Taxonomic status of *Tangara cyanomelaena* (Wied, 1830), an east brazilian atlantic forest endemic

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Recebido em 17/10/2007. Aceito em 04/04/2009.

RESUMO: Status taxonômico de *Tangara cyanomelaena* (Wied, 1830), um endemismo da Floresta Atlantica do leste brasileiro. A saíra-diamante é amplamente distribuída na Amazônia e nas matas atlânticas do leste da América do Sul, incluindo pelo menos quatro subespécies reconhecidas. Este estudo revê o status taxonômico de *Tangara velia cyanomelaena*, que ocorre apenas no leste brasileiro. A análise de espécimes taxidermizados enfocou a coloração da plumagem e a morfometria. A análise morfométrica comparativa incluiu uma estatística descritiva, análise de variância (ANOVA) e de função discriminante (DFA). As análises mostraram uma inequívoca diagnose morfológica e, conseqüentemente, resultaram no reconhecimento de *Tangara cyanomelaena* como espécie válida com base no conceito filogenético. Essa espécie difere de todos os táxons incluídos no gênero por possuir o peito e os flancos azulcelestes (cor 66 de Smithe, 1975), enquanto que *T. velia* possui o peito e os flancos mais escuros, variando do azul-esmaltado (70) ao violeta-espectral (72). A análise estatística, por sua vez, apontou que *T. cyanomelaena* é maior que *T. velia*, e que as espécies são significativamente diferentes do ponto de vista morfométrico.

PALAVRAS-CHAVE: Tangara velia, Tangara cyanomelaena, taxonomia, conservação.

ABSTRACT: The Opal-rumped Tanager is widespread in Amazonia and Atlantic Forest of eastern Brazil, with at least four subspecies. This study reviews the taxonomic status of *Tangara velia cyanomelena*, which occurs in eastern Brazil. Analyzes focused on plumage coloration and measurements and included descriptive statistics, Analysis of Variance (ANOVA) e Discriminant Function (DFA). The results provided unequivocal morphological diagnoses. *Tangara v. cyanomelaena* differs from all other members of the genus in having the breast and flanks sky blue. Statistical test demonstrated that the morphometric data of *T. v. cyanomelaena* have some means significantly different from those of *T. velia* complex. Given its clear diagnosability, inferred long-term independent evolution, and allopatric distribution, we consider that henceforth *Tangara cyanomelaena* should be treated as a separate species under the phylogenetic species concept from *T. velia* complex.

KEY-WORDS: Tangara velia, Tangara cyanomelaena, taxonomy, conservation.

Birds are amongst the most diverse groups of terrestrial vertebrates (Chiappe and Dyke 2002), but taxonomy at the level of species still poses many problems. Most Neotropical bird species are polytypic, that is they are divided into subspecies. These latter have been described under a variety of different conceptual parameters, and vary from those that exhibit only gradual variation across large areas of the continent, to others that represent extremely well-defined forms (Raposo 2001a). The Neotropical genus *Tangara* is generally considered to comprise 49 species (Sibley and Monroe 1990) and 130 subspecies (Peters 1970), and contains some of the most strikingly colourful representatives of the Emberizidae (Burns and Naoki 2004).

The Opal-rumped Tanager *Tangara velia* (Linnaeus, 1758) presents a disjunct distribution, being known from forests in the Amazon basin and the Atlantic Forest in eastern Brazil. In addition to nominate *T. v. velia*, which

occurs over the Guianan Shield (Pinto 1944, Peters 1970), the following races have been recognized in Amazonia: Tangara velia iridina (Hartlaub, 1841; described from Peru), occurring over much of western Amazonia, including Colombia, south-western Venezuela and Amazonian Ecuador, Peru and Bolivia (Pinto 1944, Peters 1970), and Tangara velia signata (Hellmayr, 1905; described from Pará, Brazil), occurring south of the Amazon, in Pará (Pinto 1944, Peters 1970). The Amazonian taxa of T. velia are very similar to each other, differing only in the relative tones of blue on the forecrown, breast, flanks, wing-coverts, and fringes of the remaining wing-feathers (Hellmayr 1936, Ridgely and Tudor 1989); in stark contrast, the race from eastern Brazil, T. v. cyanomelaena (Wied, 1830), is quite different from all of the remaining races, especially in its much paler underparts. Ridgely and Tudor (1989) pointed to the complete lack of contact between T. v. cyanomelaena and the Amazonian populations, which taken together with the striking plumage differences suggested to them that two species might be involved, an arrangement followed by Sibley (1996). Here, we test the validity of the taxon *T. cyanomelaena* and describe geographical variation in the *T. velia* complex.

