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# Taxonomic revision of the *Bothrops neuwiedi* complex (Serpentes, Viperidae) with description of a new species

**Vinícius Xavier da Silva[1] and Miguel Trefaut Rodrigues[2]**

[1] Departamento de Ciências Biológicas, Universidade Federal de Alfenas, 37130-000, Alfenas, MG, Brazil. E-mail: vinic@unifal-mg.edu.br.
[2] Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, 05508-900, São Paulo, SP, Brazil. E-mail: mturodri@usp.br.

**Abstract**

**Taxonomic revision of the *Bothrops neuwiedi* complex (Serpentes, Viperidae) with description of a new species.** Using a principal components analysis of morphological data of 1,759 specimens, we detected that the *Bothrops neuwiedi* complex (with 12 subspecies) is, actually, comprised of 7 full species, differing mainly by qualitative characteristics. One species was nominal. Five subspecies were elevated to the species level. *Bothrops iglesiasi* and the remaining *B. neuwiedi* subspecies entered in the synonymy of these six species. A new species is described. The new classification includes: *Bothrops neuwiedi* (synonyms: *B. n. goyazensis, B. n. meridionalis, B. n. paranaensis* and *B. n. urutu*), *B. diporus, B. lutzi* (synonyms: *B. n. neuwiedi, B. n. piauhyensis* and *B. iglesiasi*), *B. mattogrossensis* (synonym: *B. n. bolivianus*), *B. pauloensis, B. pubescens,* and the new species. This new species is characterized by stippled supralabials, instead of the conspicuous supralabial blotches present in other species of this complex. It is further characterized by an inconspicuous postorbital stripe and by 15-27 white-edged trapezoidal dorsolateral dark blotches throughout the body, 5-9 intersupraoculars (usually 7), 1-2 rows of small scales between the subocular and fourth supralabial, 8-9 supralabials (rarely 7 or 10), prelacunal separated from second supralabial, 9-13 infralabials (usually 10-11), 21-26 midbody dorsal scale rows (usually 23), 157-181 ventrals in males, 158-182 ventrals in females, 41-50 divided subcaudals in males, 37-47 in females. The pair of spots at the base of the dorsolateral blotches, typical of the *B. neuwiedi* complex, is generally diffuse, conferring to the whole blotch the aspect of a transverse saddle. The stippled aspect of the supralabials also appears in other scales throughout the rest of the body. This color pattern and the diffuse borders of the blotches confer a marbled pattern to this snake. We compare the new species with all related congeners, provide comments upon its distribution, and present an artificial identification key for the species of *B. neuwiedi* complex.

**Keywords:** Serpentes, Viperidae, Crotalinae, *Bothrops neuwiedi* complex, taxonomic revision, species description, South America.

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**Resumo**

**Revisão taxonômica do complexo *Bothrops neuwiedi* (Serpentes, Viperidae) com descrição de uma nova espécie.** Usando análise de componentes principais de dados morfológicos de 1759 espécimes, nós detectamos que o complexo *Bothrops neuwiedi* (com 12 subespécies) é, na verdade, formado por 7 espécies plenas, que podem ser distingüidas principalmente por caracteres qualitativos. Uma espécie é a nominal. Cinco subespécies foram elevadas ao nível de espécies. *Bothrops iglesiasi* e as subespécies de *B. neuwiedi* restantes entraram na sinonímia dessas seis espécies. Uma nova espécie é descrita. A nova classificação inclui: *Bothrops neuwiedi* (sinônimos: *B. n. goyazensis, B. n. meridionalis, B. n. paranaensis* e *B. n. urutu*), *B. diporus, B. lutzi* (sinônimos: *B. n. neuwiedi, B. n. piauhyensis* e *B. iglesiasi*), *B. mattogrossensis* (sinônimo: *B. n. bolivianus*), *B. pauloensis, B. pubescens* e a nova espécie. Esta nova espécie é caracterizada por apresentar supralabiais pontuadas, ao invés das manchas conspícuas presentes nas demais espécies do complexo. Caracteriza-se também por apresentar faixa pós-orbital inconspícua, 15-27 manchas dorsolaterais escuras, margeadas de branco e com formato trapezoidal, 5-9 intersupraoculares (geralmente 7), 1-2 linhas de pequenas escamas entre a subocular e a quarta supralabial, 8-9 supralabiais (raramente 7 or 10), prelacunal separada da segunda supralabial, 9-13 infralabiais (geralmente 10-11), 21-26 linhas de escamas dorsais no meio do corpo (geralmente 23), 157-181 ventrais nos machos, 158-182 ventrais nas fêmeas, 41-50 subcaudais divididas nos machos, 37-47 nas fêmeas. O par de pintas na base de cada mancha dorsolateral, típico do complexo *B. neuwiedi*, geralmente é difuso, conferindo à mancha o aspecto de uma sela transversal. O aspecto pontilhado das supralabiais também aparece nas demais escamas ao longo do corpo. Este padrão de coloração, juntamente com as bordas difusas das manchas, conferem um aspecto marmóreo a esta serpente. Comparamos a espécie nova com todos os congêneres relacionados, fornecemos comentários sobre distribuição geográfica e apresentamos uma chave artificial de identificação para as espécies do complexo *B. neuwiedi*.

**Palavras-chave:** Serpentes, Viperidae, Crotalinae, complexo *Bothrops neuwiedi,* revisão taxonômica, descrição de espécie, América do Sul.

## Introduction

*Bothrops* (sensu stricto) comprises about 36 species. Of these, 21 are found in Brazil. Most species present a sharply defined canthus rostralis, an unelevated snout, and a wide variation in scale counts: 3-14 intersupraoculars, 7-9 supralabials, 9-11 infralabials, 21-29 midbody dorsal scale rows, 139-240 ventrals, and 30-86 subcaudals, which are typically divided (Campbell and Lamar 2004). Descriptions and drawings of *Bothrops* skulls can be seen in Brattstrom (1964), Gomes and Puorto (1993), and Campbell and Lamar (2004). The everted hemipenis usually extends over 8-11 subcaudals and is deeply divided. Its sulcus spermaticus bifurcates at the level of subcaudals 1-3 and extends to the apex of each lobe. The hemipenis itself is divided at the level of subcaudals 2-4. The base of the asulcate side of the organ base is naked, whereas the sulcate side generally has small spinules. Calyces appear from the middle of the lobes to the distal extremity (Campbell and Lamar 2004).

Vellard (1946) was the first to separate two groups of *Bothrops* using hemipenis morphology. In his southern group, characterized by a hemipenis with short and calyculate lobes rounded distally, he included *Bothrops neuwiedi, Bothrops alternatus*, and *Bothrops cotiara*. Burger (1971) described the *atrox, neuwiedi, alternata* (=*alternatus*), and *ammodytoides* groups. The *neuwiedi* group included *Bothrops iglesiasi, Bothrops itapetiningae*, and the 12 subspecies of *B. neuwiedi*. Pesantes-Segura *et al.* (unpublished manuscript, in Campbell and Lamar 2004) recognized six groups of *Bothrops* according to a phenetic analysis of 25 hemipenial characteristics. For them, the *neuwiedi* group included *B. iglesiasi, B. erythromelas, B. andianus, B. neuwiedi.* The tendency of recent phylogenetic studies is to identify the *neuwiedi* group as composed by *B. neuwiedi* and *B. erythromelas* (Werman 1992, Moro 1996, Salomão *et al.* 1997, 1999, Wüster *et al.* 2002), the specific status of *B. iglesiasi* having been questioned since Campbell and Lamar (1989) and Brazil (1996).

The monophyly of the *neuwiedi* group is apparently supported, among other characteristics, by the presence of a divided lacunolabial (the character is independently present in the *alternatus* group) and characteristized by an extremely long hemipenis with a base dividing at level of subcaudals 7-8, moderately attenuated lobes, and few (28-35) spines on each lobe (Campbell and Lamar 2004). *Bothrops erythromelas*, associated with semiarid Caatinga areas of northeastern Brazil, is mainly distinguished from the *B. neuwiedi* complex by a lower number of ventrals [139-158 vs. 157-189] (Campbell and Lamar 2004).

*Bothrops neuwiedi* was regarded as a taxonomic complex comprising 12 subspecies distributed throughout open areas of South America, occurring in Brazil, Peru, Bolivia, Paraguay, Argentina and Uruguay (Peters and Orejas-Miranda 1986, Reyes and Onofre 1997). The species was originally described by Wagler in 1824, having as type-locality the State of Bahia, Brazil (Peters and Orejas-Miranda 1970, 1986, Hoge and Romano-Hoge 1981a, b, Grantsau 1991, Romano-Hoge 1996, Vanzolini 1996). As a holotype was not designated for the species, Hoogmoed and Gruber (1983) identified the male ZSM 2348/0, of the Spix collection in the Museum of Natural History of München (Germany), as the lectotype of *Bothrops neuwiedi* Wagler, 1824.

After Wagler described *B. neuwiedi* in 1824, several subspecies were described without, however, revising or correctly assessing the geographic variation within the group. The descriptions of these subspecies were based on the coloration and patterns of the body and head markings, because meristic characteristics overlapped (Amaral 1925, 1927, 1930c, 1933b). The recognized subspecies were: *Bothrops neuwiedi neuwiedi* Wagler, 1824, *B. n. bolivianus* Amaral, 1927*, B. n. diporus* Cope, 1862*, B. n. goyazensis* Amaral, 1925*, B. n. lutzi* (Miranda-Ribeiro, 1915)*, B. n. mattogrossensis* Amaral, 1925*, B. n. meridionalis* Müller, 1885*, B. n. paranaensis* Amaral, 1925*, B. n. pauloensis* Amaral, 1925*, B. n. piauhyensis* Amaral, 1925*, B. n. pubescens* (Cope, 1870), and *B. n. urutu* Lacerda, 1884.

The orthography "*neuwiedii*" (with two "i") was used beginning with Wagler (1830) and continued unabated, until Hoge (1966) reverted to the original spelling "*neuwiedi*", as originally proposed by Wagler (1824).

In 1925, Amaral described nine subspecies of *B. neuwiedi*: *B. neuwiedii neuwiedii, B. neuwiedii bahiensis, B. neuwiedii goyazensis, B. neuwiedii mattogrossensis, B. neuwiedii minasensis, B. neuwiedii paranaensis, B. neuwiedii pauloensis, B. neuwiedii piauhyensis* and *B. neuwiedii riograndensis. B. n. riograndensis*, previously described as *Trigonocephalus pubescens* (Cope 1870), became *B. n. pubescens* (Hoge 1959, 1966). *B. n. minasensis*, previously described as *Bothrops* *urutu* (Lacerda 1884), became *B. n. urutu* (Amaral 1937, Hoge 1966). *B. n. bahiensis*, previously described as *Lachesis lutzi* (Miranda-Ribeiro 1915), became *B. n. lutzi* (Amaral 1930a, b, Hoge 1966).

In 1927, Amaral described *B. neuwiedii boliviana*. Currently this subspecies is *B. neuwiedi bolivianus* (Hoge, 1966). In 1930, *B. neuwiedii meridionalis* was described (Amaral, 1930c), but this taxon was already recognized as *Bothrops diporus* (Cope 1862); so this subspecies was named *B. n. diporus* (Cochran 1961, Hoge 1966). *B. neuwiedii fluminensis* was the last subspecies described by Amaral (1933b). As it had already been described as *Bothrops atrox meridionalis* by Müller (1885), its name was altered to *B. neuwiedi meridionalis* (Hoge 1966).

