

## Alpha taxonomy of the *Xiphorhynchus spixii* species group with the validation of *X. juruanus* Ihering, 1904

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O trabalho revê o complexo específico *Xiphorhynchus spixii* que se distribui na região amazônica. Além de confirmar o status específico de *X. spixii* (ao sul do rio Amazonas, da margem leste do Tapajós, até o Maranhão) e de *X. elegans* (no interflúvio Madeira–Tapajós) o presente estudo valida *X. juruanus*, como uma espécie filogenética de ampla distribuição a oeste do rio Madeira, ocorrendo no Brasil, na Bolívia, no Peru, no Equador e na Colômbia. Esta última espécie passa a incluir os táxons *insignis*, *ornatus* e *buenavistae*, antes considerados subespécies de *X. elegans*. A variação geográfica dessas espécies é descrita.

The species group *Xiphorhynchus spixii* occurs over a vast region from the Colombian Andes and Bolivia into north-west Brazil and south along the right bank of the rio Amazonas to Mato Grosso, Pará, Tocantins and Maranhão<sup>14</sup>. Indeed, it is one of the most complex and debated species groups within the genus.

Cory & Hellmayr<sup>6</sup> stated that taxa within the group *spixii* are probably conspecific, also raising the possibility that *X. pardalotus* is merely a geographic substitute, i.e. yet another subspecies distributed north of the rio Amazonas. No subsequent author has linked *X. pardalotus* to the group in question, but some have tended to treat the entire complex as conspecific<sup>9,18,20,22,29</sup>. *X. ocellatus* and *X. obsoletus* were considered closely related to this complex by Raikow<sup>19</sup>, who removed *X. elegans* from the group and considered it only indirectly related to *X. spixii*. Haffer<sup>9</sup> and Aleixo<sup>1</sup>, however, recognised two species as valid: *X. spixii* (Maranhão to the rio Tapajós) and *X. elegans* (of the Tapajós/Madeira interfluvium to Bolivia), including *X. e. juruanus* (western Amazon, from south-east

Peru and Bolivia to the rio Madeira), *X. e. insignis* (Peru), *X. e. ornatus* (north-west Peru, Ecuador, south Colombia) and *X. e. buenavistae* (north-east Colombia).



Figure 2. Comparison between the dorsal spots of *Xiphorhynchus juruanus* and *X. elegans*. From right to left: *X. elegans* (AMNH 148470, Porto Velho); *X. juruanus* (AMNH 309317, Brasil); *X. juruanus* (AMNH 240413, Peru); *X. juruanus* (AMNH 407167, Ecuador); *X. juruanus* (AMNH 460242, Colombia) (Marcos A. Raposo)

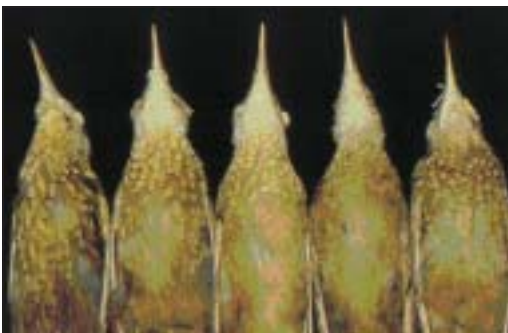


Figure 1. Comparison between the ventral spots of *Xiphorhynchus juruanus* and *X. elegans*. From right to left: *X. elegans* (AMNH 148470, Porto Velho); *X. juruanus* (AMNH 309317, Brasil); *X. juruanus* (AMNH 240413, Peru); *X. juruanus* (AMNH 407167, Ecuador); *X. juruanus* (AMNH 460242, Colombia) (Marcos A. Raposo)



Figure 3. Detail of the ochre lines along the rachis of the upperwing-coverts, ending in small spots on feathers, which is the diagnostic character of *Xiphorhynchus elegans* (Marcos A. Raposo)

*X. spixii*<sup>13</sup> was described on the basis of *Dendrocolaptes tenuirostris* Spix, 1824 (type lost), homonym of *Dendrocolaptes tenuirostris* Lichtenstein, 1818 (= *Lepidocolaptes fuscus*). Cory & Hellmayr<sup>6</sup> proposed Pará as the type locality. The species' small size is comparable to that of *X. obsoletus*<sup>14,22</sup>, from which it is distinguished by having more ochraceous plumage and a longer bill. It also differs from *X. ocellatus*, which it approaches in size, by its paler guttate spotting, more sharply demarcated and more amply distributed over the belly and mantle. *X. s. spixii* occurs in *terra firme* forest south of the rio Amazonas, from Maranhão west to the rio Tapajós. The occurrence of *X. spixii* in Ceará, mentioned by Teixeira *et al.*<sup>24</sup>, proved false and was based on the incorrect identification of an immature specimen of *X. picus* (corrected in Teixeira *et al.*<sup>25</sup>). Cory & Hellmayr<sup>6</sup> included *Xiphorhynchus fraterculus*<sup>21</sup>, described on the basis of a single specimen obtained in Santarém, Pará, as a junior synonym of *X. spixii*.

