

THE *ASPHONDYLIA* (CECIDOMYIIDAE: DIPTERA) OF
CREOSOTE BUSH (*LARREA TRIDENTATA*) IN
NORTH AMERICA

RAYMOND J. GAGNÉ AND GWENDOLYN L. WARING

(RJG) Systematic Entomology Laboratory, PSI, Agricultural Research Service, USDA,
% U.S. National Museum NHB 168, Washington, D.C. 20560, USA; (GLW) Museum
of Northern Arizona, Rt. 4, Box 720, Flagstaff, Arizona 86001, USA.

Abstract.—Fifteen species of gall midges of the genus *Asphondylia* that form complex galls on leaves, stems, or buds of creosote bush are described. Fourteen of the species are new to science, the other is redescribed. One other species that was caught in flight and is similar to the leaf gall makers of *Larrea* is also redescribed. The *Asphondylia* spp. on creosote bush appear to be a monophyletic group and are treated as the *Asphondylia auripila* species group.

Key Words: Complex galls, Southwestern desert, gall midges

Fifteen distinct kinds of complex galls growing on leaves, stems, and buds of *Larrea tridentata* (Sessé & Mocino ex DC.) Cov. (Zygophyllaceae) were found by G. L. Waring during the course of an ecological study of this plant. Each type of gall is formed by a different species of the genus *Asphondylia*, all of them except one new to science. In this paper we describe or redescribe these gall midges and place them in context with one another and with the rest of the genus. The natural history, ecology, and natural enemies of these flies have been or will be treated separately in Waring (1987), Waring and Price (1989a, b), and Waring (in preparation).

Larrea tridentata, or creosote bush, is a dominant member of southwestern desert plant communities from Texas to California (Mabry et al. 1977, Waring 1986). It is a perennial, evergreen shrub, and one of the most drought-tolerant plants in southwestern United States. *Larrea* is restricted to the New World and is one of many taxa of plants and animals that show a disjunct distribu-

tion between the southwestern North American and South American deserts. *Larrea tridentata* is the only species of *Larrea* in North America, while four others occur in southern South America (Waring 1986).

Asphondylia is a large, cosmopolitan genus of 247 described species (Foote 1965, Gagné 1968, Gagné 1973, Gagné in press, Gagné in prep., Harris 1980, Skuhrová 1986). To date, 67 species have been described from the Nearctic Region (Gagné in prep.). Almost as many more Nearctic species are known but not yet described (Gagné 1989). Gagné (1989) listed the described and undescribed Nearctic species and their hosts and discussed *Asphondylia* in general. A thorough generic analysis of the tribe (as a supertribe) to which the genus belongs was done by Möhn (1961). The Nearctic species of *Asphondylia* have not been revised since Felt (1916), but recent studies were made of a monophyletic group of eight species that occurs on Chenopodiaceae in California (Hawkins et al. 1986).

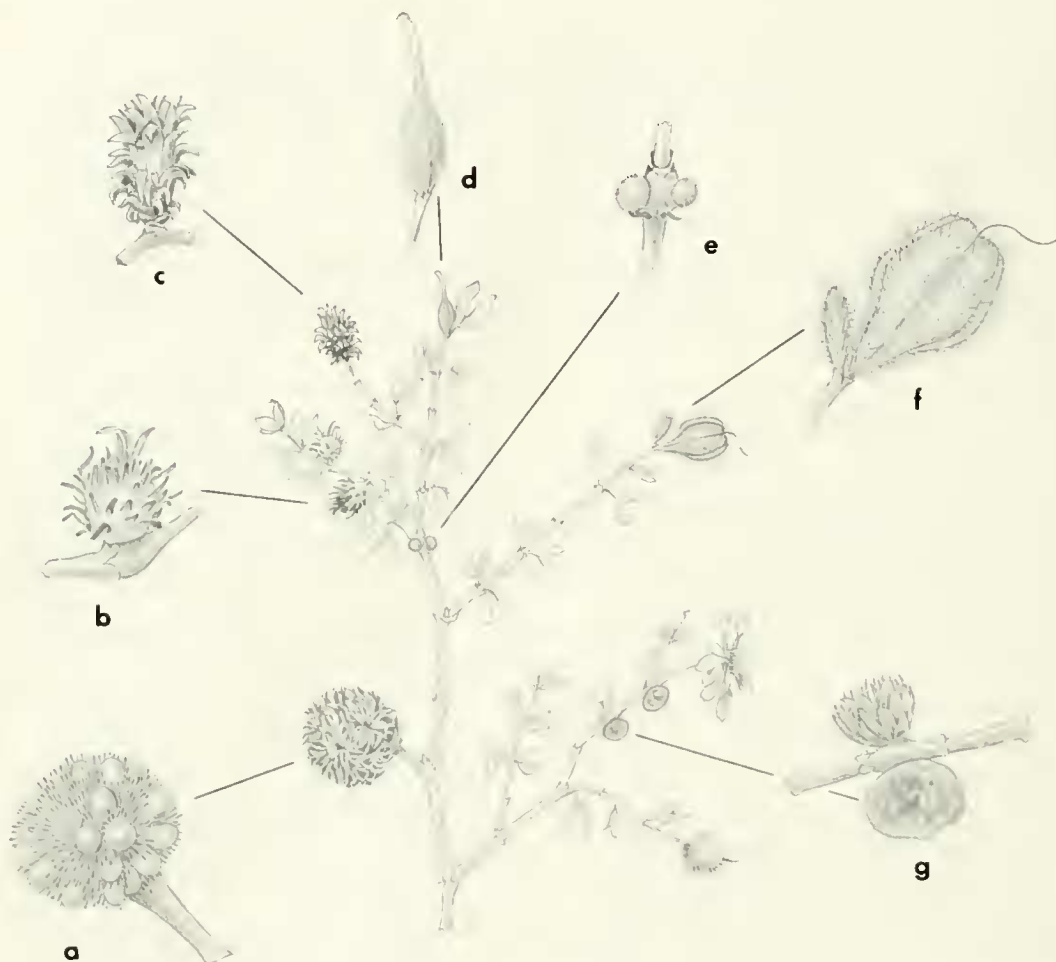


Fig. 1. Stem and bud galls of *Larrea tridentata* formed by *Asphondylia* spp. Sprig of plant in 1 \times , details of galls in 3 \times . 1a: Stem gall of *A. auripila*, the detail with outer leaves removed to show the individual cells beneath; b, stem galls of *A. foliosa*; c, stem gall of *A. rosetta*; d, apical bud gall of *A. apicata*; e, node galls of *A. bullata*; f, flower gall of *A. florea*; g, stem galls of *A. resinosa*, the resin of one of the enlarged pair removed to show detail.

and of *Asphondylia websteri* Felt, an apparent generalist known from some Fabaceae and other plants (Gagné and Wuensche 1986, Gagné and Woods 1988). In addition, one of us (RJG) made a survey for this study of certain characters on all known described Nearctic species.

Asphondylia adults are between 1–5 mm in length and are relatively robust with cylindrical antennae, large eyes, and an almost complete covering of scales. They are generally brown to dark brown, but some

species, such as *Asphondylia monacha* Osten Sacken and relatives, have black- and white-banded legs and are otherwise covered with black scales. Females have a rigid, protrusible, needlelike ovipositor (Figs. 7, 8) with which they insert their eggs into living plant tissue. Larvae are generally white to yellow, have three instars, and always occur singly, either taking up the entire gall or an individual cell in aggregate galls. The last instar is robust and has a spatula (Figs. 35–47), a hard, brown to black dermal struc-

