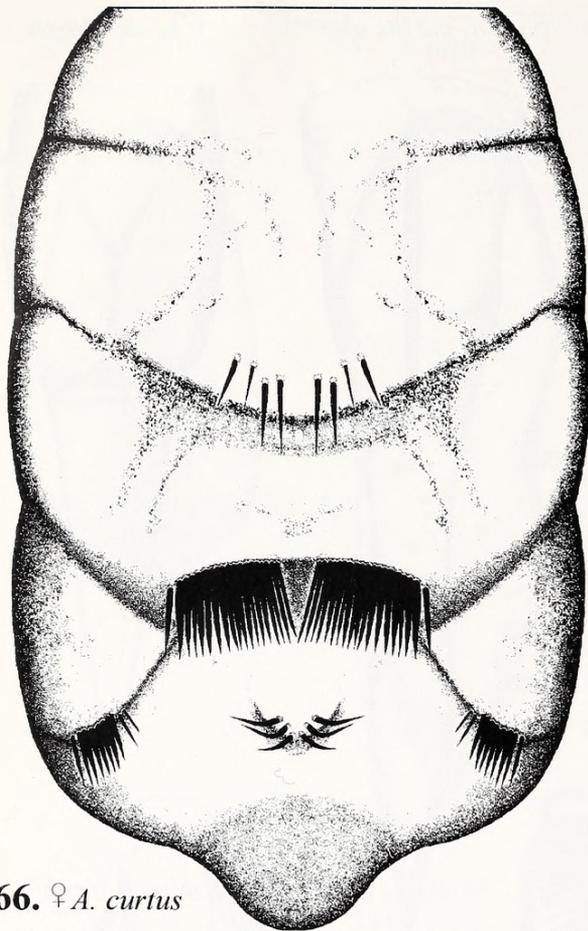


63. *A. borealis*

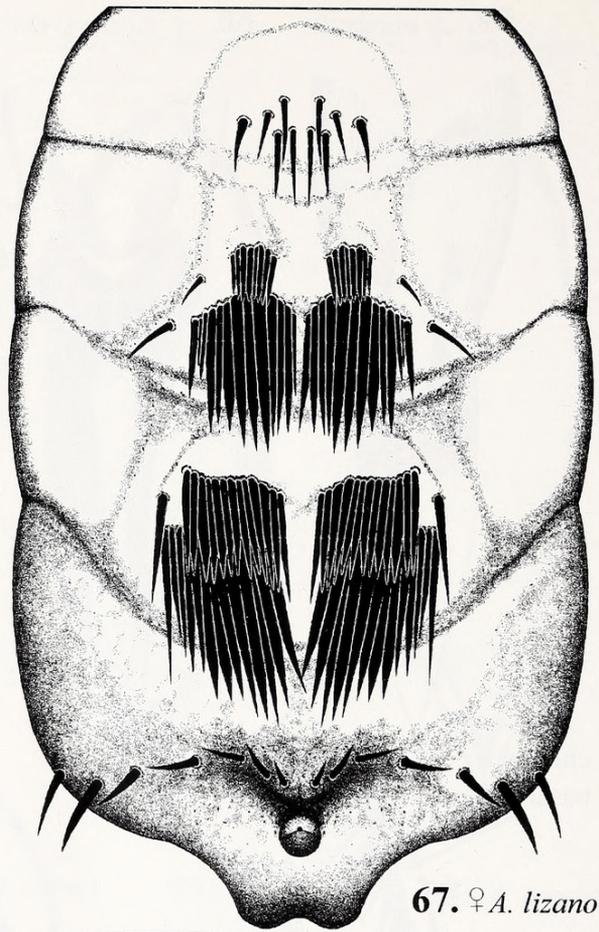
64. Phorid species 3246

65. *A. anfractus*

Figures 59-65. 59-62. Stylets, dorsal (except Fig. 60). 63-65. Tarsomere 1 of left hind leg, anterior (apex at bottom).



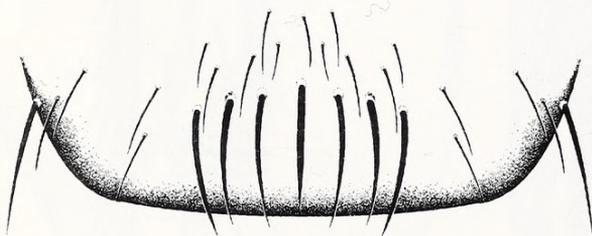
66. ♀ *A. curtus*



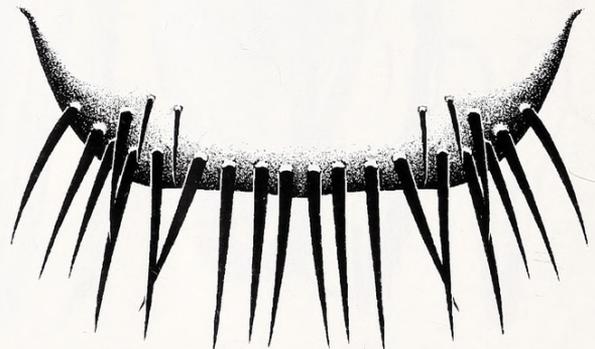
67. ♀ *A. lizanoi*



68. ♂ *A. emphysemus*



69. ♀ *A. atavus*



70. ♂ *A. lizanoi*

Figures 66-70. 66-67. Venter of abdomen. 68. Wing. 69-70. Apex of venter of abdominal segment 6.

The *A. antennatus*-infragroup is a newly proposed assemblage, based on an apparent reversal of the rounded dorsal apex of the ovipositor. This infragroup contains *A. antennatus* and *A. insulanus*, a sister-group pair I recognized previously (Brown, 1993); it also includes *A. brunnipes*, a species that was placed in this infragroup in some previous analyses (Brown, 1993, fig. 110).

The relationships within the *A. wheeleri*-infragroup were discussed previously (Brown, 1993), as were those of the *A. truncaticercus*-infragroup (Brown, 1994b). One change is that *A. gemursus* Brown is now considered a basal member of the *A. wheeleri*-infragroup.

In general, the relationships of the Costa Rican *Mesophora* fauna are relatively well known. Even taxa known only from one sex can be placed within at least a subgroup. I am unable to classify the Dominican Republic species, however, as most are known from males only. Many of these males are relatively similar (*A. pilatus*, *A. secundus*, *A. echinatus*, and *A. crassus*) and do not show any strong divergence from a generalized *Mesophora*.

Apocephalus Coquillett, 1901

Subgenus *Mesophora* Borgmeier, 1937

DIAGNOSIS. Abdominal glands of female dark. Ovipositor primitively with anteroventral notch. Larval mandible with lateral projection; larval spiracular region rounded, densely spinulose; terminal segments of larva lacking large processes (Brown, 1993). One species (*A. absentis*) lacks wing vein R_{2+3} .

Apocephalus apivorus new species

(Figs. 1, 18–19, 51, 59)

SPECIES RECOGNITION. This species can be distinguished from all other *Apocephalus* by the short wing vein CuA_1 , which does not reach the wing margin. It will not key to subgenus *Mesophora* in Borgmeier's (1971) most recent key to *Apocephalus* species.

DESCRIPTION.

General Characters. Body length 1.5–1.8 mm. Frons yellow to brown. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with long anterior and long posterior setae. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, evenly colored throughout. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 attenuated, not reaching wing margin. Halter yellow.

Male. Lower fronto-orbital seta present. Upper fronto-orbital seta present. Flagellomere 1 yellow,

pyriform, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres are slender. Costal vein not thickened. Abdominal tergites dark brown to mostly dark, with yellow markings. Venter of abdomen yellow. Venter of segment 6 with distinct, black setae, ventral setae in a single row. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 19). Right side of epandrium with prominent, darkly sclerotized, dorsolateral ridge (Fig. 18). Right surstylus short, rounded, with ventral carina absent. Cercus brown. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

Female. Lower fronto-orbital seta present, close to eye (Fig. 1). Upper fronto-orbital seta present. Flagellomere 1 yellow, pyriform. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly brown, but tergite 6 yellow. Venter of abdomen yellow, but segment 6 dark gray. Venter of segment 3 with few dark setae. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, long, thick, evenly spaced, arranged in relatively straight line. Venter of segment 6 without sclerite. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6–7 without distinct sclerite. Ovipositor dorsally broad (Fig. 51), anterodorsal portion broad, rounded. Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet with lateral barbs. Dorsal sclerite consisting of two long processes (Fig. 59).

GEOGRAPHICAL DISTRIBUTION. Manaus, Brazil; Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This is hypothesized to be the most relatively primitive species of *Mesophora*.

WAY OF LIFE. This species parasitizes male stingless bees of the species *Cephalotrigona* (formerly *Trigona*) *capitata* (F. Smith) (Apidae: Meliponinae). Detailed information about life history is given in a separate publication (Brown, in press). This is the first species of *Apocephalus* known to attack meliponine bees.

DERIVATION OF SPECIFIC EPITHET. This species is named for the larval habit of eating bees.

HOLOTYPE. ♂, COSTA RICA: Heredia, La Selva Biological Station, 10.43°N, 84.02°W, 25–26.vi.1993, B.V. Brown, reared from male *Trigona capitata* (LACM) [LACM ENT 001075].

PARATYPES. BRAZIL: Pará, Oriximiná, 1.8°S, 53.83°W, 1♂, 13.x.1992, J. Rafael, Malaise trap (INPA); COSTA RICA: Heredia, Chilamate, 10.45°N, 84.08°W, 1♂, v.1989, P. Hanson, Malaise trap, primary forest (LACM), La Selva Biological

Station, 10.43°N, 84.02°W, 15.ii-1.iii.1993, ALAS, 1♂, Malaise trap M/07/22, 1♂, Malaise trap M/10/25 (INBIO), 36♀, 19-25.vi.1993, B.V. Brown, attacking male *Trigona capitata* (LACM, INBIO, MCZ, USNM, MICR, CMNH), 65♂, 66♀, 25-26.vi.1993, B.V. Brown, reared from male *Trigona capitata* (LACM, MCZ, USNM, MICR, CMNH), 1♀, 26.vi.1993, attacking female *Trigona dorsalis* (LACM), Puntarenas, 24 km W Piedras Blancas, 8.77°N, 83.4°W, 1♂, ii-iii.1989, 2♂, ix-xi.1989, P. Hanson, Malaise trap, 200 m (LACM).

