

# Hidden Taxonomic Diversity within *Chrysoperla plorabunda* (Neuroptera: Chrysopidae): Two New Species Based on Courtship Songs

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**ABSTRACT** Two new species and one new combination in the green lacewing genus *Chrysoperla* are presented, based principally on species-specific features of their substrate-borne, vibrational courtship songs. The three are North American taxa with broad geographical ranges. All were previously considered part of a single species, variously referred to as *C. plorabunda* (Fitch) (a Nearctic species) or *C. carnea* (Stephens) (a holarctic species that includes *C. plorabunda*). An analysis of morphological characters of the adult body surface, wings, and male and female reproductive anatomy failed to reveal any consistent differences among the species that could be used to identify them, even though some statistically significant differences in wing shape emerged from the study. The new species are *C. adamsi* and *C. johnsoni*, with broadly overlapping geographical ranges in western North America. The name *C. plorabunda* is redefined to include only those individuals with courtship songs corresponding to an eastern North American population. As now restricted, *C. plorabunda* nonetheless ranges from the east to west coasts of North America and south at least to the Mexican border.

**KEY WORDS** *Chrysoperla* spp., songs, speciation

OUR UNDERSTANDING OF the systematics of the Chrysopidae has changed radically during the past 30 yr. Until quite recently, most species of green lacewings were placed almost by default in the genus *Chrysopa* Leach 1815, which became unwieldy and ill-defined as a consequence. Steinmann (1964) was among the first to suggest that it be subdivided into more meaningful taxonomic units, and he proposed four subgenera, including *Chrysoperla*, to group lacewings sharing certain patterns of color and spotting on the head. Tjeder (1966) greatly developed and modified Steinmann's classification, defining eight monophyletic subgenera of *Chrysopa* sensu lato principally in terms of male and female genital structures. Only in 1977 were *Chrysoperla* and two other subgenera given full generic status and delineated further by ecological and lifehistory traits (Séméria 1977). Others of Tjeder's subgenera were later raised to generic rank by Hölzel (1970), Aspöck et al. (1980), and Brooks & Barnard (1990). The last work extensively reviews and revises the generic classification of the chrysopids of the world.

Despite the value of generic subdivision, confusion is now apparent at lower taxonomic levels. Recently, chrysopid taxonomists have been

forced to recognize two informal "species complexes" within *Chrysoperla*, the *rufilabris* group and the *carnea* group, possessing distinctive genal (facial) markings, male genitalia, wing proportions, ecophysiological traits, and courtship behavior (Bram & Bickley 1963, Tauber & Tauber 1983, Henry 1989). Although the *rufilabris* group seems reasonably tractable, the *carnea* group clearly is taxonomically difficult. In particular, some members of the group are so similar in most morphological and ecological respects that species boundaries cannot be determined (Adams & Penny 1987). In the same way, other species, including *Chrysoperla carnea* (Stephens) itself, are now seen to be complexes of cryptic, sibling species, separated principally by differences in their courtship songs (Henry 1985b, 1991, 1992; Wells & Henry 1992a).

*Chrysoperla carnea* has undergone a series of rapid, unstable changes in its taxonomic status. Originally described as a common green lacewing from the British Isles by Stephens (1835), it was later defined to include morphologically identical forms from across most of Europe and Asia. Eventually, even its North American analogue, *C. plorabunda* (Fitch), was synonymized with paleartic *C. carnea*, based on detailed morphological and anatomical comparisons (Tjeder 1960). However, eastern and western hemisphere populations were then shown to possess completely different courtship songs, suggesting once again that they be recognized as distinct

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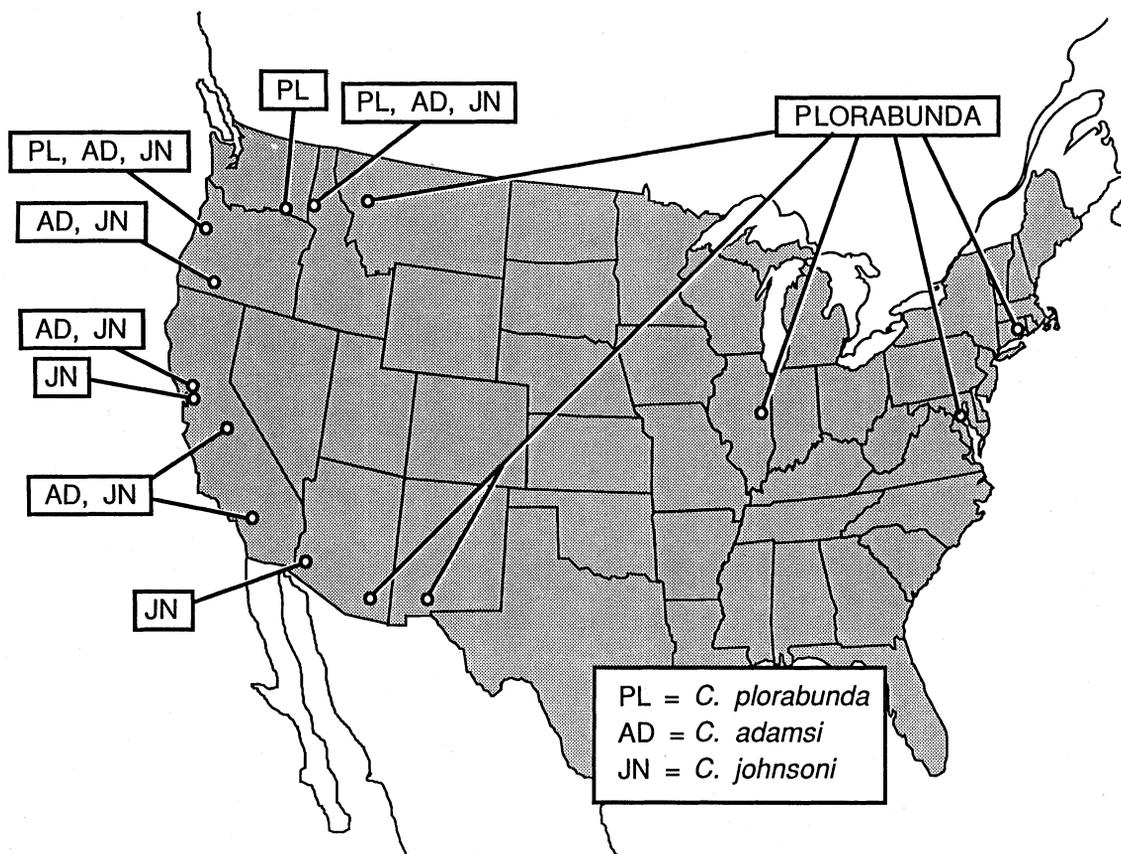


