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A HYBRID *OPORORNIS PHILADELPHIA* × *GEOTHLYPIS TRICHAS*, WITH COMMENTS ON THE TAXONOMIC INTERPRETATION AND EVOLUTIONARY SIGNIFICANCE OF INTERGENERIC HYBRIDIZATION

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ABSTRACT.—A wood-warbler collected in 1955 near New Haven, Connecticut, originally identified as *Oporornis philadelphia*, proves to be a hybrid *O. philadelphia* × *Geothlypis trichas*. The hybrid indicates the existence of substantial genetic compatibility between the parental species. Two different classifications of *Oporornis* and *Geothlypis* are consistent with the genetic similarity implied by the hybrid, but in the absence of phylogenetic evidence, the provisional continued recognition of *Oporornis* and *Geothlypis* is suggested on phenetic and nomenclatural grounds. Although the number of intergeneric paruline hybrids (10) is greater than the number of intrageneric hybrids (4, other than between species-pairs), the inference that hybridization is more common between phylogenetically distant species than between closer relatives is not warranted because several of the genera involved in the hybridizations are probably paraphyletic. *Received 17 Dec. 1984, accepted 19 Jan. 1987.*

On 21 September 1955, the late David H. Parsons, formerly Chief Preparator at the Peabody Museum of Natural History, Yale University, collected an unusual wood-warbler in a scrubby clearing in deciduous woodland at West Rock, Hamden, Connecticut, 4 km NW of the New Haven Green, New Haven. The specimen was cataloged as a Mourning Warbler (*Oporornis philadelphia*) in the ornithological collection of the Peabody Museum (YPM 6958). David A. Sibley brought the specimen to my attention and suggested that it was not a Mourning Warbler but a hybrid between *Oporornis philadelphia* and the Common Yellowthroat

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Mourning Warbler *(Oporornis philadelphia,* top),
Common Yellowthroat *(Geothlypis trichas,* bottom),
and hybrid *O. philadelphia* X *G. trichas* (YPM 6958, middle).
All are males in first basic plumage. Watercolor and gouache by David A. Sibley.

(*Geothlypis trichas*). A detailed study of the specimen, presented here, confirms this diagnosis.

DESCRIPTIONS

I compared the specimen with series of fall adult male and first-year male specimens of *O. philadelphia* and *G. trichas* at the Peabody Museum of Natural History (Yale University), the American Museum of Natural History, and the University of Kansas Museum of Natural History. The specimen resembles a fall adult male Mourning Warbler, but its crown is brownish-olive instead of gray, its back brownish-olive instead of greenish, and its throat white instead of gray. The label indicates that the specimen is a male (testes not enlarged). The age of the specimen was not determined during its preparation, but it appears to be a first-year bird because remnants of natal down adhere to the tips of the rectrices. First-year males of *O. philadelphia* and *G. trichas* are variable, but differ from adults primarily in the colors of the head and breast. Typical first-year male *O. philadelphia* have a yellowish-white chin, limited black on the upper breast, no blackish neutral gray on the lores, a broken buffy orbital ring, and brownish-olive feathers on the crown and face. Some individuals lack black on the breast and have a yellow throat; others approach the fall adult male condition. First-year male *G. trichas* have traces of black in the malar and auricular regions, varying from a few feathers to a nearly complete "mask," but usually have little (if any) black on the forehead or gray on the head. The orbital ring is buffy to white.

The hybrid and the first-year male fall plumages of *O. philadelphia* and *G. trichas* are described below. The color terminology is that of Smithe (1975). Characters that do not differ among *O. philadelphia, G. trichas,* and the hybrid are omitted from the descriptions.

Forehead to nape.—philadelphia: olive-brown. *trichas:* forehead brownish-olive with a few (rarely many) jet black feathers with medium neutral gray tips, sometimes bordered caudally by a band of light neutral gray feathers (jet black basally) joining the superciliary line just above the eye. Top of head and hindneck brownish-olive concealing olive-gray midportions and dark neutral gray bases of feathers. *Hybrid:* brownish-olive (slightly grayer than in *trichas*) concealing medium neutral gray midportions and jet black bases of the forehead feathers and medium neutral gray midportions and bases of feathers of the rest of the crown and hindneck.

Back.—philadelphia: auxiliary olive-green (color 47). *trichas:* dark auxiliary olive-green (color 48). *Hybrid:* auxiliary olive-green (color 48) but slightly greener than in *trichas.*

Rump and upper tail coverts.—philadelphia: auxiliary olive-green (color 47) but slightly greener than back. *trichas:* auxiliary olive-green (color 48), browner than in *philadelphia* and not perceptibly greener than back. *Hybrid:* greenish-olive with a brown tinge, slightly greener than back.

Face pattern.—philadelphia: face olive-brown (most individuals) to medium neutral gray (rarely). *trichas:* face brownish-olive (most individuals) to jet black (rarely), the feathers usually tipped with light neutral gray; superciliary line brownish-olive (in birds with brownish-olive faces) to jet black rostral of eye with light neutral gray caudal of eye and bordering ear coverts (in birds with black faces). *Hybrid:* lores blackish neutral gray, cheek feathers and ear coverts dark neutral gray, and feathers of malar stripe jet black tipped with (and partly concealed by) medium neutral gray, giving the appearance of a faint "mask"; superciliary line medium neutral gray; feathers surrounding orbit blackish neutral gray basally, faintly tipped with medium neutral gray.

Chin and throat.—philadelphia: pale yellowish-white to pale spectrum yellow, bases of feathers blackish neutral gray. *trichas:* spectrum yellow concealing whitish (rarely blackish

neutral gray) bases of feathers. *Hybrid:* white with a few flecks of blackish neutral gray; feathers at edge of throat tipped with very pale spectrum yellow; bases of lower throat feathers blackish neutral gray.

Breast.—philadelphia: feathers jet black with medium neutral gray and olive-brown tips; extent of tipping variable, but black usually fully concealed on upper breast, less concealed on lower breast. *trichas:* spectrum yellow, usually tinged with orange-yellow, occasionally with brownish-olive as well; bases of feathers blackish neutral gray. *Hybrid:* upper edge of breast white with blackish neutral gray flecks and very pale spectrum yellow tips (more extensive than in chin and throat); lower breast feathers jet black and variously tipped with white, light neutral gray, and pale sulphur yellow partly concealing black; edges of lower breast citrine slightly tinged with orange-yellow.

Belly.—philadelphia: spectrum yellow. *trichas:* variable, from white with a faint brown tinge (most individuals) to pale sulphur yellow (rarely). *Hybrid:* spectrum yellow, slightly paler than in *philadelphia.*

Flanks.—philadelphia: yellowish olive-green, limited in extent and not approaching midline. *trichas:* grayish-olive with a brown tinge, closely approaching midline. *Hybrid:* auxiliary olive-green (color 48), extent as in *trichas.*

Undertail coverts.—philadelphia: spectrum yellow, centers of feathers occasionally auxiliary olive-green (color 47). *trichas:* variable, from yellowish olive-green to spectrum yellow; centers of feathers occasionally yellowish olive-green, edges spectrum yellow. *Hybrid:* light spectrum yellow, centers of feathers auxiliary olive-green (color 47).

Relative lengths of primaries.—philadelphia: primary 6 usually shorter than primaries 7, 8, and 9 (outermost) but longer than primary 5; occasionally primary 6 nearly or quite as long as the longest of the three outer primaries. *trichas:* primary 6 longer than primaries 9 and 5, occasionally longer than primaries 7 and 8. *Hybrid:* primaries, in order of decreasing length: 6, 7 = 8, 9, 5.

Tail shape.—Philadelphia: slightly rounded, rectrices more or less evenly graduated in 1.0–1.5 mm increments but rectrices 3 and 2 nearly (or quite) equal. *trichas:* rounded, rectrix 6 (outermost) ca 3 mm shorter than rectrix 5, rectrices 5, 4, and 3 more or less evenly graduated in 0.5–1.0 mm increments, rectrix 2 usually less than 0.5 mm shorter than rectrix 1. *Hybrid:* distances between tips of rectrices are 2.2 mm (rectrices 6 and 5), 1.4 mm (5 and 4), 1.2 mm (4 and 3), 0.5 mm (3 and 2), and 0.2 mm (2 and 1).

MEASUREMENTS

The linear dimensions of the hybrid (in mm, measured with dividers and a dial caliper) are: flattened wing = 60.5, tail = 50.8, bill from rostral edge of nares to tip = 8.0, tarsus = 20.7. The linear dimensions (mm) of 15 specimens each of the parental species are (range, with mean in parentheses): *philadelphia.*—wing, 62.0–67.9 (64.0); tail, 49.0–56.5 (52.6); bill, 7.0–8.3 (7.8); tarsus, 19.3–22.2 (20.5); *trichas.*—wing, 53.5–60.0 (56.7); tail, 48.5–54.5 (51.5); bill, 7.4–8.2 (7.8); tarsus, 18.5–20.9 (19.6). Except for wing length, the linear dimensions of the parental species overlap, and the hybrid's dimensions fall in the range of overlap. The wing length of the hybrid lies outside of, but between the ranges of, wing lengths of the parental species. The difference between the lengths of the wing and tail of the hybrid is 9.7 mm, falling outside of, but between the ranges of, wing-minus-tail values of *O. philadelphia* (Lanyon and Bull 1967) and of the 15 specimens of *G. trichas brachidactylus* measured in this study. The wing and tail measurements of *G. trichas campicola* (the other subspecies of Common Yellowthroat broadly sympatric with *O. philadelphia*) collected east of the Rocky Mountains are similar to those of *G. trichas brachidactylus* (Behle and Aldrich 1947).

DIAGNOSIS

The color pattern and the shapes of the bill, wing, and tail of the hybrid rule out as possible parental species all wood-warblers except *G. trichas* and the species of *Oporornis*. The colors of the head and breast rule out the Kentucky Warbler (*O. formosus*), and the black breast feathers argue against Connecticut Warbler (*O. agilis*) parentage. The pattern of black on the breast feathers argues against MacGillivray's Warbler (*O. tolmiei*) parentage, as does to some degree the locality of collection.

The hybrid specimen is intermediate between *O. philadelphia* and *G. trichas* in the colors of the crown, back, and flanks, the patterns of the face and breast, the shape of the tail, and the wing-minus-tail value. A few parental characters (e.g., wing length and shape of *trichas*, continuous yellow on the belly of *philadelphia*) have been inherited nearly intact. The white chin and throat of the hybrid are abnormal for first-year males of either species; however, the parental throat colors are partially expressed, as the black flecks, occasional pale yellow tips, and blackish bases of the throat feathers of the hybrid indicate.

THE TAXONOMIC HISTORY OF *OPORORNIS* AND *GEOTHLYPIS*

In 1858, Baird classified the Mourning and MacGillivray's warblers with the yellowthroats in *Geothlypis*. Baird (1858) nonetheless recognized the differences between the *philadelphia-tolmiei* and yellowthroat groups, which he divided into separate sections of *Geothlypis*. In the same volume Baird erected *Oporornis* for the Connecticut Warbler and the Kentucky Warbler.

Ridgway (1887) acknowledged the similarities between *philadelphia, tolmiei,* and *agilis* by placing them in *Oporornis* but at the same time reflected their similarities to the yellowthroats in maintaining *Oporornis* as a subgenus of *Geothlypis*. In 1902, Ridgway gave *Oporornis* full generic status, and since the third edition, the American Ornithologists' Union's "Check-list of North American Birds" (1910, 1931, 1957, 1983) has employed Ridgway's arrangement (1902).

It is not clear whether Ridgway considered *Oporornis* and *Geothlypis* to be closely related (he placed four quite different genera between them), but other workers (Coues 1903, Griscom and Sprunt 1957, Mayr and Short 1970) clearly have. Lowery and Monroe (1968) merged *Oporornis* and *Geothlypis*.

The classifications of these workers were derived primarily from comparison of such phenotypic characters as the proportions of the wing, leg, tail, and undertail coverts (e.g., Baird 1858, Ridgway 1902:621, Griscom in Griscom and Sprunt 1957) and song patterns (e.g., Griscom in Griscom and Sprunt 1957). Such general similarities are shared among members of several paruline genera yet are variable within any particular genus, so that the variety of treatments of *Oporornis* and *Geothlypis* is not surprising. Macromolecular and cladistic morphological data have not been informative, largely because they either pertain to the higher relationships

of the parulines (e.g., Bledsoe 1987) or are limited in extent (e.g., Raikow 1978, Avise et al. 1980). With respect to the latter studies, Raikow (1978) reported that *O. tolmiei* shares a derived condition of the M. pronator profundus with many paruline genera but not with *Geothlypis,* while Avise et al. (1980), using protein electrophoretic data, found that *O. formosus* and *G. trichas* (the only species of these genera studied) cluster tightly with one another.

DISCUSSION

The production of a hybrid between *O. philadelphia* and *G. trichas* provides strong evidence of substantial genetic compatibility between the parental species. The existence of genetic compatibility between these species and between the parental species of other paruline hybrids reviewed below indicates that parulines retain the ability to produce hybrids long after genetic isolation. These hybrids offer additional evidence that such compatibility is a general phenomenon among birds, as Prager and Wilson (1975) have suggested.

Recent classifications of *O. philadelphia* and *G. trichas* are consistent with the genetic similarity implied by the hybrid between them, either in merging *Oporornis* and *Geothlypis* (e.g., Lowery and Monroe 1968) or in listing them next to one another in linear sequence (e.g., Wolters 1982, A.O.U. 1983). Neither the evidence of hybridization nor other lines of evidence, however, resolves the phylogenetic relationships among these and other wood-warblers.

In the absence of phylogenetic information, the choice between classifications is left to rely on such provisional criteria as phenetic similarity and nomenclatural stability. In that *Oporornis* and *Geothlypis* (sensu A.O.U. 1983) are distinct from one another in their overall proportions and color patterns, and because maintenance of each genus conserves the scientific names now commonly in use, I suggest continued recognition of *Oporornis* and *Geothlypis* (sensu A.O.U. 1983).

The hybrid *O. philadelphia* × *G. trichas* is the tenth known intergeneric hybrid among wood-warblers. The others are: *Vermivora pinus* × *O. formosus* (two specimens, see Graves, in press), *Parula americana* × *Setophaga ruticilla* (Burleigh 1944), *P. americana* × *Dendroica dominica* (two specimens, see Sutton 1942), *D. fusca* × *Mniotilta varia* (Parkes 1983), *D. striata* (or possibly *D. tigrina,* Parkes 1978) × *Seiurus noveboracensis* (Short and Robbins 1967), *D. cerulea* × *M. varia* (Parkes 1978), and *Wilsonia canadensis* × *O. philadelphia* (United States National Museum, K. C. Parkes, pers. comm.). In addition, 4 intrageneric hybrid specimens (other than between primarily allopatrically distributed members of superspecies) are known: *V. ruficapilla* × *V. peregrina* (Carnegie

Museum of Natural History), *D. coronata coronata* × *D. castanea* (Banks and Baird 1978), *D. coronata auduboni* × *D. graciae* (Denver Museum of Natural History, K. C. Parkes, pers. comm.), and *D. coronata coronata* × *D. pinus* (Hubbard 1977).

Parkes (1961, 1978) interpreted the relative numbers of inter- and intrageneric paruline hybrids to mean that hybridization between distantly related species is more common than between closely related species (other than members of superspecies). Banks and Johnson (1961) reached a similar conclusion for hummingbirds. These inferences rely on the assumption that all of the members of each genus involved share a more recent common ancestor with one another than with species in other genera; that is, the genera must be monophyletic (=holophyletic of Ashlock 1971).

Unfortunately, most avian systematists have constructed genera with an "evolutionary" approach (cf. Mayr 1981) based on perceived adaptive distinctiveness as well as on phylogenetic relationship. As a result, paraphyletic genera are likely to be common in current avian classifications. For instance, avian systematists have perceived the Black-and-white Warbler (*Mniotilta varia*) as adaptively distinctive and have thus placed it in a monotypic genus. However, its plumages, anatomy, and songs suggest that its sister group might lie *among* the living species of *Dendroica.* Few would suggest that it is the sister group of all living *Dendroica.* Unless it is, the possibility exists for the parental species of a *Mniotilta* × *Dendroica* hybrid to be closer phylogenetically than the parental species of a *Dendroica* × *Dendroica* hybrid. A similar situation probably exists among the warblers of the genera *Parula* and *Vermivora.*

We do not know for sure that *Dendroica* and *Vermivora* are paraphyletic, but neither do we know that these genera are monophyletic, as the interpretation of Parkes (1961, 1978) requires. Regardless, it simply is not possible at the present to derive empirically a relationship between frequency of hybridization and phylogenetic relationship because a well-corroborated phylogeny of the wood-warblers is not available.

The confusion of "evolutionary" genera with monophyletic groups provides one example of the problems associated with eclectic or "evolutionary" classifications. It is commonly assumed that the categories of such classifications convey phylogenetic information. Just how much they convey is always uncertain, however, because the phylogenetic information in eclectic classifications is necessarily implicit rather than explicit (Hull 1970). The implicit nature of such information is not a problem per se, as long as users of eclectic classifications recognize the phylogenetic limitations of such arrangements. However, because most workers look to a classification precisely for phylogenetic information, it seems more

sensible to make such information explicit through methods of phylogenetic classification (Hennig 1966, Wiley 1981) than to construct groups of ambiguous meaning.

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COLOR PLATE

The Frontispiece painting by David A. Sibley has been made possible by an endowment established by George Miksch Sutton.