Apocephalus atavus new species

(Figs. 28-29, 52, 62, 69)

SPECIES RECOGNITION. This species does not key to *Mesophora* in the key of Borgmeier (1971). It can be recognized, with difficulty, as belonging to this group by the enlarged basal setulae on the hind basitarsus and by the notched ovipositor in the female.

DESCRIPTION.

General Characters. Body length 1.6-2.2 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with some setulae markedly longer than those of other rows. Wing vein R_a slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Lower fronto-orbital seta present. Upper fronto-orbital seta present. Flagellomere 1 yellow, pyriform, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly dark, with yellow markings to mostly yellow, with dark markings. Venter of abdomen yellow. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 29). Right side of epandrium without ridge (Fig. 28). Right surstylus short, rounded, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

Female. Lower fronto-orbital seta present, close to eye. Upper fronto-orbital seta present. Flagellomere 1 yellow, round. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly yellow, with some darker markings. Venter of abdomen yellow. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventrome-

dial setae of segment 6 present, long, thick, evenly spaced, arranged in relatively straight line (Fig. 69). Venter of segment 6 without sclerite. In cleared specimens, dorsal abdominal glands invisible. Intersegment 6-7 with dark sclerite. Ovipositor dorsally narrow, anterodorsal portion broad, rounded (Fig. 52). Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet without lateral barbs (Fig. 62). Dorsal sclerite forked, on long stalk (Fig. 62).

GEOGRAPHICAL DISTRIBUTION. This species is known from three middle elevation sites in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. Unknown. This species fits most parsimoniously at the base of the tree, with *A. apivorus*, but shares with the *A. borealis*-group enlarged setulae on the hind basitarsus.

DERIVATION OF SPECIFIC EPITHET. This name is based on a Latin word for ancestor, reflecting the large number of (possibly homoplastic) primitive characters of this species.

HOLOTYPE. ♂, COSTA RICA: San José, Zurquí de Moravia, 10.05°N, 84.02°W, ix.1991, P. Hanson, Malaise trap, 1600 m (LACM) [LACM ENT 000689].

PARATYPES. COSTA RICA: Puntarenas, Las Alturas, 8.95°N, 82.83°W, 3♂, i.1992, P. Hanson, Malaise trap, 1500 m (LACM), Monteverde, 10.1°N, 83.43°W, 1♂, 1-10.iii.1992, D.M. Wood, Malaise trap, 1500 m (LACM), San José, Zurquí de Moravia, 10.05°N, 84.02°W, 1♀, ix-x.1990, 1♂, x-xii.1990, 1♂, ii.1991, 3♀, iv.1991, 3♂, 4♀, v.1992, 5♂, vi.1992, 3♂, vii.1992, 1♂, 1♀, iv-v.1993, 1♂, 1♀, 1-15.vi.1993, 3♀, ix-x.1993, P. Hanson, 1♀, 7-9.iii.1995, I. Bohorquez, Malaise trap, 1600 m (LACM, MCZ, USNM, MICR, INBIO, CMNH).

Apocephalus adustus Brown, 1993

(Figs. 2, 50)

SPECIES RECOGNITION. This species was previously known only from males; it is redescribed here, including the hitherto unknown females. These females will not key to *Mesophora* in Borgmeier's (1971) key to *Apocephalus* and lack nearly all diagnostic characters of the subgenus. They can be recognized by a combination of their notched ovipositor (visible in cleared specimens only), somewhat flattened flagellomere 1 (Fig. 2), short, simple ovipositor (Fig. 50), and generally dark color with contrasting light halter.

NOTES ON VARIATION. As noted previously (Brown, 1993), this species is extremely variable in color. The length of frontal setae in females also is highly variable. Some individuals have short frontal setae and are lacking upper (but not lower) fronto-orbital setae, whereas others have longer, complete setation.

DESCRIPTION.

General Characters. Body length 1.4–2.1 mm. Frons brown. Palpus yellow. Dorsum of thorax dark brown. Pleural regions yellow, or light brown, or dark brown. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow to brown, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites dark brown. Venter of abdomen yellow, or light brown, or dark brown. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with short setae confined to posterior margin. Right side of epandrium with faint, unsclerotized dorso-lateral ridge. Right surstylus short, rounded, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

Female. Lower fronto-orbital seta present, close to eye (Fig. 2). Upper fronto-orbital seta present. Flagellomere 1 yellow to brown, pyriform, flattened. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites black, tergite 6 at least partly brown. Venter of abdomen white to gray. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, short, thin, evenly spaced, arranged in relatively straight line. Venter of segment 6 without sclerite. In cleared specimens, dorsal abdominal glands invisible. Intersegment 6–7 without distinct sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded (Fig. 50). Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet without lateral barbs. Dorsal sclerite consisting of unforked, medial process.

WAY OF LIFE. I reared this species from an undescribed species of stingless bee, which will be described in a new genus (Paul Hanson, personal communication), at Zurquí de Moravia, Costa Rica. One bee was collected because of its abnormal behavior: it was walking on the ground near

the nest entrance and seemed unable to fly. A further sample of 21 bees was collected, and of these one was parasitized. I reared two and four flies, respectively, from the two parasitized bees.

Apocephalus borealis-group

Apocephalus anfractus-subgroup

Apocephalus absentis Brown, 1993

(Figs. 4, 24–25)

NOTES. This species was previously known only from females; below the species is redescribed, including the hitherto unknown males.

SPECIES RECOGNITION. Both sexes of this species can be recognized by the sinuate row of enlarged setulae on the basal tarsomere of the hind leg, the absence of wing vein R_{2+3} , and the absence of the lower fronto-orbital seta.

DESCRIPTION.

General Characters. Body length 0.8–1.05 mm. Frons yellow to brown. Palpus yellow. Dorsum of thorax yellow to light brown. Pleural regions yellow to light brown. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, evenly colored throughout. Anteroventral row of enlarged setulae on hind basitarsus sinuate, with some setulae markedly longer than those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} absent. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Lower fronto-orbital setal absent (Fig. 4). Upper fronto-orbital seta present. Flagellomere 1 brown, slightly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Midleg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites dark brown. Venter of abdomen light brown. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with large, prominent seta near cercus. Left side of epandrium with scattered, thin setae (Fig. 25). Right side of epandrium without ridge (Fig. 24). Right surstylus short, rounded, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

Female. Lower fronto-orbital seta absent. Upper fronto-orbital seta present. Flagellomere 1 brown, pyriform. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly brown, but tergite 6 yellow. Venter of abdomen white. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, long, thick, evenly spaced, arranged in relatively straight line. Venter of segment 6 without sclerite. In cleared specimens, dorsal abdominal

glands visible, dark. Intersegment 6–7 without distinct sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded. Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet without lateral barbs. Dorsal sclerite consisting of two small processes.

GEOGRAPHICAL DISTRIBUTION. Besides being known from several sites in Costa Rica, at both middle and lower elevations, this species has also been collected at Pakitza, Peru.

Apocephalus bisetus Brown, 1993

NOTES ON SPECIES RECOGNITION. This species, known only from a single female, was separated from *A. trisetus* Brown (Brown, 1993) based on the presence of two lateral setae on the venter of segment 6 and by a different stylet shape. Some more recently collected specimens, however, have three lateral setae like females of *A. trisetus*. A summary of the differences between the species, as I recognize them, is as follows:

- A. bisetus*: 1) flagellomere 1 yellow throughout
2) 2–3 lateral setae on venter of segment 6
3) medial section of stylet short
- A. trisetus*: 1) flagellomere 1 yellow, with dark apex
2) 3 lateral setae on venter of segment 6
3) medial section of stylet long

GEOGRAPHICAL DISTRIBUTION. This species is known only from Costa Rica.

Other *Apocephalus borealis*-group Species

Apocephalus megalops new species (Figs. 5–6, 26–27, 53)

SPECIES RECOGNITION. This species can be recognized most easily by the large eyes and narrow frons.

DESCRIPTION.

General Characters. Body length 1.7–2 mm. Frons yellow, narrow (Figs. 5–6). Palpus yellow. Dorsum of thorax yellow. Pleural regions white. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with some setulae markedly longer than those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Male. Lower fronto-orbital seta absent (Fig. 5).

Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Midleg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly yellow, with dark markings. Venter of abdomen yellow. Venter of segment 6 with distinct, black setae, ventral setae in a single row. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 27). Right side of epandrium without ridge (Fig. 26). Right surstylus elongate, rounded at apex, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

Female. Lower fronto-orbital seta absent (Fig. 6). Upper fronto-orbital seta absent. Flagellomere 1 yellow, pyriform. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly yellow, with some darker markings. Venter of abdomen yellow. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, long, thick, evenly spaced, arranged in anteriorly pointed “V”. Venter of segment 6 with sclerite present. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6–7 without distinct sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded (Fig. 53). Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet with lateral barbs. Dorsal sclerite forked, on long stalk.

GEOGRAPHICAL DISTRIBUTION. This species is known from a single, middle elevation site in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This species is part of the *A. borealis*-group.

DERIVATION OF SPECIFIC EPITHET. The name is based on Greek words for large eyes.

HOLOTYPE. ♂, COSTA RICA: San José, 26 km N San Isidro, 9.5°N, 83.72°W, viii–ix.1991, P. Hanson, Malaise trap, 2100 m (LACM) [LACM ENT 000609].

PARATYPES. COSTA RICA: San José, 26 km N San Isidro, 9.5°N, 83.72°W, 2 ♀, viii–ix.1991, 1 ♂, ii–v.1992, P. Hanson, Malaise trap, 2100 m (LACM).

Apocephalus emphysemus new species

(Figs. 30–31, 68)

SPECIES RECOGNITION. The male of this species is similar to the Nearctic Region species *A. borealis* but differs by the dark brown coloring, the enlarged first flagellomere, and the normal-sized

palpus. It can be separated from other brown *Mesophora* by the swollen costal vein (Fig. 68). The female is unknown.

DESCRIPTION.

General Characters. Body length 1.5 mm. Frons brown. Palpus brown. Dorsum of thorax light brown. Pleural regions light brown. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur dark brown, evenly colored throughout, but gradually darkened at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with some setulae markedly longer than those of other rows. Wing vein R_s slender, thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellowish at base, apically darker, greatly enlarged, apically flattened, apical two thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein thickened between humeral crossvein and R_1 . Abdominal tergites dark brown. Venter of abdomen light brown. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with thick, ventral setae (Fig. 31). Right side of epandrium with prominent, darkly sclerotized, dorsolateral ridge (Fig. 30). Right surstylus short, rounded, lacking ventral carina. Cercus brown. Setae of cercus reduced in size.