The occurrence of anomalous specimens among the recognized subspecies, some previously recorded by Amaral (1933a), and the variations of color and patterns of dorsal and cephalic spots (Abalos and Baez 1963) show the complexity of this group. Some individuals disagree of the subspecies descriptions (Vanzolini 1948, Hoge 1953), and other specimens cannot be determined from the extremely variable pattern (Silva 1993). While some of the subspecies are quite different from others and could be considered full species (*B. n. urutu*, according to Hoge and Romano-Hoge 1981b), some others are difficult to distinguish (*B. n. paranaensis* and *B. n. pubescens*, according to Campbell and Lamar 1989). In some cases, the contact areas between differentiated forms and the presence of intermediate individuals (Amaral 1927, 1930c, Lema *et al.* 1984, Fernandes and Abe 1991, Lema 1994) suggest the possibility of hybrids. The need for a revision of this complex has been previously pointed out by several authors (Vanzolini 1948, Hoge 1953, Schenberg 1963, Vieira and Alves 1975, Campbell and Lamar 1989, Fernandes and Abe 1991, Silva 1993, Morato 1995).

The revision of this group has also an important impact in the medical area. Of 593.207 venomous snakes received by the Instituto Butantan, from 1900 to 1962, *B. neuwiedi* was the third more common species, with 28.965 individuals (Belluomini 1968). In certain areas, this species reaches notable densities (Fonseca 1949), being the responsible for most of the ophidic accidents (Amaral 1925, Abalos and Baez 1963, Cei 1987). Morphological variations can reflect variations of the venom and vice versa, as was already demonstrated in *Echis carinatus* (Warrell and Arnett 1976, Mebs and Kornalik 1981), *Naja naja* (Warrell 1986, Wüster and Thorpe 1989, 1991), *Vipera russeli* (Wüster *et al.* 1992a, b) and *Bothrops* complex (Furtado *et al.* 1991, Francischetti *et al.* 1998, Rodrigues *et al.* 1998). The understanding of the populations systematics in venomous snakes is essential for the production and efficient use of the antiophidic serums (Wüster *et al.* 1992b, Wüster *et al.* 1996, 1997, 1998).

Multivariate analysis of morphological characters can be better than univariate analysis to reveal patterns of variation, because conventional techniques character-by-character may be obscured by incongruent variation of each character (Wüster *et al.* 1996). This is mainly true for groups with high levels of sexual dimorphism, and ontogenetic, geographic and individual variations. The multivariate approach has been proved useful in studies of systematics and species delimitation such as Asiatic cobras (Wüster and Thorpe 1987, 1989, 1991), Russell's viper (Wüster *et al.* 1992a, b), and *Bothrops atrox* complex (Wüster *et al.* 1996, 1997).

Silva (2000) revised the *Bothrops neuwiedi* complex and published the principal taxonomic conclusions as a section (Silva 2004) of Campbell and Lamar (2004). However, as evidence for the taxonomic conclusions have not been published, and a new species discovered during the analysis still requires a description, the present publication explains and justifies the new taxonomic arrangement for the new species named and described below.

## Materials and Methods

The 1,759 specimens analyzed from 360 localities (Appendix I) are housed in the following collections: Adolpho Lutz (AL) from Museu Nacional, Rio de Janeiro, Brazil; Gregório Bondar, Universidade Estadual do Sudoeste da Bahia (CZGB-UESB), Vitória da Conquista, Brazil; Instituto Butantan (IBSP), São Paulo, Brazil; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; Museu Nacional (MNRJ), Rio de Janeiro, Brazil; Universidade Federal da Bahia (UFBA), Salvador, Brazil, and Zoologische Staatssammlung München (ZSM), München, Germany.

Seven morphological patterns (A-G), determined mainly by qualitative characteristics were recognized (Figure 1). The general morphology of the hemipenis of some specimens from each pattern was analyzed. The following morphometrical characteristics were examined: snout-vent length (SVL), tail length (TL), head length (HL), and trunk length (TRL). SVL and TL were measured with a common ruler to the nearest 1 mm. HL was taken with a dial caliper to the nearest 0.05 mm. TRL was obtained from the subtraction SVL - HL. Terminology for scale counts follows Ferrarezzi and Freire (2001) and included: intersupraocular rows (IR), dorsal cephalic scales in the sagital line beginning after internasals and ending at the level of the rictal region (DC), supralabials (S), infralabials (IF), ventrals (V), subcaudals (SC), and dorsals in the beginning (D1), and in the half of the trunk (D2). We considered the first ventral as being in the first scale wider than long. Scales between subocular and 4$^{th}$ supralabial were counted at three levels under the eye: anterior (SSS1), intermediary (SSS2), and posterior (SSS3). The number of dorsolateral blotches throughout the body (DB); shape of the dorsolateral blotch from middle trunk (SHB); rows of dorsal scales that form the principal part of dorsolateral blotch from middle trunk (RDB); and number of dorsal scales in the smallest distance between the dorsolateral blotch from middle trunk and the anterior blotch (NDB) were also considered. SHB was defined as the ratio between the number of dorsal scales that form the lower margin of the dorsolateral blotch from middle trunk and the number of dorsal scales that form the superior margin of the same blotch. DB, SHB, RDB, and NDB are illustrated in Figure 2.

Qualitative characteristics included: type of border of dorsolateral blotches (BB), presence or absence of blotches in the interspaces between two consecutive dorsolateral blotches (BI), type of ornamentation of supralabials (OS), extension of the ornamentation of supralabials (EOS), presence or absence of dorsal postcephalic stripes (DPS), keel coloration in dorsal scales (KC), and presence or absence of melanic head (M). BB can be defined (0) or diffuse (1). BI can be present (0) or absent (1). OS can be without blotches (0), with large round white blotches (1), with vertically elongated white blotches (2), with large dark blotches covering more than half of supralabial surface; the largest blotch is directly beneath the eye (3), or with small dark brown triangular blotches covering less than half of the supralabial surface, always situated throughout the suture between two supralabials (4). EOS can be more conspicuous in all supralabials (0), in supralabials of the anterior half of the mouth (1), or in supralabials of the posterior half of the mouth (2). DPS can be absent (0), short (1), or long (2). KC can be of the same color as dorsal scales (0) or white (1). M can be absent (0) or present (1).

For testing sexual dimorphism within the seven patterns, first, the normality and the homogeneity of variances were analyzed. The normality of the samples for numerical characteristics was analyzed by Kolmogorov-Smirnov test and the homogeneous variances were analyzed by ANOVA test. When these two criteria were not infringed, sexual dimorphism was analyzed by Student's t test. If the compared samples did not have normal distributions or homogeneous variances, sexual dimorphism was verified by a Kolmogorov-Smirnov test. Numerical characteristics with sexual differences were shown separately for males and females in the descriptive statistics for all seven patterns of the complex from samples of all geographic distribution in South America (Table 1). In addition, the comparision between sexes included linear regressions of TLxSVL and HLxTRL, according to Vanzolini (1993).

Principal Components Analysis (PCA) was used to study the morphological variation among offsprings in this complex (Xavier 2001). The same analysis was used here as a hypothesis-testing for the segregation among the patterns A-G. Clusters of specimens of same pattern separated from other patterns in the PCA graphics were taken as an indication of different evolutionary lineages or species. Each individual above 290mm SVL was considered as one operational taxonomic unit (OTU), separately for males and females, throughout most of localities from occurrence area in the South America (Figure 3). The exclusion of the litters (specimens with less than 290mm SVL) and the analysis separated by sex prevent minor influences from ontogenetic variation and sexual dimorphism, respectively. Only well preserved specimes in which the pattern type could be identified beyond reasonable doubt were considered. The PCA included nine numerical characteristics (D1, V, SC, IR, SSS1, DB, SHB, RDB, and NDB) and seven qualitative characteristics (BB, BI, OS, EOS, DPS, KC, and M). The 15 variables were standardized and a matrix of Pearson correlation was produced. The cases missing data for one of the variables in the pair involved in the correlation were excluded. The central part of the pattern distribution (Figure 3) was covered by four PCAs including pattern groups A+C+D, B+C+D, C+D+E, and A+B+E. The western part of the distribution was covered by a PCA including pattern types E+F+G, the south and southeast by a PCA including patterns B+F+G. The contributions of each variable analyzed to the first three principal components for males and females in all PCAs are present in the Appendix II. The component loadings of each pattern in the PCA graphs show confidence ellipse with 75% of the values. After PCA, the comparison of the different patterns with the type material permitted the atribution of names to the patterns A-G.

## Results

Differences in hemipenis morphology among patterns were not found; the general appearance of the hemipenis of the *B. neuwiedi* complex is shown in Figure 4. Table 1 presents the descriptive statistics of the scale counts and qualitative characteristics among seven morphological patterns (A-G) of the *Bothrops neuwiedi* complex. This table and the linear regressions showed the following tendencies for females: smaller subcaudal counts, larger ventral counts, shorter tails and longer SVL than males. Nevertheless, morphometric and meristic characteristics did not distinguish patterns due to the wide overlapping.The PCA graphs are shown in Figures 5 to 10, and the contributions of each characteristic to the first three components for both sexes are shown in the Appendix II. In the PCA, the percent of total variance explained by the first two componentes presented values between 34.7 and 50.8% for males, and 33.7 and 56.1% for females (Appendix II). In general way, the PCA graphs tended to separate the morphological patterns (Figures 5 to 10). When, for instance, two or three specimens of different patterns appeared together but the confidence ellipses (75% of the values) did not show overlapping, the patterns were considered distinct. This is the case of the patterns A+C+D in the combination of components 1x2 for both sexes, and in the combination 1x3 for males (Figure 5). In the combination 1x3 for females, patterns A and D did not separate (Figure 5). Nevertheless, this was not a problem. When two patterns did not segregate in one of the sexes, they appeared separated in the same component combinations of the other sex, as the pattern pairs A+D, A+E, and F+G (Figures 5, 8, and 9). In the same way, when two patterns did not segregate in one of the component combinations (1x2 or 1x3), they segregated in other combination, as the pattern pairs C+D and F+G (Figures 6, 7, and 10). According to Appendix II, the majority of the more informative characteristics in the segregation among patterns were qualitative characteristics. The separation among patterns A+C+D (Figure 5) occurred throughout principal component 1, mainly with the contribution of the variables KC, OS, EOS, DB, and M for both sexes. The patterns A and D were also showed differences throughout component 2 with some different characteristics for males (SHB, BI, OS, EOS, and BB) and females (EOS, OS, KC, V, and RDB). The patterns B+C+D (Figure 6) showed segregation in the component 1. The characters that more contributed for this were OS, DPS, BI, and M for both sexes. In males and females of this PCA the pattern D appeared separated from patterns B and C throughout component 2 with the contribution of V, SC, NDB, BB, and DB for males, and V, SC, IR, BB, and MI for females. These differences also appear in the Table 1. The component 1 also differentiated the pattern E from pattern pair C+D (Figure 7) throughout characters OS, EOS, BI, and M for both sexes. The patterns C and D appeared separated throughout component 2 with contribution of the characters BB, NDB, IR, and V for both sexes too. In the PCA of the patterns A+B+E (Figure 8), B separated from A+E throughout component 1 with the contribution of EOS, DPS, IR, and D1 for both sexes. The pattern A showed differences from pattern E throughout component 2 in males (more significative contributions of SC, V, OS, BB, KC) and component 3 in females (more significative contributions of DB, RDB, SSS1, NDB, SHB). In the analysis of patterns E+F+G (Figure 9), the pattern E segregated from F+G throughout component 1 in males and females with principal contributions of DPS, IR, and SHB. Between F and G, the differences appeared throughout component 2 for males (characters IR, SC, OS, EOS, and V) and component 3 for females (characters EOS, DB, NDB, V, and SC). In the PCA of the patterns B+F+G (Figure 10), B separated from F+G throughout component 1 with contribution of EOS, OS, IR, and D1 for both sexes. Between F and G, males and females were segregated throughout component 2 by the characteristcs OS, DPS, and DB. The Table 1 of some way corroborated the differences among the seven patterns A-G. The medium values of IR, VM, D1, and SSS1 were the least for the pattern A. In the variables VF, SCF, and SCM the least medium values were found in the patterns A and D. Patterns A and C presented least and largest medium values of DB, respectively. The largest medium value of SHB was observed in the pattern F. The least medium values of RDB appeared in the patterns A and C. Patterns C and F presented largest and least medium values of NDB, respectively. KC only appeared in the pattern A. BI and BB were exclusive of the patterns B, E, F, and G. DPS separated pattern F from two groups: A+C+D+E and B+G. M only appeared in the pattern C. OS segregated the patterns in five groups: A, B, C+D, E+F, and G. EOS segregated the patterns in three groups: A, B+C+D+G, and E+F. These tendencies of segregation among the patterns were shown in Figure 1. The comparison of the different patterns with type-material is summarized in discussion below.