*X. elegans*<sup>16</sup> was described on the basis of specimens from Engenho do Capitão Gama, Mato Grosso, and is characterised, according to Cory & Hellmayr<sup>6</sup>, by the large ochraceous, ovoid ocelli distributed over the entire back from the nape to the uropygium. It has rufous shoulders, and the upperwing-coverts possess an ochraceous streak along the rachis, terminating in a small spot. It also has broad fan-shaped spots on the neck and breast, a straight dark bill and yellowish lower mandible. *X. elegans* occurs in the Madeira–Tapajós interfluvium and its headwaters, where it occasionally comes into close proximity with the parapatric forms of *X. spixii juruanus* and *X. s. spixii*. A possible intergradation between this form and *X. spixii* near the headwaters of the Tapajós, around Rio Peixoto de Azevedo, has been used to justify treating it as a subspecies of *spixii*<sup>9,20,22,29</sup>. Although Zimmer<sup>29</sup> and subsequent authors proposed to treat all forms in the group as subspecies of *X. spixii*, Ridgely & Tudor<sup>20</sup>, with the subsequent support of Haffer<sup>9</sup> and Aleixo<sup>1</sup>, contended that *X. spixii* might be considered a species, while all other taxa would remain subspecies of *X. elegans*.

*X. elegans juruanus*<sup>12</sup>, classified on the basis of material from the rio Juruá, is immediately distinguished from *X. s. spixii* and *X. elegans* by its smaller size and fewer breast spots, and the near absence of dorsal spots. It lacks the narrow ochraceous streaks on the upperwing-coverts of *X. elegans*. Moreover, it has a bright white throat patch and straight dark bill very similar to that of *X. elegans* but different from *X. e. insignis*<sup>6,11</sup>. It occurs on the left bank of the rio Madeira, south of the rio Amazonas and north to the lower rio Ucayali in Peru. Zimmer<sup>29</sup>, however, concluded that material from the left bank of the lower rio Madeira

(Rosarinho, Porto Velho and Manaqueri) more closely matched specimens of *X. elegans* and that the species therefore occurs on both sides of the river. There is much disagreement in the literature on this point. Most recently, Ridgely & Tudor<sup>20</sup> and Haffer<sup>9</sup> agreed that *X. spixii juruanus* occurs in all localities immediately west of the Madeira, except Rosarinho, from where morphological variants requiring further study are known<sup>9,29</sup>.

*X. elegans insignis*<sup>10</sup> is based on a specimen from Samiría, Peru. At the time of its description, Hellmayr was unaware of the description of *juruanus* by Ihering<sup>12</sup>, and as a result the two descriptions overlapped considerably. Hellmayr<sup>11</sup> presented his diagnosis in relation to the form described by Ihering only after the latter had sent him two specimens of *X. s. juruanus*, an adult and immature. However, given the considerable individual variation in these forms, insufficient material was available for more than initial remarks, limited to the more sharply curved and paler bill of *X. e. insignis*. In the original description, *X. e. insignis* was distinguished from *X. elegans* by its more stripe-like dorsal markings confined to the nape. In addition, its coloration was, in general, reportedly darker than *elegans*, including the ground colour of the pileum, which is dusky in *X. e. insignis*. As in *X. s. juruanus*, the median streaks on the upperwing-coverts characteristic of *X. elegans* are absent in *X. e. insignis*. Cory & Hellmayr<sup>6</sup> added that, in comparison to *X. e. insignis*, *X. s. juruanus* has spots both smaller and more confined to the upper body. Hence, he argued, *X. e. insignis* occupied the entire eastern portion of the region in which the complex occurred, from the left bank of the Ucayali in Peru to Colombia. Zimmer<sup>29</sup> concluded that all material examined from Sarayacu and Orosa to the east consisted of typical *X. s. juruanus*, whereas forms from the upper Ucayali were substantially different and matched Hellmayr's diagnosis in respect of bill and pileum coloration, and the mantle and ventral spots. Zimmer also suggested the possibility of intergradation with *juruanus* and, in noting the existence of morphological variation north of the rio Amazonas, concluded by describing two new taxa, *X. s. ornatus* and *X. s. similis*.

