STILL ANOTHER PARULID INTERGENERIC HYBRID (*MNIOTILTA* × *DENDROICA*) AND ITS TAXONOMIC AND EVOLUTIONARY IMPLICATIONS

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ABSTRACT.—An odd-looking wood warbler collected 24 April 1954 near Cameron, on the Gulf coast of Louisiana, originally identified as a melanistic *Mniotilta varia*, proves to be a hybrid *Mniotilta varia* × *Dendroica cerulea*. The specimen, an adult male, is intermediate between the parent species in almost all characters of size, proportions, and plumage pattern. In virtually all published lists of Parulidae, the genus *Mniotilta* appears first in sequence. This is shown to be a historical accident, based on a generic key published over a century ago. *Mniotilta* is a derivative of *Dendroica*, but its legs and feet have become distinctively modified for tree trunk foraging. Having occupied and become modified for a new adaptive zone, the species *varia* should continue to be placed in the monotypic genus *Mniotilta*. Hybrid parulids are reviewed, and the theory reiterated that selective pressures favoring evolution of reproductive isolating mechanisms have been strongest among closely related (=congeneric) species. Such selective pressures have been weaker between more distantly related species, as likelihood of mismatings was lower. All but one parulid hybrids involve either species-pairs or members of different genera. This is not a phenomenon of oversplit genera in the Parulidae. *Received 29 November 1977, accepted 13 March 1978.*

ON 24 April 1954, Thomas L. Kemper, a member of a field party from Northwestern University, collected an odd-looking wood warbler on Willow Island, 3½ mi ESE of Cameron, Cameron Parish, Louisiana. The specimen, originally intended to be used in a fat assay project, was rescued by the late Dr. George H. Lowery, Jr., who believed it to be a melanistic Black-and-white Warbler (*Mniotilta varia*). The study skin was so catalogued in the Museum of Zoology, Louisiana State University (LSUMZ 20311). Knowing of my interest in plumages, Robert J. Newman showed me this warbler when I was visiting L.S.U. in 1970. A quick examination of the specimen suggested to me that it was not an aberrant Black-and-white Warbler, but a hybrid between that species and the Cerulean Warbler (*Dendroica cerulea*). At the request of Dr. Lowery, I made a detailed study of the specimen in November 1977, which confirmed my original diagnosis. I am indebted to Drs. Lowery and Newman for the opportunity to study this hybrid. Dr. Lowery, Richard C. Banks, and Burt L. Monroe, Jr. read the manuscript and provided helpful suggestions for its revision.

MATERIALS AND METHODS

The Louisiana specimen was compared in detail with a selected series of 15 April and May male specimens each of *Mniotilta varia* and *Dendroica cerulea*. The series were chosen to exclude first-year (SY of bird-banding terminology) birds, on the chance that these might differ from older birds in size or color. As pointed out by Dwight (1900), male Black-and-white Warblers in their first spring may be recognized by their worn, brownish primary coverts (and, it should be added, alulae); the amount of black or white on the chin and throat is not a reliable age character. First-year male Cerulean Warblers also have worn, brownish primary coverts and alulae, and the outer edges of their remiges are pale blue-green, not cerulean blue. The hybrid is clearly an older bird, in its second or later spring (ASY of bird-banding usage). Measurements made include those of the flattened wing, tail, bill from anterior edge of nostril, tarsus, hallux minus claw, and hallux claw (chord). Wing, tail, and tarsus were measured to the nearest 0.5 mm, the latter two with dividers; the other measurements were made to the nearest 0.1 mm with dial calipers. Weights of May male Black-and-white Warblers and of May and June male Cerulean Warblers were taken from the banding files of Powdermill Nature Reserve, the Carnegie Museum of

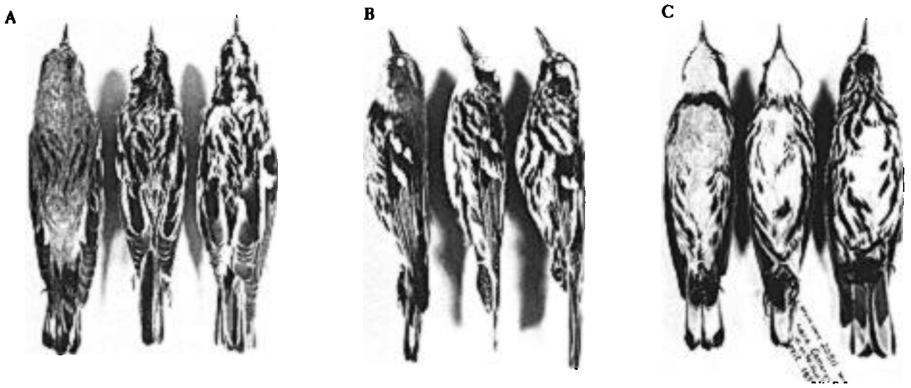

Fig. 1. Adult male specimens of Cerulean Warbler (*Dendroica cerulea*), left; Black-and-white Warbler (*Mniotilta varia*), right; and hybrid, center. **A.** Dorsal aspect; **B.** lateral aspect; **C.** ventral aspect.

Natural History field station near Rector, Pennsylvania. In the comparisons below, the hybrid is always described last; either *varia* or *cerulea* may be described first, depending on the easiest wording of comparisons.

COLOR AND PATTERN

At first glance the Louisiana specimen looks like a Black-and-white Warbler with the white stripes of the upperparts replaced by blue-gray, and with a white rather than black or striped throat, but with a black band across the upper breast (Fig. 1). The original identification as an abnormally plumaged *Mniotilta* is understandable. In detailed analysis, the specimen proves to be intermediate between the hypothesized parent species in almost all characters. In a few instances, the character state of one of the parents has been inherited intact.

Crown.—*cerulea*: blue (tips of feathers), with two variable, often partly concealed blackish lateral stripes on the posterior portion, rarely reaching forward beyond the eye. Bases of all crown feathers blackish. *varia*: two broad black stripes separated by a white stripe that reaches or almost reaches the bill. Central stripe never as wide as the distance between the blackish stripes in *cerulea*. Bases of crown feathers dark gray. *Hybrid*: sides of crown black. Feathers of central stripe gray at the very base, followed by a concealed white area, then a black tip bearing long blue-gray terminal barbs. The effect is of a blue-gray central stripe spotted with black; the concealed white central portions of the feathers of mid-crown show if the plumage is at all disarranged.

Face pattern.—*varia*: a white superciliary line from the base of the bill to the nape, forming the upper margin of a white circumorbital ring. This eye-ring complete, or occasionally broken with a few black feathers at the posterior margin. *cerulea*: a very faint pale blue to whitish postocular line in some individuals only; no white eyering. *Hybrid*: a white superciliary line as in *varia*, but shorter posteriorly, ending about 6 mm behind the eye instead of reaching the nape. Some of the white feathers of the superciliary line have tiny blackish terminal or subterminal bars. A white eyering, interrupted posteriorly.

Both species have a "mask" extending from the lores under the eyes to the cheeks and ear coverts. In *cerulea* this varies from just perceptibly darker blue than the crown, as in the specimen photographed, to distinctly blackish. In some specimens there are a few pale or whitish feathers just below the eye. In *varia* the mask is black, with, again, many specimens having a few white feathers just below those of the eyering. In the hybrid, the loral feathers are white with black tips. The cheeks are black, with a white subocular mark as in the more strongly marked individuals of *varia*. Just posterior to the black cheeks, most *varia* have an area of mixed black and white feathers, giving a spotted or longitudinally streaked appearance. This is also present in the hybrid, but the white is replaced by gray.

Back.—*varia*: interalar area heavily streaked with black and white, the effect created by black feathers with wide white margins. *cerulea*: gray-blue, with highly variable black streaking. In some individuals, the back appears as blue feathers with black shaft-streaks, whereas in more strongly marked birds, these back feathers appear black with blue margins. In none is the black as dominant as it is in *varia*. *Hybrid*:

back with more black than in any *cerulea* seen, more like *varia*, but the feather margins gray, more nearly neutral and less bluish than on the crown.

Rump.—*cerulea*: clear blue-gray, paler and less blue than on the crown or back. *varia*: black, with the lateralmost feathers having wide outer webs. *Hybrid*: blue-gray, with the individual feathers narrowly cross-barred with black.

Upper tail coverts.—*cerulea*: black with blue-gray margins. *varia* and *hybrid*: black with white edges on outer web only.

Tail.—*varia*: R [=rectrix] 6 (outermost) narrowly edged with white on black outer web for a varying distance from the base; R 2–5 with outer edge pale neutral gray; R 1 with a narrow black center between broad margins of neutral gray. Except for a narrow inner margin, no white on R 2–3. On R 4 a similar white inner margin and sometimes a white tip. R 5–6 have the white of the inner web extending to the tip of the feather. *cerulea*: outer margin of R 6 black, with no light edging; R 2–5 narrowly edged with blue on outer web; R 1 narrowly edged with blue on outer and white on inner web. Inner webs of R 2–6 all with large white areas (diminishing in size from outer to inner) which *do not* extend to the tip of the feather. *Hybrid*: outer margin of R 6 black as in *cerulea*; outer edges of R 2–5 gray, slightly bluish; outer edge of R 1 gray, broader and less blue than in *cerulea*. Margin of inner web of R 1 white as in *cerulea*, but for about the basal ¾ of the feather there is a gray area between the white of the margin and black of the center. R 2–6 with white areas as in *cerulea*, but reduction in size from outer to inner more marked, with that of R 2 being a small irregular centrad extension of the white of the margin of the inner web. Unlike the white tail areas of *cerulea*, those of the hybrid reach the tail tip on R 5–6, and almost to the tip on R 4.

Throat.—*varia*: highly variable (not correlated with age). Extremes are white with a scattered few black feathers, and virtually solid black. In most the black (at least posteriorly) is mixed with white, giving a streaked appearance. *cerulea* and *hybrid*: pure white.

Breast band.—*varia*: not differentiated from black of throat in most specimens, but in some individuals of white-throated extremes, one or more rows of black streaks across the breast form a broken band. *cerulea*: a distinct breast band of varying width, very rarely interrupted at center. This band is actually black, but is overlapped by terminal barbs of white feathers lying just anterior, giving the illusion in many individuals that the breast band is dark blue. *Hybrid*: breast band in the same place as in *cerulea*, but composed of white-edged black feathers, giving the effect of a row of short black longitudinal streaks.

Sides and flanks.—*cerulea*: a series of longitudinal streaks along sides and flanks beginning at sides of the breast band. These, like the breast band, are black but partly overlapped by white barbs, giving an illusion of dark gray or even dark blue-gray. *varia*: streaks broader, not overlapped by white, and extending farther toward the midline. *Hybrid*: streaks intermediate in every way.

Under tail coverts.—*varia*: black with broad white margins. *cerulea* and *hybrid*: pure white.

Wing.—*varia*: tertials black with white outer margin; remaining remiges dark gray with pale gray outer and white inner margins. Edges of primary coverts pale neutral gray. Greater coverts tipped with white (forming the posterior wing bar), but without pale edging on outer margins. Some specimens have tiny white spots at the tips of some of the remiges. *cerulea*: inner webs of tertials black, outer webs blue-gray, with narrow whitish margin that extends around tip of feather to inner web. Remaining remiges almost black (i.e. darker than in *varia*), with pale blue outer and white inner margins. Edges of primary coverts bluish. Greater coverts tipped with white as in *varia*, but each covert edged with blue-gray on outer margin. No white tips to remiges. *Hybrid*: pattern of tertials as in *varia*, but margins pale neutral gray with a white outer edge. Color of remiges intermediate between those of *varia* and *cerulea*, with outer edgings faintly bluer gray than those of *varia*. Edges of primary coverts distinctly bluer than in *varia*. Greater coverts with pale outer margins as in *cerulea*, but neutral gray rather than blue-gray. A tiny but distinct white spot at the tip of each remex from primary 5 inward.