## Discussion

*Initial considerations*

According to the evolutionary concept of species (Wiley 1978, 1981), one of the most important criteria for species recognition is the independence between two lineages, as an evidence of different historical fates.

**Table 1** - Comparison of scale counts and qualitative characters among seven morphological patterns (A-G) of the *Bothrops neuwiedi* complex. IR = intersupraocular rows; DC = dorsal cephalic scales in the sagital line beginning after internasals and ending at the level of the rictal region; S = supralabials; IF = infralabials; VF = ventrals in females; VM = ventrals in males; SCF = subcaudals in females; SCM = subcaudals in males; D1 = initial dorsals; D2 = midbody dorsals; SSS1 = scales between subocular and 4th supralabial counted in anterior level under the eye; SSS2 = scales between subocular and 4th supralabial counted in intermediary level under the eye; SSS3 = scales between subocular and 4th supralabial counted in posterior level under the eye; DB = number of dorsolateral blotches throughout body; SHB* = shape of the dorsolateral blotch from middle trunk; RDB = rows of dorsal scales that form the principal part of dorsolateral blotch from middle trunk; NDB = number of dorsal scales in the smallest distance between the dorsolateral blotch from middle trunk and the anterior blotch; KC = keels with the same color as dorsal scales; BI = blotches in the interspaces between two consecutive dorsolateral blotches; BB = border of dorsolateral blotches; DPS = dorsal postcephalic stripes; M = melanic head; OS** = ornamentation of supralabials; EOS = extension of the ornamentation of supralabials. The values for each variable include mean ± standard deviation/range/n, respectively.

| Char | A | B | C | D | E | F | G |
|---|---|---|---|---|---|---|---|
| **IR** | 6.16+1.42/3-9/71 | 8.919+1.267/5-12/470 | 7.751+1.423/4-11/381 | 6.954+1.340/4-10/65 | 6.663+1.323/3-12/398 | 7.919+1.252/5-12/186 | 7.862+1.076/5-11/109 |
| **DC** | 23.1+2.63/17-31/70 | 26.287+2.026/21-33/471 | 25.253+2.174/19-31/375 | 23.646+2.253/19-29/65 | 25.253+2.102/20-32/388 | 25.916+2.327/19-33/179 | 25.294+1.712/21-30/109 |
| **S** | 7.95+0.39/7-9/71 | 8.056+0.525/6-11/468 | 7.992+0.475/6-10/377 | 8.000+0.395/7-10/65 | 7.921+0.464/6-10/394 | 8.137+0.454/7-10/183 | 8.064+0.477/7-10/109 |
| **IF** | 10.2+0.86/8-12/71 | 10.757+0.848/7-13/469 | 10.607+0.817/8-13/374 | 10.138+0.704/8-12/65 | 10.532+0.816/8-13/395 | 11.087+0.910/9-13/183 | 11.055+0.731/9-13/109 |
| **VF** | 168.541+6.049/154-182/37 | 173.011+5.500/161-193/273 | 176.451+5.075/159-194/215 | 168.676+5.943/158-182/34 | 177.492+4.071/162-187/236 | 179.779+3.993/168-190/104 | 176.661+4.121/169-188/59 |
| **VM** | 165.667+3.342/160-173/33 | 168.863+5.070/152-185/197 | 172.013+4.591/160-185/155 | 168.226+6.217/157-181/31 | 172.988+3.878/162-183/161 | 176.462+4.728/166-191/80 | 171.404+4.297/164-181/47 |
| **SCF** | 39.171+4.069/34-50/35 | 42.292+3.201/31-51/260 | 43.901+3.417/33-54 | 39.563+3.202/32-47/32 | 46.295+3.113/37-55/234 | 44.010+3.422/37-56/102 | 43.358+3.409/35-51/53 |
| **SCM** | 43.800+2.821/40-50/30 | 48.066+3.283/39-56/183 | 49.660+3.870/41-64/150 | 45.483+2.886/41-52/29 | 52.248+3.428/40-61/157 | 50.962+3.383/43-59/79 | 48.500+2.411/41-53/46 |
| **D1** | 23.3+1.44/20-28/71 | 26.472+1.630/21-32/464 | 24.786+1.841/19-31/370 | 24.138+1.540/21-28/65 | 24.378+1.452/20-30/392 | 25.430+1.689/20-34/186 | 25.132+1.685/21-30/106 |
| **D2** | 22.8+1.38/21-27/73 | 25.461+1.411/22-30/473 | 23.995+1.490/21-29/382 | 23.492+1.276/21-27/65 | 24.483+1.293/21-28/402 | 25.263+1.430/20-30/186 | 25.425+1.359/22-29/106 |
| **SSS1** | 1.17+0.38/1-2/69 | 1.865+0.389/1-3/466 | 1.612+0.494/1-3/340 | 1.524+0.503/1-2/63 | 1.497+0.506/1-3/390 | 1.796+0.456/1-3/181 | 1.887+0.350/1-3/97 |
| **SSS2** | 1.18+0.39/1-2/69 | 1.732+0.467/1-3/466 | 1.541+0.511/1-3/340 | 1.381+0.490/1-2/63 | 1.497+0.506/1-3/390 | 1.818+0.428/1-3/181 | 1.784+0.438/1-3/97 |
| **SSS3** | 1.73+0.44/1-2/69 | 2.140+0.377/1-3/465 | 2.018+0.392/1-3/338 | 1.889+0.406/1-3/63 | 2.000+0.296/1-3/390 | 2.083+0.348/1-3/181 | 2.082+0.312/1-3/97 |
| **DB** | 25.2+4.20/18-35/64 | 20.545+2.153/14-29/468 | 17.564+2.710/3-25/369 | 20.629+2.847/16-29/62 | 22.212+2.757/16-33/405 | 20.716+2.755/10-28/183 | 22.971+2.864/17-35/103 |
| **SHB*** | 1.508+0.321/1-2.5/28 | 2.777+1.287/1-8/226 | 1.912+0.719/1-7/103 | 1.572+0.264/1.2-2.333/47 | 2.292+0.940/1.2-7/171 | 3.814+2.189/1.25-14/177 | 2.463+1.040/1-6/98 |
| **RDB** | 4.571+0.573/4-6/28 | 6.133+0.736/4-9/226 | 4.922+0.682/3-7/103 | 5.128+0.969/4-10/47 | 5.439+0.841/3-8/171 | 6.068+0.788/4-8/177 | 5.939+1.200/4-12/98 |
| **NDB** | 2.963+1.344/1-7/27 | 3.296+1.191/0-9/226 | 5.136+1.766/2-16/103 | 3.234+1.237/1-6/47 | 2.965+1.106/0-7/171 | 2.503+1.188/0-6/177 | 3.000+0.854/1-5/97 |
| **KC** | white keels | present | present | present or white keels | present | present | present |

*Table 1 - continued.*

| Char | A | B | C | D | E | F | G |
|---|---|---|---|---|---|---|---|
| **BI** | present or absent | present | present or absent | present or absent | present | present | present |
| **BB** | diffuse | defined | diffuse or defined | Diffuse | defined | defined | defined |
| **DPS** | absent | short | absent | Absent | absent | long | short |
| **M** | absent | absent | present | Absent | absent | absent | absent |
| **OS**** | 2 | 1 | 0 | 0 | 3 | 3 | 4 |
| **EOS** | posterior half | all | all | All | anterior half | anterior half | all |

*SHB estimated by the ratio between the number of dorsal scales forming the inferior margin of the dorsolateral blotch from middle trunk and the number of dorsal scales that form the superior margin of the same blotch.

**0 = without blotches; 1 = with large round white blotches; 2 = with vertically elongated white blotches; 3 = with large dark blotches (covering more than half of supralabial surface), the largest blotch is directly beneath the eye; 4 = with small dark brown triangular blotches (covering less than half of supralabial surface), always situated throughout the suture between two supralabials.

Populations or lineages can be independent, even though some their individuals hybridize. Therefore, the presence of some intermediary specimens do not impede the segregation of two lineages. What prevents this segregation is a wide and intense gene flow. If the gene flow was wide and intense, there is not formation of recognizable discrete units. If the multivariate analysis based on a conjunct of morphological characters obtained recognizable discrete patterns, it was considered a evidence that those patterns are isolated in nature, even though 3 or 4 intermediary specimens be present. It is essential to name those patterns in order to a reference framework allow other studies (molecular, larger samples, and/or different morphological characters) testing the independence among the patterns hypothesis.

In taxonomic complex of continental distribution as *B. neuwiedi* complex the reproductive isolation between remote popoulations (as patterns A and G, for instance) is almost certain. The problem is in close different populations and in the presence of specimens with intermediary phenotype. It is the classical case of the subspecies concept problem. Historically, the subspecies idea was born among ornithologists and lepidopterists of museums at the turn of the 20th century: "a population occupying a definite geographic area, throughout which it intergrades over short distances with similar populations occupying adjacent areas". This concept, however, when applied in practice, suffered abuses such as 1) the idea that subspecies are subordinated to a species; 2) the consideration of subspecies as "incipient" species; 3) the use of subspecies as synonym of variety; 4) the use of subspecies designations for insular populations (Vanzolini 1986, 1992). The misinformation resulting from the arbitrary use of this category resulted in some authors suggesting that it lost its sense (Wiley 1978, 1981) and would be abandoned (Wilson and Brown 1953, Frost *et al*. 1992). In view of the criticisms of the subspecies concept, we do not plan to recognise subspecies within the *B. neuwiedi* complex.