*X. elegans ornatus*<sup>29</sup> was described on the basis of a specimen from Puerto Indiana, near the rio Napo in Peru. It closely resembles *X. elegans* but is brighter and has larger ventral and dorsal spots. The bill is pale grey except the base of the lower mandible, whereas *X. elegans* has a dark bill. According to Zimmer<sup>29</sup>, both possess a similar pattern of median streaks along the rachis of the upperwing-coverts, but *X. s. ornatus* is darker cinnamon on the wings, tail and rump. It is distinguished from *X. e. insignis* by even larger ventral and dorsal spots, and by its deeper

ochraceous ventral spots. The throat is deep buff, not white as in *X. e. insignis* and *X. s. juruanus*. It occurs in northern Peru and on the left bank of the rio Amazonas from the rio Napo region to eastern Ecuador, north to eastern Colombia and east to the vicinity of São Paulo de Olivença, Brazil. Several specimens clearly identifiable as *X. s. juruanus* were available from the same area as the sample of *X. s. ornatus* taken at the latter locality. Zimmer<sup>29</sup>, expressing surprise at the presence of the two forms in the same locality and south of the Solimões, suggested that as the two were not collected on the same day they had been taken in different habitats, and plausibly even on opposite banks of the river. Todd<sup>26</sup>, in contrast, accepted that they had all been collected from one area and concluded that they were species, given that if they were subspecies they would reproduce freely and lose their diagnostic characters. He also claimed that specimens of the two had been taken on the same day, but this was subsequently emphatically refuted by Haffer<sup>9</sup>, who suggested that those of *X. s. ornatus* had been collected from an island in mid-river, c.500 m from the south bank of the Amazonas. Thus, they could be considered subspecies, as their potential reproductive compatibility was restored. After describing a degree of individual and geographic variation for his new subspecies, Zimmer<sup>29</sup> realised that an even more distinct form was present further north, in Buena Vista, upstream of Villavicencio, and described it as subspecies named for its place of origin.

*X. elegans buenavistae*<sup>29</sup>, was initially described as *X. s. similis* but its name was subsequently corrected, also by Zimmer<sup>30</sup>, because *Dendroplex similis*<sup>16</sup>, a synonym of *X. obsoletus*, preoccupied the name *similis*. The holotype is from Buena Vista, Colombia. This form closely resembles *X. elegans*, but is distinguished by a paler bill, less rufous shoulders and merely obsolete streaks along the rachis of its coverts and scapulars. It differs from *X. e. ornatus* in its overall greyer coloration, distinctly more ochraceous and smaller dorsal and ventral spots, and whiter throat, albeit not as white as *X. e. insignis*, from which it also differs in the larger size and distribution of its dorsal and ventral spots. *X. e. buenavistae* occurs from the eastern slopes of the Colombian Andes to the Orinoco basin. Closing his description, Zimmer raised the possibility of intergradation with *X. s. ornatus*, but did not reach a conclusion on the subject.

Here we review the alpha taxonomy of the *X. spixii* species group, adopting the concept of species proposed by Nelson & Platnick<sup>15</sup>. It should be noted that the results obtained using these parameters do not differ substantially from those that would be achieved if other supposedly phylogenetic concepts were deployed (for a review of such species concepts, see de Pinna<sup>17</sup>).

## Materials and methods

A total of 751 specimens was analysed, 308 of *X. spixii* and 443 of *X. elegans* (including *X. e. juruanus*, *X. e. insignis*, *X. e. buenavistae* and *X. e. ornatus*). This material included the types of *X. spixii ornatus* (AMNH 231998; for museum acronyms see below), *X. spixii similis* (AMNH 122088), *Dendroornis ocellata juruana* (MZUSP 3535), *Dendroornis elegans* (syntype NHM 89520522), *X. obsoletus parvimaclulatus* (ANSP 104157) and *Dendroornis fraterculus* (USNM 120928). Our work focused on plumage coloration and morphometric characters (length of wing, tail and exposed culmen).

Material analysed was from the following institutions: Museu Paraense Emílio Goeldi, Belém (MPEG), Museu Nacional/Universidade Federal do Rio de Janeiro (MNRJ), Museu de Zoologia da Universidade de São Paulo (MZUSP), Field Museum of Natural History, Chicago (FMNH), Museum of Natural History, University of Kansas, Lawrence (MNHUK), Museum of Natural Science, Louisiana State University, Baton Rouge (LSUMZ), American Museum of Natural History, New York (AMNH), National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), Academy of Natural Sciences, Philadelphia (ANSP); Museum of Comparative Zoology, Harvard (MCZ), Muséum National d'Histoire Naturelle, Paris (MNHN), Natural History Museum, Tring (NHM) and Museum für Naturkunde Alexander Humboldt, Berlin (MFN).

## Results

Our analysis demonstrated that three taxa, *X. spixii*<sup>13</sup>, *X. elegans*<sup>16</sup> and *X. juruanus*<sup>12</sup>, should be recognised as species, confirming the conclusions of Haffer<sup>9</sup> and Aleixo<sup>1</sup> in relation to the independence of the first two and validating, for the first time, *X. juruanus*. The taxa *X. s. insignis*, *X. s. ornatus* and *X. s. buenavistae* should henceforth not be considered taxonomically for lack of possible diagnosis and because they were consistently found to represent geographic variants of the senior synonym *X. juruanus*.