GEOGRAPHICAL DISTRIBUTION. Known from a single site in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This species is probably the sister-species of *A. borealis*.

DERIVATION OF SPECIFIC EPITHET. This name is based on a Greek word for swelling, referring to the enlarged costa.

HOLOTYPE. ♂, COSTA RICA: San José, Zurquí de Moravia, 10.05°N, 84.02°W, ix.1991, P. Hanson, Malaise trap, 1600 m (LACM) [LACM ENT 000646].

Apocephalus wheeleri-group

Apocephalus curtus-subgroup

Apocephalus lizanoi new species

(Figs. 20–21, 57, 67, 70)

SPECIES RECOGNITION. The male of this species is extremely similar to that of *A. curtus* but differs by the shape of the epandrium, which in *A. lizanoi* has a well-defined lateral ridge (Figs. 20–21), and by the less flared right surstylus in *A. lizanoi* (Fig. 20). The presumed female of this species differs from that of *A. curtus* by the pattern of ven-

tral setation (Fig. 67) and by the structure of the ovipositor (Fig. 57).

There is no direct evidence linking the female specimens with the one known male, other than that they were collected together. This species along with *A. curtus* and *lemmiscus* new species (see below) form a species complex that requires further attention. Rearing a series of males and females would be helpful, but the hosts are still unknown.

DESCRIPTION.

General Characters. Body length 1.7–2.3 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, evenly colored throughout. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly dark, with yellow markings. Venter of abdomen white. Venter of segment 6 with distinct, black setae, ventral setae in a single row (Fig. 70). Venter of segment 6 without sclerite. Epandrium globular, band-shaped, shorter than height, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 21). Right side of epandrium with faint, unsclerotized dorsolateral ridge (Fig. 20). Right surstylus short, rounded, lacking ventral carina. Cercus brown. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

Female. Lower fronto-orbital seta absent. Upper fronto-orbital seta present. Flagellomere 1 yellow, greatly enlarged, subequal to eye height, apically flattened. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly yellow, with some darker markings. Venter of abdomen yellow. Venter of segment 3 with few dark setae (Fig. 67). Venter of abdominal segment 4 with dense combs of setae. Venter of abdominal segment 5 with dense combs of setae, with sclerite present. Venter of abdominal segment 6 with short median spine, without lateroventral patch of setae. Ventromedial setae of segment 6 present, short, thick, evenly spaced, arranged in relatively straight line. Venter of segment 6 with sclerite present. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6–7 with dark sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded (Fig. 57). Anteroventral

margin of ovipositor with deep, posterior projection. Posterodorsal apex of ovipositor rounded. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor rounded. Stylet without lateral barbs. Dorsal sclerite consisting of unforked, medial process.

GEOGRAPHICAL DISTRIBUTION. Known from three middle elevation sites in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This species is closely related to *A. curtus* and *A. lemniscus* new species (see below).

DERIVATION OF SPECIFIC EPITHET. This species is dedicated to Señor Jorge Arturo Lizano, owner of the property at the incredibly diverse Zurquí de Moravia site.

HOLOTYPE. ♂, COSTA RICA: Puntarenas, Las Alturas, 8.95°N, 82.83°W, x.1991, P. Hanson, Malaise trap, 1500 m (LACM) [LACM ENT 000859].

PARATYPES. COSTA RICA: Puntarenas, Las Alturas, 8.95°N, 82.83°W, 1 ♀, x.1991, 7 ♀, i.1992, 5 ♀, v.1992, 3 ♀, vi. 1992, P. Hanson, Malaise trap, 1500 m (LACM, MCZ, USNM, MICR, INBIO), San José, Braulio Carrillo National Park, 10.12°N, 83.97°W, 2 ♀, vi–xi.1990, P. Hanson, Malaise trap, 1000 m (LACM), Zurquí de Moravia, 10.05°N, 84.02°W, 1 ♀, v.1992, P. Hanson, Malaise trap, 1600 m (LACM).

Apocephalus curtus Brown, 1993
(Figs. 56, 60–61, 66)

SPECIES RECOGNITION. Further coincident collections, along with other subtle character agreements with male specimens, confirmed my suspicion that *Apocephalus* species female C (of Brown, 1993) is the unnamed female of *A. curtus*. Females of this species are recognized by the dense patches of thick, black setae on the venter of the abdomen (Fig. 66), which are patterned differently than those of *A. lizanoi* (Fig. 67).

NOTES ON VARIATION. One male specimen has the ventral setae of the abdomen, which are usually elongate (as Fig. 70), reduced to tiny stubs.

DESCRIPTION.

General Characters. Body length 1.9–2.2 mm. Frons yellow. Palpus yellow. Dorsum of thorax light brown. Pleural regions yellow. Scutellum of same color as dorsum of thorax to darker than and contrasting with dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, evenly colored throughout. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_5 slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-

thirds with narrowest part greater than one-half basal width. Palpus enlarged, with setae reduced, thin, short, stubby. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly dark, with yellow markings. Venter of abdomen white. Venter of segment 6 with distinct, black setae, ventral setae in a single row. Venter of segment 6 without sclerite. Epandrium globular, band-shaped, shorter than height, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae. Right side of epandrium with faint, unsclerotized dorsolateral ridge. Right surstylus truncate, apically flared, lacking ventral carina. Cercus brown. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

Female. Lower fronto-orbital seta absent. Upper fronto-orbital seta present. Flagellomere 1 yellow, pyriform. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly yellow, with some darker markings. Venter of abdomen yellow. Venter of segment 3 bare. Venter of abdominal segment 4 lacking dense setal combs. Venter of abdominal segment 5 with dense combs of setae, without sclerite (Fig. 66). Venter of abdominal segment 6 without short median spine, with lateroventral patch of setae. Ventromedial setae of segment 6 present, short, thick, in medial group, arranged in relatively straight line. Venter of segment 6 with sclerite present. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6–7 with dark sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded (Fig. 56). Anteroventral margin of ovipositor with deep, posterior projection. Posterodorsal apex of ovipositor rounded. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor extremely widely rounded. Stylet without lateral barbs (Figs. 60–61). Dorsal sclerite consisting of unforked, medial process (Fig. 61).

GEOGRAPHICAL DISTRIBUTION. This species is known only from Zurquí de Moravia in San José Province, Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This species and *A. lemniscus* might be most closely related, based on the flared right surstylus. Discovery of the female of *A. lemniscus* is necessary to allow further resolution of these relationships.

Apocephalus lemniscus
new species
(Figs. 3, 22–23)

SPECIES RECOGNITION. The head of this species (Fig. 3) is strikingly different from *A. curtus* and *A. lizanoi*: flagellomere 1 is relatively small and dark brown in color, and the upper fronto-orbital seta is present. In *A. lemniscus*, the venter of segment 6 has two rows of large setae, rather than a single row as found in *A. curtus* and *lizanoi* (Fig. 70). The pattern of epandrial setation and shape of

the surstylus also is different from those of the other two species. The female is unknown.

DESCRIPTION.

General Characters. Body length 2 mm. Frons yellow. Palpus yellow. Dorsum of thorax light brown. Pleural regions light brown. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, evenly colored throughout. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Lower fronto-orbital seta absent (Fig. 3). Upper fronto-orbital seta present. Flagellomere 1 brown, pyriform, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly dark, with yellow markings. Venter of abdomen yellow. Venter of segment 6 with distinct, black setae, ventral setae in two rows. Venter of segment 6 without sclerite. Epandrium globular, band-shaped, shorter than height, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae. Right side of epandrium without ridge. Right surstylus truncate, apically flared, lacking ventral carina. Cercus brown. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. Known from a single site in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This species possibly is the sister-taxon of *A. curtus*.

DERIVATION OF SPECIFIC EPITHET. This name is derived from a Latin word for band or ribbon, referring to the short, narrow epandrium.

HOLOTYPE. ♂, COSTA RICA: San José, 6 km N San Gerardo, 2800 m, 9.95°N, 84.05°W, viii.1993, P. Hanson, Malaise trap (LACM) [LACM ENT 001433].

Apocephalus wheeleri-subgroup

Apocephalus niveus new species

(Figs. 32–33, 58)

SPECIES RECOGNITION. This species can be recognized in part by the distinctive white color of flagellomere 1 (in females only), the legs, and pleural region.

DESCRIPTION.

General Characters. Body length 1.4–1.7 mm. Frons yellow. Palpus yellow. Dorsum of thorax light brown. Pleural regions white. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs white.

Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula, or with four enlarged setulae besides apical, or with two enlarged setulae, one apical, one at midpoint. Hind femur white, evenly colored throughout. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellowish at base, apically darker, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites dark gray, with tergite 6 yellow. Venter of abdomen white. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 33). Right side of epandrium with faint, unsclerotized dorsolateral ridge (Fig. 32). Right surstylus short, rounded, lacking ventral carina. Cercus brown. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

Female. Lower fronto-orbital seta absent. Upper fronto-orbital seta present. Flagellomere 1 white, pyriform. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly brown, but tergite 6 yellow. Venter of abdomen white. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, long, thick, in lateral group of three, arranged in anteriorly pointed "V". Venter of segment 6 with sclerite present. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6–7 without distinct sclerite. Ovipositor dorsally narrow (Fig. 58), anterodorsal portion broad, rounded. Anteroventral margin of ovipositor smooth, without notch. Posterodorsal apex of ovipositor rounded. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor rounded. Stylet without lateral barbs. Dorsal sclerite forked, on long stalk.

GEOGRAPHICAL DISTRIBUTION. This species is known from low and middle elevation sites in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. Based on the presence of thick, dark seta on the venter of segment 6 in females, this species is hypothesized to be the sister taxon of the rest of the *A. wheeleri*-subgroup.

DERIVATION OF SPECIFIC EPITHET. This name is based on a Latin word for snow-white, referring to the white-colored body parts.

HOLOTYPE. ♂, COSTA RICA: Limon, 7 km W Bribri, 9.58°N, 82.88°W, ix–xi.1989, P. Hanson,

Malaise trap, 50 m (LACM) [LACM ENT 000802].

PARATYPES. COSTA RICA: Limon, 7 km W Bribri, 9.58°N, 82.88°W, 3♂, 3♀, ix–xi.1989, P. Hanson, Malaise trap, 50 m, altered forest (LACM), 16 km W Guapiles, 10.15°N, 83.92°W, 1♂, iii–v.1990, 1♀, i–iv.1991, P. Hanson, Malaise trap, 400 m (LACM), San José, Zurquí de Moravia, 10.05°N, 84.02°W, 1♂, v.1992 (LACM).