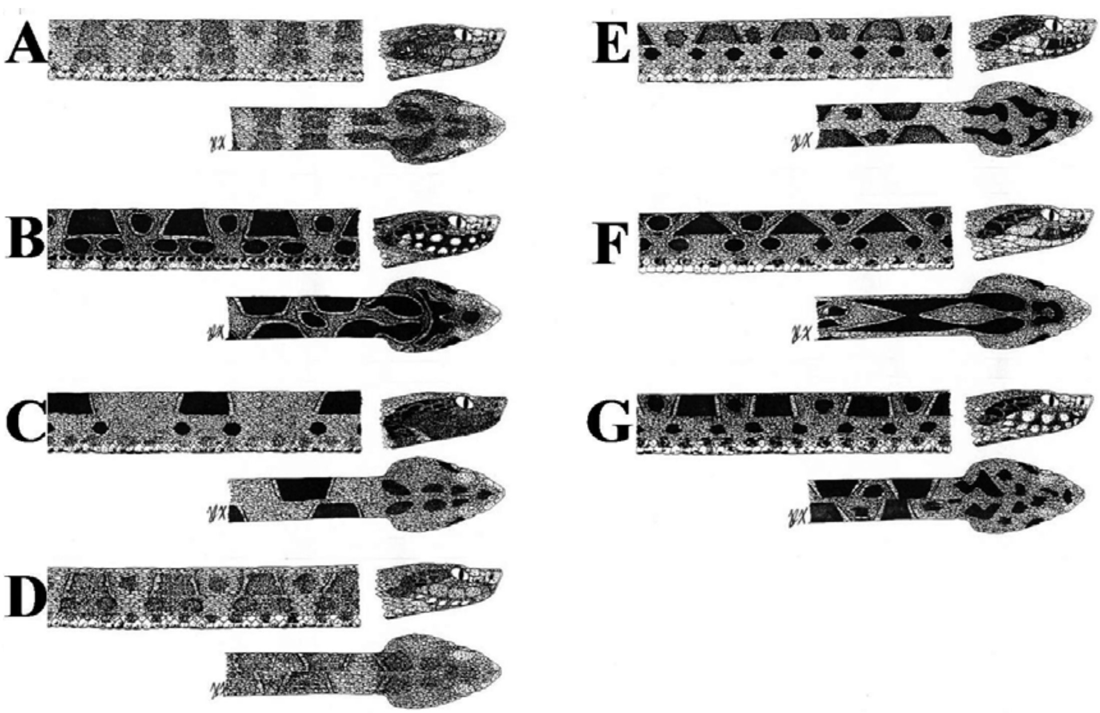



**Figure 1 -** Morphological patterns A-G of the *Bothrops neuwiedi* complex. Lateral view of the midbody, lateral and dorsal view of the head.

Wagler (1824) described *Bothrops neuwiedi*, recording as the type-locality the "province of Bahia", which in fact corresponds to the State of Bahia, Brazil (Peters and Orejas-Miranda 1970, 1986, Hoge and Romano-Hoge 1981a, b, Grantsau 1991, Romano-Hoge 1996; Vanzolini 1996). No holotype was designated; Hoogmoed and Gruber (1983) identified the male ZSM-2348/0, from Spix collection in the Museum of Natural History of München (Germany), as the lectotype of *Bothrops neuwiedi* Wagler, 1824. This specimen, collected by J. B. Spix in Brazil, had no label to confirm its exact origin, but is very similar to the specimen of plate XXII, fig. 1 of Wagler (1824), particularly the position of the mouth and fangs (Hoogmoed and Gruber 1983). Access to the photographs of this specimen (Figure 11) and surveyed characteristics for Hoogmoed and Gruber (1983) allowed us to conclude that this lectotype presents pattern B. Figure 11 shows two arrays of scales between the subocular and the 4$^{th}$ supralabial, borders of the dorsal spots with well marked contours and vestiges of the characteristic large spherical white spots in the supralabials of this pattern.

Among the individuals that presented pattern A, there is type-material of three formal taxa: *Lachesis lutzi* Miranda-Ribeiro, 1915 (holotype AL 5337 from Santa Maria da Vitória, Rio Corrente, BA) (Figure 12A-B), *Bothrops iglesiasi* Amaral, 1923 (holotype IBSP 561 from Regeneração, PI and the paratypes IBSP 551-560, IBSP 562, IBSP 563, IBSP 565-568, IBSP 3100 from Regeneração, PI; IBSP 1673 from Fazenda Grande, right edge from Rio Gurguéia, PI; IBSP 1285 from Teresina, PI) and *Bothrops neuwiedii*

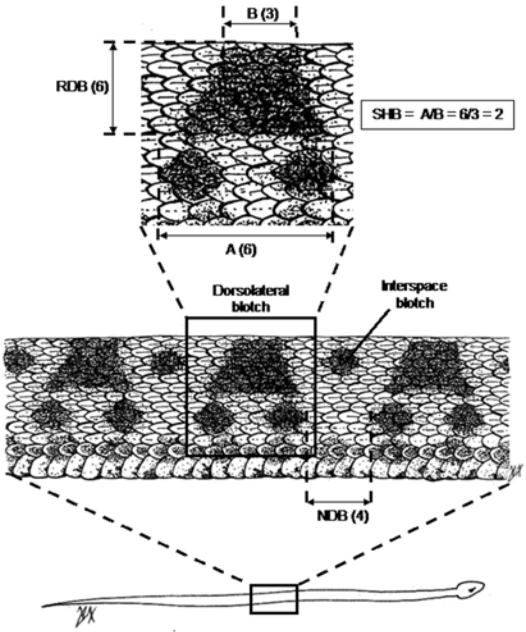



**Figure 2** - Lateral view of the midbody of the *Bothrops neuwiedi* complex. SHB = shape of the dorsolateral blotch from middle trunk; RDB = rows of dorsal scales that form the principal part of dorsolateral blotch from middle trunk; NDB = number of dorsal scales in the smallest distance between the dorsolateral blotch from middle trunk and the anterior blotch. SHB is estimated by the ratio between the number of dorsal scales that form the lower margin of the dorsolateral blotch from middle trunk (A) and the number of dorsal scales that form the superior margin of the same blotch (B).


**Figure 3** - Distribution map of the seven patterns (A-G) of the *Bothrops neuwiedi* complex in South America subdivided in three areas for PCA analysis. Black triangles = pattern A, white circles = pattern B, white squares = pattern C, white stars = pattern D, black circles = pattern E, white triangles = pattern F, black squares = pattern G.

*piauhyensis* Amaral, 1925 (holotype IBSP 1672 from Fazenda Grande, right edge from Rio Gurguéia, PI) (Figure 12C to F). A principal components analysis (PCA) including males of these three taxa (the number of females was low) did not separate these specimens (Figure 13).

Among the specimens with pattern B are the holotypes of the following subspecies: *Bothrops neuwiedii bahiensis* Amaral, 1925 (IBSP 3012 from Itiúba, BA) (Figure 14A-B), *B. neuwiedii*

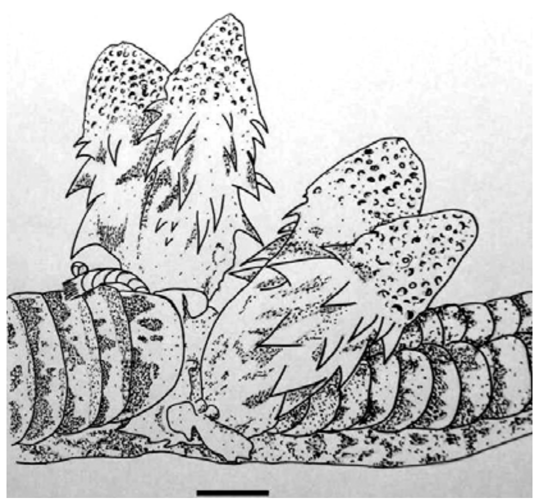


**Figure 4** - Hemipenis of *Bothrops neuwiedi* (MZUSP 4917), asulcate side. Line = 5mm.

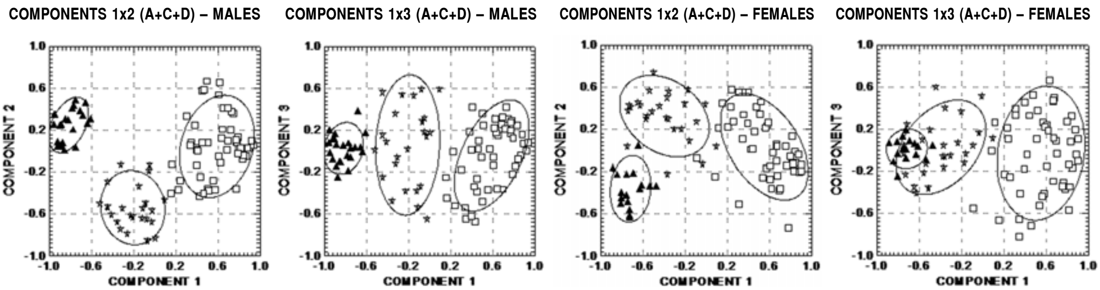



**Figure 5** - PCA graphs with combinations of components 1x2 and 1x3 for males and females of the patterns A, C, and D. Black triangles = pattern A, white squares = pattern C, white stars = pattern D.

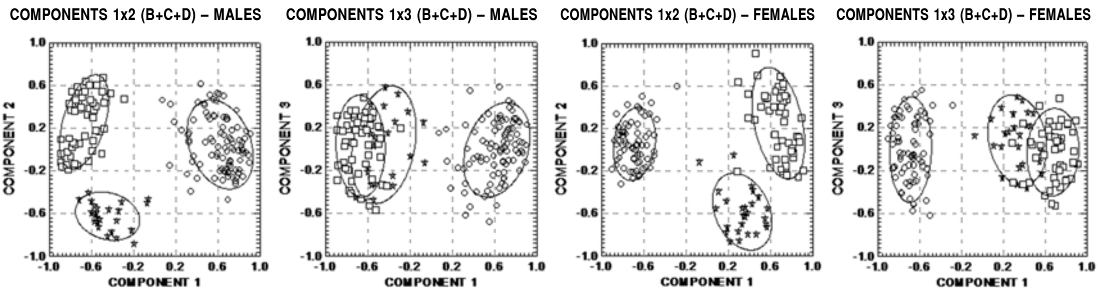



**Figure 6** - PCA graphs with combinations of components 1x2 and 1x3 for males and females of the patterns B, C, and D. White circles = pattern B, white squares = pattern C, white stars = pattern D.

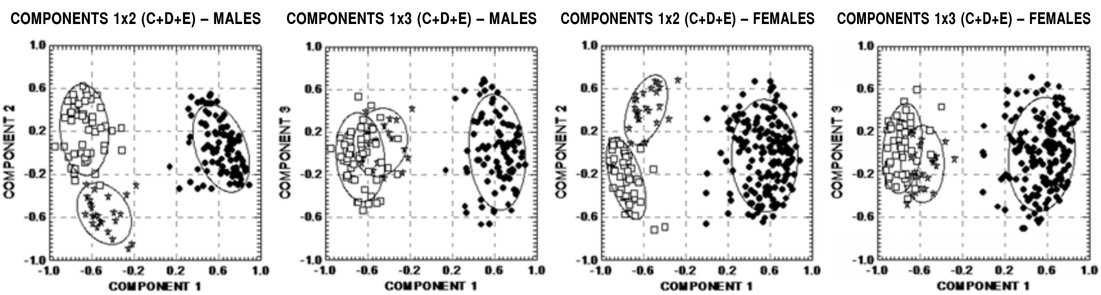



**Figure 7** - PCA graphs with combinations of components 1x2 and 1x3 for males and females of the patterns C, D, and E. White squares = pattern C, white stars = pattern D, black circles = pattern E.

*minasensis* Amaral, 1925 (IBSP 3015 from Antônio Justiniano, MG) (Figure 14C-D), *B. neuwiedii fluminensis* Amaral, 1933b (IBSP 7806 from Barcelos, RJ and the paratypes IBSP 6154, IBSP 6402, IBSP 7424, IBSP 7602, IBSP 7603, IBSP 7604 from São Sebastião of Campos, RJ) (Figure 14E-F), *B. neuwiedii goyazensis* Amaral, 1925 (IBSP 3016 from Ipameri, GO) (Figure 14G-H) and *B. neuwiedii paranaensis* Amaral, 1925 (IBSP 3014 from Castro, PR) (Figure 14I-J).