The three valid species of the complex are re-described below.

*Xiphorhynchus spixii* (Lesson)

*Picolaptes spixii* Lesson, 1831; p. 314.

*Dendroornis fraterculus* Ridgway, 1888; p. 88.

*Type material*: Holotype missing. Pará is the type locality suggested by Cory & Hellmayr<sup>6</sup>.

*Diagnosis*: *X. spixii* is the member of the complex that is most easily distinguished due to the oval shape of the breast feathers and their distribution (Fig. 2), which give the birds a scaly appearance. It

**Table 1.** Descriptive morphometrics of males and females from the three phylogenetic species in the species group. *X. juruanus* is divided arbitrarily into sample A (specimens from Brazil, Bolivia, extreme north-east Peru) and sample B (central and northern Peru, Ecuador, Colombia).

Population	Sex	Wing	Tail	Bill
<i>X. spixii</i>	Male	99.44 (3.89)	79.58 (3.51)	29.53 (1.35)
		160	155	115
	Female	94.41 (2.85)	75.49 (2.99)	28.89 (1.49)
		93	84	87
<i>X. elegans</i>	Male	97.23 (2.80)	79.15 (4.10)	29.87 (1.50)
		66	65	64
	Female	91.06 (2.90)	71.49 (3.65)	29.23 (1.57)
		59	62	62
<i>X. juruanus</i> A	Male	100.42 (4.04)	80.54 (3.51)	32.46 (1.78)
		62	59	63
	Female	94.19 (2.80)	75.30 (3.45)	31.49 (1.66)
		52	53	51
<i>X. juruanus</i> B	Male	98.31 (3.42)	78.07 (3.67)	32.25 (1.77)
		54	53	52
	Female	93.02 (3.09)	72.83 (3.41)	30.56 (1.72)
		45	46	45

First row: mean and standard deviation (in parentheses). Second row: number of specimens

is immediately distinguished from *X. elegans* and *X. juruanus* by its oval-shaped pectoral spots, which are fan-shaped in the latter two. The ventral spots of *X. spixii* occur on the throat and breast, becoming gradually more elongated until they become stripes on the abdomen. It also differs from *X. juruanus* by the broader distribution of dorsal spots.

**Variation:** Males larger. There is a slight tendency for specimens from near the headwaters of the rio Tapajós to have less elongated spots and less chestnut plumage. This is especially conspicuous in specimens from the upper rio Cururu (4 specimens MNRJ, not yet registered with accession numbers) and the Serra do Cachimbo (MZUSP 38348, 38345 and 38349) but no sign of intergradation with *X. elegans* was detected. In Alta Floresta, the two occur on opposite sides of the rio Teles Pires, confirming their respective diagnoses. It should also be noted that if hybridisation occurred between them, it would be characterised as secondary contact, as indicated by the molecular phylogeny proposed for the genus by Aleixo<sup>1</sup>, who grouped *X. elegans* and the populations included here as *X. juruanus* within a monophyletic taxon.

**Descriptive morphometrics:** See Table 1.

**Distribution:** Occurs from Maranhão, on the banks of the rios Turiaçu and Buriticupu, west to the rio Tapajós, with its northern distribution delimited by the rio Amazonas. Distributional limits elsewhere are within the vicinity of Conceição do Araguaia to the south-east and the rio Teles Pires, rio Cururu (Pará) and the Serra do Cachimbo (Fig. 1).

**Geographic representation of the series: Brazil.**

**Pará:** Acará (2), right bank of the rio Teles Pires, opposite Alta Floresta (5), Altamira (2), Alto Cururu (4), Ananindeua (4), Apehu (1), Arumatéua (2), Aveiros (6), Baião (4), Belém (70), sites along the Belém–Brasília highway (13), Benevides (3), Bujaru (1), Cachimbo (4), Caldeirão (1), Capanema (1), Capim (53), Carajás (9), Castanhal (1), Caxiricatuba (3), Conceição (1), Diamantina (2), Fordlândia (3), Igarapi-açu (1), Ipixuna (1), Irituia (2), Jacundá (4), Jamanxim (1), Javá-guará? (1), Marajó (9), Mirituba (1), Mocojuba (1), Ourém (6), Paragominas (3), Peixe Boi (1), Piquiatuba (1), Providência (3), rio Guamá (4), rio Iriri (1), rio Tocantins (1), Santa Isabel (1), Santana do Araguaia (18), Santarém Novo (1), Santo Antônio do Prata (1), São Félix do Xingu (4), Tapajós? (2), Tapará (1), Tapiringá? (1), Tauari (1), Tucunará (2), Tucuruí (8), Utinga (6), Vilarinho do Monte (3), Vitória (1). **Maranhão:** Açailândia (1), Alto da Alegria (3), Alto Turiaçu (3), Buriticupu (6), Carutapera (1), Flor do Prado (2), Itaizal (1). **Tocantins:** Couto Magalhães (2).

