

# Revision of Velvet Ant Genus *Dilophotopsis* Schuster (Hymenoptera: Mutillidae) by Using Molecular and Morphological Data, with Implications for Desert Biogeography

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**ABSTRACT** Taxonomy of the wide-ranging Nearctic velvet ant genus *Dilophotopsis* Schuster (Hymenoptera: Mutillidae) is reviewed using molecular and morphological comparisons. The validity of the four designated subspecies of *Dilophotopsis concolor* (Cresson) is examined. *Dilophotopsis concolor paron* (Cameron) is morphologically and molecularly distinct from the other three subspecies, and it is raised to the species level [*D. paron* (Cameron), nov. stat.]. *Dilophotopsis concolor crassa* (Viereck) and *Dilophotopsis concolor laredo* Schuster are morphologically indistinguishable from the nominative subspecies *D. concolor concolor*, and they are considered junior synonyms of this species. A key to the species of *Dilophotopsis* is provided. The distributions of *Dilophotopsis* species, as well as the genetic variation within *D. concolor*, are associated with individual arid lands, and they indicate that this genus will be useful in the study of the historical biogeography of the North American arid lands.

**KEY WORDS** Sphaerophthalminae, ITS1, ITS2, phylogeography

Phylogeographic analyses of wide-ranging taxa are useful for investigating the historical biogeography of North America's arid lands (Ayoub and Riechert 2004, Jaeger et al. 2005, Devitt 2006, Douglas et al. 2006), which are defined as the warm and cold deserts and the xeric shrublands (Omernik 1987, Ricketts et al. 1999). Phylogeographic analyses compare molecular patterns of divergence to past geologic and climatic events to determine the factors influencing the diversification of an organism or group of organisms (Riddle 1995, Orange et al. 1999). Specifically for North America, Neogene mountain building events and Pleistocene climate change are thought to be important in the evolution of the desert biota (Riddle et al. 2000, Jaeger et al. 2005, Douglas et al. 2006). Although many studies have provided valuable insight into the evolution of the North American desert biota, few have treated both the warm and cold deserts along with the other arid lands. A wide-ranging species found in all of these areas is needed for such an analysis. *Dilophotopsis concolor* (Cresson) (Hymenoptera: Mutillidae) may be an excellent candidate, because it is one of the most wide-ranging Nearctic velvet ants being found from southern Canada to central Mexico and from Baja California to Kansas. Before this species can be used in biogeographic analyses, species and subspecies boundaries, as well as more extensive geographic distribution data, need to be determined.

The velvet ant genus *Dilophotopsis* Schuster contains two species, *Dilophotopsis stenognatha* Schuster

and *Dilophotopsis concolor* (Cresson), both of which are nocturnal. Unlike the wide-ranging species *D. concolor*, *D. stenognatha* is restricted to the Sonoran Desert. The genus was originally described by Schuster (1958) based on males only. Since its description, the females of *D. stenognatha* and of a subspecies of *D. concolor* have been described (Mickel 1963, Pitts et al. 2007). *Dilophotopsis* is thought to be sister to *Acrophotopsis* Schuster (Pitts and McHugh 2002) and both aforementioned genera sister to *Schusterphotopsis* Pitts (Pitts 2003a). *Dilophotopsis* can be easily separated from these other genera (Manley and Pitts 2003). Little information is available on the biology of *Dilophotopsis*. The only known host record is of *Dilophotopsis concolor crassa* (Viereck) parasitizing a species of *Tachysphex* Kohl (Pitts 2003b).

Four geographically isolated subspecies of *D. concolor* were recognized by Schuster (1958), Mickel (1965), and Ferguson (1967): *D. c. concolor*, *D. c. crassa*, *Dilophotopsis concolor laredo* Schuster, and *Dilophotopsis concolor paron* (Cameron). These subspecies are doubtful, however, based on taxonomic history and a preliminary evaluation of morphology presented here. Many subspecies of other nocturnal mutillids have proven to be invalid, especially those described by Schuster, because he used too few specimens to quantify geographical variation (Ferguson 1967, Pitts 2007). The validity of the subspecies of *D. concolor* is further weakened by the characteristics used to differentiate them. The main distinguishing features are differences in integumental color. Ferguson (1962) showed that pigmentation in other spha-

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erophthalmine mutillids was affected by the temperature and humidity during development and studies on a related genus, *Dasymutilla* Ashmead, also suggest that integument color is not taxonomically reliable (Pilgrim et al. 2008). As such, the validity of the subspecies of *D. concolor* needs further investigation.

This article reports on morphological and molecular examinations that test the legitimacy of the four subspecies of *D. concolor*. The species-specific loci first and second internal transcribed spacer (ITS1 and ITS2) regions are used to determine the genetic variation among the *Dilophotopsis* species and subspecies. Genetic distances are compared with interspecific distances known from other sphaerophthalmine mutillids (Pilgrim and Pitts 2006) to determine species and subspecies boundaries.

### Materials and Methods

**Sampling.** Specimens were collected from sites across western North America from 2002 to 2007 by using blacklight traps, florescent lantern traps, and by hand. All specimens were placed directly into 95% ethanol, and those used for molecular examination have been labeled as voucher specimens and deposited in the Department of Biology Insect Collection, Utah State University, Logan, UT (EMUS). All holotypes were examined and compared with molecular voucher specimens.

**Morphological Analysis.** All specimens were examined with a Wild M-5 stereomicroscope, and all measurements were made with an ocular micrometer. Mandibular ratios were calculated by dividing the width at the ventral tooth, the excision after the ventral tooth, and the greatest apical width by the width at the base of the mandibles. Male genitalia were dissected from the specimens by using minuten pins and placed in genitalia capsules with glycerin. Genitalia were observed with a light microscope and illustrated using a camera lucida.

Specimens were borrowed from or deposited into the following collections: ANSP, Department of Entomology, Academy of Natural Sciences, Philadelphia, PA, USA; BMNH, Department of Entomology, The National History Museum, London, United Kingdom; CSCA, California State Collection of Arthropods, California Department of Food and Agriculture, Sacramento, CA, USA; CIDA, Albertson College of Idaho Collection, Orma J. Smith Museum of Natural History, Albertson College of Idaho, Caldwell, ID, USA; CISC, Essig Museum of Entomology, Department of Entomological Sciences, University of California, Berkeley, CA, USA; CNCI, Canadian National Collection of Insects, Centre for Land and Biological Resources Research, Biological Research Division Agriculture, Ottawa, Canada; CSUC, C. P. Gillette Arthropod Biodiversity Museum, Department of Entomology, Colorado State University, Fort Collins, CO, USA; CUIC, Cornell University Insect Collection, Department of Entomology, Cornell University, Ithaca, NY, USA; EMUS, Department of Biology Insect Collection, Utah State University, Logan, UT, USA; LACM, Insect Col-

lection, Los Angeles County Museum of Natural History, Los Angeles, CA, USA; SEMC, Snow Entomological Museum, University of Kansas, Lawrence, KS, USA; SRSC, Insect Collections, Sul Ross State College, Alpine, TX, USA; TAMU, Department of Entomology Insect Collection, TX A&M University, College Station, TX, USA; UAIC, Department of Entomology Collection, University of Arizona, Tucson, AZ, USA; UCDC, The Bohart Museum of Entomology, University of California, Davis, CA, USA; UCRC, UCR Entomological Teaching and Research Collection, University of California, Riverside, CA, USA; and UMSP, University of Minnesota Insect Collection, St. Paul, MN, USA.