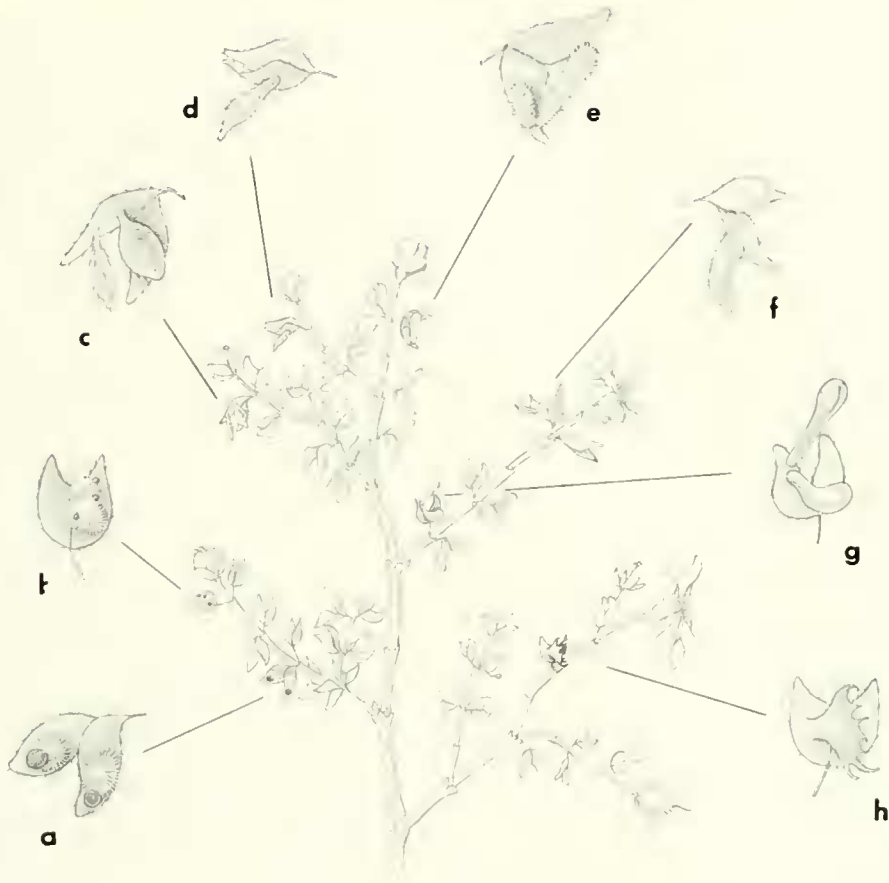


Fig. 2. Leaf galls of *Larrea tridentata* formed by *Asphondylia* spp. Sprig of plant in 1 \times , details of galls in 3 \times . 2a: Galls of *A. barbata*; b, galls of *A. villosa*; c, galls of *A. discalis*; d, gall of *A. silicula*; e, galls of *A. pilosa*; f, gall of *A. fabalis*; g, galls of *A. clavata*; h, galls of *A. digitata*.

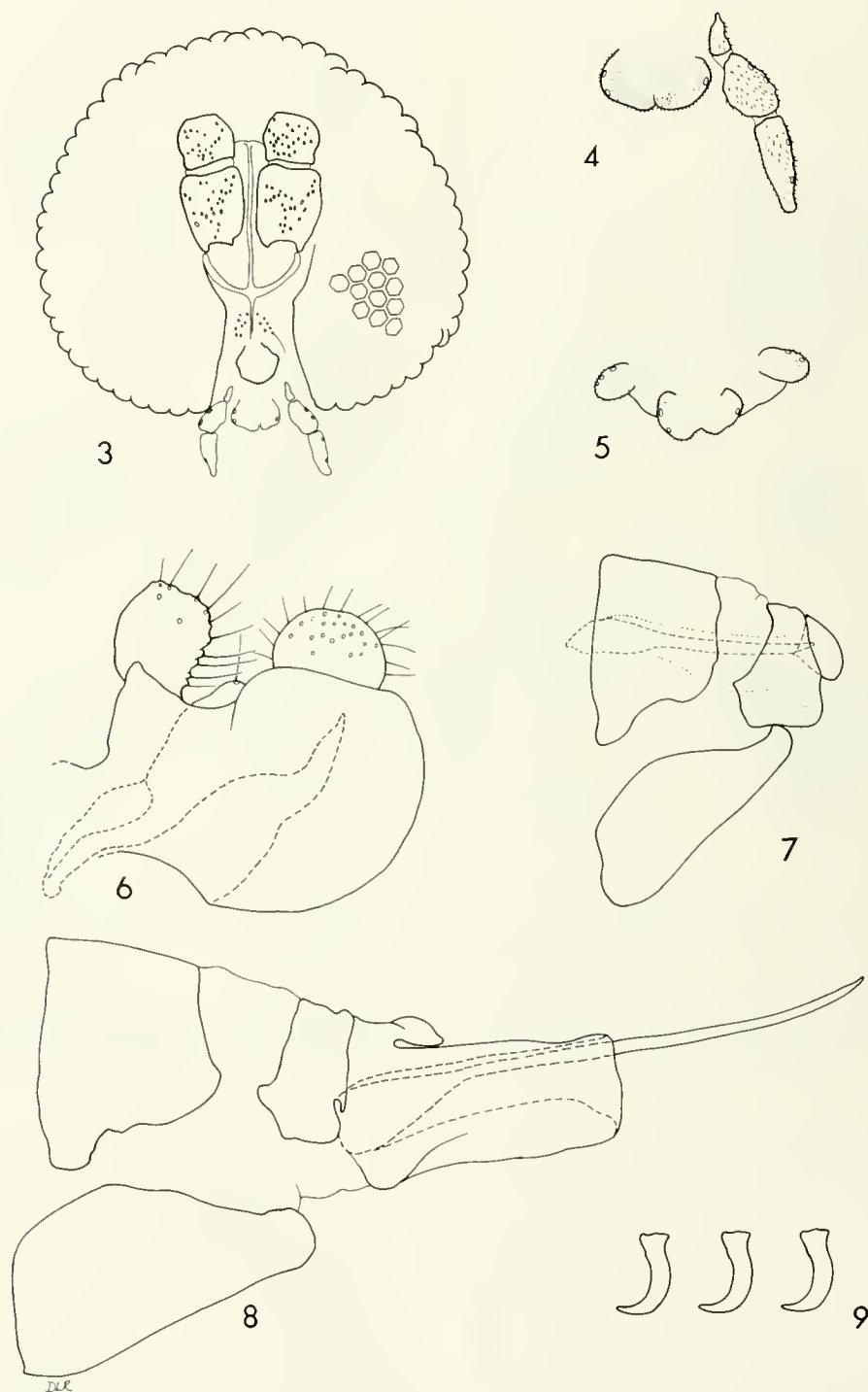
ture on the first segment of the thorax. All species in the genus pupate in the galls. The pupa is also robust, and its integument is hard and brown or black. Its head has horns of various kinds and dorsally the abdomen is covered with spines, all of which serve to effect escape from the galls.

Of the 15 species of *Asphondylia* associated here with as many different kinds of galls on *Larrea*, *Asphondylia auripila* Felt is the only one previously described. One other species, *Asphondylia brevicauda* Felt, is known from a single female without host association. That female is similar to those from six kinds of galls on creosote bush but without associated immature stages cannot

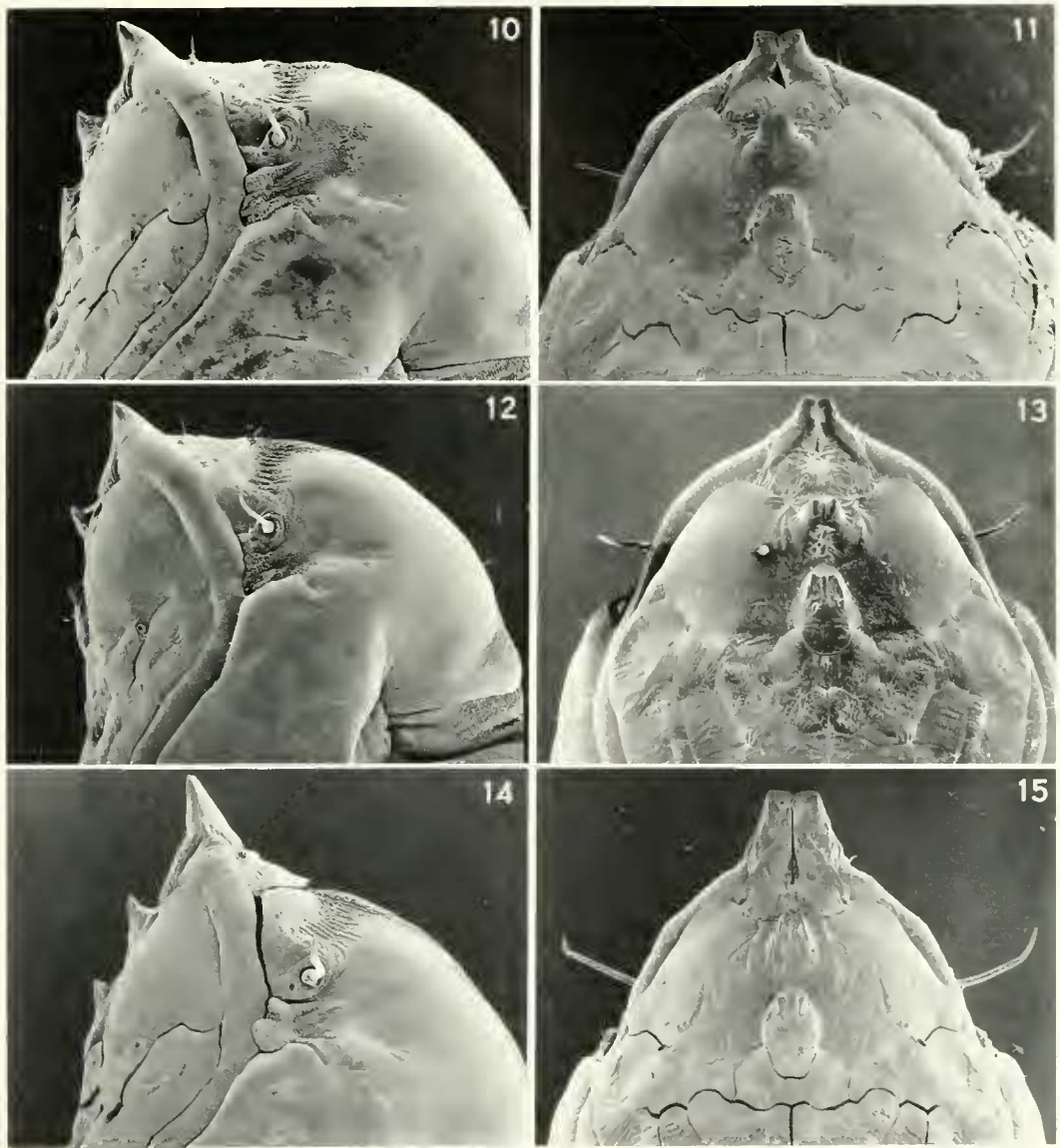
be relegated to any one of the six species. It is redescribed here as a sixteenth species but not treated further in our discussion of the *auripila* group.