*Xiphorhynchus elegans* (Pelzeln)

*Dendrornis elegans* Pelzeln, 1868; p. 45.

**Type material:** Holotype from Engenho do Capitão Gama, Mato Grosso, syntypes in Natural History Museum, Tring, and Naturhistorisches Museum, Vienna.

**Diagnosis:** Distinguished from other species by fan-shaped spots (Fig. 1) distributed over the entire undersurface to the abdomen, without becoming



stripes as in *X. spixii* and not confined to the breast as in *X. juruanus*. Also distinguished from all populations of the two latter species by ochraceous streaks along the rachis of the upperwing-coverts, ending as small spots (Fig. 3). It has a darker throat than the parapatric populations of *X. juruanus*, from which it is also distinguished by ochraceous ocelli covering almost its entire mantle (Fig. 2), whereas the latter has a striped dorsum. *X. elegans* is similar to populations of *X. juruanus* north of the rio Amazonas (previously named *X. s. ornatus* and *X. s. buenavistae*), although *X. elegans* has a less cinnamon plumage, a darker bill and smaller pectoral spots confined to the apical portion of each feather. The pectoral spots of *X. elegans* also differ in being less elongated in the proximal and median portion, thus lacking the conical shape described for some populations of *X. juruanus*.

**Variation:** *X. elegans* is highly homogeneous throughout its distribution, and no sexual dimorphism has been observed in coloration. Males are larger on average. Specimens from Rosarinho (AMNH 282269, 282271, 282272 and 282273), previously considered intermediate between *X. juruanus* and *X. elegans*<sup>9,29</sup>, matched the diagnosis of *X. elegans*, possessing marked lesser wing-coverts and intermediate spots. The presence of dorsal spots

and ochraceous throat are additional characters of *X. elegans*.

**Descriptive morphometrics:** See Table 1.

**Distribution:** Occurs south of the rio Amazonas where it is confined to the Tapajós–Madeira interfluvium (Fig. 4), and known as far west as the banks of the rio Sepotuba (MNRJ 13346) near Cáceres (Mato Grosso). To the south-west, its distribution appears to be delimited by the rio Guaporé, except in Bolivia, where it crosses this river.

**Geographic representation of the series: Brazil.**

**Pará:** Alta Floresta, left bank of the rio Teles Pires (6), Itaituba (1), Uruá (1), Urucurituba (1), Vila Braga (4); **Amazonas:** left bank of the rio Aripuanã (5), rio Theodore Roosevelt (2), Rosarinho (5); **Mato Grosso:** Engenho do Capitão Gama (1), Jacaré (1), right bank of the rio Aripuanã (Cachoeira Dardanelus) (5), Rio Peixoto de Azevedo (6), Salto Grande do Sepotuba (1), Teles Pires (3); **Rondônia:** Aliança (3), Alvorada do Oeste (6), Cachoeira Nazaré (29), Calama (5), Jiparaná (2), Ouro Preto do Oeste (6), Pedra Branca (10), Porto Velho (4), Príncipe da Beira (1), rio Anari (4), rio Jamari (1), São João do Norte (1), UHE Samuel (8). **Bolivia. Santa Cruz:** Velasco (16), Serranía de Huanchaca (9).

