

American Museum Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK 24, N.Y.

NUMBER 2251

JULY 8, 1966

Systematic Notes on the Bird Family Cracidae. No. 6 Reviews of Nine Species of *Penelope*

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The present paper completes my study of the genus *Penelope* and reviews the following species: *P. montagnii*, *P. ortonii*, *P. albipennis*, *P. dabbenei*, *P. superciliaris*, *P. argyrotis*, *P. jacucaca*, *P. ochrogaster*, and *P. pileata*. The other four species of the genus are *P. marail*, *P. purpurascens*, *P. jacquaçu*, and *P. obscura* which were reviewed in earlier papers in this series (1964, 1966), *P. marail* in 1964 and the other three species in 1966. In these studies of *Penelope*, I have illustrated the range of all the species by maps and given a list of the specimens examined with the exception of *P. marail*. To remedy this lack, I give a list of the specimens of *P. marail* in the present paper and illustrate its distribution in figure 2.

This study was based on the material in the collection of the American Museum of Natural History, and the collections of the Academy of Sciences of Philadelphia, the British Museum (Natural History), the Carnegie Museum, the Chicago Natural History Museum, and the United States National Museum of the Smithsonian Institution. I am indebted to the authorities of these institutions for their cooperation, the help given me during my visits, and for lending me selected specimens for further study. I also want to express my appreciation to Mr. Jean Delacour, Dr. Kenneth C. Parkes, and Mr. François Vuilleumier for discussing with me some of the forms reviewed in this paper.

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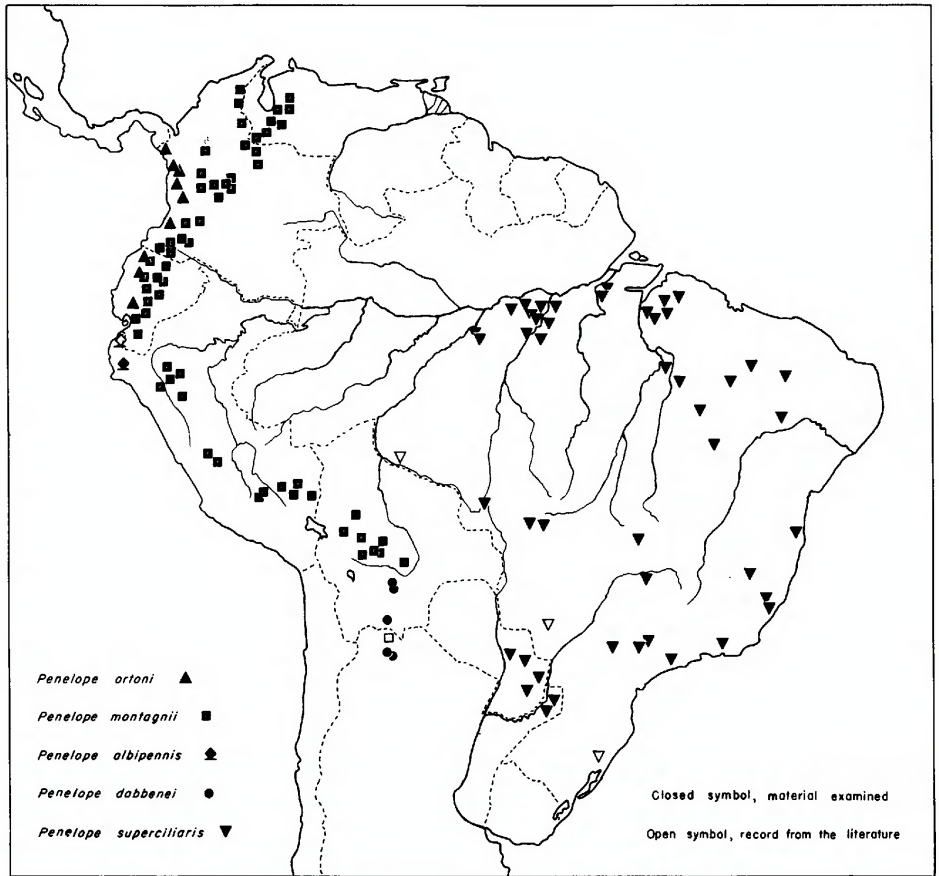


FIG. 1. Distribution of *Penelope ortoni*, *Penelope montagnii*, *Penelope albipennis*, *Penelope dabbenei*, and *Penelope superciliaris*.

Penelope montagnii

Penelope montagnii ranges in the Andes and their foothills from the Sierra de Perija in Colombia and Venezuela, and from the State of Trujillo in Venezuela, south to extreme northern Salta in Argentina. Its range is illustrated in figure 1, in which are shown the localities of the specimens that I have examined, but a number of records of *P. montagnii* (and also of *P. ortoni* and *P. superciliaris*) were omitted from regions where they are too crowded to be mapped with clarity. The record for Argentina is recent and was supplied by Olrog (1960) who reported two specimens of *P. montagnii sclateri* collected at Los Toldos, not far from the Bolivian border, by J. Gomez in February, 1960. This record was included on my map because it constitutes the southernmost for the species. Hitherto, *P. montagnii*

had not been collected or reported south of central Bolivia. This species ascends higher than any other species of *Penelope*, and the highest records indicated for the specimens that I have seen were 12,000 feet in the Central Andes of Colombia, 10,000 for Ecuador, 9400 for Peru, and 8500 for Bolivia. Los Toldos is at an elevation of 2000 meters (about 6562 feet) according to Olrog.

Penelope montagnii has been studied recently by Vuilleumier (1965, pp. 17-19) who combined with it three forms that I consider are separate species: *P. ortonii* Salvin, 1874, *P. dabbenei* Hellmayr and Conover, 1942 (which is a new name for *Penelope nigrifrons* Dabbene, 1918, preoccupied by *Penelope nigrifrons* Lesson, 1831, a synonym of *Pipile jacutinga* Spix, 1825), and *P. albipennis* Taczanowski, 1877. Some doubts about the status of *albipennis* had been expressed by Peters (1934, p. 13) who suggested that it might be a partial albino of *ortonii*, and Olrog (1960) suggested that *dabbenei* is "probably . . . an ecological form of *montagnii*." With these exceptions, *ortonii*, *dabbenei*, and *albipennis* have always been considered to be distinct species, an opinion that is certainly supported by my study.

Penelope montagnii and *Penelope ortonii*

The ranges of *P. montagnii* and *P. ortonii* meet and seem to overlap slightly in western Ecuador and perhaps neighboring southwestern Colombia, and the two birds are far too distinct morphologically to be conspecific.

Penelope ortonii is chiefly restricted to low elevations, although it ascends to at least 5100 feet in western Colombia, whereas *montagnii* is chiefly restricted to higher elevations, but their ranges overlap in western Ecuador in the regions of Paramba and Mindo. This overlap was inferred by Hellmayr and Conover (1942) when they reported that they had examined specimens of both species from Paramba, but this information received no comment from Vuilleumier. Hellmayr and Conover were correct, however, because I have seen three specimens of *P. ortonii* and two of *P. montagnii atrogularis* from that locality. The altitude at which the latter were taken was not indicated, but the specimens of *ortonii* were collected at 600 meters (about 1968 feet), 800 meters (about 2624 feet), and at 3000 feet. The two species may not have been taken at exactly the same altitude, but apparently the two are found in the valley of the Rio Mira in the vicinity of Paramba. Presumably, the range of *ortonii* ascends upward in the forest of the valley, *P. ortonii* meeting *P. montagnii atrogularis* at Paramba or a few miles above it.

This distribution is suggested by the statements of Chapman (1926, p. 714) concerning Paramba, which does not appear on standard maps. He

TABLE 1

MEASUREMENTS OF ADULT MALES OF *Penelope ortonii*, *Penelope albipennis*, *Penelope montagnii*,
Penelope dabbenei, *Penelope superciliaris*, *Penelope argyrotis*, *Penelope jacucaca*, *Penelope ochrogaster*,
 AND *Penelope pileata*

(The numbers in parentheses in the range denote the size of the sample. The standard deviation was not computed for samples of fewer than five.)

Species and Subspecies	Wing	Tail	Tarsus	Exposed Culmen
<i>P. ortonii</i>				
Mean	269.30	235.83	55.92	26.50
Range	256–295 (24)	215–263 (24)	50–60 (24)	24–31 (24)
σ	8.50	11.32	2.58	1.82
<i>P. albipennis</i> ^a	336	325	90	47 ^b
<i>P. m. montagnii</i>				
Mean	255.20	234.88	55.55	26.27
Range	240–280 (40)	212–260 (39)	50–63 (40)	22–32 (40)
σ	9.30	12.81	2.61	1.71
<i>P. m. atrogularis</i>				
Mean	249.73	223.67	56.10	26.27
Range	235–264 (11)	215–245 (9)	52–59 (11)	24–29 (11)
σ	9.32	9.13	2.50	1.26
<i>P. m. brooki</i>				
Mean	244.70	221.0	54.20	26.30
Range	225–260 (10)	207–240 (9)	50–59 (10)	23–28 (10)
σ	12.34	11.69	3.08	1.41
<i>P. m. plumosa</i>				
Mean	240.0	233.44	54.0	26.63
Range	227–250 (16)	222–245 (16)	50–58 (16)	23–30 (16)
σ	5.86	6.27	2.24	1.65
<i>P. m. sclateri</i>				
Mean	263.16	239.88	57.37	26.0
Range	246–273 (19)	223–255 (18)	53–63 (19)	23–29 (19)
σ	7.21	9.84	2.94	1.71
<i>P. dabbenei</i>				
Mean	303.14	301.0	67.57	27.43
Range	292–310 (7)	290–323 (7)	65–70 (7)	26–29 (7)
σ	6.81	11.69	2.08	1.11
<i>P. s. superciliaris</i>				
Mean	252.21	270.0	68.10	29.80
Range	243–262 (23)	250–285 (23)	63–72 (23)	28–32 (23)
σ	5.80	10.17	2.57	1.21
<i>P. s. jacupemba</i>				
Mean	251.36	269.68	67.0	29.0
Range	236–272 (25)	240–300 (25)	63–73 (25)	26–32 (25)
σ	8.32	13.46	3.28	1.54

TABLE 1—(Continued)

Species and Subspecies	Wing	Tail	Tarsus	Exposed Culmen
<i>P. s. major</i>				
Mean	259.23	275.0	69.0	29.0
Range	245–270 (9)	250–300 (9)	67–72 (9)	26–33 (9)
σ	9.16	12.84	1.83	2.14
<i>P. a. argyrotis</i>				
Mean	275.61	256.67	53.0	27.30
Range	254–302 (21)	235–275 (21)	48–57 (21)	25–32 (21)
σ	11.56	10.02	2.21	1.57
<i>P. a. colombiana</i>				
Mean	263.42	254.21	54.53	27.90
Range	248–281 (19)	240–276 (19)	51–60 (19)	25–30 (19)
σ	9.81	9.95	2.58	1.44
<i>P. a. barbata</i>				
Mean	261.16	257.0	56.83	27.67
Range	254–267 (6)	242–270 (5)	52–62 (6)	25–30 (6)
σ	5.84	9.87	3.52	1.72
<i>P. jacucaca</i>				
Mean	312.80	307.0	77.40	31.20
Range	302–340 (5)	280–335 (5)	70–86 (5)	29–33 (5)
σ	13.83	22.49	5.35	1.32
<i>P. ochrogaster</i>				
Mean	337.0	339.0	79.50	33.0
Range	333, 341 (2)	338, 340 (2)	77, 82 (2)	32, 34 (2)
<i>P. pileata</i>				
Mean	319.05	323.05	81.70	34.23
Range	295–333 (13)	290–345 (13)	73–89 (13)	29–38 (13)
σ	10.89	14.92	4.69	2.58

^a Measurements quoted from Taczanowski (1886, p. 271); an unsexed and very worn adult measured by me has a wing length of 337+, tail length 302+, tarsus length 78, and exposed culmen 34.

^b Probably denotes the total length of the bill.

wrote that it was at an altitude of 3500 feet, and, judged by his map, it seems to be situated at about latitude 0° 50' N., longitude 78° 28' W. He stated that Paramba is "A farm on the western bank of the Rio Mira [and] is in the forest region, but the open country commences 2 to 3 miles further up the Mira." Additional information was given by Brown (1941, p. 840) who said that Paramba is "An hacienda on the Rio Mera [*sic*] in the tropical forest of the western slope of the Andes. . . . Parts of the valley are very dry, others support a good stand of forest." Brown did not indicate the altitude, but he seems to be incorrect in placing Paramba at

TABLE 2

MEASUREMENTS OF ADULT FEMALES OF *Penelope ortonii*, *Penelope albipennis*, *Penelope montagnii*,
Penelope dabbenei, *Penelope superciliaris*, *Penelope argyrotis*, *Penelope jacucaca*,
Penelope ochrogaster, AND *Penelope pileata*

(The numbers in parentheses in the range denote the size of the sample. The standard deviation was not computed for samples of fewer than five.)

Species and Subspecies	Wing	Tail	Tarsus	Exposed Culmen
<i>P. ortonii</i>				
Mean	260.43	228.10	53.70	26.04
Range	244-280 (23)	210-248 (23)	49-57 (23)	22-29 (23)
σ	9.02	9.54	2.71	1.75
<i>P. albipennis</i> ^a	325	325	78	51
<i>P. m. montagnii</i>				
Mean	247.44	234.37	54.22	26.45
Range	231-261 (23)	210-253 (24)	50-60 (23)	21-32 (24)
σ	6.64	11.98	2.26	2.02
<i>P. m. atrogularis</i>				
Mean	244.56	223.0	55.10	25.67
Range	232-252 (9)	212-232 (9)	52-59 (9)	24-27 (9)
σ	7.38	8.84	2.14	1.29
<i>P. m. brooki</i>				
Mean	238.62	218.28	53.46	26.10
Range	223-255 (11)	200-228 (11)	49-57 (11)	24-28 (11)
σ	9.17	9.17	2.01	1.44
<i>P. m. plumosa</i>				
Mean	232.87	223.50	53.12	25.12
Range	213-245 (8)	212-242 (8)	51-55 (8)	23-28 (8)
σ	10.55	9.91	1.45	1.45
<i>P. m. sclateri</i>				
Mean	252.0	237.81	56.32	25.32
Range	240-277 (16)	226-250 (16)	53-59 (16)	23-28 (16)
σ	6.99	6.68	1.75	1.41
<i>P. dabbenei</i>				
Mean	293.75	285.0	66.0	27.50
Range	285-303 (4)	270-295 (4)	65-67 (4)	25-31 (4)
<i>P. s. superciliaris</i>				
Mean	243.48	267.25	66.30	29.10
Range	228-258 (21)	243-290 (20)	63-73 (21)	27-32 (21)
σ	7.66	12.91	2.39	1.32
<i>P. s. jacubempha</i>				
Mean	244.84	263.10	65.0	27.48
Range	230-260 (19)	240-285 (19)	60-69 (19)	25-32 (19)
σ	7.22	11.98	2.69	1.39
<i>P. s. major</i>				
Mean	247.0	262.0	65.72	28.0
Range	243-250 (6)	250-270 (6)	63-68 (6)	27-29 (6)
σ	2.09	8.12	1.89	1.33

TABLE 2—(Continued)

Species and Subspecies	Wing	Tail	Tarsus	Exposed Culmen
<i>P. a. argyrotis</i>				
Mean	265.15	252.70	53.25	26.65
Range	254–281 (20)	240–265 (20)	49–59 (20)	25–30 (20)
σ	7.04	6.41	2.64	1.31
<i>P. a. colombiana</i>				
Mean	254.21	254.57	53.38	26.70
Range	242–268 (16)	230–268 (16)	49–59 (16)	25–28 (16)
σ	6.40	9.53	2.84	1.18
<i>P. a. barbata</i>				
Mean	251.10	239.20	55.83	27.33
Range	241–256 (6)	230–258 (5)	52–62 (6)	25–30 (6)
σ	5.41	8.63	3.34	1.62
<i>P. jacucaca</i>				
Mean	287.75	283.75	74.50	28.75
Range	277–302 (4)	270–305 (4)	67–80 (4)	26–30 (4)
<i>P. ochrogaster</i>	327 (1)	345 (1)	79 (1)	29 (1)
<i>P. pileata</i>				
Mean	306.44	314.55	78.34	31.56
Range	292–315 (9)	297–326 (9)	73–87 (9)	30–32 (9)
σ	9.04	10.48	4.18	1.43

^a Measurements quoted from Taczanowski (1886, p. 271); the measurement of the bill probably denotes that of the total length of the bill.

"1° 11' N., 78° 21' W." Such a location would put Paramba in Colombia north of the Rio San Juan which forms the frontier between Ecuador and Colombia. If some parts of the valley of the Rio Mira near Paramba offer a choice of habitat, it explains perhaps the occurrence of the two species in this region.

The two species have been collected also at Mindo, which is south of Paramba at an altitude of 4086 feet, at about latitude 0° 03' S., longitude 78° 48' W. Mindo is the type locality of *P. ortonii*, and from this locality I have examined a specimen of *P. montagnii atrogularis* that was shot at 1200 meters (about 3937 feet) by Gomez in 1939. To be sure, Salvin (1874, p. 326) stated in the description of *P. ortonii* that its type and "single specimen obtained . . . was shot near a place called Mindo . . . at an elevation of about 6,000 or 7,000 feet," but Hellmayr and Conover have remarked that "Mindó being only a little over 4,000 feet above sea level, the altitude indicated by Salvin cannot be correct." It appears, therefore, that the two species have been taken at virtually the same altitude and locality, and I may add that I have examined about half a dozen specimens each of the

two species from various localities (though not the same) in the general vicinity of Mindo.

It is possible also that the ranges of the two species meet or approach closely in southwestern Colombia in the valley of the upper Rio San Juan, because I have seen a specimen of *P. montagnii atrogularis* that was taken at Mayasquer in 1941 by von Sneider. The altitude was not indicated, but, according to de Schauensee (1948, p. 310), the birds were collected by von Sneider between 1300 and 2700 meters, or between about 4260 and 8850 feet.

The actual zone of overlap between *P. ortoni* and *P. montagnii* is probably narrow and may have been promoted by man-made changes, such as deforestation, but the evidence given above shows that they are not strict geographical representatives. I also cannot agree with Vuilleumier's statement that "*Penelope ortoni* is certainly closely related to *P. montagnii atrogularis* (color of upper parts and crown), and *montagnii plumosa* (color of under parts), and should be included in *montagnii*, of which it is a representative in the lowlands of western Colombia and western Ecuador." The distribution is discussed above. The similarity postulated by Vuilleumier is flatly contradicted by the facts.

The morphological differences that separate these birds are very sharp. The crest of *P. ortoni* is very poorly developed for a *Penelope*, and its feathers are rounded, dark brown, and uniform in coloration, whereas the crest of all the races of *P. montagnii* is well developed and consists of feathers that are more or less elongated and attenuated and invariably edged with silvery gray, the shape of the feathers and the width of the pale edges varying geographically. In addition, the feathers of the hind neck, mantle, malar region, sides of the neck, and upper wing coverts are strictly uniform in coloration in *P. ortoni*. They have no pale edges of any kind, whereas the feathers of the malar region and sides of the neck are conspicuously edged with gray in all the races of *P. montagnii*, and those of the hind neck, mantle, and coverts are also edged with gray (or buff in the case of the mantle and coverts) to a geographically variable degree. Vuilleumier implied that the coloration of the upper parts and crown is similar in *P. ortoni* and *P. montagnii atrogularis*, but, although the ground coloration is brown in both, this implication ignores the conspicuous differences in pattern mentioned above, differences in color pattern being an important taxonomic character in *Penelope* which distinguish a number of species. The color of the under parts is not similar in *P. ortoni* and *P. montagnii plumosa*, the latter being bright rufous below the breast as against sepia brown in *P. ortoni*, and the pattern of the markings is also quite different. In *P. montagnii plumosa*, the pale edges of the feathers do not meet

at the tip and form streaks which become progressively narrower and more scanty on the center of the abdomen, whereas the pale markings of *P. ortonii* are broad, meet at the tip, become more conspicuous on the abdomen and extend farther down. Also, the throat of *P. ortonii* is much less feathered than that of the populations of *P. montagnii*, which range from Venezuela south to Peru, and it is a considerably bigger bird (tables 1 and 2). No intermediates between *P. ortonii* and *P. montagnii* are known.

Some of the morphological characters of *P. ortonii* are, in fact, rather unusual for *Penelope*, and this observation led Hellmayr and Conover (1942, p. 145) to remark that "*Penelope ortonii* is rather an isolated species," an observation that has been confirmed by my own study of this genus. The nearest relative of *P. ortonii* is not clear to me, but it does not appear to be *P. montagnii*.

Penelope albipennis

Penelope albipennis is extinct and one of the rarest birds in the world, as it is known from only three specimens, which were collected in the departments of Tumbes and Piura in northwestern Peru. Peters (1934, p. 13) stated that it was a "unique" form, but it was actually known for a long time from two specimens: the type (a male) which was collected by Stolzmann on December 18, 1876, at Santa Lucia near Tumbes and which is now in the collection of the Natural History Museum of Poland in Warsaw, and a female which was collected on January 10, 1877, by M. Jelski at the Hacienda de Pabur near Piura and which is in the collection of the Museo de Historia Natural Xavier Prado of Lima. But in 1963 I "discovered" a third specimen, an unsexed adult, in the collection of the British Museum (Natural History) which had been received in exchange with the Museo Xavier Prado. This specimen is labeled also "Hacienda de Pabur," but the date at which it was taken and the name of the collector are not mentioned, although there is good reason to believe that it may have been the young bird that was taken alive by Jelski at Hacienda de Pabur on January 10, 1877, when he shot its mother. Jelski gave it to Stolzmann who gave (1886, p. 272) a long account of this bird which he raised and eventually gave to Raimondi in Lima. The bird became a great pet but was accidentally killed.

I found later that my "discovery" had been anticipated by Morrison (1948), but his belief that the specimen in Lima is the type of *albipennis* is incorrect, because the only specimen available to Taczanowski (1877) when he described *albipennis* was the one that Stolzmann had collected at Santa Lucia. Morrison mentioned also Raimondi's pet and wrote that there was no record that it was preserved as a specimen, which is true,

but I am not sure that he is correct when he wrote that the specimen showed no sign of having been a captive, because it is extremely worn, more so than one would expect for a wild bird. It also seems logical that Raimondi would have preserved a bird that he knew to be rare, very difficult to procure, and on the verge of extinction.

The specimen in London differs from all known forms of *Penelope* by having the eight outer pairs of primaries white, but more or less dusky at the base and tip. The ninth primary is brown except at the center which is whitish. I have not seen the other two specimens, but the meticulous description of the type by Taczanowski (1877), and of the type and the female (1886, p. 271), leave no doubt whatever that the three specimens are similar. This point is important, and two other observations that have a direct bearing on the status of *P. albipennis* concern the feathers of the crest, which are edged with grayish white, and the large size of the three specimens. In the unsexed specimen, which I have examined, the wing measures 337 mm. and the tail 302, but these measurements can conservatively be increased by another 10 mm., as the tips of the feathers are very badly worn. The tarsus measures 78 mm. The measurements given by Taczanowski (1886, p. 271) are: male, wing, 336; tail, 325; tarsus, 90; female, wing, 325; tail, 325; tarsus, 78.

In 1877, Taczanowski considered the possibility that the specimen he had was a partial albino, but he rejected this interpretation because Stolzmann assured him repeatedly that all the birds he had seen had white wings, "*M. Stolzmann avant de se procurer l'exemplaire a répété plusieurs fois dans ses lettres, que toutes les Pénélopes qu'il a vues au vol dans cette localité avaient l'extrémité des ailes blanches, ce qui m'a décidé à le considérer comme forme distincte.*"

Peters (1934) and Vuilleumier (1965), who have revived the theory that *albipennis* is only an albinistic variant, seemed to discount the statements of Stolzmann, but Stolzmann was reliable and painstaking, and he said (1886) that he undertook no fewer than eight trips to collect this bird. He did not find it every time, but the mangroves into which *albipennis* had retreated because of persistent persecution were virtually inaccessible, and he was able to shoot only three birds, only one of which he secured. But he saw others and estimated that the population of the Santa Lucia swamps consisted of about 15 pairs, although it may well have been more numerous but difficult to count because of the terrain. I may add that *P. albipennis* was collected also at Hacienda de Pabur, about 205 kilometers south of Santa Lucia, and that Stolzmann said he had no doubt that it is or was found at other localities from the border of Ecuador, where it had been reported at the mouth of the Rio Zurumilla, south

through Lambayeque and Nancho to the valley of the Rio Chicama in Trujillo. The statements of Stolzmann and the fact that all the three birds in existence have white wings make it most unlikely that *P. albipennis* is only an albinistic variant.

Peters (1934) and Vuilleumier (1965) went further than Taczanowski (who did not revive the albinistic theory in 1886), and suggested that *P. albipennis* is a partial albino of *P. ortoni*. This interpretation can be rejected at once because *P. ortoni* is very much smaller than *P. albipennis* (tables 1 and 2) and the feathers of its crown are perfectly uniform in coloration and they lack the pale edges of those of *P. albipennis* (and also those of *P. montagnii* as emphasized above). Males of *P. ortoni*, which are larger than females, measure in 24 specimens: wing, 256–295 (269.30); tail, 215–263 (235.83); and tarsus, 50–60 (55.92).

Vuilleumier (1965), to support his belief, mentioned a series in the collection of the Academy of Sciences of Philadelphia "collected by A. de Buey in the Choco"¹ in which a number of specimens are in a very abnormal plumage which he interpreted as partial albinism. In these birds, which I have examined, some of the primaries, secondaries, rectrices, primary and upper wing coverts, and feathers of the crown, sides and back of the neck, breast, abdomen, and back are isabelline white, buff, or cinnamon to an extremely individually variable extent, but other specimens in the series have the normal plumage of *P. ortoni*. The pale feathers appear "bleached," but fading is not the correct interpretation, because only individual feathers here and there are involved, and some of them are darker at the tip than on the protected base of the feather. We are not dealing with a plumage stage either, because the pale and normal feathers show about the same degree of wear, but it is of interest to note that some of these birds are molting and that the new feathers which are still growing are all brown and normal in coloration. This abnormality probably reflects some physiological disturbance but does not seem to be a true case of albinism. Moreover, these abnormal birds do not throw any light on the status of *P. albipennis* because they are similar in size to *P. ortoni*, and their normal feathers are also identical to those of *P. ortoni*.

The other subspecies of *Penelope* that approach the range of *P. albipennis* are *P. montagnii atrogularis*, *P. montagnii plumosa*, *P. argyrotis barbata*, and *P. purpurascens aequatorialis*. The feathers of the crown are edged with pale

¹ Alto del Buey is the name of an isolated mountain in the Choco, not the name of a collector. The specimens concerned were collected by von Sneidern at Alto del Buey on the Rio Jurubida between June 9 and 20, 1940, and on July 5, 1940, on the Rio Baudo side of Alto del Buey.

gray (as in *P. albipennis*) in the first three birds, but their measurements are all very much smaller than those of *P. albipennis*. In *P. purpurascens aequatorialis* the feathers of the crown are uniform in coloration (as in *P. ortonii*), and *aequatorialis* is a larger bird than *P. albipennis*. It also differs from *P. albipennis* in other respects, being strongly rufous on the lower back, rump, lower abdomen, crissum, and upper and under tail coverts, whereas these parts are all dark olive in *P. albipennis*.

In conclusion, I do not believe that *P. albipennis* can be regarded as other than a very distinct species which apparently became extinct toward the end of the nineteenth century as the result of persistent persecution. Stolzmann (1886) has fortunately left us an account of this bird in life, but it is incomplete and was made under abnormal conditions when it was on the verge of extinction. The color of the soft parts mentioned by Taczanowski (1877, 1886), and on the label of the specimen that I have seen, indicates that the bare skin of the face was dark purplish blue, the bare skin of the throat orange or red, the bill bright blue with a blackish tip, and the feet red or brownish red. Taczanowski mentioned also that the iris was pale brown.

Penelope dabbenei

Penelope dabbenei is a large species, with a mean wing length of about 300 mm., which is poorly represented in collections and not well known. Its range is restricted and extends along the lower slopes of the eastern Andes from the departments of Chuquisaca and Tarija in southern Bolivia south to the region above Calilegua in eastern Jujuy in Argentina, or to about latitude 23° 47' S. Its range and that of *P. obscura bridgesi* overlap, and the range of *dabbenei* may overlap also that of *P. montagnii sclateri*, or, if not, the ranges of these two birds approach very closely in Argentina (fig. 1). The three species seem to inhabit more or less the same zone in the forest and have been taken at about the same altitudes in Argentina—*dabbenei* from 5900 to 6500 feet, *montagnii* at 6500 feet, and *obscura* a little lower at 5000 feet.

The nearest relative of *dabbenei* seems to me to be *obscura*, not *montagnii* with which *dabbenei* has been said to be allied and even conspecific. The conspecificity is suggested by the fact that *dabbenei* is more similar in size and coloration to *obscura* than it is to *montagnii*, and it has a brown tarsus in life. The tarsus is black or blackish brown in life in *obscura*, but is red in *montagnii*. This character is important because a sharp difference in the color of the skin is apparently of species importance in *Penelope* (Vaurie, 1966). To be sure, *dabbenei* and *obscura* are not conspecific. They are sympatric, but if the fact were not known one could infer that they

are not conspecific by noting that the bare skin of the face is red in life in *dabbenei*, as against dark slaty blue in *obscura*, but, as the skin of the face is dark slaty blue also in *montagnii*, it seems to follow that *montagnii* is not conspecific with *dabbenei*.

The differences in the color of the skin in life were not taken into consideration by the authors who believed that *dabbenei* and *montagnii* are closely related. Hellmayr and Conover (1942) stated that *dabbenei* "judging from the slender, pale brown legs and the presence of a shallow gular lappet is allied to *P. m[ontagnii] sclateri*." Such an argument is not convincing, as all the species of *Penelope* have a gular lappet, the tarsus of *dabbenei* is not slender but very distinctly larger and thicker than that of *P. montagnii sclateri*, and the tarsus of the latter is red in life, not brown, as stated above.

Olrog (1960) went further than Hellmayr and Conover, and, in the English summary of his paper, he pointed out that although "the relation between [*P. montagnii*] and *Penelope dabbenei* is somewhat problematic . . . the latter probably ought to be considered as an ecological form of *montagnii*." In the Spanish text, he wrote that apparently *dabbenei* inhabits a more humid type of highland forest than *montagnii*, but added that such a possibility had not been completely confirmed. Vuilleumier (1965) stated that Olrog (1960) has "rightly showed that *dabbenei* . . . is only a subspecies of *montagnii*." But Olrog was more cautious, and, in his subsequent check list of the birds of Argentina (1963), he listed *dabbenei* formally as "*Penelope (montagnii) dabbenei*," which expresses some doubt about its taxonomic status.

Olrog (1960) took into consideration only the differences in the coloration of the plumage and in measurements. He dismissed the former as not important and only relative and doubted that an appreciable difference in size exists, although the fact that *dabbenei* is larger than *P. montagnii sclateri* is evident at a glance without taking measurements. He wrote that in his measurements the wing length of the largest female of *P. montagnii sclateri* is only 2 mm. shorter than that of the smallest female of *P. dabbenei*; the wing lengths he gave as 252–271 in eight males, and 249–273 in nine females, of *P. montagnii sclateri*, versus 285–320 in eight males, and 275–299 in six females, of *P. dabbenei*. These measurements are a composite series, as only nine of the 31 were taken by Olrog, one was quoted from Hellmayr and Conover (1942), and the other 21 were taken from Bond and de Schauensee (1943). In 46 specimens that I have measured, the wing length measures 246–273 (263.16) in 19 males, and 240–277 (252.0) in 16 females, of *P. montagnii sclateri*, 292–310 (303.14) in seven males, and 285–303 (293.75) in four females, of *P. dabbenei*.

The measurements taken by different workers are apt to vary by a few millimeters, especially in the case of such large birds, but, although the range of the measurements is roughly comparable in Olrog's series and mine, the mean wing length, which is the most significant indication of relative size, was not given by Olrog. In this instance, the mean wing length of male *dabbenei* is about 40 mm. greater than that of male *P. montagnii sclateri*, and the mean of the females is nearly 42 mm. greater, a very important difference.

I did not measure a female of *dabbenei* with such a small wing length of 275 mm., as Olrog did. On the other hand, *dabbenei* can be even larger than my measurements indicate, as Olrog measured a male with a wing of 320 mm., as against 310 for the largest male I measured. It is possible that the female of *dabbenei* with a wing length of 275 mm. was not fully adult, and hence was small, as it is not always possible in the Cracidae to be certain that a specimen is a fully adult bird or not.

Olrog (1960) stated that the tarsus is about equal in length in *P. montagnii sclateri* and *P. dabbenei*, measuring "58" in the former and "60" in the latter, but these measurements are not confirmed by mine, or by the measurement of the specimen of *dabbenei* reported by Hellmayr and Conover (1942), the length of the wing of which was included by Olrog in his measurements. The tarsus in this bird (a male) measures 70 mm., according to Hellmayr and Conover, although, when I examined it, I measured its tarsus as 68 mm. In the series that I have measured, the mean length of the tarsus, in round numbers, is 57 in males and 56 in females of *P. montagnii sclateri*, as against 67 in males and 66 in females of *P. dabbenei*.

The wing and the tarsus are therefore much longer in *P. dabbenei* than in *P. montagnii sclateri*, and the difference in size between the two species is even greater in the case of the length of the tail (tables 1 and 2). It is difficult to account for the sharp difference in measurements (not to speak of the sharp differences in the colors of the skin of the face and tarsus) by a difference in ecological requirements, which is only relative according to Olrog. A difference in ecology in congeneric birds that inhabit more or less the same zone in the forest would, moreover, strengthen rather than weaken the probability that they are not conspecific. In short, it seems clear that *montagnii* and *dabbenei* are not conspecific. I believe also that they are not closely related and that the closest relative of *dabbenei* is very probably *obscura*, as stated above.

The measurements of *P. obscura* may be added for comparison. The lengths of the wing and tarsus measure, respectively: 291–346 (328.1), 72–85 (78.5) in 19 males, 298–335 (322.0), 72–84 (77.5) in nine females,

of *P. obscura bridgesi*; 304–323 (315.4), 70–81 (75.0) in five males, 270–309 (294.0), 71–79 (74.1) in eight females, of *P. obscura bronzina*; and 301–305 (303.6), 68–77 (72.3) in three males, and 285–301 (290.3), 65–72 (68.0) in three females, of nominate *obscura*. The last-named is similar in size to *dabbenei*, but, as one might expect, *P. obscura bridgesi* which overlaps *dabbenei* is appreciably larger, the difference in size being less well marked than that between *dabbenei* and *P. montagnii sclateri*.

GEOGRAPHICAL VARIATION IN *Penelope montagnii*

Penelope montagnii varies geographically, the variation, which is chiefly clinal, involving differences in size (tables 1 and 2), the feathering of the throat, the development of the gray margins of the head, the markings on the mantle, upper wing coverts, breast, and abdomen, and the ground coloration of the back, rump, and under parts. There are also variations in the color of the bill which is paler at the tip in some subspecies than in others. Six subspecies have been described, but it seems to me that the geographical variation is adequately represented by the recognition of only five.

1. *Penelope montagnii montagnii* Bonaparte, 1856, type locality, "Nouvelle Grenade," i.e., Colombia. The type is a trade skin from Bogota, and Chapman (1917, p. 194) has suggested El Piñon, above Fusagasuga, Cundinamarca, Colombia, as the type locality. In the nominate race, the throat is heavily feathered, with the exception of a bare spot of restricted size in the center, and all the feathers of the throat, malar region, sides and back of the neck, superciliary streak, and crown are very well margined with pale ashy gray. The pale margins of the feathers of the mantle are usually not well developed, being obsolete in some specimens, and when present are restricted chiefly to the upper mantle; on the lower part of the mantle and on the upper wing coverts, the whitish or buffy edges are replaced by narrow rufous edges. The pale margins of the under parts are well developed, however, and are continuous around the tip of the feather, giving the under parts a "scalloped" appearance. The ground color of the back is dark warm brown, the rump and upper tail coverts are chestnut, and the ground color of the abdomen is more or less russet, contrasting with the ground color of the breast which is dark olive brown. The bill is brownish, with a paler tip.

This subspecies ranges from the Sierra de Perija in Colombia and Venezuela, and the Andes in the State of Trujillo in Venezuela, south through the Eastern and Central Andes of Colombia to Nariño, but the southern limits of its range are difficult to define because it intergrades along the slopes of the Andes of Nariño with *atrogularis* in the west and

with *brooki* in the east. The population from the eastern slopes was called *brooki* by de Schauensee (1964, p. 63). The only specimens that I have seen from this region are two from the region of Puerres which are about intermediate between nominate *montagnii* and *brooki* but more similar to the latter. Specimens that I have seen from the southwestern slopes of Nariño are indistinguishable from *atrogularis*, but, farther north, *atrogularis* most probably intergrades with nominate *montagnii*. The zone of intergradation must be very extensive, because all the specimens that I have seen from the Central Andes from Cauca north to Caldas are more or less intermediate. This intermediate population has been discussed by Hellmayr and Conover (1932). It varies individually but is best referred to nominate *montagnii*. The account of the subspecific characters of nominate *montagnii* given above was based by me on specimens from Venezuela, the Sierra de Perija, and from the Eastern Andes south to and including Cundinamarca, where nominate *montagnii* is constant.

2. *Penelope montagnii atrogularis* Hellmayr and Conover, 1932, type locality, Alaspungo, western Ecuador. This subspecies averages a little smaller than nominate *montagnii*, but differs chiefly from it by being distinctly less heavily feathered on the throat, and by having narrower and fainter pale edges on the feathers of the malar region, sides and back of the neck, superciliary streak, and crown. On the throat of *atrogularis*, the feathers are restricted to the upper throat and chin and are blackish and more decomposed than in nominate *montagnii*. The ground color of the abdomen is darker than in nominate *montagnii*, less russet, and the tip of the bill is paler. *Atrogularis* ranges from the southwestern slopes of the Andes of Nariño in Colombia, southward through western Ecuador to Azuay.

3. *Penelope montagnii brooki* Chubb, 1917, type locality, Baeza, eastern Ecuador. Chapman (1926, p. 153) stated, "It is probable that the type came from *above* not *at* Baeza," and Hellmayr and Conover (1942, p. 152) accepted this modification of the type locality. I see no reason to modify the type locality, because the label of the type, which I have examined, mentions only Baeza which is situated at an altitude of 1908 meters and hence is not impossible as a locality. Chapman may have been influenced by his series that had been collected by the Olallas "above Baeza," which he referred to as "topotypes."

This subspecies presents some characters of both nominate *montagnii* and *atrogularis*, but it differs from them by being distinctly duller and darker, less rufescent on the back, rump, upper tail coverts, and under parts. The rump and upper tail coverts are auburn and the back is bronzy-brown, with a faint greenish gloss, whereas the rump and upper

tail coverts are chestnut and the back is warm brown in nominate *montagnii* and *atrogularis*. The extent of the feathering on the throat of *brookii* is similar to that of *atrogularis*, but the feathers are even more blackish and decomposed. The pale grayish margins of the feathers of the malar region, sides of the neck, superciliary streak, and crown are about as well developed as in nominate *montagnii*, but those of the hind neck, upper mantle, breast, and abdomen are better developed than in the latter, broader and more conspicuous. The tip of the bill is paler than in *atrogularis*, yellowish, and contrasts with the dark base. Typical *brookii* seems to be restricted to eastern Ecuador, but the eastern slopes of the Andes of Nariño in Colombia are probably best included in the range of *brookii*, although the population from this region is apparently somewhat intermediate between *brookii* and nominate *montagnii*.

4. *Penelope montagnii plumosa* Berlepsch and Stolzmann, 1902, type locality, Maraynioc, Junin, Peru. Synonym: *Penelope montagnii marcapatensis* Blake, 1962, type locality, Chilichili, Marcapata, Cuzco, Peru. This subspecies differs distinctly from nominate *montagnii*, *atrogularis*, and *brookii*, which form one group, and belongs to a second group composed of *plumosa* and *sclateri*. The geographical variation is clinal in both groups, and presumably the two groups are connected by intermediate forms, but I have not seen a specimen that is truly intermediate.

The subspecies of the second group (*plumosa* and *sclateri*) differ from the subspecies of the first group by being brighter below, more rufescent, and by having the pale margins of the feathers of the under parts restricted to the sides of the individual feather and lacking at the tip, thus giving to the under parts a streaked rather than scalloped appearance. The pale edges are also better developed on the head, mantle, and upper wing coverts. *Plumosa* differs from *sclateri* by averaging distinctly smaller (tables 1 and 2), by being much better feathered on the upper throat, which is very scantily feathered in *sclateri*, and by having the feathers of the superciliary streak and malar region less profusely variegated with pale gray, whereas the streak and malar region are very "silvery" in *sclateri*. On the other hand, the pale edges are very much better developed on the hind neck and upper mantle of *plumosa*, as the hind neck of *sclateri* is uniformly brown, not streaked, and the upper mantle is virtually uniform, showing only a few faint streaks. *Plumosa* is also more profusely streaked below than *sclateri*, more rufous below, more brownish above, less bronzy-green, than *sclateri*. The bill is dark in both subspecies, uniform in coloration.

The range of *plumosa* is restricted to eastern Peru, but it grades into *sclateri* in the southeast. One specimen from Huaisampilla, northeast of Paucartambo, which I have seen in the British Museum, shows a tendency

toward *sclateri*, and this tendency is shown to a progressively greater degree by three specimens from the region of Marcapata, southeast of Paucartambo, and by a small series of five specimens from the region of Oconeque, southeast of Marcapata, but all these birds are much more similar to *plumosa* from farther north in Peru than they are to *sclateri* from Bolivia. It is very clear that the geographical variation is clinal. The specimens from Marcapata are in the collection of the Chicago Natural History Museum, and those from Oconeque are in the collections of the Academy of Natural Sciences of Philadelphia and of the American Museum of Natural History.

The birds from Marcapata and Oconeque were named *marcapatensis* by Blake (1962), but, as this form represents only a stage on the cline, it seems to me that its nomenclatural separation is not warranted. I believe, therefore, that *marcapatensis* should be synonymized with *plumosa* to which it is "nearest" as stated by Blake. Some other populations of this species are intermediate on clines, as mentioned above, and it seems sufficient to call attention to them without separating them as subspecies.

5. *Penelope montagnii sclateri* G. R. Gray, 1860, type locality, Bolivia. The locality or region where the type was taken is not known, but the type locality of *sclateri* is restricted herein to the Yungas de la Paz which seem to have been visited by T. C. Bridges, the collector. This well-differentiated subspecies was compared to *plumosa* above. It inhabits the yungas of Bolivia, south to the Departamento de Santa Victoria in extreme northern Salta, Argentina.

Penelope superciliaris

Penelope superciliaris has a very great range which extends (fig. 1) from the right bank of the Rio Guaporé and the Rio Madeira eastward through Brazil, south of the Amazon, to northeastern Para and south to eastern Paraguay, Misiones in northeastern Argentina, and Rio Grande do Sul in southeastern Brazil. It differs from all the other species of *Penelope* by having the scapulars, upper wing coverts, and secondaries conspicuously edged with rufous ocher or chestnut. The presence of a superciliary streak is not peculiar to *P. superciliaris*, as it is present in a number of other species of *Penelope*. It varies geographically, the variation affecting chiefly the width and shade of the rufous edgings, although the development of the superciliary streak, general coloration, and size vary also geographically. The geographical variation is slight, but three subspecies can be recognized.

Penelope superciliaris superciliaris Temminck, 1815, type locality, "Brésil, et plus particulièrement dans le district de Para," restricted to the region of

Belem by Oliveira Pinto (1964, p. 106). Synonym: *Penelope superciliaris pseudonyma* Neumann, 1933a, type locality, "Rio de Cumana," i.e., Rio Canuma, an affluent of the Rio Madeira. This subspecies ranges from the Guaporé and Madeira eastward to Para. It varies individually, but the specimens I have seen show no evidence of geographical variation. Neumann (1933a) renamed this subspecies *pseudonyma* after shifting the type locality of *superciliaris* Temminck to Bahia, discussing the type locality at greater length in a subsequent paper (1933b), but Hellmayr and Conover (1942) have shown conclusively that Neumann's action was totally unwarranted.

Penelope superciliaris jacupemba Spix, 1825, type locality, Presidio de São João, near Rio de Janeiro. Synonyms: *Penelope superciliaris argyromitra* Neumann, 1933a, type locality, Veadeiros, northwest of Forte, central Goyaz; and *Penelope superciliaris ochromitra* Neumann, 1933a, type locality, Lagoa da Missão, near Parnagua, southern Piauhy. This subspecies replaces nominate *superciliaris* from Maranhão southward through eastern and central Brazil, but not south to the states of Santa Catharina and Rio Grande do Sul where it is replaced by *major*. It differs from nominate *superciliaris* by being paler, duller, more grayish above, having the rufous edges on the scapulars, coverts, and secondaries paler and wider, and its superciliary streak better defined, varying individually from grayish or buffy white to ochraceous, whereas it is not ochraceous in nominate *superciliaris*. The individual variation is more pronounced in *jacupemba* than in nominate *superciliaris* and has been discussed by Hellmayr (1929) and Hellmayr and Conover (1942).

The specimens that I have seen from Goyaz and the Mato Grosso, including a paratype of *argyromitra*, differ in no way geographically from birds from Rio de Janeiro and São Paulo, and it is certain that *argyromitra* is not valid. Peters (1943) believed that it was, after comparing the type of *argyromitra* (which is in the collection of the Museum of Comparative Zoölogy) with specimens from the lower Tapajoz, but the latter are nominate *superciliaris* and hence are distinct, whereas the comparison should have been made with *jacupemba*.

The superciliary streak is more ochraceous, as a rule, in the specimens from Maranhão, Piauhy, and northern Goyaz, than in specimens taken farther south from Bahia to São Paulo, and those from Maranhão, Piauhy, and northern Goyaz average also somewhat paler above. But, as some individuals from the south match others from the north, and my material confirms the degree of individual variation noted by Hellmayr (1929), it is best to synonymize *ochromitra* with *jacupemba*. The amount of material that I saw was considerably larger than that examined by Hellmayr.

Penelope superciliaris major Bertoni, 1901, type locality, latitude 25° 43' S. on the Rio Parana, southeastern Paraguay. This subspecies ranges from eastern Paraguay and Misiones to Santa Catharina and Rio Grande do Sul in southeastern Brazil and is not strongly differentiated, but in *major* the rufous edges of the scapulars, coverts, and secondaries are considerably narrower than in *jacupemba* and nominate *superciliaris*. The upper parts are also darker, more olive, and the wing averages a little longer in *major* (tables 1 and 2). The characters of *major* appear to be more constant than those of the other two subspecies.

Penelope argyrotis

Penelope argyrotis differs from all the other species of *Penelope* by having the brown tail feathers broadly tipped with auburn, cinnamon, or dingy white more or less tinged with cinnamon; a pale tip is present on the top and central pair of feathers but is more restricted and less well defined than on the outer pairs. The fact that the tail is not uniform in coloration in *P. argyrotis* probably implies that *Penelope* is not distantly related to *Ortalis*, in which the outer tail feathers are broadly tipped with chestnut, cinnamon, or white in all the species. Nevertheless, *P. argyrotis* is a true *Penelope* and not intermediate between that genus and *Ortalis* in any other character. Moreover, the pattern of the tail is not identical as the central pair is dark in *Ortalis*, not tipped, whereas the pale tips on the outer pairs are much better developed than in *P. argyrotis*, in some cases invading virtually the whole of the feather. The difference in pattern seems, however, to be only one of degree.

Penelope argyrotis inhabits (fig. 2) southwestern Ecuador and northwestern Peru, the Santa Marta Massif, and the Andes of Colombia and Venezuela, ranging in the Andes from the Sierra de Perija south to at least the regions of Cachiri in Santander and the Rio Negro in northern Boyaca in the Eastern Andes of Colombia, and east through the Andes and cordilleras of northern Venezuela to Monagas.

The populations of Ecuador and Peru (*barbata*) and of Santa Marta (*colombiana*) are very well differentiated from each other and from the population (nominate *argyrotis*) of the Sierra de Perija and the Andes, and are isolated, or are probably isolated geographically, from nominate *argyrotis*. The isolation is obvious in the case of *barbata*, but the ranges of *colombiana* and nominate *argyrotis* are close (it is impossible to illustrate a gap in distribution in fig. 2 as the scale of the map is too small). I believe that such a gap exists, however, because *colombiana* and nominate *argyrotis* are very distinct and not connected by intermediates. All the specimens of *colombiana* that I have seen, and all those on record, have been collected

only in the Santa Marta Massif. The specimens (“*albicauda*”) of nominate *argyrotis* that have been collected nearest to the range of *colombiana* were taken in the Sierra de Perija southeast of Fonseca and south of Villanueva. This fact suggests that the lowlands that separate the Santa Marta Massif from the Sierra de Perija are probably not suitable ecologically for this species. *Penelope argyrotis* apparently is not found below a certain elevation in Colombia and Venezuela, as all the specimens that I have seen with a

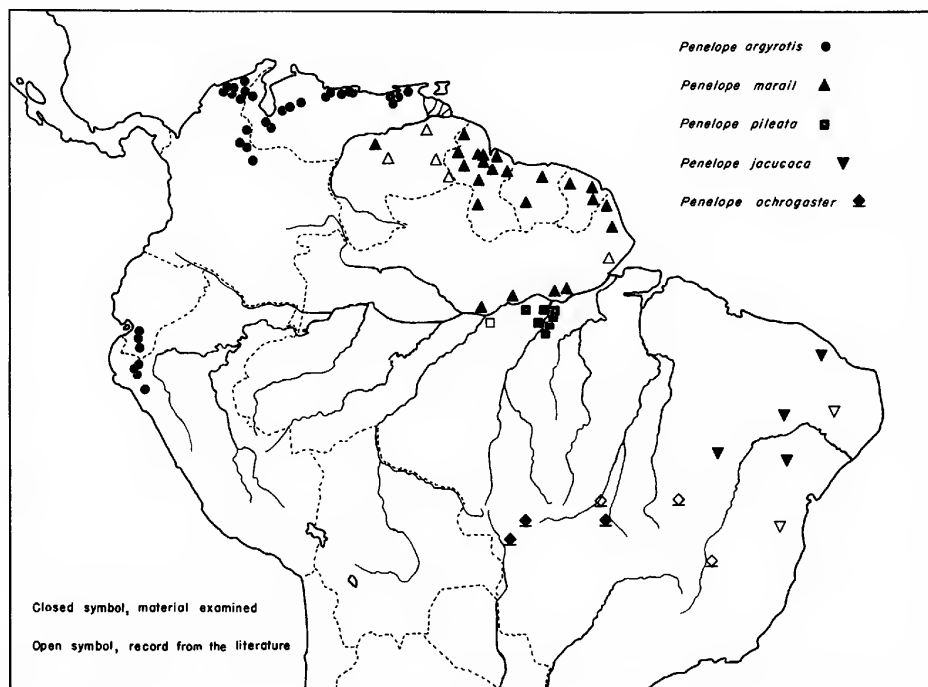


FIG. 2. Distribution of *Penelope argyrotis*, *Penelope marail*, *Penelope pileata*, *Penelope jacucaca*, and *Penelope ochrogaster*.

record of altitude were taken between about 1100 and 2400 meters, with the exception of two from the eastern extremity of the range in Venezuela which were collected, respectively, at 450 and 950 meters. The highest altitude in the gap between the Santa Marta Massif and the Sierra de Perija that I have found is 280 meters, but much of this region is considerably lower than this altitude. In Peru, *P. argyrotis* has been taken slightly above 3000 meters.

Penelope argyrotis was reviewed by Hellmayr and Conover (July, 1932) who recognized three subspecies, nominate *argyrotis*, *colombiana*, and *barbata*, which are very well differentiated and represent separate evolution-

ary trends. The wing length of nominate *argyrotis* averages distinctly longer than that of *colombiana* and *barbata* which are about similar in size (tables 1 and 2), nominate *argyrotis* and *colombiana* differing from *barbata* by the feathering of the chin and upper throat. In *barbata*, these regions are fully feathered, the feathers being webbed and normal in shape, and brown, edged with grayish white, whereas the chin and upper throat are virtually bare in nominate *argyrotis* and *colombiana* and have only a few scanty and fully decomposed blackish feathers that are usually restricted to the center of the chin and upper throat. *Barbata* is also considerably darker than nominate *argyrotis* and *colombiana*, more blackish brown, less olive-brown, above, and less rufescent below, more vermiculated with blackish brown, less olive-brown, above, and less rufescent below, more vermiculated with blackish brown. The pale edges of the feathers of the upper back and upper wing coverts, which are well developed in nominate *argyrotis* and *colombiana*, are more reduced and fewer on the back in *barbata* and are lacking or are only very faintly suggested on the coverts.

Penelope argyrotis colombiana differs very distinctly from nominate *argyrotis* by the shape and color pattern of the feathers of the crest, and also by the development of the superciliary streak and malar stripe, and the color of the pale edges of the feathers of the upper back and upper wing coverts. In *colombiana*, the feathers of the crest are narrower than in nominate *argyrotis*, distinctly more attenuated, less rounded at the tip, and they are completely edged with grayish white along the entire length, whereas the grayish edges are interrupted and present only on the feathers of the forehead in nominate *argyrotis*. The superciliary streak and malar stripe of *colombiana* are much less distinct than in nominate *argyrotis* in which the streak and stripe are pale silvery gray and very conspicuous, and all the pale edges of the feathers of the back and coverts are duller in *colombiana*, more buffy, less pure white, than in nominate *argyrotis*.

I agree completely with the revision of Hellmayr and Conover (July, 1932), but after that revision four additional forms were named. I believe they should not be recognized, as they are all based on trivial or minor characters and serve only to obscure the geographical variation of the species as a whole. These four forms and the synonymy of the species are as follows:

Penelope argyrotis barbata Chapman, 1921, type locality, Taraguacocha, Zaruma-Zaraguro trail, Cordillera de Chilla, El Oro, southwestern Ecuador. Synonym: *Penelope inexpectata* Carriker, 1934, type locality, Porculla Pass, Lambayeque, northwestern Peru. Specimens from Peru differ from the birds of Ecuador only by averaging slightly paler on the sides of the face, but the difference is very trivial, and Hellmayr and Conover (1942)

synonymized *inexpectata* with *barbata*. Carriker, who proposed *inexpectata* as a full species, was apparently not even aware of the existence of *barbata*.

Penelope argyrotis colombiana Todd, 1912, type locality, Las Taguas, Santa Marta, Colombia.

Penelope argyrotis argyrotis Bonaparte, 1856, type locality, Caracas, Venezuela. Synonyms: *Penelope argyrotis olivaceiceps* Todd, 1932 (November), type locality, San Rafael, near Cumanacoa, Sucre, Venezuela; *Penelope argyrotis albicauda* Phelps and Gilliard, 1940, type locality, La Sabana, Rio Negro, Perija district, Zulia, Venezuela; and *Penelope argyrotis mesaeus* Conover, 1945, type locality, Pamplona, Santander del Norte, Colombia. The specimens that I have seen from Merida, Trujillo, Lara, Carabobo, and the Distrito Federal (typical nominate *argyrotis*) have, as a rule, a somewhat paler brown crest than birds (*olivaceiceps*) from Anzoategui, Monagas, and Sucre, and average slightly less dark above than birds (*mesaeus*) from northern Boyaca, northern Santander, and Norte de Santander, but all the differences are slight, or relatively so, and furthermore are not constant. They do not warrant nomenclatural recognition. The birds (*albicauda*) from the Sierra de Perija are better differentiated, but they differ from nominate *argyrotis* only by a single character which is of minor importance when we consider the geographical variation of the species as a whole. The tips of the tail are paler than in specimens from the rest of the range of nominate *argyrotis*, varying individually from cinnamon to dingy buffy or grayish white, although individuals that represent the most rufous extreme in *albicauda* can be matched by an occasional specimen of nominate *argyrotis*; birds with whitish tail tips seem, however, to be restricted to the Sierra de Perija.

Penelope jacucaca, *Penelope ochrogaster*, and *Penelope pileata*

Penelope jacucaca, *P. ochrogaster*, and *P. pileata* are restricted to Brazil (fig. 2): *jacucaca* to northeastern Brazil, *ochrogaster* to central Brazil from eastern Goyaz and Minas Gerais west to the Mato Grosso, and *pileata* to the south bank of the Amazon from the lower Madeira to the lower Tapajoz rivers. They are clearly related, as more than one author has emphasized, and are large species in which some of the characters of *Penelope* have become most highly evolved. *Pileata* is the most colorful and glossy species of *Penelope* and the only one in which the color of the hind neck and back is dichromatic, the hind neck and upper part of the mantle being chestnut and the rest of the back, wings, and upper surface of the tail a rich dark and glossy olive-green. The under parts are bright chestnut, including the "thighs." *Ochrogaster* is similar to *pileata* below but is brown above, uniform in coloration, and less glossy. *Jacucaca* is warm

brown above and below; it has the general coloration of the other species of *Penelope*, but the color pattern of its head is more striking than in any other species. It is less glossy than *pileata* and *ochrogaster*.

In *jacucaca*, the feathers of the crest are sooty black and uniform in coloration, except on the forehead where they are edged with pure white to an individually variable degree. The black crown is very boldly emphasized by two broad bands of pure white over the orbital region, which join across the forehead and are separated from the bare skin of the face by a narrow band of pure black which ends behind the ear coverts. This band of black is present also in *ochrogaster* and *pileata* but is better developed, continuing along the edge of the bare skin to the sides of the neck and around the base of the throat. *Jacucaca* differs also from the other two species by having weaker feet and different proportions, the tail being shorter than the wing in *jacucaca*, whereas the reverse is true in *pileata* and *ochrogaster* (tables 1 and 2).

The crest differs in the three species. It is black in *jacucaca*, as stated, and consists of long, narrow, and fully webbed feathers which lie flat on the crown. The crest is not so well developed in *ochrogaster*, and its feathers are very narrow (only about half of the width of those of *jacucaca*) and dull reddish brown, with faint buffy or grayish edges, but they are fully webbed; the supraorbital band is poorly developed and dingy, very much less distinct than in *jacucaca*. The crest feathers of *pileata* are long and of about the same width as those of *jacucaca*, but they are not normal in structure, being almost wholly decomposed and very "hairy," and do not lie so flat as in *jacucaca*, the crest being more "bushy." The feathers are virtually all buffy white (with the result that the supraorbital band has vanished), except for the shaft which is brown and the tips which are more or less tinged with cinnamon or pale auburn, especially the posterior feathers.

The description given above shows that the three species have some characters in common, the most important of which is probably the presence of a narrow band of black along the edge of the bare skin, the other similarities consisting of the large size of the species and of the similarity in the color of the under parts in *pileata* and *ochrogaster*. But the dissimilarities are more numerous and seem equally important to me. They consist in the fact that *jacucaca* is warm brown above and below, not glossy green above, not chestnut below, that the color of the hind neck and back are uniform in *ochrogaster*, not dichromatic, in very clear-cut variations in the structure and color of the crest, development and color of the supra-orbital bands, and a difference in proportions in the case of *jacucaca*.

It has been suggested that the three birds are conspecific, and the de-

cision to treat them as one species was made by Vuilleumier (1965). I certainly agree that they are related, but it seems to me that they have become too well differentiated morphologically to be still conspecific. My study of all the species of *Penelope* has shown that a number of forms that are far more similar morphologically than *jacucaca*, *ochrogaster*, and *pileata* are, in fact, separate species, and I do not believe that *jacucaca* and *ochrogaster* would interbreed if they came into contact. The possibility that they might come into contact cannot be dismissed, because *jacucaca* and *ochrogaster* are apparently both rare (especially *ochrogaster*), if we judge by the material in existence, and their ranges are not perfectly known. The records that are available so far indicate that the range of *ochrogaster* extends east to the Rio São Francisco in Minas Gerais and northeast to the Rio São Domingos in eastern Goyaz, whereas the range of *jacucaca* extends south to southern Piauhy and southern and central Bahia. In other words, the gap in distribution is relatively narrow, but if the two birds are conspecific one would normally expect some convergence in characters rather than the very strong dissimilarity that exists. The gap between the range of *pileata* and the ranges of *jacucaca* and *ochrogaster* is far too great for one to speculate on the possibility of secondary contact and suggests, I believe, that *pileata*, which has a very restricted range, is likely to continue to evolve along separate lines, re-enforcing reproductive isolation.

SPECIMENS EXAMINED

Penelope ortonii

COLOMBIA: Rio Jurado, 1 ♂; Rio Jurubida, Alto del Buey, 5 ♂, 5 ♀; 5100 feet, on the Rio Baudo side of Alto del Buey, 1 ♂; Rio Baudo, 1 ♀; Quibdo, 1 ♂, 1 ♀; near Jimenez, 1 ♂, 1 ♀; La Costa, Tambo, 4 ♂, 4 ♀; Rio Mechengue, 2 ♂; Rio Docampado, Rio Capivo, 1 ♀; Sabaletas, Valle, 1 ♂.

ECUADOR: Paramba, 1 ♂, 2 ♀; Achotal, below Paramba, 2 ♂, 1 ♀; Santo Domingo de los Colorados, 1 ♂, 3 ♀; Gualea, 1 unsexed; Cachabi, 1 ♀; Rio Bogota, 1 ♀; above Bucay, 1 unsexed; Milpe Mindo, 5 ♂; Huila Mindo, 2 ♀.

Penelope albipennis

PERU: Hacienda da Pabur, near Piura, 1 unsexed.

Penelope dabbenei

BOLIVIA: Rio Azuero, Chuquisaca, 2 ♂; Tomina, Chuquisaca, 3 ♂, 2 ♀; Pinos, Tarija, 1 ♂, 1 ♀.

ARGENTINA: San Francisco, 60 kilometers on the road from Ledesma to Valle Grande, Jujuy, 1 ♂; Cerro Calilegua, Jujuy, 1 ♀.

Penelope montagnii montagnii

VENEZUELA: *Trujillo*: Paramo de las Rosas, 1 ♀; Teta de Niquitao, 1 ♀; La

Cuchilla, 3 ♂, 1 ♀. *Merida*: Montañas de Merida, 1 ♂; Sierra Nevada, 2 ♂; Montañas de Limones, 1 ♂, 1 ♀; Valle, 4 ♂, 2 ♀; Paramo de Frias, 1 ♀; Heights of Tabay, 2 ♂; Paramo El Escorial, 1 ♂, 1 ♀; Paramo de la Culata, 1 ♀; Rio Mucujun, 2 ♂, 1 ♀; no locality, 1 unsexed.

COLOMBIA: *Magdalena*: Above Airoca, Sierra de Perija, 1 ♂, 1 ♀; south of Teta, Sierra de Perija, 1 ♂; Cerro Pintado, Sierra de Perija, 1 ♂; Laguna de Junco, Cerro Pintado, Sierra de Perija, 1 ♂, 1 ♀. *Norte de Santander*: Paramo de Tama, 2 ♂; Alto del Pozo, 1 ♂, 1 ♀; Pamplona, 1 ♂. *Boyaca*: Peña Blanca, 4 ♂, 4 ♀; Boca del Monte, 2 ♂, 1 ♀. *Cundinamarca*: Subia, 2 ♂, 1 ♀; El Piñon, above Fusagasuga, 1 ♂; Paramo de Choachi, 1 ♂; Rio Balcones, Guasca, 2 ♂, 2 ♀; vicinity of Bogota, 1 unsexed. *Caldas*: Zancudo, 2 ♂, 1 ♀; La Leonera, 1 ♂, 1 ♀; Paramo de Santa Isabel, 4 ♂, 1 ♀, 1 unsexed. *Cauca*: Coconuco-Paletera, 6 ♂, 6 ♀, 1 unsexed young; Almaguer, 1 ♂. *Huila*: La Plata, 1 ♂, 1 ♀; Valle de las Papas, 1 ♀. "Interior of New Granada," 2 unsexed.

Penelope montagnii atrogularis

COLOMBIA: *Nariño*: Mayasquer, 2 ♂, 1 ♀; Chiles, 1 ♂, 1 ♀; El Guabo, 1 ♂.

ECUADOR: Alaspungo, 3 ♂ (including type of *atrogularis*); Chaloya, 2 ♂, 1 ♀; Paramba, 2 ♀; Lloa Urabuco, 2 ♂, 1 ♀; Yana-Urcu, 2 ♀; Pucara, 1 ♀; near Piganta, 1 ♂; Piganta, 1 ♂, 2 ♀; above Huigra, 2 unsexed; Mindo, 1 ♂; near Mindo, 1 ♂; San Jorge, 1 ♂; Nono, 1 ♀; no locality, 1 unsexed.

Penelope montagnii brooki

COLOMBIA: *Nariño*: Near Pasto, 1 unsexed; Guanderal, Puerres, 1 ♀; Chorreado, Puerres, 1 ♂.

ECUADOR: Baeza, 1 unsexed (type of *brooki*); above Baeza, 3 ♂, 3 ♀; upper Sumaco, 2 ♂, 3 ♀; below Papallacta, 1 ♀; Cuyuya (not located, but apparently near Papallacta), 2 ♂, 2 ♀; Cañon del Rio Pita, 1 ♀; "Ambato" 1 ♂, 1 ♀; Montes Anagumba, 1 ♂, 1 ♀; La Merced, 1 ♂; Huagropamba, 1 young; San José, 2 unsexed; no locality, 1 unsexed.

Penelope montagnii plumosa

PERU: Huacapistana, 2 ♂, 1 ♀; Maraynioc, 1 ♀; San Pedro, south of Chachapoyas, 1 ♂; La Lejia, north of Chachapoyas, 1 ♀; Molinopampa, near Chachapoyas, 1 ♂; 10 miles east of Molinopampa, 1 ♂, 1 ♀; Leymebamba, 1 ♂, 1 ♀; Compan, 1 unsexed; Tambo Venes Mountains east of Balsas, 2 ♀; mountains east of Balsas, 1 ♀; Torontoy, canyon of the Urubamba, 3 ♂; Santa Rita, canyon of the Urubamba, 2 ♂, 2 unsexed; Huaisampilla, northeast of Paucartambo, 1 unsexed; Chilichili, Marcapata, 1 ♂ (type of "*marcapatensis*"); San Andres, Marcapata, 1 ♀; Limacpunco, Marcapata, 1 ♀; Oconeque, 4 ♂, 1 ♀.

Penelope montagnii sclateri

BOLIVIA: *La Paz*: Sandillani, 2 ♂, 1 ♀; Tilotilo [near Sandillani], 2 unsexed; Yungas "south of 16°," 1 unsexed; no locality, but probably Yungas de la Paz, 1 unsexed (type of *sclateri*). *Cochabamba*: Incachaca, 11 ♂, 9 ♀, 2 downy young; San Jacinto, 2 ♂, 1 ♀; San Cristobal, 1 ♂, 1 ♀; Cocapata, 1 unsexed; El Palmar, 2 ♂, 3 ♀; Chapare, El Palmar, 2 ♂; Yungas de Cochabamba, 2 ♀. *Santa Cruz*: Samaipata, 1 ♀. Bolivia, no locality, 3 unsexed.

Penelope superciliaris superciliaris

BRAZIL: Borba, Rio Madeira, 2 ♂; Rio Canuma, 1 ♀ (type of "*pseudonyma*"); Lagoa Andira, 1 ♂, 5 ♀; Serra de Parintins, 1 ♂; Caxiricatuba, Rio Tapajoz, 3 ♂, 2 ♀; Pinhel, Rio Tapajoz, 2 ♂, 1 ♀; Boim, Rio Tapajoz, 1 ♂; Tauary, Rio Tapajoz, 6 ♂, 4 ♀; Limoal, Rio Tapajoz, 1 ♀; Igarapé Bravo, Rio Tapajoz, 1 ♂, 1 ♀; Mirituba, Rio Tapajoz, 1 ♂; Villa Braga, Rio Tapajoz, 1 ♂, 1 ♀; Tapaiuna, Rio Tapajoz, 1 ♂; Fordlandia, Rio Tapajoz, 1 ♀; Colonia do Mojuy, near Santarem, 1 ♀; Porto de Moz, Rio Xingu, 1 ♀; Rio Majary, Rio Xingu, 1 ♂; Villarinho do Monte, Rio Xingu, 1 ♀; Baião, Rio Tocantins, 1 ♂, 2 ♀; Ipomonga, Rio Capim, 1 ♂; Resaca, Rio Capim, 1 unsexed; Serraria Cabral, Rio Acara, 1 ♂; Villa Acara, Rio Acara, 1 ♂; Buenos Ayres, Rio Acara, 1 ♂, 1 unsexed; Igarapé Assu, 1 ♀; Para, no locality, 2 unsexed.

Penelope superciliaris jacupemba

BRAZIL: Boa Vista, Maranhão, 1 ♂; Tranqueira, Maranhão, 2 ♀; Miritiba, Maranhão, 1 ♀; São João dos Patos, Maranhão, 1 unsexed; Flores, Maranhão, 1 unsexed; Fazenda Inhumá, alto Parnahyba, Maranhão (?), 2 ♀; Corrente, Piauí, 1 ♂, 2 ♀, 1 unsexed; Deserto, Piauí, 1 ♂, 1 ♀; Piauí, no locality, 1 ♀; Bahia, no locality, 2 unsexed; Boa Vista, São Antonio, Goyaz, 1 ♂; Annapolis, Goyaz, 5 ♂; Nova Roma, Goyaz, 1 ♀; Tapirapoan, Mato Grosso, 1 ♂; Chapada, Mato Grosso, 4 ♂, 7 ♀, 1 unsexed; Serra da Chapada, Mato Grosso, 3 ♂, 2 ♀; São Francisco, Campanario, Mato Grosso, 1 ♂, 1 unsexed young; Teófilo Otoni, Minas Gerais, 1 ♂; Rio Jordão, Minas Gerais, 1 ♀; Lagoa Juparana, Espírito Santo, 2 ♂; Pão Gigante, Espírito Santo, 1 ♂; Rio de Janeiro, 3 unsexed; Victoria, São Paulo, 4 ♂; Fazenda Cayoa, Salto Grande do Rio Paranapanema, São Paulo, 2 ♂; Fazenda Varjão, 4 kilometers north of the mouth of the Rio dos Dourados, São Paulo, 1 ♂, 1 ♀; Barra do Rio dos Dourados, São Paulo, 1 ♀; São Vicente, near Santos, São Paulo, 1 ♂; Rio Parana, no locality, 1 unsexed.

Penelope superciliaris major

PARAGUAY: Cerro Amambay, 40 kilometers southwest of Capitan Bado, 4 ♂, 2 ♀; 43–46 kilometers east of the Rio Paraguay at latitude 23° 24' S., longitude 57° 10' W., 2 ♂, 2 ♀; upper Rio Iguazu, 1 unsexed; Colonia Independencia, east of Villa Rica, 1 ♂.

ARGENTINA: Puerto Segundo, Misiones, 2 ♂, 1 ♀; 10 kilometers on the Arroyo Urugua-i, Misiones, 1 ♂, 1 ♀; 30 kilometers on the Arroyo Urugua-i, 1 ♂.

Penelope argyrotis argyrotis

VENEZUELA: *Sucre*: San Rafael, near Cumanacoa, 3 ♂ (including type of "*oliveiceps*"), 3 ♀. *Monagas*: Cerro Negro, Caripe, 1 ♀; Rio Neveri, 1 unsexed. *Anzoategui*: Bergantín, 1 ♂. *Distrito Federal*: El Limón, 1 ♂; Puerto de la Cruz, 1 ♂. *Carabobo*: Cumbre de Valencia, 3 ♂, 1 ♀; Las Guigas, 1 ♀. *Lara*: Cubiro, 1 ♂. *Trujillo*: Guamito, 2 ♀; Paramo de Las Rosas, 1 ♂, 1 ♀, 1 chick. *Merida*: Capaz, 2 ♂, 3 unsexed; Montañas de Capaz, 1 unsexed; La Azulita, 2 ♂, 1 ♀. *Zulia*: La Sabana, Rio Negro, 1 ♀ (type of "*albicauda*").

COLOMBIA: La Africa, south of Villanueva, Sierra de Perija, 1 ♀; Tierra Nueva, Sierra Negra, southeast of Fonseca, Sierra de Perija, 3 ♂, 3 ♀; Monte Elias, Sierra Negra, Sierra de Perija, 1 ♀; Eroca, Sierra de Perija, 2 ♀; Pamplona, Norte de

Santander, 1 ♂, 1 ♀ (type of "*mesaeus*"). Buenos Aires, Norte de Santander, 1 ♂, 1 ♀; Cachiri, Santander, 1 ♀; Rio Negro, northern Boyaca, 1 ♂; "interior of New Granada," 1 unsexed.

Penelope argyrotis colombiana

COLOMBIA: Magdalena, Santa Marta: El Libano, 1 ♂, 2 unsexed, Vista Nieve, 2 ♂, 1 ♀; Cincinnati, 2 ♂, 3 ♀, 4 immature birds and chicks; Las Vegas, 1 ♂, 2 ♀, 1 chick; Las Taguas, 3 ♂ (including type of *colombiana*); San Lorenzo, 4 ♂, 2 ♀; Los Croros, old trail Fonseca-Rio Hacha above Loma Larga, 4 ♂, 1 ♀; San José, Rio Guatapuri, 1 ♂, 2 ♀; Chendocua, Rio Guatapuri, 1 ♂, 1 ♀; Chinchicua, 4 ♀.

Penelope argyrotis barbata

ECUADOR: Loja, Malacatos, 3 ♂, 1 ♀; Loja Huaico, 1 ♂; San José, 1 ♂, 1 ♀; Taraguacocha, 1 ♀ (type of *barbata*).

PERU: Taulis, northeast of Pacasmayo, 2 ♀; Palambla, Piura, 1 ♀; Huanca-bamba, Piura, 1 ♂.

Penelope jacucaca

BRAZIL: Guaramiranga, district of Pacoti, Serra do Baturité, Ceara, 1 ♂; Lama-rão, Bahia, 2 immature ♂, 1 immature ♀; Deserto, Piauh, 1 ♀; Corrente, Piauh, 2 ♂, 2 ♀; no locality, 2 ♂, 2 ♀.

Penelope ochrogaster

BRAZIL: Engenho do Pari, near Cuyaba, Mato Grosso, 1 ♂ (type or cotype of *ochrogaster*), Descalvados, Mato Grosso, 1 ♂; Rio Araguaya, Goyaz, 1 ♀.

Penelope pileata

BRAZIL: Caxiricatuba, Rio Tapajoz, 2 ♂, 2 ♀; Piquiatuba, Rio Tapajoz, 1 ♂; Tauary, Rio Tapajoz, 4 ♂, 2 ♀; Boim, Rio Tapajoz, 2 ♀; Pinhel, Rio Tapajoz, 2 ♀, 1 unsexed; Fordlandia, Rio Tapajoz, 1 ♂; Serra de Parintins, 1 ♂; "south bank of the Amazon," 1 ♂, 1 ♀; no locality, 3 ♂, 1 ♀, 2 unsexed.

Penelope marail marail

BRITISH GUIANA: Bartica, 3 ♂, 3 unsexed; Bartica Grove, 1 ♂; Kalacoon, 2 ♂, 1 ♀; Waremia River, 1 ♂, 5 unsexed; Mazaruni River, 1 ♂; Kartabo, 2 ♂; Tumatumari, 1 ♂; Kamakusa, 2 ♂, 2 ♀; Itubirisi River, 3 unsexed; Supenaam River, 2 unsexed; Kamakabra Creek, 2 unsexed; Ourumee, 1 ♀; Moraballi Creek, 1 ♂, 1 ♀; Berbice, 1 ♂, 1 ♀; Oko Mountains, 1 ♀; Quonga, 2 unsexed; Demerara, 1 ♀; Great Savannas, 1 ♂, 3 unsexed; no locality, 1 ♀.

SURINAM: Kaiserberg airstrip, Zuid River, 2 ♂; Lelydorp, 1 ♂; "interior of Surinam," 1 ♂, 2 ♀.

FRENCH GUIANA: Tamanoir, 2 ♂, 1 ♀; Ipoucin, 2 ♂, 1 ♀; Mana River, 1 ♀.

BRAZIL: Uaçã Swamp, 1 ♂; Rio Cunany, 1 ♂.

Penelope marail jacupeba

VENEZUELA: Upper Caura River, 1 ♂.

BRAZIL: Faro, 2 ♂, 4 ♀; Lagoa Cuipeva, 2 ♂, 2 ♀; Igarrapé Arriba, 1 ♀; Obidos, 2 ♂, 1 ♀.

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