Fig. 1. Geographical distribution of the three sibling species of the *C. plorabunda* complex in the United States. Open circles are collecting sites referred to in the text.

species (Henry 1983). This view was challenged almost immediately by Garland (1985) on morphological grounds, who reunited *C. plorabunda* with *C. carnea*; even the former's conifer-associated sibling, *C. downesi* (Smith), was included in his synonymy. At present, then, there is no consensus on how to treat *C. carnea* and its close relatives around the globe.

Recent field, behavioral, and acoustical work on *C. plorabunda* in North America has clearly demonstrated that three song morphs of the taxon, designated P1, P2, and P3, are reproductively isolated from one another by their substrate-borne, vibrational courtship songs and should be considered distinct species (Henry & Wells 1990; Henry 1991, 1992; Wells & Henry 1992a, 1992b). Although these biological species have few if any external features to identify them, they represent real phylogenetic diversity within the Nearctic branch of the *C. carnea* complex and suggest that efforts at synonymizing taxa within this group of species using traditional morphological criteria are not appropriate. Here, we describe the three species, including one

new combination and two species that are new. Every effort was made to find anatomical differences between adults of these taxa, but courtship songs remain the only reliable way to tell them apart. Therefore, summary descriptions of the songs are included as necessary parts of the individual species descriptions. Results of additional analyses of the songs of these new species can be found elsewhere (Henry & Wells 1990; Henry 1991, 1992).

#### Materials and Methods

**Specimens.** Individuals for morphological and acoustical analysis were obtained between 1979 and 1992 from the North American sites shown in Fig. 1. Numbers of insects and precise sites of collection are included in the descriptions of each species. The holotype and several paratypes each of *C. adamsi* and *C. johnsoni* have been deposited in the Entomology Division of the Yale Peabody Museum of Natural History (YPM), Yale University, New Haven, CT. Additional paratypes and voucher specimens have

**Table 1. Means ( $\pm$ SEM) of wing features for the three species of the *C. plorabunda* complex from North America. Also shown are the results of an ANOVA to determine significant differences among species**

	North American species			F	P	df
	<i>C. plorabunda</i> (n = 13)	<i>C. adamsi</i> (n = 10)	<i>C. johnsoni</i> (n = 24)			
Forewing						
Inner gradates	5.923 $\pm$ 0.178	5.900 $\pm$ 0.180	5.750 $\pm$ 0.150	0.3412	0.7128	44
Outer gradates	6.615 $\pm$ 0.266	6.100 $\pm$ 0.314	6.417 $\pm$ 0.146	1.0436	0.3608	44
Hindwing						
Inner gradates	5.385 $\pm$ 0.180	5.100 $\pm$ 0.233	5.000 $\pm$ 0.135	1.3844	0.2612	44
Outer gradates	6.231 $\pm$ 0.303	6.100 $\pm$ 0.233	6.125 $\pm$ 0.125	0.0986	0.9063	44
Forewing: length/width	2.892 $\pm$ 0.029	3.071 $\pm$ 0.037	3.036 $\pm$ 0.020	10.7514	0.0002	43
Hindwing: length/width	2.907 $\pm$ 0.032	3.071 $\pm$ 0.035	3.019 $\pm$ 0.021	7.4462	0.0017	43
Forewing/hindwing: length	1.093 $\pm$ 0.009	1.098 $\pm$ 0.004	1.095 $\pm$ 0.004	0.1377	0.8717	43

been placed in the personal collection of Charles S. Henry and in the Connecticut State Museum of Natural History (CSMNH), University of Connecticut, Storrs.

**External Morphology.** Wing and body morphology was examined using Wild and Olympus stereoscopic dissecting microscopes, fitted with camera lucida drawing-tube accessories. All measurements were performed and calibrated using an eyepiece graticule in conjunction with an external micrometer disk. For improved accuracy, fore- and hindwings on one side of the body of each specimen were removed and mounted in glycerin on slides. Body color and markings were determined from live and pinned rather than alcoholic specimens.

An analysis of variance (ANOVA) was used to test for the existence of differences among the three species in several wing features (Table 1). Scheffé's contrast test (Scheffé 1953) was then used to compare pairs of means, to determine which species was responsible for any measured differences. All statistical analyses were performed with the PC software package *CSS: Statistica 3.1* (StatSoft 1992).