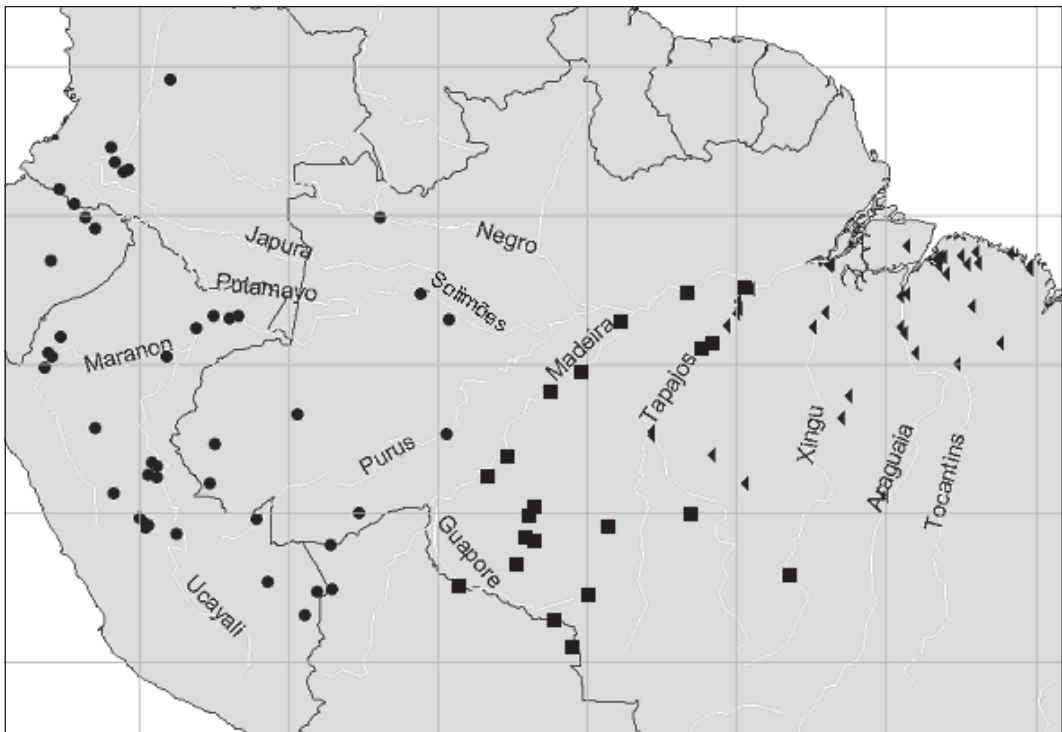


Figure 4. Map showing distributions of the examined specimens of ● *Xiphorhynchus juruanus*, ■ *X. elegans* and ▲ *X. spixii*.

*Xiphorhynchus juruanus* (Ihering)

*Dendroornis ocellata juruana* Ihering, 1904; p. 436.

*Dendroornis insignis* Hellmayr, 1905; p. 55.

*Xiphorhynchus spixii ornatus* Zimmer, 1934; p. 7.

*Xiphorhynchus spixii similis* (= *buenavistae*) Zimmer, 1934; p. 9.

*Xiphorhynchus obsoletus parvimaclulatus* Carriker, 1934; p. 323<sup>4</sup>.

*Type material*: Holotype from the banks of the rio Juruá, housed in the Museu de Zoologia da Universidade de São Paulo.

*Diagnosis*: *X. juruanus* possesses pronounced geographic variation. The Brazilian and Bolivian populations, which are geographically close to *X. elegans*, are distinguished from the latter by their smaller fan-shaped pectoral spots confined to the breast, and the dorsal spots reduced to stripes. In addition, they lack the latter's ochraceous stripes on the upperwing-coverts and have a more whitish throat. These populations of *X. juruanus* differ from *X. spixii* in the shape and distribution of spots, which are large, oval and rather diffuse in the latter. Peruvian, Ecuadorian and Colombian populations of *X. juruanus* (previously named *X. e. insignis*, *X. e. ornatus* and *X. e. buenavistae*) vary considerably but are distinct from *X. spixii* by having ventral spots that are conical and fan-shaped, rather than ovoid, and by having a pale bill, whereas both *X. spixii* and *X. elegans* have a dark bill, as do the Brazilian and Bolivian populations of *X. juruanus*. They also differ from *X. elegans* in having larger spots.

*Variation*: No sexual dimorphism detected in respect of plumage coloration. The young approximate to the pattern observed in other species of *Xiphorhynchus*, in that they are more chestnut and have a smaller, darker bill. They present pronounced modifications in body spots, which may be larger in some individuals (e.g. AMNH 824056).

Our analysis confirmed that *X. juruanus* also presents considerable geographic variation in respect of characters historically used for diagnostic purposes. In the area of contact with *X. elegans*, the belly spots are similar in shape to those of the latter, but much smaller and confined to the breast. Spots become larger in populations further from the rio Madeira, towards Ecuador and Colombia, confirming the observations of Zimmer<sup>29</sup>. The same applies to the dorsal spots, which are larger in the western range of *X. juruanus*. Localities near the rio Madeira (e.g. Porto Velho) have merely incipient dorsal spots appearing as stripes. In Porto Pardo, Porto Maldonado and the rio Manu (all in Madre

de Dios, Peru) and Nicolas Suarez (Pando, Bolivia), the dorsal and ventral spots are slightly larger, but the bill remains black (e.g. AMNH 82456 and 824057). Around Lagarto, Santa Rosa, Puerto Bermudez, the rio Linlla Pichis, Tingo María and Chuchurras, in the upper rio Ucayali region, a number of specimens have larger spots and paler bills (e.g. AMNH 240408 and 240411), typical of the synonym *X. e. insignis* (agreeing with Hellmayr<sup>10</sup>). In this region it is still possible to find some with black bills (AMNH 239365). North along the left bank of the Ucayali these characteristics are even more distant from typical *X. juruanus*, in Yarina Cocha, dpto. Loreto and thence to dpto. Amazonas (e.g. Huampami, Urakusa and La Poza), where the predominant phenotype is rather closer to the holotype of *X. s. ornatus*. The latter predominates east in the region of the rio Napo and north in Ecuadorian localities such as Archidona, Limoncocha and Santa Cecilia (Napo). Colombian populations closely resemble *X. elegans* except for their larger, more cinnamon-coloured pectoral spots, less ovoid dorsal spots and paler bill in most specimens.

