

Biosystematics of *Nasonia* (Hymenoptera: Pteromalidae): Two New Species Reared from Birds' Nests in North America

D. CHRISTOPHER DARLING¹ AND JOHN H. WERREN²

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ABSTRACT *Nasonia* generally is regarded as a monotypic genus that includes only *N. vitripennis* (Walker), a cosmopolitan parasite of the pupae of cyclorrhaphous Diptera. Two new species of *Nasonia* are described from North America that parasitize blowfly pupae (Diptera: Calliphoridae: *Protocalliphora*) in birds' nests: *N. giraulti* Darling (type locality: Cambridge, Ontario) and *N. longicornis* Darling (type locality: Kelowna, British Columbia). Lectotypes are designated for two subjective synonyms of *N. vitripennis*: *N. brevicornis* Ashmead and *Mormoniella brevicornis* Ashmead. Behavioral and genetic data are summarized that corroborate the morphological analysis. An identification key is provided and morphological and distributional information are summarized for the three species of *Nasonia* in North America. *Nasonia vitripennis* has been the subject of numerous ecological, behavioral, and evolutionary studies, and many of these studies may be compromised by the recognition of more than one species and failure to deposit documented voucher specimens. Two species of *Nasonia* are routinely collected from the same blowfly puparium (*N. vitripennis* and *N. giraulti* in eastern North America, *N. vitripennis* and *N. longicornis* in western North America) and careful identifications and a large series of voucher specimens are required in any field study of *Nasonia*.

KEY WORDS Insecta, *Nasonia*, *Nasonia vitripennis*, birds' nests, voucher specimens

THE PARASITIC WASP, *Nasonia vitripennis* (Walker), has been used extensively in ecological, genetic, behavioral, and evolutionary research (Pimentel et al. 1963, Whiting 1967, van den Assem 1976, Werren 1987). In particular, this species has been used extensively in studies of sex determination and sex ratio evolution because the wasp is able to control the sex of individual offspring behaviorally (Wylie 1966; Holmes 1972; Werren 1980, 1983), and harbors various genetic elements that distort the sex ratio (Werren et al. 1981, Skinner 1985, Werren et al. 1986, Werren & van den Assem 1986, Skinner 1987, Werren et al. 1987, Nur et al. 1988).

Nasonia vitripennis was previously believed to be the only species in the genus. However, field collections from birds' nests throughout North America have revealed the existence of two new species of *Nasonia*, both of which are geographically widespread. The three species can be distinguished on morphological, behavioral, and genetic criteria. Hybrid dysgenesis and some premating isolation also occur. The purpose of this paper is to present a diagnosis and revised generic description of *Nasonia*, an identification key to the species of *Nasonia*, descriptions of two new species from North America, some general behavioral and ge-

netic data that support the taxonomic decisions, and information on the biology of the new species.

Materials and Methods

This study is based on specimens of *Nasonia* reared from more than 850 birds' nests collected throughout North America between 1986 and 1988 and from collections in the following institutions: British Museum (Natural History), London (BMNH); Canadian National Insect Collection, Ottawa (CNC); Illinois Natural History Survey, Champaign (INHS); National Museum of Natural History, Washington, D.C. (USNM); North Carolina State University (NCSU); and Royal Ontario Museum, Toronto (ROM). For all series of specimens pinned material was examined; slide preparations were made of forewing and antenna of both males and females for most series. A total of 360 slides were prepared and examined and these are associated with individual pinned specimens by number (Appendix).

Structure and Sculpture. Morphological terms follow Graham (1969), Richards (1977), and Bouček (1988), except that "prepectus" is used instead of "postspiracular sclerite" (Gibson 1985) and the thorax + propodeum (first true abdominal segment) is referred to as the "mesosoma," and the remainder of the abdomen is referred to as the "metasoma." Metasomal tergites are designated T1, T2, and so on. The metasoma consists of two distinct functional units—the "petiole" (T1), and the "gaster." The antenna consists of the basal scape,

¹ Department of Entomology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6 Canada and Department of Zoology, University of Toronto, Toronto, Ontario M5S 1A1, Canada.

² Department of Biology, University of Rochester, Rochester, N.Y. 14627.

the pedicel, two annelli (A1, A2), and ten funicular segments (F1–F10); F8–F10 are referred to collectively as the club. Measurements of antennal segments and the club do not include the peduncle. Sculpture types follow Harris (1979).

Measurements. The terms length (L), width (W), and height (H) are maximum values obtained by rotating the specimen. Measurements and abbreviations are as follows: A2, length of annellus 2 in dorsal view; CL, club length in lateral view; EH, eye height; F1, F2, length of funicular segment 1, 2 in lateral view; HH, head height in frontal view; HL, head length in dorsal view; HW, head width in frontal view; M, length of marginal vein; MS, length of malar space; MSC, length of mesoscutum along midline; MN, length of metanotum along midline; OOL, length of ocular-ocellar line; PED, length of pedicel in lateral view; PM, length of postmarginal vein; PN, length of pronotum along midline; POL, length of postocellar line; PROP, length of propodeum along midline; PW, width of pronotal collar; S, length of stigmal vein; SC, length of scutellum along the midline; SL, scape length; SM, length of submarginal vein; TL, total body length (including ovipositor); WL, wing length; and WW, wing width.

Metric comparisons are based on 10 males and 10 females collected throughout the range of each species in North America (Appendix). Measurements from the head, mesosoma, and metasoma were taken through a stereomicroscope using a digital filar micrometer. Measurements of wings and antenna were taken through a compound microscope using a calibrated ocular reticle. After the measurements were taken and the descriptive ratios calculated, coefficients of variation (CV) were examined. For all ratios in which the CV exceeded 10%, the maximum and minimum measurements were remeasured to minimize the inclusion of erroneous data in the final data set. Sexually dimorphic and species-specific metric descriptors were evaluated with nonparametric Mann-Whitney *U* tests (SAS-PC [1987], Procedure NPARIWAY, Option WILCOXON).

Descriptions. The three species of *Nasonia* included here form the basis for a generic redescription. This description summarizes only those features common to the three included species. Ratios statistically different at either the 0.01 or 0.001 significance levels are treated in the individual species accounts. The complete description for a species consists of this generic description with the appropriate values from Table 1 and the species description.

Nasonia Ashmead, 1904

Nasonia Ashmead, 1904. Type species: *Nasonia brevicornis* Ashmead, by original designation.
Mormoniella Ashmead, 1904. Type species: *Mormoniella brevicornis* Ashmead, by original designation.

The taxonomic confusion created by the description of two genera based on the same type species in the same work has subsided with *Nasonia* now being used almost exclusively in recent literature (see Burks 1979 for summary).

Identification and Diagnosis. The genus *Nasonia* can be readily identified using standard taxonomic works for Pteromalidae (Peck et al. 1964, Graham 1969). Care must be taken when using identification keys for pupal parasites of muscoid flies (Rueda & Axtell 1985, Hoebeke & Rutz 1988). The transverse ridge on the anterior margin of the pronotum (Fig. 1 and 2) is not as distinct as in *Muscidifurax* (Rueda & Axtell 1985, couplet 2; figure 10) and the fringe of short setae on the apex of the forewing is absent in some species and often lost in specimens collected or stored in fluid preservatives—e.g., ethanol (Fig. 27–30).

The *Dibrachys* group of the Pteromalidae was established for 14 genera, including *Nasonia* (Wallace 1973), and a diagnosis of the group and a key to species were presented, both of which are of little use with respect to *Nasonia*. In fact, the diagnosis and key are inconsistent; the *Dibrachys* group is characterized as lacking a strongly developed nucha but the couplet terminating in *Nasonia* states that the nucha is prominent. The key also requires that *Nasonia* have a weakly indicated occipital carina and transverse funicular segments, which is not the case for males of *N. vitripennis* or for the new species of *Nasonia* described herein.

Diagnosis. Hymenoptera: Chalcidoidea: Pteromalidae. Face protuberant at level of toruli; occiput without a distinct carina; clypeus with oblique rugae laterad, without teeth or lobes; antenna 13-segmented, with 2 annelli (1, 1, 2, 6, 3), inserted at level of ventral margin of eyes; pedicel short, less than one-third scape length (Fig. 33–44); pronotum without distinct carina, notauli incomplete, strongly impressed anteriorly and ending abruptly (Fig. 1 and 2); mesoscutum and scutellum with delicate, imbricate reticulations (Fig. 3 and 4); hind tibia with a single apical spur; propodeum with distinct strongly reticulate nucha (Fig. 5–8); marginal vein of uniform thickness throughout, stigmal vein shorter than postmarginal (Fig. 9–28); metasoma sessile, petiole short and inconspicuous; ovipositor sheaths short, less than half length of hind tibia; metasomal tergites 2–5 not strongly excised along hind margin.

Redescription. *Female:* Head, mesosoma and metasoma dark green to black with faint green to bronze iridescent reflections, most distinct on mesosoma; mandible and tegula yellow; antennal scape and pedicel yellow; flagellum brown; coxae concolorous with mesosoma, trochanters and femora brown, except apex of femora yellow, concolorous with tibiae and tarsi, pretarsi brown. Forewing hyaline, veins light yellow. *Head:* in dorsal view transverse, 1.3–1.5 width of pronotum, width about twice head length; in frontal view subquadrate, width 1.3–1.4 height; face protuberant at level of

Table 1. Morphometric comparisons of males and females of species of *Nasonia*

	Females, $\bar{x} \pm SD$ (range)				Males, $\bar{x} \pm SD$ (range)			
	<i>vitripennis</i> (n = 10)	<i>giraulti</i> (n = 10)	<i>longicornis</i> (n = 10)	U test ^a	<i>vitripennis</i> (n = 10)	<i>giraulti</i> (n = 10)	<i>longicornis</i> (n = 10)	U test
Length (mm)	2.13 ± 0.15 (1.83-2.34)	1.96 ± 0.10 (1.79-2.15)	2.11 ± 0.16 (1.90-2.40)	* /* /	1.57 ± 0.16 (1.38-1.91)	1.51 ± 0.17 (1.22-1.82)	1.70 ± 0.08 (1.61-1.80)	/** /*
WL/TL	0.87 ± 0.03 (0.83-0.91)	0.85 ± 0.04 (0.80-0.93)	0.86 ± 0.06 (0.80-1.00)	* / /	0.62 ± 0.05 (0.50-0.69)	0.81 ± 0.06 (0.73-0.91)	0.72 ± 0.05 (0.65-0.78)	***/**/***
WL/WW	2.35 ± 0.09 (2.21-2.50)	2.20 ± 0.09 (2.07-2.41)	2.30 ± 0.12 (2.17-2.59)	** /* /	3.66 ± 0.17 (3.31-3.86)	2.42 ± 0.03 (2.25-2.56)	2.74 ± 0.02 (2.65-2.89)	-/-/-
MS/EH	0.45 ± 0.04 (0.40-0.54)	0.53 ± 0.03 (0.48-0.57)	0.49 ± 0.03 (0.45-0.53)	** /* /*	0.35 ± 0.03 (0.28-0.41)	0.40 ± 0.02 (0.35-0.43)	0.34 ± 0.02 (0.31-0.37)	** /**/
SL/EH	0.80 ± 0.05 (0.74-0.86)	0.83 ± 0.04 (0.77-0.88)	0.83 ± 0.03 (0.77-0.87)	/ /	0.81 ± 0.04 (0.73-0.88)	0.78 ± 0.05 (0.73-0.87)	0.75 ± 0.04 (0.68-0.84)	/ /**
OOL/POL	0.57 ± 0.04 (0.49-0.63)	0.59 ± 0.04 (0.54-0.64)	0.59 ± 0.06 (0.50-0.71)	/ /	0.53 ± 0.06 (0.43-0.61)	0.50 ± 0.04 (0.43-0.57)	0.50 ± 0.03 (0.45-0.54)	/ /
HW/HL	2.05 ± 0.12 (1.90-2.35)	2.12 ± 0.06 (2.01-2.20)	2.09 ± 0.08 (1.99-2.22)	* / /	2.02 ± 0.09 (1.91-2.22)	2.02 ± 0.08 (1.91-2.13)	1.97 ± 0.09 (1.80-2.10)	/ /
HW/HH	1.40 ± 0.11 (1.32-1.70)	1.42 ± 0.14 (1.34-1.75)	1.34 ± 0.03 (1.29-1.39)	/ /*	1.58 ± 0.19 (1.38-1.93)	1.37 ± 0.04 (1.31-1.42)	1.40 ± 0.03 (1.37-1.44)	***/ /**
HW/PW	1.38 ± 0.08 (1.26-1.54)	1.39 ± 0.03 (1.35-1.46)	1.35 ± 0.05 (1.29-1.47)	/* /	1.62 ± 0.04 (1.56-1.70)	1.55 ± 0.05 (1.49-1.65)	1.50 ± 0.03 (1.46-1.56)	** /* /***
PN/MS	0.19 ± 0.03 (0.16-0.24)	0.17 ± 0.02 (0.13-0.19)	0.21 ± 0.02 (0.18-0.24)	* /***/	0.22 ± 0.03 (0.17-0.27)	0.18 ± 0.02 (0.15-0.21)	0.22 ± 0.03 (0.17-0.26)	** /**/
MSC/W	0.58 ± 0.04 (0.51-0.65)	0.53 ± 0.02 (0.51-0.56)	0.57 ± 0.03 (0.53-0.63)	** /**/	0.60 ± 0.05 (0.55-0.68)	0.55 ± 0.03 (0.51-0.61)	0.59 ± 0.03 (0.56-0.66)	/* /
SC/MS	0.91 ± 0.04 (0.85-0.99)	0.95 ± 0.04 (0.87-0.98)	0.91 ± 0.08 (0.79-1.02)	/ /	0.88 ± 0.07 (0.79-1.02)	0.95 ± 0.04 (0.86-1.00)	0.95 ± 0.07 (0.84-1.09)	* / /
MN/PROP	0.24 ± 0.05 (0.19-0.35)	0.29 ± 0.04 (0.24-0.34)	0.29 ± 0.02 (0.26-0.32)	* / /*	0.24 ± 0.06 (0.16-0.33)	0.23 ± 0.03 (0.18-0.28)	0.27 ± 0.02 (0.23-0.30)	/** /
SM/M	2.35 ± 0.20 (2.08-2.74)	2.40 ± 0.16 (2.19-2.71)	2.43 ± 0.16 (2.14-2.66)	/ /	2.21 ± 0.16 (1.97-2.49)	2.21 ± 0.19 (1.75-2.44)	2.34 ± 0.16 (2.07-2.51)	/ /
PM/M	0.94 ± 0.09 (0.81-1.08)	0.78 ± 0.05 (0.69-0.83)	0.83 ± 0.07 (0.75-0.95)	***/ /*	0.85 ± 0.05 (0.78-0.95)	0.75 ± 0.05 (0.65-0.85)	0.80 ± 0.05 (0.74-0.88)	***/ /*
S/M	0.66 ± 0.06 (0.55-0.79)	0.61 ± 0.04 (0.57-0.68)	0.63 ± 0.04 (0.54-0.68)	/ /	0.56 ± 0.06 (0.47-0.67)	0.55 ± 0.04 (0.49-0.63)	0.56 ± 0.04 (0.50-0.64)	/ /
S/PM	0.71 ± 0.05 (0.62-0.79)	0.78 ± 0.05 (0.72-0.84)	0.76 ± 0.05 (0.69-0.85)	** / /*	0.66 ± 0.05 (0.59-0.74)	0.73 ± 0.05 (0.64-0.77)	0.70 ± 0.06 (0.62-0.80)	** / /
S/WW	0.26 ± 0.01 (0.24-0.27)	0.22 ± 0.01 (0.21-0.24)	0.23 ± 0.01 (0.22-0.26)	***/ /**	0.41 ± 0.04 (0.35-0.47)	0.24 ± 0.02 (0.22-0.27)	0.27 ± 0.02 (0.25-0.30)	-/**/-