MATERIALS AND METHODS

Galls were collected when fully developed and were separated by type. Some galls were cut open to obtain samples of larvae, which were preserved in 70% alcohol. The remainder of the galls were isolated in plastic bags with absorbent tissue paper in order to rear adult gall midges and parasitoids. The bags were kept at room temperature and out of direct light. After adults had emerged, they and their pupal exuviae were kept in



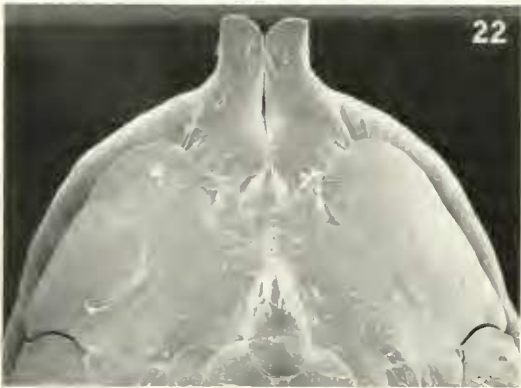
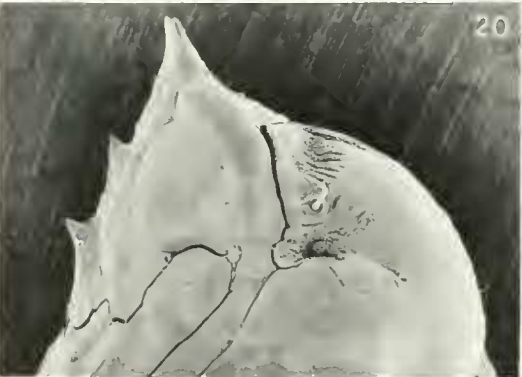
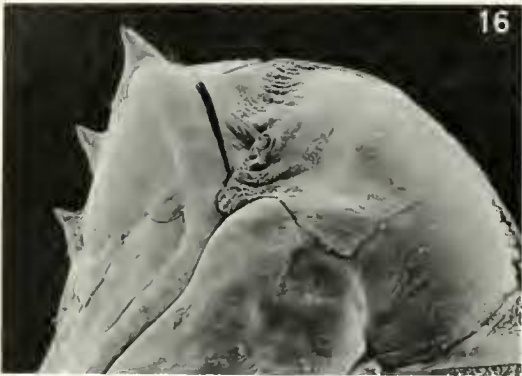
Figs. 3-9. Adult structures of *Asphondylia* spp. 3, Head of *A. clavata*, frontal view. 4, Detail of mouthparts of Fig. 3. 5, Detail of mouthparts of *A. barbata*. 6, Male genitalia of *A. resinosa*, lateral. 7, Abdominal segments 7 to end of female *A. clavata*, lateral. 8, Same, *A. resinosa*. 9, Fore, mid, and hind tarsal claws, *A. resinosa*.



Figs. 10–15. Pupal heads of *Asphondylia* spp., lateral view on left, ventral on right. 10, 11, *A. auripila*. 12, 13, *A. fohosa*. 14, 15, *A. resinosa*.

70% alcohol. Examples of the galls were kept either in alcohol or dry.
For microscopic examination, examples of larvae and adults were mounted on slides in Canada balsam according to the technique outlined in Gagné (1989). Samples of pupae were critical-point dried and placed on stubs for SEM photos. Terminology of

adult body parts follows that of McAlpine et al. (1981); larval terminology follows that in Gagné (1989).
The species from *Larrea* are described here in a fashion comparable to that of the species on *Atriplex* in Hawkins et al. (1986) and of *A. websteri* in Gagné and Wuensche (1986). We believe the *Asphondylia* spp. on



Larrea to be monophyletic, so will refer to them collectively here as the *Asphondylia auripila* group. Because so many characters are common to all the creosote bush species, a combined description of the group is made at the outset to avoid repetition in the individual descriptions that follow.

The descriptions and redescrptions of these species are in alphabetical order so they can be easily found, but the plates of figures treat the species in natural groupings. All types and other material examined are deposited in the National Museum of Natural History in Washington, D.C.

The 14 new species are given adjectival names that describe some aspect of their galls, either their shape or their position on the plant: *apicata* = apical; *barbata* = bearded or hairy; *bullata* = knobby; *clavata* = clubshaped; *digitata* = digitate; *discalis* = platelike; *fabalis* = beanshaped; *florea* = of the flower; *foliosa* = leafy; *rosetta* = rosette; *pilosa* = hairy; *resinosa* = resinous; *silicula* = podlike; *villosa* = hairy.

DESCRIPTION OF THE *ASPHONDYLIA AURIPILA* SPECIES GROUP

Adult.—*Color:* Eyes black. Face and frons yellowish. Occiput brown beneath covering of long hairs. Antenna brown. Thorax: scutum dark jade green, pruinose; scutellum brown with long setae; pleura brown; wing membrane iridescent, the veins brown; halter yellow to dusky; legs covered with white scales. Abdomen dark brown beneath the thick covering of setae and setiform scales. The setae and setiform scales covering the thorax and abdomen may be silvery (*clavata*, *pilosa*, *barbata*, and *rosetta*) or golden (*auripila* and *resinosa*) (not de-

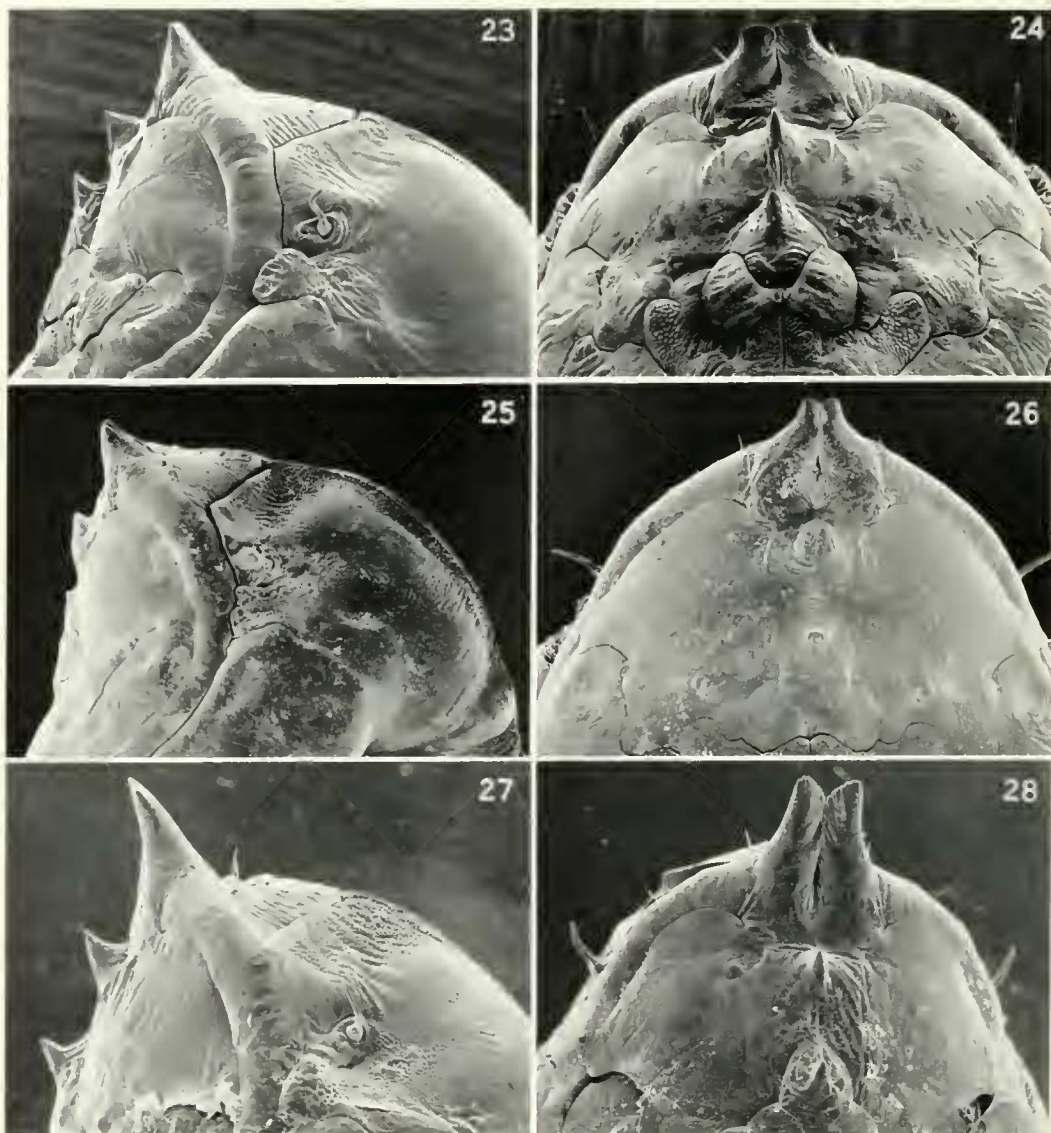
terminable in most species because most available adults were preserved in alcohol instead of dry on pins).