It should be stressed that this transition does not occur on the banks of the rio Amazonas, where populations continue to present the typical phenotype of *X. juruanus* as far as the lower Ucayali, on the opposite bank of the mouth of the rio Napo, and at Iquitos. In this area, specimens from the right bank of the rio Amazonas correspond to the morphotype *X. s. juruanus* (e.g. specimens from Orosa, AMNH 232006, 232002, 232005 and 232008) while specimens from the left bank correspond to former *X. s. ornatus* (e.g. one from the rio Mazan; AMNH 407167), giving the impression of an abrupt transition.

The same variation is observed in size. Populations of *X. juruanus* from north-west Peru, Ecuador and Colombia are conspicuously closer in morphometrics to *X. elegans* than Brazilian and Bolivian populations of *X. juruanus*. This pattern of variation matches what Brown & Wilson<sup>4</sup> term 'character displacement'.

*Descriptive morphometrics*: Table 1 summarises mensural data for *X. juruanus*. Specimens were arbitrarily divided into sample A, comprising those from Brazil, Bolivia and extreme north-east Peru (previously named *X. s. juruanus*), and sample B, comprising the rest (previously named *X. e. insignis*, *X. e. ornatus* and *X. e. buenavistae*). The purpose of this was to test whether populations geographically more distant from *X. elegans* were closer to the latter in morphometrics. Indeed, it was generally observed that mensural data from sample B were closer to *X. elegans* than those of sample A, particularly the wing and tail measurements of males. With regard to tail measurements, sample A specimens of *X.*

*juruanus* were significantly larger than *X. elegans* ( $p < 0.05$ ), whereas sample B specimens were not.

**Distribution:** *X. juruanus* occurs from the left banks of the Madeira and Guaporé west, as far as La Poza, Huampami and Nazareth, dpto. Amazonas (Peru). South, it occurs along the eastern slopes of the Andes to Nicolas Suarez, dpto. Pando (Bolivia), and Astillero, Porto Pardo and Porto Maldonado in the region of the río Manu, dpto. Madre de Dios (Peru). North, it also occurs on the left bank of the río Solimões, occupying the region of the río Napo in the vicinity of Iquitos, and extending into Ecuador in dpto. Napo (e.g. Archidona, Limoncocha, the río Manu and Santa Cecilia) and Colombia in dptos. Putumayo, Caquetá, Cauca and Meta (in Villavicencio and Buena Vista).

**Geographic representation of the series:** **Bolivia.** **Pando:** Nicolas Suarez (14). **Brazil. Amazonas:** Boca Lago Tefé (1), Estirão do Equador (8), Igarapé Grande (8), João Pessoa (8), rio Caitauhará (1), rio Juruá (1), Santa Cruz (5), Santo Isidoro (3), Tefé (1), Vila Bela Imperatriz (1); **Acre:** Cruzeiro do Sul (9), Iquiri (1), rio Branco (2), Vila Taumaturgo (Seringal Oriente on the rio Juruá) (1); **Rondônia:** Porto Velho, left bank of the rio Madeira (1). **Colombia. Cundimarca:** Bogotá (8); **Meta:** Buena Vista (1), Montanhas Macarenas (1), rio Duita (7), Villavicencio (5); **Cauca:** Moscopan (2); **Caquetá:** Morelia (2), Puerto Venecia (2); **Putumayo:** Guascayco (1); **Sucre:** rio Linlla Pichis (1). **Ecuador. Napo:** Archidona (1), Concepcion (5), Limoncocha (15), rio Manu (1), rio Pacayacu (1), rio Payamino (1), Santa Cecilia (8), San José Nuevo (1); **Pastaza:** Aucayacu (2). **Peru. Amazonas:** Huampami (4), La Poza (3), Nazareth (2), Urakusa (3); **Huánuco:** Águas Calientes (1), Calientillo (1), Chuchurras (1), El Indio (1), Tingo Maria (1); **Madre de Dios:** Altamira (1), Napo (1), Puerto Maldonado (4), Puerto Pardo (4), rio Tambopata (3); **San Martín:** El Tingo (1), Saposoa (3); **Loreto:** Balta (4), Chayauitas (1), Estacion Ecologica Pitheia (2), Iquitos (28), Oroza (5), Pebas (1), Quebrada Vanilla (25), Yurimaguas (1); **Pasco:** Puerto Bermudez (2), Navati Mission (1); **Puno:** Astillero (3), Huacamayo (3), Puerto Vessup (8), rio Pachitea Nebil (1), rio Ucayali (6), Santa Rosa (6) Yarina Cocha (1); **Ucayali:** Lagarto (10), Pucallpa (12). **Imprecise localities:** rio Mazan (1), 'Ecuador' (1). 'Colombia' (5), Madre Dios (1).

## Discussion

**Taxonomic definitions:** As they are clearly diagnosable and allopatric, *X. juruanus* and *X. elegans* cannot be considered conspecific as proposed by Ridgely & Tudor<sup>20</sup>, Haffer<sup>9</sup> and Aleixo<sup>1</sup>. From the material we examined it can be inferred that there is only one area of possible contact between *X.*

*elegans* and *X. spixii*: this lies in the vicinity of the Serra do Cachimbo, Pará, on the border with Mato Grosso. Nevertheless, all of the specimens of *X. spixii* from this area (e.g. four uncatalogued specimens in MNRJ and three in MZUSP, 38345, 38348 and 38340) and those of *elegans* (e.g. MPEG 33617, 33618, 33619, 33620, 33621, 33622) are perfectly diagnosable.

Records relating to specimens that supposedly match the diagnosis of the synonym, *X. j. ornatus*, for the right bank of the rio Amazonas in São Paulo de Olivença are most probably the result of imprecise labelling, as hinted by Zimmer<sup>29</sup> *contra* Todd<sup>26</sup>. A similar case may also have occurred with specimens collected around Oroza (AMNH 232006, 232002, 232005 and 232008), which present pronounced variation in dorsal and ventral spots. It must be stressed that the Olalla brothers employed several local hunters to collect birds<sup>18</sup>, thus some 'mislabelling' is perhaps to be expected, and may be true for those specimens from São Paulo de Olivença.

If, however, the material was taken from the right bank of rio Amazonas, Oroza must represent a transition site from typical *X. juruanus* to the more spotted form, distributed further east and north. It should be noted that the site is close to the mouth of the rio Ucayali and that strongly spotted forms predominate on the opposite bank of the latter river.

That the transition is abrupt around the mouth of the rio Ucayali and that populations may be isolated in this area does not justify validation of *X. e. insignis* (which would have priority over Zimmer's *X. s. buenavistae* and *X. s. ornatus*), as the transition in the southern distribution is gradual and characteristic of primary contact, which was corroborated by the molecular analysis of Aleixo<sup>1</sup>.

**Group phylogeny:** Bledsoe *et al.*<sup>3</sup> and Raikow<sup>19</sup> concluded that the species group is not monophyletic and excluded *X. elegans* from it. However, their findings (which used the same character matrix) have not been employed here because of major inconsistencies. In separating *X. elegans* from the *X. spixii* group, both studies used (see Raikow<sup>19</sup>) two specimens of *X. elegans* (LSUMZ 83715 and FM 330388) and a single *X. spixii* (LSUMZ 114412). FM 330388 was taken from the rio Jiparaná, Rondônia, and thus pertains to true *X. elegans*, whereas LSUMZ 83715 is from the province of Napo (Ecuador, 00°24'S 73°37'W), where *X. juruanus* occurs (labelled *X. elegans ornatus* in LSUMZ collection). Additionally, the specimen of *X. spixii* used in the previous studies is from Quebrada Vanilla, at the mouth of rio Napo (Peru), and is therefore another specimen of *X. juruanus* (identified as *X. spixii juruanus* in the collection). As mentioned earlier, *X. spixii* occurs only in Brazil, from the right bank of rio Tapajós west. The large

phylogenetic distance attributed to two specimens of the same species (LSUMZ 114412, 83715) therefore represents the potential negative effects of poor sampling combined with inconsistent terminals (polytypic species) within a phylogenetic analysis.

We consider that biogeographic patterns (parapatry), coloration and morphometrics to be highly indicative of the complex being monophyletic, thus agreeing with the phylogeny proposed by Aleixo<sup>1</sup>. The ‘character displacement’ described for *X. juruanus* / *X. elegans* is also typical of closely related populations<sup>4</sup>. At the same time, *X. juruanus* and *X. elegans* both have fan-shaped breast spots of a shape that is unique in the family (see diagnoses) and derived from that found in *X. spixii*, which in turn occurs in many related species, such as *X. obsoletus*, *X. ocellatus* and *Lepidocolaptes fuscus* (= *X. fuscus*; see García-Moreno & Silva<sup>8</sup> and Aleixo<sup>1</sup>). This, combined with the difficulty of diagnosing some populations of *X. juruanus* as distinct from *X. elegans*, indicates that they form a sister group derived from the same ancestral stock as *X. spixii*.

Considering that the cladogenesis of the group occurred dichotomously and that rivers have contributed decisively to the formation or maintenance of currently extant groups, our findings point to an area cladogram broadly congruent with that presented by Bates *et al.*<sup>2</sup> for the oscines (see their Fig. 3a). The group comprising the areas referred to as Belém, Pará 1 and Pará 2 would be a sister group of the one comprising Rondônia, Inambari and Napo. The latter, in turn, would be divided into Rondônia and Inambari–Napo subgroups. However, this cladogram is not consistent with the hypothesis that Bates *et al.*<sup>2</sup> propose as the most parsimonious for the ‘total passerine data set’ (see Bates’ Fig. 3b).

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