Table 1. Continued

	Females, $\bar{x} \pm SD$ (range)				Males, $\bar{x} \pm SD$ (range)			
	<i>vitripennis</i>	<i>giraulti</i>	<i>longicornis</i>	U test ^a	<i>vitripennis</i>	<i>giraulti</i>	<i>longicornis</i>	U test
	(n = 19)	(n = 20)	(n = 24)		(n = 14)	(n = 12)	(n = 27)	
SL (microns)	279.6 ± 28.1 (198-323)	259.0 ± 16.3 (234.5-288)	287.8 ± 17.8 (246.5-311)	** /*** /	259.9 ± 26.3 (216-296)	224.2 ± 24.6 (160-254.5)	255.5 ± 20.1 (210-297)	** /*** /
SL/W	4.56 ± 0.34 (4.00-5.22)	4.64 ± 0.26 (4.17-5.09)	4.84 ± 0.22 (4.35-5.15)	/ * / **	4.20 ± 0.37 (3.76-4.97)	4.51 ± 0.27 (3.90-4.85)	4.53 ± 0.22 (4.15-4.96)	* / / **
SL/PED	2.59 ± 0.15 (2.24-2.86)	2.82 ± 0.15 (2.40-3.07)	2.62 ± 0.06 (2.50-2.75)	*** / *** /	2.46 ± 0.12 (2.16-2.73)	2.76 ± 0.09 (2.63-2.91)	2.59 ± 0.09 (2.46-2.78)	*** / *** / ***
PED/F1	2.60 ± 0.21 (2.19-2.96)	1.87 ± 0.18 (1.59-2.37)	2.38 ± 0.18 (2.05-2.71)	*** / *** / **	2.48 ± 0.20 (2.16-2.83)	1.74 ± 0.21 (1.45-2.08)	2.25 ± 0.19 (2.00-2.66)	*** / *** / **
F1/W	0.65 ± 0.05 (0.56-0.72)	0.77 ± 0.04 (0.70-0.84)	0.73 ± 0.05 (0.63-0.82)	*** / * / ***	0.81 ± 0.08 (0.66-0.98)	1.01 ± 0.08 (0.86-1.13)	0.94 ± 0.06 (0.81-1.08)	*** / ** / ***
A2/F1	0.50 ± 0.07 (0.40-0.63)	0.37 ± 0.04 (0.30-0.47)	0.44 ± 0.05 (0.35-0.55)	*** / *** / *	0.47 ± 0.06 (0.36-0.54)	0.38 ± 0.05 (0.31-0.46)	0.47 ± 0.05 (0.41-0.59)	** / *** /
CL/SL	0.51 ± 0.03 (0.45-0.55)	0.54 ± 0.03 (0.48-0.59)	0.51 ± 0.02 (0.48-0.54)	* / *** /	0.55 ± 0.05 (0.42-0.63)	0.66 ± 0.04 (0.62-0.74)	0.58 ± 0.03 (0.51-0.64)	*** / *** /
CL/W	1.69 ± 0.06 (1.56-1.80)	1.85 ± 0.09 (1.67-1.99)	1.89 ± 0.09 (1.72-2.06)	*** / / ***	2.11 ± 0.11 (2.00-2.27)	2.50 ± 0.11 (2.28-2.72)	2.40 ± 0.16 (2.06-2.62)	*** / / ***

See Materials and Methods for discussion of characters and specimens used in the quantitative analysis.

^a Nonparametric statistical comparison by Mann-Whitney *U* test, *N. vitripennis* and *N. giraulti* / *N. giraulti* and *N. longicornis* / *N. vitripennis* and *N. longicornis*: *, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001 (SAS Institute 1987); —, diagnostic character, i.e., ranges do not overlap.

toruli; OOL shorter than POL, OOL/POL 0.5–0.7; scape shorter than eye height, SL/EH 0.7–0.9; head sculpture imbricate above, finely reticulate on supra-clypeal area and anterior of malar space; antennal scrobe shallow; clypeus distinct, indicated by change in sculpture, laterad with oblique rugae, without teeth or lobes; malar sulcus indistinct; eye with minute hairs; occipital region with weak transverse rugae, occipital carina absent. Antenna 13-segmented, with 2 annelli (1, 1, 2, 6, 3), inserted at level of ventral margin of eyes; pedicel less than one-third scape length. *Mesosoma*: notaulus incomplete, strongly impressed anteriorly and ending abruptly (Fig. 1 and 2); mesoscutum and scutellum with delicate imbricate reticulations (Fig. 3 and 4), except with distinct raised reticulations anterior to transcutal line (Fig. 2); SC/MS 0.8–1.1; pronotum campanulate, wider than long, without distinct transverse anterior carina (Fig. 1 and 2); apex of scutellum slightly emarginate; propodeum with distinct strongly reticulate nucha, sculpture alveolate, with median carina and plicae (Fig. 5–8); metanotum 0.2–0.3 length of propodeum; prepectus narrowly triangular; hind tibia with single apical spur. *Forewing*: length 0.8–1.0 total body length; marginal vein of uniform thickness throughout, length 2–3 submarginal vein; stigmal vein shorter than postmarginal, uncus usually with 4 sensilla; club length about one-half scape length and 1.5–2 maximum width. *Metasoma*: sessile, petiole short and inconspicuous; gaster with fine reticulations on basal fovea, laterotergites, and T4–7; T1–5 not strongly excised along hind margin; T1 longer than following two terga combined; pygostyle not elongate, inconspicuous; ovipositor short, sheaths only slightly exposed beyond tip of gaster.

Male: As in female except as noted. Head, mesosoma and metasoma iridescent blue-green with green to bronze reflections, color more brilliant; antenna light yellow; femora, trochanters, tibiae and tarsi light yellow, concolorous with antenna, pretarsi brown. Forewing hyaline, veins brown. *Head*: wider relative to width of pronotum, HW/PW 1.5–1.7; OOL about one-half POL; antennal scrobes deeper; occipital region with more distinct transverse rugae; antenna inserted above level of ventral margin of eyes; club longer, ≈ 0.6 –0.7 scape length, and narrower, length greater than twice maximum width. *Mesosoma*: forewing variable in shape, stigmal vein shorter, 0.5–0.7 marginal vein. *Metasoma*: gaster with fine reticulations only on laterotergites and T4–7. Genitalia: basiparamere ventrally with broadly rounded median lobe, sublateral lobes, and elongate paramere; paramere about as long as digitus and longer than sublateral lobe; paramere and sublateral lobe each with 1–2 setae; digitus with 3–4 large teeth; aedeagus about as long as basiparamere.

Key to the Species of *Nasonia*

Care must be taken when identifying female specimens that have been stored in or mounted

from fluid preservatives. This treatment results in the loss of most or all of the marginal setae on the forewing that are characteristic of *N. vitripennis* (Fig. 27–30). In these cases, slide-mounted forewings are necessary for accurate identification of the females of this species. Slide-mounts of forewing and antenna are also necessary to distinguish females of *N. giraulti* and *N. longicornis* with confidence. The morphological differences between these two species are subtle, but distributional data can assist in the identification; there are no known cases of sympatry between *N. giraulti* and *N. longicornis* (Fig. 51). The illustrations in Fig. 45–50 have been scaled to a marginal vein length of 0.27 mm to illustrate the differences in length and shape of the stigmal veins. Males can be identified with certainty because of diagnostic differences in wing shape, but care must be taken in basing the identification of females on associated males. Both *N. giraulti* and *N. longicornis* are sympatric with *N. vitripennis* over wide areas of North America.

- | | | |
|--------|---|--------------------------------|
| 1 | Males. Antenna with flagellum yellow (Fig. 33–38) | 2 |
| 1' | Females. Antenna with flagellum brown (Fig. 39–44) | 4 |
| 2(1) | Forewing short and narrow, length greater than 3 times maximum width, with long discal and marginal setae (Fig. 9 and 10); scape spindle-shaped in lateral view, pedicel longer than F1 + F2 (Fig. 33 and 34) [cosmopolitan] ... <i>N. vitripennis</i> | |
| 2'(1) | Forewing longer and broader, length less than 3 times maximum width, with shorter discal and marginal setae (Fig. 11–14); scape parallel-sided in lateral view, pedicel shorter than or equal to F1 + F2 (Fig. 35–38) [North America] | 3 |
| 3(2') | Forewing triangular (Fig. 11 and 12), stigmal vein angulate, not smoothly curved (Fig. 11, 12, and 45); scape linear, funicular segments and club with short setae (Fig. 35 and 36) [western North America] | <i>N. longicornis</i> , n. sp. |
| 3'(2') | Forewing broader and rounded (Fig. 13 and 14), similar in shape to female, stigmal vein smoothly curved, not angulate (Fig. 13, 14, and 45); scape with a distinct dog-legged bend, funicular segments and club with long setae (Fig. 37 and 38) [eastern North America] | <i>N. giraulti</i> , n. sp. |
| 4(1') | Forewing with fringe of marginal setae (Fig. 15, 27, and 29) or at least setal sockets present (Fig. 28 and 30), stigmal vein elongate, with numerous setae on upper surface, stigma irregular in outline (Fig. 16–18, 48, and 50); scape spindle-shaped, pedicel longer than F1 + F2 (Fig. 39 and 40) [cosmopolitan] ... | <i>N. vitripennis</i> |