Head (Figs. 3–5): **Antenna:** scape broadest distally, 1.6–1.8 times length pedicel, pedicel about as wide as long; first flagellomere 2.1–2.3 times length of scape, evenly cylindrical. Eye facets close together, hexagonoid. Frons with 5–20 setae per side, variable in number within a species. Labellum reduced in size, laterally with 0–4 (usually 2–3) setae and setulose, and medially with 4–6 short, basiconic setae. Palpus 1 or 2–3 segmented: when 1 segmented, usually elongate spherical, tapering at the apex, and with 2–5 scattered setae; when 3 segmented, first segment always short and narrower than the second and with 0–3 setae, and the second and third segments sometimes fused or only partly separated, the second widest and usually shorter than the third, which tapers to a pointed end; second and third segments each with 2–10, mostly lateral setae.

Thorax: Wing length 1.5–4.7 mm. Scutum with 2 dorsocentral and 2 lateral rows of long setae mixed with setiform scales. Anepisternum with scales on dorsal half, anepimeron covered with scales. Claws (Fig. 9) of all legs and both sexes subequal in size and similar in shape, as long as empodia.

Abdomen: Male terminalia as in Fig. 6, homogeneous within the species group. Ovipositor (Figs. 7, 8) 1.0–2.7 times as long as seventh sternite.

Pupa.—Antennal horns variably shaped (Figs. 10–34). Upper frontal horn simple or bifid. Lower frontal horn simple or trifid. Prothoracic spiracle usually short, curved anteriorly, but shaped otherwise on one species. Abdominal tergites 2–8 each with,



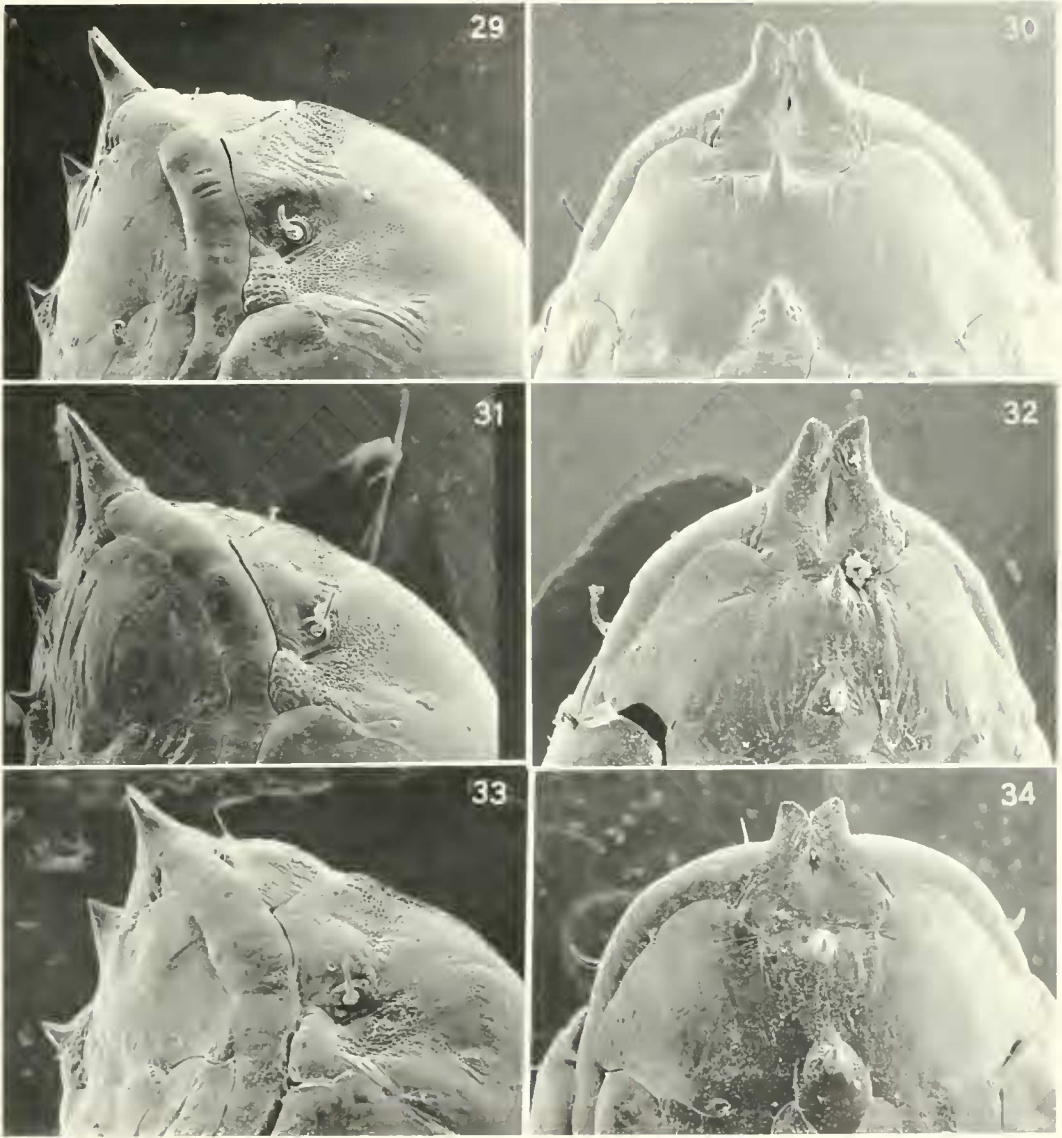
Figs. 23–28. Pupal heads of *Asphondylia* spp., lateral view on left, ventral on right. 23, 24, *A. bullata*. 25, 26, *A. pilosa*. 27, 28, *A. digitata*.

from posterior margin, a row of stout spines, a bare space, another row of stout spines followed by scattered, much smaller spines, these diminishing in size and growing sparser toward anterior margin of sclerite.

Larva.—Papillar pattern as for *Asphondylia* (Möhn 1955, 1961) but with only 2 or 3 ventral thoracic papillae instead of the primitive 6 in 2 groups of 3 each per side

and with the terminal papillae reduced to 1 pair, which are greatly reduced and usually difficult to detect. Spatula various (Figs. 35–47), some species having the large spatula with 4, subequal, anterior teeth, but most showing some reduction in area and change in shape. The area around the spatula may or may not be sclerotized and pigmented.

Remarks.—*Asphondylia clavata* and *A.*



Figs. 29–34. Pupal heads of *Asphondylia* spp., lateral view on left, ventral on right. 29, 30, *A. discalis*. 31, 32, *A. fabalis*. 33, 34, *A. silicula*.

pilosa are indistinguishable from one another, as are *A. barbata* and *A. villosa*, but each of the four forms a distinct gall. We treat these four species as distinct, presuming that the different galls are a function of differences in the larval salivary secretions that direct the shape of the galls. Those two pairs of species and the remainder of the species from each of the other kinds of galls

are distinct on the basis of some anatomical characters.