**Male Genitalia.** To prepare male terminalia for study, the last four or five abdominal segments were clipped from the body, placed in a 10–15% solution of KOH, and heated on the lowest setting of a laboratory hotplate for 2 h. The specimen was then rinsed with distilled water and stained for 2–3 min in a drop of 5% Chlorazol Black E aqueous solution. After another rinse with distilled water, the genitalic structures (gonarcus and tignum) were teased from the softened abdomen and mounted in glycerin on a microscope slide under a cover slip. The mounted structures were then drawn to scale using a camera lucida attachment on an Olympus dissecting microscope, as above. After study, all

parts of the abdominal terminus were stored in microvials containing glycerin, with the corresponding insect.

**Female Genitalia.** Female specimens were prepared for study by clipping off the terminal segments of the abdomen and clearing these in a hot 10% KOH solution for 5–10 min or in cold 10% KOH overnight. After clearing, the specimen was rinsed in distilled water and transferred to 80% ethanol or directly to glycerin. The dorsal surface of the abdomen was then removed to reveal the internal reproductive system. The area was treated with a 5% aqueous solution of Chlorazol Black E for <1 min and then flushed with distilled water.

Accurate spatial location of ducts in the internal reproductive system requires proper orientation of the specimen to permit comparison with other specimens. All observations of the seminal receptacle and the attached fertilization canal were taken from a dorsal view, with the bursa copulatrix in its normal horizontal position and with the seminal receptacle, fertilization canal, and vagina lying beneath it. Examination of other features may require folding or removing a portion of the lateral exoskeleton. A compound microscope was needed to resolve fine details of some internal structures.

**Song Features.** The vibrational songs of each of the species were recorded, digitized, and analyzed using methods described in earlier papers (Henry & Wells 1990; Henry 1991, 1992). The oscillographs and sonographs shown in Fig. 10 represent typical songs reconstructed from several thousand measured signals, and the mean values shown in the description for each species are drawn from 44 *C. plorabunda*, 65 *C. adamsi*, and 102 *C. johnsoni*. Observations of males and females of a given species were pooled because the songs were not sexually dimorphic.

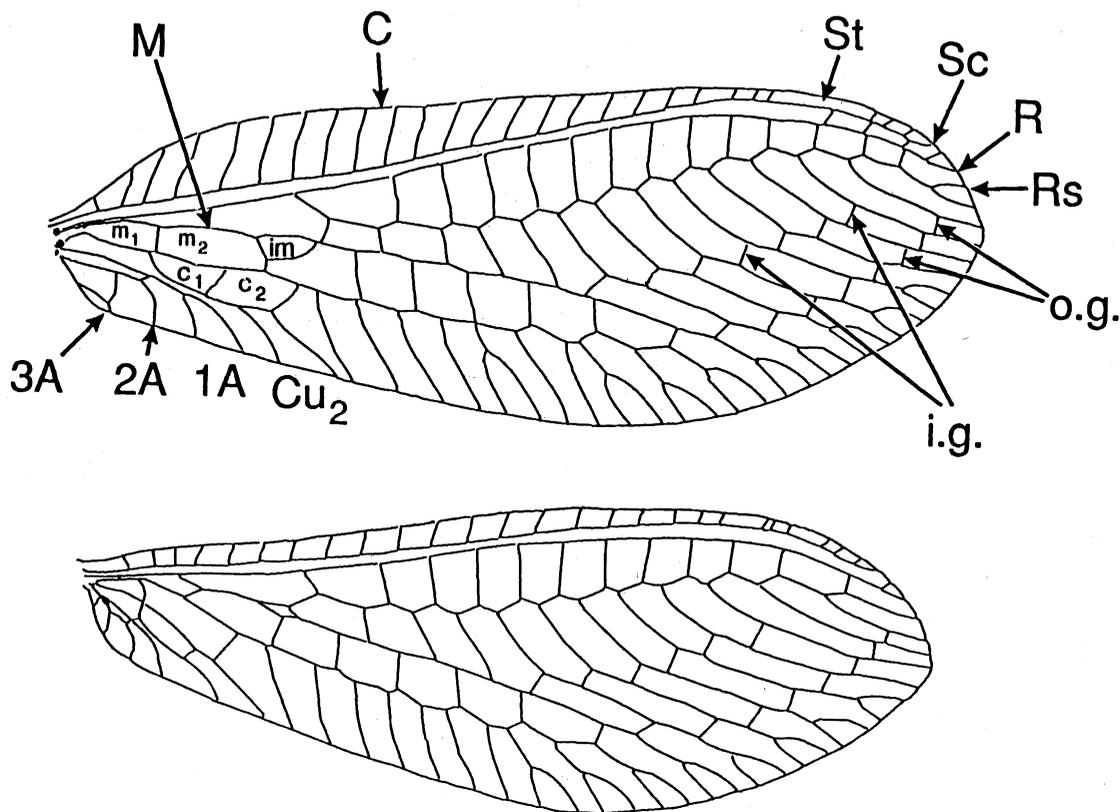


Fig. 2. Wings of *C. plorabunda*, typical of all members of the *Chrysoperla carnea* species group.  $c_1$  and  $c_2$ , 1st and 2nd cubital cells;  $Cu_2$ , 2nd cubital vein; i.g., inner gradate veins; im, intramedian cell; M, media;  $m_1$  and  $m_2$ , 1st and 2nd median cells; o.g., outer gradate veins; R, radius; Rs, radial sector; Sc, subcosta; St, pterostigma; 1A-3A, 1st-3rd anal veins.

### Species Descriptions

As discussed in more detail below, morphological and anatomical variation was as great within as among the three species described here. Therefore, a common description is given first, which applies to the three species equally. Following that is a shorter description of the unique features of each species, emphasizing the courtship songs.