METHODS

A total of 83 specimens pertaining to all *Tangara velia* subespecies was analysed (including 35 *T. v. cyanomelae-na*), held in the following institutions: Museu Nacional,

Universidade Federal do Rio de Janeiro (MNRJ), Museu Paraense Emílio Goeldi, Belém (MPEG), Universidade Federal de Pernambuco, Recife (UFPE), Departamento de Zoologia da Universidade Federal de Minas Gerais, Belo Horizonte (DZUFMG), and the Museu de Zoologia da Universidade de São Paulo (MZUSP). Because of the relatively few specimens available pertaining to the Amazonian taxa and their relative similarity (they differ only in the tone of blue on the forecrown, wing-coverts, and fringes of the remaining wing-feathers; see Figure 1), all specimens from the ranges of T. v. velia (Linnaeus, 1758), T. v. iridina (Hartlaub, 1841), and T. v. signata



FIGURE 1: Ventral view of typical individuals of *Tangara cyanomelaena* and *T. velia* complex. From right to left: *T. cyanomelaena* (MNRJ 38140, topotype) and *T. velia* (from left to right: MNRJ 29902 – Serra do Navio, AP; MNRJ 9809 – Murutucu, PA; and MNRJ 12130 – Vila Braga, rio Tapajós, PA), showing the significant differences in underparts pattern, including the paler blue breast and flanks of *T. cyanomelaena*, and the paler chestnut / cinnamon ventral region of *T. cyanomelaena*, which is apparent in the majority of individuals of this taxon.

Table 1: Plumage pattern relating to diagnostic characters. Typical pattern of *T. cyanomelaena* and typical pattern of *T. velia* complex.

Chamatan	Character state (follow	wing Smithe 1975)
Character	T. velia complex	T. cyanomelaena
Forehead	Bright blue (colour 70) or spectral violet (colour 72)	yellow band
Breast	Bright blue (colour 70) or spectral violet (colour 72)	Sky blue (colour 66)
Flanks	Bright blue (colour 70) or spectral violet (colour 72)	Sky blue (colour 66)
Vent	Amber (colour 36)	Cinnamon (colour 139)

(Hellmayr, 1905) are generally referred to hereafter as *Tangara velia* complex. Photographs of the holotypes of *T. v. iridina* and *T. v. signata* were also analysed. A complete list of the material examined is presented in the Appendix.

Additionally, GMK conducted a morphological (plumage colour) examination of four (three male, one female) *T. v. velia* and 30 (17 male, ten female and three unsexed) specimens of *T. v. iridina* collected in Venezuela and held at the Colección Ornitología Phelps, Caracas (COP), as well as 19 *T. v. cyanomelaena* (from Bahia, Pernambuco, Rio de Janeiro, and Goiás), 32 *T. v. velia* (from the Guianas), 14 *T. v. iridina* (Colombia, Ecuador and Peru) and a single *T. v. signata* (Pará, Brazil), at The Natural History Museum, Tring (NHM). No measurements were taken and these specimens were not included in the statistical analyses.

Our analysis of those specimens held in Brazilian institutions focused on plumage coloration (using Smithe 1975) and morphometric characters (wing-length, taillength, bill-length and bill-width at the nares). The software STATISTICA (2001) was used for descriptive analysis and application of the following tests: normality, homoscedasticity (Levene Test), Analysis of Variance (one-way ANOVA), and Discriminant Function Analysis (DFA). All ANOVAs were one-way to evaluate significant mean differences between *T. v. cyanomelaena* and Amazonian specimens of *T. velia*. Statistical significance was accepted at P < 0.05 throughout.