We give no key to species of the *auripila* group. There is little use in trying to sort adults caught in flight when they are so similar to other asphondylia and when so many species of the genus are still undescribed. The best way to identify these species is by their distinctive galls as drawn in Figs. 1

and 2. If a larva or pupa is associated with the gall, it would be a good idea to confirm the gall determination by comparing the larval spatula or pupal head with the figures given in this paper for the particular species.

Asphondylia apicata Gagné,
NEW SPECIES

Diagnosis.—This species forms an apical leaf bud gall (Fig. 1d). The spatula (Fig. 40) resembles slightly those of *A. florea* (Fig. 46) and *A. rosetta* (Fig. 39), but the pupal antennal horn of *apicata* (Fig. 19) is wider and more splayed than in the other two species. The ovipositor of all three species is approximately as long, somewhat elongate for the *auripila* group.

Description.—*Adult*: Wing length: male, 2.7 mm ($n = 1$); female, ? mm ($n = 1$ with teneral wings). Labellum with 1–3 setae. Palpus 3 segmented, first segment smallest with 0–1 setae, third segment longer than the second and pointed apically, each with 1–3 setae laterally. Ovipositor 2.4 times as long as seventh sternite, curved dorsally at tip.

Pupa (Figs. 18, 19): Antennal horns long, flattened dorsoventrally, broad and serrate anteriorly in frontal view. Upper and lower frontal horns simple, the lower smaller than the upper in lateral view. Prothoracic spiracles short, curved.

Last instar: Spatula (Fig. 40) with 2 rounded, anterior teeth; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (specimen on left under left cover slip on slide), from apical leaf bud gall on *Larrea tridentata*, dog track, Black Canyon City, Arizona, 2-10-88, G.

Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 2-10-88 (7 pupae, 4 larvae); Interstate Hwy 17, Carefree exit, 10 mi N Phoenix, 9-15-87 (3 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-1-80 (5 pupae), 3-1-81 to 5-1-81 (6 pupae, 7 larvae), 9-15-85 (♂, ♀, 3 larvae). CALIFORNIA: Death Valley National Monument, 2-17-69, J. Wheeler (pupa).

Asphondylia auripila Felt

Asphondylia auripila Felt 1907: 14.

Diagnosis.—This species forms a leafy stem gall that is always found in a large aggregation (Fig. 1a). Several characters are common to *auripila*, *resinosa* and *foliosa*, including the large size, the bifid upper and trifid lower frontal pupal horn, and the robust spatula with two large lateral and two much shorter medial teeth on the anterior margin. The pupa of *auripila* (Figs. 10, 11) resembles more closely that of *foliosa* with the shorter antennal horn and prothoracic spiracle, but the two differ in the width of the pupal horn.

Description.—*Adult*: Wing length: male, 4.7 mm ($n = 1$); female, 4.5–4.9 mm ($n = 4$). Labellum with 1–5 setae. Palpus 3 segmented, the first smallest with 0–1 setae, the second and third sometimes partially fused, each with 2–7 setae, mostly laterally. Ovipositor 1.4 times as long as seventh sternite ($n = 3$), curved dorsally at tip.

Pupa (Figs. 10, 11): Antennal horns short, nearly rectangular in frontal view. Upper frontal horns large but shallowly bifurcate, lower frontal horn wide, weakly trifurcate.



35



36



37



38



39



40

Prothoracic spiracles short, not recurved apically.

Last instar larva: Spatula (Fig. 38) deeply divided anteriorly with 4 pointed teeth, the 2 inner much shorter than the outer; lateral edge of anterior margin of spatula curved laterally; area surrounding spatula only weakly sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Types.—Lectotype male, here designated, emerged from globular, green gall growing at the junction of branchlets of *Larrea tridentata*, collected 1-8-1897, Tucson, Arizona, H. G. Hubbard, emerged 2-6-1897, USDA #7320, USNM Type #29221, on slide. Paralectotype, 1 male, also on slide, same data as lectotype.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 9-15-87 (2 ♂, 2 ♀, 18 pupae, 6 larvae); Saguaro National Monument, East, 20 mi E Tucson, 2-23-80 (3 pupae), 8-29-80 (♂, 2 ♀, 5 pupae, larva), 3-1-81 to 5-1-81 (4 pupae, larva), 8-23-83 (11 pupae, 13 larvae), 9-15-86 (2 ♀, 3 pupae, 9 larvae); Tucson (type series; see under type heading). CALIFORNIA: Victorville, 4-4-1918, E. Bethel, Felt notebook #a2891 (♂). MEXICO, SINALOA: Caborca, Lukeville Rd., 1-10-63 (2 larvae). TEXAS: Carlsbad Hwy, 10-6-1940, R. A. Alexander.

Asphondylia barbata Gagné, NEW SPECIES

Diagnosis.—This species and *villosa* are indistinguishable, but their galls, although showing some resemblance, are distinctly different. Both are squat leaf galls with a rugose, hairless patch at the base. That of

villosa is covered for almost its entire length with long hair (Fig. 1b), while that of *barbata* is covered for only slightly more than half its length with short hair. As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long, wide, apically serrate antennal horn, and simple, large frontal horns. The spatula has two elongate teeth but has a short shaft.

Description.—*Adult:* Wing length: female, 1.5–1.7 mm (n = 4). Labellum with 2–3 setae. Palpus with one segment bearing 3–5 setae laterally. Ovipositor 1.1 times as long as seventh sternite (n = 4).

Pupa (as in Fig. 22): Antennal horns long, flattened dorsoventrally, broad and serrate apically in frontal view. Upper and lower frontal horns simple, of approximately the same length. Prothoracic spiracles short, curved anteriorly.

Last instar larva: Spatula (as in Fig. 42) with 2 prominent, long teeth almost as long as the rest of the shaft; area surrounding spatula not modified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (on slide), from hairy leaf gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 8-31-83, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 8-15-87 (pupa); Hwy Alt. 89, 1 mi E Cottonwood, 8-15-87 (2 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-1-80 (5 pupae, 12 larvae), 9-15-82 (♀), 8-1-83 (2 ♀), 8-31-83 (3 larvae).



A. auripila species group																
Leaf Galls							Stem Galls				Bud Galls			Other Asphondylia		
clavata	pilosa	barbata	digitata	discalis	fabalis	silicula	villosa	auripila	foliosa	resinosa	apicata	bullata	florosa	rosetta	atriplicis	websteri
2	2	1	1	1	1	1	1	3	3	3	2	2	2	2	2,3	1,2,3
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	0
0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
1	1	1	1	1	1	1	1	2	2	3	3	3	3	2	3	2,3
1	1	1	1	1	1	1	1	2	2	2	1	1	1	1	1	1,2
1	1	1	1	1	1	1	1	2	2	2	1	1	1	2	2	1,2
0	0	2	2	2	2	2	1	1	1	2	2	2	2	0	0	0
0	0	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0
1	1	2	2	2	2	2	2	2	2	2	2	2	2	1	1	0
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0

1. Wing length short (1), medium (2), or long (3).*
2. Labella large with many setae and covered with setulae (0) or reduced in size, with sparse vestiture (1) or without (2).
3. Palpus with three segments (0) or one (1).
4. Ovipositor short (1), medium (2), or long (3).*
5. Upper frontal horn simple (1) or bifid (2).*
6. Lower frontal horn simple (1) or trifid (2).*
7. Spatula with only inner teeth reduced (1) or with reduced teeth and shaft (2).*
8. Area around spatula pigmented (0) or unpigmented (1).
9. Lateral papillae reduced from five pairs (0) to three pairs (1) or two (2).
10. Terminal papillae reduced from four to two pairs (0) or one pair (1).

Fig. 48. Character matrix of selected characters for the *Asphondylia auripila* species group and three other units, the *A. atriplicis* species group, *A. websteri*, and other Nearctic *Asphondylia*. Similar species are grouped together to show patterns more readily. Characters 1-4 are of the adult, 5-6 of the pupa, and 7-10 of the larva. For those characters followed by an asterisk no polarity is implied and the numbers in the matrix indicate only character states observed (1, 2, 3). For those characters without an asterisk, 0 indicates a plesiomorphic character state and 1 and 2 apomorphic character states.

Asphondylia brevicauda Felt

brevicauda Felt 1908: 295 (*Asphondylia*).

Diagnosis.—This species, known from one female caught in flight, could fit any one of several species treated as new here, viz. *barbata*, *digitata*, *discalis*, *fabalis*, *silicula*, and *villosa*. Because larvae and pupae are needed to distinguish among these species, *brevicauda* cannot be referred with certainty to any particular one of those gall makers. It would be expeditious to apply the name *brevicauda* to one of them. Then, we would not have to carry the name *brevicauda* as an available but meaningless entity. Nevertheless, it would not be scientific to apply such a name at random to a taxon to which it did not certainly belong.