#### Common Description, *Chrysoperla plorabunda* sensu lato (Figs. 2-10)

Based on 73 males and 64 females, pinned and in alcohol. Other general features and natural history as in *Chrysoperla* spp. (Brooks & Barnard 1990, 204-206).

**Color. Reproducing Adult:** Body ground color light green to dark green, occasionally yellowish green, with pale creamy to yellow or reddish yellow stripe present on midline of dorsum from vertex to terminus of abdomen; some popula-

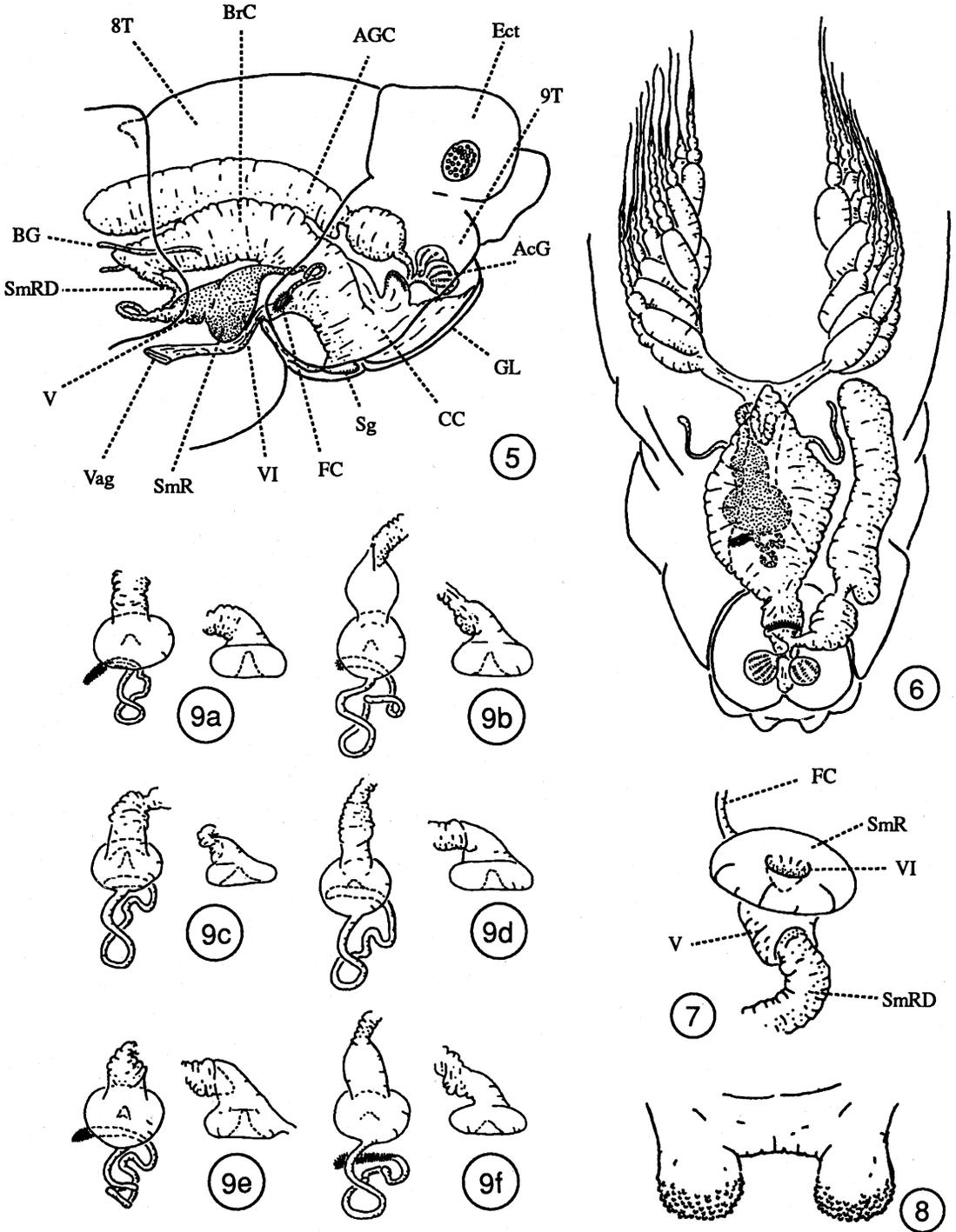
tions extensively marked segmentally with brown or reddish brown patches as described below. **Overwintering Adult:** Body ground color yellowish brown, brown, or reddish brown in most populations, but in others green to dark green, with a waxy suffusion.

**Head.** Face short; eyes metallic green or gold, prominent but more so in male than female; vertex green to yellow or creamy white, frons yellow-green to brownish yellow, both unmarked; genae between compound eyes and mandibles marked with a black or dark brown stripe usually flanked by lighter reddish brown pigmentation. Maxillary palpi black-lineate. Antennae pale yellowish but slightly darker toward tips, unmarked, approximately as long as body, with scape and pedicel short, swollen; flagellomeres slender, longer than wide.

**Thorax.** Prothorax as long as or slightly longer than mesothorax; pronotum green with paler dorsal midline stripe, with or without more or less extensive brown or reddish brown patches on lateral and front margins. Middorsal stripe on







**Figs. 5-9.** 5. Internal female reproductive system of typical member of the *C. carnea* species group, lateral view. AcG, accessory glands; AGC, accessory gland chambers; BrC, bursa copulatrix; BG, bursal gland; CC, copulatory chamber; Ect, ectoproct; FC, fertilization canal; GL, gonapophysis lateralis; SmR, seminal receptacle; SmRD, seminal receptacle duct; Sg, subgenitale; Vag, vagina; V, vela; VI, ventral impression; 8T, eighth tergite; 9T, ninth tergite. Terminology after Pupedis (1985). 6. Internal female reproductive system of typical member of the *C. carnea* species group, dorsal view. 7. Seminal receptacle of *C. johnsoni*, oblique view. FC, fertilization canal; SmR, seminal receptacle; SmRD, seminal receptacle duct; V, vela; VI, ventral impression. 8. Generalized subgenite, ventral view. 9. Seminal receptacles, dorsal and lateral views, all to same scale. (a) *C. carnea*, (b) *C. downesi*, (c) *C. plorabunda*, (d) *C. adamsi*, (e) *C. johnsoni*, (f) *C. rufilabris*.

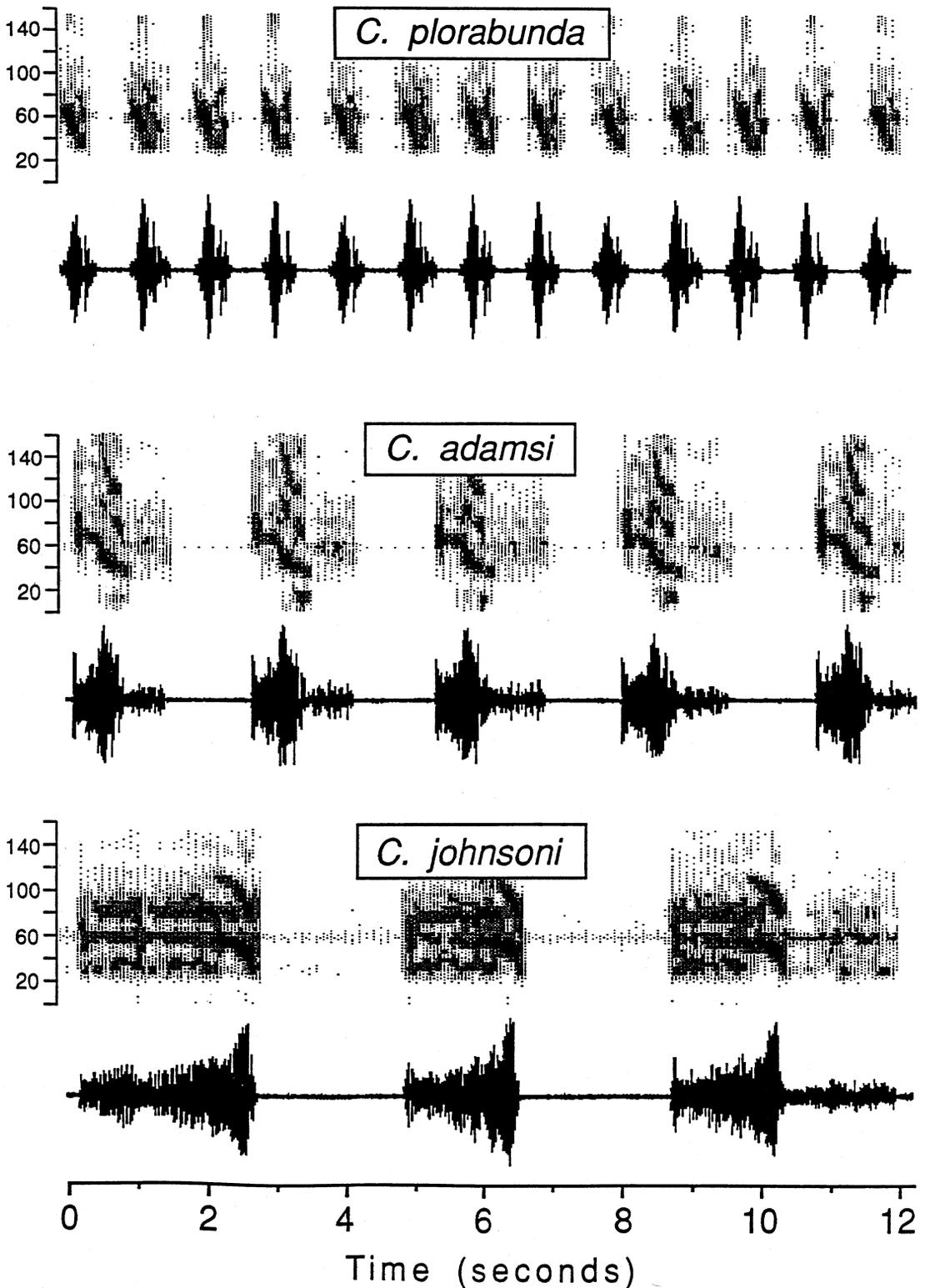


Fig. 10. Oscillographs (solid traces) and sonographs (shaded traces) depicting the courtship songs of *C. plorabunda*, *C. adamsi*, and *C. johnsoni*. The duration, spacing, and amplitude structure of the volleys (pulses or syllables) are shown in the oscillographs, whereas frequency (tonal or pitch) information is graphed on the sonographs using the same time axis. Numbers shown on the vertical axis are in cycles per second (Hz).

