6 October 2003
PROC. ENTOMOL. SOC. WASH.
105(4), 2003, pp. 995–1033

A KEY TO THE PUPARIA OF 27 SPECIES OF NORTH AMERICAN *PROTOCALLIPHORA* HOUGH (DIPTERA: CALLIPHORIDAE) FROM BIRD NESTS AND TWO NEW PUPARIAL DESCRIPTIONS

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Abstract.—Keys are provided to the puparia of 27 species of North American *Protocalliphora* Hough (Diptera: Calliphoridae) (bird nest blow flies) for which puparia are known. Previously undescribed puparia are described for two species, *P. brunneisquama* Sabrosky, Bennett, and Whitworth and *P. hesperia* Shannon and Dobroscky, and the 25 remaining species are redescribed. Hosts, distribution, and habits are discussed for each. A table of bird hosts and associated bird blow fly parasite species is included.

Key Words: bird blow flies, bird hosts, bird parasites, Calliphoridae, keys, Diptera, North America, *Protocalliphora,* puparia

Species of the genus *Protocalliphora* Hough are obligate blood-sucking parasites of nestling birds. They are rarely collected using conventional insect collecting techniques, most are found only in bird nests. The taxonomy of this genus in North America was poorly understood until Sabrosky et al. (1989) redescribed the 11 known species and described 15 new species. Their work also included a detailed review of previous taxonomic and biological studies on *Protocalliphora.*

Bennett and Whitworth, co-authors with Sabrosky, subsequently published three articles which elaborated further on the life history, ecological relationships, and pathogenicity of *Protocalliphora* (Bennett and Whitworth 1991, 1992; Whitworth and Bennett 1992). Whitworth (2002, 2003) recently described three new species of *Protocalliphora,* bringing the total number of species known in North America to 29.

Sabrosky et al. (1989) also provided several keys, the most useful being based on reared material with matched males, females, and puparia. The key to single males is usually reliable for specimens in good condition, but the key to single females is reliable for only about 10 species. Keys to third instar larvae were provided for 16 species and to puparia for 22 species. Third instar larvae are not included in the present study, because, when larvae are available, they should be allowed to pupate and adults emerge. This provides both adults and puparia for identification. Some species are best identified by puparia, while others have distinctive adults. Nests collected more than 10 days or so after young fledge have only empty puparia and this is the form of *Protocalliphora* most frequently collected.

Bennett (1957) conducted pioneering research on the identification of *Protocalliphora* puparia. He identified numerous puparial features, which could be used to separate species, and developed techniques to prepare puparia for identification. His efforts were included in Sabrosky et al. (1989), but there was little opportunity to test his keys prior to publication. Subsequently, I have encoun-

tered a variety of problems with them. Although photos of each species were provided, many were of poor quality and of little value in support of the key. No other illustrations for immatures were included and, without them, interpretation of some of the terminology is confusing. The puparial key relies heavily on the length of prothoracic fringe spines, as measured in larvae. But this character is useless for puparia since the prothoracic region is inverted during pupation making the measurement of individual spines impossible. For this character to be used, third instar larvae would also be needed. Bennett's puparial key is fairly effective for specimens of the 10 or so species, which occur in southeastern Canada where his Ph.D. studies were conducted but I found the characters variable and unreliable for the same species in other areas. Descriptions of puparia for 13 species were based on specimens collected from only one geographic area and the 9 remaining puparial descriptions were based on specimens from only 2 or 3 areas. For many species, puparia were simply not available from other areas at the time keys were developed. When I began the current study, Bennett was deceased, thus making problems encountered in the keys more difficult to resolve. One complication was that Bennett did not clearly identify specimens of puparia used to write descriptions, so it was difficult to verify features. Ultimately, I obtained about 200 of his slides from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. and about 100 slides from the Memorial University of Newfoundland. Most slides contained only fragmentary data, many were identified by species names that were never used and no synonymy was ever provided. Fortunately, I was able to reconstruct data for most of his slides and integrate his material with mine for this study. I determined his measurements and descriptions were accurate based on the material he had, thus I have let his puparial descriptions stand. Because *Protocalliphora* are readily collected as empty puparia, and the available puparial key is unreliable, the current study was initiated to develop a more effective key to the puparia of North American *Protocalliphora.*

Materials and Methods

When I began studying this genus, I personally collected bird nests in Utah, Idaho, and Wyoming (Whitworth, 1977). Some were easily found, like the colonial nests of most swallow species, and the conspicuous nests of magpies and robins. For birds with nests that were difficult to locate, I enlisted the help of ornithologists who where studying birds such as raptors, chickadees, small sparrows, warblers, and vireos. More recently, I have been able to acquire many nests from nest boxes via Internet contacts with birders who send me nests once nestlings fledge. Most contributors were contacted with the help of the Cornell Birdhouse Network, which made it possible to obtain nests from throughout North America.

Nests were examined, puparia removed and counted, and if still viable, adults were reared. Unemerged puparia were either viable, parasitized or rarely dead. Dead puparia were lighter weight, adults emerged from viable puparia within about 10 days, while in parasitized puparia, wasps emerged from days to months later. Puparia were sometimes loosely scattered through nests (*P. braueri* (Hendel)), some were wrapped in dirt or hair cocoons (*P. sialia* Shannon and Dobroscky and *P. parorum* Sabrosky, Bennett, and Whitworth) or buried in dried mud (*P. hirundo* Shannon and Dobroscky). If viable puparia were available, some were sorted into individual vials so adults and puparia could be matched if mixed infestations or unusual species were suspected.

Many species were readily identified from empty puparia; some were so distinctive that they could be determined with a darkfield microscope (e.g., *P. sialia* and *P. braueri*). If identification could not be confirmed with this method, slides were made. If possible, only fully developed puparia

were selected for slides, because characters in undersized puparia are usually distorted and they may not key properly. Infested nests usually included mature puparia, but if nestlings fledged or died before some third instar larvae matured, undersized specimens resulted. Slides were prepared by heating puparia for several minutes in 10% potassium hydroxide solution in a water bath to soften and clean them, then they were rinsed in distilled water. Specimens over-heated or left in solution too long were overcleared, and this destroyed spines making specimens difficult to key, especially those with slender spines. Optimum heating times varied with the thickness and sclerotization of the puparia. Softened puparia were sectioned with microscissors into dorsum, venter, stigmatal area, prothoracic fringe, and the cephalopharyngeal mechanism was removed and mounted. The sections were then cleared in specimen clearing fluid for 1–3 days, rinsed in 95% and then 100% ethanol, then dried and mounted in Euparal. Once slides were prepared, they were dried in a convection oven at 65°C for 10–14 days. Proper drying was important, because, if the medium was not dry, specimens tended to drift to the edges of slides in the thick medium. Slides of puparia were examined with a compound microscope at up to 400×. Measurements were made with a micrometer installed in the ocular lens, calibrated to microns.

Sabrosky et al. (1989) is cited regularly throughout this work and is the only Sabrosky reference cited. Hereafter any reference to Sabrosky refers to Sabrosky et al. (1989). References to Bennett are G. F. Bennett and references to Whitworth are the author.

Over 15,000 puparia from approximately 3,000 infested bird nests of 99 bird species were examined for this study. Material was studied from 46 of the 48 contiguous United States (*Protocalliphora* has not been found in Florida and Louisiana), Alaska, throughout Canada, and Greenland. About half of the material examined was from Bennett and Whitworth's early studies, as well as the collections of other researchers prior to 1992. Since 1992, a total of 4,077 nests of 79 bird species were examined by the author. Of these, 41% (1,691) from 52 bird species were infested with 20 species of *Protocalliphora* (Table 1).

Since this study began in 1992, no new material has been acquired for *P. avium* Shannon and Dobroscky, *P. bicolor* Sabrosky, Bennett, and Whitworth, *P. rognesi* Thompson and Pont (previously *P. chrysorrhoea* (Meigen)), *P. fallisi* Sabrosky, Bennett, Whitworth, *P. hesperioides* Sabrosky, Bennett, and Whitworth, *P. seminuda,* Sabrosky, Bennett, and Whitworth, or *P. tundrae* Sabrosky, Bennett, and Whitworth. Immatures for *P. beameri* Sabrosky, Bennett, and Whitworth and *P. sapphira* Hall, have never been collected. For *P. avium, P. bicolor, P. fallisi, P. hesperioides,* and *P. tundrae* I relied on Bennett's slides for key characters. I was also able to get a few puparial specimens of each of these species from series of adults in museums. I prepared slides of these puparia and verified that Bennett's slides matched the species, since many of his slides did not have correct species names. For *P. rognesi* and *P. seminuda* I was able to re-examine specimens retained from my study conducted between 1969–1975 (Whitworth 1977). A total of about 4,150 slides were prepared for all 27 species for which puparia were available.

Most puparial characters used here are defined in Sabrosky et al. (1989) where a glossary of terms is provided. Sketches of important characters are included here since they were lacking in Sabrosky. Puparia of *Protocalliphora* have a variety of characters which are useful for distinguishing species. The most important are found in the stigmatal area (Fig. 1) and on the venter (Figs. 8–9) and dorsum. The cuticle of most species is thickly covered with spines and often has folds or ridges.

Spines on puparia are extensions of the cuticle and most are reclinate, which appears to help larvae maintain their position in the

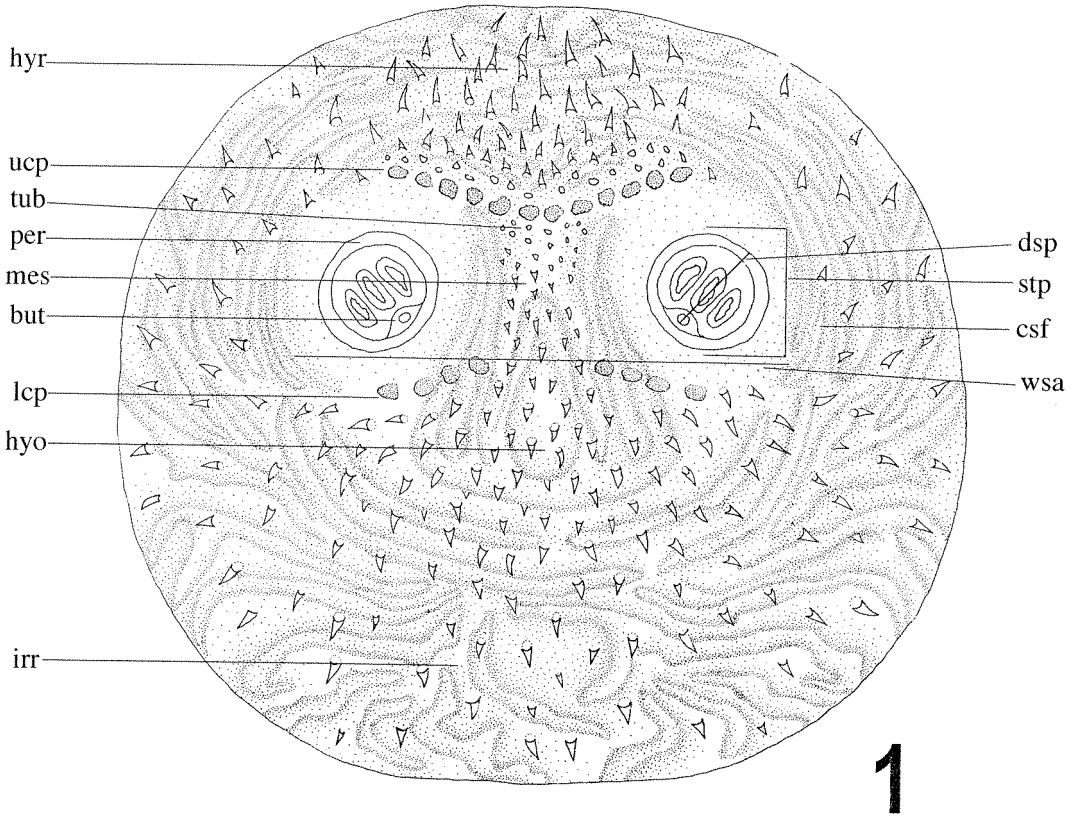
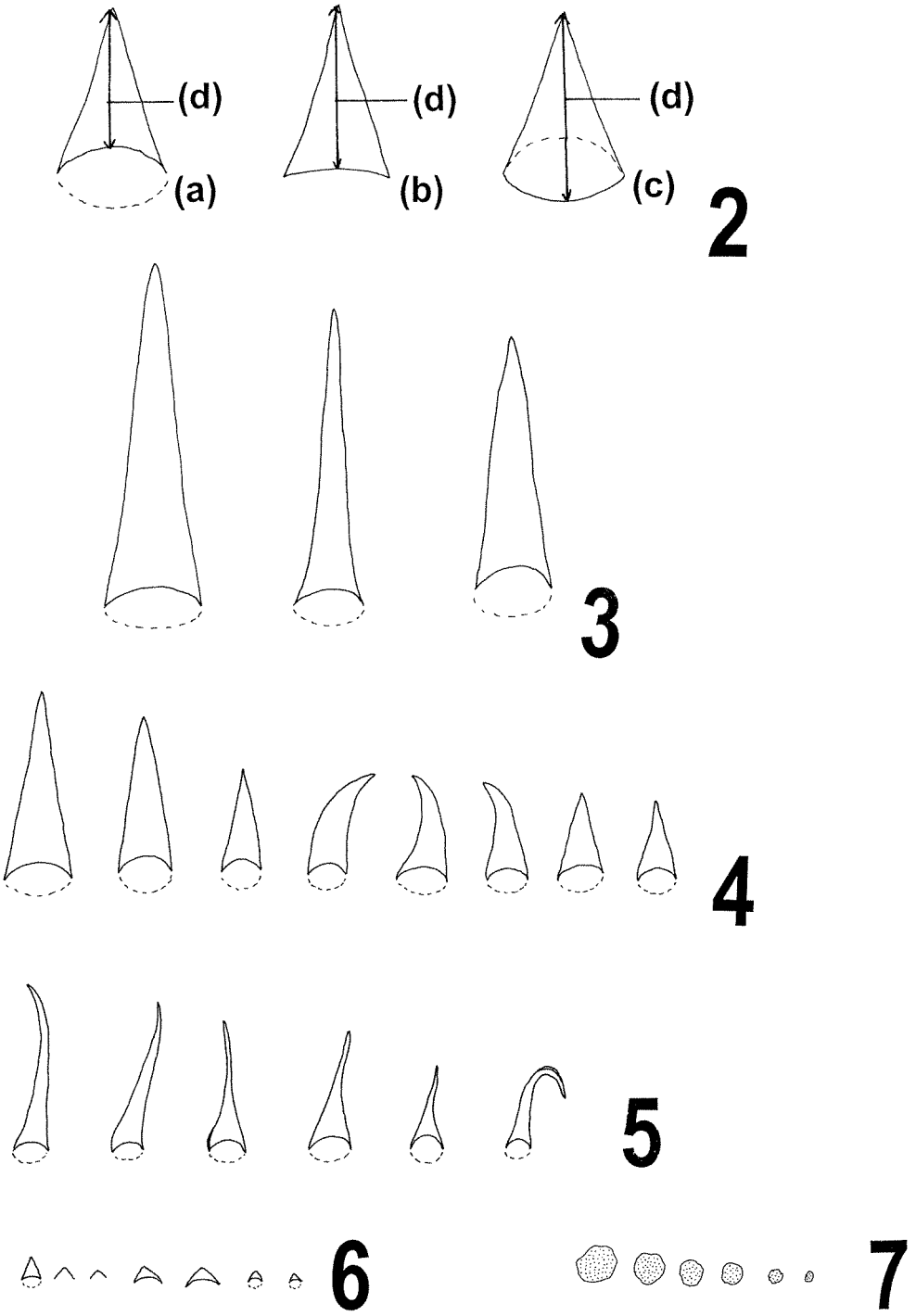


Fig. 1. Diagrammatic view of stigmatal area. but = button; csf = circumstigmatal folds; dsp = diameter of stigmatal plate; hyo = hypostigmatal region; hyr = hyperstigmatal region; irr = irregular folds; lcp = lower cuticular plaques; mes = mesostigmatal region; per = peritreme; stp = stigmatal plate; tub = tubercles; ucp = upper cuticular plaques; wsa = width of stigmatal area at level of the buttons (line is drawn below the buttons to reduce clutter).

nest, especially when feeding on nestlings (Fig. 2a). Some spines are upright and appear in profile (Fig. 2b), while some, especially in the stigmatal area, are proclinate (Fig. 2c). Most spines are translucent and appear 2-part, composed of a spine base and the spine, with spines in profile, the base is not visible. In most species, some spines are reduced to tubercles, which is the spine base with no spine projection (Fig. 7). Spine length is an important character (see Fig. 2 for how to measure; measurements vary with orientation of the spine). Spine lengths given in Sabrosky were averages of several spines in each area. I found averages tended to obscure differences between species, so in this work the longest spines in an area were measured. The longest spines on the dorsum are usually near the center of each segment. Exceptionally long, aberrant spines were not included. All spine measurements were made at 400× and spines were classified as long, medium, short, reduced to tubercles, or absent (Figs. 3–7). Spines also vary in thickness and are medium or slender (Figs. 4–5).

