

THE CONDOR

VOLUME 63

SEPTEMBER-OCTOBER, 1961

NUMBER 5

INTERGENERIC HYBRIDS IN THE FAMILY PIPRIDAE

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The Neotropical manakins of the family Pipridae include a number of strikingly sexually dimorphic species whose males gather at communal displaying areas, to which females come and at which copulation takes place without the formation of a lasting pair bond. Such a pattern of reproductive behavior is found in certain families of birds, notably the grouse and birds of paradise, in which hybridization is especially common. Sibley (1957) gave some attention to the family Pipridae in his paper on sexual dimorphism and hybridization, although he knew of only a single supposed hybrid in this family. The present paper will review briefly the manakins previously identified as probable hybrids and will offer evidence of intergeneric hybrid origin of additional unique manakin specimens.

The only hybrid manakin mentioned by Sibley was "*Chiromachaeris coronata*" Boucard, 1879. Hellmayr (1929:75), who had examined the unique type, had "little doubt that this supposed species is nothing but a hybrid between *Manacus manacus* (subsp.) and one of the yellow-headed varieties of *Pipra erythrocephala*." Comparison of males of the hypothesized parent species with Boucard's plate and Hellmayr's description suggests that "*Chiromachaeris coronata*" may well be such a hybrid, although the identification of the *Pipra* parent is perhaps less certain than that of the *Manacus manacus* parent. Sibley (1957:178) made the following statement concerning this hybrid: "It is of interest that the males in these two species, although differing in many plumage characters, both have areas of orange-yellow on the head. It is tempting to speculate that such similar characters may have been the basis for the 'mistake' in identification by the female which led to this instance of hybridization." But *Manacus manacus* has no "area of orange-yellow on the head," and Dr. Sibley has written me that this statement was based on his erroneous impression that *M. vitellinus*, a yellow species, was conspecific with *M. manacus*. The two species are sympatric in northern Colombia.

Another record of a supposed intergeneric hybrid in the Pipridae was called to my attention by Mr. Thomas E. Lovejoy III, of Yale University. Gyldenstolpe (1951: 241-242) published a description and photograph of a specimen from Redempçao, Rio Purús, Brazil, which he identified tentatively as *Teleonema f. filicauda* x *Manacus manacus* subsp. Although, as Gyldenstolpe points out, no species of *Manacus* is presently known from the Purús basin, *M. manacus* is common on other tributaries of the Amazon and may yet be found on the Purús. Except for this apparent absence of one of the supposed parent species at the collecting locality, Gyldenstolpe presents a convincing case for the hybrid origin of his specimen. In fact, the shape of the rectrices of Gyldenstolpe's bird recalls, as he mentions, the lost unique type of "*Pipra heterocerca*" Sclater, 1860. The description of the latter specimen suggests to me that it may well have been a hybrid between *Teleonema filicauda* and a race of *Pipra aureola* or *P. fasciicauda*; either of the latter could have supplied certain of the color characters present in the hybrid and not in *Teleonema filicauda*. The genera *Pipra* and *Teleonema* appear to be closely related, the latter being characterized only by the peculiar filiform structure of the rectrices of both sexes.

Another "species" of manakin known only from a unique type is *Muscicapa luteoce-*

phala Lesson, which Hellmayr (1906:326) assigned to the genus *Heterocercus*. Although Hellmayr states that this specimen, of unknown geographic origin, is structurally typical of *Heterocercus*, his description of its color together with its uniqueness suggest that this specimen should be re-examined with the possibility of hybrid origin in mind.

Todd (1925:97) described as *Pipra anomala*, sp. nov., a single specimen collected at Santarem, Amazon River, Brazil, on May 1, 1919, by Samuel M. Klages. Todd called attention to the fact that certain of the bird's characters, notably the pattern of the sides of the head and the shortness of the outermost rectrices, were without counterpart elsewhere in the genus *Pipra*. Hellmayr (1929:15-16) mentioned also the large size and especially large bill (for a *Pipra*) of *anomala*. He suggested that "the type may not be quite mature," although Todd had said that it "at first sight looks as if it were a young bird, but upon closer examination seems to be fully adult." These conjectures about age were apparently based on the peculiar mixture of green and black on the bird's back, although this is not attributable to molt; the individual feathers are part green, part black. Hellmayr (1929) and Meise (1938:154) accepted *Pipra anomala* Todd as a valid species.

While going over the manakins in the Carnegie Museum recently in another connection, I had occasion to re-examine the still unique type of *Pipra anomala*. Certain of its characters reminded me of a species currently placed far from *Pipra*, and further study has convinced me that "*Pipra anomala*" Todd is actually a hybrid between *Pipra aureola aurantiicollis* and *Heterocercus linteatus*, both of which are found at Santarem. I am happy to say that Mr. Todd fully agrees with this identification, the evidence for which follows.

The genus *Heterocercus*, as conceived by Hellmayr (1929), contained four "species." One is the problematical *H. luteocephalus* (Lesson), mentioned previously. Best known is *H. linteatus* (Strickland), widely distributed in Brazil south of the Amazon. *Heterocercus flavivertex* is found north of the Amazon, in Brazil, southern Venezuela and eastern Colombia. Another form, *H. aurantiivertex*, may prove to be a western race of *flavivertex*; it is known only from one young and three adult males from Ecuador and a tentatively identified young male from Perú (Hellmayr, 1929:91; de Schauensee, 1953:35). Members of this genus are rather large for manakins, and they are characterized particularly by having strongly graduated tails, with the outermost rectrices much shortened and narrowed. The seventh primary is longest, with the eighth and sixth equal. In *Pipra* the tail is short and square, and the eighth and seventh primaries are equal. Rictal bristles are poorly developed in *Heterocercus* (not absent as indicated by Hellmayr, 1910:3, in key), and they are fairly well developed in *Pipra*.

TABLE 1

MEASUREMENTS, TO NEAREST 0.5 MILLIMETER, OF ADULT MALE MANAKINS

Species	No.	Wing (flat)	Tail	Bill ¹
<i>Pipra aureola aurantiicollis</i>	10	60.5-64.5 (63.0)	25-29 (27.85)	6.5-7.5 (7.15)
" <i>Pipra anomala</i> " (type)		74	39	8
<i>Heterocercus linteatus</i>	10	87-91 (88.75)	50.5-54.5 (52.15)	8-9.5 (8.8)

¹Measurements of bill are from anterior edge of nostril.

In these structural characters, the type specimen of "*Pipra anomala*" falls between *Pipra* and *Heterocercus*. As mentioned by Todd, the outermost rectrices of his specimen are decidedly shorter than the rest and are also narrowed; the rest of the tail is square,

like that of a *Pipra* but longer. The bill is intermediate in size and shape between those of *Pipra aureola* and *Heterocercus linteatus*. Rictal bristles are of about the same length as those of the *Pipra*, but are more slender. The seventh primary is longest, as in *Heterocercus*, but it is barely longer than the eighth, which exceeds the sixth as it does in *Pipra*.

Males of *Heterocercus linteatus* have a silky white throatpatch, with elongated erectile feathers at the corners, which are used in a frontal display (illustrated by Sick, 1959:274). In the type of "anomala," the throat is pale orange, but the corner feathers can be seen to be slightly elongated.

In color, "*Pipra anomala*" appears almost completely intermediate, as shown on the color plate (see frontispiece). In *H. linteatus* there is a relatively small orange crownpatch. In *P. aureola* the entire crown and anterior mantle are composed of feathers fading from brilliant scarlet at the tip through yellow to white at the base. In "anomala" the crown and nape (but not the mantle) are of an orange approximating that of the crownpatch of *linteatus*, but with the feathers fading to white at the base as in *aureola*. The back, wings and tail are a mixture of the olive green of *linteatus* and the black of *aureola*; there is no trace of the sharply defined white patch on inner webs of remiges typical of the latter species.

On the underparts, the throat, as mentioned, is midway between the silky white of *linteatus* and the orange-yellow of *aureola*. At first sight, the breast is a pale, "washed-out" version of that of *aureola*. The bases of the feathers, however, are white in *aureola*; in the presumed hybrid they are blackish as in *linteatus*. The horseshoe-shaped black breastband of *linteatus* is represented in "anomala" by narrow black patches at the positions of the "arms" of the horseshoe. The abdomen differs from that of either of the presumed parents in being yellowish white, washed with olive gray on the flanks (the latter somewhat as in *linteatus*). The under tail coverts of *aureola* are black, the feathers nearest the vent having pale yellow bases. In *linteatus* the under tail coverts are pale

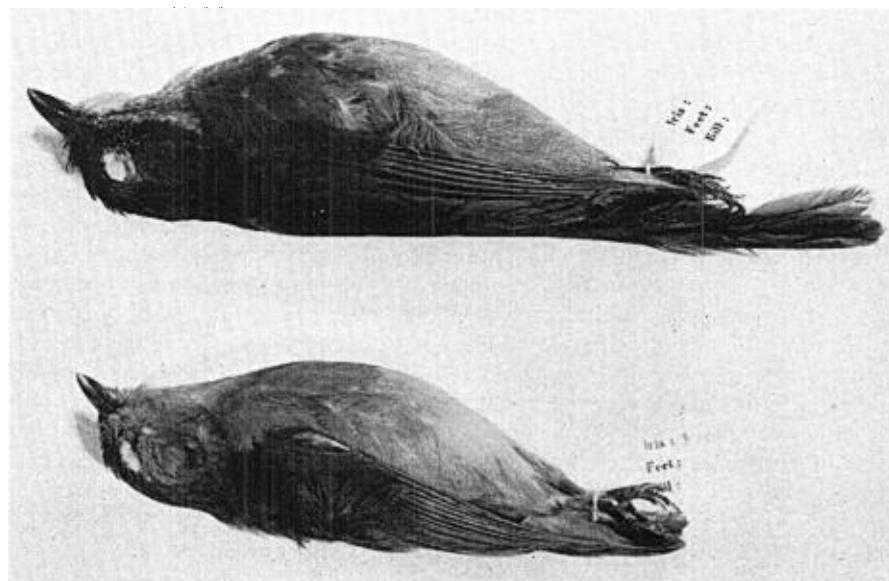


Fig. 1. Adult females of *Heterocercus linteatus* (upper) and *Pipra aureola aurantiicollis* (lower). Both figures are three-fourths natural size.

chestnut. In "anomala" these feathers are dark gray, with the bases white washed with pale orange.

One of the most interesting characters of "anomala" is the face pattern mentioned by Todd as being unique in the genus *Pipra*. Whereas in *Heterocercus linteatus* the entire head, except for the orange crownpatch and white throat, is black, in "anomala" only a facial "mask," somewhat interrupted at the lores, is black. There is no black at all on the head of *Pipra aureola*. In the northern species *Heterocercus flavivertex* (figured by Hellmayr, 1910: pl. 1, fig. 6) the greenish color of the back continues forward to the base of the bill, surrounding the bright crownpatch, with only a mask of blackish beginning just in front of the eye. This pattern in *H. flavivertex* suggests that the related *H. linteatus* carries the genetic potential for a similar mask, obscured by the development of black over the entire facial area. In the presumed hybrid, "anomala," the factor for the facial mask has been inherited and finds phenotypic expression.

In Sibley's discussion of *Manacus manacus* and *Pipra erythrocephala* as the presumed parents of "*Chiromachaeris coronata*," he mentioned the close similarity of their females. Although females of all sexually dimorphic manakins are rather plain, those of *Pipra aureola* and *Heterocercus linteatus* differ in size, proportions, and color as much as almost any two species in the family (see fig. 1). The similarity of the females is of less significance in analyzing hybridization in the Pipridae than in other families, as has been emphasized by Sick (1959:298), because of the courtship pattern in which females seek out males on their communal displaying grounds.

If, as the evidence seems to show, "*Pipra anomala*" is indeed a hybrid between *Heterocercus linteatus* and *Pipra aureola*, there can be little doubt that Hellmayr erred in placing *Heterocercus* at the end of the Pipridae and separating it from *Pipra* by such peculiar genera as *Massornis*, *Schiffornis* and *Sapayoaa*. As suggested by its general appearance and by the relative simplicity of its courtship patterns (Sick, 1959:274), *Heterocercus* is a less specialized manakin than is *Pipra*, and it should probably stand somewhat before *Pipra* in a linear sequence of genera. The reproductive behavior of *Heterocercus* differs sufficiently from that of *Pipra* that Dr. Sick, knowing both genera in life, was most reluctant to accept the idea of the hybrid origin of "*Pipra anomala*" until I sent him color slides of the pertinent skins.

Sibley (1957) has emphasized that genera in families of birds exhibiting great sexual dimorphism have all too often been based on male secondary sex characters which, having developed as reinforcements to reproductive isolation, may mask true close relationships. While this is undoubtedly true, I wonder whether the seeming overabundance of intergeneric as opposed to intrageneric hybrids may possibly be something other than an artifact based on oversplitting of genera. It occurs to me that selection favoring means of "preventing hybridization" would be most important among more closely related species. The less closely related two species are, the less chance there would appear to be for a reproductive "accident" resulting in hybridization. There would have been little selective pressure against such remote crossings simply because the situation would arise so infrequently. Behavioral and other isolating mechanisms would be developed to keep apart the closely related, essentially sympatric species which most frequently come into contact with one another during the reproductive season. Thus among the manakins we have no record of a hybrid between, say, two species of *Pipra*, but all reported hybrids appear to be intergeneric. This phenomenon may also appear in families in which a pair bond is formed, but in which a number of both closely and distantly related species may be sympatric. In the wood warblers, family Parulidae, a number of hybrids or presumed hybrids are known. Intergeneric hybrids include two

Vermivora x *Oporornis*, one *Parula* x *Setophaga*, and two *Parula* x *Dendroica* ("Sutton's Warbler," which may not be a hybrid but probably is). Except for these few intergeneric combinations, the only other wood warbler hybrids known to me are between what are rather obvious species-pairs, more closely related to one another than to any other species, which have probably evolved their divergences relatively recently. These include *Vermivora pinus* x *V. chrysoptera*, *Dendroica castanea* x *D. striata*, *Dendroica townsendi* x *D. occidentalis*, and especially *Dendroica coronata* x *D. auduboni*. The latter pair could probably best be considered as conspecific in view of the apparently unimpeded gene flow between the two forms. Another pair probably in this latter category consists of *Oporornis philadelphus* and *O. tolmiei*; these are so similar that hybrids are difficult to identify as such but equivocal specimens do exist.

Thus, among the Parulidae we have, at one extreme, hybrids between species-pairs some of which may not even be "good" species, and at the opposite extreme, intergeneric hybrids. Yet, particularly in the forests of northeastern North America, there are many species of sympatric congeneric parulids among which hybridization is not known to occur. This suggests that some particularly effective isolating mechanisms have developed among the North American wood warblers. These mechanisms rarely break down, but when they do, it is either among the closely related pairs, or between species so distantly related and so improbable as mates that no selection against such a crossing has developed. It is this latter situation that seems to have a parallel among the manakins, and it is of interest to note that Banks and Johnson (1961) independently came to virtually the same conclusion, based on their study of hybridization in North American hummingbirds.

Clearly this is a subject in which actual field observations in areas of sympatry would be highly illuminating, but the infrequency of "reproductive accidents" suggests that observers must be both persevering and fortunate to be able to contribute much toward our knowledge of how mixed matings come about or are prevented. Dr. David Snow, who has studied manakin behavior intensively in Trinidad, Panamá and British Guiana, has sent me the following notes, which he has kindly permitted me to quote: "I have seen, on two or three occasions only, ♀-plumaged (probably juvenile) *Manacus manacus* and *Pipra erythrocephala* associating together, with a certain amount of tentative display behaviour. On the one occasion when I knew the sex (by banding) of the *Manacus*, a definite juvenile ♂ *Manacus* was displaying quite persistently to a ♀-plumaged *Pipra*, which from its aggressive behaviour and incipient display movements was almost certainly a juvenile ♂; though the display of *Manacus* was typical of that which is normally directed to a ♀. Clearly one cannot make much out of such isolated observations, but they do suggest that there may at times be enough interaction between the two species for an occasional (abnormal?) individual to form a permanent attachment to the other species." Dr. Snow goes on to suggest that actual hybridization may come about if a young female has been closely associated with the "wrong" species as a juvenile. His observations of mating behavior together with certain structural differences suggest to him that, when *Manacus* and *Pipra* are involved, the latter is more probably the male.

Dr. Snow also raises the point that in the areas he has studied, manakins found together are nearly all of different genera. "Congeneric species are more often in different habitats ('avoiding' competition), so that a mating with a bird of another species is likely to be intergeneric simply because manakins of other genera are more likely to be at hand." This is undoubtedly true, and is one of the factors involved in the more efficient reproductive isolation between congeneric than between generically different

species. We must still determine the factors contributing to such reproductive isolation in areas in which congeneric species ARE found together.

ACKNOWLEDGMENTS

This paper was critically read in manuscript by W. E. Clyde Todd, David Snow, E. Thomas Gilliard, and Paul Slud. I am grateful for their comments and suggestions.

SUMMARY

Although the reproductive behavior of many species of Pipridae resembles that found in families characterized by relatively frequent hybridization, only two hybrid manakins have hitherto been reported: *Chiromachaeris coronata* Boucard = *Manacus manacus* x (probably) *Pipra erythrocephala*, and *Teleonema filicauda* x (probably) *Manacus manacus*. It is suggested that *Pipra heterocerca* Sclater may = *Teleonema filicauda* x *Pipra aureola* or *P. fasciicauda*, and that *Heterocercus luteocephalus* (Lesson) may be of hybrid origin. Evidence is presented to support the theory that *Pipra anomala* Todd = *Pipra aureola* x *Heterocercus lineatus*. It is suggested that selection against hybridization has developed most strongly among closely related species of birds, partly through geographical and ecological isolation, but allowing occasional intergeneric hybridization between unlikely combinations of parents.

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