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Phenetic relationships among the warblers in the *Dendroica virens* complex and a record of *D. virens* from Sonora, Mexico.—Four species of warblers of western North America are closely related to the eastern Black-throated Green Warbler (*Dendroica virens*): the Black-throated Gray (*D. nigrescens*), Townsend's (*D. townsendi*), Hermit (*D. occidentalis*), and Golden-cheeked (*D. chrysoparia*) warblers (Mengel 1964). These species seem to be related closely, but there is debate about their taxonomy. For example, *D. townsendi* and *D. occidentalis* hybridize where their ranges overlap in Oregon and Washington (Jewett 1944, Morrison and Hardy 1983) and may be conspecific. Mayr and Short (1970) regard *D. chrysoparia* as a subspecies of *D. virens* and suggest that *D. virens, D. occidentalis,* and *D. townsendi* comprise a superspecies complex, with *D. nigrescens* a close relative of the complex. The A.O.U. Check-list (AOU 1983:613) states that "*D. townsendi, D. occidentalis, D. virens* and *D. chrysoparia* appear to constitute a superspecies." These opinions are based on the birds' geographic distributions and a "largely subjective" evaluation of plumage patterns and song (Mengel 1964). Other than Morrison's (1983) study of morphometric variation within *D. townsendi,* there are no published analyses of the size variations within this complex. The present analyses of the *D. virens* complex (including *D. nigrescens*), based on measurements of 21 skeletal features, provide information about the phenetic variation among these warblers, and confirm the identity of a skeletal specimen in the collection of the University of Kansas, Museum of Natural History (KU 37136). KU 37136 was collected 20 December 1956 by A. A. Alcorn 21 miles SSE of Nogales, Sonora. It was eviscerated in the field, dried, and sent to KU, where it was identified as *D. virens* before being prepared as a skeleton. It is not known who identified the bird, or on what basis (presumably plumage characters). Other than this individual, there are no specimens of *D. virens* from Sonora (S. M. Russell, pers. comm.).

Methods.—I measured the following specimens (adult males unless otherwise noted): 13 *D. townsendi*; 6 *D. occidentalis*; 35 *D. virens* (12 females); 18 *D. nigrescens* (2 females); 1 *D. chrysoparia.* With the exception of two specimens from Mexico (KU 37136 and one from Veracruz), all of the *D. virens* used were from the northeast, and thus on geographic grounds are not *D. v. waynei.* With the exception of *D. virens,* these were all of the adult male specimens of these species available in the following collections: Royal Ontario Museum, University of Michigan, Burke Museum University of Washington, University of Kansas, U.S. National Museum, and Delaware Museum of Natural History. I did not attempt to obtain samples of females (with the exception of *D. virens*) because only small numbers are available. KU 37136 is a male.

I measured 21 skeletal features (Table 1) on each specimen, as described by Robins and Schnell (1971), except that gonys length is their "minimum mandible length" (gonys with rhampotheca removed), synsacrum width is width across the antitrochanters, bill length (skull) is length of the premaxilla from the base of the skull, and bill length (nost.) is length

TABLE 1

CORRELATIONS (IF > 0.30) BETWEEN COMPONENTS AND CHARACTERS FROM 74 SPECIMENS OF THE *DENDROICA VIRENS* COMPLEX

Variable	Component 1	Component 2	Component 3
Skull length	0.84		
Skull width	0.40		
Bill length (skull)	0.63	−0.35	0.45
Bill length (nost.)	0.37	−0.67	0.34
Nasal bone width	0.41	−0.46	−0.52
Interorbital width	0.40		−0.63
Mandible length	0.81	−0.36	
Gonys length	0.36	−0.63	0.30
Coracoid length	0.74		
Scapula length	0.74		
Femur length	0.83		
Tibiotarsus length	0.76	0.41	
Tarsometatarsus length	0.64	0.42	0.36
Humerus length	0.73		
Ulna length	0.84		
Carpometacarpus length	0.87		
Hallux length	0.67	0.35	
Sternum length	0.86		
Sternum depth	0.65		
Keel length	0.82		
Synsacrum width	0.59		−0.45
Eigenvalue	9.88	2.05	1.82
Percent total variance explained	47.0%	9.8%	8.6%

of the premaxilla from the anterior edge of the nostril. I used only nearly complete specimens. If a specimen was missing only a few characters, I estimated missing values as the means for the appropriate species and sex. (The sample sizes given above were the numbers used in the analyses; other specimens were measured but were not used because of missing values.) KU 37136 was complete. I used principal component analysis (PCA) (NTSYS, 1982, program FACTOR) on a matrix of correlations among the untransformed characters to ordinate the 74 specimens.

Results.—Correlations between many variables and Principal Component 1 (PC1) are high. Several measures of long bones (femur, ulna, carpometacarpus), sternum, and bill length (mandible length, and perhaps skull length) have correlations >0.80 (Table 1). Therefore, this component can be interpreted as measure of overall size (including bill size), although it doubtless contains some information about shape as well (Somers 1986). Because the correlations are positive, the largest birds are to the right on the PC1 axis. PC2 primarily contrasts bill length with leg and toe lengths; PC3 contrasts bill and tarsometatarsus lengths with nasal bone and synsacrum widths (Table 1). PC2 and PC3 have approximately the same eigenvalues, and therefore it is not possible to interpret them precisely (Gibson et al. 1984), although they nonetheless give information on grouping the specimens. The first three components together explain 63% of the total variation in the data matrix.

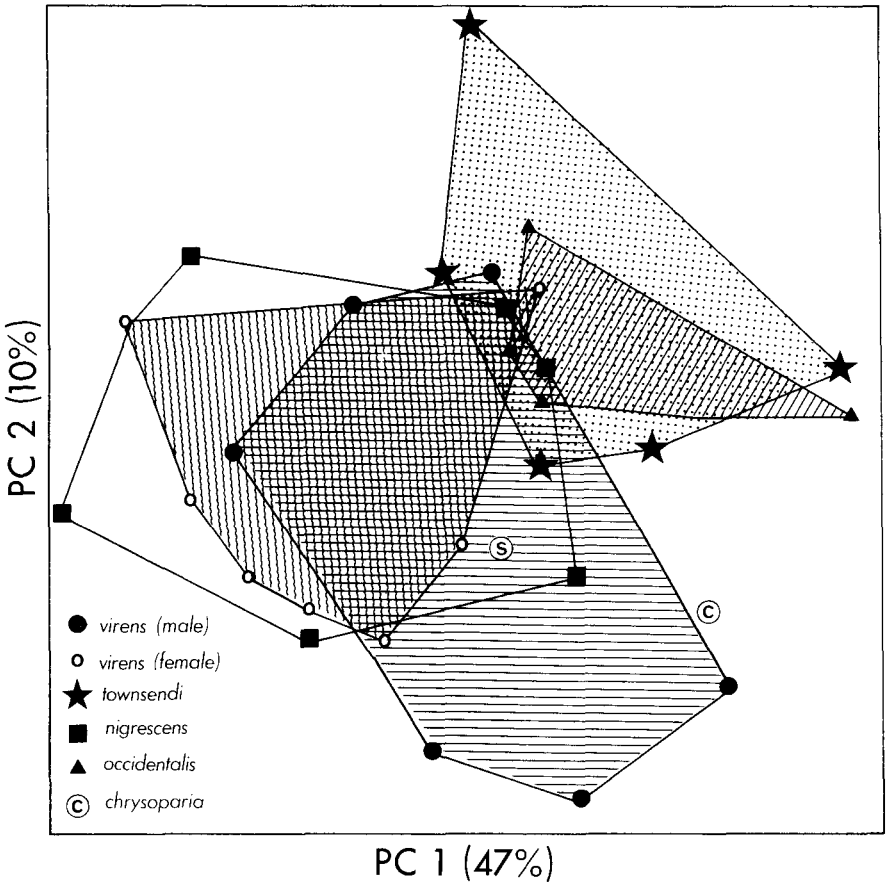

FIG. 1. Two-dimensional plot showing the phenetic relationship among 74 specimens in the *Dendroica virens* complex in a space defined by Principal Components 1 and 2. The percentages of the total variation among the 74 specimens and 21 variables explained by the respective axes are in parentheses. Specimen "S" is KU 37136, a putative specimen of *D. virens* from Sonora.

Figure 1 shows the positions of the 74 specimens in the space defined by Principal Components 1 and 2. There is extensive overlap between *D. occidentalis* and *D. townsendi* and between *D. virens* (male and female) and *D. nigrescens*. *D. virens*, and especially *D. nigrescens*, are generally "smaller" (to the left on PC1) than *D. townsendi-D. occidentalis*. Likewise, female *D. virens* are smaller on the average than males, and the two smallest *D. nigrescens* are the only two females in the sample. The amount of size dimorphism in *D. virens* is similar to that of other *Dendroica* warblers (Rising, unpubl. data). The single specimen of *D. chrysoparia* is near, but outside, the cluster of *D. virens*. There is little overlap between the *D. virens-D. nigrescens* and *D. townsendi-D. occidentalis* groups. KU 37136

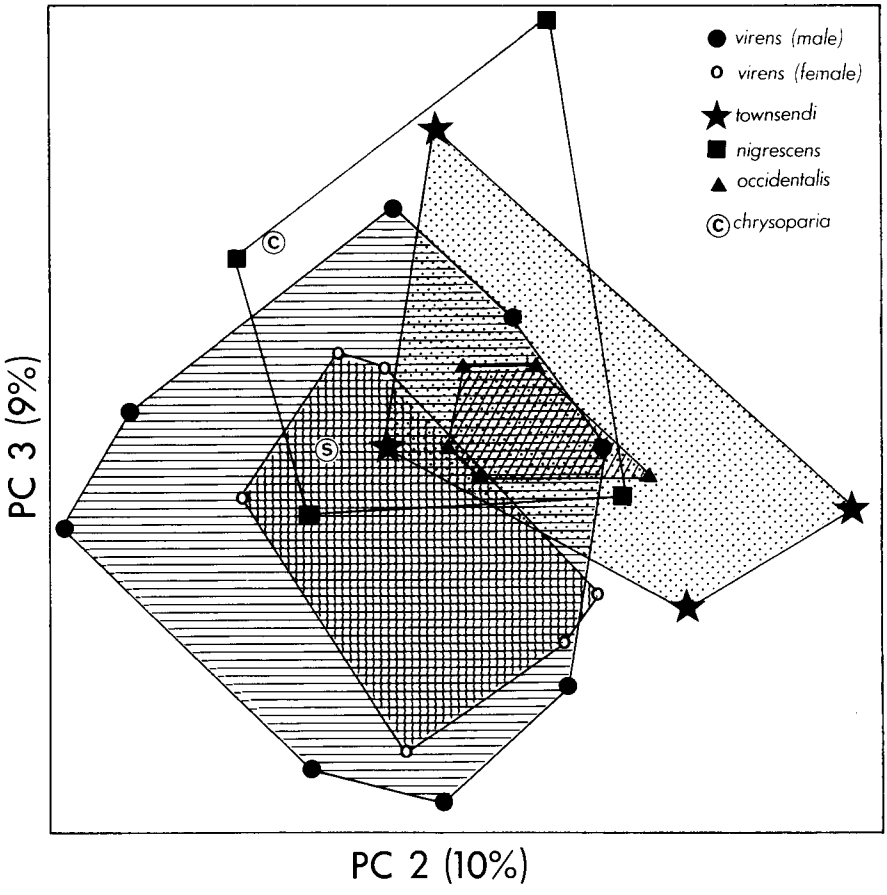

FIG. 2. Two-dimensional plot of phenetic relationships defined by Principal Components 2 and 3 (see caption to Fig. 1).

("S") clusters in the middle of male *D. virens* (as it was identified) and is outside the range of *D. townsendi*, the similar species most likely to occur in Sonora in December. Phenetically, KU 37136 could be *D. nigrescens*, but it is unlikely that the two would be confused on the basis of feather characters. There is extensive overlap among all of the species in the PC2 by PC3 space (Fig. 2). In that plot, *D. chrysoparia* again falls outside, but close to, *D. virens* space and is within *D. nigrescens* space. Again, KU 37136 is outside of the phenetic range of *D. townsendi*.

Discussion.—A superspecies complex consists of two or more allopatric species of "... relatively recent monophyletic origin which are much more closely related to each other than to any other species" (AOU 1983:xiv). Mengel's (1964) scenario for the evolution of this complex assumes that these birds comprise such a complex. He proposed that all of the western members of the complex (perhaps excepting *D. chrysoparia*) were derived from

an eastern ancestor of present-day *D. virens.* He postulated a series of colonizations of the west of such "pro-*virens*" birds through the northern boreal forests, perhaps during major Pleistocene interglacial periods. He suggested that *D. nigrescens* was descended from the oldest of these western colonizations and *D. occidentalis* and *D. townsendi* from more recent ones. The present-day hybridization of *D. townsendi* and *D. occidentalis* certainly indicates a high degree of genetic similarity between these two taxa, and they doubtless have a recent common ancestor. *D. chrysoparia* may be a relictual population of a once more widespread eastern species, probably not much different from *D. virens,* or, alternatively, a remnant of a once widespread early western differentiate.

Phenetic similarity of the sort that I have quantified could easily be due to convergence. Nevertheless, these analyses show that there is a close phenetic similarity between *D. townsendi* and *D. occidentalis,* the two taxa in the complex that frequently hybridize. *D. virens* and *D. nigrescens,* the two taxa most distantly related to each other in Mengel's scenario, are also essentially identical with regard to the features analyzed here; thus it seems appropriate to include *D. nigrescens* in the *D. virens* complex. The one specimen of *D. chrysoparia* falls close to the *D. virens* cluster, but it is more like *D. townsendi-D. occidentalis* on the PC1 axis (which explains 47% of the variation among the specimens). Therefore, either hypothesis concerning its history is consistent with its phenetic placement. KU 37136 is confirmed as a specimen of *D. virens* from Sonora.

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