For color plumage analysis, categories for the different conditions of independently analyzed characters were defined using Smithe (1975) (Table 1). The same conditions were applied to both sexes as, apparently, there is no sexual dimorphism in plumage. Nonetheless, the possibil-



FIGURE 2: Forehead view of *Tangara cyanomelaena* and *T. velia* complex. From right to left: *T. cyanomelaena* (MNRJ 38140, topotype) and *T. velia* (from left to right: MNRJ 29902 – Serra do Navio, AP; MNRJ 9809 – Murutucu, PA; and MNRJ 12130 – Vila Braga, rio Tapajós, PA), showing conspicuous yellow frontal band on the forehead. Despite being less conspicuous, this latter feature is also present in individuals of *T. velia signata*.

IABLE 2: Mean mensural values for four characters amongst males and females of T. cyanomelaena and T. velia complex. Mean (x), standard deviation (SD), minimum (min) and maximum scores (max), and total number of specimens analysed for each character (n)

•			•																	
		Bill	Bill-length (mm)	nm)			Bill-	Bill-width (mm)	(mı			Tail-]	Tail-length (mm)	lm)			Wing	Wing-length (mm)	nm)	
	×	SD	Min	max	и	×	SD	min	max	u	×	SD	min	тах	u	×	SD	min	max	u
T. cyanomelaena																				
Males	16.18	16.18 00.78 15.00 17.10	15.00		12	04.73	00.30	04.20 05.25	05.25	13	52.54 01.95		49.00	56.00	13	72.42	01.93	69.50	70.80	13
Females	15.32	15.32 00.73 14.20 16.50	14.20		_	04.74	00.30	04.15 05.00	05.00	_	50.13 02.54	02.54	45.50 54.00	54.00	_	69.42	01.92	66.50	71.55	8
T. velia																				
Males	14.20	14.20 00.64 12.65 15.60	12.65	15.60	32	04.36	00.41	03.90	05.25	35	48.51 02.90		42.00	55.50	36	71.04	03.18	60.85	09.9/	36
Females	14.24	14.24 00.99 12.90 15.75	12.90	15.75	∞	04.47	00.46	03.50 04.85	04.85	∞	48.00	03.02	43.50	51.50	8	68.72	02.50	66.10	70.55	8

ity that such dimorphism exists was not discarded during the analyses, the two sexes being analyzed independently. Juvenile specimens or those in moult were not considered in either the morphometric or plumage analyses.

We adopted the species concept outlined in Nelson and Platnick (1981), *i.e.* the Phylogenetic Species Concept.

RESULTS

Plumage analysis – Tangara v. cyanomelaena differs from all other members of the genus in having the breast and flanks sky blue (colour 66 in Smithe 1975), whereas in T. velia complex has much darker breast and flanks, varying from bright blue (70) to spectral violet (72) (Figure 1). No specimens intermediate between T. velia complex and T. v. cyanomelaena were found. T. cyanomelaena also frequently presents two other plumage characters, although these cannot quite be considered diagnostic. In general, the majority of individuals possess a conspicuous yellow frontal band on the forehead and a clearly maroon-coloured ventral region (colour 139), which latter is deeper and less extensive in T. velia complex (colour 36) (Figure 1 and 2).

In the absence of the holotype of *T. v. cyanomelaena* (see Taxonomy), we found a topotype (MNRJ 38140) which can briefly be described as follows: forehead with a yellow band (colour 55) and bright blue (colour 70) above the bill base, over the lores, cheeks and ear-coverts; crown, nape and upperparts dark grey (colour 82); all wing-coverts bright blue (colour 70); primaries and secondaries black with green edges (colour 64); rump yellow and rectrices blackish gray (colour 82) with bright blue (colour 70) edges; chin and throat blue (colour 70); upper breast blackish gray (colour 82) with some feathers largely sky blue (colour 66), and lower breast and flanks entirely sky blue (colour 66); abdomen, thighs and undertail-coverts cinnamon (colour 139). The same plumage pattern found in the topotype can be observed in other specimens of T. v. cyanomelaena throughout its distribution.