MEASUREMENTS, PROPORTIONS, AND WEIGHT

In most linear measurements the Black-and-white Warbler averages larger than the Cerulean, although in a small sample there is only a slight average difference in weight (see Table 1). The wing length of the hybrid falls within the overlap of the samples of the parental species. The tail of the hybrid is 1 mm longer than the longest *cerulea* measured, and 1.5 mm longer than the shortest *varia*. With a larger sample of *cerulea*, the tail length as well as the wing length would undoubtedly fall within the overlap. The bill of the Black-and-white Warbler is distinctly longer than that of the Cerulean, and in this measurement the hybrid matches the former. The tarsal lengths of the two species are almost identical, such that the tarsus of the hybrid matches either a small *varia* or an average *cerulea*. It is in the size of the foot, particularly the elongation of the hallux and its claw, that we find the major difference between

TABLE 1. Measurements and weights (range, mean in parentheses) of adult male *Mniotilta varia*, *Dendroica cerulea*, and hybrid

Measurement (mm)	*Mniotilta* (N = 15)	Hybrid	*Dendroica* (N = 15)
Flattened wing	66–71.5 (69.7)	68	65–69.5 (67.1)
Tail	45.5–52 (49.0)	47	41–46 (44.0)
Bill from anterior edge of nostril	8.3–10.2 (9.2)	8.8	7.1–8.4 (7.5)
Tarsus	16–17.5 (16.6)	16	15–17 (15.9)
Hallux minus claw	7.0–8.8 (7.7)	5.9	4.2–5.7 (4.8)
Chord of hind claw	5.3–7.0 (6.1)	5	3.5–4.9 (4.3)
Hallux and claw/tarsus	0.747–0.939 (0.832)	0.681	0.503–0.618 (0.564)
Weight (g)	*Mniotilta* (N = 9)	Hybrid	*Dendroica* (N = 5)
	9.1–12.1 (10.4)	8.6	9.0–10.0 (9.5)

Mniotilta and *Dendroica*. Ridgway's key (1902: 428) separates a monotypic taxon "Mniotiltae" from all other wood warblers by the character state "Hallux longer than [vs. "much shorter than"] inner toe with claw, about equal to [vs. "much shorter than"] frontal length of tarsus." Both the hallux and its claw are longer in *varia* than in *Dendroica cerulea*, with no overlap. The hallux of the hybrid is intermediate in length, falling within the zone of non-overlap of measurements of the parent species; the same is true of the hind claw. As indicated in Ridgway's key, the ratio of total hallux length (including claw) to tarsus approaches unity in *M. varia*, whereas in *D. cerulea* the total hallux is only about half the length of the tarsus. This ratio in the hybrid is again intermediate.

In his characterization of the genus *Mniotilta*, Ridgway (1902: 432) describes the outer toe as being longer than the inner. He omits these toe proportions in his characterization of *Dendroica* (p. 497), but in *D. cerulea* the outer toe is scarcely if at all longer than the inner, whereas it is decidedly so in *Mniotilta*. In the hybrid, the outer toe is very slightly longer than the inner, much as in extreme examples of *D. cerulea*.

The hybrid weighed 8.6 g, and, according to the label notation, had only a trace of fat. This is slightly less than any individual of either parental species (of the same age and sex and approximately similar season) in the small sample available. The Gulf Coast locality of collection of the hybrid suggests that it may have just made a landfall after a trans-Gulf flight and thus have been near its minimum weight, although both parental species usually arrive in Louisiana well before 24 April (Lowery 1974). Given a larger sample size, a small adult male of either of the parental species would probably match the weight of the hybrid.

DISTRIBUTION

The Black-and-white and Cerulean warblers breed sympatrically over a large area of deciduous woodlands of the eastern United States (see maps in Robbins et al. 1966). The relatively early collection date of the hybrid, 24 April, precludes any deductions as to the geographic origin of the hybridization, as the bird was clearly a migrant. Although both species are well-known migrants in Louisiana, the Black-and-white Warbler does not breed in the southern third of the state, and breeding of the Cerulean has yet to be proved anywhere in the state (Lowery 1974). The label of the hybrid indicates that the preparator found only the left testis, the size of which is given as 4 mm, compatible with a pre-breeding condition. Both species are known to be trans-Gulf migrants (Stevenson 1957), and, as mentioned previously, the coastal locality of collection suggests that the hybrid, too, had crossed the Gulf of Mexico on at least its second spring migration.

TAXONOMIC IMPLICATIONS

The monotypic genus *Mniotilta* has been placed at the head of the family Parulidae (formerly Compsothlypidae, Mniotiltidae, or Sylvicolidae) in every edition of the American Ornithologists' Union Check-list of North American birds since the first (1886). Allowing for changes in generic names, the sequence of the first several genera has remained *Mniotilta–Protonotaria–Limnothlypis–Helmitheros–Vermivora–Parula–Dendroica* in every edition. In accordance with the conventions of such linear arrangements, one would suppose that *Mniotilta* was considered to be most closely related to *Protonotaria*, than to *Limnothlypis*, and so on. Griscom (in Griscom and Sprunt 1957: 12) called *Mniotilta, Limnothlypis, Helmitheros* and *Protonotaria* "a series of related genera," rearranging them slightly from the A.O.U. sequence. His "suggested reclassification" (p. 349) maintains the same sequence, but merges *Limnothlypis* and *Helmitheros*. Of *Mniotilta*, he stated (loc. cit.): "It is strikingly distinct in color pattern, creeping habits and the important structural [characters of toe proportions]," thus seemingly negating to some extent his earlier placement of *Mniotilta* as part of the "series of related genera."

Sharpe (1885) stated that he admitted the same genera of "Mniotiltidae" as did Baird (1864), but, although he did not so state, he rearranged the sequence of Baird's genera. Baird began with *Mniotilta*, whereas Sharpe followed the sequence *Leucopeza–"Helminthotherus"* (=*Helmitheros* + *Limnothlypis*)*–Vermivora–Protonotaria–Mniotilta–Parula–Dendroica*. Sharpe chose to begin his key to genera with the condition of the rictal bristles, which divided the wood warblers into four groups. The first four genera listed formed the first group, with "rictal bristles obsolete or entirely absent," and *Mniotilta* heads the second group, with feeble but nevertheless evident rictal bristles. Within this second group, *Mniotilta* keys out uniquely in the first couplet, based on toe proportions.

In the most recent classification of the Parulidae, Lowery and Monroe (1968) departed from the A.O.U. sequence by removing *Limnothlypis, Helmitheros*, and *Protonotaria* from a position just before *Dendroica* and its relatives to one just after. However, *Mniotilta* still leads the list.

I believe the consistent placement of *Mniotilta* at the head of the Parulidae to be based on the work of Baird (1864), or possibly an earlier paper with similar conclusions. It has nothing to do with the former status of *Mniotilta* as the type genus of the family "Mniotiltidae" as has been suggested to me; in Baird's time the family was called Sylvicolidae. In Baird's key (p. 166), the first group that segregates out is the "Mniotilteae" or "Creeping Warblers." The critical part of Baird's key characterization of this group reads as follows: "Basal joint of inner toe adherent for its basal half; basal joint of outer toe, and part of the next, adherent (in all other *Sylvicolidae* the inner toe cleft nearly to the base, and second joint of outer toe free)." Baird then added: "Hind toe lengthened, nearly equal to the middle; the digit considerably longer than the claw." In his "Mniotilteae" Baird included the two genera *Mniotilta* and *Parula*. The statement about the long hind toe does indeed apply to *Mniotilta*, but *Parula* seems a strange bedfellow for the Black-and-white Warbler. Examination of specimens indicates that the hind toe of *Parula* may be slightly longer in relation to the middle toe that is true of *Dendroica*, but in this particular comparison the hind toe of *Mniotilta* is *much* longer. In the more important comparison of hind toe and tarsal lengths, *Parula* does not differ from *Dendroica*. The mean hallux/tarsus ratio of *Dendroica cerulea* (Table 1) was 0.564, and that of *Parula americana* (4 adult males) was 0.532, whereas in *Mniotilta* this ratio was 0.832. As for the matter of toe adhesion, the alcoholic specimens examined of *Mniotilta* matched Baird's description, but no noticeable difference was found between the toes of *Parula americana, Dendroica caerulescens*, and *D. dominica* (we lack alcoholics of *D. cerulea*). And, as Griscom (in Griscom and Sprunt 1957: 11) pointed out, the amount of adhesion of the basal phalanges of toes in parulids "unhappily . . . proves to be a matter of specific variation in *Vermivora* and *Dendroica*, and is of doubtful generic value."

In short, the traditional lead position of *Mniotilta* in all classifications except Sharpe's since at least 1864 reflects nothing more nor less than the possession by this genus of a useful character, the proportions of the toes and tarsus, that will separate it from all other Parulidae, and thus it can be sorted out in the first couplet of a dichotomous key. It has nothing to do with relationships as indicated by other criteria, and certainly nothing to do with modern concepts of "primitive" or "advanced" taxa. Baird, Sharpe, Ridgway, and other authors of their period simply listed the genera in the same sequence as they sorted out in their keys.

What, then, are the true relationships of *Mniotilta*? Mayr and Short (1970) considered this genus to be of "uncertain relationships," but added perceptively that "its relatives will probably be found among the dendroicas." In point of fact, if it were not for the legs and feet, the Black-and-white Warbler would be a perfectly acceptable member of *Dendroica*. Ridgway (1902) mentioned no other structural characters in his diagnoses of *Mniotilta* and *Dendroica* that would serve to separate the two genera. The black and white pattern, considered "strikingly distinct" by Griscom, would not be out of place in a genus that includes such species as *Dendroica striata* and *D. pharetra*; Griscom actually made the same observation elsewhere in the same book (in Griscom and Sprunt 1957: 12). The white tail patches are like those of *Dendroica*; although the pattern of white in the rectrices of *Mniotilta varia* differs from that of *D. cerulea* as described earlier, it is quite similar to that of other members of the genus such as *D. kirtlandii* and *D. dominica*. The bill of *M. varia* is substantially longer than that of *D. cerulea*, the species with which it has been compared in this paper, but it cannot match the elongated bill of *Dendroica dominica stoddardi* in actual length. In relative length, the bill/tail ratio of even the longest-billed population of *M. varia* (Ridgway 1902), 0.25, is the same as that of *Dendroica angelae* and *D. dominica albilora*, and less than the 0.28 of *D. d. dominica* (Kepler and Parkes 1972). There is nothing in the general life history of the Black-and-white Warbler other than its creeper-like foraging habits that would be out of place in a *Dendroica*; certain species of that genus frequently forage on vertical surfaces, most especially *D. dominica* (which Catesby [1731] called the "Yellow-throated Creeper"!). Parenthetically, the latter species, which resembles the Black-and-white Warbler in its long bill, tail pattern, certain other aspects of plumage pattern, and foraging habits, does *not* depart from other *Dendroica* in toe and tarsus proportions, although the feet are larger overall than are those of comparably-sized congeners.

I have no doubt that the Black-and-white Warbler represents an offshoot of *Dendroica*, modified structurally for a specialized mode of foraging. In this it resembles the American Redstart (*Setophaga ruticilla*), another wood warbler of obvious *Dendroica* ancestry but adapted structurally and behaviorally for aerial, "flycatching" foraging (Parkes 1961b). Both of these species have entered new specialized adaptive zones and have evolved appropriate structural modifications such that their inclusion within the genus *Dendroica* would make that genus, diverse as it is, difficult to define. I advocate continued recoginition of both of the monotypic genera *Mniotilta* and *Setophaga*. Both should be placed directly after *Dendroica* in a linear sequence of genera. As each has evolved in a different direction from *Dendroica* ancestors, it matters little which genus is listed first, as the true relationships in this group cannot be expressed in a linear sequence.

EVOLUTIONARY IMPLICATIONS

Buried within one of my papers (Parkes 1961a) that some students of Parulidae may have overlooked, as it dealt primarily with quite a different group of birds (the Pipridae), are a couple of paragraphs calling attention to certain phenomena pertaining to hybridization among the wood warblers. I noted that all known hybrids (or birds deduced to be hybrids) in this family were between obvious species-pairs that had probably evolved their differences rather recently, or else between members of two genera. Examples of the first kind cited included *Dendroica coronata* × *D. auduboni* (now considered conspecific), *Dendroica castanea* × *D. striata*, *D. townsendi* × *D. occidentalis*, and *Vermivora pinus* × *V. chrysoptera*. Another pair of species that I then thought probably to be in this category was *Oporornis philadelphia* and *O. tolmiei*, on the basis of reportedly equivocal specimens that might be hybrids. A recent analysis has shown that certain specimens must indeed be considered to be hybrids between these two species, although other reported "hybrids" are merely individual variants of one of the species (G. A. Hall, in press).

Intergeneric hybrids mentioned in the 1961 paper were of *Vermivora* × *Oporornis* (*V. pinus* × *O. formosa* and *V. pinus* × *O. philadelphia* [see McCamey 1950]), *Parula* [*americana*] × *Setophaga* [*ruticilla*], and two specimens of *Parula* [*americana*] × *Dendroica* [*dominica*], the so-called "Sutton's Warbler." Since that time another combination has been reported by Short and Robbins (1967), who described a specimen considered to represent *Seiurus noveboracensis* × *Dendroica striata* (having handled this specimen, I agree that it is *Seiurus noveboracensis* × *Dendroica* sp., but am not wholly satisfied that *D. tigrina* has been eliminated as a possible parent). The present paper adds another combination, *Mniotilta* × *Dendroica*, to the list of parulid intergeneric hybrids.

Conspicuously missing among the list of hybrid wood warblers are any between any of the many sympatric congeneric species other than the species-pairs listed above. Thus we have no known instances of hybridization between any two of the three species of *Seiurus*, and only a single instance (see beyond) among the swarm of species of *Dendroica* that breed in northeastern coniferous and mixed forests (*D. magnolia, tigrina, caerulescens, coronata, virens, fusca,* and the *castanea*/*striata* species-pair). Other groups of *Dendroica* breed sympatrically in other habitats. Although it is understandable that hybrids from the Neotropics would be much less likely to be detected than those from the Nearctic, nevertheless I know of no reported hybrids in the large genus *Basileuterus*, which includes several sympatries, nor between the wide-ranging *Myioborus miniatus* and any of its more local congeners with which it is sympatric. Impressed by this phenomenon, I ventured the proposal in my 1961 paper that selection pressures favoring the evolution of reproductive isolating mechanisms would be strongest among closely related (= congeneric) sympatric 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." This conjecture was based on hybridization patterns in both the Pipridae and Parulidae. Interestingly enough, Banks and Johnson (1961) independently came to virtually the same conclusion, based on their study of hybridization in North American hummingbirds. This interpretation has been criticized by Short and Robbins (1967) and by Short (1969); in both of these papers the reader is referred to an earlier paper by Short and Phillips (1966) for further explanation of the objections to the Parkes/Banks and Johnson theory. Short and Phillips discuss only the Banks and Johnson paper, as they were dealing with hybrid hummingbirds. They attribute the frequency of intergeneric hummingbird hybrids to the generic oversplitting of the family Trochilidae, such that there are virtually no sympatric congeneric species of this family in North America, according to the current classification. The only sentence addressing itself to the theoretical question of the nature of the selection pressures for evolution of isolating mechanisms is this: "However, if modern phylogenetic ideas are correct, then intrageneric hybridization between closely related birds should be more common than intergeneric hybridization between more distantly related species." We are not told which "modern phylogenetic ideas" apply to this prediction. This is unfortunate, as the prediction simply does not hold for the Parulidae, as shown above. In this family, intergeneric hybrids between more distantly related species are, in fact, more common than intrageneric hybrids; other than those involving species-pairs, only a single intrageneric parulid hybrid has been reported (*Dendroica coronata* × *D. striata*; Banks and Baird 1978). This lone example does not seriously affect the thesis of this paper. Of the five intergeneric hybrids described for the Pipridae (Parkes 1961a), only one (*Teleonema* × *Pipra*) is an artifact of generic oversplitting in that family. Intergeneric hybridization in the Parulidae can be considered such an artifact only by stretching the generic concept well beyond the limits suggested by our most devout lumpers, past and present. That such a criticism may well be correct with respect to the Trochilidae does not justify its extension to the Parulidae and Pipridae. Admittedly *Parula* is close to *Dendroica*, and some (e.g. Griscom, in Griscom and Sprunt 1957) have advocated their merger along with *Vermivora* (Griscom even added *Peucedramus*, which is probably not even a wood warbler!). I have suggested that both *Setophaga* and *Mniotilta* are closely related to *Dendroica*. But I know of no ornithologist who has suggested that *Vermivora* and *Oporornis* should be considered congeneric; the latest revision (Lowery and Monroe 1968) lists no fewer than eight genera between *Vermivora* and *Geothlypis* (into which these authors, perhaps unwisely, merged *Oporornis*).

But let us assume that a lumper insists that hybridization "proves" that *Vermivora* and *Oporornis* should be considered congeneric, and that the various hybrid combinations "prove" that *Dendroica, Seiurus, Parula*, and *Setophaga* should all be combined with *Mniotilta* (which has nomenclatural priority in this group). It is true that all of these hybrids would now automatically have become "intrageneric"—but this will have served only to obscure the point being made here, which is that selection has operated to improve reproductive isolation between *closely related species* that are sympatric, and not (or not as rigorously) to do so between more distantly related species. Calling all of these birds one genus does not make the American Redstart more closely related to the Northern Parula than they are when the genera *Setophaga* and *Parula* are recognized. Surely the group of sympatric species of *Dendroica* species of northeastern forests listed earlier, among which only a single hybrid combination is known, are more closely related to one another than any of them is to the Northern Waterthrush or the Black-and-white Warbler, both of which have hybridized with *Dendroica* sp.

The phenomenon of wood warblers hybridizing with distant relatives, currently considered as being in different genera, and not with sympatric congeners, is a real one. The fact that these morphologically divergent species are able to produce viable young merely reflects the status of the Parulidae as a relatively rapidly evolving group; in several bird families that are undoubtedly older than the Parulidae (e.g. Anatidae, Phasianidae), members have remained genetically compatible long after they have evolved major morphological and behavioral differences. Critics of the relatively simple notion that there have been different levels of selective pressures affecting reproductive isolation among closely and distantly related sympatric species must do more than just lump the genera and turn their backs to the problem—they must provide a better alternative theory.

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