



Aberrant colourations in wild snakes: case study in Neotropical taxa and a review of terminology

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Abstract. The criteria used by previous authors to define colour aberrancies of snakes, particularly albinism, are varied and terms have widely been used ambiguously. The aim of this work was to review genetically based aberrant colour morphs of wild Neotropical snakes and associated terminology. We compiled a total of 115 cases of conspicuous defective expressions of pigmentations in snakes, including melanin (black/brown colour), xanthins (yellow), and erythrins (red), which involved 47 species of Aniliidae, Boidae, Colubridae, Elapidae, Leptotyphlopidae, Typhlopidae, and Viperidae. Most of them were hypopigmented conditions, mainly amelanism, but also anerythrism, axanthism, hypomelanism, leucism, piebaldism, and albinism (total absence of pigments). Hyperpigmented aberrancies were mostly melanism and xanthism, plus a few instances of erythrism. No associations with diurnality and fossorial behaviour were observed, neither for blanched nor hyperpigmented aberrancies. A discussion of the terms most commonly used for wild snakes is provided, with an account of cases of aberrant colourations in other South American reptiles. Finally, we propose a simple classification framework of wild snake colour aberrancies based on predominant dorsal colour and eye pigmentation for the adoption of a standardized terminology, which may be applicable to other squamates and chelonians. We advocate the use of a more accurate terminology in the scientific literature that would avoid the use of confusing terms like “partial albinism”.

Key words. Albinism, amelanism, anerythrism, axanthism, erythrism, leucism, melanism, Neotropical snakes, piebaldism, xanthism.

Introduction

Skin colours of snakes are remarkably variable, serving purposes such as concealment, mimicry, warning signals, and also thermoregulatory advantage (NORRIS & LOWE 1964, BECHTEL 1978). This diversity relies on the distribution and pigment production by specialized skin cells called chromatophores: melanophores, and xanthophores that include the erythrophores (BECHTEL 1978). The melanophores, located in the dermis and epidermis, produce eumelanin (black/brown) or phaeomelanin (pale red/yellowish) that are stored in organelles called melanosomes, and the xanthophores produce pteridines that are stored in the pterinosomes; xanthophores and erythro-

phores, located usually in the dermis, are responsible for yellow and red respectively, determined by the ratio of carotenoids and pteridines in each cell (BAGNARA 1966). Additional types of colour-functional cells lacking pigments are the guanophores and iridophores located in the dermis, which contain fine particles of guanine and layers of purines, respectively, and produce different colours and hues depending on cell disposition and the arrangement of crystals (BAGNARA et al. 1968; ROHRLICH & PORTER 1972, GOSNER 1989).

Conspicuous deviations from the typical skin colour of a given species are widespread in the animal kingdom, with examples of excessive and reduced pigmentation (WITKOP 1975). Snakes are no exception, with several in-

herited chromatic aberrancies (hereafter CA) producing atypical colourations (e.g., BECHTEL 1991, KRECSÁK 2008, THAKUR & TRIVEDI 2018). Some of these expressions are presumed to compromise protection against predators or solar radiation, consequently lowering fitness and survivorship (BECHTEL & BECHTEL 1981, KRECSÁK 2008). These ecological handicaps were thought to explain the overall low frequency of CA in wild populations, especially those based upon hypopigmentation, commonly referred to as albinism (AMARAL 1932a, BECHTEL 1995). The generalized concept of albinism in vertebrates is regarded as an inherited defect that will negatively affect the normal production of melanin (WITKOP 1988). In humans, it is a well-studied hereditary syndrome expressing itself in variably atypical amounts of melanin in the skin, hair, and eyes (WITKOP 1985).

BÉRNILS & MOURA-LEITE (1991) classified colour anomalies of snakes, distinguishing inherited CA from those defects of the dorsal pattern that can be inherited (WOLF & WERNER 1994) but also could be a result of incubation conditions (CLAUSE & BECKER 2015). The description and classification of CA in snakes is challenging due to the intricate mechanisms of skin colour production and the varied hereditary effects of the different chromatophore types (PRÜST 1984; BECHTEL 1995). These defects are yet scarcely studied with regard to the genes involved and their expression mechanisms (DAVIS RABOSKY et al. 2016, IWANISHI et al. 2018). Although some authors attempted to classify them based upon diminished, missing, or overexpressed pigments (HARRIS 1970, DYRKACZ 1981, PRÜST 1984, BECHTEL 1995), no general consensus has yet been reached. A wide range of vaguely defined terms have instead been used, particularly for conditions involving diminished colourations (BECHTEL 1995). A reduced production or complete absence of melanin has usually been termed albinism, taking a cue from the condition affecting humans, sometimes specifying it further as complete, oculocutaneous, pure, total or true albinism (AMARAL 1927, BECHTEL & BECHTEL 1989, BECHTEL 1991; HOSHING et al. 2013, KUMBAR et al. 2016). The terms albinistic, albinoid, albinotic, and partial albino/albinistic are equally imprecise, but have liberally been employed (e.g., HARRIS 1970, DYRKACZ 1981, MIRANDA et al. 1985, ESQUEDA et al. 2005, MAHABAL & THAKUR 2014, GEZOVA et al. 2018). Moreover, they were also used for what actually constitutes piebaldism and leucism (PRADO 1939, NICÉFORO 1958), two well-known hereditary defects of melanin expression that have been widely recorded in vertebrates. Wild piebald and leucistic snakes are predominantly white with pigmented eyes, commonly presenting piebalds large pigmented blotches (BECHTEL 1991, 1995).

Herein, we present as a case study the available information about CA in wild Neotropical snakes, report new cases, and review the terminology historically used. We propose standardization for future descriptions, and provide further data on other reptiles from the region and references on this topic about non-Neotropical snakes.

Materials and methods

We analysed published cases of CA in wild snakes from South America, Middle America, and the Caribbean region, considered as reports of a conspicuous reduction (hypopigmentation) or overexpression (hyperpigmentation) of at least one dorsal colour beyond the usual colour variation of species/populations or polychromatism (NEILL 1963). Aberrancies were classified based on the predominant colour and eye pigmentation following HARRIS (1970) if both could be assessed from the text or illustrations: 1) Hypopigmentation (HYPO) of dorsum: amelanism, lack of melanin expression (dark colours), including eyes; hypomelanism, diminished melanin expression with pigmented eyes; axanthism, lack of xanthins (yellow colour); hypoxanthism, diminished xanthins; anerythrism, lack of erythrins (red colour); hypoerythrism, diminished erythrins; leucism, white, plus patternless and pigmented eyes; piebaldism, predominantly or patchily white with pigmented eyes; albinism, total absence of pigments, including in the eyes. 2) Hyperpigmentation (HYPER) of dorsum: erythrism, melanism, and xanthism, overexpressed erythrins, melanin, and xanthins respectively; being partial if indications of the species' pattern remain. When one or more colours were completely or partially substituted by another, we considered only the overexpression.

We additionally recorded the following ecological habits of snakes: fossorial (FO), non-fossorial (NFO; arboreal, aquatic, terrestrial), diurnal (DI), and nocturnal (NO). Associations between the number of species with contrasting ecological attributes (nocturnal/diurnal; fossorial/non-fossorial) and contrarious CAs (HYPER/HYPO; amelanism/melanism, AMEL/MEL) were tested in 2×2 tables using Fisher's exact test (FET). We added to the dataset of published work and internet resources some new cases from Uruguay and Brazil observed by the authors and photographic records obtained from local people. Snake taxonomy follows UETZ et al. (2020).

Results

We compiled 115 cases of CA in wild Neotropical snakes representing 47 species of Colubridae ($n = 56$; 49.1%), Viperidae ($n = 41$; 36.0%), Boidae ($n = 5$; 4.4%), Elapidae ($n = 7$; 6.1%), Typhlopidae ($n = 3$; 2.6%), Aniliidae ($n = 1$; 0.9%), and Leptotyphlopidae ($n = 1$; 0.9%). Categorization of the CA of each case according to our classification framework based on the colourations of dorsum and eyes, allowed the identification of 10 basic types that are represented in Figure 1.

Classification of a CA type using our criteria was possible in 87 examples of 42 species, of which most were instances of hypopigmentation ($n = 52$; 59.8%), mainly amelanism ($n = 26$), followed by a few cases of leucism ($n = 5$), piebaldism ($n = 11$), hypomelanism ($n = 6$), anerythrism ($n = 2$), and single occurrences of axanthism and albinism. The hyperpigmentation records ($n = 35$, 40.2%) were

mostly melanism (n = 19) and xanthism (n = 13), plus a few aberrant erythristic snakes (n = 3). The taxonomic distribution of these instances of CA is summarized in Table 1, and some examples are provided in Figures 2–4. Raw data is presented in Supplementary Table S1; we were unable to classify some reports published by AMARAL (1927a, 1927b, 1932a), HOGE (1952), NICÉFORO (1958), BÉRNILS et al. (1990), GIRAUDO (2001), FREITAS (2003), DUARTE et al. (2005), and ORTIZ et al. (2017), due to their omission of critical information to us.

Instances of hypopigmented CA have been described by various authors in a rather erratic manner, often referring to them as albinism, oculocutaneous albinism, and partial, complete or full albinism. The external characters previously used to differentiate the various expressions of “albinism” were explicit only occasionally and include varied and sometimes poorly defined criteria relating to body colouration and the pigmentation of the eyes and/or tongue (Table 2). Consequently, mismatches with our classification were commonplace. For instance, nearly all previously

reported cases that were classified by us as amelanism and hypomelanism had not been referred to as such by other authors. Previous regional works did not recognize cases of piebaldism (n = 7). Conversely, our classification of the hyperpigmentation type was not congruent with previous reports by other authors only in two cases of xanthism (see Supplementary Table S1).

Associations of CA with ecological attributes (see Table 3) proved to be not significant: HYPER/HYPO vs. DI/NO, $P = 0.086$; HYPER/HYPO vs. FO/NFO, $P = 0.129$; AMEL/MEL vs. DI/NO $P = 1.0$; AMEL/MEL vs. FO/NFO $P = 0.201$.

Discussion

Albinism, hypomelanism and amelanism

Our dataset indicates that CAs known for wild Neotropical snakes are varied and are represented in a broad taxonomic range. Most common CAs are those related to the pro-

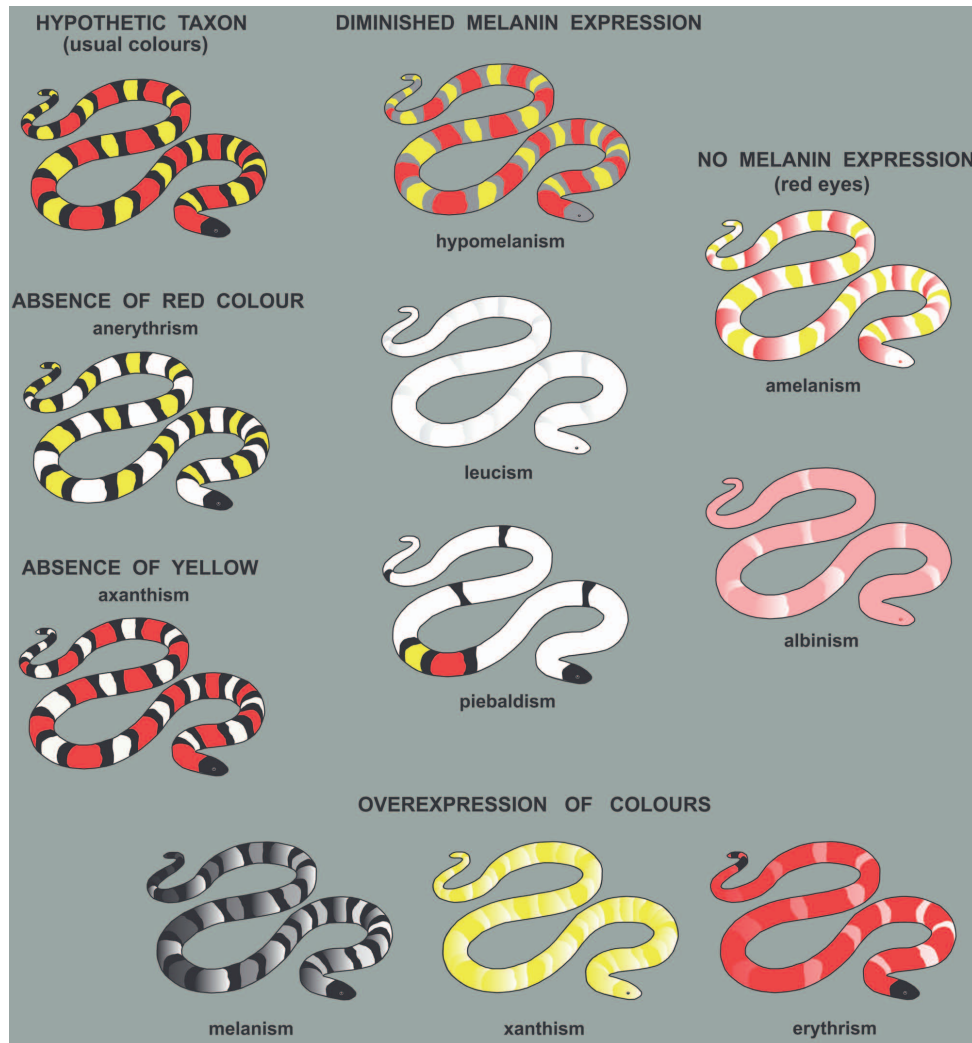


Figure 1. Schematic representation of major conspicuous colour aberrancies in wild snakes.

Aberrant colourations in wild snakes

Table 1. Colour aberrancies (CA) in wild Neotropical snakes. PM, pigmented; NP, not pigmented.

Dorsal colour variation	Extent	Eyes	CA	CA in previous reports (number of works)	Total occurrence (number of cases)	
Black	Partial	PM	Hypomelanism	Partial albinism (2), hypomelanism (1), leucism (1), xanthism (1).	<i>Bothrops</i> (2), <i>Dipsas</i> (1), <i>Drymarchon</i> (1), <i>Erythrolamprus</i> (1), <i>Philodryas</i> (1).	
	Absence	Total	NP	Amelanism	Albinism (9), total albinism (5), partial albinism (3), amelanism (2), complete albinism (1), full albinism (1).	<i>Crotalus</i> (3), <i>Oxyrhopus</i> (3), <i>Xenodon</i> (3), <i>Boa</i> (2), <i>Dipsas</i> (2), <i>Philodryas</i> (2), <i>Micrurus</i> (4), <i>Bothrops</i> (1), <i>Erythrolamprus</i> (1), <i>Geophis</i> (1), <i>Leptodeira</i> (1), <i>Lygophis</i> (1), <i>Ninia</i> (1), <i>Phalotris</i> (1).
	Over-expression	Partial	PM	Melanism	Melanism (4).	<i>Lygophis</i> (5), <i>Bothrops</i> (4), <i>Erythrolamprus</i> (1), <i>Phalotris</i> (2).
Yellow	Absence	Partial	PM	Hypoxanthism	Not reported.	Not identified.
	Over-expression	Total	PM	Axanthism	This study.	<i>Erythrolamprus</i> (1).
	Absence	Partial	PM	Xanthism	Xanthism (7), albinism (1), leucism (1), not provided (1).	<i>Crotalus</i> (4), <i>Bothrops</i> (5), <i>Dipsas</i> (1), <i>Epicrates</i> (1).
Red	Over-expression	Total	PM	Xanthism	Xanthism (1).	<i>Bothrops</i> (2).
	Absence	Partial	PM	Anerythrism	Not reported.	Not identified.
	Over-expression	Total	PM	Anerythrism	Anerythrism (1), “nigrismus” (1).	<i>Corallus</i> (1), <i>Micrurus</i> (1).
All	Absence	Partial	PM	Erythrism	Erythrism (1), not provided (1).	<i>Anilius</i> (1), <i>Micrurus</i> (1), <i>Oxyrhopus</i> (1).
	Total	PM	Erythrism	Not reported.	Not identified.	
		NP	Piebaldism	Albinism (4), leucism (1).	<i>Atractus</i> (1), <i>Boiruna</i> (4), <i>Pseudoboa</i> (2).	
Total	PM	Leucism	Leucism (3), albinism (1).	<i>Atractus</i> (3), <i>Boa</i> (1), <i>Mastigodryas</i> (1).		
	NP	Albinism	Total albinism (1).	<i>Amerotyphlops</i> (1).		

duction and distribution of melanin, mainly in the shape of amelanism and melanism. The majority of previous reports about aberrant hypopigmentation usually quoted it as albinism (e.g., SAZIMA & DI-BERNARDO 1991). Albinism, from Latin “albus” (white), was first coined to indicate a defective melanin expression in humans (WITKOP 1985). BECHTEL (1995) defined snake albinism as “a congenital decrease or absence of melanin in the skin, mucosa, and eyes”. However, it was traditionally applied to CAs not involving melanin expression (BECHTEL 1995, SUNTRARACHUN et al. 2015; THAKUR & TRIVEDI 2018). Its usage in Neotropical snakes often included both melanin-related defects and others like xanthism (e.g., AMARAL 1933–1934).

Snake albinism in a strict sense applies to the complete lack of functional chromatophores in the skin and eyes. In general, colouration defects related to diminished melanin expression are difficult to categorise because the absence of black pigment may have variable effects on the remaining colours, falsely suggesting, for instance, a case of xanthism (BECHTEL 1995). In Neotropical snakes, these were the most common CAs and traditionally also the most problematic ones to classify. A few instances of hypomelanism in Neotropical species showed normal patterns with less intense black/brown (e.g., LEMA 1960, VARGAS 2015, MENDONÇA et al. 2020). Most of the other records were examples of amelanism, which goes along with pigmentless (reddish) eyes like in albinism (e.g., PRADO & BARROS 1940, RENAULT & SCHREIBER 1949, HOGE & BELLUOMINI 1957–1958, VILLA &

RIVAS 1971, MIRANDA et al. 1985, VEIGA & TEIXEIRA 1993, DE LA TORRE-LORANCA et al. 2006, SCROCCHI et al. 2006, VALENCIA et al. 2009, TRAVAGLIA-CARDOSO et al. 2014, MACHÍN et al. 2018, LOPES et al. 2019).

Red and/or yellow colours are supposed to be more intense once they are not obscured by melanin (BECHTEL 1995), as has been observed in amelanistic *Erythrolamprus miliaris* (DA SILVA et al. 2010) and *Philodryas patagoniensis* (Fig. 2G). Remarkably, in amelanistic *Micrurus lemniscatus* (PAREDERO et al. 2017) and *M. pyrrhocryptus* (this study) both colours appeared fairly smoothed, and the red stripes were altered to orange in a *Phalotris lemniscatus* (ABEGG et al. 2015, Fig. 2C). This is probably due to the lack of phaeomelanin (pale red/yellowish colour) in amelanistic snakes, a variant of melanin known from other vertebrates but recently discovered also in reptiles (ROULIN et al. 2013). In normally dark species like *Amerotyphlops brongersmianus*, amelanism may result in a pink colouration (MIRA-MENDES et al. 2017), but this putative albinism to the eye deserves careful study. Besides, we know of a report of amelanism in the Neotropical lizard *Tropidurus semitaeniatus* (FLORÊNCIO et al. 2019). Amelanism in non-Neotropical snakes was commonly reported as albinism (e.g., KRECSÁK 2008, SHEDD 2013, HOSHING et al. 2013, ADIMALLAIAH & VYAS 2015, GEZOVA et al. 2018), but also as hypomelanism (WHITFORD et al. 2018), and sometimes explicitly used as a synonym (i.e., HOGAN & SMITH 1998). The consideration of an incomplete albinism because of

Table 2. Criteria used by different authors to classify “albinism” in Neotropical snakes. * extracted/translated by the authors.

Author	Reported anomaly	Criteria		Colour aberrancy matching	
		Body colouration	Pink/red eyes		Pink/red tongue
MIRANDA et al. (1985)	Partial albinism	Diminished dark pigmentation. *	–	YES	Albinism, amelanism.
NORONHA et al. (2013)	Partial albinism	“...total absence of tegument pigmentation...”	YES	–	Albinism, amelanism.
ABEGG et al. (2014)	Partial albinism	“...absence of melanin in certain body regions, with the skin presenting a white color with pigmented zones, or producing lighter shades of the common colors...”	–	–	Albinism, amelanism, hypomelanism, piebaldism.
VALENCIA et al. (2009)	Albinism	“...homogeneous, ...with single dominant color...”	–	–	Albinism, leucism, piebaldism, others depending on species.
ORTIZ et al. (2017)	Albinism	“...partial or complete inability of an organism to produce melanin.”	–	–	Albinism, amelanism, hypomelanism, leucism, piebaldism.
LOPES et al. (2019)	Albinism	“...absence of skin pigmentation, ...and occasionally, partial or total absence of dorsal and dorsolateral patterns...”	YES	YES	Albinism, leucism.
VEIGA & TEIXEIRA (1993)	Oculocutaneous albinism	Uniformly white body (unpigmented).*	YES	YES	Albinism, amelanism.
MIRANDA et al. (1985)	Complete albinism	Absence of dark pigmentation.*	YES	YES	Albinism, amelanism.
PRADO & BARROS (1940)	Total albinism	Absence of melanin.*	YES	–	Albinism, amelanism.
BÉRNILS et al. (1990)	Total albinism	Faded dorsal pattern.*	YES	YES	Albinism, amelanism.
DA SILVA et al. (2010)	Total albinism	“...lack of skin pigmentation...”	YES	YES	Albinism, amelanism.
ABEGG et al. (2015)	Total albinism	“...pinkish-yellow, yellow or white body...”	YES	YES	Albinism, amelanism.
MIRA-MENDES et al. (2017)	Total albinism	“...decrease or absence of melanin in the skin, mucosa, and eyes...”	–	–	Albinism, amelanism, hypomelanism.

Table 3. Lifestyles of Neotropical snakes for which reports of colour aberrancies exist (number of species). * includes fossorial taxa.

Habit	Hypopigmentation		Hyperpigmentation	
	Amelanism	Other	Melanism	Other
non-fossorial	11	11	8	9
fossorial	7	5	1	2
diurnal	8	7	4	0
nocturnal*	10	9	5	11

the lack of melanin expression was rarely made explicit by indicating the particular deficiency, for instance as an “amelanistic partial albino” (i.e. ANTONIO & BARKER 1983, CLARK et al. 1983, HERMAN 1983, HUDSON & CARL 1983). A few case reports classify such cases just as “amelanism” (i.e., JONES & FRIEDMAN 2015, HOLT & DOLLAR 2018).

Autosomal recessive and non-allelic inheritance of albinism were indicated for captive *Pantherophis guttatus* and *Pituophis melanoleucus* (BECHTEL & BECHTEL 1962, BECHTEL 1980, BECHTEL & BECHTEL 1981). Likewise, hypomelanism in *Pantherophis obsoletus* is autosomal recessive (BECHTEL & BECHTEL 1981). SAENKO et al. (2015) dem-

onstrated that a retrotransposon insertion in the oculocutaneous albinism type II gene (*OCA2*) was responsible for an amelanistic phenotype in *P. guttatus*. Besides, IWANISHI et al. (2018) recently identified a non-sense mutation in the TYR gene (which encodes the tyrosinase enzyme involved in the first step of the conversion of tyrosine to melanin) as the cause of one of the two amelanistic phenotypes known from *Elaphe climacophora* in Japan.