Morphometric analysis – Tests for normality (Kolmogorov-Smirnov Test) and homogeneity (Levene Test) demonstrated that the morphometric data could serve as statistically valid parameters in our analyses. An ANOVA showed that T. v. cyanomelaena males have on average greater bill-length (P < 0.01), bill-width (P < 0.01), and wing-length (P < 0.01) means significantly different from those of T. velia complex males; among females, only bill-length (P < 0.01) average was greater in T. v. cyanomelaena are generally larger than those of T. v. velia whilst female T. v. cyanomelaena is longer billed than T. v. velia (see

Table 2). In males, the DFA revealed a strong segregation between T.v. cyanomelaena (100%) and T.v. velia (100%) with statistically significant confidence intervals. The ANOVA also revealed sexual dimorphism in T.v. cyanomelaena, as males have longer wings than females (P < 0,01). No such dimorphism was observed in T.v. velia (see Table 2).

Taxonomy – Given its clear diagnosability, inferred long-term independent evolution, and allopatric distribution, we consider that henceforth *Tangara cyanomelaena* should be treated as a separate species from *T. velia*.

The holotype of *T. cyanomelaena*, which originally formed part of the Wied collection, has been lost for more than a century (Allen 1889, Hellmayr 1936). Whilst the rest of his collection resides at the American Museum of Natural History (New York), the type of *T. cyanomelaena* cannot be located (M. LeCroy *in litt.* 2006), and thus was unavailable for the present study. Nonetheless, analysis of the topotype from Ilhéus (MNRJ 38140), Bahia, and Wied's original description (Wied 1830) of a black and blue 'Tangara' with yellow on the forehead and rump, a

greyish-blue belly and cinnamon undertail-coverts, provide clear support for the present-day application of the name *T. cyanomelaena*.

During this study we considered the possibility of designating a neotype for *T. cyanomelaena*, in order to avoid future complications in applying this name. However, the *International code of zoological nomenclature* (1999) clearly indicates (Art. 75) that a neotype is only required in cases of extreme necessity to resolve complex taxonomic issues. In the present case, the matter is rather straightforward, as Wied's description clearly indicates the provenance of the type specimen on which it was based, and specimens of *T. cyanomelaena* from throughout the taxon's range exhibit strong homogeneity in plumage (diagnostic characters), strongly indicating that it must be maintained as the only species of eastern Brazil without future subdivisions.

DISCUSSION

Tangara cyanomelaena have been considered subspecies of *T. velia* due to their relatively similar appearance

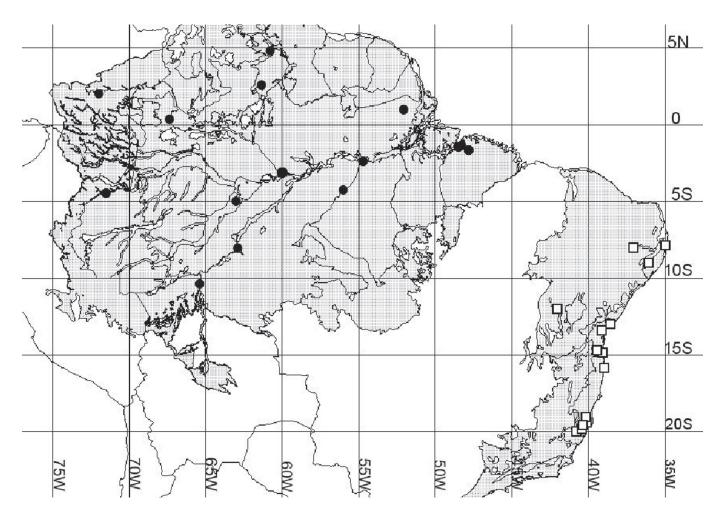


FIGURE 3: Distribution of *Tangara cyanomelaena* (white squares) and *T. velia* complex (black circles). *T. cyanomelaena* is restricted to the Atlantic Forest in eastern Brazil and never comes into contact with *T. velia*.

and allopatric ranges (Figure 3), though decisions in such cases always involve intrinsically subjective opinions regarding species status, which has generated much criticism of the Biological Species Concept (e.g. Snow 1997), and led to disparate treatments of similar cases (Raposo 2001b). For this and other reasons, the conceptual logic underlying the Biological Species Concept has been much criticized (vide Wilson and Brown 1953, Ehrlich 1961, Sokal and Crovello 1970, Rosen 1978, 1979, Nelson and Platnick 1981, Wiley 1978, Cracraft 1983, 1989, 1992, Donoghue 1985, Futuyma 1992, Mckitrick and Zink 1988, Nixon and Wheeler 1990, Zink 1997).

Some taxonomists, especially those working in the early 20th century, have treated the subtlest of geographical variation in size or coloration found among bird populations as subspecies (Barrowclough and Flesness 1996), despite that such characters frequently change very gradually (clinally) over large continental landmasses and, for this reason, are not meritorious of nomenclatural recognition, as they do not permit the delimitation of well-defined units.

It is worth mentioning that none of the concepts of subspecies which has historically been utilised in ornithology (e.g. Mayr 1942; Mayr and Ashlock 1991) is comparable with that of phylogenetic species (but see Remsen 2005), as proposed by Cracraft (1983), who defined such an entity as 'the smallest diagnosable cluster of organisms within which there is a parental pattern of ancestry and descent'. The notion of ancestry under such a system is not directly related to reproductive isolation. The relatively small number of studies that have attempted revisions of specific groups in birds under a Phylogenetic Species Concept (hereafter PSC) have rarely found that even a majority of named subspecies warrant recognition. In a recent revision of a polytypic species, Xiphorhynchus elegans, Raposo and Höfling (2003) considered just two of five currently recognised subspecies to represent phylogenetic species, whilst in a similar revision of the entire genus Xiphorhynchus, Raposo (2001) treated just 20% of named subspecies as phylogenetic species, considering the remainder of available names to represent examples of individual or minor geographic variation. A similar case is presented by the Spot-backed Puffbird Nystalus maculatus, wherein the form *N. m. striatipectus* met the requirements of species rank under the PSC, but N. m. parvirostris and N. m. pallidigula were treated as insignificant geographical variants (Silva 1991). In this respect, it is clearly that not so that subspecies and phylogenetics species can be regarded as virtually synonymous, as affirmed for Remsen (2005). Affirmations of this type, in addition to lacking any solid basis, discourage the revision of specific complexes and, consequently, contribute to continued the obfuscation of biogeographical patterns.

On the other hand, some past authors described as subspecies geographically well-defined forms, which today

are being increasingly treated specifically, regardless of the species concept employed. It is reasonable to admit under the perspective of the Biological Species Concept (*sensu* Mayr and Ahshlock 1991) that diagnostic and allopatric forms should be treated as separate species, despite any lack of indubitable evidence for reproductive isolation.

An example of this is the present case. *Tangara cyanomelaena* merits specific status based on its diagnosably different and unique plumage. It is noteworthy that Hellmayr (1936), who considered *T. cyanomelaena* a subspecies of *T. velia*, nonetheless commented on its distinction from other subspecies 'Tanagrella velia cyanomelaena (Wied), though readily distinguished from the preceding forms by the pale bluish gray coloration of the breast and sides...'. Our results also corroborate the observation by Ridgely and Tudor (1989) concerning the distinctiveness and possible specific status of *T. cyanomelaena*.

A recent phylogeny of the genus *Tangara* recognised the Opal-crowned Tanager *T. callophrys* as the sister-species of *T. velia* (Burns and Naoki 2004). Genetic material for *T. velia* was only available from Amazonia (dpto. Pando, Bolivia, and Rondônia, Brazil), thus leaving the position of *T. cyanomelaena* within the genus unknown. Even though *T. callophrys* is also very similar to *T. velia* at least in plumage characters (Sick 1997), it cannot be eliminated that the more radically different *T. cyanomelaena* is also sister to *T. velia*.

We have also found some morphological variation in T. velia complex (which never approaches T. cyanomelaena in its plumage), suggesting the need for a revision of Amazonian populations. The population of T. velia in the Guianan Shield is plainly diagnosable compared to those from the rio Negro and south of the Amazon. Specimens from Amapá (MNRJ 29900 and 29902; T. v. velia) have the flanks and wing and tail-coverts deep blue and the face greenish blue, unlike those from the rios Negro and Tapajós (T. v. iridina, which has priority, and T. v. signata) which have the face, wing-coverts and flanks violet. At one locality (Carabobo, on the upper río Cuyuni), in Bolívar state, south-east Venezuela, three of the four available specimens show all of the relevant characters of T. v. velia, but there is also a male (COP 46683) which appears to have all the characteristics of the T. v. iridina morphotype, namely its lack of any trace of greenish elements in the blue parts of the plumage, which are all more brilliantly coloured, with the rump patch being brighter straw yellow. Furthermore, the black of the upperparts is more solid, deeper, and less brownish, and the cinnamon on the underparts is also more characteristic of T. v. iridina (though this is individually variable in extent), being much deeper (more saturated). Future studies of the taxonomy and validity of T. v. iridina will require more specimens from the headwaters of the rios Amazonas and Negro, as well as a detailed analysis of the group's nomenclature.

ACKNOWLEDGEMENTS

We are grateful to the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) for their support of M.A. Raposo (proc. Instalação E-26/ 170.871/2003 and Primeiros Projetos E-26/170.642/2004) and Liliane Seixas. We also thank Paul Sweet and Shannon Kenney for sending photographs of the holotype of T. v. signata held in the American Museum of Natural History; Eric Pasquet for assistance at the Paris museum; Luís Fábio Silveira likewise for his inestimable help in the Museu de Zoologia da Universidade de São Paulo; Marcos Rodrigues and Marcelo Vasconcelos at the Departamento de Zoologia da Universidade Federal de Minas Gerais, Belo Horizonte; Alexandre Aleixo at the Museu Paraense Emílio Goeldi, Belém; Mark Adams and Robert Pr s-Jones at the Natural History Museum, Tring; and Robin Restall and Miguel Lentino at the Colección Ornitología Phelps, Caracas. We are also greatly indebted to Daniel Firme, Carlo Rodrigo Abreu, and Daniela Ingui for their critical reviews of the manuscript.

LITERATURE CITED

- Allen, J.A. (1889). On the Maximilian types of South American birds in the American Museum of History. *Bull. Amer. Mus. Nat. Hist.*, 2:1-218
- Barrowclough, G.F. and Flesness, R.N. (1996). Species, subspecies and races: the problem of Units of Management in conservation. In: Kleiman, D.G., Allen, M.E., Thompson, K.V., Lumpkin, S. and Harris, H. (eds.) Wild mammals in captivity: principles and techniques. Chicago: University of Chicago Press.
- Burns, K.J. and Naoki, K. (2004). Molecular phylogenetics and biogeography of Neotropical tanagers in the genus Tangara. Mol. Phyl. and Evol., 32:838-854.
- Chiappe, L.M. and Dyke, J.G. (2002). The mesozoic radiation of birds. Ann. Rev. Ecol. Sys., 33:91-124.
- Cracraft, J. (1983). Species concepts and speciation analysis. In: Johnston. R.F. (ed.) Current ornithology, 1. New York: Plenum Press.
- Cracraft, J. (1989). Species as entities of biological theory. In: Ruse, M. (ed.) What the philosophy of biology is. Dordrecht: D. Reidel.
- Cracraft, J. (1992). The species of birds-of-paradise (Paradisaeidae): applying the phylogenetic species concept to a complex pattern of diversification. *Cladistics*, 8:1-43.
- Donoghue, M. J. (1985). A critique of the biological species concept and a recommendation for a phylogenetic alternative. *Bryologist*, 88:172-181.
- Ehrlich, P.R. (1961) Has the biological species concept outlived its usefulness? *Syst. Zool.*, 10:167-176.
- Futuyma, D.J. (1992). *Biologia evolutiva*. Ribeirão Preto: Sociedade Brasileira de Genética/CNPq.
- Hellmayr, C.E. (1936). Catalog of birds of the Americas and adjacent islands. *Field Mus. Nat. Hist. Publ. Zool. Ser.*, 13(9).
- International Commission for Zoological Nomenclature (ICZN). (1999). *International code of zoological nomenclature.* Fourth edn. London, UK: International Trust for Zoological Nomenclature.
- Mayr, E. (1942). Systematics and the origin of species. New York: Columbia University Press.
- Mayr, E. and Ashlock, P.D. (1991). Principles of systematic zoology. Singapore: McGraw-Hill.
- McKitrick, M.C. and Zink, R.M. (1988). Species concepts in ornithology. *Condor*, 90:1-14.