One of the individuals analyzed with pattern C is the holotype of *Bothrops neuwiedii pauloensis* Amaral, 1925 (IBSP 3013 from

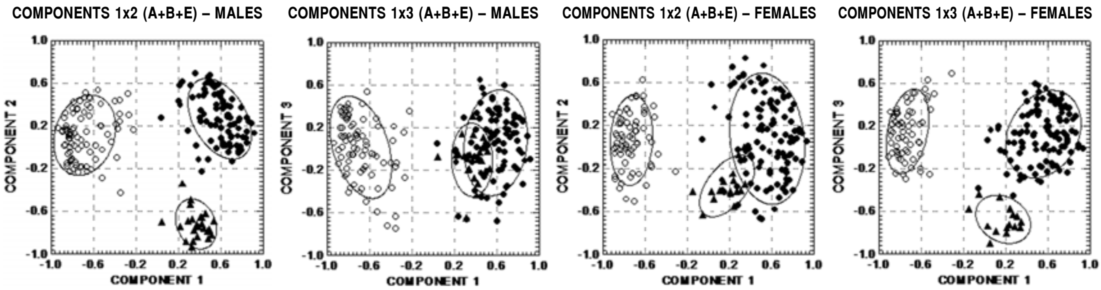



**Figure 8** - PCA graphs with combinations of components 1x2 and 1x3 for males and females of the patterns A, B, and E. Black triangles = pattern A, white circles = pattern B, black circles = pattern E.

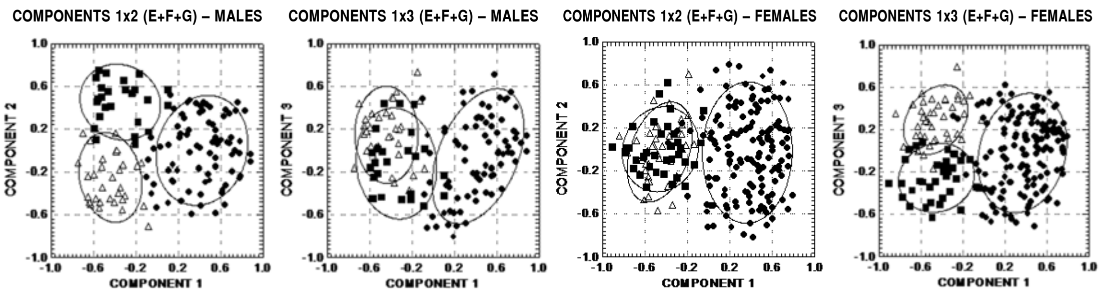



**Figure 9** - PCA graphs with combinations of components 1x2 and 1x3 for males and females of the patterns E, F, and G. Black circles = pattern E, white triangles = pattern F, black squares – pattern G.

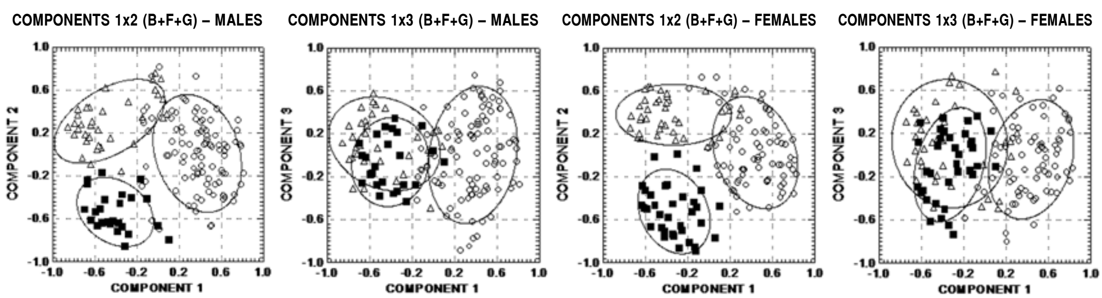



**Figure 10** - PCA graphs with combinations of components 1x2 and 1x3 for males and females of the patterns B, F, and G. White circles = pattern B, white triangles = pattern F, black squares – pattern G.

Leme, SP) (Figure 15A-B). No type-material was associated with pattern D. Among the samples with pattern E are the holotype of *Bothrops neuwiedii mattogrossensis* Amaral, 1925 (IBSP 3011 from Miranda, MS) (Figure 15C-D) and the paratype of *Bothrops neuwiedii boliviana* Amaral, 1927 (MZUSP 6478 from Buenavista, Provincia de Sara, Departamento de Santa Cruz, BOL) (Figure 15E-F). In the case of pattern F were included the holotype of *Bothrops neuwiedii meridionalis* Amaral (1930c) (IBSP 5316 from Embarcación, Salta), and the paratypes from Argentina (IBSP 5317 from Charata, Chaco; IBSP 5318 from Km 151,

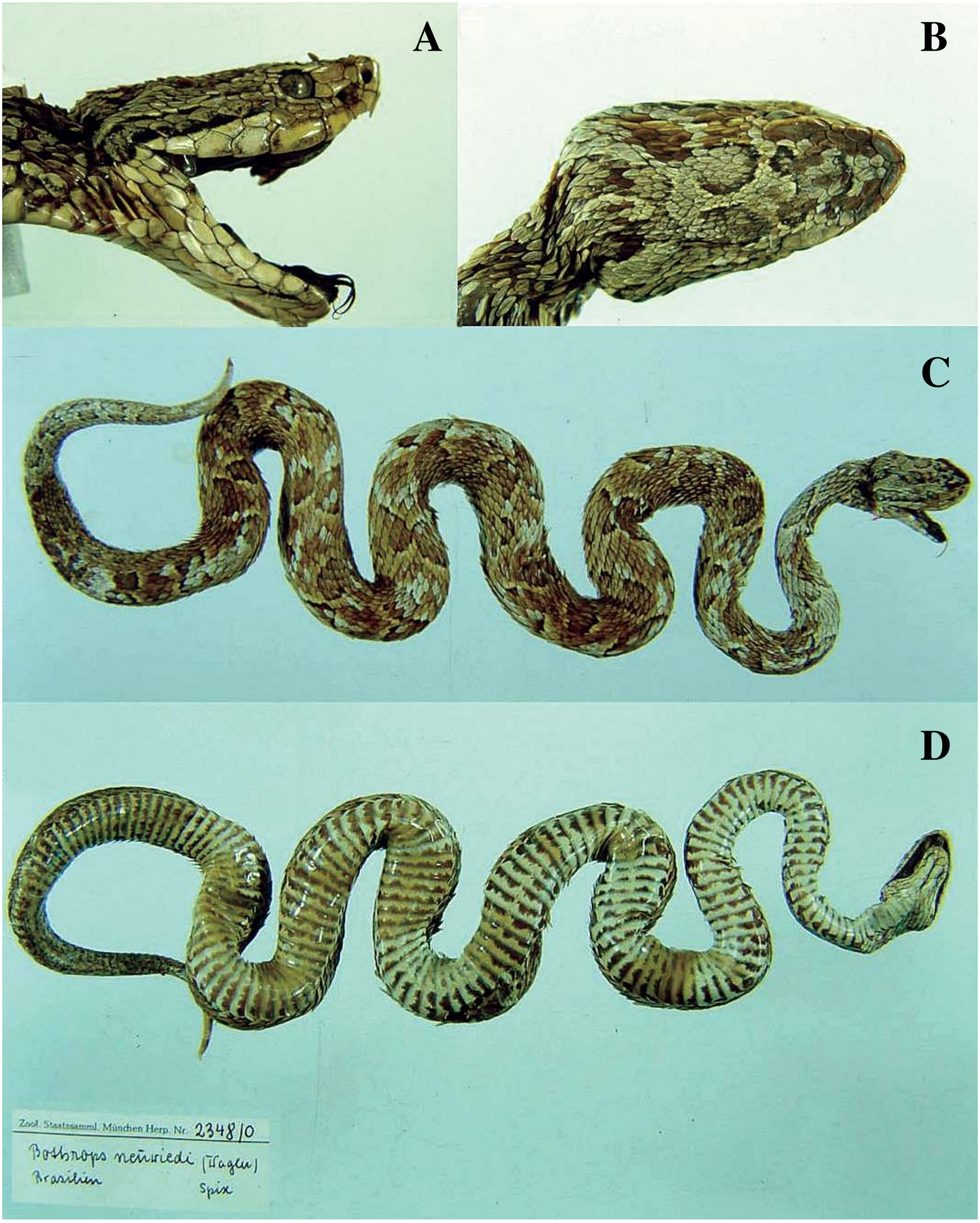



**Figure 11** - Lectotype of *Bothrops neuwiedi* Wagler, 1824 from Zoologische Staatssammlung München (ZSM), München, Germany. Male specimen ZSM 2348/0, colected in Brazil by J. B. Spix. A) Lateral view of the head. B) Dorsal view of the head. C) Dorsal view of the body. E) Ventral view of the body. Photographs by M. Müller.