**Range, Habitat, and Ecology.** *Chrysoperla plorabunda* sensu stricto is transcontinental, ranging from northern Canada to Florida and Mexico (Fig. 1). It is the only member of this complex that occurs in eastern North America. It occupies a wide range of open habitats, including grasslands, cultivated fields, and the edges of deciduous forests. It is rarely but occasionally encountered in coniferous forests of the northeastern states, where it is generally replaced by and easily confused with the closely related *C. downesi*. In western North America, two or even all three species co-occur in many areas, often syntopically (Fig. 1). There, specimens may be taken in meadows, cultivated fields and fruit groves, chaparral, mixed second-growth forests, or undisturbed coniferous forests. These lacewings overwinter as adults, in most populations turning from green to reddish brown or yellowish brown in the fall in response to decreasing or short day lengths (Sheldon & MacLeod 1974). Like all *Chrysoperla*, the three species feed principally on nectar and honeydew as adults (Hagen et al. 1970), although certain local populations may require the visual stimulation of soft-bodied insect prey to terminate reproductive diapause (Tauber & Tauber 1986a). Larvae are typical aphid-lions, actively searching out and consuming plantlice and other soft-bodied arthropods on a variety of herbaceous plants, shrubs, and trees.

*Chrysoperla plorabunda* (Fitch) new combination

(Figs. 2, 3, 4, 9c, and 10)

*Chrysopa plorabunda* Fitch 1856: 88 (in part); Bickley & MacLeod 1956: 192.

*Chrysoperla plorabunda* (Fitch) 1856: 88; Henry 1983: 299 (in part).

*Chrysoperla carnea* (Stephens) 1835: 103 (in part); Tjeder 1960: 148; Garland 1985: 753.

**Holotype.** 1 ♀, complete, no date, locality, collector, or other data; Museum of Comparative Zoology "Diptera room" (MCZ holotype # 10493). Forewing length, 11.45 mm, forewing width, 4.14 mm. Crossveins and gradate veins not darkened. Color faded, markings indistinct.

**Paratypes.** Adult morphology based on 46 specimens: 5 ♂♂, 4 ♀♀, Ft. Grant, AZ; 3 ♂♂, 2 ♀♀, Las Cruces, NM; 3 ♂♂, 2 ♀♀, Mary's Peak, OR; 3 ♂♂, 6 ♀♀, Moscow, ID; 2 ♂♂, 1 ♀♀, St. Ignatius, MT; 3 ♂♂, 4 ♀♀, Storrs, CT; 3 ♂♂, 1 ♀♀, Walla Walla, WA; 2 ♂♂, 2 ♀♀, Washington, DC. Courtship song based on 44 individuals: 7 Mary's Peak, OR; 23 Moscow, ID; 10 Storrs, CT; 4 Walla Walla, WA (see Henry & Wells [1990] for locality details).

**General.** Color, wing and body morphology, genitalia, measurements, and bionomics as in general description (Table 1; Figs. 2–8, and 9c). Dark gradate veins and crossveins generally ab-

sent in all known populations. Forewing longer than wide by a factor of 2.75–3.11 (2.89), hindwing by 2.74–3.14 (2.91). Adults of all known populations acquire autumnal coloration.

**Courtship Song** (25°C). Vibrational song simple, repetitive, consisting of a single volley (syllable) of abdominal vibration ≈600 ms in length and repeated once per second for several seconds to 1 min (top of Fig. 10). Sexual partners duet by exchanging volley for volley, resulting in rapid, coordinated acoustical interactions during courtship. Measurements: volley duration, 380–800 ms (629.00); volley interval (start of a volley to the start of the next), 980–1,560 ms (1,207.68); number of volleys per song, one.

**Variation.** Morphological variation as in general description, except dark gradates and crossveins rare or absent. *C. plorabunda* from eastern North America rarely associated with conifers or evergreens but commonly found in coniferous forests of Pacific Northwest. Songs remarkably invariant across continent but tending toward a slightly lower initial volley vibrational frequency (pitch) in northwestern populations (Henry & Wells 1990).

**Range and Habitat.** Distributed over much of North America from sea level to >3,000 m; in United States from Maine to Florida, Texas, and eastern Arizona, across midwest, and westward to Pacific coast of Oregon and Washington (Fig. 1). Apparently not present, or possibly rare, in California and western Arizona and is the only one of the three species found east of Great Plains. Distributional pattern in Rocky Mountain states unknown. No known significant habitat restrictions.

*Chrysoperla adamsi* Henry, Wells & Pupedis, new species  
(Figs. 4, 9d, and 10)

*Chrysoperla plorabunda* (Fitch) 1856: 88; Henry 1983: 299 (in part).

**Holotype.** 1 ♂, Philomath (Mary's Peak), Oregon, 28-IX-89, on immature Douglasfir (*Pseudotsuga menziesii*), C. S. Henry & M. M. Wells; YPM holotype # E151, in alcohol. Forewing length, 11.52 mm, forewing width, 3.71 mm. Color faded, markings indistinct. Crossveins and gradate veins not darkened; other morphology and genitalia as in common description. Courtship song as described below.

**Paratypes.** Adult morphology based on 39 specimens: 3 ♂♂, 2 ♀♀, Badger, CA; 3 ♂♂, 1 ♀, Forest Home, CA; 5 ♂♂, 4 ♀♀, Mary's Peak, OR; 3 ♂♂, 1 ♀, Medford, OR; 5 ♂♂, 2 ♀♀, Moscow, ID; 3 ♂♂, 7 ♀♀, Vacaville, CA. Courtship song based on 65 individuals: 23 Badger, CA; 25 Forest Home, CA; 7 Mary's Peak, OR; 2 Medford, OR; 1 Moscow, ID; and 7 Vacaville, CA (see Henry [1991] for locality details).

