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THE NATURE OF THE VARIABILITY IN THE
VARIABLE SEEDEATER IN PANAMA
(*SPOROPHILA AMERICANA*: EMBERIZINAE)

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Abstract.—Detailed examination of variation in *Sporophila americana* in Panama necessitates major changes in the stated ranges and nomenclature of the subspecies found there. The name *hicksii* (Lawrence, 1865) is revived for white-throated black and white birds on the Pacific coast of Panama from Veraguas east through Darién (skipping the Canal Zone), the Caribbean coast in San Blas, and south in western Colombia to Valle. The currently recognized name *chocoana* (Meyer de Schauensee, 1950) becomes a synonym of *hicksii*. It is suggested that the type locality of *hicksii* should be Buenaventura, Colombia, instead of Panama. Black-throated black and white birds from the Pacific slope of Costa Rica and Chiriquí may now be known under the resurrected name *hoffmanni* Cabanis, 1861. The nearly black subspecies *corvina* (Sclater, 1859) extends along the western Caribbean coast of Panama and in the Canal Zone intergrades with *hicksii* to form a hybrid zone in which no pure parental types occur. The long-used but dubiously applicable name "*aurita*" (Bonaparte, 1850) is tentatively applied to these intergrades and the specimens are analyzed by the use of a hybrid index.

As its name implies, the Variable Seedeater, *Sporophila americana*, has been regarded as being so variable in the adult male plumage, particularly in Panama, as to defy interpretation in terms of normal geographic variation. This idea became so fixed in the earlier literature that contrary information was often ignored. No recent attempts have been made to examine series of specimens from Panama to elucidate distributional patterns there. By current taxonomic practices there are three subspecies of *Sporophila americana* recognized in Panama: *S. a. corvina*, a nearly all black form found on the Caribbean slope of western Panama north to Mexico; *S. a. aurita*, a supposedly extremely variable black and white form found on the Pacific slope of Costa Rica and Panama to the Canal Zone and on both slopes east of the Canal to Darién, where it is supposedly replaced by a more constant white-throated form, *S. a. chocoana*, inhabiting easternmost Panama and Pacific Colombia south to the Río Dagua. The development of this classification may be traced through the publications of Sclater (1871), Chapman

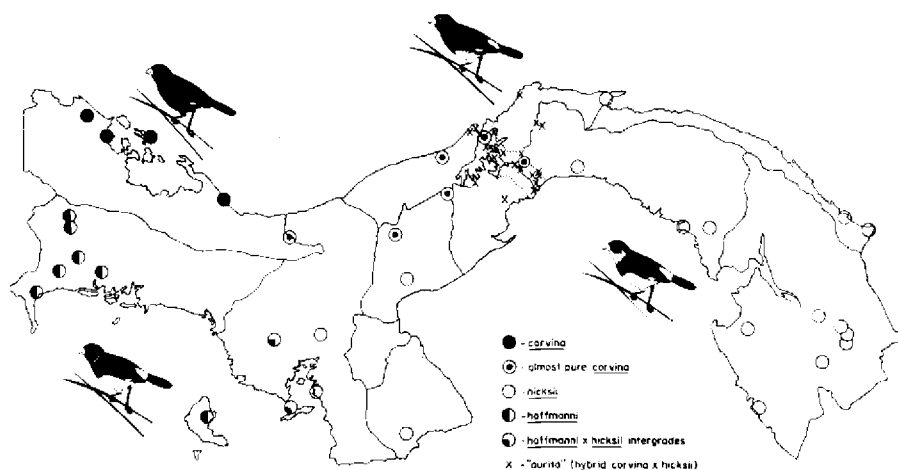


Fig. 1. Distribution of the forms of *Sporophila americana* in Panama, based on specimens examined in this study.

(1926), Hellmayr (1938), Meyer de Schauensee (1950, 1952) and Eisenmann (1957).

Not all of the observations below are entirely original, but their significance has not hitherto been appreciated. I shall not attempt to treat the history of each conclusion, as this may be found in the references just cited. The classification I shall propose differs considerably from that above. For this reason and because the nomenclatural changes I shall propose are rather intricate, I shall begin by presenting my conclusions first and documenting them beyond.

The revised distribution and nomenclature of *S. americana* in Panama is shown in Fig. 1. No change in status is required for the black populations from the western Caribbean coast, *S. a. corvina*. Much of the rest of the isthmus is occupied by a black and white subspecies, with a white rump and throat, which occurs in most of Panama east of the Canal Zone and west of the Canal Zone on the Pacific slope to central Veraguas. The name *hicksii* is resurrected for this subspecies, with *chocoana* falling into synonymy. A similar subspecies, but with a black throat, is found from western Veraguas, including Isla Coiba, west along the Pacific slope through Costa Rica. The name *hoffmanni* is revived for this form. The only birds showing great variability are restricted to the area of the Canal Zone, where populations consist entirely of intergrades between *corvina* and *hicksii*, and where no pure parental types occur. The name "aurita," the application of which is dubious in any case, is tentatively used for these intergrades.

Sporophila americana corvina (Sclater)

Spermophila corvina Sclater, 1859, Proc. Zool. Soc. London 1859:379.
Playa Vicente, Oaxaca, Mexico.

Spermophila badiiventris Lawrence, 1865, Ann. Lyc. Nat. Hist. N.Y. 8:172.
Greytown, Nicaragua. Type re-examined for this study.

Characters.—Adult males almost entirely black, with only the speculum of the wing and midline of belly white. Speculum smaller than in *hicksii*. Females and subadult males are markedly darker and more sooty than in other subspecies, but have not been considered in determining the distribution or extent of intergradation in any of the forms.

Range.—Caribbean slope of southeastern Mexico, south through Bocas del Toro, Panama. The few specimens known from the Caribbean slope between Bocas del Toro and the Canal Zone are nearly pure *corvina*, but show faint traces of white on the sides of the neck. I have designated these as "0+" in the hybrid index discussed in the account of *S. a. "aurita,"* but have listed these specimens below under *corvina*.

Specimens examined (only specimens from Costa Rica and Panama are listed although others were examined).—COSTA RICA. GUANACASTE: ca. 3 miles E Tilarán, 950 m (1, LSU); Arenal, 500 m (1, LSU). ALAJUELA: Naranjo (1, USNM); Villa Quesada (1, USNM). HEREDIA: Puerto Viejo (1, LSU). CARTAGO: Bonilla (6, USNM; 4, AMNH); Guayabo (3, USNM); Tucurrique (1, AMNH); Aquiares (1, AMNH). SAN JOSE: Carillo (3, AMNH; 1, USNM). LIMON: Cariari (4, WFVZ); Finca La Lola, Río Madre de Dios (1, WFVZ); Jiménez (2, USNM); San Bernardo (1, USNM); Sipurio (2, USNM); Uva (1, USNM); Limón (3, AMNH); Guápiles (2, AMNH); Siquirres (1, AMNH); Atalanta (2, AMNH).

PANAMA. BOCAS DEL TORO: Almirante (5, USNM; 4, AMNH); Changuinola (1, USNM); Cocoplum (7, ANMH); "Bocas del Toro" (1, ANSP). The following were ranked "0+," or almost pure *corvina*, in the hybrid index discussed below: VERAGUAS: Río Calovévora, Caribbean slope (1, AMNH); COCLE: Tigre, head of Río Guabal (1, USNM); El Uracillo, Río Negro (1, USNM). COLON: Chilar, Río Indio (1, USNM). CANAL ZONE: Gatun (1, USNM); Gamboa Pipeline Road (1, USNM).

Sporophila americana hicksii (Lawrence)

Spermophila hicksii Lawrence, 1865, Ann. Lyc. Nat. Hist. N.Y. 8:171.
"Panama" (probably = Buenaventura, Colombia, see below). Type re-examined for this study.

Spermophila aurita chocoana Meyer de Schauensee, 1950, Proc. Acad. Nat. Sci. Phila. 52:138, Nuquí, Chocó, Colombia.

Characters.—Adult males with throat, sides of neck, lower breast and abdomen, rump, undertail coverts, and speculum white; pectoral band and variable amount of chin black.

Range.—Pacific coast of Panama from central Veraguas and the Azuero Peninsula east (skipping the Canal Zone) through Panamá Province and Darién, the Atlantic slope in San Blas, south along the Pacific slope of Colombia to the vicinity of the Río Dagua, Valle.