Apocephalus antennatus-infragroup

Apocephalus antennatus

Malloch, 1913

(Figs. 7, 15)

Apocephalus leptotarsus Brown, 1993 new synonymy

NOTES ABOUT SYNONYMY. My previous description of *A. leptotarsus* as a separate species was based on an error: the surstylus of this species does not bear a medial carina.

NOTES ABOUT VARIATION. Some specimens from Costa Rica assigned to this species have the tip of the hind femur darkened, whereas North American specimens, and those from Colombia, lack this darkening. All other species of *Mesophora* are consistently one or the other, so this difference might represent some real distinction between the Costa Rican and other species. I can find no structural characters to support this differentiation, however.

Also, some specimens have no extra setulae on the venter of mid tarsomere 2. This is not correlated with any other variation, but it adds weight to the idea that *A. antennatus* is a highly variable species or a cryptic species complex.

NOTES ABOUT DISTRIBUTION. Previously, I tentatively concluded that this species was not limited to the Nearctic Region. Further collections show this to be true; there are now many specimens from the Neotropical Region: from Costa Rica, the Dominican Republic, and Mexico.

WAY OF LIFE. Nearctic Region hosts of this species, several species of fireflies (Coleoptera: Lampyridae), were listed previously (Brown, 1994a). Recently, I also reared *A. antennatus* from a diurnal, non-luminous species of *Lucidota* (Coleoptera: Lampyridae) at Monteverde, Costa Rica. This was a different firefly species from *L. atra*, a host I reported previously.

Apocephalus longistylus

Brown, 1993

(Fig. 16)

NOTES ABOUT DESCRIPTION. The female of *A. longistylus* lacks the lower fronto-orbital seta, not the "middle" (=upper) fronto-orbital seta, as I originally stated (Brown, 1993).

WAY OF LIFE. I reared adult males of this species from a species of *Bicellonycha* (Lampyridae) at Zurquí de Moravia, Costa Rica.

Apocephalus wheeleri-infragroup

Apocephalus mortifer

Borgmeier, 1937

NEW MATERIAL EXAMINED. This species, previously known only from Brazil, was collected in Central America: 1♂, COSTA RICA: San José, Zurquí de Moravia, 10.05°N, 84.02°W, ix.1991, P. Hanson, Malaise trap, 1600 m (LACM).

Apocephalus tritarsus

Brown, 1993

NOTES ON VARIATION. Newly collected Costa Rican specimens of this species differ from the original specimens from Mexico by the dark brown color of the halter and cercus.

WAY OF LIFE. I reared this species from a diurnal, non-luminous lampyrid of the genus *Lucidota* at Monteverde, Costa Rica. The beetle was a different species than that from which *A. antennatus* was reared (see above).

Unplaced Species

Apocephalus micrepelis

Brown, 1993

NOTES ABOUT DESCRIPTION. This species was previously known only from the holotype male. Additional specimens (CMNH, LACM) have brought to light a previously unnoticed character: males have a few ventral setae on abdominal segment 6.

Apocephalus pilatus new species

(Figs. 34–35)

SPECIES RECOGNITION. Males of this species are similar to those of *A. antennatus*, but the palpal setae are not shortened, the surstylus is more rounded, and the large setae near the cercus are more posteroventrally placed. The female is unknown.

DESCRIPTION.

General Characters. Body length 1.5–1.8 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick,

moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly yellow, with dark markings. Venter of abdomen yellow. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with large, prominent seta near cercus. Left side of epandrium with scattered, thin setae (Fig. 35). Right side of epandrium with prominent, darkly sclerotized, dorsolateral ridge (Fig. 34). Right surstylus short, rounded, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. This species is known only from the Dominican Republic.

PHYLOGENETIC RELATIONSHIPS. Unknown.

DERIVATION OF SPECIFIC EPITHET. The name of this species is derived from a Latin word for dense, referring to the number of setae on the left side of the epandrium.

HOLOTYPE. ♂, DOMINICAN REPUBLIC: Pedernales, Las Abejas, 38 km NNW Cabo Rojo, 18.13°N, 72.63°W, 15.vii.1987, J. Rawlins, R. Davidson, Malaise trap, 1250 m (CMNH) [LACM ENT 000897].

PARATYPES. DOMINICAN REPUBLIC: Pedernales, Las Abejas, 38 km NNW Cabo Rojo, 18.13°N, 71.63°W, 2♂, 15.vii.1987, J. Rawlins, R. Davidson, Malaise trap, 1250 m (CMNH, LACM), 3.3 km NE Los Arroyos, 18.25°N, 71.75°W, 1♂, 16–18.vii.1990, L. Masner *et al.*, sweep samples, wet montane forest, 1450 m (CMNH).

Apocephalus crassus new species

(Figs. 40–41)

SPECIES RECOGNITION. This is another species whose male is similar to that of *A. antennatus*, but it differs by the sparse, thicker setae on the left side of the epandrium and the absence of a large seta near the cercus. The female is unknown.

DESCRIPTION.

General Characters. Body length 2.4 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick,

moderately long, pointed. Midleg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly yellow, with dark markings. Venter of abdomen yellow. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with thick, ventral setae (Fig. 41). Right side of epandrium with prominent, darkly sclerotized, dorsolateral ridge (Fig. 40). Right surstylus short, rounded, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. This species is known only from the Dominican Republic.

PHYLOGENETIC RELATIONSHIPS. Unknown.

DERIVATION OF SPECIFIC EPITHET. The name is from a Latin word for thick, referring to the enlarged setae of the left side of the epandrium.

HOLOTYPE. ♂, DOMINICAN REPUBLIC: Pedernales, 3.3 km NE Los Arroyos, 18.25°N, 71.75°W, 16–18.vii.1990, L. Masner *et al.*, sweep samples, wet montane forest, 1450 m (CMNH) [LACM ENT 000895].

Apocephalus prolixus

new species

(Figs. 42–43)

SPECIES RECOGNITION. Males of this species resemble those of *A. longistylus* and *A. prolatus* by their elongate right surstylus but differ by having a small palpus and no ventral abdominal setae. The epandrium is greatly depressed, like that of *A. insulanus* (Brown, 1993, figs. 5, 26), but unlike *A. insulanus* there are large setae on both sides of the epandrium (Figs. 42–43). The female is unknown.

DESCRIPTION.

General Characters. Body length 1.5–1.8 mm. Frons yellow. Palpus yellow. Dorsum of thorax light brown. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, evenly colored throughout. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow to brown.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed to with setae reduced, thin, short, stubby. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal ter-

gites mostly yellow, with dark markings. Venter of abdomen white. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium markedly depressed, approximately as long as high, with large, prominent seta near cercus. Left side of epandrium with scattered, thin setae (Fig. 43). Right side of epandrium with prominent, darkly sclerotized, dorsolateral ridge (Fig. 42). Right surstylus elongate, rounded at apex, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. This species is known only from the Dominican Republic.

PHYLOGENETIC RELATIONSHIPS. Unknown.

DERIVATION OF SPECIFIC EPITHET. The name is from a Latin word for elongate, referring to the long epandrium.

HOLOTYPE. ♂, DOMINICAN REPUBLIC: Pedernales, Las Abejas, 38 km NNW Cabo Rojo, 18.13°N, 71.63°W, 1♂, 15.vii.1987, J. Rawlins, R. Davidson, Malaise trap, 1250 m (CMNH) [LACM ENT 000888].

PARATYPE. DOMINICAN REPUBLIC: Pedernales, 3.3 km NE Los Arroyos, 18.25°N, 71.75°W, 1♂, 16–18.vii.1990, L. Masner *et al.*, sweep samples, wet montane forest, 1450 m (LACM).

Apocephalus secundus new species

(Figs. 36–37)

SPECIES RECOGNITION. The male of this species can be recognized by the enlarged palpus and the enlarged setula on the second tarsomere of the mid leg. The female is unknown.

DESCRIPTION.

General Characters. Body length 1.7 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick, elongate, apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus enlarged, with setae reduced, thin, short, stubby. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly yellow, with dark markings. Venter of abdomen yellow. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cer-

cus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 37). Right side of epandrium with prominent, darkly sclerotized, dorsolateral ridge (Fig. 36). Right surstylus short, rounded, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. This species is known only from the Dominican Republic.

PHYLOGENETIC RELATIONSHIPS. Unknown.

DERIVATION OF SPECIFIC EPITHET. The name is a Latin word for second, referring to the second tarsomere of the mid leg, which has an elongate apical seta.

HOLOTYPE. ♂, DOMINICAN REPUBLIC: Pedernales, Las Abejas, 38 km NNW Cabo Rojo, 18.13°N, 71.63°W, 1♂, 15.vii.1987, J. Rawlins, R. Davidson, Malaise trap, 1250 m (CMNH) [LACM ENT 000893].

Apocephalus echinatus

new species

(Figs. 38–39)

SPECIES RECOGNITION. Males of this species are recognized by the extremely dense setae on the epandrium. The female is unknown.

DESCRIPTION.

General Characters. Body length 1.8–2.2 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg bare. Hind femur yellowish-brown, evenly colored throughout. Anteroventral row of enlarged setulae on hind basitarsus straight, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly dark, with yellow markings. Venter of abdomen yellow. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with dense, thicker setae (Fig. 39). Right side of epandrium without ridge (Fig. 38). Right surstylus short, rounded, lacking ventral carina. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. This species is known only from the Dominican Republic.

PHYLOGENETIC RELATIONSHIPS. Unknown.

DERIVATION OF SPECIFIC EPITHET. This name is based on a Latin word for spiny, referring to the dense setae on the left side of the epandrium.

HOLOTYPE. ♂, DOMINICAN REPUBLIC: Pedernales, 5 km NE Los Arroyos, 18.25°N, 71.75°W, 33♂, 17–18.vii.1990, C. Young *et al.*, Malaise trap (CMNH) [LACM ENT 001155].

PARATYPES. DOMINICAN REPUBLIC: Independencia, Sierra de Neiba, 5.5 km NNW Angel Feliz, 18.68°N, 71.78°W, 1♂, 21–22.vii.1992, J. Rawlins *et al.*, Malaise trap, dense cloud forest, 1750 m (CMNH), Pedernales, 3.3 km NE Los Arroyos, 18.25°N, 71.75°W, 1♂, 16–18.vii.1990, L. Masner *et al.*, sweep samples, wet montane forest, 1450 m (CMNH, LACM), 5 km NE Los Arroyos, 18.25°N, 71.75°W, 32♂, 17–18.vii.1990, C. Young *et al.*, Malaise trap (CMNH, LACM, USNM, MCZ).

