18 December 1992
PROC. BIOL. SOC. WASH.
105(4), 1992, pp. 834–840

DIAGNOSIS OF A HYBRID ANTBIRD (*PHLEGOPSIS NIGROMACULATA* × *PHLEGOPSIS ERYTHROPTERA*) AND THE RARITY OF HYBRIDIZATION AMONG SUBOSCINES

Gary R. Graves

Abstract.—*Phlegopsis barringeri* Meyer de Schauensee, 1951, is suggested to be a hybrid between *Phlegopsis nigromaculata* and *P. erythroptera.* This represents the first case of hybridity in the large monophyletic assemblage of New World suboscines comprising the woodcreepers, antbirds, ovenbirds, and tapaculos (parvorders Thamnophilida and Furnariida). The rarity of hybridization among suboscines (Suborder Tyranni) may result from the absence of song learning in this assemblage, resulting in vocal stereotypy within populations and the reduction of mate recognition error by females.

Hybridization in birds occurs most frequently in sexually dimorphic species with polygynous breeding systems (Sibley 1957). More than half of all known cases of hybridization in nature occur in four avian families or tribes: Anatidae (ducks, geese, and swans), Phasianidae (grouse and pheasants), Trochilidae (hummingbirds), and Paradisaeini (birds of paradise) (Gray 1958) (taxonomy of Sibley & Monroe 1990). The apparent absence or low frequency of hybridization in other lineages may reflect reality or the failure of biologists to detect it (Graves 1990). Only a few cases of hybridization have been detected among New World suboscines (e.g., Parkes 1961, Short & Burleigh 1965, Tyler & Parkes 1992), which constitute a quarter ($n = 1097$) of all Western Hemisphere species.

Meyer de Schauensee (1951) described a relatively large and spectacular species of antbird, the Argus Bare-eye (*Phlegopsis barringeri*), from a unique specimen collected on the Río Rumiyaco, Department of Nariño, Colombia. Determining whether a unique specimen represents a valid species, a hybrid, or a genetic variant of a previously described species can be a Herculean task. However, because hybrids have no standing in zoological nomenclature, the burden of proof rests upon a taxonomist to reject hybridity before conferring species status (Graves 1990). Meyer de Schauensee compared the specimen of *P. barringeri* with three morphologically similar taxa but failed to address hybridity. That possibility was raised by Willis (1979), who suggested parenthetically that *P. barringeri* was a hybrid between the Black-spotted Bare-eye (*P. nigromaculata*) and Red-winged Bare-eye (*P. erythroptera*), which overlap broadly in western Amazonia from eastern Colombia (Hilty & Brown 1986) south to northern Bolivia (Parker & Remsen 1987).

My analysis of *P. barringeri* confirmed Willis' hunch. The proposed hybrid origin of the specimen (*P. nigromaculata* × *P. erythroptera*) cannot be rejected. Here I present a diagnosis of the hybrid antbird, the first known example of hybridity in the parvorders Thamnophilida and Furnariida (Sibley & Monroe 1990), a monophyletic assemblage representing 131 genera and 560 species of woodcreepers, antbirds, ovenbirds, and tapaculos. I then briefly discuss a correlate of hybridization frequency in suboscines (Suborder Tyranni), the absence of song learning.

Materials and Methods

I compared the holotype of *Phlegopsis barringeri* (adult male, Academy of Natural Sciences Philadelphia (ANSP), No. 162,675) directly with specimens of *P. nigromaculata* and *P. erythroptera* from Ecuador under natural light. A complete description of *P. barringeri,* which will not be repeated here, can be found in Meyer de Schauensee (1951). Series of *Phlegopsis* and nearly all other species of antbirds were examined at the following institutions: American Museum of Natural History; Carnegie Museum of Natural History; Museu Paraense "Emilio Goeldi," Belem; Museum of Natural Science, Louisiana State University (LSUMNS); Museu de Zoologia, Universidade de São Paulo; and the National Museum of Natural History, Smithsonian Institution. Measurements of wing chord, tail length from point of insertion of central rectrices to tip of longest rectrix, tarsus length, hallux (plus claw) length, bill length from anterior edge of nostril, and bill width at anterior edge of nostril were made with digital calipers to the nearest 0.1 mm.

In order to visualize morphological variation in two dimensions, I used principal components analysis of log transformed data. Unrotated principal components were extracted from covariance matrices (Wilkinson 1989). P-values of <0.05 were regarded as significant for two-sample t-tests.

Diagnostic assumptions and methods of hybrid diagnosis based on plumage characters and morphology follow Graves (1990). For brevity, I refer to *Phlegopsis barringeri* as a "hybrid" throughout the text.

Results

Potential parental species.—Because the hybrid strongly resembles species of *Phlegopsis* in plumage pattern and color (Fig. 1) and because its collection locality is known, determination of the potential parental species seems straightforward: species of *Phlegopsis,* and related genera, *Myrmoborus, Hypocnemis, Myrmochanes, Sclateria, Percnostola, Myrmeciza, Pithys, Gymnopithys, Myrmornis, Rhegmatorhina,* and *Hylophylax,* that occur in Amazonian forest of Colombia and Ecuador.

Soft part colors.—The hybrid had bare reddish orbital skin (now faded), an apomorphic character of *Phlegopsis* among the Thamnophilida. The size of the orbital patch in the hybrid is intermediate between that of *P. nigromaculata* (larger) and *P. erythroptera* (smaller). This character alone suggests that the two species of *Phlegopsis* were the hybrid's parents. Other "bare-eyed" antbirds have smaller patches of bluish-gray or bluish-white orbital skin in life, which fades to gray in specimens. Hybrids between a species of *Phlegopsis* and a species from another genus would probably, although not certainly, have a small orbital patch with traces of melanization (gray in dried skin).

Plumage characters.—Because the hybrid was male, the plumage diagnosis focused on aspects of male plumage. Meyer de Schauensee (1951:3) noted "this new species combines in some ways characters found in both *P. nigro-maculata* and *P. erythroptera,* and has others not found in either." A careful examination of the hybrid confirms his observation (Fig. 1). No combination of potential parental species, except *Phlegopsis nigromaculata* and *P. erythroptera,* could have produced the distinctive characters of the hybrid: (1) unmarked glossy black head, throat, and breast; (2) brown mantle with contrasting spots; and (3) black and rufous-cinnamon remiges, rectrices, and upper- and undertail coverts. Significantly, the hybrid lacks any trace of pale markings on the head, throat, and breast, or an interscapular patch (found in one or more species of *Myrmoborus, Hypocnemis, Myrmochanes, Myrmeciza, Myrmornis,* and *Hylophylax*). Most elements of the hybrid's plumage pattern and color are easily identified as intermediate character states or mosaics of characters of *Phlegopsis nigromaculata* and *P. erythroptera.* However, the buff and rufous

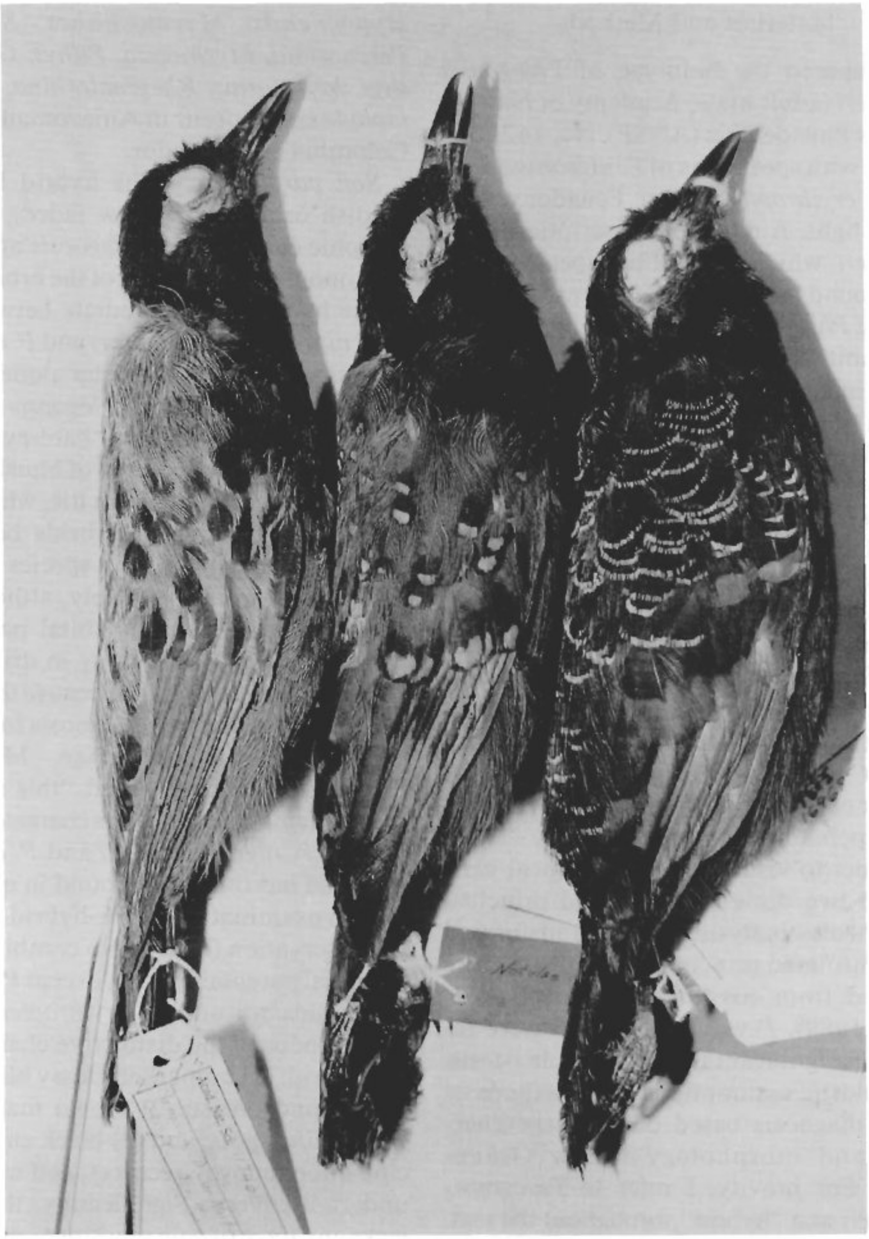

Fig. 1. Lateral views of adult males (from left to right): *Phlegopsis nigromaculata*, "*P. barringeri*" (ANSP 162,675; =*P. nigromaculata* × *P. erythroptera*), and *P. erythroptera*. Note ocelli on wing coverts and back of hybrid.

ocelli encircled by drop-shaped black spots on the feather tips of the mantle and wing coverts of the hybrid are not found in either parental species. By comparison, back feathers in *P. nigromaculata* are olivaceous-brown with a terminal black spot (rounded triangle). The color pattern in *P. erythroptera* is markedly different—back feathers are entirely black with a narrow white subterminal band (back feathers of juvenile males

Table 1.—Ranges and means of measurements (mm) of adult male *Phlegopsis nigromaculata, P. erythroptera,* and their hybrid (="*P. barringeri*"). *Phlegopsis* specimens are from Ecuador and north of the Río Amazonas in Peru. Significant *P*-values indicate that means of *Phlegopsis* species are different (two-tailed *t*-test).

	P-value	*Phlegopsis nigromaculata* ($n = 15$)	*Phlegopsis erythroptera* ($n = 8$)	*P. nigromaculata* × *P. erythroptera* (ANSP 162,675)
Wing	NS	87.1–94.0	88.6–93.6	
		90.9	91.4	93.7
Tail	<0.001	58.5–64.5	59.6–68.0	
		61.6	65.2	61.9
Tarsus	<0.001	29.2–32.4	30.1–33.3	
		30.6	32.2	31.2
Hallux	<0.01	18.5–20.9	19.7–21.3	
		19.8	20.6	20.4
Bill length	<0.05	12.0–14.6	11.9–13.7	
		13.2	12.6	12.8
Bill width	<0.01	4.6–5.7	4.5–5.0	
		5.2	4.8	5.2

have broad rufous edges, e.g., LSUMNS 110,210). Pattern elements in the hybrid may be interpreted by identifying probable homologues in the parental species. For example, the black spots of the hybrid and *P. nigromaculata* are probably homologous, while the buffy ocelli of the hybrid are homologous with the subterminal white bands in *P. erythroptera*. This suggests that during feather development in the hybrid, the subterminal band inherited from *P. erythroptera* invaginated to form an ocellus within the black spot. Less complete ocellations are found on the tertials and secondaries of the hybrid, where the terminal black spot failed to enclose the irregularly shaped ocellus.

This example offers rare insight into the complexity of genetic control of plumage patterns in antbirds. Because different pigments are believed to be encoded by different genes, even within the same feather tract (Buckley 1982), a minimum of five genes or gene complexes and their modifers appear to control the color pattern of back feathers in *Phlegopsis,* including those for: (1) ground color (expressed in both parental species and hybrid); (2) presence or absence of terminal spot (expressed in *P. nigromaculata* and hybrid); (3) color of terminal spot (expressed in *P. nigromaculata* and hybrid); (4) presence or absence of subterminal band or ocellus (expressed in *P. erythroptera* and hybrid); and (5) color of subterminal band or ocellus (expressed in *P. erythroptera* and hybrid). Serial patterns among feather tracts suggest that some genes affect several plumage tracts, for example, the terminal (or subterminal) black spots on the back, wings, and tail of *Phlegopsis nigromaculata.*

External morphology.—Variation of morphological characters of avian hybrids falls within the ranges exhibited by their parental species (Buckley 1982, Graves 1990), reflecting a polygenic mode of inheritance. As expected, the size of the hybrid antbird conformed to this pattern (Table 1). *Phlegopsis nigromaculata* and *P. erythroptera* are morphologically similar and the percent difference between their character means is small: wing (0.6%); tail (5.8%); tarsus (5.2%); hallux (4.0%); bill length (4.8%); and bill width (8.3%). Measurements of the hybrid fall at or between the means for five of the six characters measured on parental species. Meyer de Schauensee's (1951:3) observation that the hybrid had larger feet than other *Phlegopsis* is erroneous.

Most potential parental species are considerably smaller in all morphological di-

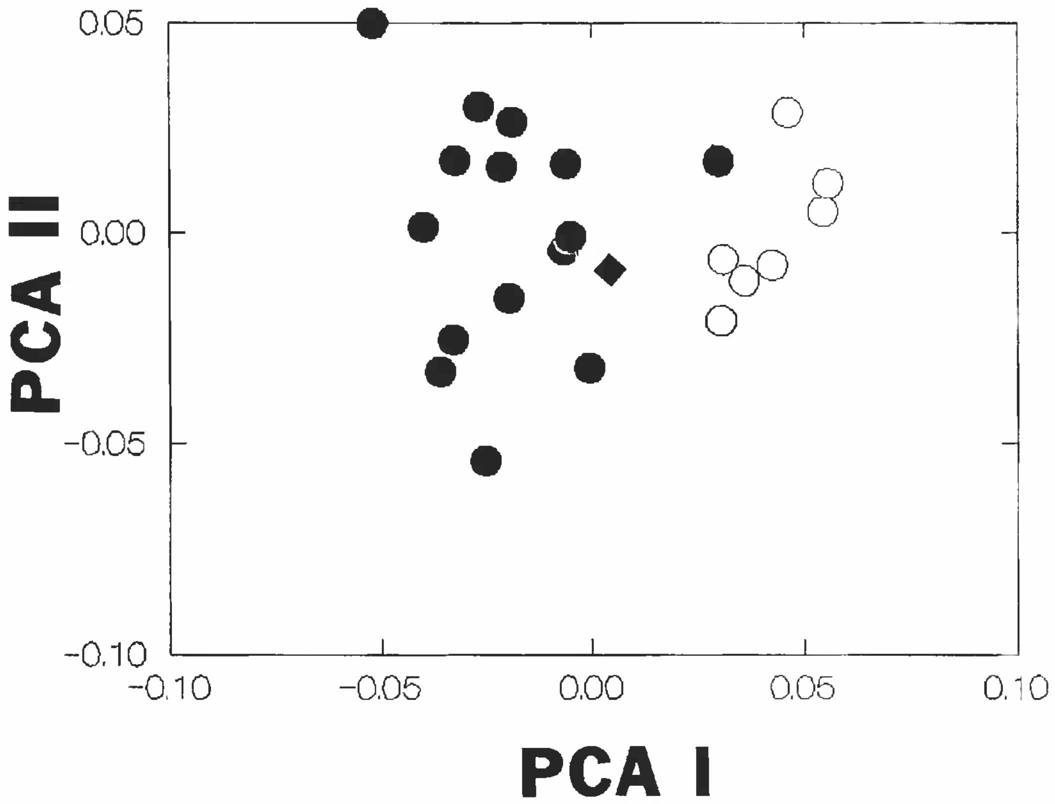

Fig. 2. Bivariate plot of principal component factor scores of *Phlegopsis nigromaculata* (=filled circles), *P. erythroptera* (=hollow circles), and their hybrid (=◇), "*P. barringeri.*"

mensions than the hybrid, including all taxa of *Myrmoborus, Hypocnemis, Myrmochanes, Sclateria, Percnostola, Pithys, Gymnopithys,* and *Rhegmatorhina. Myrmeciza fortis, M. melanoceps, M. hyperythra,* and *Myrmornis torquata* approach the size of *Phlegopsis,* but can be eliminated as parents of the hybrid on the basis of plumage characters. Morphological relationships of *Phlegopsis* species and the hybrid are shown by first two axes of a principal components analysis (Fig. 2, Table 2). Factor scores for the hybrid are nearly centered between the clusters of scores for the parental species. Intermediacy in complex shape variables, controlled by a multitude of genetic loci, constitutes strong evidence for the hybridization hypothesis. Had the factor scores of the hybrid fallen outside the envelope of scores of the proposed parental species, this particular hybrid hypothesis could have been rejected. From a statistical standpoint, the likelihood that a third valid species of *Phlegopsis* would be intermediate in size and shape between two other remarkably similar, sympatric species seems remote.

In summary, both plumage and morphological data are consistent with the hypothesis that *Phlegopsis barringeri* Meyer de Schauensee represents a hybrid between *Phlegopsis nigromaculata* and *P. erythroptera.* The name *Phlegopsis barringeri* is thus available only for the purpose of homonymy in taxonomy.

Discussion

Rarity of hybridization among the suboscines appears to be a real phenomenon rather than an artifact of taxonomic practices.

Table 2.—Factor loadings for the first two principal components from analysis of *Phlegopsis nigromaculata, P. erythroptera,* and their hybrid, "*P. barringeri*" (ANSP 162,675) (see Fig. 2).

Variable	Principal component axes	
	I	II
Wing	0.001	0.006
Tail	0.013	0.006
Tarsus	0.012	0.008
Hallux	0.011	0.001
Bill length	−0.010	0.021
Bill width	−0.024	−0.001
Variance explained		
Percent	48.1	25.2

This position is supported not only by the cumulative record of avian hybridization (Gray 1958), but by several monographic works where extensive museum series of suboscine specimens were carefully studied (e.g., Wetmore 1972).

The causes of this phylogenetic correlation are unknown. However, I speculate that the absence of vocal learning among suboscines (Nottebohm 1972, Kroodsma 1988) may be a factor. These species develop basic patterns of vocalizations without auditory feedback and do not imitate songs or phrases of other species. Furthermore, geographic variation in song is reduced or absent (e.g., Lanyon 1978, Payne & Budde 1979), resulting in stereotypy of vocalizations within regional populations of a species. As a consequence, females may be less likely to make species recognition errors during mate selection. The prevalence of dull, weakly patterned, or sexually monomorphic plumages among the suboscines, especially the Thamnophilida and Furnariida, suggests that vocalizations are the primary isolating mechanism between species in this assemblage.

Acknowledgments

I thank R. C. Banks, M. Isler, K. C. Parkes, K. V. Rosenberg, and M. B. Robbins for comments on the manuscript, and Robbins and F. B. Gill for permission to examine the hybrid antbird. Museum work was supported by grants from the Frank M. Chapman Fund of the American Museum of Natural History, and the Research Opportunities Fund and Neotropical Lowland Research Program, Smithsonian Institution.

Literature Cited

Buckley, P. A. 1982. Avian genetics. Pp. 21–110 *in* M. Petrak, ed., Diseases of cage and aviary birds. 2nd ed. Lea and Febiger, Philadelphia, 680 pp.

Graves, G. R. 1990. Systematics of the "green-throated sunangels" (Aves: Trochilidae): valid taxa or hybrids?—Proceedings of the Biological Society of Washington 103:6–25.

Gray, A. P. 1958. Bird hybrids. Commonwealth Agricultural Bureaux, Bucks, England, 390 pp.

Hilty, S. L., & W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, 836 pp.

Kroodsma, D. E. 1988. Contrasting styles of song development and their consequences among passerine birds. Pp. 157–184 *in* R. C. Bolles & M. D. Beecher, eds., Evolution and learning. Lawrence Erlbaum, Hillsdale, New Jersey.

Lanyon, W. E. 1978. Revision of the *Myiarchus* flycatchers of South America.—Bulletin of the American Museum of Natural History 161:429–627.

Meyer de Schauensee, R. 1951. Colombian zoological survey. Part IX. A new species of ant-bird (*Phlegopsis*) from Colombia.—Notulae Naturae 241:1–3.

Nottebohm, F. 1972. The origin of vocal learning.—American Naturalist 106:116–140.

Parker, T. A., & J. V. Remsen, Jr. 1987. Fifty-two Amazonian bird species new to Bolivia.—Bulletin of the British Ornithological Club 107:94–107.

Parkes, K. C. 1961. Intergeneric hybrids in the family Pipridae.—Condor 63:345–350.

Payne, R. B., & P. Budde. 1979. Song differences and map distances in a population of Acadian flycatchers.—Wilson Bulletin 91:29–41.

Short, L. L., Jr., & T. D. Burleigh. 1965. An intergeneric hybrid flycatcher (*Contopus* × *Empidonax*) from Idaho.—Proceedings of the Biological Society of Washington 78:33–37.

Sibley, C. G. 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds.—Condor 59:166–191.

———, & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.

Tyler, J. D., & K. C. Parkes. 1992. A hybrid Scissor-tailed Flycatcher × Western Kingbird specimen from southwestern Oklahoma.—Wilson Bulletin 104:178–181.

Wetmore, A. 1972. The birds of the republic of Panama. Pt. 3. Smithsonian Miscellaneous Collections 150 (3).

Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinios.

Willis, E. O. 1979. Comportamento e ecologia da Mae-de-Taoca, *Phlegopsis nigromaculata* (D'Orbigny & Lafresnaye) (Aves, Formicariidae).—Revista Brasilia Biologica 39:117–159.

Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.