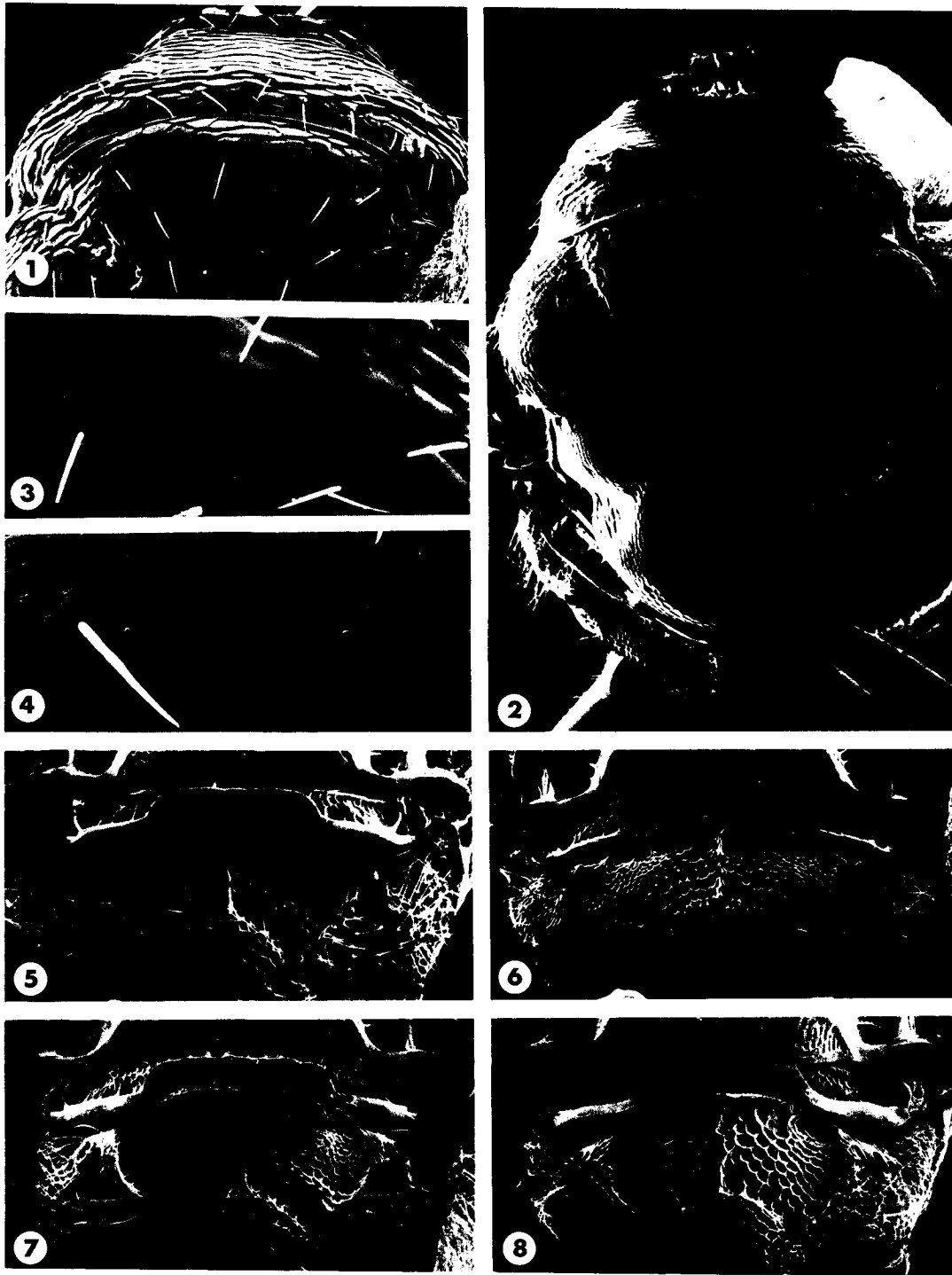


Fig. 1-8. Scanning electron micrographs, *Nasonia* species. (1) *N. giraulti*, pronotum. (2) *N. longicornis*, dorsal view of mesosoma. (3-4) Sculpture on anterior of mesoscutum. (3) *N. longicornis*. (4) *N. giraulti*. (5-8) Propodea. (5 and 7) *N. giraulti*. (6) *N. longicornis*. (8) *N. vitripennis*.

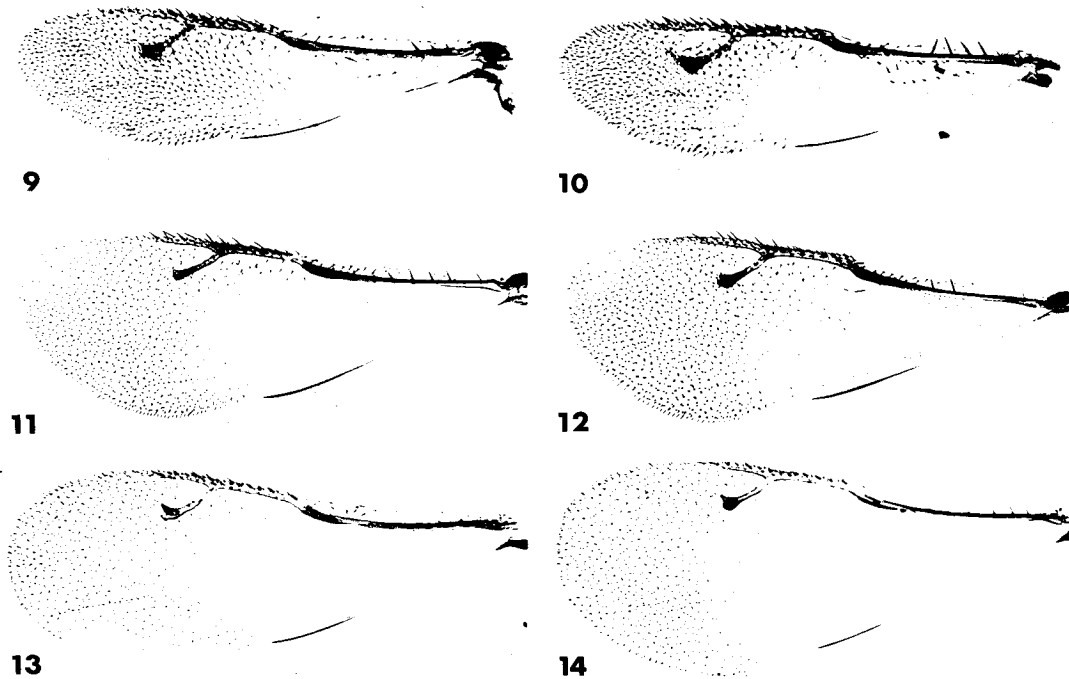


Fig. 9-14. Intra- and interspecific variation in male forewing. (9 and 10) *N. vitripennis*. (11 and 12) *N. longicornis*. (13 and 14) *N. giraulti*.

- 4'(1') Forewing without fringe of marginal setae (Fig. 19, 23, 31, and 32), without distinct setal sockets, stigmal vein shorter with few setae on upper surface, stigma with even outline (Fig. 20-22 and 24-26); scape parallel-sided, pedicel shorter than or equal to F1 + F2 (Fig. 41-44) [North America] 5
- 5(4') Forewing with distinct and darker discal setae (Fig. 19 and 32), stigmal vein angulate, with inflection point near base (Fig. 20-22), in closer proximity to postmarginal vein (Fig. 46); funicular segments transverse, pedicel longer relative to F1 and scape (Fig. 41 and 42) [western North America] *N. longicornis*, n. sp.
- 5'(4') Forewing with inconspicuous and lighter discal setae (Fig. 23 and 31), stigmal vein smoothly arched (Fig. 24-26), not in as close proximity to postmarginal vein (Fig. 46); funicular segments quadrate, pedicel shorter relative to F1 and scape (Fig. 43 and 44) [eastern North America] *N. giraulti*, n. sp.

***Nasonia vitripennis* (Walker)**
 (Fig. 8-10, 15-18, 27-30, 33, 34, 39, 40, and 47-51)

A complete discussion of the taxonomic history of this species is included in Graham (1969) and

will not be repeated here. For this study the major concern is the synonymy of *Nasonia brevicornis* with the Old World species *N. vitripennis*. This synonymy was first published by Gahan (1927), and there is no reason to question this synonymy based on a recent comparison of the primary types of these two species.

Type Material. *Pteromalus vitripennis* Walker: Lectotype ♀ (BMNH; examined), designated by Graham 1969: 779. Type Locality: London, England. *Dicyclus pallinervosus* Walker: Holotype ♀ (BMNH; examined). Type Locality: Madeira. *Stictototus insuetus* Walker: Lectotype ♀ (BMNH; examined) designated by Graham 1969: 780. Type Locality: Madeira. *Nasonia brevicornis* Ashmead: LECTOTYPE ♀ (USNM; present designation), "Algonquin, Ill. 6.18.95-114," "4595," "Type No 12318 U.S.N.M." [red, printed], "*Nasonia brevicornis* ♀ Ashm.," [in Ashmead's handwriting], and lectotype label. Type Locality: Algonquin, Illinois, USA. PARALECTOTYPES: 3 ♀♀, all from Algonquin, Illinois; 6.24.95-114, 4593 [USNM], 6.2.95-114, 4644 [USNM], and 7.3.95-115, 4572 [INHS]. The lectotype is in excellent condition. Slide preparations were not made of the forewing and antenna because Girault's long series of topotypic plesiotypes was available for study (see Girault & Sanders [1909] for a discussion of this type material). *Mormoniella brevicornis* Ashmead: LECTOTYPE ♀ (USNM; present designation), "City Can Ut 2.7," "*Mormonia brevicornis* ♀ Ashm.," [in Ashmead's handwriting], and lectotype label. Type Locality:

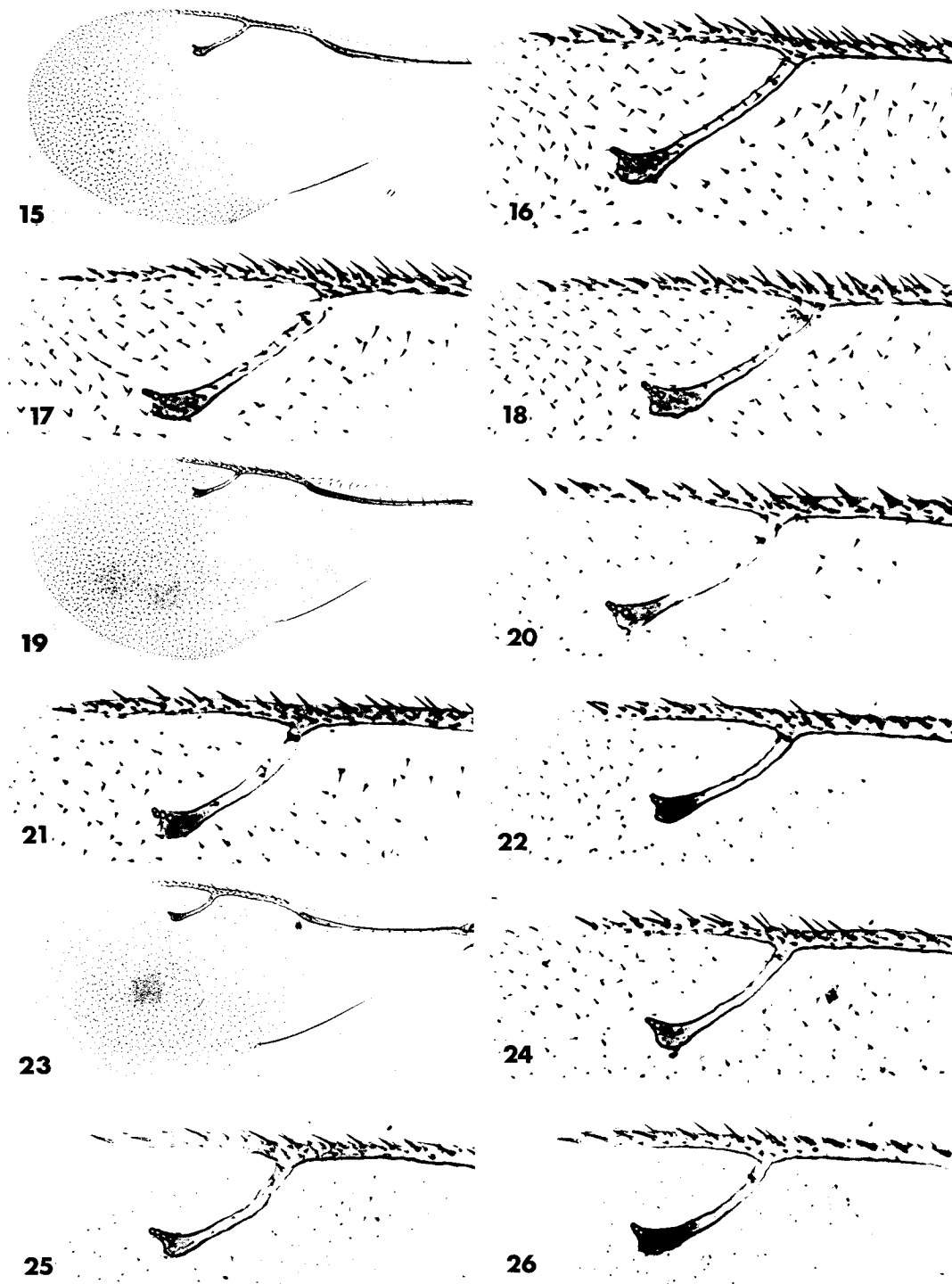


Fig. 15-26. Intra- and interspecific variation in female forewing. (15-18) *N. vitripennis*. (19-22) *N. longicornis*. (23-26) *N. giraulti*.

Utah (?), USA. The name *Mormonia* is regarded as a misspelling of *Mormoniella*. This specimen is in very poor condition; the head and metasoma are missing. Fortunately, a flagellum is glued to the

point; the funicular segments are transverse, a diagnostic character for *N. vitripennis*.

The type material of the subjective synonyms of *N. vitripennis* was examined to determine if either

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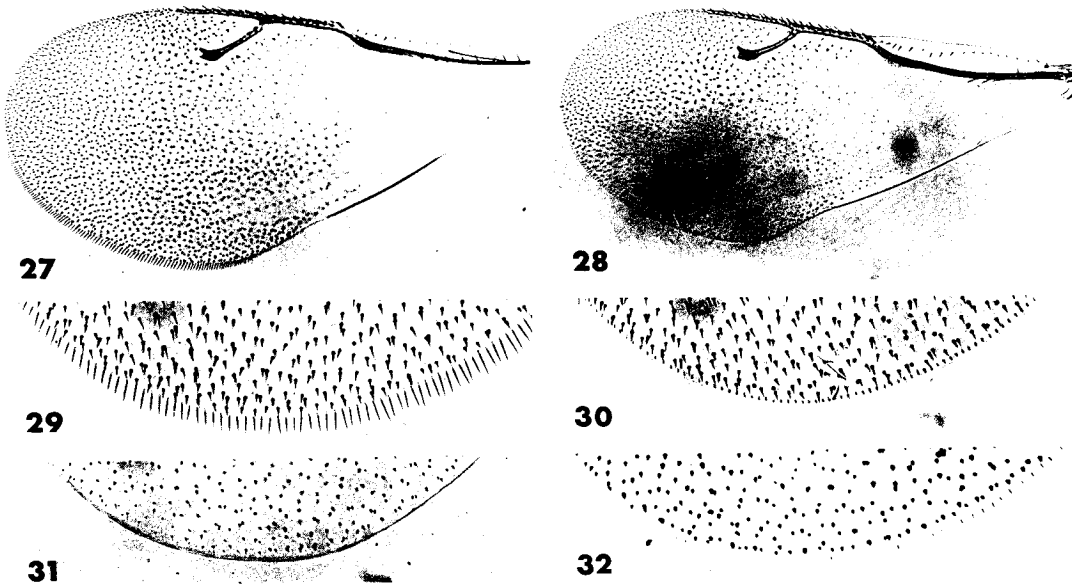


Fig. 27-32. Intra- and interspecific variation in female forewing. (27 and 28) *N. vitripennis*. (29-32) Wing apex. (29 and 30) *N. vitripennis*. (31) *N. giraulti*. (32) *N. longicornis*.

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of the newly recognized species in North America was represented. This does not seem to be the case, but the primary types are all females unassociated with males and slides were not prepared. The type material of *Pteromalus abnormis* Boheman, 1858, was not examined, but illustrations in the original

description clearly indicate that the males are brachypterous—i.e., the synonymy with *N. vitripennis* is supported. *Pteromalus muscarum* Hartig is another accepted synonym of *N. vitripennis*. The synonymy of *P. muscarum* and *N. vitripennis* was proposed by Graham (1969) based on a study of

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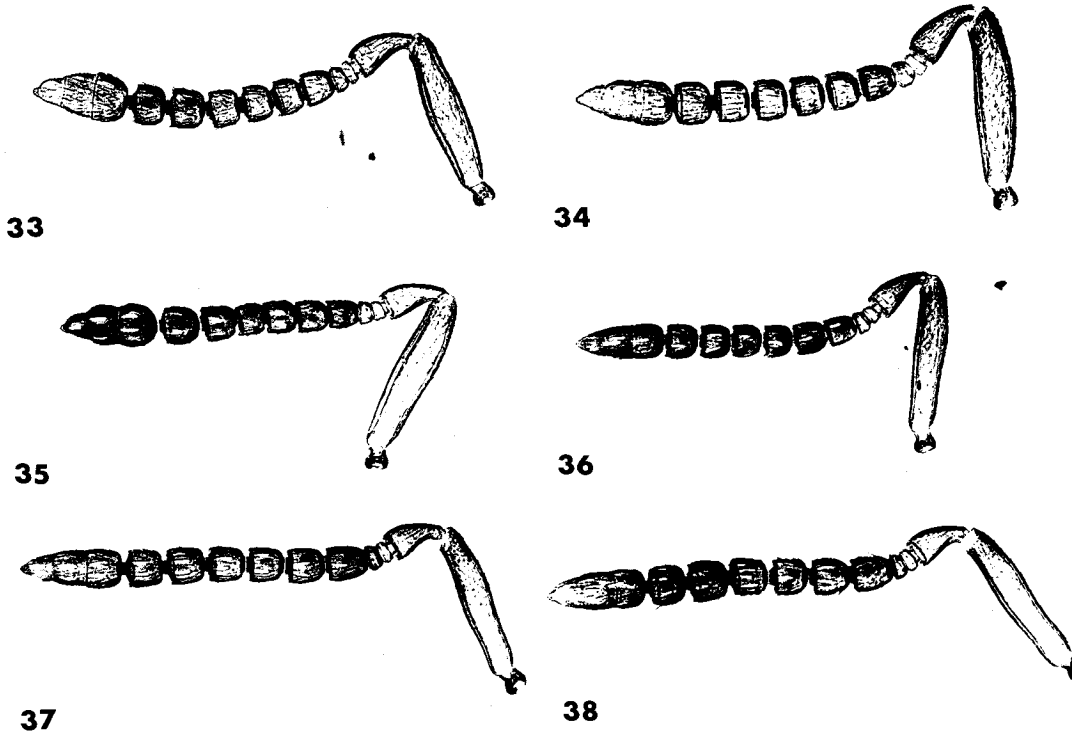


Fig. 33-38. Intra- and interspecific variation in male antenna. (33 and 34) *N. vitripennis*. (35 and 36) *N. longicornis*. (37 and 38) *N. giraulti*.

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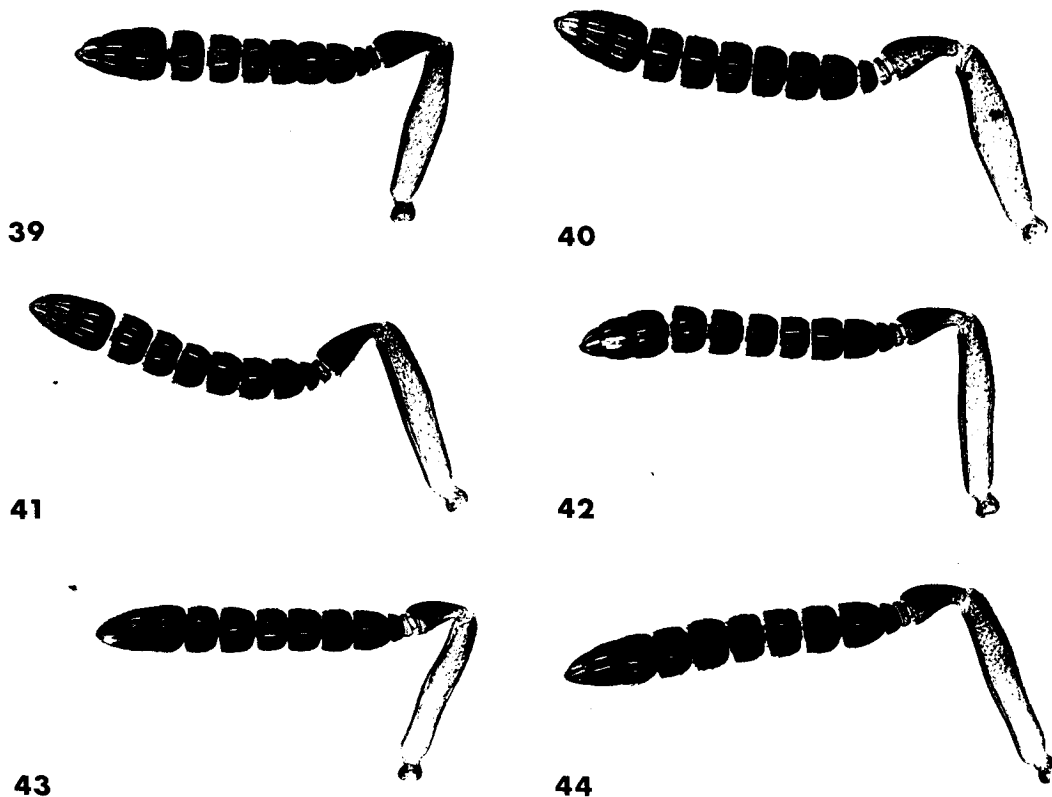


Fig. 39-44. Intra- and interspecific variation in female antenna. (39 and 40) *N. vitripennis*. (41 and 42) *N. longicornis*. (43 and 44) *N. giraulti*.

the type material that includes both males and females.

Diagnosis. Both sexes of *N. vitripennis* can be recognized by the structure of the antenna; the spindle-shaped scape and elongate pedicel (Fig. 33, 34, 39, and 40) are apparent usually without resorting to slide-mounted material. Males of *N. vitripennis* are distinctly brachypterous and can be immediately recognized by the short, narrow, setose forewings (Fig. 9 and 10). Females are most easily identified in pinned or living specimens by the setation of the forewing. Both the darker discal setae and the fringe of apical setae (Fig. 15-18, 27, and 29) will distinguish this species from congeners. Slide-mounts of the forewing are on occasion necessary to confirm identifications. The longer, straighter, setose stigmal vein and the irregular outline of the stigma, incorporating many setae, will provide unequivocal identification as *N. vitripennis* (Fig. 15-18, 48, and 50). Note: marginal setae are usually absent in specimens that have been stored in fluid or slide-mounted, but in these cases the setal sockets are usually visible at the wing margin (Fig. 28 and 30; cf. Fig. 27 and 29).

Material Examined. The following is a listing of specimens (mostly reared series) of Old World *Nasonia* examined at the BMNH: Locality (month collected; host; * if slides made of forewing and antenna).

AUSTRALIA: New South Wales (Ex: sheepfly [Calliphoridae: *Lucilia*]); Rydalmeve (II; Ex: Lab culture?, *). CHINA, Peiping (Ex: *Lucilia sericata*; *). EGYPT (Ex: *Chrysomyia albipes* and *Sarcophaga*). ENGLAND, Warwicks, Wellesbourne (VI; Ex: *Calliphora erythrocephala* and *Lucilia* sp.; *); Slough (V; blackbird nest); Surrey (VII; Ex: nest of spotted flycatcher). FRANCE, Hyeres (VI; Ex: *Sarcophaga*). GERMANY, Berlin (V, VI; Ex: *Protophthora* in nest of tit). GREECE, Levandia (X; Ex: *Beotia* ?). HOLLAND (Ex: Lab culture, LII; *). KOREA, Suigen (VIII; Ex: tachinid fly parasite of silkworm; *). PALESTINE, Jerusalem (V; Ex: *Chrysomyia marginalis*; *). RHODESIA, Gatooma (X-III; Ex: *Musca humilis* and ? *Chrysomyia marginalis*). SOUTH AFRICA, Dohne (IX; Ex: *Stomoxys calcitrans*; *); Pretoria (II; Ex: *Lucilia sericata*). SWITZERLAND, Zurich (VI, Ex: *Crataerina pallida* [Hippoboscidae] in nest of common swift). YUGOSLAVIA, Belgrade (IX; Ex: *Sarcophaga*).

North America material is listed in the Appendix.