Species Recognized but Not Named

The following species are represented by a single sex only: males of the *A. anfractus*-group or females of the other groups.

Phorid Species 3251 ♀ (Fig. 11)

A. limai Prado; Brown, 1993 (misidentification)

SPECIES RECOGNITION. The two specimens of this unnamed species have a different ovipositor structure than that of *A. limai*. My previous use of the name was in part because both taxa lack the upper fronto-orbital setae, but this character state is now known to be fairly widespread. This species belongs in the *A. borealis*-group.

DESCRIPTION.

General Characters. Body length 2.9–3.1 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with some setulae markedly longer than those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Female. Lower fronto-orbital seta absent (Fig. 11). Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, subequal to eye height, apically flattened. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites yellow. Venter of abdomen yellow. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, long, thick, evenly spaced, arranged in relatively straight line.

Venter of segment 6 without sclerite. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6–7 with dark sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded. Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet without lateral barbs. Dorsal sclerite forked, on long stalk.

MATERIAL EXAMINED. PANAMA: Chiriqui, Potrerillos, 1♀, 25.vii.1964, A. Broce, light trap, 975 m (USNM) [LACM ENT 000638]; VENEZUELA: Yacambu, 1♀, 10.v.1981, H.K. Townes, 365 m (LACM) [LACM ENT 000629].

Phorid Species 3223 ♀ (Figs. 12, 54)

Species recognition. This is one of two species that have ovipositors closely resembling those of *A. borealis*. Unlike females of *A. borealis*, species 3223 is darker in color and has flagellomere 1 enlarged and apically flattened.

DESCRIPTION.

General Characters. Body length 2.2 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with basal setulae markedly longer than those of other rows. Wing vein R_s slightly swollen, thicker than costa. Wing vein R_{2+3} thin. Wing vein CuA_1 reaches wing margin. Halter brown.

Female. Lower fronto-orbital seta absent (Fig. 12). Upper fronto-orbital seta present. Flagellomere 1 yellow, greatly enlarged, subequal to eye height, apically flattened. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly yellow, with some darker markings. Venter of abdomen yellow. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, long, thick, evenly spaced, arranged in relatively straight line. Venter of segment 6 without sclerite. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6–7 without distinct sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded (Fig. 54). Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed, but broadly rounded before apex. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet with lateral barbs. Dorsal sclerite consisting of two long processes.

GEOGRAPHICAL DISTRIBUTION. Known from a single middle elevation site in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This species is clearly part of the *A. borealis*-subgroup, possibly a female of *A. emphysemus*.

MATERIAL EXAMINED. COSTA RICA: San José, Zurquí de Moravia, 10.05°N, 84.02°W, 1♀, v.1991 [LACM ENT 000640], 2♀, ix-x.1993 [LACM ENT 001496, 001492], P. Hanson, Malaise trap (LACM).

Phorid Species 3246 ♀

(Figs. 13, 55, 64)

SPECIES RECOGNITION. This female is also similar to that of *A. borealis* but has the lower fronto-orbital seta present and is darker in color. Also, the extremely enlarged setulae of the hind tarsomere of species 3246 is diagnostic (Fig. 64).

DESCRIPTION.

General Characters. Body length 1.9 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, markedly longer than those of other rows (Fig. 64). Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Female. Lower fronto-orbital seta present, slightly medially displaced (Fig. 13). Upper fronto-orbital seta present. Flagellomere 1 yellow, pyriform. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly yellow, with some darker markings. Venter of abdomen yellow. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, long, thick, evenly spaced, arranged in relatively straight line. Venter of segment 6 without sclerite. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6-7 with dark sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded (Fig. 55). Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed, but broadly rounded before apex. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet with lateral barbs. Dorsal sclerite consisting of unforked, medial process.

GEOGRAPHICAL DISTRIBUTION. Known from a single middle elevation site in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This species also is clearly part of the *A. borealis*-subgroup; it might also be the female of *A. emphysemus*.

MATERIAL EXAMINED. COSTA RICA: San José, Zurquí de Moravia, 10.05°N, 84.02°W, 1♀,

x-xii.1990, P. Hanson, Malaise trap (LACM) [LACM ENT 00614].

Phorid Species 3247 ♀

SPECIES RECOGNITION. This species is similar to *A. megalops* and species 3251 but differs by having a large patch of ventral setae on a sclerotized area of segment 6. The ovipositor is similar to that of species 3251 (see Brown, 1993, fig. 52).

DESCRIPTION.

General Characters. Body length 1.5 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus straight, with some setulae markedly longer than those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Female. Lower fronto-orbital seta absent. Upper fronto-orbital seta present. Flagellomere 1 yellow, greatly enlarged, subequal to eye height, apically flattened. Palpus small, with setae normal, thick, moderately long, pointed. Color of abdominal tergites mostly yellow, with some darker markings. Venter of abdomen yellow. Venter of segment 3 bare. Venter of abdominal segment 5 lacking dense setal combs, without sclerite. Ventromedial setae of segment 6 present, long, thick, evenly spaced, scattered. Venter of segment 6 with sclerite present. In cleared specimens, dorsal abdominal glands visible, dark. Intersegment 6-7 with dark sclerite. Ovipositor dorsally broad, anterodorsal portion broad, rounded. Anteroventral margin of ovipositor with notch. Posterodorsal apex of ovipositor pointed. In lateral view, posteroventral apex of ovipositor straight. Posteroventral apex of ovipositor pointed. Stylet with lateral barbs. Dorsal sclerite consisting of unforked, medial process.

GEOGRAPHICAL DISTRIBUTION. This species is known only from the Dominican Republic.

PHYLOGENETIC RELATIONSHIPS. This species is part of the *A. borealis*-group, although not closely related to *A. borealis*.

MATERIAL EXAMINED. DOMINICAN REPUBLIC: Pedernales, Las Abejas, 38 km NNW Cabo Rojo, 18.13°N, 71.63°W, 1♀, 15.vii.1987, J. Rawlins, R. Davidson, Malaise trap, 1250 m (CMNH) [LACM ENT 000628].

Phorid Species 3250 ♂

(Figs. 44-45)

SPECIES RECOGNITION. The males of this species are superficially similar to those of *A. antennatus* but differ by the dark brown halter and the different genitalia.

DESCRIPTION.

General Characters. Body length 1.5–2.1 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions white. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus slightly sinuate, with all setulae short, subequal to those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds with narrowest part greater than one-half basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly dark, with yellow markings (tergite 6 yellow). Venter of abdomen white. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 45). Right side of epandrium with prominent, darkly sclerotized, dorsolateral ridge (Fig. 44). Right surstylus short, rounded, lacking ventral carina. Cercus brown. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. This species has been collected at two middle elevation sites in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. These males probably belong to the *A. anfractus*-subgroup, previously known only from females. They could be males of *A. bisetus*, *A. gracilis*, *A. moraviensis*, or *A. trisetus*.

MATERIAL EXAMINED. COSTA RICA: Limon, 16 km W Guapiles, 10.15°N, 83.92°W, 1♂, iii–v.1990 [LACM ENT 000856], P. Hanson, Malaise trap, 400 m (LACM), 7 km W Bribri, 9.58°N, 82.88°W, 1♂, ix–xi.1989 [LACM ENT 000848] (LACM), San José, Zurquí de Moravia, 10.05°N, 84.02°W, 2♂, iv.1991 [LACM ENT 000845, 000858], 1♂, v.1991 [LACM ENT 000851], 4♂, vi.1991 [LACM ENT 000786, 000790, 000791, 000792], 8♂, v.1992 [LACM ENT 000833, 000834, 000835, 000839, 000840, 000841, 000843, 000852], 2♂, vi.1992 [LACM ENT 000832, 000850], 1♂, 1–15.vi.1993 [LACM ENT 000844], P. Hanson, Malaise trap, 1600 m (LACM).

Phorid Species 3252 ♂
(Figs. 14, 46–47)

SPECIES RECOGNITION. Males of this species can be separated from other *Mesophora* by the dis-

tinctly narrowed flagellomere 1 (Fig. 14) and the presence of ventral setae on segment 6.

DESCRIPTION.

General Characters. Body length 1.2–1.4 mm. Frons brown. Palpus yellow. Dorsum of thorax light brown. Pleural regions light brown. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellowish-brown. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus sinuate, with some setulae markedly longer than those of other rows. Wing vein R_s slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter brown.

Male. Frons opaque. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellow, greatly enlarged, apically flattened, apical two-thirds narrowed to one-third basal width. Palpus small, with setae normal, thick, moderately long, pointed. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly dark, with yellow markings. Venter of abdomen white to yellow. Venter of segment 6 with distinct, black setae (but few and scattered), ventral setae in a single row. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with anterior part short, straight, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 47). Right side of epandrium with faint, unsclerotized dorsolateral ridge (Fig. 46). Right surstylus short, rounded, lacking ventral carina. Number of setae on right surstylus many. Cercus brown. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. This species is known from a single middle elevation site in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. This species is a male of the *A. anfractus*-subgroup and thus possibly of the Costa Rican species *A. bisetus*, *A. gracilis*, *A. moraviensis*, or *A. trisetus*. Apparently this species and species 3253 are sister taxa, based on the following putative synapomorphies: 1) flagellomere 1 narrowed apically (Fig. 14), and 2) apicoventral setula of each tarsomere of mid leg enlarged.

MATERIAL EXAMINED. COSTA RICA: San José, Zurquí de Moravia, 10.05°N, 84.02°W, 2♂, x–xii.1990 [LACM ENT 000880, 000882], 2♂, iii.1991 [LACM ENT 000876, 000877], 2♂, iv.1991 [LACM ENT 000885, 000887], 1♂, v.1991 [LACM ENT 000878], 1♂, vii.1991 [LACM ENT 000883], 1♂, v.1992 [LACM ENT 000879], 2♂, vii.1992 [LACM ENT 000881, 000884], P. Hanson, Malaise trap, 1600 m (LACM).

Phorid Species 3253 ♂

(Figs. 48–49)

SPECIES RECOGNITION. Males of this species can be separated from the similar males of species 3253 by the enlarged palpus and absence of ventral setae on abdominal segment 6.

DESCRIPTION.