The stigmatal region is divided into the hyperstigmatal, mesostigmatal, hypostigmatal, and is bounded by circumstigmatal folds (Fig. 1). Spines in the lower hyperstigmatal area are shorter while those above are longer. Spines in the upper mesostigmatal area are often reduced to tubercles with longer spines below. Spines in the upper hypostigmatal area are shorter, while



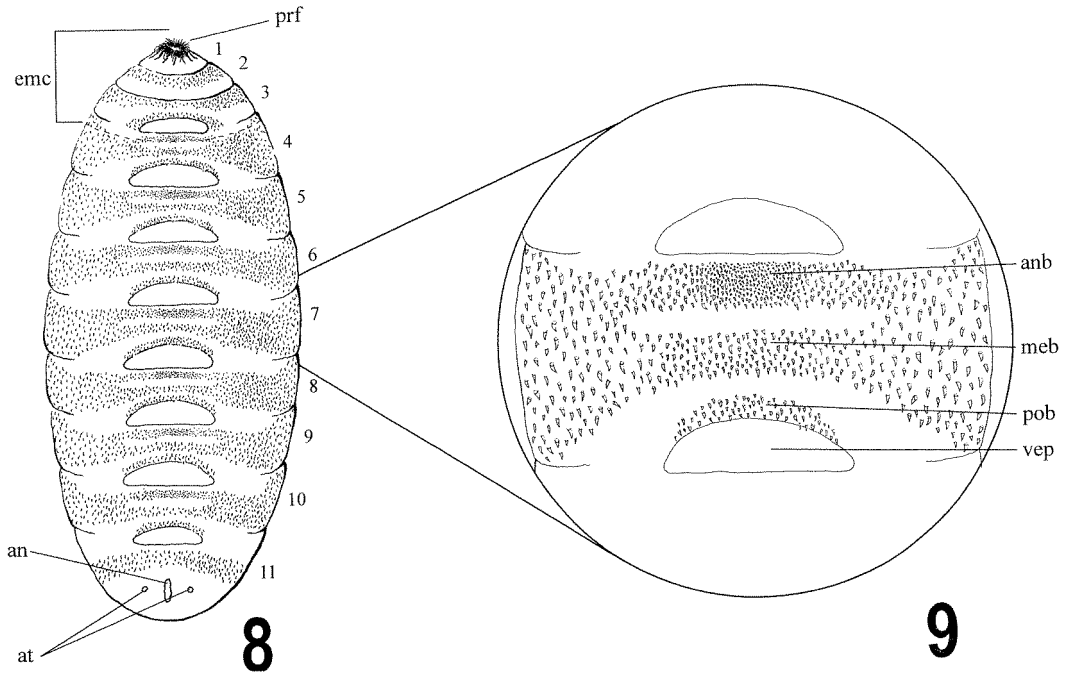
Figs. 2–7. Puparial spines. 2, How to measure: (a) reclinate; (b) profile; (c) proclinate; (d) measurement of spine length. 3, Long spines. 4, Medium spine width. 5, Slender spine width. 6, Short spines. 7, Tubercles. All examples of Figs. 3–7, 450×.

those below are longer. The stigmatal region may have pronounced folds (Fig. 21a, *P. aenea* Shannon and Dobroscky), moderate folds (Fig. 22a, *P. asiovora* Shannon and Dobroscky), faint folds (*P. halli* Sabrosky, Bennett, and Whitworth) or folds absent (Figs. 25a, 26a, *P. interrupta* Sabrosky, Bennett, and Whitworth, *P. metallica* Townsend). Bennett used the term folds for the stigmatal area and ridges for the venter and dorsum, folds were considered larger than ridges. This terminology is continued here for consistency, although some species have very large ridges and others have smaller folds.

Ridges of the dorsal and ventral cuticle may be pronounced (Fig. 21c, *P. aenea*), moderate (*P. parorum*), faint or absent (Fig. 25b, *P. interrupta*). This character is somewhat variable, but with practice can be useful for distinguishing some species. In some species with broad ridges (*P. hirundo, P. lata* Sabrosky, Bennett, and Whitworth), ridge width is a useful character. The venter normally has 3 distinct spine bands, the anterior, medial, and posterior bands on each segment, bounded by ventral pads (Figs. 8–9). On each segment the anterior band varies little between species, while the medial band may be regular (Fig. 10a, *P. sialia*), thinned in the center with opposing spines (Fig. 10b, *P. halli*), irregular and thinned in the center (Fig. 10c, *P. cuprina,* [Hall]), thinned in center not irregular (Fig. 10d, *P. bennetti* Whitworth) interrupted (Figs. 10e, 22b, *P. asiovora*), or center reduced to tubercles (Fig. 10f, *P. interrupta*). In species with reduction in the medial band, reduction usually progresses toward the rear. The posterior band is sometimes reduced or absent, especially to the rear (Figs. 14a, b, *P. halli*). This condition is also present in *P. aenea, P. fallisi,* and *P. tundrae*. Because of this reduction, ventral band ratio measurements will generally be lower to the rear in those species. In some species, the posterior band is reduced steadily to the rear, in others reduction does not occur until the last segment. This character is useful when present, but is variable within species. *Protocalliphora halli* exhibits the full range of variation from no reduction in the posterior band in some specimens, to extreme reduction in others. If in doubt, measure the ventral band ratio in an anterior and posterior segment to verify if reduction is occurring.

The ventral band ratio is an important species character but can be difficult to measure properly. This ratio is determined by measuring the sum of band widths of ventral bands and dividing it by the total distance between margins of ventral pads (Figs. 8–9, see Sabrosky, for details). Normally, bands should be measured in the center of each segment. In some species, the medial band is reduced or divided in the middle where band width is usually measured (Fig. 10e, 22b, *P. asiovora,* Fig. 10f, *P. interrupta*). When this condition was encountered, I measured band width to one side of the gap. When measuring band widths, I assumed there was no space between the rear of the posterior band and the adjacent ventral pad. Rarely, a distinct gap is present, if so, the actual band width is measured. Bands may be broad which produces a high ratio (Fig. 11, 29d, *P. spatulata* Sabrosky, Bennett, and Whitworth), to narrow with a low ratio (Fig. 12, *P. halli*). Bennett (in Sabrosky) advised ignoring small spines and tubercles when measuring bands, and I concur. However, some species like *P. parorum* (Fig. 13, 27b) and *P. bennetti* have medial and anterior bands with a broad row of tiny spines to the rear of the main band. When this condition was encountered, I included the small spines in the measurement. Finally, when puparia are heavily ridged as in *P. hirundo* and *P. rugosa* Whitworth, bands can be so distorted that they are very difficult to measure (Whitworth 2002). It may be necessary to measure several specimens to get an accurate measurement of ventral band ratio in these species.

The prothoracic fringe is a band of long spines on the anterior margin of the protho-



Figs. 8–9. 8, Diagrammatic view of venter. prf = prothoracic fringe; emc = emergence cap; an = anus; at = anal tubercle. 9, Expanded view of segment number 7, anb = anterior band; meb = medial band; pob = posterior band; vep = ventral pad.

racic segment of larvae and puparia. This character is unique to most of the genus *Protocalliphora* (Figs. 8, 15), although this character is absent in puparia of *P. braueri.* It is of minimal value for distinguishing puparia of most species, which have an average total diameter of about 350 μ, but it is useful for identifying *P. sialia* and *P. occidentalis,* which have exceptionally long fringe (500–800 μ) (Fig. 15b). *Protocalliphora interrupta* has an unusually short fringe, which averages 225 μ (200–250 μ), while *P. parorum* has a longer than average fringe of 425 μ (400–450 μ). Another character that was studied was the cephalopharyngeal mechanism. Unfortunately, it proved variable within species and was often distorted when mounted on a slide. If a better method can be found to prepare it for study, it may prove to have useful characters.

Problems were encountered calculating the distance across the stigmatal plates at the level of the buttons as explained in Sabrosky. After measuring numerous specimens, it was determined that when Bennett made this measurement he did not stop at the outer margins of the plates (as defined in the text), but extended it to the full width of the stigmatal area, roughly delineated by the circumstigmatal folds. Rather than remeasure everything to conform with the definition provided in Sabrosky, I have redefined this measurement as the width of the stigmatal area, at the level of the buttons (Fig. 1). Another problem was encountered measuring the diameter of the stigmatal plate. This measurement is defined in Sabrosky as extending from the top of the peritreme through the ventral slit to the bottom of the button (Fig. 1). However, McAlpine et al. (1981) define the stigmatal plate as bounded by the peritreme and technically the full diameter of the plate would extend past the button to the bottom of the peritreme. Again, rather than remeasure everything, the measurement, as defined in Sabrosky, is used for all measurements in this study.

Bennett included a variety of puparial measurements, such as the diameter of stigmatal plates, stigmatal ratio, distance between buttons, and width across stigmatal plates (Fig. 1). I have included these measurements in my descriptions, because they help characterize species. However, they have proven to be of little value in the keys and vary primarily with the size of the puparia.

Results

I have identified 18 new bird hosts and 90 new host-parasite relationships since the publication of Sabrosky (Table 1). Thirty-six of the host-parasite relationships were from material I collected, the remaining 54 relationships were from other researcher's studies, and most were confirmed from material sent to me for identification.

To aid species identification, I have prepared a list of 160 infested bird species and the species of *Protocalliphora* known from their nests (Table 1). New relationships from other studies are identified by citation, if published, or if unpublished the researcher's name and affiliation are given. This table combines data from Sabrosky where bird hosts were listed by *Protocalliphora* species. When using puparial keys, it is important to check known host-parasite relationships, new relationships identified from puparia alone should be determined with caution. Puparia of similar species can be difficult to distinguish, but when hosts and species range are considered, distinctions may be made with confidence.

Most fly pupae found in bird nests in North America are *Protocalliphora*. Occasionally, sarcophagids or other genera of calliphorids are found in nests, usually associated with carrion. These latter taxa are more common in the nests of hawks and owls, which feed dead animals to nestlings. They also may be found in nests where nestlings have died. Sarcophagid puparia may be distinguished by having posterior spiracles in deep cavities and the dorsal cornu of the cephalopharyngeal mechanism deeply incised. Calliphorid puparia have posterior spiracles exposed at the apex of the terminal abdominal segment, and the dorsal cornu is not incised. Puparia of the subgenus *Protocalliphora* are distinguished by the presence of a prothoracic fringe and three distinct ventral spine bands (Figs. 8–9). Larvae of the subgenus *Trypocalliphora* lack a prothoracic fringe, the ventral medial band is absent, and the ventral anterior and posterior bands are weak or absent. Most scavenger calliphorid species have strong ventral anterior spine bands, or bands of spines associated with intersegmental areas.

The following key separates 27 species of *Protocalliphora* puparia. Some species are still poorly known, and key characters selected for them may be variable, making keying difficult. Species with puparia unknown and not included in the key are *P. beameri* Sabrosky, Bennett, and Whitworth and *P. sapphira* (Hall).

Key to Puparia of North American *Protocalliphora*

1. Dorsal cuticular spines very sparse; ventral medial spine bands absent from all segments, anterior and posterior spine bands reduced or absent to rear; prothoracic fringe absent; spines in all regions less than 10 μ; obligatory subcutaneous nestling parasite. *Protocalliphora* (*Trypocalliphora*) (one species in this subgenus) . . . . . braueri
– Dorsal cuticular spines numerous; three distinct ventral spine bands on, at least, anterior segments (Figs. 8–9); distinct fringe on the anterior end of the prothoracic segment (Figs. 8, 15a, b); puparia covered with spines, ranging from tubercles (Fig. 7) to short spines (Fig. 6), or long spines (Fig. 3), spines may be medium (Fig. 4), or slender (Fig. 5); not normally subcutaneous. *Protocalliphora* (*Protocalliphora*) (28 North American species in this subgenus, puparia known for 27 species) 2
2. Center of medial spine band interrupted on at least some segments (Figs. 10e, 22b), interruption usually narrow and may be incomplete or with no interruption in a few specimens in a series; hyperstigmatal spines usually 25 μ or less, a few to 30 μ; mesostigmatal folds moderate; ridges of dorsum and venter faint to absent; ventral band ratio 0.63 (0.57–0.68/10) (usually in open nests of larger birds

Table 1. Bird species infested by species of *Protocalliphora*.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Blackbirds	1	Brewer's—*Euphagus cyanocephalus*	*asiovora, braueri, interrupta, metallica* (1), *occidentalis, seminuda, sialia*
	1	red-winged—*Agelaius phoeniceus*	*fallisi, interrupta, metallica* (1), *shannoni*
	1	yellow-headed—*Xanthocephalus xanthocephalus*	*braueri, hirundo, interrupta, *metallica* (W, 1)
Bluebirds	251	eastern—*Sialia sialis*	*asiovora* (1), **braueri* (W, 2), **deceptor* (W, 1), *hirundo, sialia* (247)
	73	mountain—*Sialia currucoides*	*occidentalis* (73)
	194	western—*Sialia mexicana*	**braueri* (W, 15), **parorum* (W, 1), **seminuda* (F, 1), *occidentalis* (178)
	37	mountain or western—*sialia* spp.	*occidentalis* (37)
Buntings		indigo—*Passerina cyanea*	*metallica*
		lazuli—*Passerina amoena*	*metallica*
		snow—*Plectrophenax nivalis*	*tundrae*
Bushtit		*Psaltriparus minimus*	*hesperioides*
Cardinal	1	northern—*Cardinalis cardinalis*	*deceptor* (1), *metallica*
Catbird	2	grey—*Dumetella carolinensis*	*avium, metallica* (2), *shannoni*
Chat	2	yellow-breasted—*Icteria virens*	*metallica, *interrupta* (R-1, 1), **spenceri* (R-1, 1)
Chickadees	10	black-capped—*Poecile atricapillus*	**bennetti* (3), **braueri* (W, 1), **deceptor* (W, 3), *parorum* (3), *shannoni*
	7	*boreal—*Poecile hudsonicus*	**bennetti* (M)
	25	Carolina—*Poecile carolinensis*	**bennetti* (W, 3), *deceptor* (22)
	5	chestnut-backed—*Poecile rufescens*	*parorum* (5)
	71	mountain—*Poecile gambeli*	*braueri, occidentalis* (1), *parorum* (70), *sialia* (1)
	2	*Poecile* spp.	*braueri* (2)
Cowbird		brown-headed—*Molothrus ater*	*deceptor, shannoni*
Creeper		brown—*Certhia americana*	*parorum*
Crow		American—*Corvus brachyrhynchos*	*asiovora, avium, deceptor, occidentalis*
Cuckoo		black-billed—*Coccyzus erythropthalmus*	*metallica*
Dipper	2	American—*Cinclus mexicanus*	*aenea* (2), **braueri* (H)
Dove	1	mourning—*Zenaida macroura*	*asiovora, cuprina, *metallica* (W, 1)

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Eagles		bald—*Haliaeetus leucocephalus*	*avium*
		golden—*Aquila chrysaetos*	*asiovora, braueri*
Falcons		gyrfalcon—*Falco rusticolus*	*avium*
		peregrine—*Falco peregrinus*	*avium*
		prairie—*Falco mexicanus*	(possible) *asiovora*
Finches		Cassin's—*Carpodacus cassinii*	*hesperia*
	1	house—*Carpodacus mexicanus*	*asiovora, braueri, cuprina, hesperia, hesperioides, *interrupta* (W, 1)
Flickers		northern (common)—*Colaptes auratus*	
	2	northern red shafted—*Colaptes auratus cafer*	*lata* (2)
		northern yellow shafted—*Colaptes auratus auratus*	*sialia*
Flycatchers		alder—*Empidonax alnorum*	*bicolor, braueri, metallica*
		*acadian—*Empidonax virescens*	**deceptor* (R)
	26	ash-throated—*Myiarchus cinerascens*	**parorum* (D, 4), *occidentalis* (22)
	1	dusky—*Empidonax oberholseri*	*cuprina* (1), *hesperioides*
	2	great-crested—*Myiarchus crinitus*	*braueri, deceptor, sialia* (2)
		pacific-slope (western)—*Empidonax difficilis*	*cuprina, hesperioides*
		willow—*Empidonax traillii*	*cuprina*
Goldfinches		American—*Carduelis tristis*	*bicolor, braueri, cuprina, metallica, shannoni*
		unidentified	*hesperioides*
Grackle	1	common—*Quiscalus quiscula*	*aenea, bicolor, braueri, deceptor, fallisi, hirundo, metallica, shannoni, sialia*
Grosbeaks		blackheaded—*Pheucticus melanocephalus*	*braueri*
		blue—*Guiraca caerulea*	*metallica*
		pine—*Pinicola enucleator*	**hesperia* [1](W), **spenceri* (M)
Hawks		broad-winged—*Buteo platypterus*	*avium*
		Cooper's—*Accipiter cooperii*	*asiovora, avium*
		ferruginous—*Buteo regalis*	*asiovora*
		northern goshawk—*Accipiter gentilis*	*avium, lata, asiovora*
		northern harrier—*Circus cyaneus*	*avium*
		red-shouldered—*Buteo lineatus*	*avium*
		red-tailed—*Buteo jamaicensis*	*avium, lata, asiovora*
		Swainson's—*Buteo swainsoni*	*asiovora, avium*