Distribution. *Nasonia vitripennis* currently is regarded as a cosmopolitan species and there is no reason to refute this contention based on the material examined in this study. However, care should be exercised in the identification of specimens from Central or South America, especially those that are

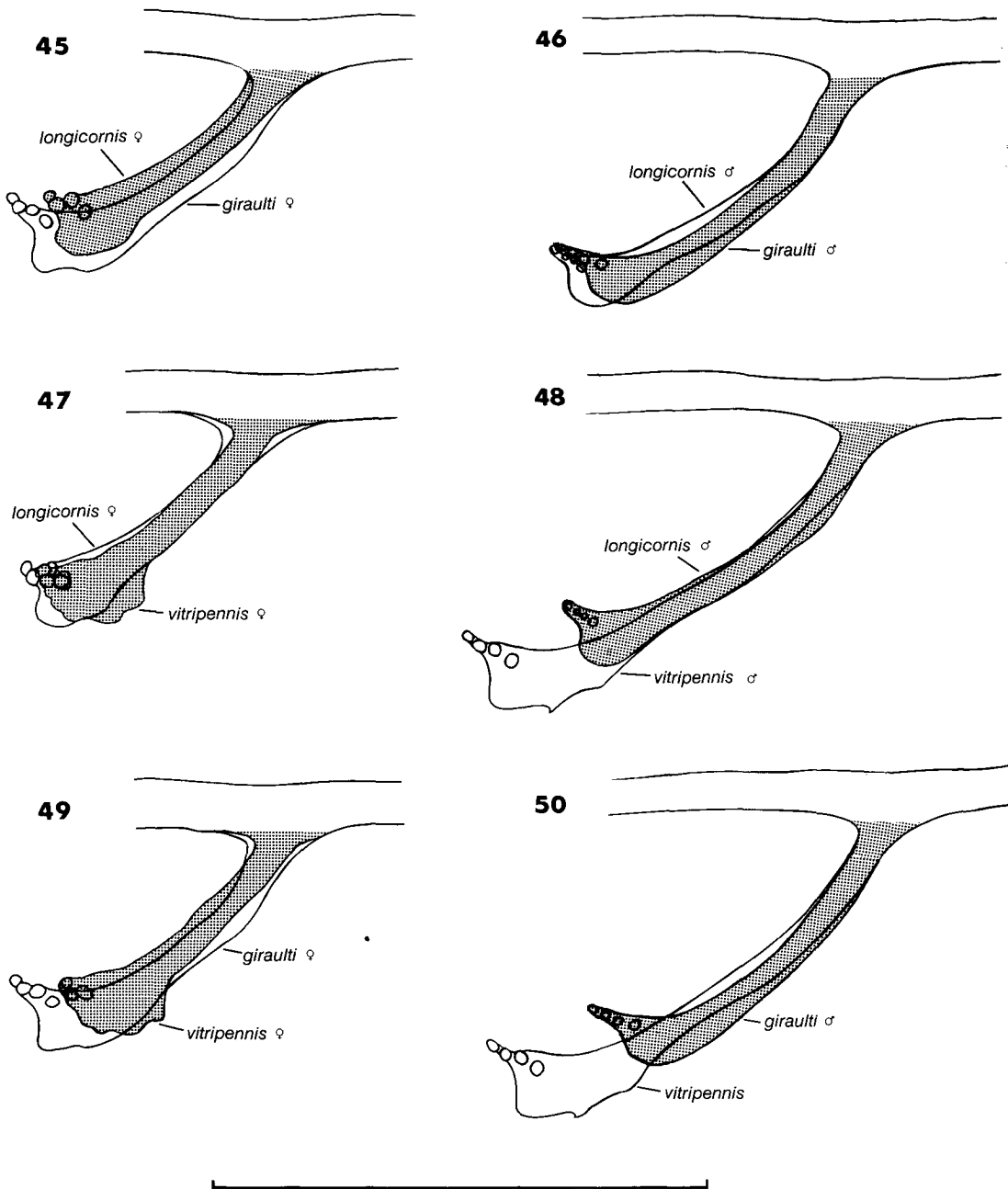


Fig. 45-50. Comparison of stigmal veins. (45, 47, and 49) Males. (46, 48, and 50) Females. (45) *N. giraulti* and *N. longicornis* (stippled). (46) *N. giraulti* (stippled) and *N. longicornis*. (47) *N. vitripennis* (stippled) and *N. longicornis*. (48) *N. vitripennis* and *N. longicornis* (stippled). (49) *N. vitripennis* (stippled) and *N. giraulti*. (50) *N. vitripennis* and *N. giraulti* (stippled). All illustrations prepared with camera lucida and marginal vein. Scale line = 0.27 mm.

associated with birds' nests. This species is widely distributed in North America (Fig. 51) and is routinely sympatric with *N. giraulti* and *N. longicornis*, often collected from the same birds' nest and frequently from the same blowfly pupa.

Hosts. The range of hosts attacked by *N. vitri-*

pennis has been tabulated (Peck 1963, Burks 1979) and will not be repeated here. Many of these records are dubious, based on literature records and usually without a clear indication of voucher specimens (e.g., egg parasite of the spruce budworm [Lepidoptera: Tortricidae] [Tothill 1923]). The dis-

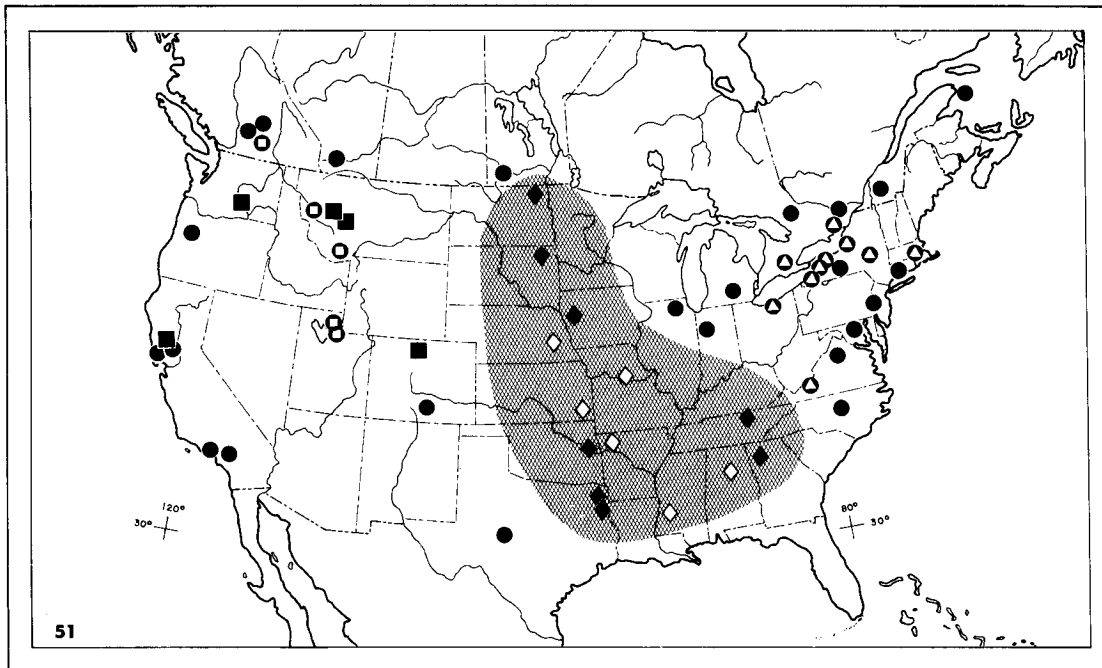


Fig. 51. Collection localities and distribution of *Nasonia* species in North America: *N. vitripennis* (circles); *N. giraulti* (triangles); *N. longicornis* (squares). Composite symbols signify sympatry. Diamonds indicate localities where nests were examined but *Nasonia* was not collected: ◆, blowflies collected; ◇, blowflies not collected.

covery of additional species of *Nasonia* in North America further compromises these summaries. Based on the current study, *N. vitripennis* is regarded as a pupal parasite of cyclorrhaphous Diptera, primarily the families Calliphoridae and Sarcophagidae, that frequent a variety of habitats including poultry and livestock manure, decaying carcasses, and birds' nests.

Redescription. *Female*: Length 1.8–2.3 mm. *Head*: length of malar space 0.40–0.54 eye height. Antenna (Fig. 39 and 40): scape spindle-shaped in lateral view, expanded medially, anterior and posterior margins divergent, not parallel, length 4.0–5.2 maximum width, pedicel very long, 2.2–3.0 F1, longer than F1 + F2; funicular segments transverse, length of F1 0.56–0.72 width; F2 shorter than F1; club 0.45–0.55 scape length, robust, length less than twice width, 1.6–1.8. *Mesosoma*: PN 0.16–0.24 MSC; dorsellum with upper margin scalloped and not emarginate along midline (Fig. 8). Forewing (Fig. 15–18, 27–30): length 2.2–2.5 maximum width; with distinct dark discal setae and fringe of marginal setae, denser distad postmarginal vein; postmarginal vein long, 0.81–1.1 marginal and 1.27–1.61 stigmal vein; stigmal vein long, 0.24–0.27 wing width, straight, without inflection point, with many setae along upper surface; stigma large and angular, incorporating many discal setae. *Metasoma*: T1 finely reticulate dorsad, surface sculpture not differentiated from laterotergite.

Male: As in female except as noted. Length 1.4–

1.9 mm. *Head*: in frontal view more quadrate, width 1.4–1.9; length of malar space 0.28–0.41 eye height. Antenna (Fig. 33 and 34): scape length 3.8–5.0 maximum width; funicular segments more quadrate, length of F1 0.7–1.0 width; club length 0.42–0.63 scape length, length about twice width, 2.0–2.3. *Mesosoma*: dorsellum with upper margin not distinctly scalloped, emarginate along midline. Forewing (Fig. 9 and 10): very short and narrow, length only 0.5–0.7 total body length, 3.3–3.9 maximum width; with longer discal and marginal setae; stigmal vein 0.35–0.47 wing width, smoothly curved and in closer proximity to postmarginal vein; stigma elongate and not abruptly differentiated from stigmal vein, without distinct uncus.

Nasonia giraulti Darling,
new species

(Fig. 1, 4, 5, 7, 13, 14, 23–26, 31, 37, 38, 43–46, 49, 50, and 51)

Type Locality. Canada, Ontario, Cambridge.

Type Material. HOLOTYPE ♀: "Canada, Ontario: Waterloo Co., 1 mi S Cambridge, 43°15'N × 80°18'E, 9 Aug 1988, D. C. Darling & J. Thomson-Delaney," "Ex: *Protocalliphora* pupa (ME37-1) in eastern bluebird nest." PARATYPES (50 ♀♀, 25 ♂♂): 18 ♀♀, 8 ♂♂, same exact data as holotype, from same pupa (ME37-1); 32 ♀♀, 17 ♂♂, same data as holotype, except from different pupae in same nest (ME37-

2, ME37-3, ME37-4, ME37-5, ME37-8). D. Chris Darling slide no. 1148/49, 1152/53, 1166/67, 1171/72 (♀ forewing/antenna); 1146/47, 1150/51 (♂ forewing/antenna).

Additional Material Examined. See Appendix.

Type Repository. HOLOTYPE: Royal Ontario Museum, Toronto, Canada. Paratypes widely distributed, including ROM, USNM, CNC, BMNH, AEI, ANIC, NCSU.

Etymology. Named for A. A. Girault, one of the most prolific and dedicated students of the Chalcidoidea. Girault was justifiably outraged by the original taxonomic treatment of *Nasonia* (Ashmead 1904) and only begrudgingly accepted Ashmead's nomenclatural priority. He redescribed *N. vitripennis* (as *N. brevicornis*) and conducted the first detailed work on the biology of chalcidoid parasites of Diptera (Girault & Sanders 1909, 1910).

Diagnosis. Both sexes of *N. giraulti* can be distinguished from the congeneric species by the structure of the antenna; the angulate, parallel-sided scape and short pedicel are usually apparent without resorting to slide-mounted material (Fig. 37, 38, 43, and 44). In addition, the male antenna of *N. giraulti* has longer setae than the other species (Fig. 37 and 38; cf. Fig. 33-36). Females of *N. giraulti* have more quadrate funicular segments than *N. longicornis* females (Fig. 43 and 44; cf. Fig. 41 and 42). *N. giraulti* females lack the fringe of marginal setae and the numerous setae on the upper surface of the stigmal vein that are characteristic of *N. vitripennis* females (Fig. 23-26, 31; cf. Fig. 15-18, 27-30) and the discal setae are less distinct than in the females of the other two species. Males of *N. giraulti* have the longest and broadest forewings in the genus; there is very little sexual dimorphism in the shape of the forewing. The ratio of wing length to wing width is diagnostic for males of the 3 described species: *N. giraulti*, 2.25-2.56 cf. *N. vitripennis*, 3.31-3.86; *N. longicornis*, 2.65-2.89. Slide-mounts of the forewing are usually necessary to distinguish females of *N. giraulti* and *N. longicornis* on the basis of the shape of the stigmal vein (Fig. 46): smoothly arched without a distinct inflection point in *N. giraulti* (Fig. 24-26) and angulate and in closer proximity with the postmarginal vein in *N. longicornis* (Fig. 20-22).

Additional Material Examined. See Appendix.

Distribution. *N. giraulti* is known only from eastern North America, where it is broadly sympatric with *N. vitripennis* (Fig. 51). This species and *N. vitripennis* often are collected from the same birds' nest and occasionally from the same blowfly pupa. To date, *N. giraulti* has not been collected in sympatry with *N. longicornis*.