**General.** Color, wing and body morphology, genitalia, measurements, and bionomics as in general description (Table 1; Figs. 2–8, and 9d). A few dark gradate veins and crossveins variably present in populations from central California (Vacaville and Badger). Forewing longer than wide by a factor of 2.84–3.25 (3.07), hindwing by 2.91–3.25 (3.07). Geographic distribution of autumnal coloration unknown.

**Courtship Song** (25°C). Vibrational song simple, repetitive, consisting of a single long volley (syllable) of abdominal vibration  $\approx 1,400$  ms in duration and repeated once every 3 s for several seconds to 1 min (middle of Fig. 10). Last portion of each volley is a low-intensity "rumble" of erratic abdominal vibration. Sexual partners duet by exchanging volley for volley, resulting in slow-paced but coordinated acoustical interactions during courtship. Measurements: volley duration, 950–1,950 ms (1,366.68); volley interval (start to start), 1,800–6,550 ms (3,261.83); number of volleys per song, one.

**Variation.** Morphological variation as in general description. Songs remarkably invariant across known geographical range (Henry 1991).

**Range and Habitat.** Distributed over much of western North America, from sea level to  $>3,000$  m; in United States from northern Idaho and Washington south to southern California (Fig. 1). Not found east of Great Plains. Distributional pattern in Rocky Mountain states unknown. No known significant habitat restrictions.

**Etymology.** This species is named in honor of Phillip A. Adams, one of the principal architects of modern lacewing systematics and a good friend of C.S.H. He has helped on many occasions with collecting and identifying *Chrysoperla* in southern California, including this taxon, and his advice on difficult questions of systematics and phylogeny has been of incalculable value.

***Chrysoperla johnsoni* Henry, Wells & Pupedis,**  
new species  
(Figs. 4, 7, 9e, and 10)

*Chrysopa mohave* Banks 1938: 118 (in part); sensu Tauber & Tauber 1973b: 729.

*Chrysoperla carnea* (Stephens), var. *mohave* (in part); sensu Tauber & Tauber 1973a: 1164.

*Chrysoperla plorabunda* (Fitch) 1856: 88; Henry 1983: 299 (in part).

**Holotype.** 1 ♂, Philomath (Mary's Peak), Oregon, 28-IX-89, on immature Douglasfir (*Pseudotsuga menziesii*), C. S. Henry & M. M. Wells; YPM holotype # E152, in alcohol. Forewing length, 11.95 mm, forewing width, 3.88 mm. Color faded, markings indistinct. Crossveins and gradate veins not darkened; other morphology and genitalia as in common description. Courtship song as described below.

**Paratypes.** Adult morphology based on 52 specimens: 5 ♂♂, 5 ♀♀, Badger, CA; 5 ♂♂, 4 ♀♀, Berkeley, CA; 2 ♂♂, 1 ♀, Forest Home, CA; 5 ♂♂, 7 ♀♀, Mary's Peak, OR; 2 ♂♂, 1 ♀, Medford, OR; 5 ♂♂, 2 ♀♀, Moscow, ID; 3 ♂♂, 5 ♀♀, Quartzite, AZ. Courtship song based on 102 individuals: 11 Badger, CA; 31 Berkeley, CA; 1 Forest Home, CA; 21 Mary's Peak, OR; 1 Medford, OR; 22 Moscow, ID; and 15 Quartzite, AZ (see Henry [1992] for locality details).

**General.** Color, wing and body morphology, genitalia, measurements, and bionomics as in general description (Table 1; Figs. 2–8, and 9e). Many dark gradate veins and crossveins present in populations from central California, especially Strawberry Canyon, Berkeley. Forewing longer than wide by a factor of 2.74–3.19 (3.04), hindwing by 2.82–3.25 (3.02). Geographic distribution of autumnal coloration unknown, but individuals collected near Moscow, ID, and in the Kofa Mountains of southwestern Arizona (Quartzite) overwinter without changing from deep green (unpublished data), whereas those from Strawberry Canyon turn brown as winter approaches (Tauber & Tauber 1981). Even in summer, specimens from Strawberry Canyon are pale yellow-green with pronounced development of red or reddish brown patches, possibly correlated with aestivation (Tauber & Tauber 1973a, 1986b).

**Courtship Song** (25°C). Vibrational song (shortest repeated unit or SRU) complex, consisting of several long volleys (syllables) of abdominal vibration  $\approx 2,800$  ms in duration and repeated within the song every 4.5 s (bottom of Fig. 10). Last portion of terminal volley of each song is a low-intensity "rumble" of erratic abdominal vibration. Sexual partners duet by exchanging multisyllabic SRUs, resulting in slow-paced but coordinated acoustical interactions during courtship. Measurements: volley duration, 980–5,850 ms (2,836.85); volley interval (start to start), 2,050–7,250 ms (4,626.08); number of volleys per song, 2–6 (2.48); total song duration, 3.2–34.3 s (10.59).

**Variation.** Morphological variation as in general description, except Strawberry Canyon (Berkeley) population consistently different from others in color and crossvein-gradate pigmentation. Songs show gradual, clinal change in temporal features latitudinally across known geographical range, such that northern populations have shorter, more closely spaced volleys at a given temperature than southern ones (see Henry [1992] for detailed analysis).

**Range and Habitat.** Distributed over much of western North America, from sea level to  $>3,000$  m; in United States from northern Idaho and Washington south to southern California and western Arizona (Fig. 1). Not found east of Great Plains. Distributional pattern in Rocky Mountain

states unknown. No known significant habitat restrictions.

**Etymology.** This species is named in honor of our friend and colleague, James B. (Ding) Johnson, who has provided many representatives of the taxon from Idaho to Arizona and who has contributed substantially to deciphering species differences within *C. plorabunda* s. lat.