General Characters. Body length 1.3–1.4 mm. Frons yellow. Palpus yellow. Dorsum of thorax yellow. Pleural regions yellow. Scutellum of same color as dorsum of thorax. Scutellum with short anterior and long posterior seta. Legs yellow. Venter of tarsomere 2 of mid leg with row of thin setulae and thick apical setula. Hind femur yellowish-brown, with abrupt, distinctive darkening at apex. Anteroventral row of enlarged setulae on hind basitarsus sinuate, with some setulae markedly longer than those of other rows. Wing vein R_5 slender, subequal to or thinner than costa. Wing vein R_{2+3} well developed. Wing vein CuA_1 reaches wing margin. Halter yellow.

Male. Frons opaque. Lower fronto-orbital seta absent. Upper fronto-orbital seta absent. Flagellomere 1 yellowish at base, apically darker, greatly enlarged, apically flattened, apical two-thirds narrowed to one-third basal width. Palpus enlarged, with setae reduced, thin, short, stubby. Mid leg with tarsomeres all slender. Costal vein not thickened. Abdominal tergites mostly dark, with yellow markings. Venter of abdomen yellow. Venter of segment 6 bare. Venter of segment 6 without sclerite. Epandrium globular, approximately as long as high, with anterior part short, straight, with setae near cercus not markedly larger than other epandrial setae. Left side of epandrium with scattered, thin setae (Fig. 49). Right side of epandrium with prominent, darkly sclerotized, dorsolateral ridge (Fig. 48). Right surstylus short, rounded, lacking ventral carina. Number of setae on right surstylus many. Cercus yellow. Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium.

GEOGRAPHICAL DISTRIBUTION. This species is known from two middle elevation sites in Costa Rica.

PHYLOGENETIC RELATIONSHIPS. See *Apocephalus* 3252, above.

MATERIAL EXAMINED. COSTA RICA: San José, 26 km N San Isidro, 9.5°N, 83.72°W, 1♂, ii-v.1992, P. Hanson, Malaise trap, 2100 m (LACM) [LACM ENT 000875], Zurquí de Moravia, 10.05°N, 84.02°W, 1♂, iv.1991, P. Hanson, Malaise trap, 1600 m (LACM) [LACM ENT 000886].

IDENTIFICATION

**Key to Males of Neotropical Region
Mesophora Species**

- 1 Anterior face of hind femur with abrupt, distinctive darkening at apex 2
- Anterior face of hind femur evenly colored throughout (posterior face may have distinctive darkening) 17

- 2 (1) Palpus enlarged, inflated, subequal to eye height (Figs. 16–17) 3
- Palpus small, normal in appearance, shorter than eye height (Fig. 15) 7
- 3 (2) Apical two-thirds of flagellomere 1 narrowed abruptly to one-third basal width (Figs. 9, 14); flagellomere 1 yellowish at base, apically darker 4
- Flagellomere 1 broader, yellow 5
- 4 (3) Setae of cercus and proctiger of normal size, longer and thicker than short setae of epandrium (Figs. 48–49); anteroventral row of enlarged setulae on hind basitarsus sinuate (Fig. 65); left side of epandrium with scattered, thin setae (Fig. 48); number of setae on right surstylus many (Fig. 49) **Phorid species 3253**
- Setae of cercus and proctiger markedly reduced, subequal to short setae of epandrium (Brown, 1993, figs. 8, 29); anteroventral row of enlarged setulae on hind basitarsus straight; left side of epandrium with thick, ventral setae (Brown, 1993, fig. 8); number of setae on right surstylus two, or three
- *Apocephalus brevicercus* Brown
- 5 (3) Venter of segment 6 with distinct, black setae *Apocephalus prolatus* Brown
- Venter of segment 6 bare 6
- 6 (5) Right surstylus short, rounded (Fig. 36); left side of epandrium with scattered, thin setae (Fig. 37)
- *Apocephalus secundus* new species
- Right surstylus elongate (similar to Fig. 42); left side of epandrium with thick, ventral setae (Brown, 1993, fig. 14)
- *Apocephalus longistylus* Brown
- 7 (2) Halter brown 8
- Halter yellow 11
- 8 (7) Venter of segment 6 with distinct, black setae; frons brown; anteroventral row of enlarged setulae on hind basitarsus sinuate; flagellomere 1 apical two-thirds narrowed to one-third basal width (Fig. 14) **Phorid species 3252**
- Venter of segment 6 bare; frons yellow; anteroventral row of enlarged setulae on hind basitarsus straight; flagellomere 1 apical two-thirds with narrowest part greater than one-half basal width 9
- 9 (8) Upper and lower fronto-orbital seta present (similar to Fig. 1); anteroventral row of enlarged setulae on hind basitarsus with some setulae markedly longer than those of other rows (similar to Fig. 63); flagellomere 1 pyriform; cercus yellow
- *Apocephalus atavus* new species
- Upper and lower fronto-orbital seta absent (similar to Fig. 5); anteroventral row of enlarged setulae on hind basitarsus with all setulae short, subequal to those of other rows; flagellomere 1 greatly enlarged,

- apically flattened (similar to Fig. 5); cercus brown 10
- 10 (9) Epandrium globular, approximately as long as high (Figs. 44–45); pleural regions white **Phorid species 3250**
- Epandrium markedly depressed, longer than height (Brown, 1993, figs. 5, 26); pleural regions yellow or light brown ***Apocephalus insulanus* Borgmeier**
- 11 (7) Venter of segment 6 with distinct, black setae ***Apocephalus megalops* new species**
- Venter of segment 6 bare 12
- 12 (11) Epandrium with large, prominent seta near cercus (Figs. 34–35) 13
- Epandrium with setae near cercus not markedly larger than other epandrial setae 14
- 13 (12) Palpus with setae normal, thick, moderately long, pointed (similar to Fig. 5) ***Apocephalus pilatus* new species**
- Palpus with setae reduced, thin, short, stubby (Fig. 15) ***Apocephalus antennatus* Malloch**
- 14 (12) Epandrium markedly depressed (Brown, 1993, figs. 5, 26); left side of epandrium with scattered, thin setae; cercus brown ***Apocephalus insulanus* Borgmeier**
- Epandrium globular; left side of epandrium with short setae confined to posterior margin (Brown, 1993, fig. 20), or with thick, ventral setae (Fig. 41); cercus yellow 15
- 15 (14) Frons brown; dorsum of thorax dark brown; left side of epandrium with short setae confined to posterior margin ***Apocephalus adustus* Brown**
- Frons yellow; dorsum of thorax yellow; left side of epandrium with thick, ventral setae 16
- 16 (15) Right surstylus short, rounded, lacking ventral carina (Fig. 40) ***Apocephalus crassus* new species**
- Right surstylus elongate, pointed (Brown, 1993, fig. 33); ventral carina short, extended partially across surstylus ***Apocephalus angustistylus* Brown**
- 17 (1) Venter of segment 6 with distinct, black setae 18
- Venter of segment 6 bare 22
- 18 (17) Halter yellow; epandrium not band-shaped 19
- Halter brown; if lighter-colored, then epandrium short, band-shaped (Figs. 20–23) 20
- 19 (18) Flagellomere 1 pyriform; scutellum with long anterior and long posterior setae; wing vein CuA₁ attenuated, not reaching wing margin; upper and lower fronto-orbital seta present ***Apocephalus apivorus* new species**
- Flagellomere 1 greatly enlarged, apically flattened; scutellum with short anterior and long posterior seta; wing vein CuA₁ reaches wing margin; upper and lower fronto-orbital seta absent ***Apocephalus micrepelis* Brown**
- 20 (18) Flagellomere 1 pyriform (Fig. 3), brown; upper fronto-orbital seta present; ventral setae in two rows ***Apocephalus lemniscus* new species**
- Flagellomere 1 greatly enlarged, apically flattened, yellow; upper fronto-orbital seta absent; ventral setae in a single row (Fig. 70) 21
- 21 (20) Palpus small, with setae normal, thick, moderately long, pointed; right surstylus short, rounded (Fig. 20) ***Apocephalus lizanoi* new species**
- Palpus enlarged, with setae reduced, thin, short, stubby (similar to Fig. 16); right surstylus truncate, apically flared (Brown, 1993, fig. 42) ***Apocephalus curtus* Brown**
- 22 (17) Apical two-thirds of flagellomere 1 narrowed to one-third basal width (Fig. 9) 23
- Apical two-thirds of flagellomere 1 broader (similar to Fig. 5) 26
- 23 (22) Palpus brown; dorsum of thorax and pleural regions dark brown; cercus brown 24
- Palpus, dorsum of thorax, pleural regions and cercus yellow 25
- 24 (23) Frons opaque; legs, including hind femur dark brown; flagellomere 1 brown; epandrium with anterior part bulging anteriorly; number of setae on right surstylus three (see figures in Brown, 1994b) ***Apocephalus satanus* Brown**
- Frons glossy; legs, including hind femur yellowish-brown; flagellomere 1 yellowish at base, apically darker; epandrium with anterior part straight; number of setae on right surstylus one (see figures in Brown, 1994b) .. ***Apocephalus nitifrons* Brown**
- 25 (23) Palpus enlarged, with setae reduced, thin, short, stubby (similar to Fig. 16); epandrium with anterior part elongate; right side of epandrium, beside ventral setae, with numerous lateral setae; number of setae on right surstylus two (see figures in Brown, 1994b) ***Apocephalus grandiflavus* Brown**
- Palpus small, with setae normal, thick, moderately long, pointed; epandrium with anterior part short, straight; right side of epandrium, beside ventral setae, with one to three lateral setae; number of setae on right surstylus one to many ***Apocephalus truncaticercus* Brown**
- 26 (22) Mid leg with tarsomere 1 expanded; right surstylus with ventral carina present 27
- Mid leg with tarsomeres all slender; right surstylus lacking ventral carina 29