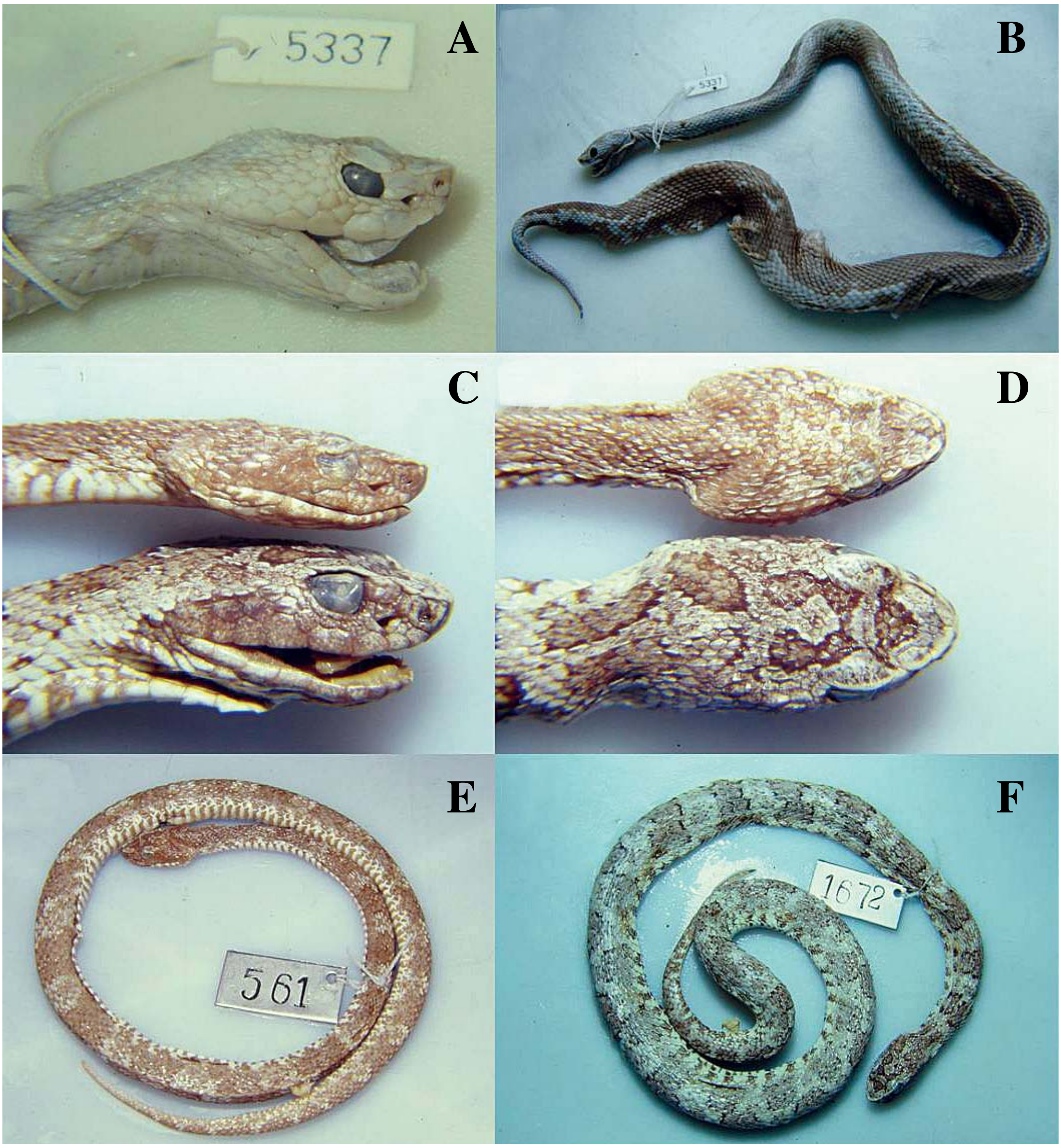



**Figure 12** - Type-material associated to pattern A. A) Lateral view of the head of the holotype of *Lachesis lutzi* Miranda-Ribeiro, 1915 (AL-5337 from Santa Maria, Rio Corrente, BA). B) General view of the holotype of *Lachesis lutzi* Miranda-Ribeiro, 1915. C) Lateral view of the head of the holotypes of *Bothrops iglesiasi* Amaral, 1923 (IBSP-561 from Regeneração, PI, up) and *Bothrops neuwiedi piauhyensis* Amaral, 1925 (IBSP-1672 from Fazenda Grande, right edge of Rio Gurguéia, PI, down). D) Dorsal view of the head of the holotypes of *Bothrops iglesiasi* (up) and *Bothrops neuwiedi piauhyensis* (down). E) General view of the holotype of *Bothrops iglesiasi*. F) General view of the holotype of *Bothrops neuwiedi piauhyensis* (down).

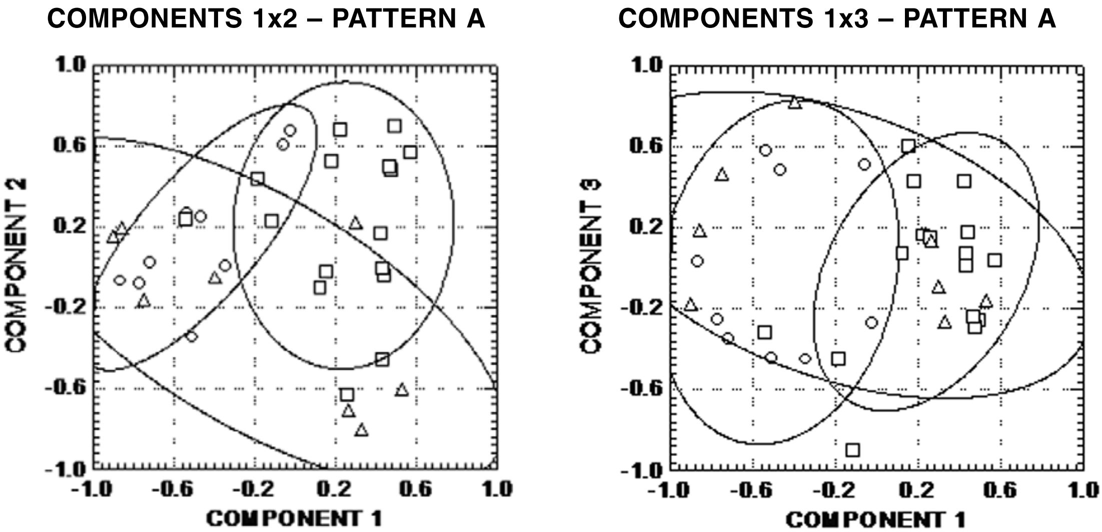



**Figure 13** - PCA graphs with combinations of components 1x2 (left) and 1x3 (right) for males with pattern A. White circles = *Bothrops iglesiasi*, white squares = *Lachesis lutzi*, white triangles = *Bothrops neuwiedii piauhyensis*.

Formosa; IBSP 5319 from Cordoba; IBSP 5320 from Km 644, Santiago del Estero; IBSP 5321 from Villa Alberdi, Tucumán) (Figure 15G-H). The type-material that presented pattern G was the holotype of *Bothrops neuwiedii riograndensis* Amaral, 1925 (MZUSP 1476 from Itaqui, RS in the area 2) (Figure 11I-J).

*Attribution of names*

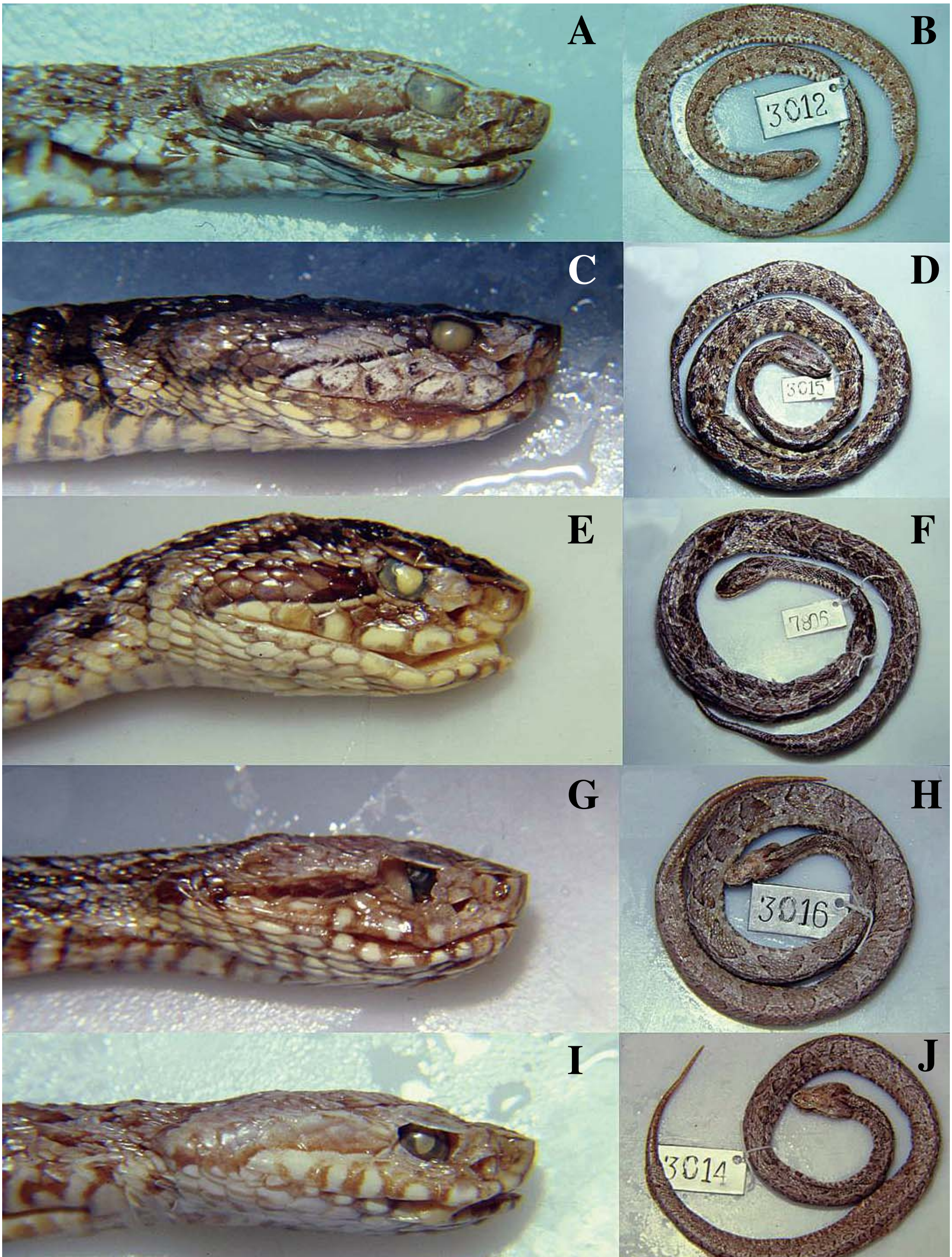
Pattern B

In 1884, Lacerda described *Bothrops urutu* from "province of Minas Gerais", but the holotype was never found (McDiarmid *et al.* 1999). *Bothrops atrox meridionalis* was described by Müller in 1885 from Andaraí, RJ. As the holotype was not designated, Golay and collaborators (1993) reported the NMBA 2564 specimen (Naturhistorisches Museum Basel, Switzerland) from Andaraí as the lectotype.

In 1925 Amaral described *Bothrops neuwiedii minasensis*, *Bothrops neuwiedii bahiensis*, *Bothrops neuwiedii goyazensis* and *Bothrops neuwiedii paranaensis* among other subspecies of the group. However, the type-locality of the first subspecies was mistakenly identified as Francisco Justiniano, MG, instead of Antônio Justiniano, MG. The analysis of the respective holotypes showed that all presented pattern B.

Amaral (1933b) also described *Bothrops neuwiedii fluminensis* from the eastern State of Rio de Janeiro. The holotype and paratypes analyzed also showed pattern B. In 1937, Amaral described *Bothrops urutu* Lacerda, 1884 as *Bothrops neuwiedii urutu*, having *Bothrops*

**Figure 14** - Type-material associated to pattern B. Lateral view of the head (left) and general view of the body (right). A-B) Holotype of *Bothrops neuwiedii bahiensis* Amaral, 1925 (IBSP-3012 from Itiúba, BA). C-D) Holotype of *Bothrops neuwiedii minasensis* Amaral, 1925 (IBSP-3015 from Antônio Justiniano, MG). E-F) Holotype of *Bothrops neuwiedii fluminensis* Amaral, 1933b (IBSP-7806 from Barcelos, RJ). G-H) Holotype of *Bothrops neuwiedii goyazensis* Amaral, 1925 (IBSP-3016 from Ipameri, GO). I-J) Holotype of *Bothrops neuwiedii paranaensis* Amaral, 1925 (IBSP-3014 from Castro, PR).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*neuwiedii minasensis* Amaral, 1925 as synonym. Hoge, in 1966, described *Bothrops atrox meridionalis* Müller, 1885 as *Bothrops neuwiedi meridionalis* and placed *Bothrops neuwiedii fluminensis* Amaral, 1933b in its synonymy. Therefore, *Bothrops neuwiedi* Wagler, 1824 was the first available name for specimens presenting pattern B; the other mentioned names were included in its synonymy. After Hoge (1966), the use of "*neuwiedi*" with one "i" was retoken, as originally proposed.

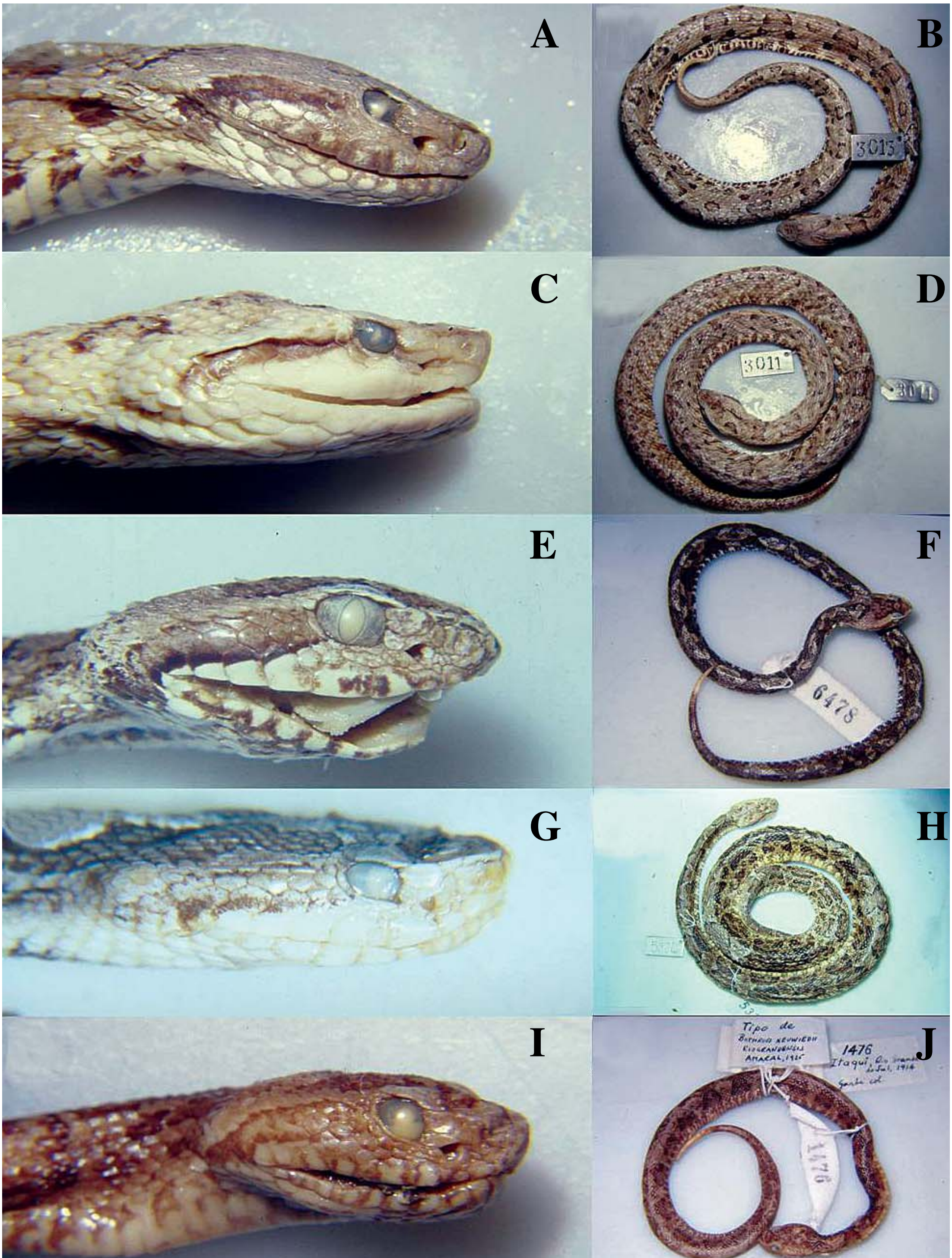
Pattern A

Miranda-Ribeiro described *Lachesis lutzi* in 1915. The analysis of the holotype and of the author's description confirmed that the specimen has pattern A. Despite the extremely discolored aspect of this specimen, the excellent description of Miranda-Ribeiro is sufficient for a certain identification. Some of the characteristics of this pattern included the unique array of scales between the subocular and the 4$^{th}$ supralabial; intermediate intersupraoculars tending to increase or coalesce; characteristic ornamentation of the supralabials and white keels in some scales. Additionally, spots whose borders are already few marked as in pattern A tend to lose coloration more easily, hence the whitish aspect of the holotype (Figure 12A-B).

In 1923, Amaral described *Bothrops iglesiasi*. Holotype and paratypes presented pattern A. *Bothrops neuwiedii piauhyensis* described by Amaral in 1925 also possessed pattern A. It has been suspected that *B. iglesiasi* and *B. n. piauhyensis* could be synonymous (Campbell and Lamar 1989). These taxa were previously known from few specimens, and were described from very close localities in the State of Piauí, based on specimens collected by Francisco Iglésias, for the Instituto Butantan, from 1912 to 1919 (Iglésias 1958a, b). One of the paratypes of *B. iglesiasi* (IB 1673), for example, is from the same locality of the *B. n. piauhyensis* holotype (IB 1672). However, the most confusing report suggesting the synonymy of these two taxa is in Brazil (1996). According to this author, after the removal of Afrânio do Amaral from the Instituto Butantan because of several irregularities, two notebooks of the deceased João Florêncio Gomes were found in a closet. In one notebook, several new species of snakes were described, including *Lachesis iglesiasi* dated on 1913. However, in another notebook, João Florêncio Gomes changed the classification that originally referred to *Lachesis iglesiasi*, inserting "*neuwiedi* var.". Doubt about whether this pattern represented a new species or a variety of *Bothrops neuwiedi* may explain why Gomes postponed publishing data on this species. Amaral (1923) nevertheless published the description of *B. iglesiasi* after Gomes died, without any mention of him. These aspects and the analysis of the *B. n. piauhyensis* and *B. iglesiasi* holotypes, both presenting pattern A, allowed for the synonymy of the two taxa (Figure 12C-F).

In 1925, Amaral located *Bothrops neuwiedii neuwiedii* as a subspecies considered common in the low and humid region of southern Rio Paraguaçu, in the Recôncavo Baiano, close to the capital of the State of Bahia. Although the

**Figure 15 –** Type-material associated to patterns C, E, F and G. Lateral view of the head (left) and general view of the body (right). A-B) Holotype of *Bothrops neuwiedii pauloensis* Amaral, 1925 (IBSP-3013 from Leme, SP). C-D) Holotype of *Bothrops neuwiedii mattogrossensis* Amaral, 1925 (IBSP-3011 from Miranda, MS). E-F) Paratype of *Bothrops neuwiedii boliviana* Amaral, 1927 (MZUSP-6478 from Buenavista, Província de Sara, Departamento de Santa Cruz, BOL). G-H) Paratype of *Bothrops neuwiedii meridionalis* Amaral, 1930c (IBSP-5320 from Santiago del Estero, km 644, ARG). I-J) Holotype of *Bothrops neuwiedii riograndensis* Amaral, 1925 (MZUSP-1476 from Itaqui, RS).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author presented the pholidosis data for 26 individuals, he did not designate any type-material, rendering the recognition of this subspecies uncertain. However, the recent collection of two specimens from Camaçari and one from Dias D'Ávila, both localities from the Recôncavo da Bahia, showed that pattern A is the present pattern in the area. Therefore, it is possible to attribute this pattern to *Bothrops neuwiedii neuwiedii* Amaral, 1925. In the same work, Amaral also described *Bothrops neuwiedii bahiensis* (synonym of *Bothrops neuwiedi* Wagler, 1824, as was previously demonstrated), but mistakenly considered it a synonym of *Lachesis* (*Bothrops*) *lutzi* (Miranda-Ribeiro, 1915). Amaral (1930a) then renamed *Lachesis* (*Bothrops*) *lutzi* (Miranda-Ribeiro, 1915) as *Bothrops neuwiedii lutzi*, with *Bothrops neuwiedii bahiensis* Amaral, 1925 as synonym. Of the names presented, *Bothrops lutzi* (Miranda-Ribeiro, 1915) has priority on others to refer to the animals that possess pattern A.

<u>Pattern C</u>

Amaral also described *Bothrops neuwiedii pauloensis* in 1925. The examined holotype presented pattern C. However, probably due to the long conservation period, this sample did not show the characteristic lateral melanization of the head, although the supralabials had a certain dark pigmentation (Figure 15A-B). The whitish spots in some supralabials represent an occasional variation of pattern C and differ from the great spherical white spots characteristics of pattern B (Figure 14). In pattern B, the pigmented portions are darker and the borders of the white spots in the supralabials are well defined. The pair of occipital spots tend to be longer in pattern B than C. The unique name available to refer to the animals with pattern C is *Bothrops pauloensis* Amaral, 1925.

<u>Pattern D</u>

No available name was associated with the specimens that presented pattern D. Perhaps, the intention of Amaral (1925) was to name such individuals when describing *Bothrops neuwiedii goyazensis* from Ipameri, GO. In fact, pattern D is the most common pattern in the occurrence area of this subspecies, including the type-locality. However, Ipameri was precisely one of the places that showed sympatry of individuals with different patterns (B and D). As previoulsly mentioned, the holotype chosen by Amaral possessed pattern B, for which the oldest available name is *B. neuwiedi*. Therefore, animals with pattern D represent a new species, which will be described below.

<u>Pattern E</u>

In 1925, Amaral also described *Bothrops neuwiedii mattogrossensis*. Despite the discolored aspect of this holotype (Figure 15C-D), it was possible to associate this specimen with pattern E. In addition, the type-locality (Miranda, MS) presented a wide variety of specimens, all with pattern E, without exception. This pattern was predominant also in areas close to Miranda, MS. In 1927, Amaral described *Bothrops neuwiedii boliviana*. The holotype (CM 2728 from Buenavista, Provincia de Sara, Departmento de Santa Cruz, Bolivia) and a wide variety of paratypes (Amaral 1927 and Griffin 1916) are in the Carnegie Museum (Pennsylvania, USA). One of the analyzed paratypes (MZUSP 6478) also presented pattern E with the characteristic spot of the supralabial under the eye, as well as other studied specimens from Bolivia (Figure 15E-F). Hoge (1966) modified the orthography of this name for *Bothrops neuwiedi bolivianus*. The individuals from Humaitá, in the State of Amazonas, erroneously identified as *B. neuwiedi neuwiedi* (Hoge and Romano-Hoge 1981b) also presented pattern E.

Some specimens from western distribution presented discolored body blotches and whitish general coloration. This also seems to be the case of the samples from Serranía Huanchaca, Santa Cruz, Bolivia, identified as *B. n. bolivianus* (Fig. 233, page 255 in Campbell and Lamar 1989) and of the individual from

Planalto de Alta Lídia, in the State of Rondônia (Fig. 17, page 76 in Silva 1993). In the future, these animals can be considered a new species. However, in similar way, some completely melanic specimens were also found in some localities. These anomalies of the general body pigmentation, sometimes darkening, an at other times making the specimens appear clear, are seemly more common in this pattern. These individuals were attributed to pattern E. Therefore, at this moment, judging conservatively, such forms were not considered a new species. In the future, larger samples may demonstrate the contrary. *Bothrops matto-grossensis* Amaral, 1925 is the oldest available name for animals with pattern E.

Pattern F

In 1862, Cope described *Bothrops diporus*, based on samples from the region of the Rio Vermejo, on the border of Paraguay and Argentina, maintained in the collection of National Museum of Natural History, in Washington, USA (holotype USNM 12380, formerly USNM 5401). Amaral (1930c) described *Bothrops neuwiedii meridionalis*, based on specimens from several locations in Argentina. Although the holotype and paratypes were quite discolored, they appeared to present pattern F (Figure 15G-H). The name proposed by Amaral (1930c), however, was already proposed for *Bothrops atrox meridionalis* Müller, 1885, which entered in the synonymy of *Bothrops neuwiedi* Wagler, 1824 (pattern B). In 1961, Cochran renamed *Bothrops diporus* Cope, 1862 as *Bothrops neuwiedii diporus*. In 1966, Hoge placed *Bothrops neuwiedii meridionalis* Amaral, 1930c in the synonymy of *Bothrops neuwiedi diporus* Cope, 1862. Consequently, specimens with pattern F should be referred to as *Bothrops diporus* Cope, 1862.

Pattern G

In 1870, Cope also described *Trigonocephalus* (*Bothrops*) *pubescens* based on a specimen captured by the Thayer expedition in the State of Rio Grande do Sul. No holotype was designated, but the description previously mentioned the characteristic markings in form of bars in the supralabials. In 1925, Amaral described *Bothrops neuwiedii riograndensis*. The holotype presented pattern G (Figure 15I-J). In 1959, Hoge classified *Trigonocephalus* (*Bothrops*) *pubescens* (Cope, 1870) as *Bothrops neuwiedii pubescens*, with *Bothrops neuwiedii riograndensis* Amaral, 1925 as synonym. Therefore, the name available to identify pattern G is *Bothrops pubescens* (Cope, 1870).

## Redescription of the species in alphabetical order

*Bothrops diporus* Cope, 1862, status nov.
(Figures 1F, 15G-H)

*Bothrops diporus* Cope, 1862: 347.

*Bothrops neuwiedii meridionalis* Amaral, 1930c: 66, fig. 1.

*Bothrops neuwiedii diporus* Cochran, 1961: 151.

*Bothrops neuwiedi diporus* Hoge, 1966 [1965]: 128.

Holotype - USNM 12380 (old USNM 5401). Type-locality: region of Rio Vermejo, border between Paraguay and Argentina. Specimen collected by La Plata Expedition.

Diagnosis - Prolonged postcephalic stripes present, a resultant coalition of the occipital blotches with the first pair of dorsolateral blotches of the trunk. Supralabials evenly pigmented or with large dark markings (covering more than 50% of the supralabial surface) more conspicuous in the anterior half of the mouth; the largest spot is exactly under the eye. The borders of the dorsolateral blotches have well defined contours. Dorsolateral blotches in the trunk: 10 to 28 (mode 21); usually triangular, wide and close to each other.

Description - Blunt rostral, in contact with internasals, nasals and first pair of supralabials. Internasals and canthals of the same size, in contact, a little larger than scales that separate the nasals, which are a little larger than dorsals of the head-rest. Canthals usually separate from the large and ovoid supraoculars for one scale. Second supralabial separated from prelacunal. Intersupraocular rows 5 to 11 (mode 8); 19 to 33 scales in the sagital line beginning after internasals and ending at the level of the rictal region (mode 25); 1 or 2 arrays of scales between the subocular and the 4th supralabial (mode 2); supralabials 6 to 11 (mode 8); infralabials 7 to 13 (mode 11). Dorsals in the beginning of the trunk 20 to 29 (mode 24); 20 to 29 dorsals in the half of the trunk (mode 25); 173 to 189 ventrals for females; 166 to 187 ventrals for males; 38 to 56 subcaudals for females; 44 to 59 subcaudals for males. Keel coloration equal to the coloration of the dorsal scales. Borders of the dorsolateral blotches of well defined contours, detaching them from the ground color. Blotches in the interspaces between two consecutive dorsolateral blotches usually present. Occipital blotches exceeding the line of the quadrate-mandibular articulation and joining the first pair of dosrolateral blotches, forming long postcephalic stripes. Postocular stripe with a medium width of three scales extends from the eye to the line of the labial fissure. Absence of melanism in the head. Supralabials evenly pigmented or with great dark markings (covering more than 50% of the supralabial surface) more conspicuous in the anterior half of the mouth; the largest mark is exactly under the eye. Sometimes these spots occupy the totality of the anterior supralabials, resulting in a mouth with a dark anterior half and a clear posterior half. Dorsolateral blotches in the trunk 10 to 28 (mode 21). Dorsolateral blotch from middle trunk with 1 to 5 scales in the superior margin (mode 2); 3 to 8 arrays of scales in the height of the principal part (mode 6); 4 to 9 scales in the lower margin of the principal part (modes 5 and 6); 3 to 13 arrays of scales in total height (mode 10); 5 to 14 scales in the total width (mode 7) and 0 to 6 scales separate this blotch of the anterior and posterior blotches (mode 2). Ground coloration varying from the light brown to the dark brown. Dorsolateral blotches are dark brown to black. Borders of the principal part of the dorsolateral blotches can present white margins. Ventrals usually more immaculate than in the other species.

Individual variation - Abalos and Baez (1963) described the wide variety of drawings in the spots of this species in the Province of Santiago del Estero, Argentina.

Geographic distribution (Figure 3) - Occurs in Argentina, in the Provinces of La Rioja, La Pampa, Cordoba, San Luis, Mendoza, Catamarca, Santiago del Estero, Tucumán, Jujuy, Salta, Formosa, Chaco, Santa Fé, Corrientes and Misiones (Freiberg 1939, Abalos and Bucher 1970, Abalos and Mischis 1975; Di Tada and Abalos 1976; Cei 1987). This species also occurs in Paraguay (Cei 1987) and Brazil, in the southern State of Mato Grosso do Sul and western States of São Paulo, Paraná, Santa Catarina and northwestern Rio Grande do Sul.

*Bothrops lutzi* (Miranda-Ribeiro, 1915), status nov.
(Figures 1A, 12)

*Lachesis lutzi* Miranda-Ribeiro, 1915: 4, pl.
*Bothrops iglesiasi* Amaral, 1923: 97.
*Bothrops neuwiedii neuwiedii* Amaral, 1925: 57.
*Bothrops neuwiedii piauhyensis* Amaral, 1925: 58, pl.14 (fig. 2), pl. 15 (fig. 2).
*Bothrops lutzi* Amaral, 1925: 57.
*Bothrops neuwiedii lutzi* Amaral, 1930a: 114.
*Bothrops neuwiedi neuwiedi* Hoge, 1966 [1965]: 127.
*Bothrops neuwiedi lutzi* Hoge, 1966 [1965]: 128.
*Bothrops neuwiedi piauhyensis* Hoge, 1966 [1965]: 129.

Holotype - AL 5337, adult female. Type-locality: Santa Maria, Rio Corrente (present

Santa Maria da Vitória): Bahia: Brazil. Specimen collected by Adolpho Lutz, in 1912, in an expedition in Rio São Francisco.

Diagnosis - Supralabials ornamented with small white spots prolonged vertically and usually more conspicuous in the posterior half of the mouth. Keels of some dorsal scales with characteristic white coloration. Borders of the dorsolateral blotches of little defined contour, usually forming transverse saddles where it is difficult to see the pair of secondary blotches of the dorsolateral blotches. One array of scales between the subocular and the $4^{th}$ supralabial. Central intersupraoculars with tendency to the increase or coalesce. Postocular stripe faintly defined. Dorsolateral blotches frequently of trapezoid format, narrow and close to each other, varying from 20 to 35 (modes 21 and 24).

Description - Blunt rostral, in contact with internasals, nasals and first pair of supralabials. Internasals and canthals of same size, in contact, a little larger than scales that separate the nasals, which are a little larger than dorsals of the rest of the head. Canthals usually separate from the large and ovoid supraoculars for one scale. Second supralabial separated from prelacunal. Intersupraocular rows 3 to 9 (mode 6), central intersupraoculars usually increased or fused; 17 to 30 scales in the sagital line beginning after internasals and ending at the level of rictal region (mode 24); usually one array of scales between the subocular and the $4^{th}$ supralabial; supralabials 6 to 11 (mode 8); infralabials 7 to 13 (mode 11). Dorsals in the beginning of the trunk 20 to 26 (mode 23); 21 to 25 dorsals in the half of the trunk (mode 23); 159 to 179 ventrals for females; 161 to 173 ventrals for males; 34 to 46 subcaudals for females; 40 to 50 subcaudals for males. Keel of some dorsals with characteristic white coloration. Borders of the dorsolateral blotches of undefined contour, usually forming transverse saddles where it is difficult to see the pair of secondary blotches. Blotches in the interspaces between two consecutive dorsolateral blotches are present or not. Occipital spots do not exceed the line of the quadrate-mandibular articulation. Postcephalic stripes absent. Postocular stripe with a medium width of three scales, not very marked. Melanism in the head usually absent. Supralabials with white small spots prolonged vertically. Although this ornamentation can be present in all the supralabials, the most common pattern is that such spots are more conspicuous in the posterior half of the mouth. Dorsolateral blotches in the trunk 20 to 35 (modes 21 and 24). Dorsolateral blotch in the middle trunk with 1 to 4 scales in the superior margin (modes 3 and 4), 4 to 6 arrays of scales in the height of the principal part (mode 5), 2 to 5 scales in the lower margin of the principal part (mode 4), 7 to 11 arrays of scales in the total height (mode 9), 3 to 7 scales in the total width (mode 5), 1 to 7 scales separate this blotch of the anterior blotch (mode 3) and 1 to 5 scales separate this blotch of the posterior blotch (modes 2 and 3). Ground coloration varying from cream to gray. Dorsolateral blotches are brown, brown-gray or black. Borders of the dorsolateral blotches usually do not have clearly defined white margins.

Geographic variation - Specimens collected in Camaçari and Dias D'Ávila, in the State of Bahia, presented the lowest ventral counts (154 and 156).

Geographic distribution (Figure 3) - This species only occurs in Brazil, being registered in States of Piauí, Bahia, western Pernambuco, eastern Goiás and northern Minas Gerais. This species has also been reported to occur in the locality of Americana, a town in the State of São Paulo, which may be the result of a misunderstanding or may be a relictual population.

*Bothrops mattogrossensis* Amaral, 1925, status nov.
(Figures 1E, 15C-D)

*Bothrops neuwiedii mattogrossensis* Amaral, 1925: 60, pl. 14 (fig. 6), pl. 16 (fig. 6).

*Bothrops neuwiedii boliviana* Amaral, 1927: 6, fig. 2.

*Bothrops neuwiedi bolivianus* Hoge, 1966 [1965]: 127.

*Bothrops neuwiedi mattogrossensis* Peters and Orejas-Miranda, 1970: 50.

Holotype - IBSP 3011, adult female. Type-locality: Miranda: Mato Grosso do Sul: Brazil. Specimen collected on February 25, 1922 by D. A. Correia.

Diagnosis - Uniform pigmentation in all the supralabials or big dark markings (covering more than 50% of the supralabial surface) more conspicuous in supralabials of the anterior half of the mouth. When these spots are present, the largest always meet under the eye. Dorsolateral blotches of the body with well defined contours, standing out from the ground coloration. Usually the last dorsolateral blotches of the trunk are divided vertically to the middle. Postcephalic stripes usually absent. When present, never with length larger than occipital length spots. Without melanism in the head. Postocular stripes well defined and keels always with the same coloration of the dorsal scales. Blotches in the interspaces between two consecutive blotches are present. Dorsolateral blotches in the trunk of variable formats from 16 to 33 (modes 21 and 22).

Description - Blunt rostral, in contact with internasals, nasals and first pair of supralabials. Internasals and canthals of the same size, in contact, a little larger than scales that separate the nasals, which are a little larger than dorsals of the head rest. Canthals usually separate from the large and ovoid supraoculars for one scale. Second supralabial separated from prelacunal. Intersupraocular rows 3 to 12 (mode 7); 20 to 32 scales in the sagital line beginning after internasals and ending at the level rictal region (modes 25 and 26); 1 or 2 arrays of scales between the subocular and the 4$^{th}$ supralabial; supralabials 6 to 11 (mode 8); infralabials 7 to 13 (mode 11). Dorsals in the beginning of the trunk 20 to 29 (mode 24); 21 to 28 dorsals in the half of the trunk (mode 23); 162 to 187 ventrals for females; 162 to 185 ventrals for males; 37 to 55 subcaudals for females; 40 to 61 subcaudals for males. Keel coloration equal to that of the dorsal scales. Borders of the dorsolateral blotches with well-defined contours, detaching them from the ground coloration. Blotches between two consecutive dorsolateral blotches usually present. