

A new subspecies of *Heliodoxa xanthogonys* (Aves, Trochilidae) from the southern Pantepui highlands, with biogeographical and taxonomic notes

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RESUMO. Uma nova subespécie de *Heliodoxa xanthogonys* (Aves, Trochilidae) do sul da Venezuela, com observações biogeográficas e taxonômicas. Este artigo revisa a variação biogeográfica e geográfica do Beija-flor-veludo (*Heliodoxa xanthogonys*). Diferente de outros membros do mesmo gênero, este troquilídeo é endêmico da região de Pantepui do norte da América do Sul. Baseados em distintos caracteres de coloração e de biometria na área sul da distribuição geográfica de *H. xanthogonys*, nós descrevemos uma raça até agora não reconhecida que ocorre na maior parte do sul da Venezuela, *H. xanthogonys willardi* subsp. nov. Formando uma superespécie com o táxon andino *H. jacula*, *H. xanthogonys* foi similarmente originado de descendentes da população do nordeste dos Andes que subsequentemente invadiu os platôs da Venezuela e Guiana. Palavras-Chave: Biogeografia, variação geográfica, Pantepui, *H. xanthogonys*, *H. xanthogonys willardi*, ssp. nov., Trochilidae.

ABSTRACT. This paper reviews the biogeography and geographical variation of the Velvet-browed Brilliant (*Heliodoxa xanthogonys*). Unlike other generic members, this trochilid is endemic to the Pantepui region of northern South America. Based on different colour and biometric characters within the southern range of *H. xanthogonys*, we describe a hitherto unrecognized race from southernmost Venezuela, *H. xanthogonys willardi* subsp. nov. Forming a monophylum (superspecies) with the Andean taxon *H. jacula*, *H. xanthogonys* likely originated from descendants of the northeastern Andean population that subsequently invaded the tablelands of Venezuela and Guyana.

Key Words: Biogeography, geographical variation, Pantepui, *H. xanthogonys*, *H. xanthogonys willardi*, ssp. nov., Trochilidae.

Since the middle of the 19th century the avifauna of the highlands and tepuis of southern Venezuela and adjacent parts of Guyana and Brazil (Pantepui region) has been more extensively studied (Mayr and Phelps 1967). As a result, most of the tablelands have been found to harbour a characteristic bird species assemblage, including many endemic elements.

Within the family of hummingbirds (Trochilidae), endemic Pantepui forms occur in a number of genera. Among the group of brilliants and jewelfronts, *Heliodoxa xanthogonys* is the only representative confined to the Pantepui highlands (figure 1). It has been chiefly recorded from the submontane zone (mostly between 700-2000 m) of various tepuis and sierras in the states of Bolivar and Amazonas, Venezuela, western Guyana, and northern Roraima, Brazil (Friedmann 1948, Snyder 1966, Ruschi 1986, Grantsau 1988, Sick 1993; Sánchez-Osés, unpubl. data). Until recently (Weller 1999), *H. xanthogonys* has been considered monotypic (e.g., Meyer de Schauensee & Phelps 1978).

MATERIAL AND METHODS

During a biogeographical survey of *H. xanthogonys*, a total of 42 specimens were examined for morphometric and plumage characterization. Bill length from tip to the

proximal end of operculum, wing length, and furcation of the inner- (R1) and outermost (R5) rectrices were measured to the nearest 0.1 mm. Coordinates of collecting localities of examined specimens were determined according to Paynter (1982) and Stephens and Traylor (1985). The plumage coloration was standardized by using a color guide (Smithe 1975). A nonparametric mean analysis (Student's t-test) was used to compare the subpopulations of the species (significance level $p < 0.05$).

RESULTS AND DISCUSSION

Morphologically, *Heliodoxa* species are sexually dimorphic, medium-sized trochilids (10-13 cm). Males are characterized by green upper parts, and glittering areas on frontlet and throat. In contrast, females lack most of the glittering parts but exhibit ventrally more whitish to rufous plumage with iridescent green discs. In both sexes, the tail shows a clear bifurcation, and has either olive-greenish or bluish-black coloration.