- Nelson, G.J. and Platnick, N.I. (1981). Systematics and biogeography: cladistics and vicariance. New York: Columbia University Press.
- Nixon, K.C. and Wheeler, Q.D. (1990). An amplification of the phylogenetic species concept. *Cladistics*, 6:211-233.
- Peters, J.L. (1970). Check-list of birds of the world, 13. Cambridge, MA: Mus. Comp. Zool.
- de Pinna, M.C.C. (1991). Concepts and tests of homology in the cladistic paradigm. *Cladistics*, 7:367-394.
- Pinto, O.M. de O. (1944). Catálogo de aves do Brasil e lista dos exemplares existentes na coleção do Departamento de Zoologia. Segunda parte. São Paulo: Publicação do Departamento de Zoologia.
- de Queiroz, K. (2005). Ernest Mayr and the modern concept of species. *Proc. Natl. Acad. Sci.* USA 102 suppl. 1:6600-6607.
- Raposo, M.A. (2001a). Taxonomia alfa de aves neotropicais. In: Albuquerque, J. L. B., Cândido, J. F., Straube, F. C. and Roos, A. L. (eds.) Ornitologia e conservação: da ciência às estratégias. Tubarão, SC: Ed. Unisul.
- Raposo, M.A. (2001b). Taxonomia, evolução e anatomia da siringe do gênero *Xiphorhynchus* Swainson, 1827 (Aves: Dendrocolaptidae). *Ph.D. thesis*. Universidade de São Paulo.
- Raposo, M.A. and Höfling, E. (2003). Alpha taxonomy of the *Xiphorhynchus spixii* species group with the validation of *X. juruanus* Ihering, 1904. *Cotinga*, 20:72-81.
- Remsen, J.V. (2005). Pattern, process, and rigor meet classification. *Auk*, 122:403-413.
- Ridgely, R.S. and Tudor, G. (1989). *The birds of South America*, 1. Austin: University of Texas Press.
- Rosen, D.E. (1978). Vicariant pattern and historical explanations in biogeography. *Syst. Zool.*, 27:159-188.
- Rosen, D.E. (1979). Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. *Bull. Amer. Mus. Nat. Hist.*, 162:267-376.
- Sick, H. (1997). Ornitologia brasileira. Rio de Janeiro: Ed. Nova Fronteira.
- Silva, J.M.C. (1991). Sistemática e biogeografia da superespécie Nystalus maculatus (Piciformes: Bucconidae). Ararajuba, 2:75-79.
- Smithe, F.B. (1975). Naturalist's color guide. New York: Amer. Mus. Nat. Hist.
- StatSoft, Inc. (2001). STATISTICA for Windows v. 6.0. Tulsa, OK: StatSoft.
- Sibley, C.G. (1996). Sibley's birds of the world v. 2.0. Cincinnati, OH: Thayer Birding Software.
- Sibley, C.G. and Monroe, B.L. (1990). Distribution and taxonomy of the birds of the world. New Haven, CT: Yale University Press.
- Snow, D.W. (1997). Should the biological be superseded by the phylogenetic species concept? Bull. Brit. Orn. Club, 117:110-121.
- Sokal, R.R. and Crovello, T.J. (1970). The biological species concept: a critical evaluation. *Amer. Nat.*, 104(936):127-152.
- Wied-Neuwied, M. (1830). Verzeichnis der Amphibien, Säugethiere und Vögel, welche auf einer Reise zwischen dem 13ten und dem 23sten Grade südlicher Breite im östlichen Brasilien beobachtet wurden. In: Wied-Neuwied, M. (ed.) Beiträge zur Naturgeschichte von Brasilien, 3(2). Weimar: Verlag des Landes-Industrie-Comptoirs.
- Wiley, E.O. (1978). The evolutionary species concept reconsidered. Syst. Zool., 29:76-80.
- Wilson, E.O. and Brown, W.L. (1953). The subspecies concept and its taxonomic application. *Syst. Zool.*, 2:97c111.
- Zink, R.M. (1997). Species concepts. Bull. Brit. Orn. Club, 117:97-109.