Description.—*Adult*: Wing length: female, 1.9 mm ($n = 1$). Labellum with several setae (obscured on specimen). Palpus with one segment bearing several setae. Ovipositor 1.1 times as long as seventh sternite.

Male, pupa and larva: Unknown.

Holotype.—Female, Fort Yuma, Arizona, 9-4, Coll. [H. G.] Hubbard, USNM Type No. 29219, Felt #c1040, type deposited in U. S. National Museum. No additional data have been found to indicate whether this fly was reared or only caught in flight. The H. G. Hubbard notebooks in the Smithsonian Archives were searched in vain for further information under the dates of Sept. 4 and April 9 of the years Hubbard traveled to Arizona, and there is no code number 9-4 in the Hubbard card files remaining with the Systematic Entomology Laboratory.

Asphondylia bullata Gagné,

NEW SPECIES

Diagnosis.—This species forms a short, socketed stem gall (Fig. 1e). The spatula (Fig. 41) is unique in the *auripila* group because it has four teeth but lacks the surrounding sclerotization present in all the other stem gall makers. The pupa is unique for the short

distance between the frontal horns. The ovipositor is the longest in the *auripila* group.

Description.—*Adult* (female only): Wing length: female, 2.1 mm ($n = 3$). Labellum with 1–3 setae. Palpus 3-segmented, the first smallest with 0–1 setae, the second and third subequal except the second pointed apically, each segment with 3–5 setae laterally. Ovipositor 2.8 times as long as seventh sternite ($n = 3$), curved dorsally at tip.

Pupa (Figs. 23, 24): Antennal horns short, broad anteriorly. Upper and lower frontal horns simple and about as long as antennal horns; distance between frontal horns uniquely short.

Last instar larva: Spatula (Fig. 41) with 4 anterior teeth, pair of short teeth medially and large one on either side, with long and narrow shaft not surrounded by sclerotized and pigmented area. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (specimen under left coverslip on slide), from stem gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 9-31-83, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 8-30-87 (2 pupae); Diamond Creek, river mile 225, Grand Canyon National Park, 1-5-88 (pupa); Saguaro National Monument, East, 20 mi E Tucson, 3-2-80 (♀, 3 pupae), 1-15-81 (2 ♀, 4 pupae), 3-4-81 (pupa), 9-31-83 (3 larvae).

Asphondylia clavata Gagné,

NEW SPECIES

Diagnosis.—This species and *pilosa* are indistinguishable. Galls of the two species have the same general form except that that of *clavata* is smooth (Fig. 2g), while that of *pilosa* has a thick covering of hair (Fig. 2c). The two species are unique among the *auripila* group for the presence on the larva of four subequal anterior teeth on the spatula

and three pairs of lateral papillae on each thoracic segment (Fig. 35). As with all the leaf galling asphondylia on *Larrea*, their ovipositors are among the shortest of the *auripila* group. The pupal antennal horn is shortened, the upper frontal horn is still wide enough to indicate a reduction from a bifid form, and the lower frontal horn is much reduced.

Description.—*Adult*: Wing length: male, 2.3–3.1 mm ($n = 5$); female, 2.6–2.9 mm ($n = 7$). *Color*: setae and long setiform scales silvery. Labellum with 2–3 setae. Palpus with 3 segments, the first smallest with 0–2 setae, the second and third subequal in length with 2–5 setae laterally, the third tapering to pointed apex. Ovipositor 1.0 times as long as seventh sternite ($n = 6$).

Pupa (as in Figs. 25, 26): Antennal horn short and tapered to rounded apex. Upper frontal horn short, simple, and wide. Lower frontal horn short, barely serrate.

Last instar larva: Spatula (Fig. 35) with 4 anterior teeth, the inner pair slightly shorter than the outer; area surrounding spatula sclerotized and pigmented. Three ventral papillae present on each side of thoracic segments, one singlet and one pair, seta of the singlet longest.

Holotype.—Larva (one of five specimens under cover slip on slide, the specimen at lower right), from clavate gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 8-31-83, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-84 (2 ♂, 3 ♀, 10 pupae, 16 larvae) and 3-26-88 (8 pupae, 2 larvae); Hwy Alt. 89, 1 mi E Cottonwood, 8-18-86 (♀, 14 pupae, 3 larvae); Interstate Hwy 17, Carefree Exit, 10 mi N Phoenix, 8-15-87 (5 pupae) and 3-23-88 (5 pupae, 3 larvae); Saguaro National Monument, East, 20 mi E Tucson, 3-10-80 (7 pupae, 2 larvae), 8-29-80 (♀, 5 pupae, 2 larvae), 4-15-

82 (3 ♂, 4 ♀, 8-31-83 (♂, 2 ♀, 5 pupae, 18 larvae), and 8-16-84 (2 ♂, 3 ♀, 12 pupae, 3 larvae); Tucson, 4-4-59, M. Adachi (♀, pupa). CALIFORNIA: Los Angeles (no other data; galls only). BAJA CALIFORNIA: 3-4-89 (3 larvae).

Asphondylia digitata Gagné, NEW SPECIES

Diagnosis.—This species forms a digitate, bilaterally flattened gall on the under surface of the leaf (Fig. 2h). As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long antennal horn, and simple, large frontal horns. The shape of the spatula (Fig. 41) is unique for its splayed anterior margin.

Description.—*Adult* (only females available): Wing length: female, 2.1 mm ($n = 1$). Labellum with 1–2 setae. Palpus 1 segmented with 1–2 setae. Ovipositor 1.1 times as long as seventh sternite ($n = 2$).

Pupa (Figs. 27, 28): Antennal horn elongate, serrate anteromedially. Upper and lower frontal horns simple, long, pointed.

Last instar larva: Spatula (Fig. 47) deeply divided anteriorly, the resulting sections splayed, each with a pair of subequal teeth; area surrounding spatula not sclerotized or pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of two specimens under cover slip on slide, the specimen at right), from flat, digitate leaf gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 3-4-81, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: Parashant Canyon, river mile 198, Grand Canyon National Park, 3-20-1987 (2 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-10-80 (♀, 5 pupae), 8-29-80, (♀, 6 pupae), 3-1 to 5-10-81 (pupa), 3-4-81 (6 pupae, 6 larvae), and 8-15-85 (3 pupae, lar-

va). CALIFORNIA: Los Angeles (no other data; galls only).

Asphondylia discalis Gagné,
NEW SPECIES

Diagnosis.—This species forms a circular, bilaterally flattened gall on the under surface of the leaf (Fig. 2c). This species resembles *silicula* except for a longer pupal antennal horn. As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long antennal horn, and simple, large frontal horns. The spatula (Fig. 44) is blunt, occasionally slightly bifid anteriorly.

Description.—*Adult* (teneral, removed from pupa): Labellum with 2–3 setae. Palpus with one segment bearing 3–5 setae laterally. Ovipositor subequal in length to seventh sternite (teneral).

Pupa (Figs. 29, 30): Antennal horns flattened dorsoventrally, broad and serrate apically in frontal view. Upper and lower frontal horns simple, equally long. Prothoracic spiracles curved.

Last instar larva: Spatula (Fig. 45) two blunt, slightly serrate lobes anteriorly divided only slightly, or not at all to resemble *silicula*; area surrounding spatula unmodified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of three specimens under cover slip on slide, the specimen at right), from platelike leaf gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 3-4-81, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-87 (3 pupae); Interstate Hwy 17, Carefree Exit, 10 mi N Phoenix, 8-15-87 (3 pupae); Saguaro National Monument, East, 20 mi E Tucson, 2-23-80 (2 pupae), 8-29-80 (2 pupae), 3-1-81 to 5-1-81 (6 pupae, 6 larvae), 3-13-87 (♂, ♀, 5 pupae, 2 larvae).

Asphondylia fabalis Gagné,
NEW SPECIES

Diagnosis.—This species forms a bean-shaped gall on the under surface of the leaf (Fig. 2f). As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long antennal horn, and simple frontal horns. The spatula (Fig. 43) has a short shaft and two large, widely separated anterior teeth.

Description.—*Adult*: Wing length: male, 1.6–1.7 mm (n = 2); female, 1.6–1.8 mm (n = 3). Labellum with 2–3 setae. Palpus with one segment bearing 3–5 setae laterally. Ovipositor 1.0 times as long as seventh sternite (n = 3).

Pupa (Figs. 31, 32): Antennal horn long, broad and serrate anteromedially. Upper and lower frontal horns simple, the lower smaller. Prothoracic spiracles short, curved anteriorly.