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Jays		blue—*Cyanocitta cristata*	*shannoni*
		gray—*Perisoreus canadensis*	*hesperia, shannoni*
		pinyon—*Gymnorhinus cyanocephalus*	*asiovora*
	2	*Stellar's–*Cyanocitta stelleri*	**asiovora* (W, 2)
Juncos	1	dark-eyed—*Junco hyemalis*	**spatulata* (M), **occidentalis* (R-1, 1)
		oregon—*Junco hyemalis oreganus*	*braueri, parorum*
		slate colored—*Junco hyemalis hyemalis*	*metallica*
		unidentified	*braueri, shannoni*
Kestrel	8	American—*Falco sparvarius*	*asiovora, *braueri* (W, 1), *lata, occidentalis* (5), *sialia* (2)
Kingbirds		eastern—*Tyrannus tyrannus*	*bicolor, cuprina, metallica, occidentalis, shannoni, sialia*
		western—*Tyrannus verticalis*	*braueri, cuprina, occidentalis*
Lark		horned—*Eremophila alpestris*	*braueri, seminuda, spatulata*
Magpie		black-billed—*Pica pica*	*asiovora, braueri*
Martin	19	purple—*Progne subis*	*hirundo, occidentalis, *rugosa* (2), *sialia* (17)
Meadowlarks		eastern—*Sturnella magna*	*braueri*
		western—*Sturnella neglecta*	*braueri*
Mockingbird	3	northern—*Mimus polyglottos*	*deceptor, *metallica* (W, 1), *sialia (W, 1)
Nuthatches		brown-headed—*Sitta pusilla*	possible *sialia*
	15	pygmy—*Sitta pygmaea*	**parorum* (D, 14), **occidentalis* (D, 1)
	5	red-breasted—*Sitta canadensis*	**braueri* (W, 1), *parorum, *occidentalis* (D, 5)
	14	white-breasted—*Sitta carolinensis*	**braueri* (W, 1), *occidentalis, *parorum* (D, 12), *sialia* (2)
Osprey		*Pandion haliaetus*	*avium*
Ovenbird		*Seiurus aurocapillus*	*braueri*
Owls		eastern-screech—*Otus asio*	*sialia*
	1	*ferruginous pygmy—*Glaucidium brasilianum*	**occidentalis* (P, 1)
		flamulated—*Otus flammeolus*	*occidentalis*
		great-horned—*Bubo virginianus*	*asiovora, avium, occidentalis*
		long-eared—*Asio otus*	*asiovora*
		western-screech—*Otus kennicottii*	*occidentalis*

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Phoebes		black—*Sayornis nigricans*	*halli*
	28	eastern—*Sayornis phoebe*	*aenea, *bennetti* (RE, 1), *deceptor* (27), *hirundo, sialia*
	1	Say's—*Sayornis saya*	*aenea, halli* (1), *occidentalis*
Pipit		American—*Anthus rubescens*	*spatulata*
Raven		common—*Corvus corax*	*asiovora, occidentalis, sialia*
Redstart		American—*Setophaga ruticilla*	*bicolor, spenceri*
Robin	22	American—*Turdus migratorius*	*aenea, asiovora, avium, braueri* (1), *cuprina, hesperia* (10), *metallica, occidentalis* (1), *shannoni* (10), *sialia*
Shrike		loggerhead—*Lanius ludovicianus*	*asiovora, braueri, cuprina* (possible B)
Siskin		pine—*Carduelis pinus*	*braueri*
Solitaire		Townsend's—*Myadestes townsendi*	*braueri*
Sparrows		American tree—*Spizella arborea*	*braueri*
		*Bachman's—*Aimophila aestivalis*	**deceptor* (R)
		*Brewer's—*Spizella breweri*	**braueri* (HO)
	1	chipping—*Spizella passerina*	*braueri, brunneisquama, hesperia, metallica* (1)
		field—*Spizella pusilla*	*metallica*
		fox—*Passerella iliaca*	*metallica, interrupta*
		grasshopper—*Ammodramus savannarum*	*metallica*
	28	house—*Passer domesticus*	*braueri* (19), *chrysorrhoea, occidentalis* (2), **rugosa* (W, 1), *sialia* (7)
		savannah—*Passerculus sandwichensis*	*braueri, metallica, *spatulata* (F&M)
	3	song—*Melospiza melodia*	*braueri, cuprina* (R-1, 1), *interrupta* (2), *metallica, shannoni, sialia*
	1	sparrow spp.	*metallica* (1)
		swamp—*Melospiza georgiana*	*fallisi, metallica, *shannoni* (B)
		unidentified	*braueri, metallica*
		vesper—*Pooecetes gramineus*	*braueri, metallica*
	1	white-crowned—*Zonotrichia leucophrys*	*braueri, *metallica* (W, 1), **spatulata* (F&M)
		white-throated—*Zonotrichia albicollis*	*fallisi, metallica, shannoni*
Starling	4	European—*Sturnus vulgaris*	*asiovora, *bennetti* (W, 1), *bicolor, braueri* (2), *hirundo, occidentalis* (2), **rugosa* (W, 1), *sialia*

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Swallows		bank—*Riparia riparia*	*braueri, chrysorrhoea, hirundo, metallica, occidentalis,* **rugosa* (W, 1), *sialia*
	30	barn—*Hirundo rustica*	*aenea* (1), *asiovora* (1), *braueri* (4), *chrysorrhoea, cuprina* (1), **deceptor* (W, 2), *halli* (16), *hesperia, hirundo* (2), *occidentalis, parorum, rugosa* (W, 2), *seminuda, sialia* (3)
	3	cliff—*Hirundo pyrrhonota*	*asiovora, braueri, chrysorrhoea, hirundo* (3), *occidentalis,* **rugosa* (W), *sialia*
		northern rough-winged—*Stelgidopteryx serripennis*	*metallica, sialia*
	556	tree—*Tachycineta bicolor*	**bennetti* (W, 62), *bicolor, braueri* (54), **brunneisquama* (W, 1), **deceptor* (W, 4), *hirundo* (5), *metallica* (9), *occidentalis* (160), **parorum* (D, 1), **rugosa* (W, 70), *shannoni, sialia* (190)
		unidentified	*asiovora, avium, beameri, halli, hesperia*
	35	violet-green—*Tachycineta thalassina*	*braueri* (9), *chrysorrhoea, hirundo* (1), **rugosa* (W, 9), *occidentalis* (17)
Tanager		scarlet—*Piranga olivacea*	*metallica*
Thrashers	1	brown—*Toxostoma rufum*	*metallica* (1), *shannoni*
		*sage—*Oreoscoptes montanus*	**braueri* (HO)
Thrushes	1	hermit—*Catharus guttatus*	**hesperia* (R-1, 2), *shannoni*
		Swainson's—*Catharus ustulatus*	*braueri,* **hesperia* (M), **shannoni* (M)
		veery—**Catharus fuscescens*	species unknown (R)
		varied—*Ixoreus nacvius*	**hesperia* (M)
		wood—*Hylocichla mustelina*	*bicolor, deceptor, shannoni*
Titmouse	27	*oak—*Baeolophus inornatus*	**parorum* (D, 22), **occidentalis* (D, 5)
	14	*tufted—*Baeolophus bicolor*	**deceptor* (W, 13), **sialia* (W, 1)
Towhees		spotted—*Pipilo musculatus*	**brunneisquama* (B)
	1	eastern—*Pipilo erythrophthalmus*	**deceptor* (W, 1), *metallica*
Unknown	1	unknown	*shannoni*
Veery	3	*Catharus fuscescens*	**hesperia* (R-1, 2), **shannoni* (R-1, 1)

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Vireos	4	plumbeous—*Plumbeous plumbeous*	**cuprina* (W, 4)
		red-eyed—*Vireo olivaceus*	*bicolor*
	1	solitary (blue-headed)—*Vireo solitarius*	*bicolor, *cuprina* (R-1, 1)
	1	warbling—*Vireo gilvus*	*spenceri, *cuprina* (R-1, 1)
		*yellow-throated—*Vireo flavifrons*	**braueri* (R)
Warblers		*blackpoll—*Dendroica striata*	**spenceri* (M)
		black-throated blue—*Dendroica caerulescens*	*bicolor*
		*black & white—*Mniotilta varia*	**braueri* (R)
		Canada—*Wilsonia canadensis*	*braueri*
		chestnut-sided—*Dendroica pensylvanica*	*bicolor*
	3	*hooded—*Wilsonia citrina*	**deceptor* (W, 1, R), **braueri* (R-1, 2)
		*Kentucky—*Oporonis formosus*	**braueri* (R)
	1	*McGillivray's—*Oporonis tolmiei*	**metallica* (R), **interrupta* (R-1, 1)
		Nashville—*Vermivora ruficapilla*	*metallica*
		*orange-crowned—*Vermivora celata*	**braueri* (M)
		prairie—*Dendroica discolor*	*deceptor*
	40	prothonotary—*Protonotaria citrea*	**deceptor* (W, 10, R-1, 30)
	4	*Swainson's—*Limnothlypis swainsonii*	**braueri* (RE, 1), **deceptor* (R-1, 1)
		*Townsend—*Dendroica townsendi*	**braueri* (M), **shannoni* (M), **spenceri* (M)
		Wilson's—*Wilsonia pusilla*	*braueri*
		worm-eating—*Helmitheros vermivorus*	*deceptor*
	14	yellow—*Dendroica petechia*	*bicolor, braueri, cuprina* (12), **deceptor* (W, 1), *hesperioides, metallica, spenceri* (1)
	1	yellow-rumped—*Dendroica coronata*	*bicolor, braueri, cuprina, **metallica* (M), *shannoni, **spatulata* (M), **spenceri* (M)
Waterthrushes		Louisiana—*Seiurus motacilla*	*aenea*
		northern—*Seiurus noveboracensis*	*metallica*
Waxwing	1	cedar—*Bombycilla cedrorum*	**braueri* (W, 1), *shannoni*
Woodpecker		downy—*Picoides pubescens*	*fallisi, sialia*

Table 1. Continued.

Bird Group	Infested Nests Examined in Current Study	Bird Species	*Protocalliphora* Species (Sum of species may exceed nests examined because of mixed infestations.)
Wood-pewee		western-wood—*Contopus sordidulus*	*cuprina*
Wrens	3	Bewick's—*Thryomanes bewickii*	**deceptor* (W, 2), **occidentalis* (D, 1), *parorum*
	7	Carolina—*Thryothorus ludovicianus*	*deceptor* (7)
	61	house—*Troglodytes aedon*	*aenea*, **bennetti* (W, 8), *braueri* (9), *deceptor* (6), *occidentalis* (6), *parorum* (22), *shannoni, sialia* (10)
	1	marsh—*Cistothorus palustris*	*braueri, interrupta* (1)
		unidentified	*metallica*
Yellowthroat		common—*Geothlypis trichas*	*fallisi, metallica*
Total examined = 1,691			

* New host or new host-parasite associations determined since host list was published in Sabrosky et al. (1989). All identifications confirmed by Whitworth unless indicated otherwise. Species followed by (W) were collected by author in the current study. Some new relationships were determined from old Bennett slides, labeled (B). Other host-parasite associations were taken from material submitted for identification by other researchers, including Don Dahlsten (D), University of California, Berkeley, unpublished; Jeanne Fair (F), Los Alamos, NM, unpublished; Fair & Miller (F&M) 1995; Halstead (H) 1988; Howe (HO) 1991 (species confirmed by G. F. Bennett); Matsuoka et al. (M), 1997 & unpublished in part; Glenn Proudfoot (P), Texas A&M University, Department of Wildlife and Fisheries, unpublished; Will Reeves (RE), Clemson University, South Carolina, unpublished; Revels (R) 1996 (species confirmed by C. W. Sabrosky), Mia Revels (R-1), currently Northeastern State University, Talequah, OK, unpublished, confirmed by author.

[1] Sabrosky et al. (1989) listed pine grosbeak as a host for *P. halli* from my nest #414, a re-examination revealed it actually was *P. hesperia.*

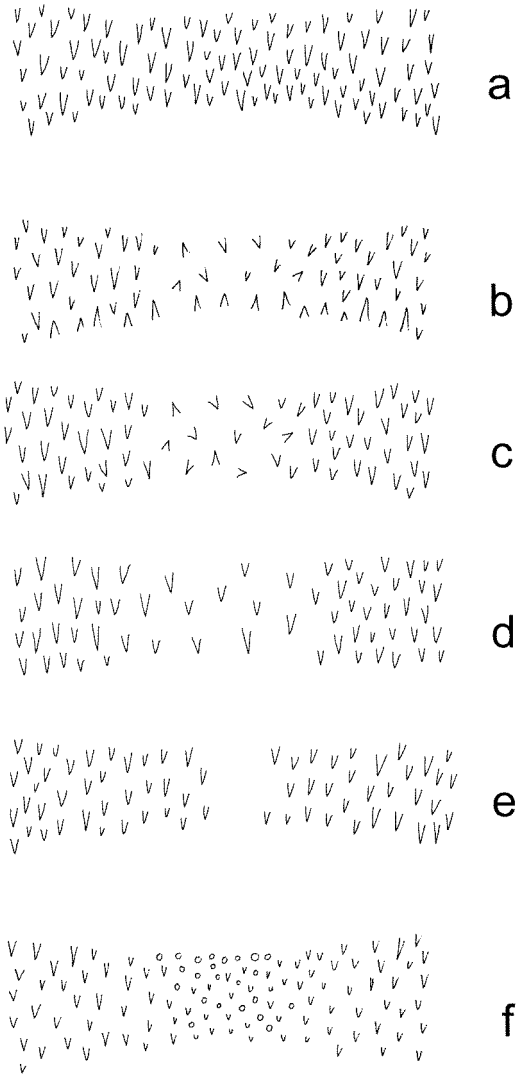


Fig. 10. Puparia, ventral medial spine band condition: (a) regular, *Protocalliphora sialia*; (b) thinned in center, irregular with opposing spines to rear, *P. halli*; (c) thinned in center, irregular, few opposing spines, *P cuprina*; (d) thinned in center, regular, rarely opposing spines, *P. bennetti*; (e) interrupted, *P. asiovora*; (f) center reduced to tubercles, *P. interrupta*.

such as magpies, raptors, or crows; western only) . . . . . *asiovora*

– Medial spine band complete, although sometimes narrowed on midline (Figs. 10a–d), or reduced to short spines or tubercles on some segments (Fig. 10f); hyperstigmatal spines, mesostigmatal folds, dorsal and ventral ridges, and ventral band ratios variable 3

3. Prothoracic fringe, when present, long, 500 μ or more in diameter, often with a large opening in center (Fig. 15b); dorsal cuticular ridges usually pronounced 4

– Prothoracic fringe 450 μ or less, central opening smaller (Fig. 15a); dorsal cuticle variable or fringe not present 5

4. Stigmatal region with numerous pronounced folds; lower portion of mesostigmatal area with distinct spines 10–20 μ (Whitworth 2003: Fig. 2a); ventral band ratio averages 0.81 (0.71–0.89); east of a line from Alaska to Kentucky . . . . . *sialia* (in part)

– Stigmatal region with folds faint or absent; lower portion of mesostigmatal area with tubercles only, sometimes a few short spines (Whitworth 2003: Fig. 2c); ventral band ratio averages 0.72 (0.57–0.85); west of a line from Montana to New Mexico and probably into Mexico . . . . . *occidentalis* (in part)

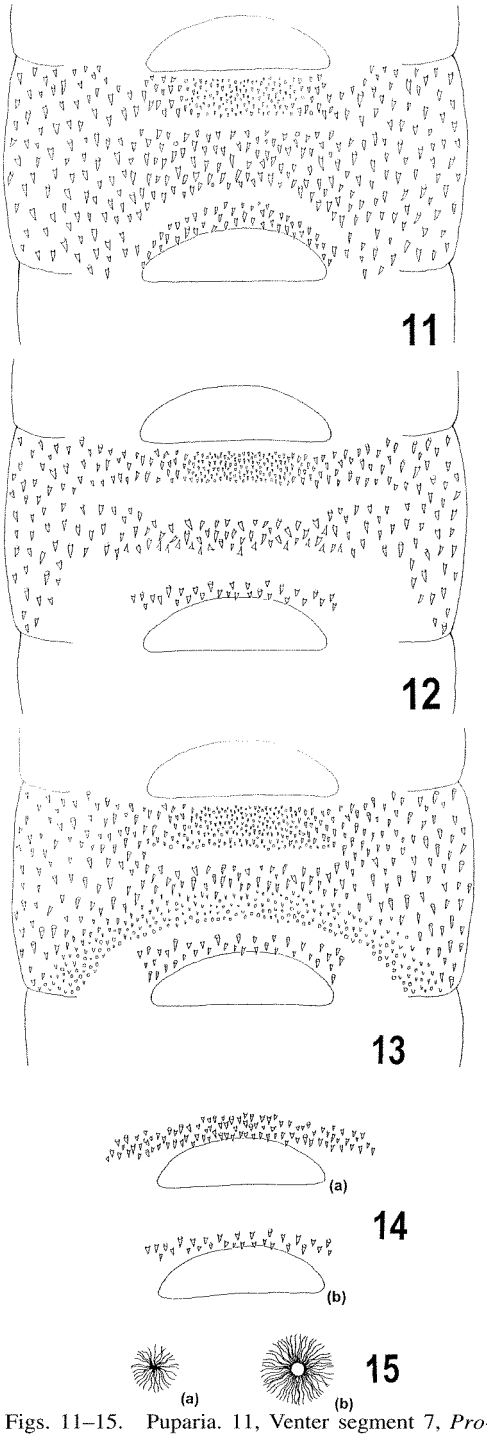
5. Hyperstigmatal, mesostigmatal, and hypostigmatal spines reduced to tubercles or short spines averaging 4–6 μ, at most 7.5 μ (Figs. 16–18, 25–26); center of medial band may be reduced to tubercles toward rear (Fig. 10f) 6

– Hyperstigmatal region with, at least, some distinct spines 10 μ or longer (Figs. 1, 19–20); center of medial band may be thinned or narrowed, but not reduced to tubercles toward rear 8

6. Posterior spine band on venter reduced or absent, especially to rear, medial spine band usually reduced to tubercles in middle, especially toward rear (Fig. 10f); mesostigmatal and hypostigmatal tubercles large (Figs. 17, 25a); prothoracic fringe short, 225 μ (200–250 μ); western only . . . . . *interrupta*

– All 3 ventral spine bands about same size, spines of medial band distinct; mesostigmatal and hypostigmatal tubercles tiny; prothoracic fringe 300 μ or more 7

7. Hyperstigmatal tubercles with spine projections visible at 400×, usually 2.5–5 μ long, rarely to 7.5 μ, tubercles appearing larger than *P. metallica* (Fig. 16), at 400× "cell-wall," border usually lacking (Fig. 18); longest spines in center of anterior ventral band usually 12.5 μ or more; eastern and midwestern only, hosts include cardinal, chickadee, fly-



Figs. 11–15. Puparia. 11, Venter segment 7, *Protocalliphora spatulata.* 12, Venter segment 7, *P. halli.* 13, Venter segment 7, *P. parorum.* 14, Posterior band reduced to rear, *P. halli, P shannoni*: (a) segment 4; (b) segment 10. 15, Prothoracic fringe: (a) *P. spatulata,* 300 μ; (b) *P. sialia,* 500 μ.

catcher, phoebe, warbler, and wren; adult male with broad surstyli, female with bluish abdomen . . . . . *deceptor*

– Hyperstigmatal tubercles without spines projections visible at 400×, individual tubercles usually bordered by circular "cell-wall," tubercles appearing as minute dots at 400× (Figs. 16, 26a); longest spines in center of anterior ventral band usually 10 μ or less; widespread, broad host range; adult male with slender surstyli, female with fifth tergite cupreous . . . . . *metallica*

8. Hyperstigmatal spines usually short, longest spines 12.5 μ, rarely to 20 μ; mesostigmatal and hypostigmatal areas with tubercles and, at most, a few short spines (Fig. 19); posterior spine bands usually reduced to rear, sometimes only last segment reduced (Figs. 14a, b) . . . . . *shannoni*

– Longest hyperstigmatal spines usually 20 μ or more; mesostigmatal and hypostigmatal areas usually with distinct spines; posterior spine bands variable 9

9. Dorsal cuticle with pronounced to moderate ridges (see Fig. 21c); most species with a high ventral band ratio of 0.65 or more; stigmatal region often with pronounced to moderate folds (absent in most *P. occidentalis*) 10

– Dorsal cuticle with ridges faint or absent (Fig. 23); ventral band ratio variable; stigmatal region usually with folds faint or absent . . . 18

10. Ventral band ratios average 0.58 (0.51–0.64) at the front, 0.48 (0.46–0.53) at the rear; posterior spine band reduced to rear (Fig. 21d); reduction may be slight, only last segment; mesostigmatal spines reduced to tubercles, or a few short spines at lower margin (Fig. 21a); known from dipper nests and 1 barn swallow nest in the west *aenea* (in part, western form)

– Ventral band ratios average 0.63 or more (aberrant individuals occasionally as low as 0.48); posterior spine band not reduced to rear; mesostigmatal spines usually not reduced 11

11. Dorsal cuticular ridges 50 μ or more wide, usually a few ridges 60–100 μ or more wide; dorsal ridges usually widely spaced (*P. hirundo,* Whitworth 2002: fig. 3a), closer together in undersized specimens 12

– Dorsal cuticular ridges usually average less than 50 μ in width; dorsal cuticular ridges more abundant and closer together (*P. rugosa,* Whitworth 2002: fig. 2c) 13

12. Mesostigmatal and upper hypostigmatal area bare, without tubercles or spines (Sabrosky: fig. 55); hyperstigmatal spines long 35–60 μ; fully developed puparia exceptionally large,

averaging 13 mm; known only in raptors and flickers in the west . . . . . *lata*

– Mesostigmatal and upper hypostigmatal spines or tubercles present; hyperstigmatal spines shorter 25–35 μ; puparia 9 mm or less; primarily in cliff and bank swallows . . . *hirundo*

13. Longest hyperstigmatal spines usually less than 30 μ (25–35 μ); stigmatal area outlined in broad irregular folds 14

– Longest hyperstigmatal spines 35 μ (35–50 μ) or more; stigmatal area variable but folds, if present, narrower and more regular 15

14. Mesostigmatal area bare or with a few scattered spines; dorsum with short spines usually 25 μ or less (25–30 μ) (Sabrosky: fig. 44); known only in the east, midwest, and Alaska, primarily in crows and raptors . . . . . *avium* (in part)

– Mesostigmatal area with dense spines to 15 μ; dorsal spines long, usually 30 μ (30–50 μ) (Whitworth 2002: fig. 2); known only in northwestern United States and British Columbia, primarily in swallows . . . . . *rugosa*

15. Almost exclusively in bank swallow nests; mesostigmatal spines distinct to 15 μ; prothoracic fringe 350–400 μ (Sabrosky: fig. 47) . . . . . *rognesi*

– Usually not in bank swallow nests; upper mesostigmatal area with tubercles, lower area with spines to 10 μ, sometimes longer; prothoracic fringe in *P. parorum* 350–450 μ, in *P. sialia* 500 μ or more 16

16. Dorsal cuticle with moderate ridges; venter with ridges usually faint or absent; anal tubercles pronounced and circular with no ridges (Figs. 20, 27a); several rows of small spines to rear of anterior and medial spine bands (Figs. 13, 27b); surstyli of adult male long and slender; primarily in nests of chickadees, wrens, and nuthatches . . . *parorum* (in part)

– Dorsal cuticle with pronounced ridges; venter with ridges moderate to pronounced; anal tubercles indistinct, ridged with irregular cuticle; few small spines to rear of anterior and medial spine band; surstyli of adult male digitate; rarely in chickadees, but found in wrens and some nuthatches 17

17. Stigmatal region usually with distinct hyperstigmatal, mesostigmatal and hypostigmatal folds, outlined by pronounced circumstigmatal folds; lower portion of mesostigmatal area with distinct spines 10–20 μ (Whitworth 2003: Fig. 2a); ventral band ratio usually higher, average 0.81(0.71–0.89); east of line from Alaska to Kentucky . . . . . *sialia* (in part)

– Stigmatal region with few, if any, folds and no circumstigmatal folds; lower portion of mesostigmatal area only with tubercles, rarely a few short spines (Whitworth 2003: fig. 2C); ventral band ratio usually lower 0.72 (0.57–0.85); west of a line from British Columbia to eastern Colorado, south to New Mexico, and probably Mexico . . . *occidentalis* (in part)

18. Posterior spine band on venter significantly reduced or absent toward rear (Figs. 14a, b); medial band thinned and often irregular or with opposing spines (Figs. 10b–d) 19

– Posterior spine band approximately equal in size on all segments, occasionally some reduction on last 2 or 3 segments to rear; medial band variable, primarily western, 2 eastern species 23

19. Hyperstigmatal spines broad at base but slender at tip (Fig. 5), longest spines 25–35 μ; ventral band ratio of last complete segment usually low, 0.37 (0.29–0.47) or less; known only from northern Canada and Greenland . . . . . *tundrae*

– Hyperstigmatal spines medium (Fig. 4), length variable; ventral band ratio variable 20

20. Western only; in nests of barn swallows, phoebes, warblers, or flycatchers; posterior band with slight to extreme reduction to rear (Fig. 14); ventral spine band ratio at rear averages 0.46 (0.38–0.62) (Fig. 15) 21

– Eastern only; posterior band usually extremely reduced to rear; ventral spine band ratio at posterior end averages 0.35 (0.29–0.47) . . 22

21. Medial spine band on last segment with spines irregular and opposing on rear edge (Fig. 10b); hyperstigmatal spines to 35 μ; usually in barn swallows or phoebes . . . . . *halli*

– Medial spine band on last segment with only a few irregular spines, and at most, a few small opposing spines (Fig. 10c); hyperstigmatal spines usually less than 30 μ; usually in warblers, flycatchers, and occasionally barn swallows . . . . . *cuprina*

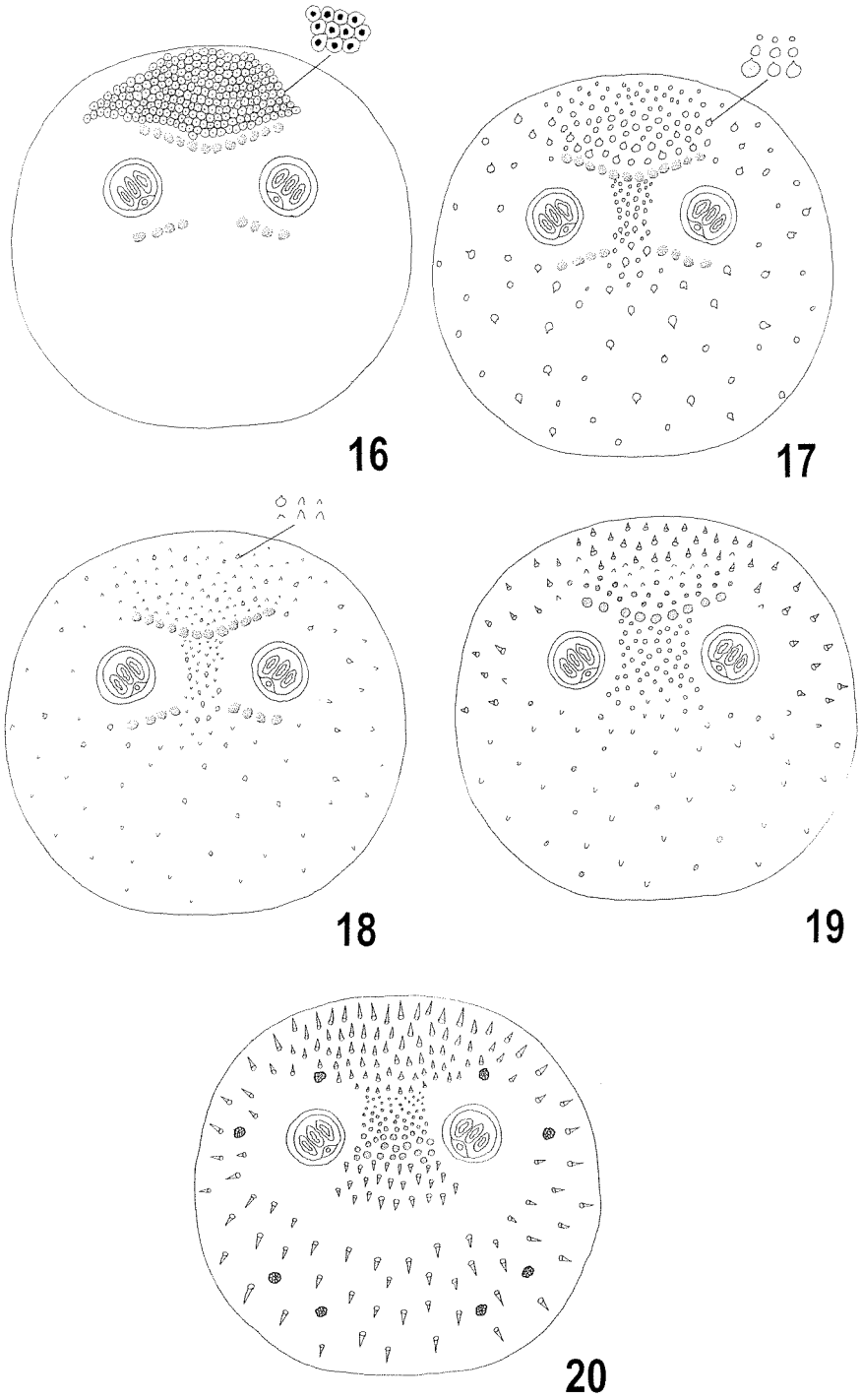
22. Posterior spine band reduced on all segments, extreme reduction or absent to rear; stigmatal spines sparse and short, most 25 μ or less; ventral band ratio to rear tends to be smaller 0.32 (0.29–0.36) (known from only two locations in Ontario) . . . . . *fallisi*

– Posterior spine band reduced or absent only toward rear; stigmatal spines closer together and longer, 25–30 μ (a few over 30 μ); ventral band ratio to rear tends to be larger 0.37 (0.31–0.47) . . . . . *aenea* (in part, eastern form)

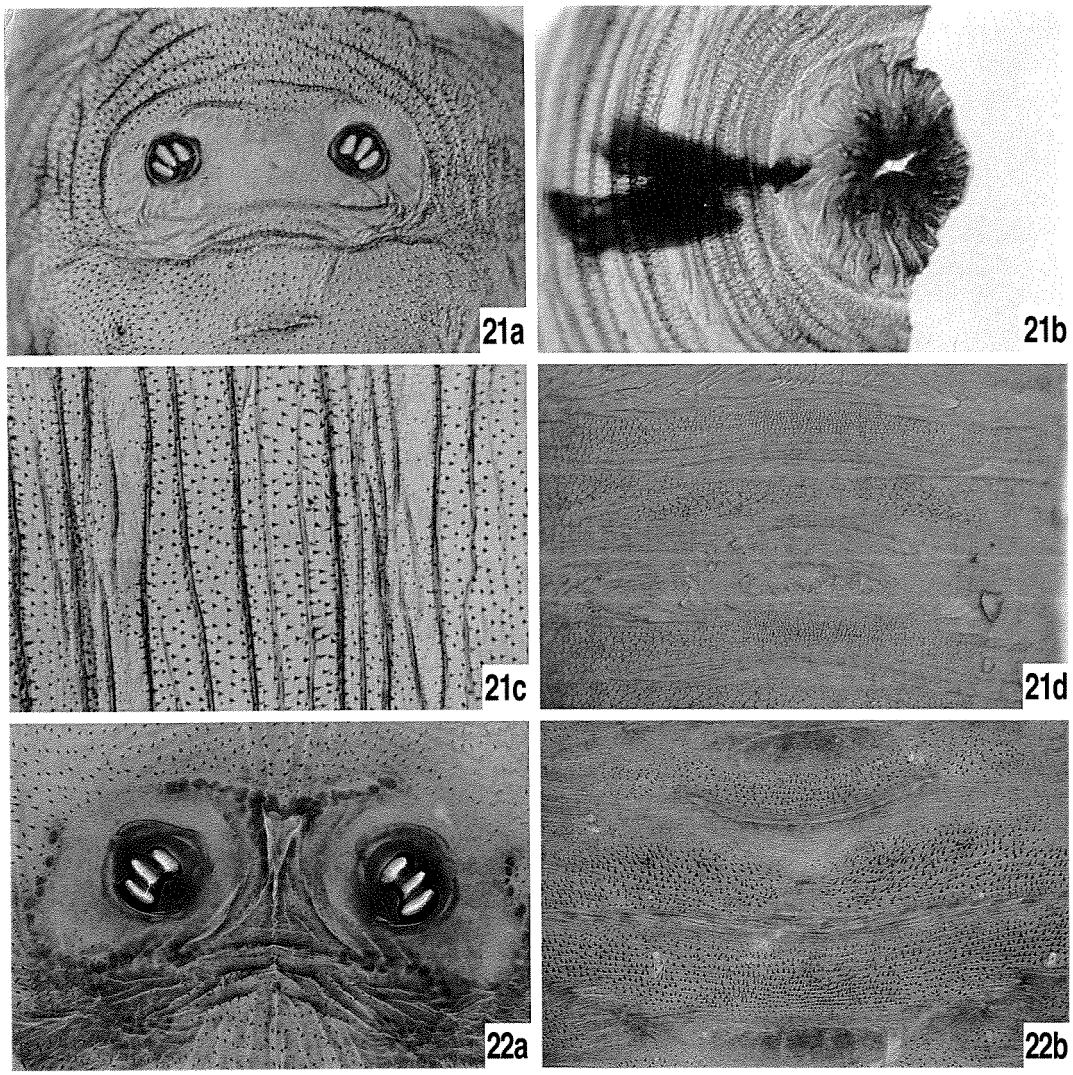
23. Hyperstigmatal spines exceptionally slender when viewed at 400× (Fig. 5); spine base may be broad, but upper half slender 24

– Hyperstigmatal spines usually medium (Fig. 4) 27

24. Known only from far eastern United States; ventral band ratio 0.63 (0.54–0.78); hyper-



Figs. 16–20. Puparia, stigmatal views. 16, *Protocalliphora metallica.* 17, *P. interrupta.* 18, *P. deceptor.* 19, *P. shannoni.* 20, *P. parorum.* Pattern of spines shown in the hyperstigmatal area of Fig. 16 occurs throughout the stigmatal area. Spines are denser than shown for Figs. 17–20.



Figs. 21–22. Puparia. 21, *Protocalliphora aenea* (top four figures): (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter. 22, *P. asiovora* (bottom two figures): (a) stigmatal view; (b) venter.

stigmatal area without folds; primarily in open nests of flycatchers and warblers *bicolor*

– Known primarily from western United States or Alaska (one record of *P. spatulata* in Canada, northeast of Wisconsin); ventral band ratio averages 0.66–1.0; hyperstigmatal area variable, no folds in one species, folds in two species 25

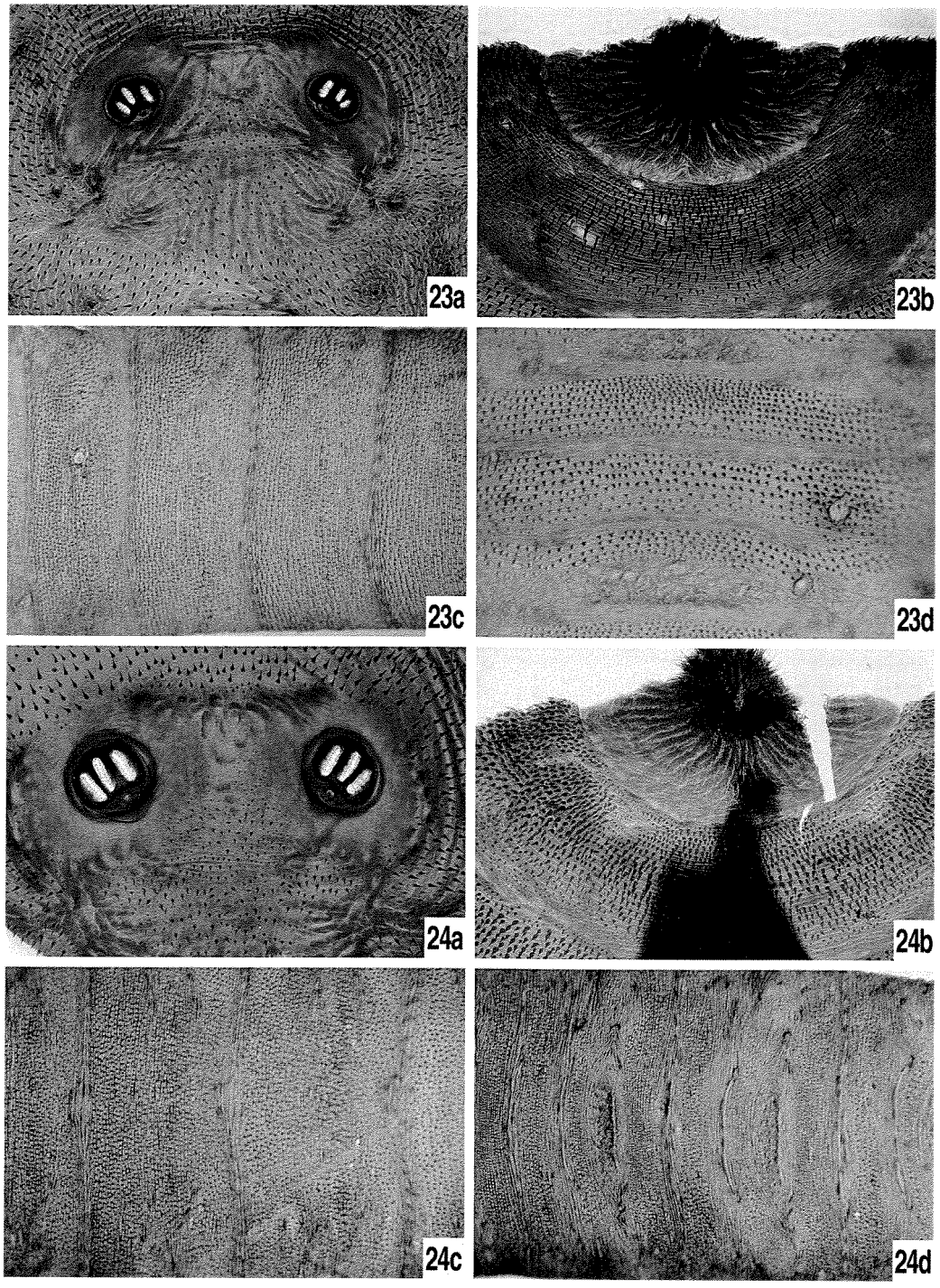
25. Mesostigmatal folds faint or absent (Fig. 30a); cuticle of hyperstigmatal area usually smooth; known primarily in warblers . . . . . *spenceri*

– Mesostigmatal folds pronounced; cuticle of hyperstigmatal area often very lumpy and uneven 26

26. Longest hyperstigmatal spines 25–30 μ; circumstigmatal folds faint to moderate; ventral band ratio averages 0.73 (0.67–0.84) (Fig. 28); known only from nests of horned lark, barn swallow, and bluebird, usually in desert habitats . . . . . *seminuda*

– Longest hyperstigmatal spines 30–50 μ; circumstigmatal folds pronounced (Fig. 29a); ventral band ratio averages 0.83 (0.72–1.0) (Fig. 11); known from nests of horned lark, rosy finch, several small sparrows, and water pipits; usually from high elevations or far north . . . . . *spatulata*

27. Mesostigmatal and hypostigmatal regions



Figs. 23–24. Puparia. 23, *Protocalliphora brunneisquama* (top four figures): (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter. 24, *P. hesperia* (bottom four figures): (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter.

with tubercles and a few short spines, spines sometimes longer and more abundant; longest hyperstigmatal and dorsal spines usually 35–50 μ (Figs. 20, 27a); broad row of small spines to rear of medial band (Figs. 13, 27b); ventral band ratios usually greater than 0.70 (0.58–0.87); prothoracic fringe 350–450 μ found in nests of chickadees, titmice, and wrens; western only ..... *parorum* (in part)

– Mesostigmatal and hypostigmatal regions with some distinct spines; longest hyperstigmatal spines 25–35 μ; ventral band ratios usually less than 0.70 (0.55–0.76); no small spines to rear of medial band or rows not as broad; prothoracic fringe 250–350 μ 28

28. Longest hyperstigmatal spines 25 μ or less, a few to 30 μ 29

– Longest hyperstigmatal spines usually 30 μ or more 31

29. Stigmatal folds broad, 0.30–0.50 μ wide, pronounced or moderate; mesostigmatal and hypostigmatal folds pronounced and irregular (Sabrosky, figs. 44a, b); ventral medial band not thinned in center; eastern or midwestern and north to Alaska; primarily in raptors and other large birds ..... *avium*

– Stigmatal folds, if present, narrower and moderate, faint or absent; mesostigmatal and hypostigmatal folds absent or, if present, faint and regular; ventral medial band, thinned in center toward rear 30

30. Spines of ventral medial band rarely irregular, never opposing on posterior segments (Fig. 10d); broad row of small spines to rear of medial band (Fig. 13, Whitworth 2002: fig. 1d); eastern United States, western Canada, and Alaska in cavity nests of chickadees, tree swallows, wrens, and starlings ..... *bennetti*

– Spines of ventral medial band include some irregular and a few opposing on posterior segments (Fig 10c); only a few rows of small spines to rear of medial band; western only, known primarily from warbler and flycatcher nests ..... *cuprina*

31. Ventral bands narrow, especially to rear, ratio usually 0.60 μ or less (Utah front averages 0.55, rear 0.45, Washington front averages 0.62, rear 0.55); found primarily in nests of barn swallows and phoebes; in Utah, sometimes posterior band much reduced to rear ..... *halli*

– Ventral bands wider, ratio usually 0.60 or more; found primarily in nests of robins, finches and chickadees 32

32. Few or no small spines to rear of medial band; very rare, usual host unknown (recorded only from a chipping sparrow and tree swallow nest); adult male with exceptionally long, slender surstyli, calypters dark brown both sexes ..... *brunneisquama*

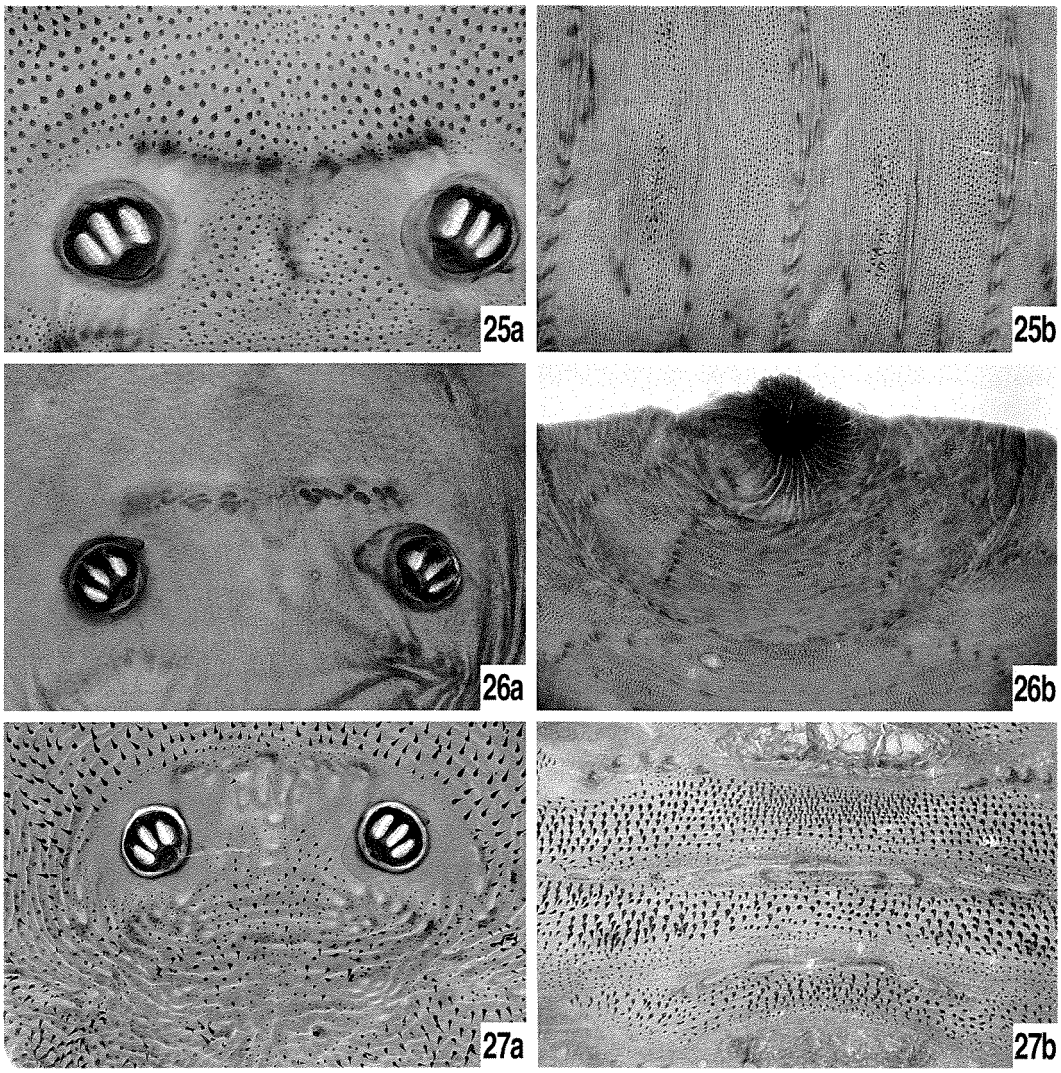
– Numerous small spines to rear of medial band 33

33. Broad rows of small spines to rear of ventral medial spine bands on many segments (Figs. 13, 27b); found in nests of chickadees, titmice, and wrens ..... *parorum* (in part)

– Some small spines to rear of ventral medial spine bands, rows not as broad; found in nests of robins and finches ..... *hesperia and hesperioides* (puparia currently indistinguishable)

Descriptions

In the discussion that follows, diagnostic characters for puparia of each species are given, voucher slides are identified, characters to distinguish similar species are discussed, and new host-parasite relationships and range expansions are given. Host-parasite data and range data from Sabrosky are also listed to help characterize species (Table 1). New descriptions of puparia are provided for two species, *P. brunneisquama* Sabrosky, Bennett, and Whitworth and *P. hesperia* Shannon and Dobroscky, which have not been previously described. Although I accept Bennett's puparial descriptions, I have identified some additional key characters that help distinguish species and these are given in the diagnoses and key. Users of the key should refer to Sabrosky and Whitworth (2002, 2003) for additional information on puparia and some useful illustrations to help distinguish puparial characters. Since no specific puparia were associated with each species in Sabrosky, I have designated voucher slides listed under each species. Where possible, voucher slides were selected from specimens used in the original puparial description or from types or paratypes for that species. If the puparia of a species demonstrates extreme variation, examples of each extreme are selected. Most slides from the original descriptions were prepared in the 1950's and some are of poor quality. Newer, better quality slides were selected if no good quality original slide is available. All voucher slides will be deposited with the Sabrosky, Bennett, and Whitworth collection of *Pro-*



Figs. 25–27. Puparia. 25, *Protocalliphora interrupta* (top two figures): (a) stigmatal view; (b) dorsum. 26, *P. metallica* (middle two figures): (a) stigmatal view; (b) prothoracic fringe. 27, *P. parorum* (bottom two figures): (a) stigmatal view, (b) venter.

tocalliphora at the National Museum of Natural History, Smithsonian Institution. Common bird names follow the "*Checklist of North American Birds*," 7th edition, American Ornithologists Union, 1998, 2002. New hosts and range expansions are noted; if new records are part of a research project the collector is identified. For new range information, the nearest town or map feature is identified.

Protocalliphora (P.) aenea Shannon and Dobroscky
(Fig. 21)

Diagnosis.—Puparia usually with posterior spine band reduced to rear and a ventral band ratio of 0.50 or less. This species has an eastern (Sabrosky: fig. 42) and a western form (Fig. 21), and they come out separately in the key. The following is a comparison of distinctive characters with the eastern

form first: dorsal cuticular ridges absent or faint vs. pronounced; mesostigmatal area with spines present vs. spines reduced to tubercles; ventral posterior spine band reduced or absent to rear vs. slight to moderate reduction to the rear; ventral band ratio averages 0.49/11 at front and 0.37/10 at rear vs. 0.58/8 at front and 0.48/8 at rear.

Voucher slides.—Eastern form: Barn swallow nest #48, Ontario, Canada, Algonquin Park, summer, 1955, Bennett. Western form: American dipper nest #4925-4, Cache County, Utah, Logan Canyon, summer 2001, Whitworth.

Similar species.—The eastern form is closest to *P. fallisi,* but *P. aenea* has less posterior band reduction and a larger ventral band ratio. The western form is similar to several species with pronounced dorsal ridges, but has a lower ventral band ratio and posterior ventral spine band reduced to rear. It is known almost exclusively from dipper nests in the west.

Hosts.—Western *P. aenea* were collected from nests of barn swallow, dipper, and Say's phoebe. Eastern *P. aenea* were collected from nests of common grackle, eastern phoebe, American robin, Louisiana water thrush, and house wren.

New range.—Collected near Kemmer, Wyoming. Sabrosky recorded western *P. aenea* from British Columbia, California, Colorado, Idaho, Oregon, Washington, and Utah; eastern *P. aenea* were recorded from Ontario, Quebec, Maine, New Hampshire, New York, Virginia, and West Virginia.

Discussion.—The eastern form of this species was never collected from eastern or midwestern United States during the current study despite the fact that six infested house wren nests and 30 infested eastern phoebe nests (known hosts) were examined within this species range. In 2001, it was found in two of three dipper nests under a bridge on Temple Fork Creek near Logan, Utah, where I had collected two nests infested with this species in 1971. It was also found in a barn swallow nest under a highway bridge near Kemmer, Wyoming. This is the first record of this species in a barn swallow nest in the west.

Sabrosky considered the possibility that the eastern and western forms of this species were separate species. They compared adult characters, found they overlapped, and concluded that the eastern and western forms represented a single species. I have compared puparia and found significant differences and, with apparent differences in host preference, I considered describing two separate species. However, I examined three *P. aenea* puparia collected by Halstead (1988) from dipper nests near Fresno, California, and they had only faint to moderate dorsal ridges and distinct spines in the mesostigmatal area unlike other western *P. aenea.* I believe it is prudent to wait until more specimens are collected in the west before determining the status of this species.

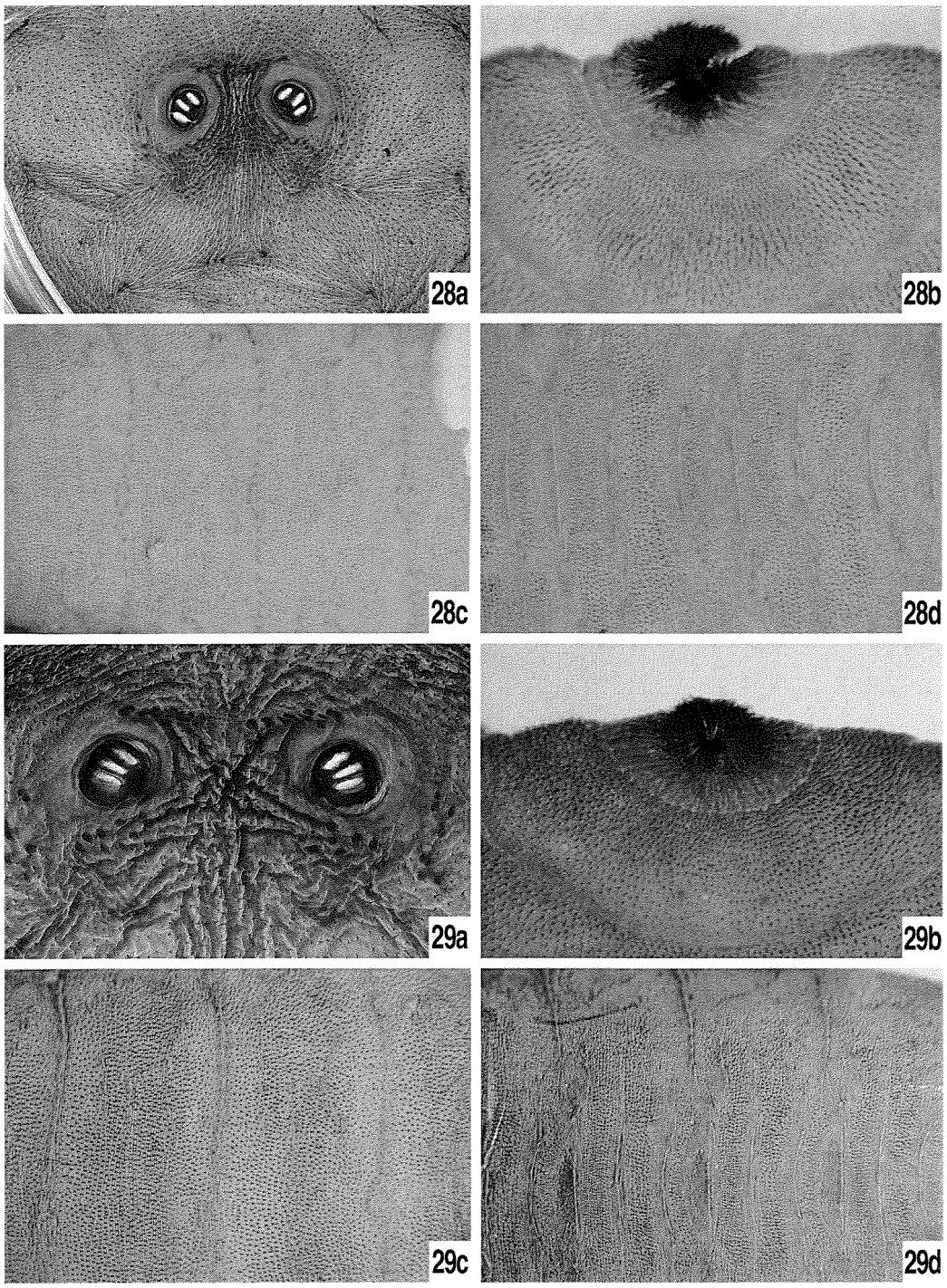
Protocalliphora (P.) asiovora Shannon and Dobroscky (Figs. 10e, 22)

Diagnosis.—The pronounced interruption on the midline of the ventral medial spine band (Figs. 10e, 22b) will usually separate this species from all others. This feature may be present on only some segments and some individuals in a series may lack it completely. Mesostigmatal folds moderate, hyperstigmatal spines dense, slender, and short, usually 25 μ or less (Fig. 22a). Dorsal and ventral ridges faint to absent.

Voucher slide.—Black-billed magpie nest, Okanogan County, Washington, June 6, 1939, W.L. Jellison, from puparial description.

Similar species.—*Protocalliphora interrupta* may have the midline of the ventral medial spine band reduced to tubercles (Fig. 10f), but in the stigmatal area all spines are reduced to tubercles (Fig. 25a). Slender hyperstigmatal spines would place with species at couplet 23 if interruption of medial spine band is missed.

New hosts.—Stellar's Jay, Tacoma, Washington. I also collected this species from a small hanging nest (bird species un-



Figs. 28–29. Puparia. 28, *Protocalliphora seminuda* (top four figures): (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter. 29, *P. spatulata* (bottom four figures): (a) stigmatal view; (b) prothoracic fringe; (c) dorsum; (d) venter.

known) high in a tree, in the Clarkston, Washington, area, this seems to be a very unusual host for this species.

Other hosts.—Sabrosky listed the species from many corvids, raptors and a variety of smaller passerines, including Brewer's blackbird, Amercian crow, mourning dove, golden eagle, house finch, northern goshawk, Cooper's, ferruginous, red-tailed and Swainson's hawks, pinyon jay, black-billed magpie, great horned and long-eared owls, common raven, American robin, loggerhead shrike, European starling, barn and cliff swallow.

Range.—Collected only in Washington in this study, Sabrosky listed it from most western states.

Discussion.—A Stellar's Jay nesting near Tacoma, Washington, had a clutch of 3 nestlings, and, about a week before they were old enough to fledge, a nestling was observed on the ground under the nest. I captured it and noticed it showed abundant scabs on its abdomen, possibly from feeding by *Protocalliphora* larvae. When I attempted to replace it in the nest, I found its two siblings had very recently died. The nestling refused to stay in the nest and ultimately disappeared. When the nest was examined, 60 mature third instar larvae were found in the nest. With the death of its siblings, larval feeding focused on the survivor and I suspect caused its premature fledging. Previous studies suggest populations of over 10 larvae per nestling make nestlings anemic (Whitworth and Bennett 1992).

Protocalliphora (P.) avium Shannon and Dobroscky

Diagnosis.—Broad, pronounced stigmatal and circumstigmatal folds, pronounced ridges on dorsum and venter (Sabrosky: fig. 44). Dorsal and ventral ridges occasionally faint, thus this species keys to two places in the key.

Voucher slide.—American crow nest #12, Algonquin Park, Ontario, Canada, summer 1951, Bennett.

Similar species.—Puparia are closest to *P. rugosa,* known only from the northwestern United States and British Columbia. The ranges of these two species do not overlap. *Protocalliphora hirundo* and *P. lata* are also similar, the former is primarily in swallow nests, the latter is found only in northwestern North America.

Hosts.—Not found in this study. Nests of favored hosts, raptors and corvids in its range, were not examined.

Range.—Eastern and midwestern United States, Canada and Alaska.

Discussion.—Sabrosky debated whether this species is distinct from its sister species *P. asiovora,* based on adult features. Puparia of *P. asiovora* are very different, leaving little doubt they are distinct species (Fig. 22).

All characters were described from Bennett's slides, some have dorsum and venter with ridges faint to absent. These slides are 50 years old, and it is uncertain if this condition actually exists, is a processing anomaly, or an effect of age.

Protocalliphora (P.) bennetti Whitworth (Fig. 10d)

Diagnosis.—Dorsal ridges faint to absent, ventral spine bands usually regular though the medial band may be thinned and irregular (Fig. 10d) and has several rows of small spines to the rear similar to *P. parorum* (Fig. 13). This species is one of several remaining after puparia of species with distinct characters have been keyed. Puparia are illustrated and described by Whitworth (2002).

Voucher slide.—Carolina chickadee nest #3351-4, Roanoke, Virginia, May, 2000, Whitworth, from type series.

Similar species.—*Protocalliphora cuprina* puparia are closest to this species, their ranges overlap in the northwestern United States and Canada. The medial band of *P. cuprina* is usually thinned with some spines irregular, but rarely opposing (Fig. 10c). Other similar species include *P. halli, P. brunneisquama, P. parorum, P. hesperia,*

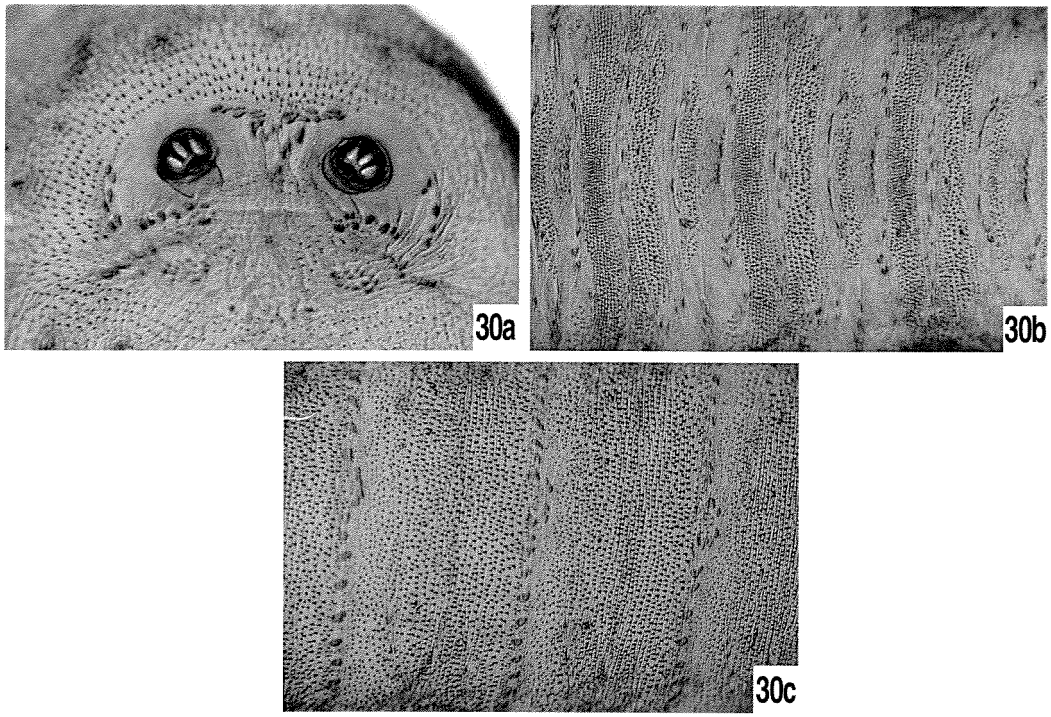


Fig. 30. Puparia. *Protocalliphora spenceri*: (a) stigmatal view; (b) venter; (c) dorsum.

and *P. hesperioides*. Adults are intermediate between *P. shannoni* and *P. sialia* and are difficult to distinguish. This species is known primarily from chickadee, tree swallow, and house wren nests, which will help distinguish it from similar species.

Hosts.—New host found in an eastern phoebe nest from Sevier County, Tennessee, submitted by Will Reeves, Clemson University. Also found in nests of boreal, black-capped, and Carolina chickadee, European starling, tree swallow, and house wren. Eastern bluebird, listed as a host in Whitworth (2002), was an error.

Range.—Sevier County, Tennessee, Whitworth (2002) also listed Alaska, Maine, Massachusetts, Minnesota, New York, Virginia, West Virginia, British Columbia, Ontario, and Saskatchewan.

Discussion.—This species was discovered while analyzing data for this study (Whitworth 2002).

Protocalliphora (P.) bicolor Sabrosky, Bennett, and Whitworth

Diagnosis.—Slender hyperstigmatal spines (Fig. 5), no posterior spine band reduction, known only from the northeastern United States, primarily in warbler and vireo nests.

Voucher slide.—American redstart nest, Holderness, Hew Hampshire, August 10, 1930, Mrs. Harding, from puparial description.

Similar species.—*Protocalliphora tundrae* has slender hyperstigmatal spines, but the posterior spine band is reduced to the rear. This species has been found only in northern Canada and Greenland. Other species with slender hyperstigmatal spines are found only in the west.

Hosts.—Sabrosky listed this species from nests of flycatchers, warblers, vireos, and American Goldfinch.

Range.—New York, New Hampshire, Wisconsin, Ontario.

Discussion.—This species was not collected during this study, though many nests were examined from its known range. Nests of favored host species were rarely collected, and most nests examined were from nest boxes. Most specimens examined were old slides from Bennett's collection. This species may be the ecological counterpart of *P. cuprina* which has similar hosts in the west.

Protocalliphora (Trypocalliphora) braueri (Hendel)

Diagnosis.—Sparse dorsal cuticular spines, ventral medial spine band absent, prothoracic fringe absent. Stigmatal folds weak in eastern material, often pronounced in the west (Sabrosky: figs. 46a, b). Larvae are obligate subcutaneous parasites.

Voucher slide.—Eastern form: House wren nest #2804-4, Hiwassee, Virginia, June 24, 1999, Whitworth. Western form: Tree swallow nest #4213-1, Umtanum Ridge, Kittitas County, Washington, July, 2000, Whitworth.

Similar species.—Most likely to be confused with sparsely spined puparia of sarcophagids or other genera of calliphorids which may be found in nests with dead nestlings. Sarcophagids have their posterior spiracles in a deep cavity, whereas spiracles in calliphorids are flush with the surrounding cuticle. Other genera of calliphorids usually have spine bands limited to the intersegmental area.

New hosts.—Black-capped chickadee, Tacoma, Washington; cedar waxwing, Eatonville, Washington; American kestrel, Saskatoon, Saskatchewan. Revels (1996) recorded it from black and white warbler, Kentucky warbler, and yellow-throated vireo. I have examined additional material from Revels, Northeastern State University, Talequah, Oklahoma, and found this species from hooded and Swainson's warbler nests collected near Idaho Falls, Idaho. Also collected from nests of American robin and European starling. Sabrosky listed numerous additional hosts.

New range.—Black Earth and Sheldon, Wisconsin. Revels (1996) recorded Arkansas. This species is widespread throughout North America, though it was considered rare in the east by Sabrosky.

Discussion.—Many Europeans place this species in the genus *Trypocalliphora* (Rognes 1985), while North Americans consider it only a subgenus of *Protocalliphora* (Sabrosky). I have followed the usage in Sabrosky for consistency, but suspect it deserves full genus status. Bennett (in Sabrosky) described larvae of this species as having a short prothoracic fringe averaging 7 μ (3–10 μ), but larvae I examined had no discernable fringe. Cais (1965) compared the larvae of three species of European *Protocalliphora.* His illustrations show no prothoracic fringe in *P. hirudo* (= *P. braueri*) while showing a prominent fringe in the other two species. Larvae of this species are obligate subcutaneous parasites while species of the subgenus *Protocalliphora* are occasionally found in ears and nares, they are almost never subcutaneous. When these immature characters are considered with the distinctive aedeagus in the male and the lack of reclinate upper orbital bristles in the female, a strong case can be made that *Trypocalliphora* deserves full genus status.

This species was common in western Oregon, western Washington, and western British Columbia, where other species of *Protocalliphora* were often uncommon. In one group of 90 infested nest boxes examined near Tacoma, Washington, 63 (70%) were infested by this species (Bennett and Whitworth 1991). This species was uncommon in the rest of the west and occasionally found throughout most of North America.

Protocalliphora (P.) brunneisquama Sabrosky, Bennett, and Whitworth (Fig. 23)

Diagnosis.—Hyperstigmatal spines to 33 μ, mesostigmatal spines 10–15 μ, ven-

tral band ratio anterior end 0.76, posterior end 0.67.

Voucher slide.—Tree swallow nest #4864-2, see data below.

Similar species.—Puparia of this species have no distinctive characters, they key near *P. parorum, P. hesperia,* and *P. hesperioides.*

Range.—Sabrosky listed it from California, Colorado, Idaho, Montana, New Mexico, Utah, and Washington.

New hosts.—Five adults were reared from 15 puparia found in a tree swallow nest from Corona, California. I previously found this species in a chipping sparrow nest in Utah, but puparia were undersized and not suitable for use in a description (Sabrosky). I have concluded the listing of brown towhee as a host for *P. lata* in Sabrosky was a misidentification and, in fact, the specimens were *P. brunneisquama.* See comments under *P. lata.*

Discussion.—Thirty-one other infested tree swallow nests were examined in California and this species was not found again. It also was not found in several hundred other tree swallow nests throughout its range, so its favored host is not likely tree swallows. Puparia of this species were not described in Sabrosky, a description follows: Length 7.2 mm (7–8 mm)/9; breadth 3.5 mm (3–4 mm)/9; posterior region (Fig. 23a): Stigmatal plates 181 μ (175–198 μ)/4; distance between buttons 580 μ (540–630 μ)/4; and width of stigmatal area across stigmatal plates 1,144 μ (1,100–1,200 μ)/4; stigmatal ratio 0.51(0.49–0.53)/4. Upper mesostigmatal area tubercles or short spines, lower area spines to 15 μ, folds absent; hyperstigmatal spines numerous, longest spines to 33 μ (25–33 μ); hypostigmatal area spines to 25 μ (15–25 μ); circumstigmatal folds faint. Dorsal cuticle (Fig. 23c): Spines to 37.5 μ (35–37.5 μ), ridges faint. Ventral cuticle (Fig. 23d): Ventral band ratio, anterior end 0.76(0.73–0.80)/4, posterior end 0.67 (0.61–0.73)/4. Diameter of prothoracic fringe 300 μ (250–350 μ)/4 (Fig. 23b).

Basis for description.—5 adults, 15 puparia, Corona, California, tree swallow nest #4864, May 29, 2001.

Protocalliphora (P.) cuprina (Hall)
(Fig. 10c)

Diagnosis.—Posterior, ventral spine band may or may not be reduced to the rear, medial band thinned on the midline toward rear, usually some irregular spines and a few opposing (Fig. 10c); longest hyperstigmatal spines to 25 μ (Sabrosky: fig. 48). Keys to two places because characters are variable. Narrow host preferences, primarily in warbler and flycatcher nests, western only.

Voucher slide.—Western wood pewee nest #1255, Franklin Basin, Cache County, Utah, August 10, 1971, Whitworth, from puparial description.

Similar species.—*Protocalliphora halli,* see discussion below.

New hosts.—Plumbeous vireo, Mt. Trumbull, Arizona; song sparrow, blue headed and warbling vireo, submitted by Revels, from Idaho Falls area, Idaho; also found in barn swallow and yellow warbler. I have examined a puparial slide prepared by Bennett labeled USNM X-20 which lists collector as Neff in California (loggerhead) shrike as host. Bennett had not written species identification on the slide, but Sabrosky listed this host for *P. asiovora* from Neff in California. I have keyed this specimen to *P. cuprina,* which would be an unusual host. It is possible Bennett misidentified this slide and if so, the listing for *P. asiovora* should be changed to *P. cuprina.* Sabrosky listed it from finches, kingbirds, wood pewees, and warblers.

New range.—Mt. Trumbull, Arizona; also found in British Columbia, Oregon, and Washington in this study. Sabrosky listed it from California, Idaho, Montana, Utah, and Wyoming.

Discussion.—Puparia of this species can be difficult to separate from numerous others, but its narrow host preferences eliminate most similar species, except *P. halli.*

This species has been found in mixed infestations with *P. halli* in barn swallow nests in Washington and Oregon. Both species have ventral medial band thinned, differences include *P. cuprina* rarely has opposing spines on medial band (Fig. 10c) vs. *P. halli* often has opposing spines on the rear margin and toward the rear (Fig. 10b); *P. cuprina* usually has shorter hyperstigmatal spines, 25 μ or less vs. 30 μ or more in *P. halli*; ventral posterior band usually with only small reductions to rear vs. some specimens with extreme reduction to the rear in *P. halli.*

Protocalliphora (P.) deceptor Sabrosky, Bennett, and Whitworth
(Fig. 18)

Diagnosis.—Hyperstigmatal spines reduced to small tubercles with tiny spine projections when viewed at 450× (Fig. 18).

Voucher slide.—Eastern phoebe nest USNM 556-236, Shenandoah, Virginia, July 21, 1956, A. Wetmore.

Similar species.—*Protocalliphora interrupta* is similar but has larger round hyperstigmatal tubercles (Figs. 17, 25a), ventral posterior spine band reduced to rear, ventral medial spine band reduced to tubercles on midline (Fig. 10f). *Protocalliphora metallica* is similar, but hyperstigmatal tubercles are usually smaller, surrounded by cell-like borders (Figs. 16, 26a), and the tubercles do not have spine projections. Occasional *P. deceptor* have hyperstigmatal tubercles with cell-like borders and no spine projections, very similar to *P. metallica.* However, *P. deceptor* tubercles are larger, and spines of anterior spine band are longer. Occasionally *P. shannoni* have short hyperstigmatal spines (2.5–7.5 μ) or tubercles and will key to *P. deceptor.* Mesostigmatal spines and tubercles in *P. shannoni* are usually very sparse, those in *P. deceptor* are usually dense. *Protocalliphora shannoni* favors robins and thrushes throughout North America, while *P. deceptor* favors chickadees, warblers, and wrens, only in eastern Northern America.

New hosts.—Eastern bluebird, Mt. Pleasant, Texas; black-capped chickadee, Coweta, Oklahoma; barn swallow, Paris, Texas; eastern towhee, Charleston, South Carolina; hooded and prothonotary warblers, Richmond, Virginia; Swainson's warbler, Ozark National Forest, Arkansas, Mia Revels; Bewick's wren, Norman, Oklahoma. Also recorded by Revels (1996) from nests of acadian flycatcher and Bachman's sparrow. Other hosts found in this study include Carolina chickadee, northern cardinal, common grackle, eastern phoebe, tree swallow, tufted titmouse, yellow warbler, Carolina wren, and house wren. Sabrosky also listed it from brown-headed cowbird, American crow, great-crested flycatcher, northern mockingbird, wood thrush, and prairie and worm-eating warblers.

New range.—Arkansas, Fayetteville; Palatine, Illinois; Ashland, Kentucky; Peru, Nebraska; Newtonville, New Jersey; Mt. Morris, New York; Ada, Oklahoma; Lebanon, Pennsylvania; Mt. Pleasant, Texas; Beaver Dam, Wisconsin; other states are Delaware, Georgia, Indiana, Missouri, North Carolina, Ohio, South Carolina, Tennessee, Virginia. Sabrosky listed it throughout the eastern United States, west to Missouri and south to Mississippi.

Discussion.—This species sometimes infests nests favored by *P. sialia* in the southeastern and lower midwestern United States where *P. sialia* was not collected (Whitworth 2003).

Protocalliphora (P.) fallisi Sabrosky, Bennett, and Whitworth

Diagnosis.—Extreme ventral posterior spine band reduction, short hyperstigmatal spines (25 μ or less), ventral band ratio at rear averages 0.32 (Sabrosky: fig. 50). Known only from Ontario.

Voucher slide.—Host not identified, nest #54-568-5, Ontario, possibly Algonquin Park, summer 1954, Bennett. The only puparia found for this species were 11 slides prepared by Bennett, most were in poor condition.

Similar species.—*Protocalliphora aenea* occurs in the same area, but has less reduction of the posterior ventral spine band and longer hyperstigmatal spines.

Hosts.—Sabrosky listed red-winged blackbird, common grackle, swamp and white-throated sparrows, rough-winged swallow, and downy woodpecker.

Range.—Known only from two locations in Ontario.

Discussion.—Key characters for this species were taken from a few poor quality slides in the Bennett collection and Bennett's description in Sabrosky. This species was not collected during this study.

Protocalliphora (P.) halli Sabrosky, Bennett, and Whitworth (Figs. 10b, 12, 14)

Diagnosis.—Posterior spine band on venter often reduced to rear. Medial spine band on venter thinned in middle, often with opposing spines on rear edge (Fig. 10b). Opposing spines are usually most evident on the last three segments, and may just involve a few spines. Posterior band variable from significant reduction to none, longest hyperstigmatal spines 30 μ or more, low ventral spine band ratios.

Voucher slides.—Three voucher slides are designated because of extreme variations in puparia of this species. Barn swallow nest #245 (TW4-4), Logan, Utah July 9, 1970, Whitworth, used by Bennett to describe puparia of this species, exhibits extreme reduction of ventral posterior band to rear. Barn swallow nest 1155-4, Logan, Utah, July 11, 1971, Whitworth from holotype series, not used by Bennett for puparial description, only slight reduction of posterior band to rear. Barn swallow nest 5186-1, Bellingham, Washington, summer 2001, Whitworth, posterior band not reduced to rear.

Similar species.—Very close to *P. cuprina* and sometimes found in mixed infestations with it. *Protocalliphora cuprina* usually has shorter hyperstigmatal spines, to 25 μ, and few opposing spines on the rear margin of the ventral medial band (Fig. 10c).

Hosts.—Known primarily from barn swallows, also black and Say's phoebes, (Sabrosky).

New range.—Scappoose, Oregon; Bellingham and Tacoma, Washington; Grants, New Mexico. Sabrosky also listed California, Utah, Wyoming, and British Columbia.

Discussion.—Puparia from Washington and Oregon did not show the extreme reduction of the ventral posterior band as described in Sabrosky. I re-evaluated all Utah material, including lot #1155, which was the basis for the puparial description, and it was accurate. However this lot was nontypical and puparia from an additional 140 *P. halli* infested nests from Utah and Wyoming rarely had such extreme reduction. I originally thought this variation represented a separate species, but all adults were similar and some posterior band reduction to the rear was observed from a variety of series throughout *P. halli's* range.

Sabrosky listed pine grosbeak as a new host for this species from my nest #414 near Logan, Utah, collected July 22, 1970. A re-examination of the material, including three puparial slides, revealed they are actually *P. hesperia.*

Protocalliphora (P.) hesperia Shannon and Dobroscky (Fig. 24)

Diagnosis.—Hyperstigmatal spines to 30 μ (rarely to 35 μ), folds faint or absent, dorsal spines to 40 μ, dorsal ridges faint to absent, ventral band ratio averages 0.65 (0.55–0.76)/25 (Figs. 24a–d).

Voucher slide.—Barn swallow nest, Gold #1, Adin Bridge, Modoc County, California, August 6, 1978, C.S. Gold, from paratypes, see description below.

Similar species.—Puparia of *P. hesperioides* are very similar, and *P. parorum* puparia with spines in mesostigmatal area are also similar, but this species has a broad row of small spines to the rear of the posterior spine band.

New hosts.—Pine grosbeak, parasite misidentified in Sabrosky as *P. halli,* see note under that species. Swainson's and varied thrush, from Steve Matsuoka, United States Geological Survey, Anchorage, Alaska; veery, from Mia Revels, Idaho Falls area, Idaho and hermit thrush, Mogollon Rim, Arizona. Sabrosky listed other hosts including American robin, house finch, and barn swallows.

Range.—Idaho Falls, Idaho; Mogollon River, Arizona, Sabrosky also listed Alaska, British Columbia, California, Oregon, Washington, and Utah.

Discussion.—Hyperstigmatal spine length was variable throughout this species range, some specimens longest spines were only 25 μ. Bennett did not describe puparia of this species in Sabrosky, therefore a description follows: Length 7.5 mm (7.1–7.7)/8; breadth 3.3 mm(3.0–3.5)/8. Posterior region: Stigmatal plates 164 μ (145–198 μ)/27 in diameter; distance between buttons 514 μ (440–650 μ)/27; and across the stigmatal plates 1,074 μ (820–1,300 μ)/27; stigmatal ratio 0.48(0.44–0.50)/27; mesostigmatal spines short to 15 μ, folds faint to absent, a few moderate; hyperstigmatal spines to 35 μ, folds faint to absent; hypostigmatal spines to 15 μ, folds moderate to absent (Fig. 24a). Dorsal cuticle: Spines to 40 μ, ridges faint to absent, rarely moderate (Fig. 24c). Ventral cuticle: Ventral band ratio 0.65(0.55–0.76)/25; ridges faint to absent (Fig. 24d). Diameter of prothoracic fringe 300 μ (275–325 μ)/10 (Fig. 24b).

Basis for description.—Alaska: 6 slides, Kenai, gray jay or thrush, June 10, 1978, G.E. Haas; 4 slides, Anchorage, varied thrush nest #KMB012, June 26, 1998, Steve Matsuoka, United States Geological Survey. California: 3 slides, Modoc County, Adin Bridge, barn swallow, August 6, 1978. Utah: Logan, 3 slides, American robin nest #350, July 17, 1970; 3 slides, Pine grosbeak nest #414, July 22, 1970; 1 slide, Cassin's finch nest #499, August 7, 1970; 8 slides, American robin nest #534, June 22, 1980; 2 slides, American robin nest #927, June 25, 1971.

Protocalliphora (P.) hesperioides Sabrosky, Bennett, and Whitworth

Diagnosis.—Puparia currently indistinguishable from *P. hesperia.* See discussion.

Voucher slide.—House finch nest, Anaheim, California, July, 1936, A.J. Basinger, from paratypes.

Similar species.—Currently puparia of this species are indistinguishable from *P. hesperia. Protocalliphora hesperioides* can be confused with *P. brunneisquama, P. cuprina, P. halli,* and *P. parorum.*

Hosts.—Sabrosky listed bushtit, house finch, goldfinch species, dusky and western flycatcher, and yellow warbler.

Range.—California, Washington, and British Columbia.

Discussion.—This species was not collected during this study, and only 10 puparia were available for study. Bennett described this species as having pronounced stigmatal folds (Sabrosky: fig. 52), but in all the material I examined (including 5 of Bennett's slides) stigmatal folds ranged only from faint to moderate. As more material becomes available, distinctive characters may be found.

Protocalliphora (P.) hirundo Shannon and Dobroscky

Diagnosis.—Broad pronounced dorsal cuticular ridges, stigmatal area with a few pronounced folds, mesostigmatal and hypostigmatal area with distinct spines (Whitworth 2002: figs. 3a, b).

Voucher slide.—Swallow species (probable cliff swallow), Ventura, California, June 23, 1949, J.N. Belkin, from puparial description.

Similar species.—*Protocalliphora lata* also has broad dorsal cuticular ridges, but the mesostigmatal and hypostigmatal areas are usually bare. *Protocalliphora rugosa* has pronounced ridges and folds, but they are more abundant and closer together than in *P. hirundo.*

Hosts.—During this study *P. hirundo* was found in nests of cliff, tree, barn and bank swallows. Sabrosky also listed the species from yellow-headed blackbirds, eastern bluebirds, common grackles, eastern phoebes, and European starlings. Sabrosky also listed it from nests of purple martins and violet-green swallows, but most of these hosts in the west were actually infested by *P. rugosa.*

Range.—During this study, *P. hirundo* was found in Washington and Oregon; Sabrosky listed it from Maine to Washington, south to southern California and north to Alaska.

Discussion.—I recently described a new species, *P. rugosa,* which Sabrosky did not distinguish from *P. hirundo* (Whitworth 2002). As adult and puparial descriptions found in Sabrosky were based on *P. hirundo,* there is no need to redescribe this species.

Bennett (in Sabrosky) described ventral band ratio averaging 0.53 (0.40–0.74); however, I measured 36 specimens from many different areas and my specimens averaged 0.65 with a range of 0.48–0.79. Occasional aberrant specimens had very low ratios, ventral band ratios were sometime difficult to measure in these heavily ridged puparia.

Protocalliphora (P.) interrupta Sabrosky, Bennett, and Whitworth (Figs. 10f, 17, 25)

Diagnosis.—Hyperstigmatal spines reduced to tubercles and short spines (Figs. 17, 25a). Posterior band on venter reduced to rear, medial band reduced to tubercles on midline (Fig. 10f). Prothoracic fringe exceptionally short, averaging 225 μ (200–250 μ).

Voucher slide.—Yellow-headed blackbird nest #104-1, Mendon, Cache County, Utah, June 18, 1970, Whitworth, from puparial description.

Similar species.—Other species with hyperstigmatal spines reduced include *P. deceptor* (Fig. 18), and *P. metallica* (Fig. 16).

New hosts.—House finch, Tacoma, Washington; yellow-breasted chat, and McGillivray's warbler, Idaho Falls, Idaho, Mia Revels. Other hosts found during this study are long-billed marsh wrens and Brewer's blackbirds. Sabrosky also listed yellow-headed, and red-winged blackbirds and song sparrow.

New range.—Idaho Falls, Idaho; Tacoma, Washington, Sabrosky also listed Utah, California, and British Columbia.

Discussion.—A long series of *P. interrupta* reared from a brewer's blackbird nest in Washington included aeneous adult females that would key to *P. aenea* in couplet 3 of the adult key in Sabrosky. I initially suspected this was a new species, but after analyzing adults and puparia of Washington and Utah material I found puparia were essentially the same. Some aeneous adult females were also found in the Utah material and this appears to be a genetic variation which is often scattered through specimens in a reared series, this condition was not noted in the original description. If males and puparia are available, these two species are readily distinguished since *P. aenea* surstyli are digitate while *P. interrupta* surstyli are slender and curved; also in puparia, the hyperstigmatal area has distinct spines vs. spines reduced to tubercles in *P. interrupta* (Fig. 17).

Protocalliphora (P.) lata Sabrosky, Bennett, and Whitworth

Diagnosis.—Broad, pronounced dorsal cuticular ridges, mesostigmatal and hypostigmatal areas few or no spines, puparia to 13 mm; the largest known species of *Protocalliphora* (Sabrosky: fig. 55).

Voucher slide.—American kestrel nest #380-1, Mendon, Cache County, Utah, July 20, 1970, Whitworth, from puparial description and type series.

Similar species.—*Protocalliphora hirundo* is similar, but the mesostigmatal and hypostigmatal areas have abundant spines and puparia are, at most, 9 mm in length.

Hosts.—Found in northern flicker, Sabrosky also listed red-tailed hawk, northern goshawk, American kestrel, and brown towhee. The identification of *P. lata* in to-

whees appears to be an error. Sabrosky mentioned the larval description for *P. lata* was based on 3 specimens from Anaheim, California. I have found 3 Bennett slides (2 larvae and 1 puparium) from Anaheim, California that list "towhee" as host. The specimens are clearly not *P. lata* and key to *P. brunneisquama.* I have concluded this was a misidentification. I dropped towhee as a host for *P. lata* and have listed it under *P. brunneisquama.*

Range.—British Columbia, California, Idaho, Oregon, Idaho, and Utah.

Discussion.—Karen Weibe, University of Saskatchewan, Saskatoon sent specimens from two northern flicker nests that I confirmed were *P. lata.* She reported seeing some large larvae (almost certainly *P. lata*) attached to flicker nestlings each year near Riske Creek, British Columbia. I also found this species in flicker nests in Utah and Idaho, but the nests were so fouled with nestling excrement that the larvae usually died before maturing (Bennett and Whitworth 1992). Karen noted that her flicker nests were sometimes not so foul and I suspect flickers are a common host for this species.

Protocalliphora (P.) metallica (Townsend) (Figs. 16, 26)

Diagnosis.—Stigmatal area covered with tiny tubercles surrounded by cell-like walls (Figs. 16, 26a). Walls occasionally not visible so only tiny tubercles are present. These features are minute and best seen at 450× in a slide mount.

Voucher slide.—Common grackle nest #144, Algonquin Park, Ontario, Canada, Summer 1955, Bennett, from puparial description.

Similar species.—*Protocalliphora deceptor* has stigmatal spines reduced, but with short spine projections (Fig. 18), *P. interrupta* has larger stigmatal tubercles (Fig. 17) and posterior spine bands reduced to the rear.

New hosts.—Northern mockingbird, Gilford, New Hampshire; mourning dove, Hanover, Michigan; white-crowned sparrow, Tacoma, Washington; yellow-rumped warbler, Anchorage, Alaska. Revels (1996) recorded it from MacGillivray's warbler. Other hosts found during this study include Brewer's blackbird, red-winged blackbird, gray catbird, sparrow sp., and tree swallow. Sabrosky listed it from many hosts.

New range.—Anchorage, Alaska and Lenoir City, Tennessee; also collected from Iowa, Illinois, Massachusetts, Maryland, Michigan, Minnesota, New Hampshire, New York, Virginia. Sabrosky found it widespread in the United States and in British Columbia.

Protocalliphora (P.) occidentalis Whitworth

Diagnosis.—Prothoracic fringe 500 μ in diameter or longer. Dorsal cuticular ridges pronounced. Stigmatal area with folds faint or absent; mesostigmatal area with spines reduced to tubercles; ventral band ratio averages 0.72; western North America. Puparial characters are illustrated in Whitworth (2003).

Voucher slides.—Mountain bluebird nest 2926-2, Eureka, Nevada, September 13, 1999, Whitworth.

Similar species.—*Protocalliphora pararum* with diameter of prothoracic fringe 450 μ or less. *Protocalliphora sialia* is very similar and was, until recently, considered the same species. See Whitworth (2003) for a detailed discussion.

New hosts.—From nests contributed by Don Dahlsten, University of California, Berkeley, red-breasted nuthatch, pygmy nuthatch, and Bewick's wren, all nests from central California, dark-eyed Junco from Idaho Falls area, Mia Revels.

New range.—Eureka, Nevada. Also collected from Arizona, California, Colorado, Idaho, Montana, New Mexico, Oregon, Utah, Washington, Wyoming, and British Columbia.

Protocalliphora (P.) parorum Sabrosky, Bennett, and Whitworth (Figs. 13, 20, 27)

Diagnosis.—Dorsal cuticular ridges usually moderate, occasionally faint or absent. Usually a broad row of small spines to the rear of the anterior and medial ventral spine bands (Figs. 13, 27b); mesostigmatal area often with spines reduced to tubercles (Figs. 20, 27a). Prothoracic fringe long, to a diameter of 450 μ. Narrow host range, primarily in chickadees, nuthatches, titmice, and wrens.

Voucher slide.—Mountain chickadee nest A2840, Modoc County, California, early 1980's, C.S. Gold, from puparial description.

Similar species.—Close to *P. occidentalis,* but the difference in prothoracic fringe diameter usually separates them (500 μ or more in *P. occidentalis* vs. 450 μ or less in *P. parorum*). *Protocalliphora parorum* tends to have distinct circular anal tubercles (Fig. 20) while *P. occidentalis* tends to have less distinct, more irregular tubercles. Dorsal cuticular ridges are usually moderate in *P. parorum* and pronounced in *P. occidentalis.* Adult males are readily distinguished: *P. parorum* surstyli are long and slender, *P. occidentalis* surstyli are digitate.

New hosts.—Western bluebirds and white-breasted nuthatch, Flagstaff, Arizona. Additional new hosts from material contributed by Don Dahlsten, University of California, Berkley, included ash-throated flycatcher, pygmy nuthatch, tree swallow, and oak titmouse. Other hosts found in this study include black-capped, mountain, and chestnut-backed chickadee, house and Bewick's wren. Sabrosky also listed brown creeper, red-breasted nuthatch, barn swallow, and Oregon (dark-eyed) junco.

New range.—Arizona, Colorado, Idaho, New Mexico, Oregon, Washington, and British Columbia, Canada. Sabrosky also listed California and Utah.

Discussion.—This species often has most mesostigmatal spines reduced to tubercles, like *P. occidentalis.* Specimens usually have a few short spines, some have no spines, and a few have abundant spines. When many distinct spines are present in the mesostigmatal area, this species is difficult to distinguish from *P. brunneisquama* and *P. hesperia.* Puparia of this species are variable throughout its range, thus it appears three times in the key.

Protocalliphora (P.) rognesi Thompson and Pont

Protocalliphora chrysorrhoea: Sabrosky et al. 1989; Bennett and Whitworth 1991, 1992; Whitworth and Bennett 1992; Koslov and Whitworth 2002.

Diagnosis.—Pronounced dorsal ridges, long hyperstigmatal spines, to 50 μ, prothoracic fringe 350–400 μ, almost exclusively in bank swallows (Sabrosky: fig. 47).

Voucher slide.—Bank swallow nest, Tok, Alaska, July 14, 1948, R. Sailer, from puparial description.

Similar species.—*Protocalliphora parorum, P. occidentalis,* and *P. sialia* are similar, but the former has only tubercles or short spines in the mesostigmatal area, and a broad row of short spines to the rear of the ventral medial spine band. The latter two have a longer prothoracic fringe over 500 μ in diameter.

Hosts.—Known almost exclusively from bank swallow nests; also recorded from house sparrow, barn swallow, and violet-green swallow.

Range.—Sabrosky recorded this species from across the northern United States, Ontario, and Alaska.

Discussion.—Thompson and Pont (1993) proposed the replacement name *P. rognesi* for the preoccupied *P. chrysorrhoea* (Meigen). While identifying samples of blow flies collected from the Kola Peninsula in Russia, I found two adult female *P. rognesi* in samples taken from flytraps (Koslov and Whitworth 2002).

Protocalliphora (P.) rugosa Whitworth

Diagnosis.—Pronounced, dense dorsal cuticular ridges, pronounced irregular folds in the hypostigmatal area, short hyperstigmatal spines (30 μ or less), mesostigmatal area with dense spines (Whitworth 2002: fig. 2a).

Voucher slide.—Tree swallow nest 1198-2, Logan Canyon, Cache County, Utah, July 17, 1971, Whitworth, from puparial description.

Similar species.—*Protocalliphora avium* is similar but has very sparse or no spines in the mesostigmatal area and a limited range which does not overlap with *P. rugosa* which is known only from the northwestern United States and British Columbia.

Hosts.—Purple martin, house sparrow, European starling, bank, barn, cliff, tree, and violet-green swallow.

Range.—Idaho, Montana, Oregon, Utah, Washington, Wyoming, and British Columbia.

Discussion.—This species was separated from *P. hirundo,* see discussion under that species. It was discovered while analyzing data for this study (Whitworth 2002).

Protocalliphora (P.) seminuda Sabrosky, Bennett, and Whitworth
(Fig. 28)

Diagnosis.—Slender hyperstigmatal spines, 30 μ or less, mesostigmatal folds moderate to pronounced (Figs. 28a–d). Ventral band ratio 0.73 (0.67–0.84).

Voucher slide.—Brewer's blackbird nest #244-6, Pocatello Valley, Oneida County, Idaho, July 5, 1970, Whitworth, from puparial description.

Similar species.—Similar to *P. spatulata,* see differences discussed under that species. *Protocalliphora spatulata* tends to favor higher elevations or occur farther north, while *P. seminuda* is often associated with desert habitat.

New hosts.—Western bluebird, Los Alamos, New Mexico, collected by J.M. Fair, Los Alamos Labs, adults only, no puparia. Sabrosky listed it from Brewer's blackbird, horned lark, and barn swallow.

Range.—Sabrosky listed the species from California, Idaho, New Mexico, Utah and Wyoming.

Protocalliphora (P.) shannoni Sabrosky, Bennett, and Whitworth
(Figs. 14, 19)

Diagnosis.—Short hyperstigmatal spines to about 12.5 μ (rarely to 20 μ), mesostigmatal and hypostigmatal spines reduced to tubercles (Fig. 19). Ventral posterior spine bands reduced to rear, sometimes only last one or two segments reduced, rarely little or no reduction.

Voucher slide.—Robin nest #190, Algonquin Park, Ontario, summer 1955, Bennett, from puparial description.

Similar species.—*Protocalliphora deceptor* has shorter hyperstigmatal spines and no reduction to the ventral posterior spine band. Occasionally *P. shannoni* has short spines or tubercles in the hyperstigmatal area and would key to *P. deceptor,* see comments under *P. deceptor.*

New hosts.—Townsend's warbler and Swainson's thrush nests contributed by Steve Matsuoka, United States Geological Survey, Anchorage, Alaska; veery, Idaho Falls area, Mia Revels. Nine puparial slides prepared by Bennett, labeled 55-147, which would be summer 1955, Algonquin Park Ontario, listed swamp sparrow as host but included no species identification. Six slides were *P. metallica,* two were *P. fallisi* and one was *P. shannoni,* which would be a new host-parasite relationship. Matsuoka also collected it from American robin and yellow-rumped warbler (under myrtle warbler in Sabrosky). Sabrosky listed *P. shannoni* from a variety of hosts.

New range.—Idaho Falls, Idaho, Waldo, Maine, and Anchorage, Alaska, also collected from New Hampshire and New York. Sabrosky found this species primarily in the northeastern and northwestern United States and Canada.

Discussion.—Sabrosky stated that east-

ern forms of this species have pronounced cuticular ridges while western forms have weak cuticular ridges. I found cuticular ridges weak in most specimens and occasionally moderate to pronounced in specimens from both the east and west. Hyperstigmatal spine length can be quite variable, from tubercles to 20 μ. Patches of longer spines may be found throughout the hyperstigmatal region, especially near the upper portion. Puparia of this species are somewhat variable, but a comparison of adults and puparia from Maine to Washington, and north from British Columbia to Anchorage, Alaska, revealed many shared features and *P. shannoni* appears to be a widespread, variable species. One adult character not mentioned in Sabrosky is the thorax of many adult females which have aeneous highlights.

Protocalliphora (P.) sialia Shannon and Dobroscky (Figs. 10a, 15b)

Diagnosis.—Prothoracic fringe usually 500 μ in diameter or longer. Dorsal cuticular ridges pronounced. Stigmatal area with pronounced folds; mesostigmatal area with distinct spines; ventral band ratio averages 0.81. Puparial characters are illustrated in Whitworth 2003.

Voucher slide.—*P. sialia*: Barn swallow nest #64, Ontario, Algonquin Park, Summer 1952, Bennett.

Similar species.—*Protocalliphora occidentalis* is very similar, see comments under that species.

New hosts.—Northern mockingbird, Allegany, Maryland and tufted titmouse, Gorton, Massachusetts.

New range.—Indiana, Illinois, Kentucky, Minnesota, Nevada, Rhode Island, Tennessee, and Saskatchewan. Also collected from Alaska, Iowa, Maine, Maryland, Massachusetts, Michigan, New York, Ohio, Pennsylvania, Vermont, Virginia, West Virginia, and Ontario. Sabrosky listed New Brunswick, Northwest Territories, Quebec, Delaware, Georgia, and South Dakota.

Protocalliphora (P.) spatulata Sabrosky, Bennett, and Whitworth (Figs. 11, 15a, 29)

Diagnosis.—Hyperstigmatal spines slender and long (up to 50 μ, Fig. 5). High ventral band ratio averaging 0.83 (0.72–0.92) (Fig. 11), circumstigmatal folds pronounced (Fig. 29a).

Voucher slide.—Horned lark nest #XII, Beartooth Pass, Park County, Wyoming, August 20, 1964, N.A.M. Verbeek, from puparial description.

Similar species.—*Protocalliphora seminuda* is similar, but has shorter hyperstigmatal spines (30 μ or less), lower ventral band ratio averaging 0.73, and circumstigmatal folds faint to moderate.

New hosts.—Savannah and white-crowned sparrows, 150 km east of Delta Junction, Alaska, Fair and Miller (1995); yellow-rumped warblers and dark-eyed juncos from Steve Matsuoka, vicinity of Anchorage, Alaska. Sabrosky listed it from horned lark and water pipit and an undetermined species of rosy finch.

Range.—Sabrosky reported this species in Alaska, California, Colorado, Montana, New Mexico, Wyoming, Northwest Territories, Ontario, and Yukon Territory.

Discussion.—Fair and Miller (1995) reported subcutaneous *P. spatulata* larvae in sparrow nestlings. However, I examined the reared series from their study, and it contained a mix of *P. braueri* and *P. spatulata.* It is likely *P. braueri* was the subcutaneous species observed (J.M. Fair, pers. comm.).

Protocalliphora (P.) spenceri Sabrosky, Bennett, and Whitworth (Fig. 30)

Diagnosis.—Slender hyperstigmatal spines, mesostigmatal folds faint or absent, ventral band ratio averages 0.71 (0.55–0.95) (Figs. 30a–c).

Voucher slide.—Warbling vireo nest #1237-3, Franklin Basin, Cache County, Utah, July 21, 1971, Whitworth, from puparial description.

Similar species.—*Protocalliphora seminuda* and *P. spatulata* are similar but have pronounced mesostigmatal folds.

New hosts.—Blackpoll, Townsend's, yellow-rumped warblers, pine grosbeak, from Steve Matsuoka, Anchorage, Alaska, yellow-breasted chat, Idaho Falls area, Mia Revels. Sabrosky listed American redstart, warbling vireo, yellow warbler and slate-colored (dark-eyed) junco.

New range.—Anchorage, Alaska. Sabrosky recorded it from British Columbia, Manitoba, Idaho, and Utah.

Discussion.—The only puparia of this species available for study were from Utah, Idaho, and Alaska. Ten puparia from Alaska had ventral band ratios averaging 0.64, while four puparia from Utah averaged 0.73 and five puparia from Idaho averaged 0.92. Bennett measured ventral band ratios in 15 specimens, including 5 from Utah, which I have, plus 10 from British Columbia, which I have not seen. His ratios averaged 0.70 (0.40–0.80) which suggests Alaska specimens have lower ratios than Utah and British Columbia specimens. The hyperstigmatal spines of Alaska specimens were broader at the base, with only tips slender, while Utah and Idaho specimens had spines uniformly slender.

Protocalliphora (P.) tundrae Sabrosky, Bennett, and Whitworth

Diagnosis.—Posterior spine band reduced to rear, hyperstigmatal spines with slender tips, ventral band ratios usually low, averaging 0.52 (0.43–0.58) to front and 0.37 (0.29–0.47) to rear (Sabrosky: fig. 64).

Voucher slide.—Snow bunting nest, Nedre midsommer Sö, Pearyland, Greenland, July 10, 1966, J.E.H. Martin, from paratypes.

Similar species.—*Protocalliphora aenea* and *P. fallisi* are similar and their ranges overlap. The slender hyperstigmatal spines should separate *P. tundrae,* but it is known from only a few specimens, and it is not certain how constant the character is.

Hosts.—Known only from the nests of snow buntings and savannah sparrows.

Range.—Known only from far northern Canada and Greenland.

Discussion.—Few samples of puparia were available, most specimens were slides from the Bennett collection.

Acknowledgments

This study was funded by my company, Whitworth Pest Solutions, Inc. Thanks to all my employees for understanding my preoccupation with this project and especially to Dana Hobbs, office manager, who frequently took time from her regular duties to assist me. Also thanks to Jennifer Shutt, technician, who skillfully processed samples and prepared slides, while a full-time college student.

I am especially indebted to hundreds of bird enthusiasts, many associated with the Cornell Birdhouse Network, who sent me over 3,000 bird nests to examine for *Protocalliphora.* Special thanks to major contributors including: Marti Anderson, Federal Way, WA; Lum Bourne, Westerville, OH; Hatch Graham, Somerset, CA; Keith Kridler, Mt. Pleasant, TX; Patricia Otto, Bellingham, WA; Alan Reid, Springfield, OR; Dean Sheldon, Greenwich, OH; and Shriley Sturts, Coeur d'Alene, ID.

Thanks also to ornithologists who sent me nests or specimens from their research, including: James Battin, Northern Arizona University, Flagstaff; Kristin Covert, Rocky Mt. Research Station, Flagstaff, AZ; Christine Custer, United States Geological Survey, Lacrosse, WI; Don Dahlsten, University of California, Berkeley; Russ Dawson, University of Northern British Columbia, Prince George; Jeanne Fair, University of Missouri, Columbia; Steve Germaine, Arizona Game and Fish, Phoenix, AZ; John Gerwin, North Carolina State Museum of Natural Science, Raleigh; Steve Matsuoka, United States Geological Survey, Anchorage, AK; Darrel Pogue, University of Texas at Tyler; Mia Revels, Northeastern State University, Tahlequah, OK; George Walter, Nisqually Tribal Biolo-

gist, Olympia, WA; Harmon Weeks, Purdue University, West Lafayette, IN; and Karen Wiebe, University of Saskatchewan, Saskatoon.

I am indebted to several entomologists and institutions for the loan of material and assistance during this study. Thanks to Wilford Hanson, Utah State University, Logan, UT; Karen Needham, Spencer Entomological Museum, Vancouver, British Columbia; James O'Hara, Canadian National Collection, Agriculture and Agri-Food Canada, Ottawa; Philip Perkins, Museum of Comparative Zoology, Harvard University, Cambridge, MA; Norm Woodley, Systematic Entomology Laboratory, USDA, Washington, DC; and Rich Zack, Washington State University, Pullman.

Thanks also to Dawn Nelson of Seattle, WA, for the drawings and Patrick Craig of Monte Rio, CA, for the photographs. Finally, thanks to my wife Faye, who has endured over 30 years of my fascination with this insect group, assisted me in the field, and given up a good part of her home for my research.

I take pleasure in dedicating this work to the late C. W. Sabrosky and G. F. Bennett, co-authors and pioneers in the study of *Protocalliphora,* who devoted much of their professional careers to studies of this genus.

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