Hosts. This species is regarded as a parasite of pupae of cyclorrhaphous Diptera that are associated with birds' nests. The type material and all other series are associated with Calliphoridae (*Protocalliphora* spp.) or with birds' nests (Appendix).

Description. Female: Length 1.8-2.2 mm. **Head:** length of malar space 0.48-0.57 eye height. An-

tenna (Fig. 43 and 44): scape cylindrical in lateral view, not distinctly expanded medially, anterior and posterior margins parallel, not divergent as in *N. vitripennis*, length 4.2-5.1 maximum width; pedicel short, 1.6-2.4 F1, only about one-half the length of F1 + F2; funicular segments more quadrate than in *N. vitripennis*, length of F1 0.70-0.84 width; F2 subequal to F1; club longer and more gracile than in *N. vitripennis*, length 0.48-0.59 scape length, and almost twice width, 1.67-1.99. **Mesosoma:** PN 0.13-0.19 MSC; dorsellum with upper margin not distinctly scalloped as in *N. vitripennis*, emarginate along midline (Fig. 6). Forewing (Fig. 23-26 and 31): length 2.1-2.4 maximum width; with discal setae lighter in color and less distinct than in *N. vitripennis* and *N. longicornis*; without fringe of marginal setae, either apically or distad postmarginal vein; postmarginal vein shorter, 0.69-0.83 marginal and 1.11-1.39 stigmal vein; stigmal vein shorter than in *N. vitripennis*, 0.21-0.24 wing width, smoothly arched, without a distinct inflection point near base, not in as close proximity to postmarginal vein as in *N. longicornis*, with only a few setae along upper surface; stigma smaller and more rounded than in *N. vitripennis*, incorporating only few discal setae. **Metasoma:** T1 glabrous dorsad, surface sculpture differentiated from finely reticulate laterotergite.

Male: As in female except as noted: Length 1.2-1.8 mm. **Head:** length of malar space 0.35-0.43 eye height. Antenna (Fig. 37 and 38): scape length 3.9-4.85 maximum width; funicular segments more quadrate, length of F1 0.9-1.1 width, with longer setae than in other species; club length 0.62-0.74 scape length, length greater than twice width, 2.3-2.7. **Mesosoma:** metanotum shorter, 0.18-0.28 length of propodeum. Forewing (Fig. 13-14): similar in shape to female, 0.7-0.9 total body length, longer than in *N. longicornis* and much longer than in *N. vitripennis*, 2.2-2.6 maximum width; stigmal vein 0.22-0.27 wing width; stigma larger.

Nasonia longicornis Darling,
new species

(Fig. 2, 3, 6, 11, 12, 19-22, 32,
35, 36, 41, 42, 45-48, and 51)

Type Locality. Canada, British Columbia, Kelowna.

Type Material. HOLOTYPE ♀: "Canada, British Columbia: Osoyoos Dist. Kelowna, 49°53'N × 119°29'E, Ex: *Protocalliphora* pupa (BC1-12) in tree swallow nest coll. 15 July 1988, H. Metke." PARATYPES (50 ♀♀, 25 ♂♂): 7 ♀♀, 2 ♂♂, same exact data as holotype, from same pupa (BC1-12); 43 ♀♀, 23 ♂♂, same data as holotype, except from different pupae in same nest (BC1-6, BC1-9, BC1-10, BC1-11, BC1-13). D. Chris Darling slides no. 1156/57, 1160/61, 1168/69 (♀ forewing/antenna); 1154/55, 1158/59 (♂ forewing/antenna).

Additional Material Examined. See Appendix.

Type Repository. HOLOTYPE: Royal Ontario Museum, Toronto, Canada. Paratypes widely distributed, including ROM, USNM, CNC, BMNH, AEI, ANIC, NCSU.

Etymology. An allusion to the longer antenna of this species relative to *N. vitripennis*, from the Latin "cornu" or horn, recalling that for many years *N. vitripennis* was referred to as *N. brevicornis*.

Diagnosis. Both sexes of *N. longicornis* can be distinguished from the congeneric species by the structure of the antenna. The scape is linear and parallel-sided (Fig. 35, 36, 41, and 42), not expanded and spindle-shaped as in *N. vitripennis* (Fig. 33, 34, 39, and 40) and not narrow and angulate as in *N. giraulti* (Fig. 37, 38, 43, and 44). Males of *N. longicornis* have shorter setae on the funicular segments and club than *N. giraulti* (Fig. 35 and 36; cf. Fig. 37 and 38) and triangular wings that are intermediate in width (Fig. 11 and 12), longer and broader than *N. vitripennis* (Fig. 9 and 10) but shorter and narrower than *N. giraulti* (Fig. 13 and 14). The ratio of wing length to wing width is diagnostic for males of the 3 described species: *N. longicornis*, 2.65–2.89, cf. *N. vitripennis*, 3.31–3.86; *N. giraulti*, 2.25–2.56. Females of *N. longicornis* can usually be distinguished from *N. vitripennis* in pinned or living specimens by the absence of apical setae on the forewing (Fig. 19 and 32; cf. Fig. 15, 27–30) and from *N. giraulti* by the darker discal setae (Fig. 20–22 and 32; cf. Fig. 24–26 and 31). In addition, the stigmal vein of females is angulate and in closer proximity to the postmarginal vein in *N. longicornis* (Fig. 19–22 and 46); not smoothly arched without a distinct inflection point as in *N. giraulti* (Fig. 23–26 and 46) or irregular in outline and much longer as in *N. vitripennis* (Fig. 15–18 and 48).

Additional Material Examined. See Appendix.

Distribution. *N. longicornis* is known only from western North America, where it is broadly sympatric with *N. vitripennis* (Fig. 51). This species and *N. vitripennis* are often collected from the same birds' nest and occasionally from the same blowfly pupa. To date, *N. longicornis* has not been collected in sympatry with *N. giraulti*.

Hosts. This species is regarded as a parasite of pupae of cyclorrhaphous Diptera associated with birds' nests. The type material and most other series of specimens are associated with Calliphoridae (*Protocalliphora* spp.) in birds' nests. Sarcophagidae and Tachinidae may also serve as hosts. *N. longicornis* has been reared in association with spruce budworm (*Choristoneura fumiferana* (Clemens), CNC), and was reported as a hyperparasite of the tachinid *Omotoma fumiferana* (Tot.) (Coppel & Smith 1957). There are no wild-caught specimens of this species associated with Sarcophagidae but this species accepts *Sarcophaga bullata* as a host in the laboratory. There are no records of this species associated with either carcasses or poultry or livestock manure.

Description. Female: Length 1.9–2.4 mm. **Head:** length of malar space 0.45–0.53 eye height. Antenna (Fig. 41 and 42): scape cylindrical in lateral view, not distinctly expanded medially, anterior and posterior margins parallel, not divergent as in *N. vitripennis*, longer than in other species, length 4.35–5.15 maximum width; pedicel long, 2.05–2.7 F1, subequal to F1 + F2; funicular segments more quadrate than in *N. vitripennis*, length of F1 0.63–0.82 width; F2 subequal to F1; club longer and more gracile than in *N. vitripennis*, length 0.48–0.54 scape length, and almost twice width, 1.72–2.06. **Mesosoma:** PN 0.18–0.24 MSC, longer than in *N. vitripennis* and *N. giraulti*; dorsellum with upper margin not distinctly scalloped as in *N. vitripennis*, emarginate along midline (Fig. 6). Forewing (Fig. 19–22 and 32): length 2.2–2.6 maximum width; with discal setae lighter in color and less distinct than in *N. vitripennis*; without a fringe of marginal setae, either apically or distad postmarginal vein; postmarginal vein shorter, 0.75–0.95 marginal and 1.18–1.45 stigmal vein; stigmal vein shorter than in *N. vitripennis*, 0.22–0.26 wing width, angulate, with distinct inflection point near base, in closer proximity to postmarginal vein than in *N. giraulti*, with only a few setae along upper surface; stigma smaller and more rounded than in *N. vitripennis*, incorporating only few discal setae. **Metasoma:** T1 glabrous dorsad, surface sculpture differentiated from finely reticulate laterotergite.

Male: As in female except as noted. Length 1.6–1.8 mm. **Head:** in frontal view more quadrate, width 1.4 length; length of malar space 0.31–0.37 eye height; scape shorter relative to eye height, SL/EH 0.7–0.8. Antenna (Fig. 35 and 36): scape length 4.15–5.0 maximum width; funicular segments more quadrate, length of F1 0.8–1.1 width; club length 0.51–0.64 scape length, length greater than twice width, 2.1–2.6. **Mesosoma:** Forewing (Fig. 11 and 12): length 0.65–0.8 total body length, intermediate to males of *N. vitripennis* and *N. giraulti*, 2.65–2.9 maximum width; stigmal vein 0.25–0.30 wing width, straighter, without distinct inflection point.

Comparative Biology

Morphology. The most obvious morphological differences between the species of *Nasonia* involve the structure of the forewing and antenna. In *Nasonia*, as in most Chalcidoidea, the courtship sequence involves several stereotypic movements with rigid temporal relationships that result in the male either establishing genital contact or dismounting (van den Assem 1976). The male forewing and antenna figure prominently in the courtship of *Nasonia* (van den Assem & Vernel 1979) and it is likely that morphological differences in the antenna (e.g., shape of the scape, size of pedicel) and the forewing (e.g., size, setation, length, and shape of stigma) would influence courtship in subtle ways that could result in unreceptivity by females. Mor-

phological differences in structures that are involved in courtship could drive sympatric speciation by the elaboration of premating isolating mechanisms or maintain reproductive isolation in secondary contact following allopatric speciation. A sexual selection explanation such as this would be consistent with two aspects of *Nasonia* morphology: 1) males of the three species are much easier to distinguish than females, and 2) the morphological differences are more extreme between sympatric species. Sexual dimorphism and species-specific differences in the structure of the male antenna have recently been reported in various groups of Chalcidoidea. Differences can be subtle, as in *Nasonia* and many other genera of Pteromalidae (Graham 1969, Darling 1986, Darling & Hanson 1986), or strongly exaggerated, as in Chalcididae (*Inoreia*, Gringell & Schaffer 1981), Eulophidae (*Mellitobia*, Dahms 1984; *Elachertus*, Schauff 1985; *Entedon*, Schauff 1988), Perilampidae (*Euperilampus* and *Perilampus*, Darling 1983), and Torymidae (*Monodontomerus*, Goodpasture 1975). Sexual selection based on the importance of wings and antenna in courtship is consistent with monotony in male genitalia (Eberhard 1985), which is common in Chalcidoidea.

Genetics and Behavior. Genetic and behavioral differences between isofemale lines were also found that are consistent with genetic divergence of the *Nasonia* species. A preliminary study of allozymes using starch-gel electrophoresis (Selander et al. 1971) has revealed fixed differences between the three species (*N. vitripennis*, five isofemale lines, Montana (NvMT5) and upstate New York (NvR5, Nv61, NvSP56, NvRO32); *N. giraulti*, five isofemale lines, Virginia (NgVA2) and upstate New York (NgSP1, NgRO60, NgRO80, NgRV); *N. longicornis*, six isofemale lines, Colorado (NlCO4) and Montana (NlMT3, NlMT5, NlMT7, NlMT8)). *N. vitripennis* has a unique electromorph at three loci (peptidase-2, glucose-6-phosphate dehydrogenase, lactate dehydrogenase), and all three species are fixed for different electromorphs of peptidase-1 (Werren & Selander, unpublished data).

Reciprocal genetic crosses were made between six isofemale lines of the three species: *N. vitripennis* (New York, NvR5), *N. giraulti* (Ohio, NgOH2; New York, NgRV; Virginia, NgVA2), *N. longicornis* (Utah, NlUT7; Montana, NlMT14). Fertile progeny were produced in all conspecific crosses, but crosses between species did not typically yield F1 hybrid females except in the case of *N. longicornis* males \times *N. giraulti* females. Less than 1% F1 hybrid progeny are inconsistently produced in the other hybrid crosses and hybrid dysgenesis also occurs in the F3 generation (Werren & Riley, unpublished data). We can conclude that there is a significant degree of postmating reproductive isolation between the species.

We have also observed differences in host preference and the tendency of larvae to enter diapause between the three species. *N. giraulti* has a signif-

icantly lower preference for *S. bullata* (Diptera: Calliphoridae) pupae than do the other species ($\chi^2 = 79.5$; $P < 0.001$). For example, when five inseminated females of each species are provided with five *S. bullata* pupae in a test tube (25°C, constant light), parasite progeny developed from 100% of the replicates for *N. vitripennis* (NvR5, $n = 112$), 100% for *N. longicornis* (NlUT7, $n = 73$; NlMT14, $n = 94$), but from a lower percentage of the replicates for *N. giraulti* (NgRV, 63%, $n = 117$; NgOH2, 92%, $n = 75$). Similarly, diapause tendency was significantly different in these experiments ($\chi^2 = 49.3$; $P < 0.001$). Diapausing larvae were not produced by *N. vitripennis* (NvR5, $n = 112$) and *N. longicornis* (NlUT7, $n = 73$; NlMT14, $n = 94$), but *N. giraulti* did produce some diapausing larvae (5.3%, NgOH2, $n = 75$; 24%, NgRV, $n = 113$).