APPENDIX

Material utilised by this study. For museum acronyms see Material and methods.

Tangara v. velia Colombia – Nova Granada: (unsexed, MZUSP 2130). Brazil – Roraima: Isabel (♀, MNRJ 12129); km 4 north of Rio Cachorro (♂, MZUSP 73480); Mucajaí, Colônia do Apiaú (♀, MPEG 46249; ♂, MPEG 46248). Amapá: Serra do Navio (♂, MNRJ 29900, 29902).

Tangara v. iridina Brazil – Amazonas: Inambu, right bank of the upper rio Negro (♂, MNRJ 37878); Lago, Tarumázinho (♂, MZUSP 62115); Manaus, Reserva Ducke (♂, MPEG 30368, 30369); rio Javari, border with Ecuador (♂, MPEG 17157, 17158; unsexed, MPEG 17156); rio Solimões, right bank at Caitaú, Uará (♀, MPEG 50196; ♂ MPEG 50194, 50195).

Tangara. v. signata Brazil – Pará: upper rio Cururú, tributary of the rio Tapajós (♂, MZUSP 42846); Benevides, km 15 on the Belém-Mosqueiro road (♀, MPEG 25099); Benevides, Retiro Nazaré, Baía do Sol (♂, MPEG 22163); Capim, between km 93 and 107 on the Belém-Brasília road (unsexed, MZUSP 45866, 45869; ♀, MZUSP 45859, 45860, 45871; ♂, MZUSP 45857, 45858, 45861-65, 45867, 45868, 45870); Murutuá (♂, MNRJ 9809); Itaituba, rio Tapajós (♂, MPEG 15054); Tanaquara, Belém (♂, MPEG 11245, ♂, MPEG 11246, 11500); Utinga, Belém (♀, MZUSP 36045; ♂, MZUSP 36042-44); Vila Braga, rio Tapajós (♂, MNRJ 12130). Rondônia: Cachoeira Nazaré, west bank of the rio Jiparaná (♂, MPEG 40294); Guajará-Mirim, rio Mamoré (♂, MPEG 23053, 23054).

Tangara cyanomelaena Brazil – Pernambuco: no locality (unsexed, UFPE 2884; ♂, UFPE 1824); Usina São José, Igarassú (♀, MNRJ 24757; unsexed, MNRJ 24758). Alagoas: no locality (♀, UFPE 3.233; ♂, UFPE 3183, 3232, 3278). Bahia: 17 km west of Valença (♂, DZUFMG 1888); Belmonte (♂, MZUSP 10326); Ilhéus (♀, MZUSP 33787, MNRJ 27988; ♂, MNRJ 22325); no locality (unsexed, MPEG 36671, 36672, MZUSP 3.044); Itabuna (♀, MZUSP 11.904, 10.327; ♂, MZUSP 10.116, 10.325); Itajuípe (unsexed, MPEG 30494). Espírito Santo: no locality (♀, MZUSP 6.243; ♂, MZUSP 6.242, 6.244); Cupido (unsexed, MNRJ 26973); north of São José (♀, MNRJ 26996; ♂, MNRJ 2500); Linhares (unsexed, MNRJ 26975); Pau Gigante municipality (♂, MZUSP 24658, 33785, 33786, MNRJ 19944; unsexed, MNRJ 19921); rio São José (♀, MZUSP 28232; ♂, MZUSP 28231).