- 27 (26) Mid leg with tarsomeres 2 and 3 expanded; right surstylus with ventral carina short, extended partially across surstylus (Brown, 1993, fig. 40). *Apocephalus tritarsus* Brown
- Mid leg with tarsomeres 2 and 3 slender; right surstylus with ventral carina long, with many short side branches, or with ventral carina long, unbroken 28
- 28 (27) Halter and flagellomere 1 yellow; venter of tarsomere 1 of midleg with scattered setulae; right surstylus with ventral carina long, unbroken (Brown, 1993, fig. 37) *Apocephalus mortifer* Borgmeier
- Halter brown; flagellomere 1 yellowish at base, apically darker; venter of tarsomere 1 of midleg with setulae confined to posterior margin; right surstylus with ventral carina long, with many short side branches (Brown, 1993, fig. 36) *Apocephalus hansonii* Brown
- 29 (26) Halter yellow 30
- Halter brown 32
- 30 (29) Left side of epandrium with dense, thicker setae (Fig. 39); epandrium with setae near cercus not markedly larger than other epandrial setae *Apocephalus echinatus* new species
- Left side of epandrium with scattered, thin setae; epandrium with large, prominent seta near cercus (Figs. 42–43) 31
- 31 (30) Epandrium markedly depressed (Figs. 42–43); right surstylus elongate *Apocephalus prolixus* new species
- Epandrium globular (similar to Figs. 36–41); right surstylus short, rounded *Apocephalus antennatus* Malloch
- 32 (29) Wing vein R_{2+3} absent; anteroventral row of enlarged setulae on hind basitarsus sinuate (similar to Fig. 65); upper fronto-orbital seta present (Fig. 4); flagellomere 1 slightly enlarged, apically flattened (Fig. 4) *Apocephalus absentis* Brown
- Wing vein R_{2+3} well developed; anteroventral row of enlarged setulae on hind basitarsus straight; upper fronto-orbital seta absent; flagellomere 1 greatly enlarged, apically flattened 33
- 33 (32) Costal vein thickened between humeral crossvein and R_1 (Fig. 68); frons and palpus brown; hind femur dark brown; left side of epandrium with thick, ventral setae (Fig. 31); setae of cercus markedly reduced, subequal to short setae of epandrium (Figs. 30–31) *Apocephalus emphysemus* new species
- Costal vein not thickened; frons and palpus yellow; hind femur yellowish-brown, or white; left side of epandrium with scattered, thin setae; setae of cercus of normal size, longer and thicker than short setae of epandrium 34

- 34 (33) Flagellomere 1, pleural regions and legs yellow; epandrium markedly depressed, with large, prominent seta near cercus (Figs. 42–43); right surstylus elongate (Fig. 42); cercus yellow *Apocephalus prolixus* new species
- Flagellomere 1 yellowish at base, apically darker; pleural regions and legs white; epandrium globular, with setae near cercus not markedly larger than other epandrial setae (Figs. 32–33); right surstylus short, rounded (Fig. 32); cercus brown *Apocephalus niveus* new species

Key to Females of Neotropical Region *Mesophora* Species

(Note: the female of *A. limai* Prado, which I have not examined, is not included in this key.)

- 1 Anteroventral row of enlarged setulae on hind basitarsus straight (Fig. 63) 2
- Anteroventral row of enlarged setulae on hind basitarsus sinuate (Fig. 65) 20
- 2 (1) Lower fronto-orbital seta present (Fig. 1), in some species displaced medially (as in Fig. 10) 3
- Lower fronto-orbital seta absent (as in Fig. 12) 7
- 3 (2) Flagellomere 1 round *Apocephalus atavus* new species
- Flagellomere 1 pyriform (Figs. 1, 8) 4
- Flagellomere 1 greatly enlarged, subequal to eye height, apically flattened (Fig. 10) *Apocephalus mortifer* Borgmeier (presumably the undescribed females of *A. hansonii* and *A. tritarsus* would key here also)
- 4 (3) Hind femur evenly colored throughout; wing vein CuA_1 attenuated, not reaching wing margin; venter of segment 3 with few dark setae *Apocephalus apivorus* new species
- Hind femur with abrupt, distinctive darkening at apex; wing vein CuA_1 reaches wing margin; venter of segment 3 bare 5
- 5 (4) Anteroventral row of enlarged setulae on hind basitarsus with all setulae short, subequal to those of other rows; halter yellow 6
- Anteroventral row of enlarged setulae on hind basitarsus with setulae markedly longer than those of other rows (Fig. 64); halter brown **Phorid species 3246**
- 6 (5) Frons and dorsum of thorax yellow; in cleared specimens, dorsal abdominal glands visible, dark *Apocephalus angustistylus* Brown
- Frons and dorsum of thorax dark brown; in cleared specimens, dorsal abdominal glands invisible *Apocephalus adustus* Brown

- 7 (2) Upper fronto-orbital seta present (e.g., Fig. 12) 8
 - Upper fronto-orbital seta absent (e.g., Fig. 7) 16
 8 (7) Flagellomere 1 pyriform (similar to Figs. 8, 17) 9
 - Flagellomere 1 greatly enlarged, subequal to eye height, apically flattened (e.g., Fig. 11) 11
 9 (8) Hind femur evenly colored throughout; halter brown; dorsum of thorax light brown; palpus small 10
 - Hind femur with abrupt, distinctive darkening at apex; halter yellow; dorsum of thorax yellow; palpus elongate (Fig. 17) **Phorid species 3136**
 (= *Apocephalus* unnamed female B of Brown, 1993)
 10 (9) Venter of abdomen with large setal combs (Fig. 66); hind femur yellowish-brown; pleural regions yellow *Apocephalus curtus* Brown
 - Venter of abdomen lacking setal combs; hind femur white; pleural regions white *Apocephalus niveus* new species
 11 (8) Either venter of segment 6 with extremely short, thin setae (*A. antennatus*, *insulanus* and *longistylus*) or venter of abdomen with large setal combs (*A. lizanoi*; Fig. 67); anteroventral row of enlarged setulae on hind basitarsus with all setulae short, subequal to those of other rows 12
 - Venter of segment 6 with large setae (similar to Fig. 69); venter of abdomen without setal combs; anteroventral row of enlarged setulae on hind basitarsus with some setulae markedly longer than those of other rows (Fig. 63) 15
 12 (11) Palpus small (similar to Fig. 15) 13
 - Palpus elongate (similar to Fig. 16) *Apocephalus longistylus* Brown
 13 (12) Venter of abdomen with large setal combs (Fig. 67); venter of segment 3 with few dark setae *Apocephalus lizanoi* new species
 - Venter of abdomen lacking setal combs; venter of segment 3 bare 14
 14 (13) In cleared specimens, dorsal abdominal glands invisible; anterodorsal portion of ovipositor broad, rounded (see figures in Brown, 1993) *Apocephalus antennatus* Malloch
 - In cleared specimens, dorsal abdominal glands visible, dark; anterodorsal portion of ovipositor narrowed, elongate (see figures in Brown, 1993) *Apocephalus insulanus* Borgmeier
 15 (11) Ventral setae of segment 6 in several rows on crescent-shaped, anteriorly pointed sternite; halter yellow **Phorid species 3247**
 - Ventral setae of segment 6 in single straight row; sternite absent; halter brown **Phorid species 3223**
 16 (7) Hind femur evenly colored throughout 17
 - Hind femur with abrupt, distinctive darkening at apex. 18
 17 (16) Palpus, dorsum of thorax and pleural regions yellow; hind femur yellowish-brown *Apocephalus grandiflavus* Brown
Apocephalus truncaticercus Brown
 (females of these two species cannot be separated at this time)
 - Palpus, dorsum of thorax, hind femur and pleural regions dark brown *Apocephalus satanus* Brown
 18 (16) Segment 6 without ventral setae; anteroventral row of enlarged setulae on hind basitarsus with all setulae short, subequal to those of other rows; in cleared specimens, dorsal abdominal glands invisible; ovipositor anterodorsal portion narrowed, elongate (Brown, 1994b, fig. 5) *Apocephalus brevicercus* Brown
 - Segment 6 with ventral setae present; anteroventral row of enlarged setulae on hind basitarsus with some setulae markedly longer than those of other rows; in cleared specimens, dorsal abdominal glands visible, dark; ovipositor anterodorsal portion broad, rounded 19
 19 (18) Flagellomere 1 greatly enlarged, subequal to eye height, apically flattened; frons broad (Fig. 11) **Phorid species 3251**
 - Flagellomere pyriform; frons narrow (Fig. 6) *Apocephalus megalops* new species
 20 (1) Lower fronto-orbital seta absent; R₂₊₃ absent; hind femur evenly colored throughout; halter brown *Apocephalus absentis* Brown
 - Lower fronto-orbital seta present; R₂₊₃ present; hind femur with abrupt, distinctive darkening at apex; halter yellow **other *A. anfractus*-subgroup species**
 (see Brown, 1993)

EVOLUTION OF HOST SELECTION

To analyze the host shift in *Mesophora*, the known hosts of the various species are plotted on the cladogram of relationships (Fig. 73). Although some progress has been made in identifying hosts of the various species, there are still large gaps in our knowledge. Only 8 of the 42 named species of *Mesophora* have been reared, and most of them only once. Still, we have enough information to speculate about the observed host shift.

All outgroups to *Mesophora* are parasites of ants, including all other species of *Apocephalus*. Therefore, ants must be considered the primitive hosts of the group. The most derived clades of *Mesophora*, those of the *A. wheeleri*-subgroup, appar-

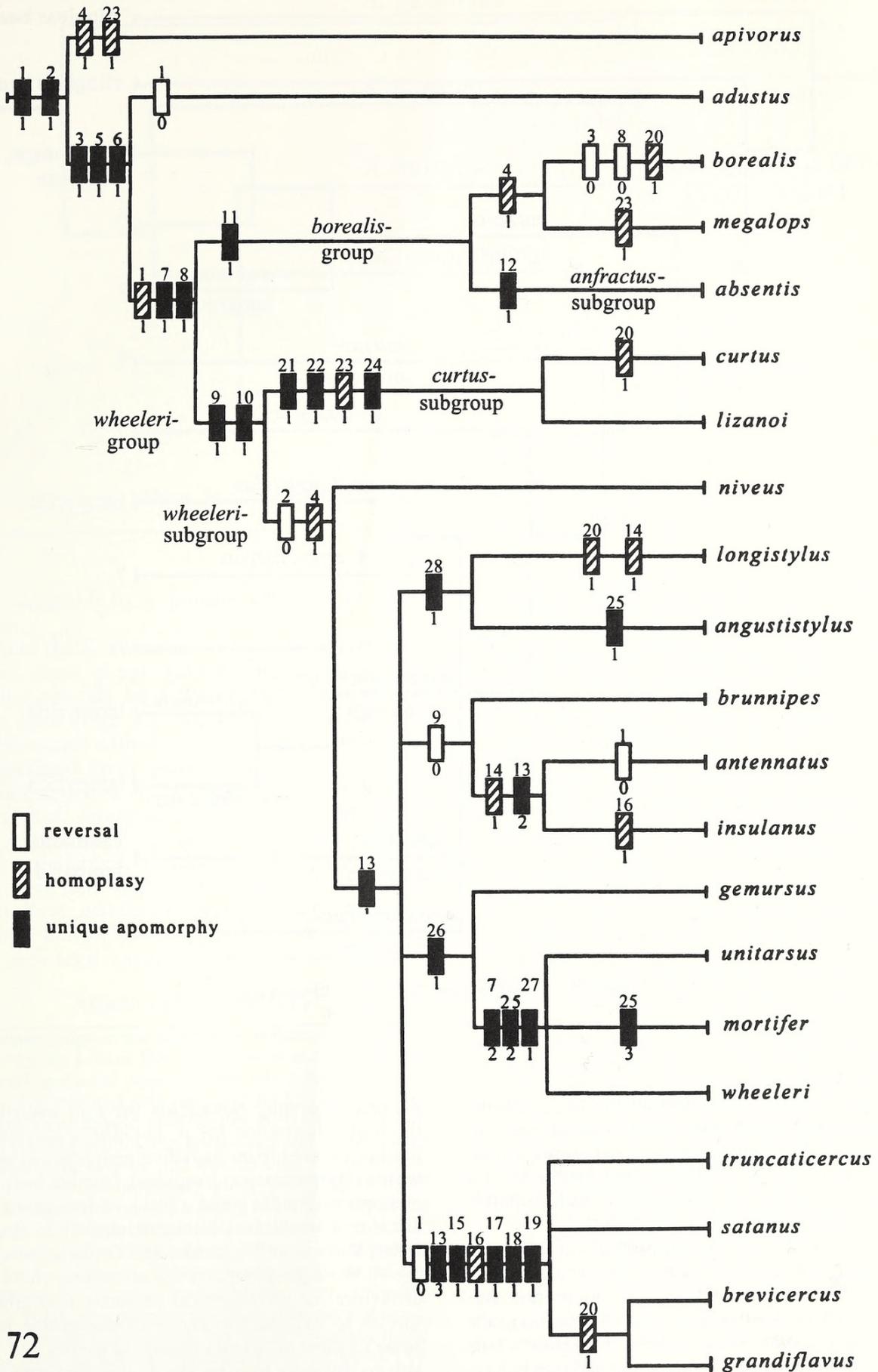


Figure 72. Preferred cladogram based on data in Table 1.

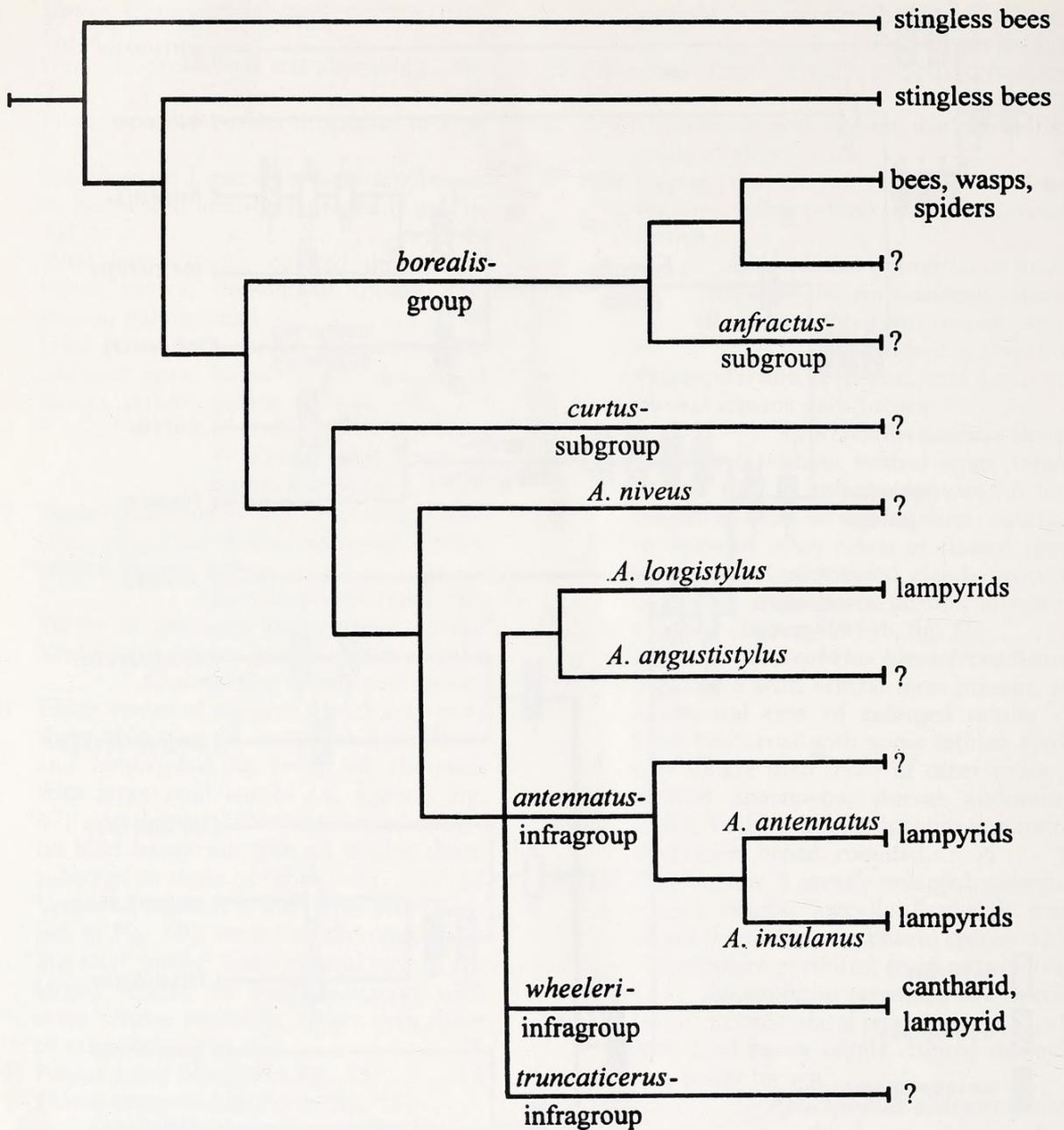


Figure 73. Hosts mapped on parasite cladogram.

ently are parasites of cantharoid beetles, including lampyrids and cantharids. Only one species, *A. mortifer*, has been reared from a cantharid, *Chauliognathus fallax*, but I also reared larvae from a different cantharid in Costa Rica; unfortunately they died soon after pupation.

Cantharoid beetles are extremely divergent hosts from ants, and the interesting question to answer is how did the flies move from ants to beetles. According to the information presented here, they first shifted from ants to stingless bees. This shift is fairly easy to understand: the physiological and behavioral adaptations necessary to shift from one social hymenopteran to another are probably relatively minor.

The next shift, from bees to beetles, is still unex-

plained. The only tantalizing piece of evidence is the host information for *A. borealis*, a species that has been reared from such divergent hosts as vespid wasps (Hymenoptera: Vespidae), bumble bees (Hymenoptera: Apidae), and a black widow spider (Araneida: Theridiidae) (Borgmeier, 1963; Brown, 1993; Disney, 1994; Ennik, 1973). Perhaps within the *A. borealis*-group, or its ancestors, there was behavioral or physiological plasticity that allowed species to expand the range of acceptable hosts. Some of these attacked cantharoid beetles and were able to diversify to form the *A. wheeleri*-subgroup.

More field work is necessary to explore this possibility and especially to find hosts of the *A. anfractus*-subgroup and the *A. curtus*-subgroup. Also, laboratory experiments to establish the range of

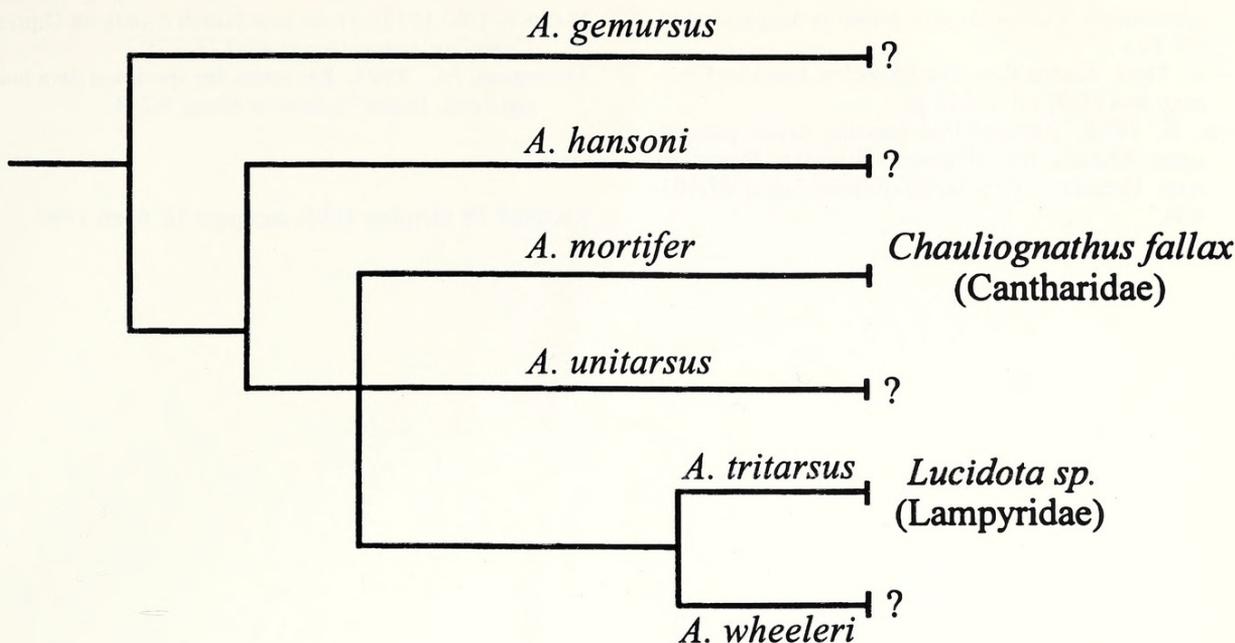


Figure 74. Host taxa mapped on cladogram of *A. wheeleri*-infracroup.

hosts acceptable to *A. borealis* would be of great interest.

Within the *A. antennatus*- and *A. wheeleri*-infracroups, there is not enough information to say whether specific host-parasite coevolution has taken place (Figs. 73–74), although such an hypothesis seems unlikely. *Apocephalus antennatus* is a generalized firefly parasite, attacking at least 5 genera throughout its extensive New World range. Although *A. insulanus* has been reared only once, from a species of *Photinus* in Peru (Brown, 1994a), it has a similarly large range and probably attacks more than one species of firefly. Less is known about the *A. wheeleri*-infracroup, and the two species with known hosts, *A. mortifer* and *A. tritarsus*, have each been reared from only a single host.

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