Piebaldism

This condition is a commonly misidentified CA of snakes. Piebald is an old English word combining “pie” in reference to the white/black plumage of magpies, and “bald” from the Greek “phalios” indicating white spotting (SPRITZ 1992). The synonym “albinistic pinto” was barely used in snakes (DYRKACZ 1981, PRÜST 1984). It is a non-progressive defect that is well studied in mammals, associated with the KIT gene (which encodes the kinase receptor proteins necessary for the development and function of the melanocytes), producing a variety of phenotypes depending on the mutation (SPRITZ 1992). GLOYD (1958) inaccurately pointed out that it resembled vitiligo, a human skin disease of undefined aetiology and not strictly genetic. Similarly,

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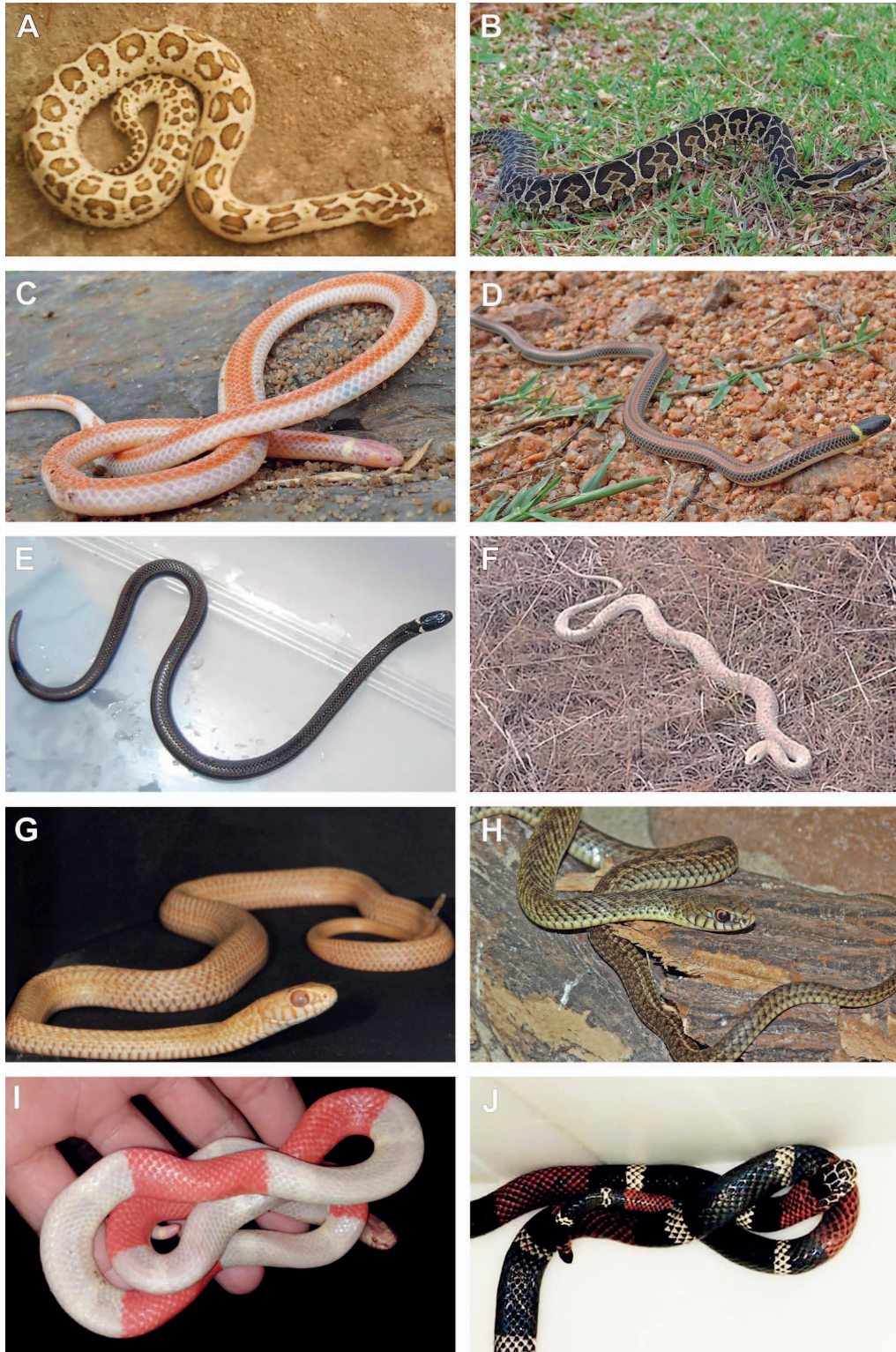


Figure 2. Colour aberrancies in Neotropical snakes related to the amount of melanin in the skin. A) hypomelanism in *Bothrops alternatus* (Maldonado, Uruguay [UY], MACHÍN et al. 2018); B) normal *B. alternatus* (Treinta y Tres [TT], UY; photo A. Sosa); C) amelanism in *Phalotris lemniscatus* (same specimen as in ABEGG et al. 2015); and D) normal specimen (TT, UY; photos A. Sosa); E) melanism in *P. lemniscatus* (Piriápolis, UY; photo IE); F) hypomelanism in *Philodryas patagoniensis* (Minas, UY); G) amelanism in *P. patagoniensis* (TT, UY, Uruguay, same specimen as in MACHÍN et al. 2018; photo CB); and H) normal specimen (TT, UY; photo A. Sosa); I) amelanism in *Micrurus pyrrhocryptus*; and J) normal specimen (Chaco, Argentina; photos Fundación Refugio Salvaje, Argentina).

the cases of progressive piebald-like depigmentation observed in captive specimens of the non-Neotropical rattlesnake *Crotalus viridis*, Burmese python *Python bivittatus*, Ball python *P. regius* (BECHTEL 1995, BROGHAMMER 2000), and also free-ranging iguanas *Ctenosaura oedirhina* from Honduras (GOODE & PASACHNIK 2016, as piebaldism), are of unconfirmed hereditary disposition. Besides, reports of leucism in the Neotropical lizards *Iguana iguana* from Colombia, and *Amphisbaena darwini trachura* and *Tropidurus hispidus* from Brazil, are likely cases of piebaldism according to their colour patterns (CHALKIDIS & DI-BERNARDO 2004, AYALA-MONEDERO & ÁLVAREZ-LEÓN 2014, SANCHES et al. 2019).

Piebald snakes show white spots, patches or a predominantly white skin (PRÜST 1984, BECHTEL 1995), and are very uncommon in the wild (DODD 2000, KORNILIOS 2014, GROSS et al. 2016). They are particularly appreciated by reptile keepers, who sometimes call them just “pieds” (BROGHAMMER 2000). In captive Ball pythons (*Python regius*), piebaldism is based upon a recessive Mendelian inheritance (BROGHAMMER 2000). Our local examples mostly concern *Boiruna maculata* (BOULENGER 1896, CEI 1993, GIRAUDO 2001, SCOTT et al. 2006, CARREIRA et al. 2018, MACHÍN et al. 2018) and *Pseudoboa nigra* (PRADO 1939, NORONHA et al. 2013) of the tribe Pseudoboini, but also single cases known from *Mastigodryas boddaerti* (NICÉFORO 1958) and *Atractus zebrinus* (this study). The first two are usually black snakes, being piebalds scarcely spotted with white (BOULENGER 1896), fairly stained white (Fig. 3A), or primarily white (e.g., GIRAUDO 2001, NORONHA et al. 2013, MACHÍN et al. 2018). The occurrence of normal colours on the head slightly extending posteriorly was constant in the studied cases and may therefore allow for differentiating them from other melanin-related defects. Although well-known as a common genetic defect in domestic mammals (MAHABAL et al. 2019), the rarity of piebaldism in wild reptiles and researchers being not familiar with colour variants in other vertebrate groups may explain the misclassifications in previous works.

Leucism

Leucism originates from the Greek word “leukos” (= white), and refers to a hereditary non-progressive defect affecting the presence of chromatophores in the skin, which turns white in the case of snakes, eventually presenting scarce iridophores (BECHTEL 1995). Leucism is symmetrical, and does not change with age (VAN GROUW 2013). The eyes are unaffected, as pigmented cells of the retinal epithelium develop independently (JACKSON 1997). Confusion regarding leucism is not exclusive to the snake literature as there is broad usage of the term for various instances of whitening plumage in birds and the coats of mammals, in which nutrition and other genetic conditions may also produce similar aberrations (VAN GROUW 2006, 2013; LUCATI & LÓPEZ-BAUCELLS 2016, ZALAPA et al. 2016). Leucistic snakes may exhibit some tiny and scattered faded stains throughout

the body colouration, added to which may be blue eyes (PRÜST 1984, ENTIAUSPE-NETO et al. 2018). Available reports from the wild are quite rare elsewhere, with most of them not recognizing instances as leucism (LAHIRI 1955, LOVE & LOVE 1979, ANTONIO & BARKER 1983, BECHTEL 1991, KRECSÁK 2008, STEPHENSON & DRACE 2014, LOBO & SREEPADA 2016, BRUNI 2017, SYLER & SY 2011, CHAUDHURI et al. 2018, MOHALIK et al. 2019), and at least in *Pantherophis obsoletus*, it is autosomal recessive (BECHTEL & BECHTEL 1985, BECHTEL 1995). Neotropical cases concern *Atractus reticulatus* (GIRAUDO & SCROCCHI 2000, ENTIAUSPE-NETO et al. 2018; Fig. 3C) and *Boa constrictor* (USA 2015). Putative ones were reported from *Mastigodryas boddaerti* (NICÉFORO 1958) and *Atractus trilineatus* (BOOS 2001). The absence of patches with normal colour(s) easily allows distinguishing them from piebald snakes. Leucism is also known from the Neotropical lizards *Gonatodes albogularis* from Colombia (GRISALES-MARTÍNEZ & ARIAS-ÁLVAREZ 2018), *Homonota taragui* from Argentina (COURTIS et al. 2015), and the freshwater Amazon turtle *Podocnemis unifilis* (ERICKSON & KAEFER 2015).

Melanism

Hyperpigmentation in polychromatic snakes is common in both Palaearctic (e.g., BECHTEL 1978, ANDRÉN & NILSON 1981, KING 2003, JABLONSKI & KAUTMAN 2017, KALLAENTZIS et al. 2018) and Neotropical species (CACCIALI 2010; BERNARDO et al. 2012). Of the types of aberrant hyperpigmentation, spontaneous melanism is likely the most common condition and possibly more frequent than widely supposed, as recognizing it necessitates observers to be familiar with a species’ normal colour range (BECHTEL 1995). As with CAs in general, the absence of one colour may be confusing as it will cause others to seemingly become enhanced. For instance, anerythristic individuals of conspicuously red snakes may be misidentified as cases of melanism, sometimes also called nigrism (BÉRNILS & MOURA-LEITE 1991). Melanism is a quite common CA in lizards, as has been documented from European species (DOMENEGHETTI et al. 2016; RECKNAGEL et al. 2018, and references therein).

The ecological correlates of melanism in reptiles are controversially discussed, including the putative advantages for thermoregulation, protection from solar irradiation and exposure to predators (BITNER & KING 2003, RECKNAGEL et al. 2018). Melanism is of simple recessive inheritance in the Common garter snake *Thamnophis sirtalis* (KING 2003), which does not apparently increase its risk of being predated upon (BITNER 2003). On the other hand, darker Swedish *Vipera berus* were suggested to benefit from better thermoregulation ability but may incur a greater predation risk in a trade-off (ANDRÉN & NILSON 1981). The underlying causes of differential melanism frequency between populations need to be studied on a case by case basis. For instance, the occurrence of island melanism like in some Mediterranean snakes such as *Eirenis*

modestus (KALAENTZIS et al. 2018) may be explained by a complex interaction of reduced gene flow, genetic drift, and selective forces (BITTNER & KING 2003).

As far as Neotropical snakes are concerned, we compiled some records of melanism from colubrids (LEMA 1985, MENEZES et al. 2014, COSTA-CAMPOS et al. 2015, BARBOSA et al. 2019, this study) and viperids (SAPORITI 1938, HOGE 1952a, DA SILVA et al. 1999, Fig.2E). Additionally, there is a single record from the lizard *Tropidurus torquatus* from Brazil (PEREIRA et al. 2014).

Erythrism and anerythrism

A variable amount of red in the colour pattern is typical of some snakes, like *Thamnophis sirtalis* (MOOI et al. 2011), and Neotropical elapids of the genus *Micrurus* (SOINI 1974, FEITOSA et al. 2015). Noticeable examples of inter-population variations are the presence/absence of red colours in the pattern that is driven by Mendelian in-

heritance like observed in the dipsadid *Sonora semiannulata* from the western United States (DAVIS RABOSKY et al. 2016), and the entirely erythristic population of the Carolina pigmy rattlesnake *Sistrurus miliarius* (PALMER 1971). On the other hand, sporadic occurrences of conspicuously aberrant red colours or erythrism are among the rarest CAs in wild snakes elsewhere (MAČÁT et al. 2016). The anomalous excess of red or brown colouration is sometimes called rufinism in the zoological literature, but is a term not traditionally used for snakes (PRÜST 1984; BECHTEL 1995). Three cases of snake erythrism from the Neotropics, involving *Anilius scytale* (CRUZ-DA-SILVA et al. 2018), *Micrurus corallinus* (this study, Fig. 4A), and *Oxyrhopus guibei* (AMARAL 1932), displayed partial substitutions of other colours by red. Anerythristic wild snakes seem to be quite rare as well (BECHTEL 1980, BECHTEL & BECHTEL 1989) and we know of only two examples from the region: *M. corallinus* (BÉRNILS & MOURA-LEITE 1991) and the Tree boa *Corallus annulatus* (LEWIS et al. 2009), with both lacking only red.



Figure 3. Piebaldism and leucism in wild Neotropical snakes. A) piebald *Boiruna maculata* (Durazno, Uruguay [UY]; dead specimen, photo CB); B) normal *B. maculata* (Chaco, Argentina, photo CB); C) leucistic *Atractus reticulatus* (Rio Grande do Sul, Brazil, same specimen as in ENTIAUSPE-NETO et al. 2018; photo L. M. Borges); D) normal *A. reticulatus* (Rivera, UY; photo CB).

Xanthism and axanthism

As quoted for red colour, snake polychromatism in Neotropical taxa may express itself in yellow variants, as is seen in *Xenodon merremii* (CACCIALI 2010) and the exceptionally beautiful yellow phase of the viperid *Bothriechis schlegelii* (GÓMEZ & BUITRAGO-GONZÁLEZ 2017). Besides, a population of entirely yellow specimens of the pelagic elapid

Hydrophis platurus (usually only yellow-bellied) is known from western Costa Rica. Being a surface feeder, this characteristic possibly helps this snake to avoid overheating in a tropical climate (BESSESEN & GALBREATH 2017). Xanthic snakes may also synthesize small amounts of melanin and have coloured eyes (BECHTEL 1995).

The term flavinism is occasionally used in the herpetological literature for exceptionally yellow specimens. How-

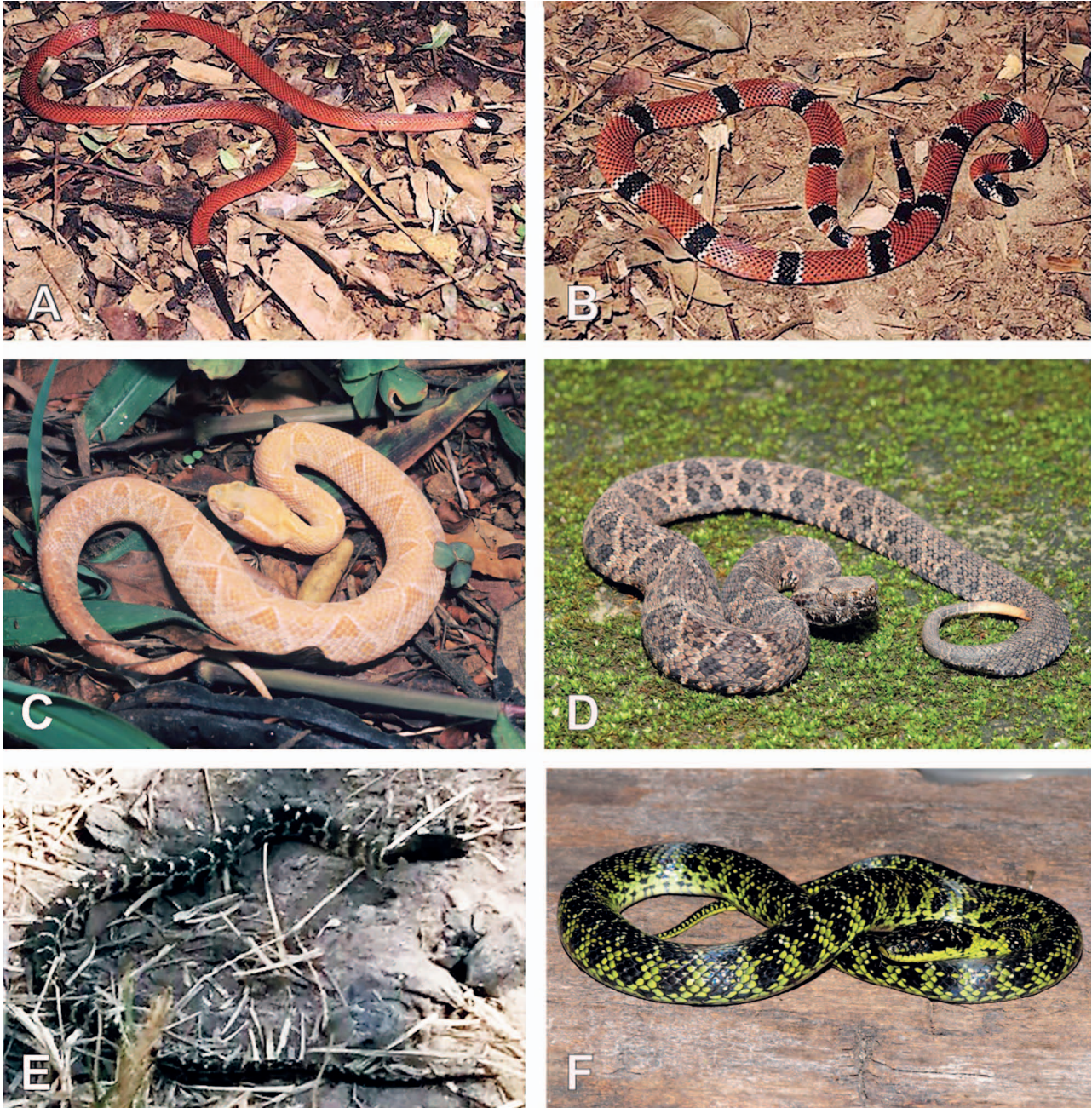


Figure 4. Non-melanin related colour aberrancies in wild Neotropical snakes. A) erythristic *Micrurus corallinus*; and B) normal specimen (Brazil [BR]; photos O. A. V. Marques); C) xanthic *Bothrops jararacussu* (Iguapé, São Paulo [SP], BR; photo O. A. V. Marques); D) normal *B. jararacussu* (Ibiúna, SP, BR; photo A. D. Abegg); E) axanthic *Erythrolamprus poecilogyrus* (Río Negro, Uruguay [UY]); and F) normal specimen (Quebrada de los Cuervos, UY; photo CB).

ever, the over-expression of yellow is sometimes hard to differentiate from the change in colouration induced by the absence of melanin in amelanistic specimens (i.e., THOMAS et al. 2002).

Xanthic CA in Neotropical snakes was seldom observed, being more common in viperids of the genera *Bothrops* (HOGE 1952a, SUEIRO et al. 2010, VARGAS 2014, DUARTE in UETZ et al. 2020, TOKUDA & COSTA 2019; Fig. 4C) and *Crotalus* (SAZIMA & DI-BERNARDO 1991, CARDOSO & PARPINELLI 2006); it was also documented from *Dipsas mikanii* (AMARAL 1933–1934) and *Epicrates crassus* (HOGE & BELLUOMINI 1957–1958). Although such CA has been claimed to protect its bearer from solar irradiation in tropical climates (BESSESEN 2012), xanthism was noted only in nocturnal species in our case study.

As far as the contrarious condition, axanthism, is concerned, we know of only a single case in wild snakes from our region, recorded by local people in *Erythrolamprus poecilogyrus* (Fig. 4E). Axanthic snakes are difficult to differentiate from anerythristic ones, and both were called “black albinos” because they stand out by exhibiting only black and brown colours (BROGHAMMER 2000).

Concluding remarks

SAZIMA & DI-BERNARDO (1991) proposed that hypopigmented CA of Neotropical wild snakes seemed to be more frequent in fossorial and nocturnal species, whose blanched phenotypes would undergo less intense predation. Our exploratory analysis on an expanded data set is not conclusive in this regard, however. It must be noticed that correlates of ecological attributes of snakes (diurnal/nocturnal, fossorial/non-fossorial) and major CA categories (hyper-/hypopigmentation, melanism/amelanism) sometimes became statistically significant, or approached significance during the computations for this work, by the addition of small amounts of new data. This indicates the weakness of our analysis with the available information, as the data matrix of taxonomical distribution of CA in Neotropical snakes is still unstable. Improved testing would require the pooling of more observations for the consideration of phylogenetic constraints, and also obtaining CA frequency estimates in snake communities, which are difficult to document given the rarity of some of the conditions and the observation bias of hard-to-find taxa (e.g., fossorial species). Additional bias underlying accumulated historical data from biological collections and large-scale surveys is created by observers possessing the ability to recognize colour aberrancies in snakes to different extents, and unequal sampling effort in different areas (BECHTEL 1980).

Interestingly, we recorded aberrant hyperpigmentation in a few fossorial species, but these CAs seem to provide no major contributions to thermoregulation, as they were also infrequent in terrestrial diurnal snakes. Even when melanism may bring about some functional advantages for snakes with regard to heat absorption, reproduction and

survival (BITTNER et al. 2002, CLUSELLA-TRULLAS et al. 2008 and references therein), such must be evaluated on a case-by-case basis. When studying the sea snake genus *Laticauda*, LORIOUX et al. (2008) did not find an association of enhanced pigmentation (melanism) with advantages for survival either regarding thermoregulation, predation, or protection solar irradiation. As was proposed by these authors for snake melanism, other aberrant colourations studied herein may be, to a great extent, fortuitous phenomena.

Additional significant gaps in our knowledge about the complex mechanism of skin colour production in snakes are the scarcity of available histological and genetic studies (GOSNER 1989, BECHTEL 1995). Despite multiple genes involved in pigmentation having been isolated and special attention having been paid to the melanocortin-I receptor (MC1r) in several amphibians, birds, mammals, and reptiles, variable or no relationships between colour variation and gene polymorphism were observed (GUO et al. 2010, HERCZEG et al. 2010, CORSO et al. 2012, BUADES et al. 2013; SUNTRARACHUM et al. 2015). Although explored to an increasing extent at molecular level, the available knowledge on snake CA genetics is still incipient (SAENKO et al. 2015, SUNTRARACHUN et al. 2015, IWANISHI et al. 2018). Routine sampling by field biologists would allow for large-scale DNA surveying in the long run, as experimental studies are expensive and time-consuming (e.g., BECHTEL & BECHTEL 1985, 1989). A desirable alternative shortcut would be the analysis of the huge amount of valuable information generated by professional snake breeders over several decades (e.g., BROGHAMMER 2000).

Finally, we advocate a more accurate use of terminology in the herpetological literature concerning common CAs in wild snakes, but more generally in squamate reptiles, particularly with regard to melanin hypopigmentation. The criteria used by previous authors to define and classify these pigmentation deficiencies in snakes were heterogeneous and often confusing, mainly with regard to the widespread use of terms like albinism and partial albinism. In any case, the occurrence of albinism, as considered herein, was greatly overestimated in the literature, and criteria for its recognition were not uniform. Vague terms like partial albinism/leucism, albinistic or albinoid should be discarded to avoid confusion, as they do not refer to specific chromatophore defects. We propose a simplified categorization framework based on just three basic colours in the dorsal and eye pigmentation, which may permit even inexperienced researchers to differentiate the most common genetically based CAs reported for wild snakes (Fig. 1).

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Supplementary data

The following data are available online:

Supplementary Table S1. Records of chromatic aberrations in Neotropical wild snakes.

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