Specimens examined.—PANAMA. VERAGUAS: Soná (5, USNM); La Colorada, Santiago (2, AMNH); E shore of Montijo Bay, 1 mile S of Angulo River mouth (2, CM); Isla Gobernadora (2, USNM; one of these is more similar to those from Isla Coiba). LOS SANTOS: Tonosí (1, USNM). COCLE: Gago (1, USNM). PANAMA PROVINCE: Pacora (1, USNM); Chiman, Río Chiman (1, USNM); Charco del Toro, Río Majé (2, USNM). SAN BLAS: Mandinga (2, USNM); Permé (2, MCZ); Puerto Obaldia (3, USNM, 1 MCZ). DARIEN: Cana (4, USNM; 3, MCZ); mouth of Río Paya, Río Tuira (1, USNM); Pucro, Río Pucro (1, USNM); Jaqué (5, USNM); El Real, Río Tuira (5, AMNH); Boca de Cupe, Río Tuira (3, AMNH); Río Sambú (1, ANSP).

COLOMBIA. CHOCO: Nuquí, Río Jurubidá (4, ANSP); Nuquí (2, USNM); Acandí (5, USNM); Juradó (1, AMNH; 1, ANSP); Río Baudonde (1, ANSP); Quibdo (1, ANSP); upper Río Baudó (1, ANSP); Andagoya (1, ANSP). ANTIOQUIA: Dabeiba, Río Sucio (1, AMNH); Villa Arteaga (2, USNM). CORDOBA: Socarré, Río Sinú (1, USNM). CALDAS: Santa Cecilia (3, ANSP). VALLE: Punta Muchimbo, Río San Juan, 1 mile S of mouth of Río Calima (2, USNM); San José (1, USNM); Buenaventura (2, USNM).

Remarks.—When Meyer de Schauensee (1950) described *chocoana*, he compared it with birds from Costa Rica, western Panama, and the Canal Zone, all of which were considered to represent *aurita* and all of which have black throats. He recognized that birds from Colombia and Darién differed in consistently possessing a white throat and he therefore segregated these under the name *chocoana*. A major problem arises here in the nature and origin of the type specimen of *hicksii* Lawrence (USNM 40300). Meyer de Schauensee (1950:139) reported that "Mr. Herbert Deignan has kindly examined the type of *hicksii* for me and writes me that although it is a white-throated example, it was collected by Hicks 'probably not far from the city of Panama.' It therefore must be regarded as an aberrant example of *S. a. aurita*."

The type of *hicksii*, which I have examined, is a perfectly typical example of *chocoana*, with a pure white throat and rump. It shows not a trace of the intergradation with *corvina* that marks "*aurita*." The specimen is labelled simply "Panama," the implication being that it came from the vicinity

of Panama City, on the Pacific slope. No such individuals with pure white throats from the vicinity of Panama City or the Canal Zone exist in any of the collections I have examined, although they have been taken on the Pacific slope both to the east and to the west of the Canal Zone area.

The type of *hicksii* was sent to S. F. Baird at the Smithsonian Institution by Fred Hicks in a lot of 54 specimens, all of which came from Panama except for 4 from Cali, Colombia, and 12 from Buenaventura, Colombia (letter of 27 December 1864 from Hicks to Baird; accession file 588, USNM). Not all of these specimens were catalogued. The type of *hicksii* was catalogued immediately following 3 specimens of the same species labelled as being from Buenaventura, one of which (USNM 40299) is now missing. These are the only other specimens of *Sporophila americana* among those collected by Hicks; the type of *hicksii* is the only one labelled as coming from Panama.

Hicks' original labels were for the most part more informative than usual for the period, and often included soft part colors and measurements, as well as locality, date, collector, and field number. Unfortunately, these were made of very fragile paper and in many instances appear to have been deliberately removed from the specimens, as is the case with the type of *hicksii*. Whoever copied the data onto the new labels often did not transfer all of the information that was on the originals and the transcriptions were also not without error. There is a specimen of the tanager *Ramphocelus flammigerus icteronotus* in the same lot as the type of *hicksii* that has "Panama" written on one side of the label and "Buenaventura" on the other.

Circumstantial evidence strongly suggests that the type specimen of *Spermophila hicksii* Lawrence came from Buenaventura, Colombia; it is unlikely to have been obtained in the vicinity of Panamá City. Even if the specimen did come from Panama, it can not be regarded as an abnormal specimen of "*aurita*," since similar white-throated populations occur on the Pacific slope of Panama both to the west and to the east of the Panamá City-Canal Zone area. The name *Spermophila aurita chocoana* Meyer de Schauensee, 1950 therefore becomes a junior synonym of *Spermophila hicksii* Lawrence, 1865 and I recommend that Buenaventura, Valle, Colombia, be regarded as the type locality of *hicksii*.

Buenaventura is at or near the southern limit of the range of *hicksii*. Meyer de Schauensee (1950) correctly recognized the Río Dagua as the approximate line of demarcation between *chocoana* (= *hicksii*) and the subspecies *ophthalmica* (Sclater, 1860; type locality Babahoyo, Ecuador), which differs in having a narrower pectoral band and whiter chin. Colombian birds from Los Cisneros, Valle (3, AMNH), Guapi, Cauca (1, USNM), and from Nariño through Ecuador are referable to *ophthalmica*.

The discovery of white-throated individuals of *hicksii* west of the Canal Zone is significant (see discussion of "*aurita*"). Although the amount of

black in the chin is variable in *hicksii*, the birds from Coclé and the Azuero Peninsula stand out in having the chin almost totally white, thus contrasting markedly with the intergrades ("aurita") to the east and with the subspecies *hoffmanni* to the west.

Sporophila americana hoffmanni Cabanis

Sporophila hoffmanni Cabanis, 1861, Journ. Orn. 9:6. Costa Rica.

Spermophila collaris Lawrence, 1865, Ann. Lyc. Nat. Hist. N.Y. 8:177.

David, Chiriquí, Panama. (Not *Loxia collaris* Boddaert.) Type re-examined for this study.

Characters.—Similar to *hicksii* but adult males with throat black, with varying amounts of white, either as a narrow collar or as discontinuous patches, on either side of the neck.

Range.—Pacific slope of Costa Rica and Panama in Chiriquí and Isla Coiba, intergrading with *hicksii* in western Veraguas.

Specimens examined.—COSTA RICA. SAN JOSE: El General (7, MCZ). PUNTARENAS: Tambor, Nicoya (3, LACM); Las Agujas (1, LACM); Pigres (1, USNM); Pozo Azul (5, CM; 1, MCZ); El Pozo del Río Grande (de Terraba) (3, MCZ; 4, CM; 2, FM; 1, ANSP); Buenos Aires (3, CM; 4, FM; 4, AMNH); Puerto Jiménez, Península de Osa (1, CM; 1, AMNH); Rincón de Osa (1, LSU; 1, WFVZ); Boruca (1, ANSP; 1, AMNH; 2, CM; 1, USNM; 1, ANSP; 7, MCZ); 13 km S of Palmar Sur (3, WFVZ); Helechaes (7, WFVZ).

PANAMA. CHIRIQUI: David (1, USNM; 1, MCZ); Divalá (1, MCZ; 1, USNM); El Volcán (4, USNM); Buena Vista (1, USNM); Puerto Armuelles (4, USNM); Boquerón (1, AMNH). VERAGUAS: Isla Coiba (7, USNM; 4, AMNH [collected by Batty, locality not reliable]).

Remarks.—Although Chapman (1926) recognized this subspecies (under the name *collaris*) and Hellmayr (1938) conceded that birds from Costa Rica and Chiriquí were generally separable from "aurita," this western subspecies is not at present recognized, due to its similarity to certain of the intergrades from the Canal Zone and the fact that, hitherto, *hicksii* was not known to occupy the intervening area. Some of the intergrades of "aurita" are indeed very similar to the western birds, but they may usually be distinguished by the lesser amount of white in the rump. Within the populations from the Pacific slope of Costa Rica and Chiriquí, there is little variation in adult male plumage. Yet because of the confusion that has long attended the concept of variation in this species, Wetmore (1957) assigned a series of seven males from Isla Coiba, which closely resemble one another and show little variation, to the subspecies *aurita*, which was then considered to be extremely variable.

The earliest available name for the black-throated western birds is *hoff-*

manni Cabanis, 1861, the original description of which clearly pertains to this population. *S. a. hoffmanni* evidently intergrades with *S. a. hicksii* in Veraguas. A series of five males from Soná are closest to *hicksii* but have more black in the chin than typical of most individuals of that subspecies. The birds from Isla Coiba are like *hoffmanni* but show a slight tendency towards *hicksii* in having the white collar mostly continuous and a few white feathers on the chin. Of two adult males from Isla Gobernadora, Veraguas, one resembles the birds from Isla Coiba whereas the other could pass as typical *hicksii*.

Sporophila americana "aurita" (Bonaparte)

Spermophila aurita Bonaparte, 1850, Consp. Gen. Av. 1(2):497 "Bras. [il]" = Panama?

Spermophila semicollaris Lawrence, 1863, Ann. Lyc. Nat. Hist. N.Y. 8:10. Lion Hill, Panama Railroad. Type re-examined for this study.

Spermophila fortipes Lawrence, 1865, Ann. Lyc. Nat. Hist. N.Y. 8:172. Line of Panama Railroad. Type re-examined for this study.

Characters.—Extremely variable, ranging from individuals similar to *hicksii*, but with slightly more black in the rump, throat, or belly, to individuals nearly as black as *corvina*; see discussion of hybrid index below.

Range.—Essentially restricted to the Canal Zone area of central Panama; known as far west as La Chorrera, western Panamá Province, and as far east as Buenaventura Island, near Portobelo, Colón, and the Candelaria and Peluca Hydrographic Stations at the head of Madden Lake.

Specimens examined.—All are from the Canal Zone or immediately adjacent parts of Panamá or Colón provinces, except where indicated, and all are from the USNM, AMNH, and MCZ collections except 3 from Gatun (ANSP) and 1 from Barro Colorado Island (FM). Hybrid index (HI) is given first, followed by number of specimens in parentheses. Aspinwall, HI-1 (1); Balboa, HI-3 (2); Barro Colorado Island, HI-5 (1); Bas Obispo, HI-1 (1); Bohio HI-4 (1); Buenaventura Island, near Portobelo, Colón Province, HI-3 (1); Candelaria Hydrographic Station, HI-3 (3); Chiva Chiva, HI-4 (1); Colón, HI-1 (1), HI-2 (1); Corozal, HI-3 (2); Curundu HI-5 (1); Fort Lorenzo, HI-1 (1); Frijoles, HI-1 (1), HI-4 (1); Gamboa, HI-2 (1); Gatun, HI-1 (5), HI-2 (7), HI-3 (4), HI-4 (1); Juan Mina, HI-1 (1), HI-3 (2), HI-4 (1), HI-5 (2); La Chorrera, western Panama Province, HI-2 (1); Lion Hill (Loma del León), HI-1 (1), HI-2 (4); HI-3 (3); HI-4 (2); Miraflores, HI-3 (1), HI-5 (1); line of Panama Railroad, HI-5 (1); "near Panama," HI-2 (2), HI-3 (4), HI-4 (1), HI-5 (1); "Panama," HI-2 (3); Peluca Hydrographic Station, HI-3 (1); Tabernilla, HI-2 (1), HI-3 (1), HI-4 (1); Río Trinidad, Agua Clara, HI-2 (1); Savanna, HI-3 (1).

Remarks.—There is considerable doubt in my mind about the proper use of the name *aurita* Bonaparte, long applied to most of the specimens of this species from Panama and Pacific Costa Rica. Bonaparte's (1850:497) entire original description reads as follows: "*Sp. aurita*, Bp. Mus. Paris. ex Bras. Similis praecedenti [*Sporophila luctuosa*]; gula pectoreque nigerrimis: sed rostro nigro et macula utrinque auriculi alba." This description could apply to many individuals from the Canal Zone or equally well to *hoffmanni* of Costa Rica and Chiriquí. Sclater (1871:15) considered the specimens he examined from "Panama and Chiriquí" to represent a single species and stated that "the typical example of *S. aurita* in Mus. Paris clearly belongs to it, though the locality (Brazil) attributed to it in the 'Conspectus' is no doubt erroneous." It is not absolutely clear that Sclater actually examined the type; Hellmayr (1938:191) could not find it at the Paris Museum in 1935. Because of Sclater's action, the type locality of *aurita* has since been taken as Panama, but neither the true identity nor the provenance of the type has been positively determined.