### Discussion

**External Morphology.** No consistent differences were found among *C. plorabunda* s. str., *C. adamsi*, and *C. johnsoni* in body color and markings. Each of the three species encompasses greener versus yellower phenotypes, as well as populations with extensive brownish or reddish spotting versus those without. The population of *C. johnsoni* in Strawberry Canyon, Berkeley, CA, represents one end of this continuum, displaying pronounced reddish brown spotting on a yellow-green ground color and unparalleled development of dark crossveins and gradates. Consequently, it has been considered part of Banks' *C. mohave*, now reduced to the rank of a variety or race of *C. carnea-plorabunda* (Tauber & Tauber 1973a). However, acoustically it is an integral part of *C. johnsoni*, and true populations of "*C. plorabunda mohave*" appear from their song features to belong to the *C. downesi* species complex (Henry 1992).

Similarly, most measurements of body or wing dimensions and proportions did not differ significantly among the three species (Table 1). One exception was found in the ratio of length to width in both fore- and hindwings: an ANOVA and Scheffé's test showed that *C. plorabunda* possessed significantly broader wings than either *C. adamsi* or *C. johnsoni*, even when the analysis was restricted to sympatric populations in the Pacific Northwest. However, the ranges of variation of these features overlapped extensively among the three species, so the value of wing aspect ratio as an identifying character is small.

**Male Genitalia.** Fig. 4 demonstrates the homogeneous morphology of the male gonarcus and tignum in representatives of the three species from different geographical regions. Even *C. downesi* from eastern New York state has genitalia that are indistinguishable from those of the *C. plorabunda* species complex (Fig. 3), and earlier work on European lacewing songs showed that *C. carnea* shared precisely the same type of male genitalia (Henry 1983). For comparison, the distinctive structures of *C. rufilabris* (Burmeister) are illustrated (Fig. 3). Clearly, characters of the male genitalia are not useful for understanding the systematics of the *C. carnea* species group of the genus *Chrysoperla*.

**Female Genitalia.** At the species level, the internal reproductive morphology of the female

chrysopterid is remarkably invariant. The virtually identical ground plan of all six species of *Chrysoperla* examined is evident even in the spatial looping of the fertilization canal (Fig. 9a-f). Only the vela shows some differences that could prove to have systematic value: when viewed from above, the vela of *C. downesi* (Fig. 9b) appears slightly more constricted at its base than it does in *C. carnea*, *C. plorabunda*, *C. adamsi*, or *C. johnsoni*. However, individual variation is considerable and has not been sufficiently evaluated. Female anatomy will probably not be useful in separating closely related taxa of the *C. carnea* species complex.

**Courtship Songs.** Each of the three species described here has a unique courtship song, but all share the same basic, frequency-modulated tonal characteristics. The songs of *C. plorabunda* and *C. adamsi* share other features as well, including single-syllable temporal structure and volley-for-volley dueting. *C. adamsi*, however, has a longer volley and a slower volley repetition rate than does *C. plorabunda*; in fact, the ranges of values of volley duration and volley interval in the two species do not even overlap. By contrast, those two features are quite similar in *C. adamsi* and *C. johnsoni* and overlap extensively. In this case, it is the multisyllabic nature of *C. johnsoni*'s song that provides an unambiguous difference between the two species: courting *C. adamsi* exchange single volleys when dueting, whereas *C. johnsoni* exchange groups of two to six volleys instead.

Although it is easy physically to confuse these species with *C. downesi* in some parts of their broad, overlapping ranges, confounding their songs is impossible. Unlike any of the three species in the *C. plorabunda* complex, *C. downesi* produces two distinctly different types of volleys in each song and displays constant or even slightly rising tonal (frequency) characteristics in each volley (Henry 1980). One of the volley types is very short and delivered at a repetition rate that far exceeds that of *C. plorabunda*, *C. adamsi*, or *C. johnsoni*, so even casual inspection of courting individuals should be sufficient to recognize *C. downesi*.

Intermediate songs have been produced in the laboratory between *C. plorabunda* and *C. johnsoni* by forced hybridization, but individuals with hybrid songs of this (or any other) type have never been found in the field (Henry 1992). In fact, laboratory hybrids exhibit significantly reduced fecundity and fertility, suggesting that modest postzygotic barriers to interspecific reproduction exist (M.M.W., unpublished data). When cultured in the laboratory, each species breeds true for its characteristic courtship song through many generations, confirming that each is a cohesive genetic unit.

**Range and Habitat.** Range alone cannot be used to identify these three species, except east

of the Great Plains, where *C. plorabunda* is present without the others and where its only possible alternative, *C. downesi*, is always a dark, intense green color. Nor is habitat useful, because each species can be found almost anywhere, especially in western North America. Much more work is needed before we can map the complete ranges of any members of the *C. carnea* species group with any confidence.

**Prognosis.** *Chrysoperla downesi*, like our earlier concept of *C. plorabunda*, is a poorly defined taxon that almost certainly includes several valid biological species, reproductively isolated by their courtship song differences (Henry 1985a). It is important to study the courtship behavior and songs of this other complex of cryptic taxa of *Chrysoperla* in much the same manner as we have done here and in earlier work. So also must studies be expanded to European and Asian members of the *C. carnea* species group, because preliminary work indicates that those also have speciated repeatedly without much morphological evidence of cladogenesis (Henry 1983). Eventually, such an approach, perhaps coupled with studies of larval anatomy and molecular characters, could produce a comprehensive understanding of the diversity, classification, and phylogeny of this difficult genus.

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