From *H. jacula*, a close relative of the subtropical northern Andes and southeastern Central America (Chapman 1931; Renner, unpubl. data), *H. xanthogonys* can be distinguished by the orange-red coloured proximal part of the lower mandible (but appears whitish in skins; *H. jacula*: bill entirely blackish) and a slightly larger throat patch.

Males of *H. xanthogonys* show a glittering green forehead and crown, a brilliant turquoise to golden green gorget with a circular violet-blue patch on the upper throat, dark golden green belly, and blue-black rectrices (with a slight dark green gleam on the dorsal side of inner rectrices). Females lack the glittering areas on throat, belly, and dorsal feathers; in ventral plumage, white portions are dominant, with greenish spots on throat and belly. Unlike males, the outer rectrices are tipped white, and the undertail-coverts show more greyish-brown instead of entirely greenish discs.

Most probably due to small sample sizes of *H. xanthogonys* in ornithological collections, geographical variation in the species has been scarcely discussed. Chapman (1931) recognized differences in throat coloration between a male from Cerro Duida and the holotype from Merume Mountains, Guyana. More recently, Meyer de Schauensee and Phelps (1978), Dickerman and Phelps (1982), and Willard *et al.* (1991) gave no indication for geographical variation within the species.

While studying a series of skin specimens collected at Serranía de la Neblina during a Field Museum of Natural History expedition in 1985 (compare Willard *et al.* 1991), we found evidence for geographical variation between northern and southern representatives of the species. Comparison with other specimens revealed that an immature female (NMNH # 325.973) from the adjacent Sierra Imeri, shares the distinct characters of the Neblina birds. Further specimens from Neblina examined in the Colección Ornitología Phelps, Caracas, all show a clear white ventral plumage, indicating that the Southern subpopulation is subspecifically distinct (COP # 64686 with note “sp. nov.?” on label). For its taxonomic recognition we propose the name:

Heliodoxa xanthogonys willardi subsp. nov.

Holotype. Deposited in The Field Museum of Natural History, Chicago, FMNH # 318.837; adult female from Amazonas, Serranía de la Neblina, Camp VII, 1800 m, collected by David E. Willard, February 1985.

Description of holotype. Bill straight, black with whitish mandible; frontlet Emerald Green [163]; postocular area white; rest of head, hindneck, upperparts, and flanks; underparts with partly Lime Green [159] discs, on chin and centrally with whitish subterminal bars on chin and upper throat becoming entirely white towards belly; uppertail-coverts Parrot Green [260]; rectrices blue-black [Jet Black 89] with a dark green-bronzy tinge, with white tips in outer three pairs; undertail-coverts basically greyish [Olive-Gray 42] with white margins.

Paratype. FMNH # 318.839; adult male from Amazonas, Serranía de la Neblina, Camp XI, 1400 m, collected by David E. Willard, 6 February 1985.

Description of Paratype. Forehead and centre of crown glittering Emerald Green [163]; postocular area white; rest of head, hindneck and upperparts to rump Emerald Green [163]; chin to lower breast glittering Emerald Green [163] with a bluish tinge; violet-blue [Ultramarine 270] patch on upper throat; belly and abdomen dark green [Parrot Green 260]; discs of undertail-coverts dark green [Parrot Green 260], narrowly fringed Cinammon [39]; tail blackish.

Diagnosis. Male differs on average from nominate form by longer wings and rectrices; the plumage shows no general differences. Females are less green in general appearance; underparts more whitish, especially on throat and breast; centre of belly white without any greenish discs; flanks, rectrices, centres of undertail-coverts emerald green; tips of outermost rectrices with broader white margins.

Distribution. Known from two collecting sites, Serranía de la Neblina and Sierra Imeri, in southern Amazonas, Venezuela, at border to Roraima, Brazil, at 500 – 1800 m.

Etymology. This taxon is named after David E. Willard, the collector of the type specimens.

Geographical variation. Males of *H. xanthogonys willardi* differ on average in wing and tail length from nominate birds (table 1), although the significance could not be tested due to small sample size ($n = 3$) of the type series that consists of two adult males and one immature bird. As the latter is similar in biometric characters to adult birds, it was included in comparison with northern representatives. Clinal variation in wing length is indicated for *H. x. xanthogonys*. For example, three males from Kamarang River, Guyana, have slightly shorter wings (61.4 – 61.8 mm) than those from Roraima and adjacent regions of southern Bolívar (62.9 – 65.3 mm, $n = 6$) as well as two birds from Cerro Duida (62.9, 65.7 mm).

In most biometric characters, the measurements of female *H. x. willardi* ($n = 7$, table 1) fall within the value range of female *H. x. xanthogonys*. Similarly to males, females of *willardi* have significantly longer wings ($p = 0.02$) than nominate birds. The immature female from Sierra Imeri was included in the analysis for the same reason as the immature male specimen.

In coloration, differences in males are rather a matter of individual than of geographical variation. For example, the throat patch varies in shape (circular to oval) and extent. In some specimens, the forecrown may be glittering golden green, whereas others show more turquoise reflections. Immature males like the one from Serranía de la Neblina (FMNH # 318.834) lack the glittering forecrown, showing a rather dark green head with rufous fringes. Ventrally, the violet-blue throat patch is reduced to about half the size of an adult male's, and central areas on throat and belly are darker greyish.

Table 1. Biometric characters of both sexes of *Heliodoxa xanthogonys* subsp., showing mean \pm s.d., sample size (in brackets), and range.

Taxon	Sex	Bill (mm)	Wing (mm)	Rectrix 1 (mm)	Rectrix 5 (mm)
<i>Heliodoxa x. xanthogonys</i>	Male	22.5 \pm 0.7 (14)	63.8 \pm 1.7 (15)	33.4 \pm 1.0 (14)	38.7 \pm 1.4 (14)
		21.1 – 24.1	60.5 – 66.5	31.7 – 35.1	34.5 – 39.9
	Female	26.3 \pm 1.1 (15)	61.6 \pm 2.9 (16)	33.7 \pm 1.1 (16)	35.7 \pm 1.0 (16)
<i>Heliodoxa x. willardi</i>		25.2 – 28.9	56.5 – 68.5	31.3 – 35.2	33.4 – 37.6
	Male	22.7 \pm 0.7 (3)	67.3 \pm 0.8 (3)	35.9 \pm 1.3 (3)	42.4 \pm 0.9 (3)
		21.9 – 23.3	66.5 – 68.0	34.4 – 36.8	41.3 – 43.1
<i>Heliodoxa x. willardi</i>	Female	26.3 \pm 0.9 (5)	63.6 \pm 0.9 (6)	33.0 \pm 1.2 (5)	35.3 \pm 1.4 (5)
		25.3 – 27.5	61.9 – 64.4	31.3 – 34.7	33.1 – 37.0

Females of subspecies *xanthogonys* show individual colour differences in various plumage features. The frontlet is golden green to dark greenish. Upperparts, flanks, and rectrices vary from weak golden green to dark bronze-green (similarly in nominate males). In the latter, the whitish tips characteristic of females are sometimes very narrow and reduced to the outermost rectrices (e.g., NMNH # 149.596). However, considering the extent of whitish parts in ventral plumage there is no distinction in the nominate females between specimens from the eastern distributional limits and those from farther southwest. As an example, a female from Cerro Marahuaca, Amazonas (NMNH # 606.017), agrees in this character with Guyanan or Roraima birds, thus being clearly different from all *willardi* females.

Systematics and speciation in *Heliodoxa*

Recent studies on genetic differentiation have thrown new light on phylogenetic aspects in *Heliodoxa* and *Polyplancta* (Gerwin and Zink 1989), thus partly solving taxonomic uncertainties expressed, e.g., by Peters (1945) and Zimmer (1951). As a main result, four species groups comprising eight species were distinguished, *H. xanthogonys*, *H. gularis/branicckii*, *H. rubinoides/jacula-leadbeateri*, and *H. schreibersii/aurescens* (formerly *Polyplancta aurescens*, compare Heynen 1999). Additionally, the widest genetic distance and higher genetic divergence in comparison with all other congeners was proven for *H. xanthogonys*, probably due to the complete isolation from the Andean *Heliodoxa* taxa and the insular range of this form (Gerwin and Zink 1989).

The present-day distribution of *Heliodoxa* suggests an Andean centre of evolution, where five species occur, of which only one is distributionally focused on the Cordilleres of southern Central America (*H. jacula*: Panamá, Costa Rica; scattered occurrence in Colombia). In the coloration pattern, *H. xanthogonys* more strongly resembles the west Andean taxon *H. jacula* (blue throat patch) than the geographically closer *H. leadbeateri* (NW Venezuela to Bolivia; green throat pattern) and the possibly parapatric *H. aurescens* (E

Colombia to E Peru, NW Brazil, very locally in S, SE Venezuela; chin blackish, throat glittering green).

A possible evolutionary scenario for *H. xanthogonys* is that the taxon evolved from descendants of the also subtropically distributed *H. jacula*. Presumably, Pleistocene fluctuations in forest vegetation enabled a proto-*xanthogonys* population to pass the tropical, partly arid lowlands of western Venezuela by long-distance emigration (see Mayr and Phelps 1967). Considering the intermediate sizes of specimens from the western cerros, we suggest that *H. xanthogonys* could have originated within the western Pantepui region where it is found, e.g., on Cerro Paraque and at Serranía Parú. Likewise, Cerro Duida has been demonstrated to be an important centre of endemism for many bird taxa (Chapman 1931) as well as other vertebrates (Müller 1973).

Subsequently, the ancestral *H. xanthogonys* population spread in an eastern direction, reaching the highlands of southeastern Venezuela and western Guyana. Southward directed invasion resulted in colonization of the Sierra Imeri and Serranía de la Neblina, supported by junctions of evergreen montane forests along the cerros bordering to Brazil (Hueck and Seibert 1972, Huber and Alarcon 1988). Based on the allopatric distributional pattern (figure 1) we conclude that the southernmost population of *H. xanthogonys* became isolated from its northern conspecifics during a glacial period in a southern Venezuelan mountain refuge (Haffer 1974, but compare Colinvaux *et al.* 2000), resulting in the subspecific differentiation of *H. x. willardi*. According to these findings, the southern subspecies of another Pantepui trochilid, *Saucerottia cupreicauda laireti*, is similarly restricted to the highlands of southernmost Venezuela and adjacent northern Roraima (Phelps and Aveledo Hostos 1988, Weller 2000).

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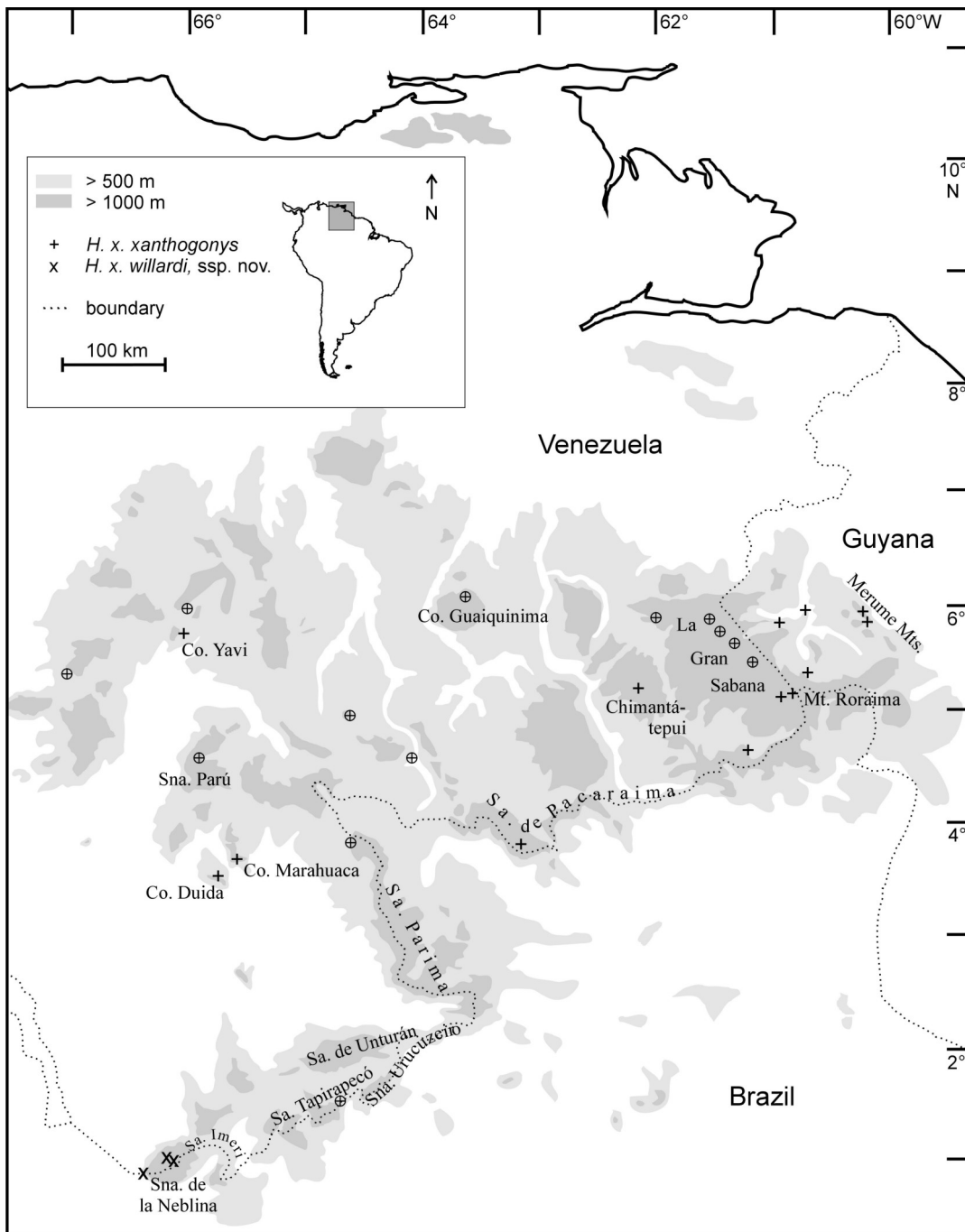


Figure 1. Distribution of *Heliodoxa xanthogonys* based on examined specimens; for localities and coordinates, see Appendix. Additional locations are (encircled) provided by Sánchez-Osés (1995).

of Natural History, New York (AMNH); The Field Museum of Natural History, Chicago (FMNH); National Museum of Natural History, Washington, D. C. (NMNH); Colección Ornitológica Phelps, Caracas (COP); and Zoologische Staatssammlung, Munich (ZSM). This project was partly supported by grants from the German Science Foundation (DFG # Schu 766/1-5), the AMNH (Collection Study Grant), the NMNH (Smithsonian Short-term Visitor Grant), and the FMNH (Field Museum Grant). We thank Carlos Sánchez-Osés (ZFMK) for providing additional skin data from the COP.

REFERENCES

- Chapman, F. W. (1931) The upper zonal bird-life of Mts. Roraima and Duida. *Bull. Amer. Mus. Nat. Hist.* 63:1-135.
- Chubb, C. (1916) *The birds of British Guiana*, v. 1. London: Quaritch.
- Colinvaux, P. A., P. E. de Oliveira and M. B. Bush (2000) Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quat. Sci. Rev.* 19:141-169

- Dickerman, R. W. and W. H. Phelps Jr. (1982) An annotated list of the birds of Cerro Urutaní on the border of Estado Bolívar, Venezuela, and Territorio Roraima, Brazil. *Am. Mus. Novit.* 2732:1-20.
- Friedmann, A. (1948) Birds collected by the National Geographic Society's expeditions to northern Brazil and southern Venezuela. *Proc. U. S. Nat. Mus.* 97:373-570.
- Gerwin, J. A. and R. M. Zink (1989) Phylogenetic patterns in the genus *Heliodoxa* (Aves: Trochilidae): an allozymatic perspective. *Willson Bull.* 101:525-544.
- Gould, J. (1861) *An introduction to the Trochilidae, or family of humming-birds*. London: Taylor and Francis.
- Grantsau, R. (1988) *Os Beija-flores do Brasil*. Rio de Janeiro: Espressão e cultura.
- Haffer, J. (1974) *Avian speciation in tropical South America*, no. 14. Cambridge: Publ. Nat. Ornith.Club.
- Huber, O. and C. Alarcon (1988) *Mapa de vegetación de Venezuela*. Caracas: Ministerio del Ambiente y de los Recursos Naturales Renovables (División de Vegetación).
- Hueck, K. and P. Seibert (1972) *Vegetationskarte von Südamerika*. Stuttgart: Gustav Fischer.
- Mayr, E. and W. H. Phelps Jr. (1967) The origin of the bird fauna of the south Venezuelan highlands. *Bull. Amer. Mus. Nat. Hist.* 136:269-328.
- Meyer de Schauensee, R. and W. H. Phelps Jr. (1978) *A guide to the birds of Venezuela*. Princeton: Princeton Univ. Press.
- Müller, P. (1973) The dispersal centres of terrestrial vertebrates in the Neotropical realm. A study in the evolution of Neotropical biota and its native landscape. *Biogeographica* 2:1-244.
- Paynter Jr., R. A. (1982) *Ornithological Gazetteer of Venezuela*. Cambridge: Mus. Comp. Zool.
- Peters, J. L. (1945) *Check-list of birds of the world*, v. 5. Cambridge.
- Ruschi, A. (1986) *Aves do Brasil. Beija-flores*, v. 5. Rio de Janeiro: Espressão e Cultura.
- Sick, H. (1993) *Birds in Brazil*. Princeton: Princeton Univ. Press.
- Smithe, F. B. (1975) *Naturalist's color guide*. New York: Amer. Mus. Nat. Hist.
- Snyder, D. E. (1966) *The birds of Guyana*. Salem: Peabody Museum.
- Stephens, L. and M. A. Traylor Jr. (1985) *Ornithological Gazetteer of the Guianas*. Cambridge: Mus. Comp. Zool.
- Weller, A.-A. (1999) Velvet-browed Brilliant *Heliodoxa xanthogonys*, p. 615-616. In: J. del Hoyo, A. Elliot and J. Sargatal (eds.) *Handbook of the Birds of the World*, v. 5. Barn-owls to Hummingbirds. Madrid: Lynx Edicions.
- _____ (2000) A new hummingbird subspecies from southern Bolívar, Venezuela, with notes on biogeography and taxonomy of the *Saucerottia viridigastercupreicauda* species group. *Orn. Neotrop.* 11: 143-154.
- Willard, D. E., S. F. Mercedes, G. F. Barrowclough, R. W. Dickerman, P. F. Cannell, S. L. Coats, J. L. Cracraft and J. P. O'Neill (1991) The birds of Serranía de la Neblina, Territorio Federal Amazonas, Venezuela. *Fieldiana (Zool.)* 65:1-80.
- Zimmer, J. T. (1951) Studies of Peruvian birds, n. 60. *Amer. Mus. Novitates* 1513:1-45.

APPENDIX

Localities of specimens examined (listed from N to S):

Heliodoxa xanthogonys xanthogonys

- Guyana: Kamarang River, 458 m, 05°54'N/60°35'W; Merume Mountains, 610-1000 m, 05°48'N/60°06'W; Mount Twek-Quay, 915 m, not located;
- Venezuela: Santa Elena Highway, km 122, 1350 m, not located; Cerro Yavi, 1600 m, 05°32'N/65°59'W; Chimantá-tepui, 1200 m, 05°18'N/62°10'W; Monte Roraima, 850-1100 m, 05°12'N/60°44'W; Arabopó, 1200-1300 m, 05°06'N/60°44'W; Cerro Urutani, Sierra de Pacaraima, 1200-1280 m, 03°46'N/63°03'W; Cerro Marahuaca, camp Jaime Benitez, 1500 m, 03°34'N/65°27'W; Cerro Duida, Primer Pico, 1280-1433 m, 03°25'N/65°40'W;

Heliodoxa xanthogonys willardi, subsp. nov.

- Venezuela: Serranía de la Neblina, Camp V, 1250 m, 00°05'N/66°00'W; Camp VI, 1800-2000 m; Camp XI, 1400 m, 00°50'N/65°56'W;
- Venezuela/Brazil: Sierra Imeri, near Salto de Hua, 1000 m, not located (W of Serranía de la Neblina).