Last instar larva: Spatula (Fig. 43) with 2 prominent teeth spread far apart and 2 tiny, inner teeth; area surrounding spatula unmodified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (leftmost of three specimens under left cover slip on slide), from stem gall on *Larrea tridentata*, dog track, Black Canyon City, Arizona, 9-15-87, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-87 (6 pupae, 8 larvae); Hwy Alt. 89, 1 mi E Cottonwood, 4-15-84 (2 pupae, 2 larvae); Parashant Canyon, river mile 198, Grand Canyon National Park, 10-1-86 (2 ♂, 3 ♀, 7 pupae, larvae); Saguaro National Monument, East, 20 mi E Tucson, 3-1-80 (4 pupae, larva).

Asphondylia florea Gagné,
NEW SPECIES

Diagnosis.—This species forms a cylindrical to pear-shaped flower gall (Fig. 1f).

The spatula (Fig. 46) shows a resemblance to that of *apicata* and *rosetta*, but both the anterior teeth and the entire spatula are longer in *florea*. The pupal antennal horn (Fig. 21) narrows anteriorly, as does that of *rosetta*, but that of *florea* is longer and is wider anteriorly. The ovipositor in all three species is approximately as long, somewhat elongate for the *auripila* group.

Description.—*Adult*: Wing length: male, 2.6–2.8 mm ($n = 4$); female, 2.5–2.7 mm ($n = 4$). Labellum with 1–2 setae. Palpus 3 segmented, the first segment with 0 setae, the second and third subequal in length, each with 1–3 setae laterally. Ovipositor 2.1 times as long as seventh sternite ($n = 4$).

Pupa (Figs. 20, 21): Antennal horns long, flattened dorsoventrally, broad and serrate apically in frontal view. Upper and lower frontal horns simple, equally long. Prothoracic spiracles normal, curved anteriorly.

Last instar larva: Spatula (Fig. 46) with 2 prominent, rounded teeth, and slight projection between; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (on slide), from flower gall on *Larrea tridentata*, Parashant Canyon, river mile 198, Grand Canyon National Park, Arizona, 5-15-88, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-87 (24 pupae, 3 larvae); Parashant Canyon, river mile 198, Grand Canyon National Park, 5-15-88 (4 ♂, 4 ♀, 6 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-4-81 (2 pupae), 4-10-84 (♂, 2 pupae); Tucson, 4-4-59, M. Adachi (pupa).

Asphondylia foliosa Gagné, NEW SPECIES

Diagnosis.—This species forms a short, leafy stem gall (Fig. 1b). Such galls are never

found in aggregate as are those of *auripila*. This species has several characters in common with *auripila* and *resinosa*, including the large size, the bifid upper frontal pupal horn and trifid lower, and the robust spatula with two large lateral and two much shorter medial teeth on the anterior margin. This species differs from the other two in the apically narrowed antennal horn.

Description.—*Adult*: Wing length: male, 3.2–3.5 mm ($n = 4$); female, 3.4–3.7 mm ($n = 4$). Labellum with 1–2 setae. Palpus usually 3-segmented, the first smallest with 0–2 setae, the second and third sometimes not completely separated, each with 5–10 setae, mainly laterally. Ovipositor 1.4 times as long as seventh sternite ($n = 2$), curved dorsally at tip.

Pupa (Figs. 12, 13): Antennal horns short, rounded in frontal view. Upper frontal horns bifurcate, lower frontal horn shorter but trifurcate, the middle projection shorter than the laterals. Spiracular horn short, curved anteriorly.

Last instar larva: Spatula (Fig. 37) deeply divided anteriorly with 4 pointed teeth, the 2 inner much shorter than the 2 outer; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of six specimens under cover slip on slide, the specimen in middle of upper row), from solitary, foliaceous stem gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 8-23-1983, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 9-15-87 (larva); Interstate Hwy 17, Carefree Exit, 10 mi N Phoenix, 9-15-87 (larva); Parashant Canyon, river mile 198, Grand Canyon National Park, 8-20-1984, (3 larvae); Saguaro National Monument, East, 20 mi E Tucson, 8-11-80 (3 pupae), 8-23-83 (11 pupae, 8

larvae), 8-18-86 (4 ♂, 6 ♀, 4 pupae, 14 larvae).

Asphondylia pilosa Gagné,
NEW SPECIES

Diagnosis.—This species and *clavata* are indistinguishable. Galls of the two species have the same general form except that that of *pilosa* has a thick covering of hair (Fig. 2e), while that of *clavata* is smooth (Fig. 2g). The two species are unique among the *auripila* group for the presence on the larva of four subequal anterior teeth on the spatula and three pairs of lateral papillae on each thoracic segment (Fig. 35). As with all the leaf galling asphondyliids on *Larrea*, their ovipositors are among the shortest of the *auripila* group. The pupal antennal horn is shortened, the upper frontal horn is still wide enough to indicate a reduction from a bifid form, and the lower frontal horn is reduced.

Description.—*Adult*: Wing length: male, 2.6–3.0 mm ($n = 5$); female, 2.5–2.9 ($n = 5$). Labellum with 0–2 setae. Palpus with 3 segments, the first smallest with 0–2 setae, the second and third subequal in length with 2–5 setae laterally, the third tapering to the pointed apex. Ovipositor 1.0 times as long as seventh sternite ($n = 3$).

Pupa (Figs. 25, 26): Antennal horn short and tapered to rounded apex. Upper frontal horn short, simple, and wide. Lower frontal horn short, barely serrate.

Last instar larva: Spatula (as in Fig. 35) with 4 anterior teeth, the inner pair slightly shorter than the outer; area surrounding spatula sclerotized and pigmented. Three ventral papillae present on each side of thoracic segments, one singlet and one pair, the seta of the singlet longest.

Holotype.—Larva (one of two specimens under cover slip on slide, the specimen at right), from clavate, pilose gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 3-2-80, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified,

collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 4-15-84 (7 ♂, 10 ♀, pupa, 7 larvae) and 8-15-85 (6 pupae, 1 larva); Parashant Canyon, river mile 198, Grand Canyon National Park, 4-3-1983 (3 pupae); Interstate Hwy 17, Carefree Exit, 10 mi N Phoenix, 8-15-87 (12 pupae); Saguaro National Monument, East, 20 mi E Tucson, 3-2-80 (3 pupae, 3 larvae), 8-29-80 (3 pupae, 3 larvae), 3-4-81 (3 larvae), and 8-31-83 (2 pupae, 2 larvae). BAJA CALIFORNIA: 3-4-89 (3 larvae).

Asphondylia resinosa Gagné,
NEW SPECIES

Diagnosis.—This species forms a short, leafy stem gall that is completely covered with hard, brown resin (Fig. 1g). This gall midge has several characters in common with *auripila* and *foliosa*, including the large size, the bifid upper frontal and trifid lower pupal horn, and the robust spatula with two large lateral and two much shorter medial teeth on the anterior margin. This is the largest species of the *auripila* group and differs from the two similar species in the elongate prothoracic spiracle that is abruptly bent anteriorly near the apex and in the shape of the spatula, which is rounded rather than angled laterally.

Description.—*Adult*: Wing length: male, 4.7 mm ($n = 1$); female, 4.5–4.9 mm ($n = 7$). Labellum with 0–1 setae. Palpus 3 segmented, the first small with 0–1 setae, the second and third subequal except the second pointed apically, each segment with 2–6 setae laterally. Ovipositor 1.7 times as long as seventh sternite ($n = 3$), curved dorsally at tip.

Pupa (Figs. 14, 15): Antennal horns long, nearly rectangular in frontal view. Upper frontal horns bifurcate, lower frontal horn short, trifurcate, middle projection longer than the lateral projections. Prothoracic spiracles long, curved anteriorly at apex.

Last instar larva: Spatula (Fig. 36) deeply divided anteriorly with 4 pointed teeth, the 2 inner much shorter than the outer; lateral edge of anterior margin of spatula curved

medially to join shaft; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of four specimens under cover slip on slide, the specimen at lower right), from solitary, foliaceous but resinous stem gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 12-4-1981, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 1-15-87 (19 pupae); Parashant Canyon, river mile 198, Grand Canyon National Park, 2-10-88 (♂, 4 ♀); Saguaro National Monument, East, 20 mi E Tucson, 2-25-80 (♂, 2 ♀, 2 pupae), 1-15-81 (4 pupae, 3 larvae); 1-15-83 (1 ♂, 6 ♀), 1-10-87 (♂, ♀, 18 pupae, 34 larvae); Tucson, 12-4-81, R. J. Gagné (4 larvae). TEXAS: El Paso, 3-23-51, J. A. Baker (pupa). MEXICO: Jalisco, 67-8948 (galls only).

Asphondylia rosetta Gagné,

NEW SPECIES

Diagnosis.—This species forms an elongate rosette gall on the stems (Fig. 1c). The spatula (Fig. 39) shows a resemblance to that of *A. apicata* and *A. florea*, but the pupal antennal horn is shorter and narrower than that of the other two species. The ovipositor of all three species is approximately of equal length, somewhat elongate for the *auripila* group.

Description.—*Adult*: Wing length: male, 3.0–3.1 mm ($n = 2$); female, 2.6–3.1 mm ($n = 5$). Labellum with 1–3 setae. Palpus 3 segmented, first smallest with 0–1 setae, the second and third subequal except the second pointed apically, each segment with 3–5 setae laterally. Ovipositor 2.3 times longer than seventh sternite ($n = 5$), curved dorsally at tip.

Pupa (Figs. 16, 17): Antennal horns short, the apex broad in frontal view. Upper and

lower frontal horns simple and long, about as long as antennal horns. Prothoracic spiracles short.

Last instar larva: Spatula (Fig. 39) with 2 rounded anterior teeth; area surrounding spatula sclerotized and pigmented. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of six specimens under cover slip on slide, the specimen at lower left), from elongate rosette gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 8-31-83, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 9-15-87 (15 pupae, 7 larvae); Parashant Canyon, river mile 198, Grand Canyon National Park, 10-5-86 (3 ♂, 4 ♀, 33 pupae, 9 larvae); Saguaro National Monument, East, 20 mi E Tucson, 2-23-80 (2 pupae), 8-29-80 (♀, pupa, larva), 8-31-83 (20 pupae, 12 larvae), 9-15-84 (4 ♀, 4 pupae, 17 larvae), 4-15-87 (2 pupae). CALIFORNIA: Los Angeles (galls only).

Asphondylia silicula Gagné,

NEW SPECIES

Diagnosis.—This species forms a podlike, elongate, bilaterally flattened gall on the under surface of the leaf (Fig. 2d). The gall midge is similar to *fabalis*, except for a shorter pupal antennal horn. As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, short antennal horn, and simple, large frontal horns. The spatula (Fig. 41) is blunt and slightly serrate anteriorly.

Description.—*Adult*: Wing length: male, 1.7 mm ($n = 1$); female, 1.6 mm ($n = 1$). Labellum with 3–5 setae. Palpus with one segment bearing 4–5 setae laterally. Ovipositor 1.0 times as long as seventh sternite ($n = 3$).

Pupa (Figs. 33, 34): Antennal horn long, broad and serrate anteromedially. Upper

and lower frontal horns simple, the lower smaller. Prothoracic spiracles short, curved anteriorly.

Last instar larva: Spatula (Fig. 44) with only indistinct serrations anteriorly; area surrounding spatula unmodified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (one of six specimens under cover slip on slide, the specimen at lower right), from podlike leaf gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 3-4-81, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 3-15-87 (10 pupae, 2 larvae); Saguaro National Monument, East, 20 mi E Tucson, 3-1-80 (♀, 12 pupae), 3-1-81 (9 pupae, 8 larvae), 9-15-84 (3 pupae, 2 larvae), 3-15-87 (♂).

Asphondylia villosa Gagné,

NEW SPECIES

Diagnosis.—This species and *barbata* are indistinguishable, but their galls are distinctly different. Both are squat leaf galls with a rugose, hairless patch at the base. That of *villosa* is covered for almost its entire length with long hair (Fig. 1b), while that of *barbata* is covered for only slightly more than half its length with short hair. As with all the leaf gall makers this species has a short ovipositor. It has a one-segmented palpus, long, wide, apically serrate antennal horn, and simple, large frontal horns. The spatula has two elongate teeth but is otherwise short.

Description.—*Adult:* Wing length: male, 1.6 (n = 1); female, 1.7–2.1 mm (n = 4). Labellum with 2–3 setae. Palpus with one segment bearing 3–5 setae laterally. Ovipositor 1.1 times as long as seventh sternite (n = 2).

Pupa (as in Fig. 22): Antennal horns long, flattened dorsoventrally, broad and serrate

apically in frontal view. Upper and lower frontal horns simple, of approximately same length. Prothoracic spiracles short, curved anteriorly.

Last instar larva: Spatula (Fig. 42) with 2 prominent, long teeth almost as long as shaft; area surrounding spatula not modified. Two ventral papillae present on each side of thorax, setae subequal in length.

Holotype.—Larva (on slide), from hairy leaf gall on *Larrea tridentata*, Saguaro National Monument, East, 20 mi E Tucson, Arizona, 9-10-84, G. Waring, deposited in National Museum of Natural History.

Other material examined (all from *Larrea tridentata* and, unless otherwise specified, collected by G. Waring).—ARIZONA: dog track, Black Canyon City, 8-15-87 (♂, 2 ♀, 11 pupae, 6 larvae); Hwy Alt. 89, 1 mi E Cottonwood, 9-1-86 (2 ♂, 2 ♀, 2 pupae); Saguaro National Monument, East, 20 mi E Tucson, 9-10-84 (pupa, larva).

DISCUSSION

More than 126 presumptive species of *Asphondylia* are known for the Nearctic Region and only 67 of them have been described, exclusive of this paper. Further, many of them are known only from adults, which are fairly homogenous in *Asphondylia*. The Nearctic species have not been revised since Felt (1916), when there were many fewer known. Nonetheless, because of recent studies of the *atriplicis* group (eight species that occur on Chenopodiaceae in California (Hawkins et al. 1986)), *A. websteri* (Gagné and Wuensche 1986), and an unpublished survey of certain characters on available stages of all known described Nearctic species, we are able to place the creosote bush species in context with the rest of *Asphondylia*.

The character matrix of Fig. 48 shows how the *auripila* group differs from other *Asphondylia* and how the species group can be further divided. The species on creosote bush share only one character state, the small adult labella with six or fewer setae and few,

scattered setulae on each (character 2). All creosote bush species have the larval lateral papillae reduced to two or three pairs (character 9), but the *atriplicis* group and *websteri* also have three pairs. Another character state, the single pair of terminal papillae (character 10), is shared by the *auripila* and *atriplicis* groups. Because these attributes result from losses, they could have evolved separately, so we are reluctant to propose a close relationship among the *auripila* and *atriplicis* groups and *websteri*. This is a common problem in determining relationships among species of *Cecidomyiidae* (Jones et al. 1983), but also among genera that share character states more indicative of life habits than of kinship (Sylvén 1975). Admittedly, the reductions within the *auripila* group could also have evolved independently more than once.

The *auripila* group sorts into three subgroups that fit well with their habits. These groups are the leaf, stem, and bud gall makers. The leaf gall makers of *Larrea*, namely *clavata*, *pilosa*, *digitata*, *discalis*, *fabalis*, *silicula*, *barbata*, and *villosa*, have in common the shortest ovipositor known in *Asphondylia*, the shaft being only about as long as the seventh sternite (character 4). The last six of these species share several losses or reductions, so differ somewhat from *clavata* and *pilosa*. The six are smaller (wing length 1.5–2.0 mm) than the medium-sized (2.1–3.1) *clavata* and *pilosa* (character 1), they have one- instead of three-segmented palpi (character 3), the larval spatula is greatly reduced in size and sclerotization (characters 7, 8), and they have lost a pair of lateral larval setae (character 9). The reduction of the adult palpus from three segments to one is unique within the *auripila* group, but the reduced larval spatula is also found in the bud gall makers. The loss of a lateral seta on each side of the spatula is shared by all the bud and stem gall makers.

The stem gall makers, *auripila*, *resinosa*, and *foliosa*, are large (wing length 3.2–4.9 mm) and females have a moderately long

ovipositor, 1.4–1.7 times as long as the seventh sternite. Its three unique character states are the reduced medial lobes of the spatula (character 7) and the bifid upper (character 5) and trifid lower pupal frontal horns (character 6).

The bud gall makers, *apicata*, *bullata*, *floreana*, and *rosetta*, are medium sized (wing length 2.1–3.1 mm), have the longest ovipositors of the *auripila* group (2.1–2.8 times as long as the seventh sternite), simple pupal frontal horns, and reduced spatulas and number of lateral papillae. The three last characters are common also to the leaf gall makers. As with the group of tiny leaf gall makers, *bullata* has lost the sclerotization surrounding the spatula (character 8).

Although our level of confidence that the *auripila* group is monophyletic could be greater, the evidence indicates that these species are the descendant of one founder species, which subsequently diverged onto the leaves, stems, and buds of *Larrea* before speciating further. We look forward to learning whether any *Asphondylia* spp. occur on other *larreas* in South America. If any do, they should shed light on the age and distribution not only of the *Asphondylia auripila* species group but also of its host.

ACKNOWLEDGMENTS

We are grateful to the following people for their help in the production of this manuscript: Deborah Leather Roney for the pencil and line drawings; Nit Malikul for taking the SEM photos; and Amnon Friedberg, Hans Roskam, and Norman Woodley for reviewing drafts of the manuscript.

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