**Molecular Analysis.** DNA was extracted, amplified, and sequenced from a total of 13 *Dilophotopsis* specimens. Three specimens from each *D. concolor* subspecies were analyzed along with two *D. stenognatha* specimens. An attempt was made to sample from various parts of the range of each *D. concolor* subspecies. DNA extraction and amplification of the two rDNA internal transcribed spacer regions ITS1 and ITS2 followed the protocols outlined by Pilgrim and Pitts (2006). Sequences were analyzed with an ABI Prism 377, 3100, or 3730 Genetic Analyzer (Applied Biosystems, Foster City, CA). All polymerase chain reaction products were sequenced in both directions, and they were combined in Sequencher 4.1 (Gene Code Corp., Ann Arbor, MI). Pairwise percentage of genetic distances between subspecies were calculated by determining the number of differences (point mutations and insertions or deletions) and dividing by the number of base pairs of the longer of the two sequences.

**Phylogenetic Analysis.** The two genetic loci were subjected to Bayesian analysis by using MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003). Sequences were analyzed as a combined data set, with each gene partitioned according to the general time-reversible model (Lanave et al. 1984) with invariant sites and gamma-distributed rate variation across sites (GTR+I+ $\Gamma$ ) and with all parameters unlinked across loci. Bayesian analyses included four independent runs, with three heated chains and one cold chain in each run. The MCMC chains were set for 3,000,000 generations and sampled every 100 generations; chains were run until the average standard deviation of the split frequencies dropped below 0.01. The burn-in period for each analysis was removed after graphical determination of stationarity. Two outgroups were included in the analysis. *Acrophotopsis eurygnatha* Schuster is closely related to *Dilophotopsis* (Pitts and McHugh 2002), and it was included. *Laminatilla lamellifera* (Schuster) was used as a more distant outgroup as *Schusterphotopsis* was not available.

### Results

**Molecular Results.** For the *D. concolor* subspecies, intrasubspecific genetic variation is lowest in *D. c. paron*, 0.13% for ITS1 and 0.10% for ITS2 (Table 1). The greatest ITS1 intrasubspecific genetic variation was in *D. c. laredo*, 0.96%, whereas the greatest vari-

**Table 1.** Intraspecific and intrasubspecific genetic variation of the ITS1 and ITS2 sequences for the species and formerly recognized subspecies of *Dilophotopsis*

Subspecies	No. specimens	ITS1		ITS2	
		intrasubspecific variation (%)		intrasubspecific variation (%)	
<i>D. concolor paron</i>	3	0.13		0.10	
<i>D. concolor concolor</i>	3	0.57		0.66	
<i>D. concolor crassa</i>	3	0.56		1.33	
<i>D. concolor laredo</i>	3	0.96		0.70	
<i>D. stenognatha</i>	2	0		N.A.	

N.A., not applicable.

ation for ITS2 was in *D. c. crassa*, 1.33% (Table 1). No intraspecific variation was discovered in the ITS1 sequences of *D. stenognatha*, intraspecific variation for ITS2 was unavailable for *D. stenognatha* because only one ITS2 sequence was obtained.

The genetic distances for both ITS1 and ITS2 reveal that the *D. c. paron* sequences are very different from the other *D. concolor* subspecies (distances are 3.01–3.59% for ITS1 and 6.71–9.84% for ITS2; Table 2). These differences are greater than the genetic distance between *D. stenognatha* and *D. concolor*, which are 2.56–2.88% for ITS1 and 5.35–6.16% for ITS2 (Table 2). All sequences have been submitted to GenBank (accession nos. EU369205–EU369234).

**Phylogenetic Results.** Bayesian analysis of the combined molecular data produced a well-resolved tree with high posterior probabilities, which is 1.0 for most nodes (Fig. 1). This topology revealed a monophyletic *Dilophotopsis* composed of three distinct groups. *D. c. paron* forms a distinct, deeply divergent clade that is sister to a clade containing the remaining three *D. concolor* subspecies (Fig. 1). *D. stenognatha* is sister to these two clades (Fig. 1). Within the large clade made up of *D. c. concolor*, *D. c. crassa*, and *D. c. laredo*, sub-clades correspond largely to individual arid regions (Fig. 2) rather than to the defined subspecies.

**Morphological Results.** Careful examination of numerous *Dilophotopsis* specimens revealed consistent morphological differences between *D. c. paron* and the remaining subspecies. Differences were found in the shape and sculpturing of the mesosternal tubercles, as well as in male genitalic morphology. No significant differences in the interocellar distances as proposed by Schuster, the male genitalia, or the mesosternal tubercles were found among *D. c. concolor*, *D. c. crassa*, and *D. c. laredo*.

Based on the above-mentioned molecular and morphological data, we are recognizing *D. c. paron* as a

distinct species in the following taxonomic section. In the discussion, we discuss the subspecies as being separate until a complete discussion of the evidence is given for our taxonomic changes.

### *Dilophotopsis concolor* (Cresson)

*Mutilla concolor* Cresson, 1865. Entomol. Soc. Phila., Proc. 4: 390. Male. Holotype. "Colorado" (ANSP).

*Mutilla nanula* Dalla Torre, 1897. Cat. Hym. 8: 65. New name for *Mutilla pygmaea* Blake, 1879. Am. Entomol. Soc. Trans. 7: 250. Female. NEW SYNONYM. Syn-type. "Colorado" (ANSP).

*Odontophotopsis alamonis* Viereck, 1904. Am. Entomol. Soc. Trans. 30: 87. Male. Holotype. Alamogordo, NM, 15 May 1902, (ANSP).

*Odontophotopsis crassus* Viereck, 1924. Can. Entomol. 56: 122. Male. NEW SYNONYM. Holotype. Oliver, British Columbia, 24 July 1923, coll. E. R. Buckell (CNCI).

*Dilophotopsis concolor laredo* Schuster, 1958. Entomol. Am. 37: 86. Male. NEW SYNONYM. Holotype. Winterhaven, TX, 9 April 1935, coll. S. E. Jones (UMSP).

*Dilophotopsis concolor utahensis* Schuster, 1958. Entomol. Am. 37: 87. Male. NEW SYNONYM. Holotype. Delle, UT, 16 July 1927, coll. J. C. Bradley (CUIC).

**Diagnosis.** This species can be differentiated from other *Dilophotopsis* species by male genitalic characters (Figs. 3–11). The external margin of the cuspis is angulate, with a dorsal carina present at the elbowed region (Figs. 3, 6, and 9), although the shape of the cuspis and the size of this carina vary to some degree. Also, the mesosternal tubercles of *D. concolor* are more peg-like than those of *D. stenognatha*, and they are glabrous on their apex (Fig. 18). This species lacks a sternal felt line. The coloration of *D. concolor* is variable; the body coloration ranges from stramineous to castaneous, and many specimens have piceous areas under the tergal felt lines and near the apices of the femora (Fig. 21). This species is moderately sized, ranging from 8 to 13 mm. The mandibles are more dilated than those of *D. stenognatha* with a mandibular ratio of 1, 0.7, 1.

**Distribution.** Widely distributed from western Kansas, Nebraska, Oklahoma, and Texas west through Arizona, the Great Basin Desert of California, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, Washington, and Wyoming; south into northern Mexico in

**Table 2.** Genetic differences (%) in the species and formerly recognized subspecies of *Dilophotopsis* (ITS1 above diagonal and ITS2 below diagonal)

	<i>D. c. paron</i>	<i>D. c. concolor</i>	<i>D. c. crassa</i>	<i>D. c. laredo</i>	<i>D. stenognatha</i>
<i>D. concolor paron</i>	—	3.13–3.59	3.05–3.44	3.01–3.57	2.57–2.71
<i>D. concolor concolor</i>	6.71–9.84	—	0–0.97	0–0.96	2.56–2.85
<i>D. concolor crassa</i>	6.88–7.16	0.67–1.34	—	0.41–1.37	2.57–2.77
<i>D. concolor laredo</i>	6.86–6.96	0.20–0.81	0.67–1.15	—	2.60–2.88
<i>D. stenognatha</i>	6.06–6.16	5.57–5.76	5.35–5.82	5.66–5.71	—

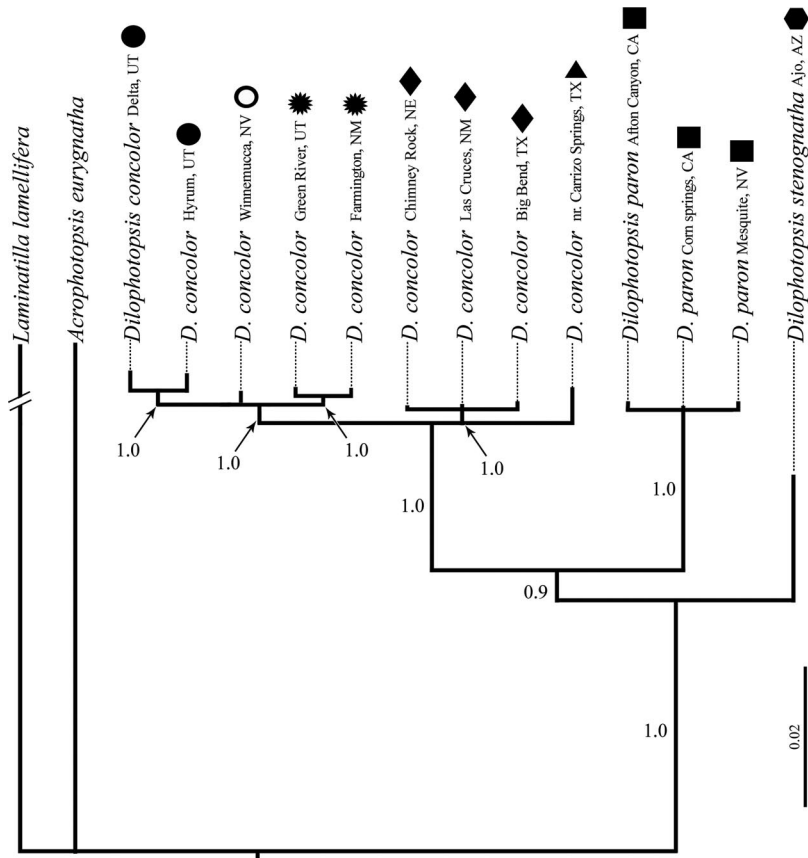


Fig. 1. Consensus tree of Bayesian analysis of the combined ITS1 and ITS2 sequences. Numbers at each branch represent posterior probabilities. Species names and collection locality are given. Symbols following collecting locality correspond to symbols on the map of North American deserts and arid lands (see Fig. 2) and mark populations forming distinct clades.

the states of Chihuahua, Coahuila, Durango, and Tamaulipas; and north to British Columbia, Canada. Absent from the Mojave and western Sonoran deserts.

**Materials Examined.** USA, Arizona: Cochise Co.: 1 male, Benson, 4 km SW, 4-VI-1991, L. R. Davis Jr. (EMUS); 1 male, Charleston, 18-IV-1966, R. F. Sternitzky (EMUS); 1 male, Portal, 4,700 feet, 7-VII-1964, 1 male, Portal, 4,700 feet, 13-VII-1964, J. H. Puckle, M. A. Mortenson and M. A. Cazier (EMUS); 1 male, Huachuca Mts., Ramsey Canyon, 1-X-1965, R. F. Sternitzky (EMUS); 1 male, Sierra Vista, Huachuca Mts., V-1965; 1 male, Sierra Vista, Huachuca Mts., 16-III-1963, R. F. Sternitzky (EMUS); Coconino Co.: 1 male, Moenkopi Sand dune Assoc., 2 miles S., F. G. Andrews, E. A. Kane (CSCA); Santa Cruz Co.: 1 male, Campini Mesa, 5 km NE Bodie Ranch, Parker Canyon, 2-7-V-2004, M. E. Irwin and F. D. Parker (EMUS); California: Inyo Co.: 1 male, Deep Springs Valley, 4 miles SW Deep Springs, V-VIII-1983, D. Giuliani (CSCA); 1 male, White Mts., Wyman Canyon, 20-VII-1967, S. Frommer (UCRC) Colorado: Bent Co.: 1 male, Hasty, 26-29-VI-1974, H. E. Evans (CSUC); Delta Co.: 1 male, Rogers Mesa, 16-VI-1998 (CSUC); Mesa Co.: 1 male, Colorado National Monument, Picnic Area, 31-V-1989, M. Weissmann and R. S. Peigler (CSUC); Moffat

Co.: 2 males, Dinosaur National Monument, 12-VII-1948, H. G. Rodeck (CSUC); Idaho: Elmore Co.: 2 males, Mt. Home, 7-VII-1931, J. Nottingham (SEMC); Kansas: Stanton Co.: 1 male (SEMC); Oklahoma: Beckham Co.: 1 male, Sayre, 8-VI-1957, Standish-Kaiser (UAIC); Montana: Jefferson Co.: 2 males, Town 2N, Range 1W, 17-VII-1926, C. B. Philip (UMSP); Nebraska: Morrill Co.: 1 male, Chimney Rock, 5-6-VIII-2006, K. A. Williams and B. Webster (EMUS); Nevada: Churchill Co.: 1 male, Sand Mt., 27-VI-1979, R. C. Bechtel, D. M. Martinelli, and R. W. Rust (UCDC); 1 male, Stillwater, 12 miles NE, 3-VI-1961, F. D. Parker (UCDC); Elko Co.: 1 male, Wells, 17-VII-1985, L. A. Stange (EMUS); Humboldt Co.: 2 males, Winnemucca, 1-VI-1969, T. R. Haig (CSCA); 5 males, Winnemucca, 10 miles N, 18-VI-2003, J. Pitts (EMUS); Pershing Co.: 3 males, Woolsey, 27-VII-1973, T. R. Haig (CSCA); 12 males, Woolsey RR Station, 6-VII-1973; 20 males, Woolsey RR Station, 6-VI-1973, T. R. Haig (CSCA); White Pine Co.: 1 male, White River Valley, Jakes Wash 20 miles SE Ely, III-VIII-1984, D. Giuliani (CSCA); New Mexico: Grant Co.: 1 male, City of Rock State park, 31-V-1965, M. E. Irwin (UCRC); Lincoln Co.: 3 males, Valley of Fire State Park, 6-VI-1977, Hanson and Knowlton (EMUS);



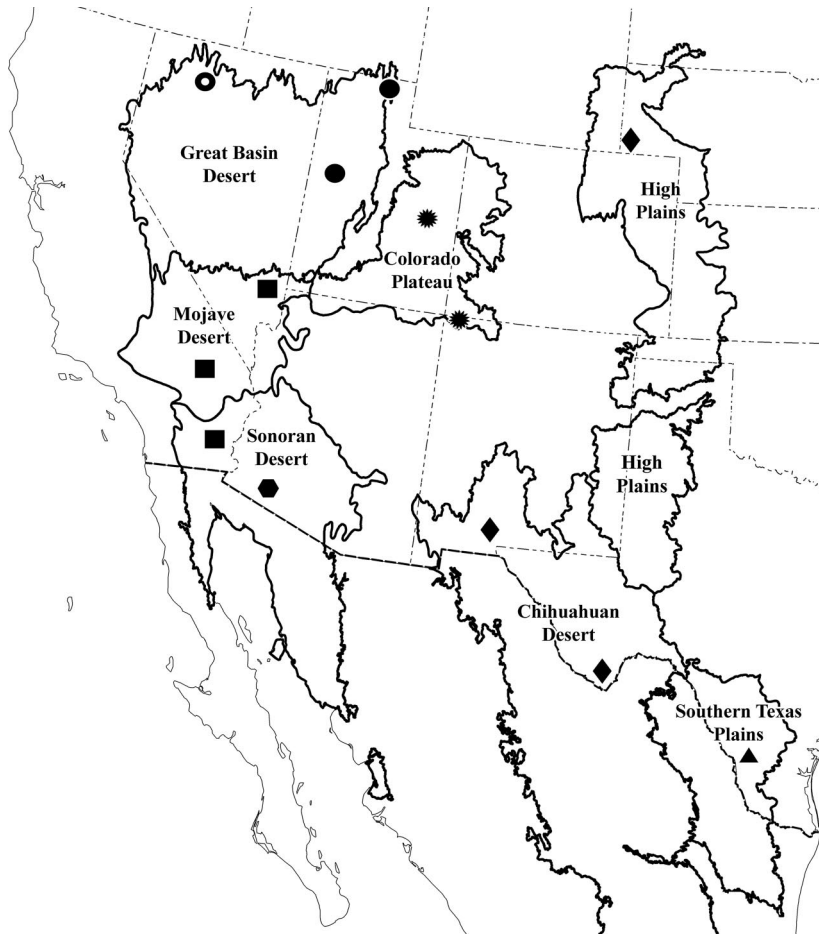
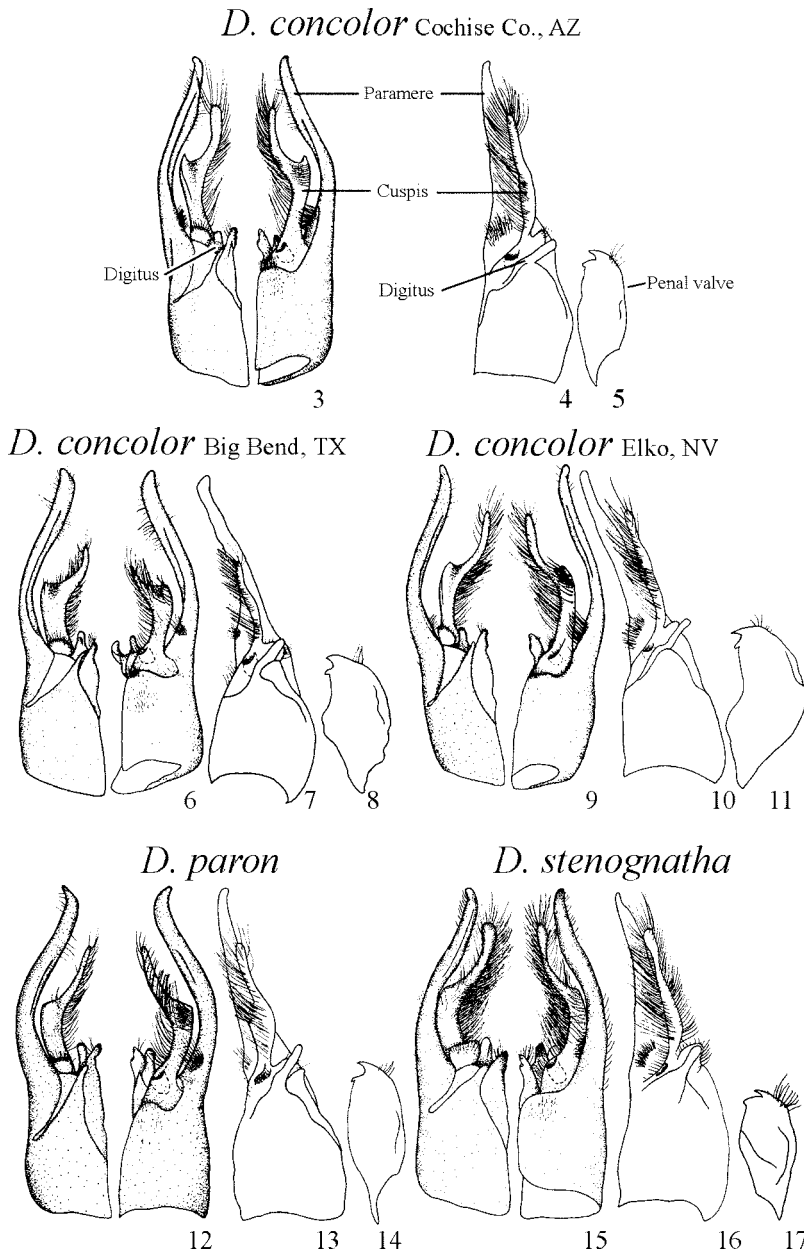


Fig. 2. Map of the North American deserts and arid lands sampled for *Dilophotopis*. Symbols mark collection localities and represent populations forming distinct clades (see Fig. 1). Desert and arid lands boundaries are modified from Omernik (1987).

Otero Co.: 1 male, Alamo Canyon, nr. Alamogordo, 29-V-1965, M. E. Irwin (UCRC); Sandoval Co.: 1 male, Jemez Springs, 1-VII-1941, R. H. Beamer (SEMC); Texas: Brewster Co.: 1 male, Alpine, 5-VIII-1991, J. Llamaz (SRSC); 2 males, Big Bend National Park, Panther Junction, 18-V-1959; 1 male, Boquillas, 13-V-1959, W.R.M. Mason (EMUS); 20 males, Big Bend Ranch State Park, 16-V-2006, K. A. Williams and J. S. Wilson (EMUS); Culberson Co.: 1 male, Van Horn, 27-VIII-1971, R. F. Denno and E. E. Grissell (UCDC); Hudspeth Co.: 1 male, Van Horn, 25 km SW, 29-V-1999, W. MacKay (EMUS); Jeff Davis Co.: 1 male, Fort Davis, 29-V-1959, W. R. Mason (EMUS); La Salle Co.: 75 males, Chaparral Wildlife Management Area, 19-21-V-2006, K. A. Williams and J. S. Wilson (EMUS); Utah: Beaver Co.: 1 male, Milford, 2-VII-1941, G. F. Knowlton and F. C. Harmston (EMUS); Box Elder Co.: 1 male, Lakeside, 13 miles SW, 10-28-VI-1982, J. Hansen (EMUS); Cache Co.: 3 males, Blacksmith Fork Canyon, 8-12-VIII-2001, W. Hanson and C. Brammer (EMUS); Emery Co.: 3 males, Temple Mountain wash, 20-VI-2005, F. D. Parker (EMUS); Garfield Co.: 2

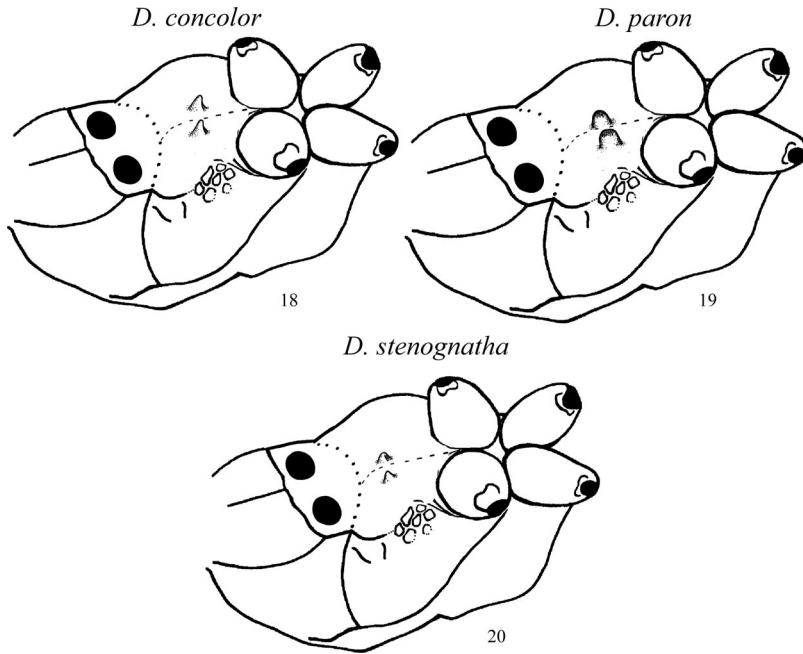
males, Calf Creek, 10 km S. Boulder, 28-VI-2002, F. D. Parker and M. Erwin (EMUS); 2 males, Capital Reef National Park, Sulfur Creek, 26-28-VI-1978, Lindahl (EMUS); Grand Co.: 2 males, Castle Valley, 8-VI-1963, G. E. Bohart (EMUS); 2 males, Crescent Jct., 1.5 miles N, 28-V-9-VI-1987, Tibbets and Nelson (EMUS); Iron Co.: 1 male, Parowan, 18-VII-1941, G. F. Knowlton and F. C. Harmston (EMUS); Juab Co.: 1 male, Nephi, 8-VII-1965, R. Dickson, W. Ewart (UCRC); Kane Co.: 6 males, Kanab, 3 miles N, 16-VII-1975, F. G. Andrews, A. R. Hardy (CSCA); 1 male, Sooner Rocks, 4-VI-2003, H. Ikerd (EMUS); Millard Co.: 1 male, White Valley, 19-V-1940, R. W. Fautin (EMUS); Salt Lake Co.: 1 male, Salt Lake City, 12-VIII-1974; 2 males, Salt Lake City, 22-30-VII-1975; 3 males, Salt Lake City, 2-10-VIII-1975; 2 males, Salt Lake City, 5-11-VIII-1975; 2 males, Salt Lake City, 16-22-VI-1976; 1 male, Salt Lake City, 28-V-8-VI-1976; 1 male, Salt Lake City, 23-29-VI-1976, Knowlton and Crowe (EMUS); San Juan Co.: 16 males, Moab, 34 miles S, 13-20-VI-1987, C. R. Nelson (EMUS); Sevier Co.: 1 male, Big Rock Candy Mts., 13-VII-1961, G. F. Knowlton (UCDC); Tooele Co.: 1



Figs. 3-17. Genitalia: dorsal view left; ventral view right; internal lateral view, penial valve removed; penial valve, lateral view. *D. concolor* (3-11), *D. paron* (12-14), and *D. stenognatha* (15-17).

male, Callao, 29-VII-1941, G. F. Knowlton and F. C. Harmston (EMUS); Uintah Co.: 1 male, Bonanza, 14-VII-1975, G. E. Bohart (EMUS); 2 males, SW Bonanza, 12-VI-1981, M. Schwartz and R. Miller (EMUS); 2 males, Vernal, 19-VII-1941, G. F. Knowlton (EMUS); Washington Co.: 3 males, Leeds Canyon, 17-VII-1980; 1 male, Leeds Canyon, 15-VII-1980, Hanson, Knowlton and Clemons (EMUS); 1 male, Snow Canyon, 15-VI-1983, W. J. Hanson (EMUS); Wayne Co.: Hanksville, 1 male, 12 miles S, 22-VII-1968, J.E.H. Martin (EMUS); Weber Co.: 2 males, Slaterville, 13-VII-

1967, G. F. Knowlton and L. E. Fronk (EMUS); Washington: Benton Co.: 1 male, Hanford Site sand dune, W. of Columbia River, 7-VI-1996, 1 male, Hanford Site sand dune, W. of Columbia River, 19-VI-1995, R. S. Zack (EMUS); 2 males, Hanford Site ALE, Rattlesnake Spring, 19-VI-1995, R. S. Zack (EMUS); 1 male, Hanford Site ALE, Lower Snively Spring, 12-VII-1995, R. S. Zack (EMUS); Wyoming: Fremont Co.: 2 males, Lander, 6-7-VII-2000, P. M. Pineda (CSUC); Hot springs Co.: 1 male, Thermopolis, route 120, 24-VI-1980, M. Pogue, R. J. Lavigne (EMUS); Canada, British



Figs. 18–20. Mesosternal armature (legs except hind coxae, sculpture and pilosity omitted). *D. concolor* (18), *D. paron* (19), and *D. stenognatha* (20).

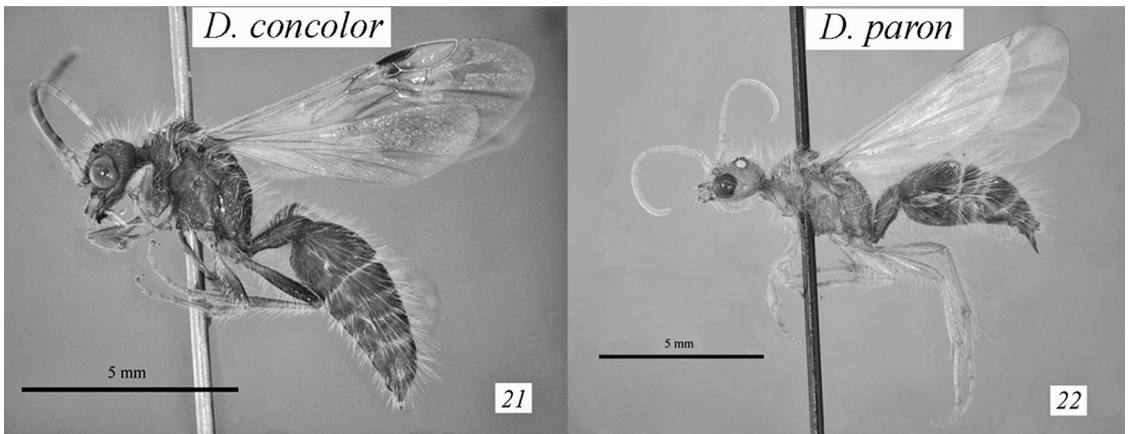
Colombia: 1 male, Oliver, 26-VII-1953, D. F. Hardwick (EMUS); Mexico, Chihuahua: 1 male, Escalón, 12 miles N, 18-IV-1961, Howden and Martin (EMUS) Coahuila: 1 male, Cuatro Ciénegas, 3 km S. along Hwy. 30, 27-XII-1988, B. N. Danforth and R. L. Minckley (EMUS); 1 male, Monclova, 21-IX-1974, W. Hanson and G. Bohart (EMUS); Durango: 1 male, Durango, 41 miles NE, 28-VII-1956, R. E. Beer (SEMC); 2 males, Metates, 21-VI-1961, R. A. Scheibuer (UAIC); 1 male, Tapias, 19-VI-1961, R. A. Scheibuer (UMSP); Tamaulipas: 1 male, Victoria, 12 miles SE, 20-IX-1974, G. Bohart and W. Hanson (EMUS); Zacatecas: 2 males, Fresnillo, 9 miles S, 18-VIII-1956, D. D. Linsdale (CISC).

Notes. Ferguson (1967) moved *Odontophotopsis crasus* Viereck into *Dilophotopsis* as a subspecies of *D. con-*

*color* and synonymized *D. c. utahensis* with it. *O. alamonis* was synonymized with *D. concolor* by Schuster (1958). *M. nanula* was synonymized with *D. c. crassa* by Pitts et al. (2007). We agree with the synonymies made by these authors. Dalla Torre (1897) misspelled *M. pygmaea* as *M. pygmaea*, and gave it a new name, *M. nanula*. Inspection of a specimen labeled as a paratype of *M. concolor* was found to be misidentified. The specimen belongs in *O. melicausa* species-group.

#### *Dilophotopsis paron* (Cameron), NEW STATUS

*Sphaerophthalma* [sic] *paron* Cameron, 1896. Biol. Central Am. 37: 88. Male. Holotype. Northern Sonora, Mexico, coll. Morrison (BMNH).



Figs. 21–22. Habitus. *D. concolor* (21) and *D. paron* (22).

*Dilophotopsis concolor sonorensis* Schuster, 1958. Entomol. Am. 37: 88. Male. Holotype. Gila bend, AZ, 24 April 1935, coll. F. H. Parker (UMSP).

**Diagnosis.** This species can be distinguished from the other *Dilophotopsis* species by the appearance of the mesosternal tubercles (Fig. 19). These tubercles are relatively wide and are shagreened on their apex. Also, the male genitalia are diagnostic; the shape of the cuspis is distinctive being more rounded rather than angulate on the external margin, and the dorsal carina is lacking compared with *D. concolor* (Fig. 12). The genitalia are much less setose than *D. stenognatha* (Figs. 12–14). This species lacks a sternal felt line. Also, like *D. concolor*, the body coloration is variable, but the legs of *D. paron* are usually stramineous with no darkening at the apices of the femora (Fig. 22). This species is moderately sized, ranging from 10 to 13 mm. The mandibles are similar to *D. concolor* with a mandibular ratio of 1, 0.6, 0.9.

**Distribution.** Restricted to the Mojave and western Sonoran deserts of Arizona, California, and Nevada, and the deserts of Baja California, and Baja California Sur, Mexico.

**Materials Examined.** USA, Arizona: Pima Co.: 1 male, Organ Pipe Cactus National Monument, 12-IV-1947, A. L. Melander (UCRC); 1 male, Sierra Pinta Mts., 16-IV-1963, C. E. Mickel (EMUS); Yuma Co.: 1 male, Sierra Pinta Mts., Heart Tank, 16-IV-1963, C. E. Mickel (LACM). California: Inyo Co.: 1 male, Lone Pine, 3-VI-2003, E. E. and K. A. Williams (EMUS); 1 male, Resting Springs, 29–30-VI-1955, Belkin et al. (LACM); 1 male, Death Valley, Saratoga Springs, 27–29-VI-1955, Belkin et al. (LACM); Kern Co.: 2 males, Three Pine Canyon, 26-V-2005, K. A. Williams (EMUS); Riverside Co.: 1 male, Cathedral City, 1-V-1945, A. L. Melander (UCRC); 2 males, Corn Springs, 10 miles. S Desert Center, 29-V-2005, E. E. and K. A. Williams (EMUS); 3 males, Deep Canyon, 16-V-1963, E. I. Schlinger (UCRC); 3 males, Joshua Tree National Monument, 27-V-1976, G. W. Byers (SEMC); 7 males, Joshua Tree National Monument, 1–4-VI-1976, L. Bezark (CSCA); 5 males, Mecca, 1-VI-1935 (LACM); 3 males, Palm Springs, 26-IV-1955, Menke and Stange; 1 male, Palm Springs, 20-V-1939; 1 male, Palm Springs, 23–24-V-1940, W. L. Swisher (LACM); 1 male, White-water Canyon, 30-V-1998, 1 male, Whitewater Canyon, 13-V-1966, M. W. Stone (UCRC, EMUS); San Bernardino Co.: 2 males, Afton Canyon, 1 mile. S Afton, 28-V-2005, E. E. and K. A. Williams (EMUS); 1 male, Hole in the Wall Camp Ground, E. Mojave scenic area, 17-VI-1993, W. F. Chamberlain (TAMU); 1 male, Morongo Valley, 19-V-1951, E. J. Taylor (UCDC); 1 male, Morongo Valley, 15-IX-1957, R. R. and M. D. Snelling (LACM); 1 male, Twenty-nine Palms, IV-1949 (LACM); San Diego Co.: 1 male, Anza Borrego State Park, 23-IV-1951, W. J. Wall (UCDC); 1 male, Borrego Springs, 11-VI-1965, J. L. Bath (UCRC); 1 male, Borrego Springs, 13-IV-1947 (LACM); 1 male, Borrego, Palm Canyon, 4-V-1945, A. L. Melander (UCRC); 3 males, Jct. Hwys. 78 and 53, 18-VIII-1987, G. C. Snelling (LACM). Nevada: Clark Co.: 1 male,

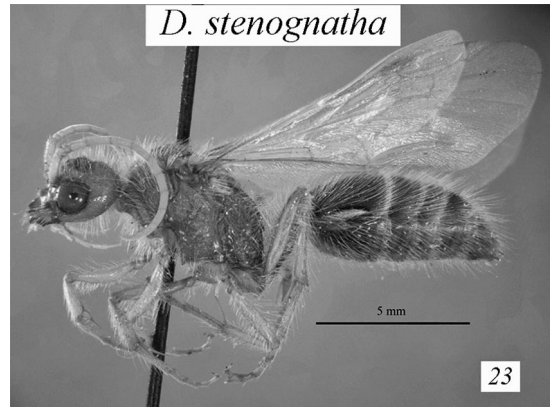


Fig. 23. Habitus of *D. stenognatha*.

Pahrump, 20 km W, 16-V-2003 (EMUS); 2 males, Pahrump, 24–25-VI-2006, K. A. Williams (EMUS); 1 male, Riverside, 4.5 miles. W, 1-V-1997, F. D. Parker (EMUS); 1 male, Toquap Wash, W. Mesquite, 24-V-2003, D. Yanega (EMUS); Nye Co.: 1 male, Ash Meadows Rd, 4.2 miles E Rt. 373, 11-VI-2001, B. Kondratieff et al. (CSUC); Mexico, Baja California: 1 male, Bahía de Los Angeles, 9/11-VIII-1993, T. Jackson (EMUS); 1 male, Bahía de Los Angeles, 2 km S., 11-IV-1977, E. M. Fisher (CSCA); 1 male, Rancho Santa Ines, 9 km S., 30-VI-1979, W. M. Clark, P. Blom and D. Ward; 1 male, Rancho Santa Ines, 9 km S., 21-VI-1981, W. M. Clark (CIDA). Baja California Sur: 2 males, Ejido Esperanza, 1 mile SW, 19-IV-1987, A. Gilbert and F. Andrews (CSCA); 16 males, Guillermo Prieto, 13 km S, El Tablón, 16–18-IV-1983, M. Wasbauer and C. Slansky (CSCA); 1 male, LA Paz, 55 km NW, 13-XI-1982, P. J. and J. O. Schmidt (LACM); 6 males, San Ignacio, 4.3 miles N, 7-IX-1985, J. P. and K.E.S. Donahue (LACM).

**Notes.** Cameron (1896) misspelled *Sphaerophthalma paron* as *Sphaerophthalma paron*. Mickel (1965) moved *S. paron* into *Dilophotopsis* as a subspecies of *D. concolor* and synonymized *D. c. sonorensis* with *D. c. paron*; we agree with his findings. The head is missing in the holotype of *S. paron*.

#### *Dilophotopsis stenognatha* Schuster

*Dilophotopsis stenognatha* Schuster, 1958. Entomol. Am. 37: 74. Male. Holotype. Tucson, AZ, 20 May 1935, coll. Bryant (UMSP).

**Diagnosis.** This species can be diagnosed from other *Dilophotopsis* species by its mandibles, which are less dilated than *D. concolor* and *D. paron*. The mandibular ratio of *D. stenognatha* is 0.9, 0.5, 0.7. Also, this species has a piceous metasoma and a castaneous head and mesosoma (Fig. 23). This species is large, ranging from 13 to 18 mm in length. The male genitalia lack a dorsal carina on the cuspis, and they are much more densely setose than other *Dilophotopsis* species (Figs. 15–17). Many specimens have a trace of a sternal felt line. The mesosternal tubercles are more triangular than other *Dilophotopsis* species, with the base obviously broader



than the apex (Fig. 20). The mesosternal tubercles of some specimens of *D. concolor* may seem similar to those of *D. stenognatha*, but the shape of the genitalia and the body coloration are sufficient to distinguish between these species.

**Distribution.** The eastern Sonoran Desert of Arizona and Sonora, Mexico.

**Materials Examined.** USA, Arizona: Pima Co.: 9 males, Organ Pipe Cactus N.M., 26-V-1976, L. Bezark (CSCA); 6 males, T13 S. R11 E. S12, 23-V-1972, E. Yensen (EMUS, CIDA); 1 male, Tucson, 5-V-1962, 1 male, Tucson, 6-V-1963, G. D. Butler (LACM); 1 male, Tucson, Saguaro Nat. Mon., 7-V-1921–VI-1961, G. D. Butler (LACM); Santa Cruz Co.: 6 males, Santa Rita Mts., Madera Canyon, 7-VIII-1947, L. Martin (LACM); Yuma Co.: 2 males, Yuma Proving Grounds, 26-VI-2001, S. L. Buchmann (EMUS). Mexico, Sonora: 1 male, Empalme, 16 Mi SE, 8-V-1953 (EMUS); 1 male, Hermosillo, 3 miles N, 25-V-1961, Howden and Martin (EMUS); 1 male, Sonoyta, 35 miles SE, 5-VI-1967, R. W. McDiarmid (EMUS).

