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A NEW SPECIES OF WARBLER (PARULIDAE) FROM PUERTO RICO

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THE West Indies are among the best known of the world's tropical regions, and our knowledge of the distribution of indigenous land birds in the Greater Antilles has been thought to be nearly complete (Bond, 1956). The last new species from the Antilles were described in 1927, the results of work in the Zapata Swamp of Cuba (Barbour and Peters, 1927) and the isolated Morne de la Selle in Haiti (Wetmore, 1927). No new species has been found in Puerto Rico in this century, and it would seem unlikely that a bird could escape detection on the island, which has a human population density now approaching 320 per square km, and less than 3,300 ha (0.4 percent of land area) of virgin forest remaining (Wadsworth, 1949). Nevertheless the discovery of extant populations of the Puerto Rican Whip-poor-will (*Caprimulgus noctitherus*) by Reynard (1962) and the Puerto Rican Plain Pigeon (*Columba inornata wetmorei*) by Leopold (1963), both previously presumed extinct (Bond, 1956, 1961), indicated that the inventory of the Puerto Rican avifauna might be incomplete.

The largest remaining forest in Puerto Rico is in the Sierra de Luquillo at the island's eastern end. In September 1968 the senior author and his wife established residence within the forest at an elevation of 770 m, and began intensive studies of the Puerto Rican Parrot (*Amazona vittata*) and the Puerto Rican Tody (*Todus mexicanus*). These studies included a series of census routes through the forest to assess seasonal and altitudinal distribution and abundance of these and other species (Kepler and Kepler, 1970). Two census routes were established in Elfin Woodland (Figure 1), a distinctive forest type confined to the higher peaks and ridges. In this forest they occasionally noticed a warbler of peculiar appearance, but were unsure of its identity because of the difficulty of seeing small birds in this habitat. The bird (see Frontispiece) showed similarities both to the Black-and-white Warbler (*Mniotilta varia*), a common North American migrant to Puerto Rico, and the Arrow-headed Warbler (*Dendroica pharetra*), a

ELFIN WOODS WARBLER, *Dendroica angelae* Kepler and Parkes

Adult (above) and immature (below)

From a tempera painting by Don R. Eckelberry

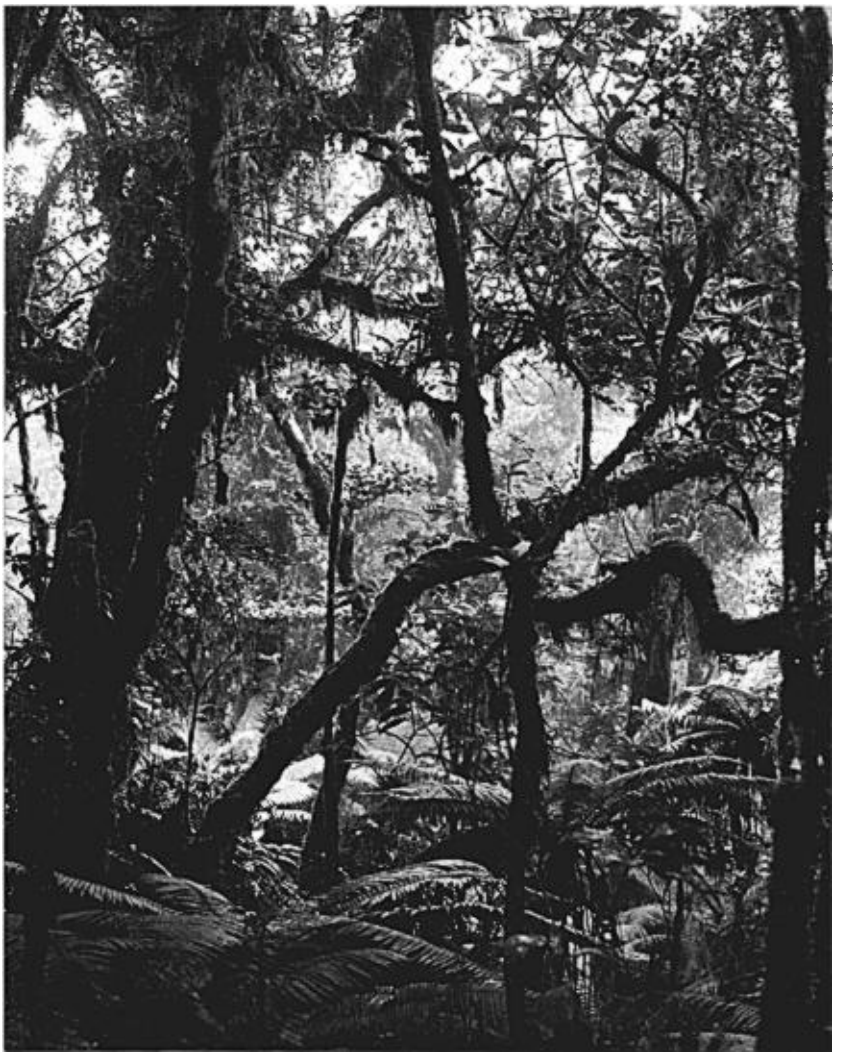

Figure 1. The Elfin Woodland, Pico del Este. This is typical of the Elfin Woodland on the higher peaks in Luquillo Forest. The treefern, *Cyathea pubescens*, is restricted to this forest type.

resident species of Jamaica. By March 1971, when Parkes visited the forest, the Keplers had concluded that the mysterious warbler must represent a species unknown to science, and invited Parkes to contribute to the primarily taxonomic aspects of its study. Serious attempts to collect a specimen began at that time. On 18 May 1971 Kepler procured a specimen on the high slopes of El Yunque Peak; it indeed proved to be

an undescribed species. During a second visit to the forest by Parkes in July 1971 three additional specimens were collected. We propose to name this distinctive new species:

Dendroica angelae, sp. nov.

ELFIN WOODS WARBLER

HOLOTYPE: U. S. National Museum No. 564,584, adult male (cranium fully pneumatized) in late stage of prebasic molt, testes approximately 0.5 mm in diameter; collected by Cameron B. Kepler on the ridge between the Río Sabana and Río Espíritu Santo valleys, approximately 2.5 km west of Highway 191 on the El Toro trail, Sierra de Luquillo, Puerto Rico (elevation 780 m), 14 July 1971.

PARATYPES: Carnegie Museum 142,928, adult [male], junction of Los Picachos and El Yunque trails, Pico El Yunque, Sierra de Luquillo, Puerto Rico (elevation 950 m), 18 May 1971; USNM 564,585, male just completing first prebasic molt, 1 km west of type locality (elevation 850 m), 16 July 1971; CM 142,929, female just completing first prebasic molt, same data as holotype. All specimens were collected by Cameron B. Kepler and prepared by Kenneth C. Parkes. The adult paratype, CM 142,928, was damaged by shot and could not be sexed internally, but was considered to be a male on the basis of behavior (singing from territorial song perches).

DIAGNOSIS: A small black and white parulid, sexes at least grossly alike (field observations), fitting Ridgway's (1902: 497) diagnosis of the genus *Dendroica*, but with an exceptionally short and rounded wing; coloration and proportions of adults bridging to some extent the genera *Dendroica* and "*Catharopeza*;" young in first basic plumage, like those of *D. pharetra* and *D. plumbea*, chiefly greenish, but with white markings of definitive plumage faintly indicated in yellow.

DESCRIPTION OF HOLOTYPE (taken from the freshly collected bird; the intricacies of the facial pattern show less clearly in the prepared specimen): UPPERPARTS: essentially black, with a slight bluish gloss; feathers of forehead and anterior half of crown edged with some white barbs, giving the effect (because of black of underlying feathers showing through) of indistinct longitudinal gray streaks; a narrow concealed white central streak on crown, which becomes more conspicuous as a short white longitudinal mark on nape; sides of head black, with *white markings* as follows—lores; a prominent eye ring (interrupted anteriorly and posteriorly by black feathers at the nasal and temporal canthi); a few small feathers in the auricular region; an indistinct superciliary line, which connects posteriorly with a prominent arcing band at the posterior margin of the auriculars, which band in turn is connected (or nearly so) with a narrow moustachial streak; a band on either side of the nape about 6 mm by 2 mm, which approaches but is separated from the postauricular band. Mantle appearing partly slate gray anteriorly, but this is an artifact of molt; where black mantle feathers have not yet fully grown out the gray bases of the adjacent feathers, normally concealed, are visible. Upper tail coverts black with white margins. UNDERPARTS: white, heavily spotted with black triangular marks (apex anterior), most densely across the lower chest, forming vaguely defined longitudinal lines; spots on throat smaller, and separated from white moustachial streak by a narrow, interrupted black line; black spots becoming streaks on flanks; midabdomen white; under tail coverts and thigh feathers dull black with extensive white tips. WINGS: black, with two prominent white wing bars formed by tips of middle and greater coverts, the anterior bar broader (ca. 4 mm versus 1 to 2 mm); a longitudinal white spot on terminal portion of outer web of tertials; a white "speculum" formed by white spots on the proximal end of the outer webs of primaries 4–8; primaries (except outermost) and secondaries otherwise with

pale gray outer margins; inner margin of remiges white; under wing coverts and axillars white. The holotype has right secondary 4 about 7 mm short of full length, and right secondary 5 old and worn; left secondary 4 missing, and left secondary 5 about 8 mm short of full length; all other remiges are new and full grown. TAIL: dull black, with a very narrow whitish margin on outer web of outer pair of rectrices, and broad slate gray edges on outer web of other rectrices; inner web of outer three pairs of rectrices with white tips, diminishing in size inwardly to a narrow white border on rectrix 3. The holotype has left rectrix 3 about ¼ full length, all the rest fresh and full grown. UNFEATHERED PARTS: iris very dark fuscous brown; tarsus and toes dark bluish gray; pads of feet grayish yellow; bill very dark gray, virtually black, with tomia lighter gray. STRUCTURE: wing formula of holotype $7 = 6 > 5 > 8 > 4 > 3 > 9 > 2 > 1$. Tail double-rounded, with rectrix 3 longest, central rectrix 1 mm shorter, outer rectrix 6.5 mm shorter. Rictal bristles moderate, longest ca. 3 mm.

DESCRIPTION OF ADULT PARATYPE: This specimen differs from the holotype as follows: streaks of forehead and crown obsolete (apparently through wear); white tips of rectrices somewhat less extensive (not due to wear alone); white marks on tertials slightly longer; remiges duller black with narrower edgings (wear); black spots on throat smaller, with a thinly spotted area between throat and chest setting off the chest markings as a poorly defined band.

DESCRIPTION OF FIRST BASIC PLUMAGE (USNM 564,585): UPPERPARTS: dark grayish green, distinctly brighter and yellower from nape to base of bill; an indistinct yellowish white longitudinal mark in midnape, 4 mm long; upper tail coverts slightly grayer than back, edged with yellowish white on outer web. FACE: eye ring as in adult but yellowish white; lores grayish white; semiconcealed postocular line yellowish white; auriculars like back but slightly browner, with yellowish white tips forming a small vertical mark where the adult has a white mark; yellowish white feathers at side of nape forming an indistinct vertical mark, again where the adult has a definite white mark. UNDERPARTS: pale, dull greenish yellow, becoming whiter on midabdomen; on many feathers of throat and breast, the individual *barbs* are of this pale yellow color, with narrow dusky tips to the *barbules*, thus narrowly outlining the entire barb—the optical effect is of a somewhat grayish yellow with short indistinct longitudinal brighter yellow streaks. Under tail coverts dull yellowish gray. WINGS: dull black, obscured at "shoulders" by broad greenish tipping of the color of the back; wing bars as in adult, but heavily washed with dull greenish yellow rather than pure white; markings on tertials similar in color but less clearly defined; "speculum" spots reduced, on primaries 5–7 only; flight feathers edged externally with color of back, slightly more whitish on four outermost primaries; inner edge of flight feathers white as in adult; under wing coverts grayish white, tipped with dull yellow. TAIL: dull black, edged with dorsal color; white tips reduced to a narrow white edge to inner margin of tip of outermost rectrix only. In this specimen, left rectrix 3 is ⅔ grown and is edged with gray as in the adult; right rectrix 1 and left rectrix 2 are missing. In view of the freshness of the remainder of the tail, it seems improbable that this gray-edged feather represents the results of a normal molt, but this must await further material.

DESCRIPTION OF FIRST BASIC PLUMAGE (CM 142,929): This specimen differs from that described above as follows: crown not brighter than dorsum, slightly brighter on the forehead only; yellowish white mark on midnape shorter (2 mm); upper tail coverts edged with yellowish white all round instead of on outer web only; "speculum" absent; white tips of rectrices not reduced, but much like those of adults.

MEASUREMENTS: See Table 1.

VOICE: Song a series of short, rapidly uttered, rather unmusical notes on one pitch, swelling in volume, and terminating with a short series of distinct double (iambic)

TABLE 1

WEIGHTS AND MEASUREMENTS OF *DENDROICA ANGELAE*[1]

Specimen	Weight	Wing (flat)	Wing (chord)	Tail	Tarsus	Bill (exposed culmen)	Bill (from anterior end nostril)
USNM 564,584 (TYPE) adult ♂	8.7	55	53.6	44.6	15.8	11.4	8.2
CM 142,928 adult [♂]	8.8	[56.5]	[54]	44.2	15.9	10.4	7.9
USNM 564,585 immature ♂	8.4	52	51.3	44.4	15.6	9.9	7.4
CM 142,929 immature ♀	8.0	53	51.3	43.3	15.2	8.4	6.9

[1] Weight in grams to nearest 0.1; measurements taken with dial calipers to nearest 0.1 mm except flat wing, taken on ruler to nearest 0.5 mm. Wing measurement of CM 142,928 is an estimate of wing length prior to present condition of wear. The short bill of CM 142,929 appears not to be fully grown.

syllables sounding slightly lower in pitch (Figure 2). The male song recorded has four terminal iambic notes, the first attached to the initial series of connected notes. The contact note heard in family groups of adults and young is a persistent repetitive series of notes similar to the song, but lacking the terminal iambic syllables. The call note, infrequently given, is a single, short metallic chip, similar in quality and duration to that of *Dendroica caerulescens*.

ETYMOLOGY: Species or subspecies of the family Parulidae (*sensu lato*, Lowery and Monroe, 1968) have already been named in honor of Adelaide, Francesca, Grace, Karlene, Laura, Lucy, Margaret, and Virginia. The authors are delighted to continue this tradition and name this distinctive new parulid for its co-discoverer, Angela Kay Kepler, who, in addition, located the El Yunque population and found the individual that became the first collected specimen. The English name is derived from the species' preferred habitat.

RANGE AND HABITAT

Believed to be confined to the Sierra de Luquillo, Puerto Rico, and primarily restricted to the Elfin Woodland of its upper slopes, individuals have been found from 640 m to 1,030 m elevation.

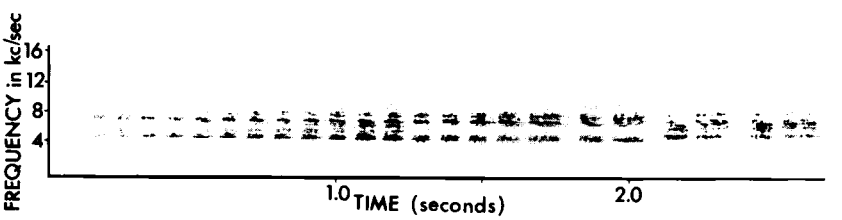

Figure 2. Sonagram of the song of *Dendroica angelae* recorded at 7½ inches per second on a UHER 4000 Report L, using a Sennheiser MD 405 L Cardioid microphone. The sonagram was made on a KAY 6061 B sound spectograph at narrow band settings.

The lower slopes of the Sierra de Luquillo are covered with a montane rain forest with an average canopy height of approximately 20 m. With increasing elevation, this forest is gradually reduced in stature, being replaced on exposed ridges and the highest peaks by stunted, gnarled trees ranging from 1 m to 8 m in height. This vegetation type is found throughout the world in suitable localities, and has been variously referred to as Cloud, Mossy, or Dwarf Forest, or Elfin Woodland (Beard, 1949; Richards, 1966; Howard, 1968). Howard (op. cit.) describes at length the characteristics of the Elfin Woodland of Pico del Oeste, and his introductory remarks present a graphic picture of this forest type as it appears in Puerto Rico: "The forest floor as well as the stems, branches, and exposed bases of the components of the forest are covered with festoons of bryophytes, almost lined with vascular epiphytes, and intertwined or overburdened with woody and herbaceous twiners" (Figure 1). The Pico del Oeste forest is enveloped in fog for more than half of all daylight hours, resulting in a 40 percent reduction in incident radiation. Rainfall normally exceeds 4,500 mm per year (Baynton, 1968). Below about 800 m the ridgetop forest may be taller and the tree *Clusia krugiana* (Guttiferae) predominates locally. The trunk bryophytes are much reduced, and the substrate is normally clear of the bryophyte layer more characteristic of higher elevations. A dense understory of the cutting sedge *Scleria canescens* may predominate locally. As in the higher Elfin Woodland, the canopy is often bound with tight masses of epiphytic vines, primarily *Marcgravia sintenisii*. Such middle-elevation forest connects the true Elfin Woodland of the three major peaks in the Sierra de Luquillo (Figure 3).

The range of *Dendroica angelae* is limited by that of the Elfin Woodland, including the contiguous vegetation of the middle-elevation ridges. Populations have been found on all the major peaks, and irregularly on the ridges joining them. The range is thus a series of narrow belts rarely exceeding 300 m in width except on the peaks, and extends from Pico El Toro northeastward approximately 6 km to the Elfin Woodland beyond Pico El Yunque, and from this ridgeline northwestward 1 km to El Cacique, southward 1 km on the ridge between the Icacos and Sabana Valleys, and southwestward approximately 5 km through Pico del Oeste to Pico del Este. The Elfin Woodland is variously bordered below by a forest of Sierra Palm (*Prestoea montana* = *Euterpe globosa*), generally on steep, rocky, protected slopes, or by a forest known as the Colorado type after its dominant tree, *Cyrilla racemiflora* (Cyrillaceae). *Dendroica angelae* does not penetrate the palm forest, which forms a sharp lower limit to its range, but is found occasionally in the Colorado zone, especially the more stunted portions where it grades into the Elfin Woodland. Only one of more than 40

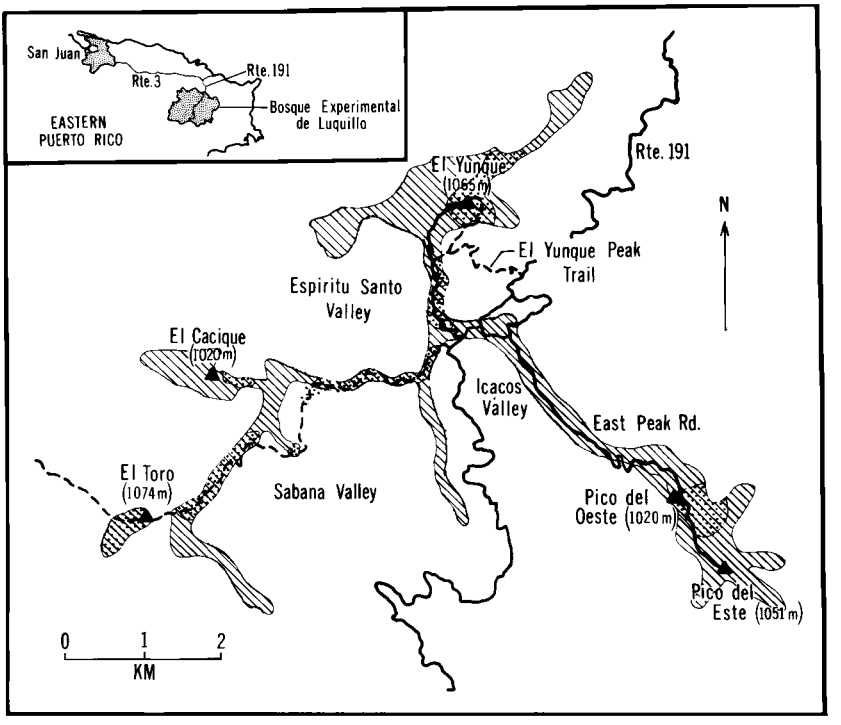

Figure 3. Map of the Luquillo Experimental Forest, showing the major peaks and valleys, the distribution of Elfin Woodland (diagonal lines), and the known range of *Dendroica angelae* (stippled areas).

locations where *D. angelae* has been sighted is beyond this range. The preferred habitat for this warbler does not exceed 450 ha (Wadsworth, 1949).

Relationships

As mentioned in the diagnosis above, the new species matches in every respect Ridgway's (1902: 497) diagnosis of the genus *Dendroica*, and we place it there without hesitation. Among the endemic West Indian warblers of this genus, certain species are obviously closely related to (and may have been derived from) mainland species (*D. pityophila* and *D. adelaidae* = *D. graciae*; *D. vitellina* = *D. discolor*), and there are resident races of the mainland species *D. petechia*, *D. dominica*, and *D. pinus*. In addition, three (now four) species of endemic Antillean *Dendroica* are rather obviously related to one another, but their affinities with mainland forms are obscure. These are *D. plumbea* of Guadeloupe, Marie Galante, and Dominica; *D. pharetra* of Jamaica; *D. angelae* of Puerto Rico; and "*Catharopeza*" *bishopi* of St. Vincent. The little-known *Leucopeza semperi* of St.

Lucia does not appear to belong to this group. Before discussing the relationships of *D. angelae* and its nearest relatives, some general observations on Antillean *Dendroica* are in order.

Ridgway (op. cit.) mentions rounded wings as a characteristic of "the distinctively Antillean types," which he lists as *D. plumbea*, *D. pharetra*, *D. adelaidae*, and *D. delicata* [= *D. adelaidae delicata*]. These rounded wings are characterized by having "the ninth primary shorter than the fifth, sometimes shorter than the fourth." *D. angelae* carries this tendency to the extreme known in *Dendroica*, with the ninth primary equal to or shorter than the third primary. In addition *angelae* is one of the shortest-winged species of the genus, both absolutely and relatively. The only *Dendroica* with an average wing length (chord, from Ridgway) in adult males of less than the 53.8 mm average of the two *angelae* specimens is *D. a. adelaidae* (49–51, mean 50 mm), which is, interestingly, the only other endemic Puerto Rican species of parulid. Among the smallest of the mainland *Dendroica* is the Prairie Warbler, *D. d. discolor*. Ridgway's wing chord measurements for adult males of this form are 55.9–59 mm, mean 57.6 mm, for 10 specimens. Measurements of Prairie Warblers banded in western Pennsylvania suggest more overlap in wing measurements between *discolor* and *angelae* than indicated above, so that the two species may conveniently be considered approximately equal in wing length. On the other hand, weights of adult male Prairie Warblers with no visible fat average only 80 percent of the weight of *D. angelae*, emphasizing the latter's shorter wing relative to body size.

In addition to the tendency for rounded wings, the West Indian warblers also tend toward longer bills (a well-known "island" phenomenon) and, to some extent, longer tarsi. In *Dendroica* in general, the tail seems to be the most stable of the linear measurements. Wing length is affected by, among other things, length of migration; bill length and tarsal length by foraging habits. Thus the most meaningful ratios to use for demonstrating tendencies in relative length among readily available measurements (i.e. chiefly those from Ridgway, 1902) use tail length as the constant.

Utilizing the bill measurement Ridgway employed, exposed culmen, we find that only one mainland species, *Dendroica dominica*, exceeds *D. angelae* in bill/tail ratio. In 20 mainland forms this ratio in adult males ranges from .17 to .22 (mean .196). In *D. d. dominica* the bill/tail ratio is .28, and in *D. d. albilora* it is .25, which is precisely the ratio in *D. angelae*. Other insular forms of *Dendroica* approach but do not exceed *D. angelae* in relative length of bill: *D. adelaidae*, .24; *D. vitellina*, .23; *D. pinus "abacoensis"* (now considered a slightly long-billed but taxonomically inseparable population of *D. p. achrustera*), .24. On the other hand some of the West Indian *Dendroica* do not show this "island effect"

in relative bill length and do not differ from mainland forms: bill/tail ratios of *D. plumbea*, .20; *D. pityophila*, .21; *D. pharetra*, .22. The answer to this apparent discrepancy will probably be found in a comparative study of foraging behavior.

The tendency toward longer tarsi in insular forms is less well-marked, but is nonetheless present. The tarsus/tail ratio of 20 mainland forms ranges from .33 to .39 (mean .362). This ratio in insular forms is as follows: *D. p. "abacoensis,"* .35; *D. angelae*, .36; *D. pharetra*, .37; *D. plumbea*, .38; *D. vitellina*, .39; *D. adelaidae*, .44. Again, differences in foraging behavior probably offset any "island effect" in some species.

The relationship of *Dendroica angelae* to *D. pharetra* of Jamaica is evident at first glance. Both are chiefly (*pharetra*) or wholly (*angelae*) black and white in definitive plumage, and both have triangular black spots on white underparts. These are heavier in *angelae*, and, in fact, the latter is in general more heavily pigmented than *pharetra*. The upperparts of *angelae* are almost solidly black rather than streaked, and the rump and upper tail coverts of *pharetra* are olive, a color without counterpart in the two adult *angelae* specimens. The outer margins of the inner remiges of *pharetra* are also edged with olive rather than gray. Except for a much reduced eye ring, the bold face and nape markings of *angelae* are without counterpart in *pharetra*. The white tail-tip spots of *angelae* are absent in *pharetra*, being replaced by rather narrow white edgings on the inner webs of the three outermost rectrices. *D. pharetra*, in fact, is the only member of its genus that lacks distinct white or yellow tail spots (Ridgway, 1902: 508). The outermost primaries of *pharetra* are edged in dull white, with a somewhat broader proximal area forming a hint of the markedly contrasting "speculum" of *angelae*. The greenish first basic plumage of *pharetra* foreshadows the definitive pattern just as is the case in *angelae*.

Bond (1956: 153) calls attention to the first basic ("immature") plumage as an indication of the relationship between *Dendroica pharetra* and *D. plumbea*; the gray, unspotted adults of *plumbea* are quite different in appearance from either *angelae* or *pharetra*, but, as in both of the latter, the first basic plumage is greenish, with the pattern of the adult foreshadowed in yellowish white. In the case of *plumbea* these markings consist of wing bars, a subocular spot, and a distinct superciliary line that connects with a broad loral spot. In one character *plumbea* connects *pharetra* and *angelae*; the shape and extent of the white tail markings are intermediate between those of the two latter species.

Before leaving *Dendroica plumbea*, we may appropriately mention that the material we have seen supports the validity of the race *D. p. guadeloupensis* Brodkorb (1931) synonymized with *plumbea* by Bond and others. The darker underparts, which may even suggest blurred spotting

on the throat and upper breast, are even more evident in young Guadeloupe specimens than in adults when compared with birds from Dominica in equivalent plumage.

The endemic parulid of the island of St. Vincent has generally been considered to represent a monotypic genus, appearing in most of the literature as *Catharopeza bishopi*. Many authors, including Ridgway (1902: 619) have commented that it is a weak genus, close to *Dendroica*. Bond (1956: 154) called it "probably an aberrant, primitive *Dendroica*." Later (1959: 6) he notes that Greenway (1958: 24) placed *bishopi* in *Dendroica*, and comments as follows: "Although this is probably justified, since morphological distinctions in *Catharopeza* are *minor*, I believe that more should be known about this bird before any such change in classification is accepted." In a later work (1967: 19), Bond considered *Dendroica* and *Catharopeza* to be subgenera of *Parula*; he cautioned, however, that the entire subgeneric classification in the 1967 paper was tentative, and would not be used in future supplements to his check-list. A wholesale "lumping" of parulid genera was rejected by Lowery and Monroe (1958: 5), and Bond's latest work (1971) continues to use the generic names *Dendroica* and *Catharopeza*.

Ridgway (loc. cit.) considered the chief structural character of *Catharopeza* to be its relatively shorter tail. A close reading of his diagnoses of *Dendroica* and *Catharopeza* will show that the tail of the latter is short primarily *in relation to the tarsus*, and, in fact, *bishopi* does have *both* a somewhat relatively short tail and relatively long tarsus, resulting in a tarsus/tail ratio of .43, exceeded only by the .44 of *D. adelaidae*. This proportion difference, as indicated by Ridgway, does not seem very important, appearing to be no more than a slight extension of the trend visible in other West Indian warblers.

The new information called for by Bond (1959) before accepting the merger of *Catharopeza* with *Dendroica* is provided by the newly discovered *D. angelae*. In several of the ways in which the plumages of *pharetra* and *angelae* differ, the latter approaches *bishopi*. The St. Vincent species, like *angelae*, is solidly black above, although duller and less glossy. It lacks, at first sight, any white markings on the dorsal surface, but close examination shows that unworn specimens have an indication of the white central crown stripe as found in *angelae*. The white spots at the tips of the rectrices of *bishopi* are similar in size and shape to those of *angelae*.

The most striking resemblance between *angelae* and *bishopi* is in the facial pattern. Both have a prominent white eye ring, although this is interrupted in *angelae*; in *bishopi* it varies exceedingly in width and shape and may even extend backward as a short postocular line (USNM 355,838). Both species have white loral spots, again rather better developed in

bishopi. Although not mentioned in any description we have seen, most specimens of *bishopi* have a concealed white superciliary exactly where *angelae* has a semiconcealed white stripe. The underparts of the two species are strikingly different at first glance; *bishopi* lacks spots, but has instead a white chin, black upper throat (variably mixed with white), followed by a white lower throat area, then a blackish breast band of variable width. The flanks are dark gray, and the midabdomen white. The only approach to the ventral pattern of *bishopi* shown by *angelae* is the tendency of the black spots to be heaviest just where *bishopi* has its breast band. The dried bill of *bishopi* specimens examined is black as in *angelae*, while in *pharetra* the base and in *plumbea* the entire lower mandible is pale.

Through the courtesy of George Reynard, Kepler has heard a tape recording of *pharetra* adults feeding young, using call notes higher pitched but otherwise closely similar to the equivalent vocalizations of *angelae*. The song of *pharetra* as described by Bond (1971: 199) appears to be similar in quality to that of *angelae* (as we might expect in view of the similarity of their feeding calls), but without the definite pattern, lacking the crescendo in the middle and the disconnected notes at the end. On the other hand, the song of *bishopi* (heard on tape by Parkes through the courtesy of Jon Barlow) is more melodious in quality than that of *angelae*, but has a remarkably similar pattern, including a crescendo and disconnected terminal notes.

The intermediacy of *angelae* between *pharetra* and *bishopi* makes the recognition of a monotypic genus for the latter untenable, and we regard *bishopi* as a species of *Dendroica*. Furthermore it is tempting to consider the four species *plumbea*, *pharetra*, *angelae*, and *bishopi* as forming a superspecies, as they are obvious geographic replacements and are more closely related to one another than to any other member of the genus. It is true that *bishopi* stands somewhat apart from the other three species in proportions, as already mentioned. It differs even more strikingly in the color of its first basic plumage, which is brown rather than greenish. On the other hand this plumage resembles that of the other three species in that it foreshadows the pattern of the adult; the sequence of white and black areas of the adult underparts is matched in buffy and dark brown in the young bird, and the eye ring and loral spot are also differentiated, although inconspicuously. It should be noted that the illustration of *bishopi* (plate 33) in Griscom and Sprunt (1957), captioned as "immature," appears to have been painted from a badly foxed adult; the pattern is that of the definitive plumage, while the color is a reddish chocolate brown quite unlike the more fuscous brown of the true "immature."

With its transfer to the genus *Dendroica*, *bishopi* becomes the largest

species of its genus, displacing *D. kirtlandii*. Three adults of *bishopi* in the Royal Ontario Museum weighed 16.0, 16.8, and 19 g. The weights of 77 breeding adult Kirtland's Warblers ranged from 12.3 to 16.0 g (Mayfield, 1960: 138).

The question naturally arises as to the position of this group of West Indian species with respect to other *Dendroica*. Ridgway (1902) placed *plumbea* and *pharetra* after *palmarum* at the end of *Dendroica*, followed by *Catharopeza bishopi*. Bond, in his various works, has followed Ridgway in this sequence except for reversing the positions of *pharetra* and *plumbea*. Lowery and Monroe (1968) substantially rearranged *Dendroica* internally, although keeping *Catharopeza* immediately following, with a footnote acknowledging the possibility that it might "prove to be no more than an aberrant *Dendroica*." They placed *plumbea* and *pharetra* near the beginning of *Dendroica*, between *caerulescens* and *pinus*.

In our search for a mainland relative of these West Indian species, our eyes lit first on the Blackpoll Warbler, *Dendroica striata*. It shares with them the lack of any color than black and white (and some olive) in the adult males, and a decidedly greenish first basic plumage. On the other hand, *striata* shares with many other mainland *Dendroica* a marked sexual and seasonal dimorphism, lacking in the West Indian forms. More important, in our judgment, is the evidence afforded by the pattern of the juvenal plumage, by which the genus *Dendroica* may be divided into two rather well-marked groups based. In one group this plumage has no spots or streaks, the underparts being silky white, grayish or yellowish, the upperparts solid gray or greenish. This plumage is held for a very short time before the advent of the first prebasic molt. In the other group the juvenal plumage is decidedly streaked or spotted below and usually above, and the completion of the first prebasic molt is at a rather later age than in the first group. Of the West Indian species under discussion, we have seen the true juvenal plumage only of *Dendroica plumbea* (USNM 355,789). It belongs without question to the first group. It has no streaks or spots, but is dull grayish green above, brownish gray on throat and breast, and silky white on the abdomen. There is an indistinct white superciliary, and the wing bars are represented by two rows of small yellowish white spots on the wing coverts. The ephemeral nature of this plumage is illustrated by the fact that the first few feathers of the first basic plumage are beginning to appear on the throat of this specimen even though the juvenal remiges are not yet fully grown.

The nature of the juvenal plumage, therefore, suggests that *Dendroica striata* is not the nearest mainland relative of *D. angelae* et al. We doubt whether, at the present time, the true affinities between the West Indian and mainland *Dendroica* species can be ascertained through examination

of skins. The clues may lie in behavioral or anatomical characters as yet unstudied. Until a definitive study of the genus *Dendroica* has been published (Lowery and Monroe credit "unpublished work of John P. Hubbard" as the partial basis for their species sequence in *Dendroica*), the best expedient is probably to continue to list *plumbea, pharetra, angelae,* and *bishopi* at the end of the genus. This group appears to have been long isolated, certainly as evidenced by their lack of resemblance to any other *Dendroica*; we question, however, whether Bond's adjective "primitive" (1956: 153) can be applied with any confidence at this time.

Plumage Sequence

This section might well have been placed earlier in the paper, but deductions about the plumage sequence of *Dendroica angelae* at present rest in part on evidence afforded by its relatives, so this discussion has been deferred until the relationships of *angelae* had been outlined.

Although the West Indies are technically "tropical," the breeding seasons of the resident *Dendroica* under discussion, so far as known, coincide approximately with those of temperate mainland species. Thus there is a well-defined annual cycle, and all young birds at a given date are within a month or two of being the same age. This is significant when it is pointed out that we know of green-plumaged (first basic) specimens of *D. plumbea* taken in every month of the year from January through June, as well as August. A green bird taken on Guadeloupe on 29 June (CM 100,607) is in worn plumage; another from the same island taken 28 June (USNM 355,788) is in the midst of a molt from a worn green plumage to the definitive gray and white plumage. A Dominica specimen (USNM 355,774) taken 12 August is in a later stage of the same molt. Guadeloupe specimens taken 18 and 22 June (USNM 355,780, 355,783) are in freshly acquired green plumage. It is obvious from these data that the first basic plumage of *Dendroica plumbea* is held for a full year. This is almost certainly true of the other species in the group as well. Of *bishopi* we have seen brown-plumaged birds from March, September, and November, and of *pharetra,* green birds from October and December. As indicated at the beginning of this paper, specimens of *D. angelae* just completing the first prebasic molt (i.e. into the green plumage) were collected in mid-July and have been seen from July through October. Although the Keplers have not observed green individuals in spring, this is not surprising, as *D. angelae* is highly elusive at this time, and the Keplers were at first only watching for black and white birds. However in the early summer of 1971, individuals seen molting from green into black and white plumage clearly suggest that these were year-old birds, homologous with the two molting *D. plumbea* described above. At this point there is no reason to doubt that the

plumage sequence of *D. angelae* resembles that of its near relatives. The absence of a prealternate molt in first-year birds makes highly unlikely the presence of such a molt in older birds, and, in fact, we have seen no evidence for the existence of more than one molt per year in any of these species.

Skutch (1954: 385–386) has written on Parulidae as follows: "The acquisition of the adult plumage is strikingly different in the migratory and non-migratory members of this family. Young males of the migratory species go south in the immature plumage, pass the winter in that plumage, and then take on the bright nuptial attire before returning to their breeding grounds in the north. In the non-migratory Central American species of *Myioborus*, *Basileuterus*, and *Ergaticus*, the sexes of which are alike, the young of both sexes acquire a plumage essentially like that of the adult soon after leaving the nest." Even if the generalization about the migratory species were accurate, which it is not, the generalization about non-migratory parulids is best confined to the three Central American genera familiar to Skutch. It certainly does not apply to the four West Indian nonmigratory species discussed here, in which the acquisition of "adult" plumage takes even longer than it does in the northern migratory species that do fit Skutch's generalization.

STATUS OF THE ELFIN WOODS WARBLER, PAST, PRESENT, AND FUTURE

One immediately wonders (and we have been asked by many colleagues) how an avian species could have escaped detection on an island as densely populated, deforested, and repeatedly studied by ornithologists as Puerto Rico. Early collections were made by Gundlach, Wetmore, Danforth, and others, and recently the Luquillo Forest has been the scene of an intensive multidisciplinary study by Odum and a host of colleagues (Odum, 1970), including avian studies by the Rechers (1966, 1970). The forest receives over one million visitors annually, many of them enthusiastic bird watchers in pursuit of local endemics. On the other hand, this forest has historically been the least known part of Puerto Rico, and the upper slopes, including parts of the Colorado forest, most of the Sierra Palm forest, and nearly all of the Elfin Woodland, have remained in virgin condition. The Elfin Woodland, crowning as it does the high peaks, is regularly enveloped in cloud or rain, and is in many places a dense, tangled thicket that resists efforts to enter it. Because of its remoteness and inhospitable character, it has apparently been neglected by past workers, and very few visitors hike the trails and roads that now enter the forest.

The Elfin Woods Warbler itself is difficult to see, and is nowhere a common bird. Its black and white or greenish plumage is inconspicuous among the twisted vegetation, and it habitually frequents the densest parts

of the canopy, particularly those thickets where vines entangle the crown, binding it into a dense, dark mat. The bird normally forages below the exposed canopy but above the lower edge of the crown of individual trees (Kepler and Kepler, MS). Even when vocalizing it is rarely seen well, and the adult can easily be mistaken for a Black-and-white Warbler, a species common in the Elfin Woodland from September to April. Immatures are similar in appearance to a number of *Dendroica* species that also winter in Puerto Rico. The song and contact notes are similar enough to those of the Bananaquit (*Coereba flaveola*), which forms ⅔ of the breeding avifauna of the Elfin Woodland, that they are easily overlooked unless one is very familiar with the bird. It is therefore really not surprising that this species has been unrecorded in the past; indeed the senior author and his wife, living at the lower edge of the Elfin Woodland, were unaware of its existence for more than a year.

Dendroica angelae is distributed irregularly within the 450 ha of available habitat. Although we have as yet few details on the spatial requirements of individuals or pairs, we have seen foraging family groups covering an area estimated to exceed 0.5 ha. A particularly dense population of five pairs near Pico del Este is distributed along a wide 500-m strip of ridgetop, indicating that the territory may approach or exceed one hectare per pair. As tracts of apparently suitable habitat lack *Dendroica angelae*, the population will probably be found to be considerably less than would be predicted by available habitat alone. We therefore estimate, as an approximation only, that the total population at present numbers fewer than 300 pairs.

The area and character of the Elfin Woodland had changed only slightly until recent years. El Cacique has never been modified, and El Toro has been disturbed by no more than a hiking trail. A trail and narrow road were built to El Yunque, the latter about 25 years ago, and communications facilities covering several hectares installed. The greatest destruction of habitat occurred in the early 1960s with the construction of a modern road to Pico del Este. Two radar towers and other facilities were built on the peak, and the combined activity may have destroyed as much as 25 ha of prime habitat on Pico del Este, nearby Pico del Oeste, and the long ridge leading to them (see Figure 14, p. B-10, in Odum, 1970). Thus human activity in the last several years may have destroyed as much as 5 percent of the Elfin Woodland.

The entire known range of the Elfin Woods Warbler lies within the boundaries of the Luquillo Experimental Forest, administered by the Institute of Tropical Forestry, U. S. Forest Service, Department of Agriculture. Convenient public access to the Elfin Woods is confined to the trails to El Yunque and El Toro (Figure 3), although other areas can

be reached by hiking restricted roads. We feel that the difficulty of access over much of the species' range will continue to prevent undue disturbance, and, in fact, the inconspicuousness of the bird itself will protect it. Under present regulations the possession of Federal and Puerto Rico Commonwealth scientific collecting permits is not sufficient for collecting within the Luquillo Experimental Forest—this can be authorized only by the director. Although the Elfin Woods Warbler does not appear to be in any immediate danger, its continued survival is entirely dependent upon the presence of its limited undisturbed habitat, and pressures against this will continue to mount. More construction of the type recently completed on Pico del Este could destroy most of the population. We urge that the fragile nature of the interaction between the Elfin Woodland and its only endemic bird species be recognized in any future planning for the development of the Luquillo Forest. In view of the species' small population and restricted range, we have recommended that *Dendroica angelae* be placed on the lists of rare and endangered species by the U. S. Department of the Interior and the International Union for Conservation of Nature and Natural Resources (IUCN).

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SUMMARY

A new species, the Elfin Woods Warbler, is described and named *Dendroica angelae*. Confined to the Elfin Woodland forest type at high elevations in the Sierra de Luquillo, eastern Puerto Rico, it belongs to a distinctive group of endemic Antillean parulids of unknown mainland affinities, including *D. pharetra* of Jamaica, *D. plumbea* of Guadeloupe and Dominica, and "*Catharopeza*" *bishopi* of St. Vincent; the latter species is here placed in the genus *Dendroica*, as its alleged generic characters are

considered less significant than its resemblances to *D. angelae*. In warblers of this group, the juvenal plumage is, so far as known, unspotted and quickly lost, and the first basic plumage is worn for a year before the definitive plumage is attained; there is no alternate plumage. The total preferred habitat of *D. angelae* comprises about 450 ha, and the population probably does not exceed 300 pairs. A combination of factors, involving difficulty of access to and passage within this small range, and the species' visual and vocal inconspicuousness, has probably caused it to be overlooked until now. It is recommended that the Elfin Woods Warbler be placed on the list of rare and endangered species.

Resumen

Se describe una nueva especie, la Reinita del Bosque Enano (Elfin Woods Warbler), y se le da el nombre de *Dendroica angelae*. Este pájaro está confinado al tipo de bosque enano, a elevaciones altas en la Sierra de Luquillo, al este de Puerto Rico. Pertenece a un grupo característico de parulidas Antillanas endémicas, aparentemente sin afinidades conocidas con las especies continentales, incluyendo las especies *Dendroica pharetra* de Jamaica, *D. plumbea* de Guadalupe y Dominica, y "*Catharopeza*" *bishopi* de San Vicente. Esta última aparece bajo el género *Dendroica* toda vez que las características genéricas alegadas a la misma son consideradas menos significativas que su semejanza al *D. angelae*. El plumaje juvenil en las reinitas de este grupo, hasta donde se conoce, no tiene marcas y desaparece rápidamente. Estas reinitas llevan su primer plumaje básico por un año antes de obtener el plumaje definitivo y no hay en ellas plumaje alterno. El habitat preferido por el *D. angelae* ocupa un área de 450 hectáreas, aproximadamente, y su población posiblemente no excede de 300 pares. Una combinación de factores que envuelven tanto la dificultad en el acceso y penetración de esta pequeña extensión de terreno, como el hecho de que este pájaro es inconspicuo tanto visualmente como en su canto, fueron posiblemente la causa de que esta especie no fuera descubierta hasta ahora. Se recomienda que la Reinita del Bosque Enano (Elfin Woods Warbler) sea puesta en la lista de especies raras y en peligro de extinción.

Literature Cited

Barbour, T., and J. L. Peters. 1927. Two more remarkable birds from Cuba. Proc. New England Zool. Club, 9: 95–97.

Baynton, H. W. 1968. The ecology of an elfin forest in Puerto Rico. 2. The microclimate of Pico del Oeste. J. Arnold Arboretum, 49: 419–430.

Beard, J. S. 1949. The natural vegetation of the Windward and Leeward Islands. Oxford Forestry Mem., 21: 1–192.

Bond, J. 1956. Check-list of birds of the West Indies, Fourth ed. Philadelphia, Acad. Nat. Sci.

BOND, J. 1959. Fourth supplement to the check-list of birds of the West Indies (1956). Philadelphia, Acad. Nat. Sci.

BOND, J. 1961. Birds of the West Indies. Boston, Houghton, Mifflin Co.

BOND, J. 1967. Twelfth supplement to the check-list of birds of the West Indies (1956). Philadelphia, Acad. Nat. Sci.

BOND, J. 1971. Birds of the West Indies, second ed. Boston, Houghton, Mifflin Co.

BRODKORB, P. 1931. Description of a new warbler from Guadeloupe, West Indies. Proc. Biol. Soc. Washington, 44: 3–4.

GREENWAY, J. C., JR. 1958. Extinct and vanishing birds of the world. Amer. Comm. Int. Wild Life Protection, Spec. Publ. 13.

GRISCOM, L., AND A. SPRUNT, JR. (Eds.). 1957. The warblers of America. New York, Devin-Adair Co.

HOWARD, R. A. 1968. The ecology of an elfin forest in Puerto Rico. 1. Introduction and composition studies. J. Arnold Arboretum, 49: 381–418.

KEPLER, C. B., AND A. K. KEPLER. 1970. Preliminary comparison of bird species diversity and density in Luquillo and Guánica Forests. Pp. E183–186 *in* A tropical rain forest (H. T. Odum, Ed.). Oak Ridge, U. S. Atomic Energy Comm. Techn. Inform. Extension.

LEOPOLD, N. F. 1963. Checklist of birds of Puerto Rico and the Virgin Islands. Univ. Puerto Rico Agr. Exp. Sta., Bull. 168.

LOWERY, G. H., JR., AND B. L. MONROE, JR. 1968. Family Parulidae. Pp. 3–93 *in* Checklist of birds of the world, vol. 14 (R. A. Paynter, Jr., Ed.). Cambridge, Massachusetts, Mus. Comp. Zool.

MAYFIELD, H. 1960. The Kirtland's Warbler. Cranbrook Inst. Sci., Bull. 40.

ODUM, H. T. (ed.). 1970. A tropical rain forest. Oak Ridge, U.S. Atomic Energy Comm. Techn. Inform. Ext.

RECHER, H. F. 1970. Population density and seasonal changes of the avifauna in a tropical forest before and after Gamma irradiation. Pp. E69–86 *in* A tropical rain forest (H. T. Odum, Ed.). Oak Ridge, U. S. Atomic Energy Comm. Techn. Inform. Ext.

RECHER, H. F., AND J. T. RECHER. 1966. A contribution to the knowledge of the avifauna of the Sierra de Luquillo, Puerto Rico. Carib. J. Sci., 6: 151–161.

REYNARD, G. B. 1962. The rediscovery of the Puerto Rican Whip-poor-will. Living Bird, 1: 51–60.

RICHARDS, P. W. 1966. The tropical rain forest. Cambridge, Cambridge Univ. Press.

RIDGWAY, R. 1902. The birds of North and Middle America, part 2. U.S. Natl. Mus., Bull. 50, part 2.

SKUTCH, A. F. 1954. Life histories of Central American birds. Families Fringillidae, Thraupidae, Icteridae, Parulidae, and Coerebidae. Pacific Coast Avifauna, No. 31.

WADSWORTH, F. H. 1949. The development of the forest land resources of the Luquillo Mountains, Puerto Rico. Unpublished Ph.D. dissertation, Ann Arbor, Univ. Michigan.

WETMORE, A. 1927. A thrush new to science from Haiti. Proc. Biol. Soc. Washington, 40: 55–56.

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