Several nomenclatural resolutions suggest themselves. One could regard the name *aurita* Bonaparte as being of undeterminable application, or one could go on the assumption that the name was correctly applied to birds from the hybrid zone in the central part of the Panamanian isthmus. In the latter case, one might attempt to apply the name *aurita*, which is the earliest available for any of the Panamanian subspecies, to one or the other of the parental phenotypes, i.e. either to *corvina* or *hicksii*. To do this successfully, one would still need the holotype of *aurita* to determine to which parental type it was most similar. Were it to prove more similar to the black subspecies, then *corvina* would become a synonym of *aurita*, thus causing endless confusion, since *corvina* is the one name that has never been applied to the more variable populations in Panama. I have adopted a compromising course by applying the name "*aurita*," in quotes, only to those individuals that are clearly intergrades between *corvina* and *hicksii*. Although this is not altogether a satisfactory resolution, this population has a circumscribed range in which neither parental phenotype occurs and in which virtually all individuals can be certainly identified as belonging to "*aurita*," as opposed to some other population. This also prevents the sudden disappearance of the name under which the majority of Panamanian birds have appeared in most of the earlier literature.

To facilitate analysis of variation in "*aurita*," I grouped adult male specimens according to the following hybrid index (HI).

HI 0.—Pure *corvina*. All black except for small white speculum and white along midline of belly. Individuals fitting this description but having faint traces of white "ears" I designated as "0+," shown in Fig. 1 as "almost pure *corvina*."

- HI 1.—More white in midline, particularly lower abdomen; some white in crissum. No, or almost no, white in rump. White "ears" present, but sometimes vestigial.
- HI 2.—Like HI 1 but more white in belly and crissum and light tips to feathers on flanks away from midline. A few white-tipped feathers on rump.
- HI 3.—White pattern of abdomen evident but suffused with black. White "ears" extending onto throat as a variable collar. Some white on chin and a little more on rump.
- HI 4.—Belly mostly whitish, rump considerably white, but little white on chin.
- HI 5.—Like *hicksii* but less white in rump.
- HI 6.—Pure *hicksii*; black with white throat, white "ears," white lower breast and abdomen, white undertail coverts, speculum, and rump (but not upper tail coverts), chin variably black, pectoral band black.

Disregarding the few "0+" specimens from outside the area of the Canal Zone, I examined 80 specimens of "*aurita*." The number in each HI category was as follows:

HI 0+	2	(3%)
HI 1	12	(15%)
HI 2	24	(30%)
HI 3	26	(33%)
HI 4	9	(11%)
HI 5	7	(9%)

Thus, 63% of the specimens could be regarded as more or less intermediate between the two parental types, 18% were more like *corvina* and 20% were more like *hicksii*. No specimens of pure parental stock occur in the area of intergradation, and this population thus constitutes a hybrid zone by Short's (1969) definition.

Eisenmann (1957:260) came close to a correct interpretation in hypothesizing that the variability of this species in Panama might be the result of "interbreeding between *aurita* and *corvina*" and that "nominate *aurita* is itself the product of some earlier contact between *corvina* and a population essentially like *ophthalmica*." It was not apparent at that time, however, that "*aurita*" was confined entirely to the Canal Zone area, nor that the "population essentially like *ophthalmica*," in the form of *hicksii*, still exists in Panama on the Pacific slope on either side of the hybrid "*aurita*" zone. Because the range of *hicksii* was obviously once continuous across the Pacific side of the isthmus, it is evident that the new development is the introgression by *corvina* genetic stock, thus creating a hybrid zone that has fragmented the distribution of *hicksii*.

The age of the establishment of the hybrid zone between *hicksii* and *corvina* is not certain, but Eisenmann's (1957:260) supposition that the forms in question "were probably not in contact" a century ago, may be doubted. The earliest specimens from the area of the Canal Zone are the types of *semicollaris* Lawrence and *fortipes* Lawrence, collected by McLeannen along the Panama Railroad in the mid-1800's. I have examined these and would classify both as HI 2 intergrades, with the type of *fortipes* having less white on the rump and more white on the chin than the type of *semicollaris*. Two other specimens collected by McLeannen I would classify as HI 2 and HI 5. Although I analyzed all the specimens of "*aurita*" from the hybrid zone by date and locality, I could detect no pattern of change through time. This may be due to lack of adequate samples taken in the 19th century. The hybrid zone has apparently been in existence for over a century and appears to be stable. The influence of *corvina* has not yet spread much beyond the Canal Zone on the Pacific slope. On the other hand, there is evidence, although slight, that the influence of *hicksii* may be spreading westward along the Atlantic slope.

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