#### Key to *Dilophotopsis* Species

1. Mandibular apex, distal to the ventral emargination, slender with parallel dorsal and ventral margins, mandibular ratio near 1, 0.5, 0.7; traces of sternal felt line retained, sometimes reduced to a group of minute punctures; metasoma piceous (Fig. 23); large, 15–18 mm. . . . . *D. stenognatha* Schuster
- Mandibles strongly dorsoventrally dilated, mandibular ratio near 1, 0.6, 1; sternal felt line completely absent; metasoma coloration variable, but never completely piceous; smaller, 8–13 mm. . . . . 2
2. Cuspis angulate on external margin, with dorsal carina on elbowed region (Figs. 3, 6, and 9); mesosternal armature triangular to peg-like with a glabrous apex (Fig. 18); femoral apices usually darkened (Fig. 21). . . . . *D. concolor* (Cresson)
- Cuspis rounded on the external margin, lacking a dorsal carina at the elbowed region (Fig. 12); mesosternal armature cylindrical with a shagreened apex (Fig. 19); femora usually stramineous throughout (Fig. 22) . . . . . *D. paron* (Cameron)

#### Discussion

Molecular tools are increasingly being used to aid taxonomists in deciphering cryptic or morphologically challenging species complexes (Pilgrim and Pitts 2006, Reimer et al. 2006, von Dohlen et al. 2006, Bergmann and Russell 2007, Pitts et al. 2007). Our molecular and morphological analysis of *Dilophotopsis* revealed that *D. concolor* includes two species that are morphologically difficult to differentiate—one species is a widespread, variable species, whereas the other species is

more localized in distribution, rather than four subspecies as Schuster (1958) proposed.

Our analysis uncovered interesting patterns of genetic divergence in *Dilophotopsis*. *D. c. paron* is separated from the other *D. concolor* subspecies by relatively high genetic distances (3% or more for ITS1 and 6% or more for ITS2). These distances are equivalent to the interspecific genetic distances of many sphaerophthalmine mutillid wasps (Pilgrim and Pitts 2006, Pitts et al. 2007). The genetic distances between *D. stenognatha* and *D. concolor* are slightly lower (2.57–2.88% for ITS1 and 5.35–6.16% for ITS2). The topology and branch lengths of the Bayesian phylogram (Fig. 1) further support the distinctiveness of *D. c. paron*.

Although there is some variation among the ITS1 and ITS2 sequences of *D. c. concolor*, *D. c. crassa*, and *D. c. laredo* (Table 2), these differences are equivalent to the intrasubspecific differences present in each individual subspecies. Additionally, the genetic differences are not consistent with the designated subspecies. The genetic variation does result in multiple well-supported sub-clades on the phylogram (Fig. 1), but these clades do not correspond to the defined subspecies. For example, the ITS1 and ITS2 sequences of *D. c. laredo* match the sequence of a *D. c. concolor* specimen from Nebraska and these specimens form a clade supported by a posterior probability of 1.0 (Fig. 1).

Additionally, the results of our morphological analysis do not support the defined subspecies. Schuster (1958) stated that *D. c. paron* was the most morphologically variable subspecies. Our research shows that *D. c. paron* is actually the least variable morphologically, as well as the least variable in the ITS1 and ITS2 sequences. This contradiction is likely a result of Schuster using inconsistent color characters to distinguish *D. c. paron* from the other subspecies. Schuster (1958) also stated that *D. c. laredo* was the most distinctive of the four subspecies based on the shape of its mesosternal tubercles and its larger ocelli. Our results, again, do not support Schuster's assertions; we found that the ocelli of *D. c. laredo* are not significantly larger than any other *D. concolor* subspecies and that the mesosternal tubercles do not differ significantly from *D. c. concolor* or *D. c. crassa*. This may be because Schuster examined few specimens of *D. c. laredo*.

Multiple morphological character states support the distinctiveness of *D. c. paron*. The male genitalia, specifically the shape of the cuspis, as well as the shape of the mesosternal tubercles, clearly distinguish *D. c. paron* from *D. c. concolor*, *D. c. crassa*, *D. c. laredo*, and *D. stenognatha* (Figs. 12–14, 18–20). Although some morphological variation exists among *D. c. concolor*, *D. c. crassa*, and *D. c. laredo*, these differences are not consistent enough to consider each of these as distinct species. The differences are mainly in the size of the mesosternal tubercles, and in the length of the carina on the cuspis (Figs. 3 and 6, and 9). Therefore, the subspecies of *Dilophotopsis* do not represent geographically isolated populations with discrete morphological characters. The morphological and molecular data suggest that *D. c. paron* should be elevated to

species, and *D. c. concolor*, *D. c. crassa*, and *D. c. laredo* are new junior synonyms of *D. concolor*.

Although the subspecies are invalid, the geographic structuring among *Dilophotopsis* species, especially within *D. concolor*, does have a geographic component. *D. paron* is restricted to the Mojave and western Sonoran deserts, as well as the deserts of Baja California. *D. stenognatha* is restricted solely to the eastern Sonoran desert of Arizona and Mexico. *D. concolor* is wide ranging from Zacatecas, Mexico, to British Columbia, Canada, and from Kansas to eastern California. Yet, this species is absent from the Mojave and western Sonoran deserts. Thus, the variation seems to be associated with specific arid lands. For example one of the sub-clades of *D. concolor* seems to be restricted to the Great Basin Desert, one sub-clade is limited to the Colorado Plateau, and one sub-clade is found in the Chihuahuan Desert and the Plains (Fig. 2).

One interesting pattern that can be derived from our preliminary phylogeographic analysis of *Dilophotopsis* is the east–west split between sister species *D. concolor* and *D. paron*. This same pattern has been observed in many arid-adapted taxa (Jaeger et al. 2005, Devitt 2006, Douglas et al. 2006). This, and the apparent isolation of *D. concolor* sub-clades to individual deserts, suggests that the *Dilophotopsis* will be useful in the study of the historical biogeography of the Nearctic arid lands. With further sampling, the study of *Dilophotopsis* potentially will add to the current body of knowledge regarding speciation in the Nearctic deserts by facilitating an analysis in both the warm and cold deserts, as well as the surrounding xeric shrublands.

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