Distribution. *N. vitripennis* is sympatric with *N. giraulti* and *N. longicornis* throughout eastern and western North America, respectively (Fig. 51). *N. vitripennis* and *N. giraulti* often occur in the same bird's nest and conservative estimates of parasitized blowfly pupae show that 24% of nests were attacked by both species at Geneseo, N.Y. ($n = 54$), and 40% of nests were attacked by both species in two sites in Ontario, Cambridge, and Chaffey's Locks ($n = 20$). In some cases, the species are microsympatric and emerge from a single puparium. For example, of 35 pupae from bluebird nest ME37 that were parasitized by *Nasonia*, 25 produced only *N. giraulti*, 8 produced only *N. vitripennis*, and 2 produced both species. There is, however, considerable local variation in both parasitism rate and parasitoid species composition. For example, nest ME49 was collected on the same day from a nest box in the same field as ME37, but all 38 parasitized pupae produced only *N. vitripennis*.

The east-west disjunction in the distributions of *N. giraulti* and *N. longicornis* cannot be explained as an artifact of inadequate sampling. Nests were collected from nest boxes at 14 sites in the central and southern United States (primarily eastern bluebird) but only 16% of the nests contained blowfly pupae ($n = 171$). In northeastern North America, a higher percentage of nests are infested with blowflies. For example, 41% of eastern bluebird nests and 60% of tree swallow nests contain blowflies based on Ontario records for 1988 (Darling & Thomson-Delaney, unpublished data). These results are consistent with the hypothesis that these two species are strongly associated with *Protocalliphora* and that this disjunction is due to the distribution of the hosts; *Protocalliphora* have not been recorded from south of Virginia (Hall 1948). *N. vitripennis* is considered widely distributed in North America (Burks 1979) but the distribution of rural populations of this species is unclear because of the frequent introductions for biological control purposes (see bibliography in Rueda & Anderson [1985]).

There are no clearcut differences in the seasonal distribution of the species in areas of symp-

Blowfly pupae from both first brood (late June) and second brood (late July) bluebird nests in Chaffey's Locks, Ontario, were parasitized by both *N. vitripennis* and *N. giraulti*.

Discussion

It may seem rather unexpected that new species should be recognized in the genus *Nasonia*. This genus has been under intense scrutiny for almost 80 yr and is clearly the most studied species of Chalcidoidea, if not the most studied species of parasitic Hymenoptera. However, most of these studies were restricted to the laboratory and most experimental work used stock cultures derived from laboratory strains. Most field studies have emphasized barnyard situations and were directed at the possibility of using *Nasonia* as a biological control agent against muscoid flies (see annotated bibliography in Rueda & Axtell 1985). In those few cases where *Nasonia* was studied in birds' nests, the primary focus was the role of the wasps as mortality factors of *Protocalliphora* blowflies (Jellison & Philip 1933, Zeleny 1976). Examination of museum collections and data from our field studies indicate that only *N. vitripennis* is associated with barnyard situations. This is fortunate for the extensive literature that has developed for this species. Few, if any, studies of *N. vitripennis* have designated voucher specimens and there must now be at least some uncertainty about species identity because of the existence of heretofore undescribed species of *Nasonia*. Clearly, voucher specimens are essential even in cases such as *Nasonia* where it seems unlikely that identification problems will surface in the future (Yoshimoto 1978).

The advantage of combining morphological and behavioral approaches is clearly indicated by our study of *Nasonia*. Two factors, one derived from morphology and one derived from behavior, combined to facilitate the recognition of these closely related species. It was essential that there were obvious differences in wing length between the males of *Nasonia* species. Without this morphological correlate, assortative mating and pre-mating isolation between the species would have been very difficult to observe and appreciate. Without laboratory studies of mating behavior, wing length variation in males could have been regarded as either a polymorphism (Askew 1971) or continuous variation (Darling & Hanson 1986). Other morphological characters are subtle and it is extremely unlikely that these "sibling" or "cryptic" species would have been detected solely on morphological grounds. Only after specimens could be sorted a priori to tentative species using wing length was it possible to extract additional morphological information by microscopic comparisons of wings and antennae. And without the genetic data it would not be certain that the reproductive isolation and hybrid dysgenesis observed in the laboratory operates in nature to maintain distinct gene pools.

Were it not for the interplay and congruence of data derived from morphology, behavior, and genetics *Nasonia* would still be regarded as a monotypic genus.

A fundamental question concerning the micro-sympatry of *Nasonia* is whether genetic divergence has occurred in sympatry or in allopatry with subsequent range extensions leading to the observed sympatry in North America. It is possible that the cosmopolitan distribution of *N. vitripennis* is a relatively recent occurrence and is a result of its association with synanthropic flies. If sympatry is recent then this species complex presents opportunities to investigate the interaction of closely related species in secondary sympatry. A prediction would be that pre-mating isolating mechanisms are actively evolving to reduce the fitness costs that are associated with hybridization. However, if *N. vitripennis* was cosmopolitan when *N. giraulti* and *N. longicornis* (or their common ancestor) differentiated then sympatric speciation is a distinct possibility. Clearly, a historical perspective is required to evaluate these and many other evolutionary scenarios.

It would be premature to present a cladistic hypothesis for the relationships of the species of *Nasonia* at this time. Our suspicion is that there are still undescribed species in North America and species identifications in other parts of the world must be regarded as tentative. In addition, there is no substantiated hypothesis for the sister group of *Nasonia* and this information is essential to even begin to investigate phylogenetic relationships of the species. A first step would be to investigate the possibility that the *Dibrachys* group (which includes *Nasonia*, sensu Wallace 1973) is monophyletic, or to demonstrate the monophyly of a restricted group of genera that includes *Nasonia*.

Species diversity in *Nasonia* is significant because it opens up new areas of study. Comparative studies will be more illuminating than the duplication of the descriptive studies that have been done with *N. vitripennis* with the newly described species. For example, it is now possible to investigate the evolution of host associations and courtship and to analyze differences in, for example, reproductive biology as possible adaptations. Such studies will require a phylogenetic framework as a starting point (Felsenstein 1985, Coddington 1988), and again there will be the need for a close interplay between studies of morphology, behavior, and genetics.

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References Cited

- Ashmead, W. H. 1904. Classification of the Chalcid flies, or the Superfamily Chalcidoidea with descriptions of new species in the Carnegie Museum, collected in South America by Herbert H. Smith. Mem. Carnegie Mus. 1: 225-555.
- Askew, R. R. 1971. Parasitic insects. American Elsevier, New York.
- Boheman, C. H. 1858. Könskillnad hos Pteromaliner. Öfver. K. Vetensk-Akad. Forh. 15: 58-59.
- Boucek, Z. 1988. Australasian Chalcidoidea (Hymenoptera). C.A.B. International, Wallingford, United Kingdom.
- Burks, B. D. 1979. Family Pteromalidae, pp. 768-835. In K. V. Krombein, P. D. Hurd, Jr., D. R. Smith, & B. D. Burks [eds.], Catalog of hymenoptera in America north of Mexico, Vol. 1. Smithsonian Institution Press, Washington, D.C.
- Coddington, J. A. 1988. Cladistic tests of adaptational hypotheses. Cladistics 4: 3-22.
- Coppel, H. C. & B. C. Smith. 1957. Studies on dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). V. *Omotoma fumiferanae* (Tot.) (Diptera: Tachinidae). Can. J. Zool. 35: 581-592.
- Dahms, E. C. 1984. Revision of the genus *Melittobia* (Chalcidoidea: Eulophidae) with the description of seven new species. Mem. Queensl. Mus. 21: 271-336.
- Darling, D. C. 1983. A review of the New World species of *Euperilampus* (Hymenoptera: Chalcidoidea), with notes about host associations and phylogenetic relationships. Quaest. Entomol. 19: 1-40.
1986. Revision of the New World Chrysolampinae (Hymenoptera: Chalcidoidea). Can. Entomol. 118: 913-940.
- Darling, D. C. & P. E. Hanson. 1986. Two new species of *Spalangiopecta* from Oregon (Hymenoptera: Chalcidoidea), with a discussion of wing length variation. Pan-Pac. Entomol. 62: 153-164.
- Eberhard, W. G. 1985. Sexual selection and animal genitalia. Harvard University Press, Cambridge, Mass.
- Felsenstein, J. 1985. Phylogenies and the comparative method. Am. Nat. 125: 1-15.
- Gahan, A. B. 1927. Miscellaneous descriptions of new parasitic Hymenoptera with some synonymical notes. Proc. U.S. Nat. Mus. 71: 1-39.
- Gibson, G. A. P. 1985. Some pro- and mesothoracic structures important for phylogenetic analysis of Hymenoptera, with a review of terms used for the structures. Can. Entomol. 117: 1395-1443.
- Girault, A. A. & G. E. Sanders. 1909. The chalcidoid parasites of the common house or typhoid fly (*Musca domestica* Linnaeus) and its allies. I. Reconstruction of the chalcidoid genus *Nasonia* Ashmead of the family Pteromalidae, with description and biology of *Nasonia brevicornis* Ashmead, species nova, its type species from Illinois. Psyche 16: 119-132.
1910. The chalcidoid parasites of the common house or typhoid fly (*Musca domestica* Linn.) and its allies. Psyche 17: 9-28.
- Goodpasture, C. 1975. Comparative courtship behavior and karyology in *Monodontomerus* (Hymenoptera: Torymidae). Ann. Entomol. Soc. Am. 68: 391-397.
- Graham, M. W. R. de V. 1969. The Pteromalidae of north-western Europe (Hymenoptera: Chalcidoidea). Bull. Br. Mus. (Nat. Hist.) Entomol. Suppl. 16.
- Grissell, E. E. & M. E. Schauff. 1981. New nearctic *Invreia* (Hymenoptera: Chalcidoidea) from lepidopterous pests of peanut. Proc. Entomol. Soc. Wash. 83: 1-12.
- Harris, R. A. 1979. A glossary of surface sculpturing. Occasional Papers in Entomology, State of California, Department of Food and Agriculture, No. 28.
- Hall, D. G. 1948. The blowflies of North America. The Thomas Say Foundation, Philadelphia.
- Hoebeke, E. R. & D. A. Rutz. 1988. *Trichomalopsis dubius* (Ashmead) and *Dibrachys cavus* (Walker): newly discovered pupal parasitoids (Hymenoptera: Pteromalidae) of house flies and stable flies associated with livestock manure. Ann. Entomol. Soc. Am. 81: 493-497.
- Holmes, H. B. 1972. Genetic evidence for fewer progeny and a higher percent males when *Nasonia vitripennis* oviposits in previously parasitized hosts. Entomophaga 17: 79-88.
- Jellison, W. L. & C. B. Philip. 1933. Faunae of nests of the magpie and crow in western Montana. Can. Entomol. 65: 26-31.
- Nur, U., J. H. Werren, D. G. Eickbush, W. D. Burke & T. H. Eickbush. 1988. A "selfish" B chromosome that enhances its transmission by eliminating the paternal genome. Science 240: 512-514.
- Peck, O. 1963. A catalogue of the Nearctic Chalcidoidea (Insecta: Hymenoptera). Can. Entomol. Suppl. 30.
- Peck, O., Z. Boucek & A. Hoffer. 1964. Keys to the Chalcidoidea of Czechoslovakia (Insecta: Hymenoptera). Mem. Entomol. Soc. Can. 34.
- Pimentel, D., W. P. Nagel & J. L. Madden. 1963. Space-time structure of the environment and the survival of parasite-host systems. Am. Nat. 97: 141-167.
- Richards, O. W. 1977. Hymenoptera, introduction and key to families, 2nd ed. Royal Entomological Society of London, London.
- Rueda, L. M. & R. C. Axtell. 1985. Guide to common species of pupal parasites (Hymenoptera: Pteromalidae) of the house fly and other muscoid flies associated with poultry and livestock manure. N.C. Agric. Res. Serv. Tech. Bull. 278.
- SAS-PC. 1987. SAS/STAT guide for personal computers, version 6. SAS Institute, Cary, N.C.
- Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson & J. B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus* I. Variation in the old-field mouse. Studies in Genetics 6: 49-90.
- Schauff, M. E. 1985. Taxonomic study of the nearctic species of *Elachertus* Spinola (Hymenoptera: Eulophidae). Proc. Entomol. Soc. Wash. 87: 843-858.
1988. The species of *Entedon* in America north of Mexico (Hymenoptera: Eulophidae). J. N.Y. Entomol. Soc. 96: 30-62.
- Skinner, S. W. 1985. Son-killer: a third extrachromosomal factor affecting the sex ratio in the parasitoid wasp, *Nasonia* (= *Mormoniella*) *vitripennis*. Genetics 109: 745-759.
1987. Paternal transmission of an extrachromosomal factor in a wasp: evolutionary implications. Heredity 59: 47-53.

- Tohill, J. D. 1923 (1922). Notes on the outbreaks of spruce budworm, forest tent caterpillar and larch sawfly in New Brunswick. *Acad. Entomol. Soc.* 8: 172-182.
- van den Assem, J. 1976. Male courtship behaviour, female receptivity signal, and size differences between the sexes in Pteromalinae (Hym., Chalcidoidea Pteromalidae), and comparative notes on other chalcidoids. *Neth. J. Zool.* 26: 535-548.
- van den Assem, J. & C. Vernel. 1979. Courtship behaviour of *Nasonia vitripennis* (Hym.: Pteromalidae): observations and experiments on male readiness to assume copulatory behaviour. *Behaviour* 68: 118-135.
- Wallace, G. E. 1973. New Pteromalidae of the *Di-brachys* group (Hymenoptera: Chalcidoidea) with a key to genera. *Ann. Carnegie Mus.* 44: 171-181.
- Werren, J. H. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. *Science* 208: 1157-1159.
1983. Sex ratio evolution under local mate competition in a parasitic wasp. *Evolution* 37: 116-124.
1987. Labile sex ratios in wasps and bees. *Bioscience* 37: 498-506.
- Werren, J. H. & J. van den Assem. 1986. Experimental analysis of a paternally inherited extrachromosomal factor. *Genetics* 114: 217-233.
- Werren, J. H., S. W. Skinner & E. L. Charnov. 1981. Paternal inheritance of a daughterless sex ratio factor. *Nature (London)* 293: 467-468.
- Werren, J. H., S. W. Skinner & A. M. Huger. 1986. Male-killing bacteria in a parasitic wasp. *Science* 231: 990-992.
- Werren, J. H., U. Nur & D. Eickbush. 1987. An extrachromosomal factor causing loss of paternal chromosomes. *Nature (London)* 327: 75-76.
- Whiting, A. R. 1967. The biology of the parasitic wasp *Mormoniella vitripennis* [= *Nasonia brevicornis*] (Walker). *Q. Rev. Biol.* 42: 333-406.
- Wylie, H. G. 1966. Some mechanisms that affect the sex ratio of *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae) reared from superparasitized house fly pupae. *Can. Entomol.* 98: 645-653.
- Yoshimoto, C. M. 1978. Voucher specimens for entomology in North America. *Bull. Entomol. Soc. Am.* 24: 141-142.
- Zeleny, L. 1976. The bluebird. How you can help its fight for survival. Indiana University Press, Bloomington.

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Appendix

The following is a listing of pinned specimens of North American *Nasonia* examined during this study: Locality (nest/pupa [Canada] or isofemale line code [USA]; first and last date collected; specimens; repository; host or host association; *, if slides made of forewing and antenna, †, if slides made and included in metric analysis). If no repository is listed, the material is in the ROM. The codes used for common host associations are as follows; nests of: B, bluebird (sp. ?); EB, eastern bluebird; WB, western bluebird; MB, mountain bluebird; TS, tree swallow.

Nasonia vitripennis

CANADA (171 ♀♀, 78 ♂♂). ALBERTA: Lethbridge (VII-5, VII-6; 2 ♀♀; CNC), Lethbridge area (1 ♀; CNC), Lethbridge, Oldman River (VI-22; 1 ♀; CNC). BRITISH COLUMBIA: Kamloops District, Kamloops (VII-18; 1 ♀; CNC; Sarcophagidae); Vavenby (1 ♀, 3 ♂♂, CNC; Sarcophagidae); Osoyoos District, Kelowna (BC1; VII-15; 15 ♂♂, 31 ♀♀; TS), (BC2; VII-15; 11 ♂♂, 6 ♀♀; WB), (BC3; VI-28; 4 ♂♂, 2 ♀♀; WB). MANITOBA: Brandon (VIII-14; 1 ♀; CNC). ONTARIO: Frontenac County, Chaffey's Locks: (BGC7-4; VII-28; 1 ♂, 6 ♀♀; EB), (GH3; V-31; 24 ♂♂, 18 ♀♀; EB), (HUD2-9; VII-1; 2 ♂♂, 2 ♀♀; TS), (HUE1-4; VI-27; 6 ♀♀, 3 ♂♂; EB; †), (HUF1-3; VII-22; 3 ♂♂, 1 ♀; TS), (ON2; VIII-16; 26 ♀♀, 7 ♂♂; EB; †); Hastings County, Stirling (VIII-11; 1 ♀; CNC; *Musca domestica*); Ottawa-Carleton, Bells Corners

(V-23; 58 ♀♀, 4 ♂♂; CNC/ROM; Diptera; †), Ottawa (VII-15; 1 ♀; CNC); Waterloo County, Kitchener (VA6-4; VIII-9; 3 ♀♀, 1 ♂, EB; †). QUEBEC: Duncan Lk. nr. Rupert (VI-11; 1 ♀; CNC; phoebe nest); Drummond County, Hemming (VII-28; 1 ♀; CNC); Gaspé-Est County, Bonaventure Island (VII-25; 1 ♀; CNC; kittiwake nest). USA (79 ♀♀, 44 ♂♂). CALIFORNIA: Alameda County, Berkeley (X-15; 5 ♀♀, 1 ♂, USNM; *Lucilia sericata*; *); Los Angeles County (4 ♀♀, 2 ♂♂, USNM; *); Riverside County, Indio (VI-5; 2 ♀♀, 2 ♂♂, USNM; *Protocalliphora*); Yolo County, Davis (VIII-25; 2 ♀♀, 1 ♂; *). COLORADO: Custer County, Westcliffe (VII-6; 7 ♀♀; USNM). CONNECTICUT: Windham County, Pomfret (2 ♀♀, 3 ♂♂; USNM; TS, *Protocalliphora*). ILLINOIS: McHenry County, Algonquin (15 ♀♀, 5 ♂♂, USNM/INHS/ROM; †), G. E. Sanders voucher specimens (INHS). INDIANA: Tippecanoe County, Lafayette (XI-19; 3 ♀♀, 1 ♂, USNM; *Phormia regina*). MARYLAND: Prince Georges County, Beltsville (X-21; 3 ♀♀, 1 ♂; USNM; *Lucilia sericata*). MASSACHUSETTS: Plymouth County, Rock (VIII-2; 1 ♀; USNM; *Protocalliphora*; *). MICHIGAN: Jackson County, Jackson (M11; V-23; 5 ♀♀, 4 ♂♂; EB; †). NEW YORK: Monroe County, Mumford (NYR5; VI-19; 5 ♀♀, 4 ♂♂; †), Rochester (R511P; VI-19; 3 ♀♀, 3 ♂♂); Tompkins County, Ithaca (III-18; 5 ♀♀, 1 ♂; USNM; *Protocalliphora*), Cornell University Laboratory culture (5 ♀♀, 1 ♂). NORTH CAROLINA: Wake County, Raleigh (laboratory reared; 3 ♂♂, 13 ♀♀; NCSU/ROM; *Musca domestica* in poultry manure). PENNSYLVANIA: Monroe County, Shawnee-on-Delaware (6 ♀♀, 2 ♂♂; USNM; *Protocalliph-*

ora; *). TEXAS: Menard County, Menard (VII-29; 1 ♀; USNM; *Protocalliphora*; *). VIRGINIA: Shenandoah Natl. Pk. (VII-21; 2 ♀♀; USNM; phoebe nest; *).

Nasonia giraulti

CANADA (62 ♀♀, 44 ♂♂). ONTARIO: Frontenac County, Chaffey's Locks: (HUF1-3; VII-22; 1 ♂, 1 ♀; TS), (ON1-1; VII-20; 18 ♀♀, 2 ♂♂; TS; *), (ON1-2; VII-20; 6 ♀♀, 4 ♂♂; TS; *), (ON1-3; VII-20; 5 ♀♀, 5 ♂♂; TS), (ON1-4; VII-20; 1 ♀, 3 ♂♂; TS), (ON1-5; VII-20; 4 ♀♀, 4 ♂♂; TS; *), (ON1-6; VII-20; 5 ♀♀, 5 ♂♂; TS; *), (ON1-7; VII-20; 2 ♀♀, 5 ♂♂; TS; *), (ON1-8; VII-20; 4 ♀♀, 1 ♂; TS), (ON2; VIII-16; 11 ♀♀, 10 ♂♂; EB; *), (HUE1-4; VI-27; 3 ♂♂; EB); Ottawa-Carleton County, Bells Corners (V-23; 2 ♀♀; CNC/ROM; Diptera; *); Waterloo County, Kitchener (VA6-4; VIII-9; 3 ♀♀, 1 ♂♂; TS; *). USA (45 ♀♀, 23 ♂♂). MASSACHUSETTS: Plymouth County, Rock (VIII-2; 1 ♂; USNM; *Protocalliphora*; *). MONTANA: Sanders County, Plains (MT7; VI-26; 1 ♀; B), (MT9; VI-11; 2 ♀♀, 3 ♂♂; B). NEW YORK: Erie County, Springville (SP1; VI-5; 5 ♀♀, 2 ♂♂; EB; *); Livingston County, Geneseo (RO60P; VI-28; 2 ♀♀, 1 ♂; TS; *); Monroe County, Mumford (MU12AH; VII-10; 3 ♀♀, 2 ♂♂; TS; *), Rochester: (RO60R; VI-28; 3 ♀♀, 2 ♂♂), (RV; VI-19; 25 ♀♀, 9 ♂♂; *); Onondaga County, Brewerton (BR2; V-29; 2 ♀♀, 1 ♂; EB; *). VIRGINIA: Giles County, Pembroke (VA2; V-27; 2 ♀♀, 2 ♂♂; EB; *).

Nasonia longicornis

CANADA (5 ♀♀, 5 ♂♂). BRITISH COLUMBIA: Laboratory reared (1 ♀, 2 ♂♂; CNC; Tachinidae); Osoyoos District, Kelowna (BC2; VII-15; 3 ♂♂, 2 ♀♀; WB), (BC3; VI-28; 2 ♀♀; WB; *). USA (104 ♀♀, 55 ♂♂). CALIFORNIA: Contra Costa County, Walnut Creek (CA4; VII-14; 4 ♀♀, 2 ♂♂; TS; *). COLORADO: Larimer County, Bellevue: (CO4; VII-6; 5 ♀♀, 1 ♂; MB; *), (CO4C; VII-6; 3 ♂♂, 3 ♀♀; *). MONTANA: Beaverhead County, Red Rock Lake: (MT11; VI-25, VII-19; 5 ♀♀, 3 ♂♂; *), (MT11E; VII-19; 2 ♀♀, 2 ♂♂; *), (MT13P; VII-19; 3 ♀♀, 3 ♂♂; *), (MT13O; VII-19; 2 ♀♀, 2 ♂♂; *); Lake County, Ronan: (MT3; V-22; 4 ♀♀, 1 ♂; MB; *), (MT3O; VI-19; 2 ♀♀, 2 ♂♂; MB; *), (MT5C; VI-22; 3 ♀♀, 2 ♂♂; WB), (MT5E; VI-23; 5 ♀♀, 2 ♂♂; WB); Lewis and Clark County, Lewis and Clark St. Pk.: (MT14; VII-8; 3 ♀♀, 1 ♂; WB; *), (MT17; VI-25; 5 ♂♂); Sanders County, Plains (MT7; VI-26; 12 ♀♀, 5 ♂♂; B; *), (MT8; VII-11; 8 ♀♀, 5 ♂♂; B; *), (MT9; VII-11; 1 ♀; B; *). UTAH: Box Elder County, Mantua (VII-7; 1 ♀, 1 ♂; USNM; TS; *); Weber County, Ogden (UT7P; VII-11; 6 ♀♀, 6 ♂♂; MB; *). WASHINGTON: Yakima County, Yakima: (WA2B; VI-16; 6 ♀♀, 2 ♂♂; WB; *), (WA2C; VI-16; 2 ♀♀, 1 ♂; WB; *), (WA4A; VI-15; 6 ♀♀, 1 ♂; WB; *), (WA4B; VI-15; 3 ♀♀, 1 ♂; WB; *), (WA4C; VI-15; 8 ♀♀, 2 ♂♂; WB; *), (WA7B; VI-19; 5 ♀♀, 1 ♂; WB; *), (WA7C; VI-18, VI-19; 5 ♀♀, 1 ♂; WB; *).