

## SHORT COMMUNICATIONS

**Evaluation of *Vermivora* × *Oporornis* hybrid wood-warblers.**—By the late 19th century, the breeding birds of the eastern United States were thought to be well known. Hence, discovery of three apparently new species of wood-warblers in the 1870s, *Helminthophaga leucobronchialis* (Brewster 1874), *H. Lawrenceii* (Herrick 1875), and *H. cinnantiensis* (Langdon 1880), was considered remarkable. Perhaps more surprising was the subsequent insight that all three taxa were hybrids (Ridgway 1880, 1885; Brewster 1881). “*H. Lawrenceii*” (Lawrence’s Warbler) and “*H. leucobronchialis*” (Brewster’s Warbler) were determined to be the hybrid offspring of the Blue-winged (*Vermivora pinus*) and Golden-winged (*V. chrysoptera*) warblers, while “*H. cinnantiensis*” (Cinnanti Warbler) was judged to be an intergeneric hybrid of *V. pinus* and the Kentucky Warbler (*Oporornis formosus*). In the era before Mendelian genetics, these were among the first recognized examples of hybridization in passerines. Brewster (1881:224) reflected the sentiments prevalent among his colleagues, “many of our leading ornithologists were incredulous as to its [hybridization] occurrence in a state of nature save among the Grouse and some of the Swimming Birds.”

Hybridization between *V. pinus* and *V. chrysoptera* is now well documented (Parkes 1951, Gill 1980). The specimen of “*H. cinnantiensis*” remains unique, and for over sixty years was the only known hybrid between *Oporornis* and *Vermivora*. In 1948, a puzzling warbler was collected in Cass County, Michigan. This specimen, which was compared with the type of *H. cinnantiensis*, was provisionally considered a hybrid between *V. pinus* and the

TABLE 1  
RANGES AND MEANS (± ONE STANDARD DEVIATION) OF MEASUREMENTS OF MALE  
*OPORORNIS PHILADELPHIA*, *O. FORMOSUS*, *VERMIVORA PINUS*, AND  
*VERMIVORA* × *OPORORNIS* HYBRIDS

Character	<i>O.</i> <i>philadelphia</i> (N = 15)	<i>O. formosus</i> (N = 15)	<i>V. pinus</i> (N = 15)	Hybrids	
				Mich.	Ohio
Wing chord	60.3–65.6	65.6–74.1	58.7–63.4	61.6	63.6
	62.8 ± 1.7	69.4 ± 2.1	61.1 ± 1.3		
Wing tip	9.7–17.2	13.6–20.8	13.5–16.0	14.2	16.0
	13.2 ± 2.4	17.7 ± 2.0	14.6 ± 0.7		
Central rectrices	47.4–52.5	47.0–52.2	43.1–49.2	44.7	45.6
	50.6 ± 1.5	49.4 ± 1.6	46.2 ± 1.5		
Outer rectrices	42.0–49.8	43.6–50.7	41.1–46.8	42.7	44.3
	46.6 ± 1.9	47.4 ± 2.1	43.9 ± 1.7		
Tarsus	19.6–21.9	19.6–22.7	16.0–17.8	18.7	18.4
	20.6 ± 0.7	21.6 ± 0.8	17.0 ± 0.6		
Culmen (from anterior edge of nostril)	7.1–8.5	7.9–8.6	7.7–8.7	8.0	NA <sup>a</sup>
	7.7 ± 0.4	8.2 ± 0.2	8.4 ± 0.2		

<sup>a</sup> Measurement not available.

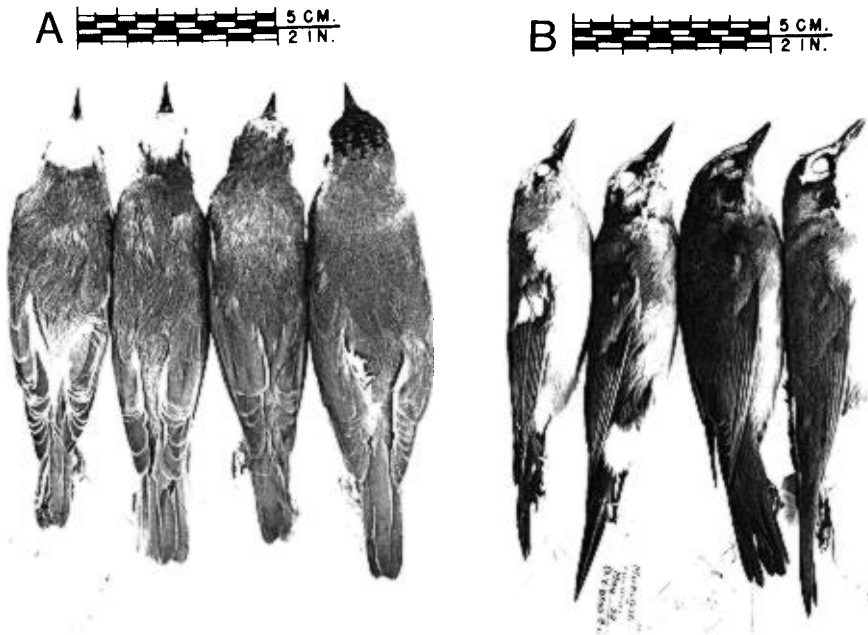


FIG. 1. Dorsal (A) and lateral (B) views of *Vermivora pinus*, *Oporornis formosus*, and presumed *V. pinus* × *O. formosus* hybrids (all males). From left to right: *V. pinus*; “Michigan” hybrid; “Ohio” hybrid; *O. formosus*. The Michigan hybrid may be the progeny of an F<sub>1</sub> hybrid back-crossed with a parental *V. pinus*.

Mourning Warbler (*O. philadelphia*) (McCamey 1950). In this paper, I reevaluate the two presumed *Vermivora* × *Oporornis* hybrid specimens.

*Specimens examined.*—“*Vermivora pinus* × *Oporornis formosus*” (Ridgway 1880); Cincinnati Museum of Natural History No. 26247 (formerly No. 1394 in the Frank W. Langdon Collection), male, collected at Madisonville, Ohio, on 1 May 1880 by Frank W. Langdon. “*Vermivora pinus* × *Oporornis philadelphia*” (McCamey 1950); Delaware Museum of Natural History No. 54985 (formerly No. 10381 in the George M. Sutton Collection), adult male, 11.4 g, testes greatly enlarged, collected at Russ Forest, Cass County, Michigan on 28 May 1948 by B. Frank McCamey.

I compared these specimens with large series of all North American parulid species in the National Museum of Natural History, Smithsonian Institution. Measurements (after Baldwin et al. 1931) of the two putative hybrids and a series of male *V. pinus*, *O. formosus*, and *O. philadelphia* were taken with dial calipers and rounded to the nearest 0.1 mm (Table 1).

I used principal components analysis (PCA) on untransformed variables to reduce the dimensionality of data and to facilitate the visualization of morphology in two dimensions. Unrotated principal components were extracted from correlation matrices (SYSTAT).

*Results.*—Because of its close resemblance to both specimens, there is little doubt that *V. pinus* is one of the parental species of both hybrids. Ridgway (1880) and McCamey (1950)

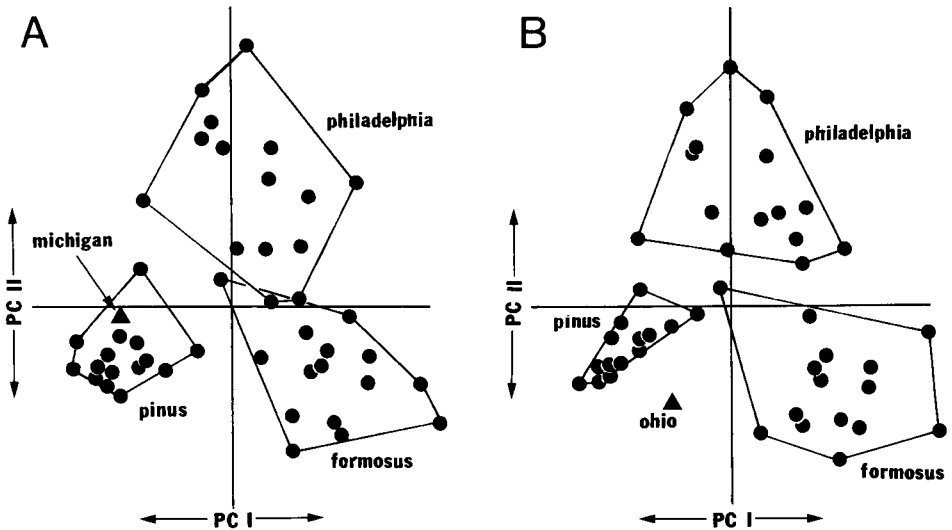


FIG. 2. Bivariate plots of factor scores from Principal Components Analysis. Separate analyses were performed for the Michigan (A) and Ohio (B) hybrids.

described the plumage intermediacy of the hybrids. Intermediacy in color or pattern, although strongly suggestive, is insufficient to prove parentage. Because the identity of *V. pinus* as one of the parents seems to be indisputable, I focussed attention on characters that are absent in *V. pinus* but shared by a hybrid and one or more species of *Oporornis*.

Unequivocal evidence of species-specific *Oporornis* parentage is found only in the crown and facial plumage of the hybrids (Fig. 1). Both hybrids have a yellow forecrown as in *V. pinus*, but differ from that species and from *O. philadelphia*, in having small black spots above each nostril (more prominent in the Michigan specimen) clearly separated from the loreal area by a yellow preocular stripe. Both hybrids have scattered black feathers, tipped with grayish olive, at the sides and rear of the hindcrown. Crown feathers of *O. philadelphia* are medium gray (base to tip) from nostrils to nape. The crown of *O. formosus* is black from the nostrils posterior to a point behind the eyes; feathers of hindcrown are tipped gray. Because crown feathers of *O. philadelphia* are uniformly gray, black spots above the nostrils and black crown feathers could only have been inherited from *O. formosus*. Other potential parental species (e.g., *Geothypis trichas*) lack black-based feathers on the hindcrown. Auricular feathers of the Ohio hybrid are black with dull yellow tips or lateral barbs. These form an obscured facial pattern nearly identical to that of *O. formosus* (the auriculars of *O. philadelphia* are uniformly gray). Under magnification, black barbs can be observed on the edges of a few auricular feathers on the Michigan bird. Again, *O. formosus* is indicated to be the *Oporornis* parent of both hybrids. Neither hybrid exhibits any trace of the extensively gray or black bib found in *O. philadelphia*. Both hybrids have yellow undertail coverts (tip of covert to tip of tail: "Ohio," 12 mm; "Michigan," 14 mm) similar in length to those of *O. formosus* (range, 12.5–22.5;  $\bar{x}$  = 15.5 mm) and *O. philadelphia* (range, 12.5–18.0;  $\bar{x}$  = 14.2 mm) but longer than in *V. pinus* (range, 15.5–21.7;  $\bar{x}$  = 18.1 mm).

The remaining plumage (e.g., wings, tail) could have been inherited from *V. pinus* or

TABLE 2  
FACTOR LOADINGS FOR THE FIRST TWO PRINCIPAL COMPONENTS FROM SEPARATE  
ANALYSES OF THE HYBRIDS

Variable	Ohio		Michigan	
	I	II	I	II
Wing chord	0.90	-0.33	0.87	-0.40
Wing tip	0.57	-0.78	0.54	-0.71
Central rectrices	0.76	0.58	0.80	0.48
Outer rectrices	0.86	0.18	0.86	0.07
Tarsus	0.87	0.18	0.88	0.14
Culmen	NA	NA	-0.20	-0.87
Variance explained				
Percent	63.8	22.4	53.9	28.0
Cumulative	63.8	86.2	53.9	81.9

either species of *Oporornis* and provide no additional information. Plumage pattern and color comparisons indicate that both specimens are *Vermivora pinus* × *Oporornis formosus* hybrids.

*Morphological analysis.*—Except for tarsus length, measurements of the hybrids were within, or narrowly outside, the range of values for *V. pinus* (Table 1). This morphological similarity is aptly demonstrated by the plot of PCA factor scores (Fig. 2, Table 2). The bill of the Ohio hybrid was broken at the tip, so separate principal component analyses were performed for each hybrid. Factor scores for both hybrids fall well outside the envelope of scores for *O. philadelphia*, corroborating the conclusion based on plumage. The Michigan hybrid falls within the envelope of scores for *V. pinus* whether or not "culmen length" is included in the analysis. The Ohio specimen, which is larger than the Michigan specimen in four of the five comparable measurements, occurs outside the *V. pinus* envelope, roughly between the centroids for *V. pinus* and *O. formosus*. This suggests a correlation between intermediacy in plumage and morphology and raises the speculation that the Ohio specimen is an F<sub>1</sub> hybrid, while the Michigan bird may represent the progeny of an F<sub>1</sub> hybrid backcrossed with a pure *V. pinus*.

*Discussion.*—The occurrence of a greater frequency of intergeneric than intrageneric hybrids has been cited as evidence supporting the hypothesis that reproductive isolating mechanisms are strongest among closely related species (Parkes 1978). Hybridization (i.e., the ability to interbreed) is thus viewed as a shared primitive character. An alternate view suggests that hybridizing parulids are closely related and are generically oversplit (e.g., Short and Robbins 1967). These hypotheses would appear to be mutually exclusive. The AOU checklist (1983), which attempted to approximate a primitive to derived sequence of genera within families, lists no fewer than nine parulid genera (*Parula*, *Dendroica*, *Catharopeza*, *Mniotilta*, *Setophaga*, *Protonotaria*, *Helmintheros*, *Limnothlypis*, *Seiurus*) in the sequence between *Vermivora* and *Oporornis* (see Parkes 1978, Avise et al. 1980). Clearly, a robust phylogeny of parulid genera must be determined to evaluate the evolutionary implications of *Vermivora* × *Oporornis* hybridization.

*Acknowledgments.*—I thank R. Davis and R. Kennedy (Cincinnati Museum of Natural History) and D. Niles (Delaware Museum of Natural History) for loaning the hybrid warblers.

R. Banks, J. Becker, P. Cannell, F. Gill, S. Lanyon, S. Olson, K. Parkes and J. Pitocchelli reviewed the manuscript.

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*Wilson Bull.*, 100(2), 1988, pp. 289–293

**Techniques for study of avian syrinxes.**—In most birds, the syrinx is located within the thoracic cavity, dorsal to the heart and ventral to the esophagus (in hummingbirds and some storks it is along the neck). The syrinx and trachea are bound to the esophagus by membrane; removal of these together, using the esophagus as a 'handle,' reduces risk of damage to the delicate bronchi and preserves membranous connections (e.g., the bronchidesmus). Removal of a syrinx from a museum specimen disrupts the heart arteries and the sternum and breast muscles along one side, but careful removal leaves a specimen largely intact and makes the syrinx available for future researchers. Dissection procedures described here follow Ames (1971:13) but are more detailed: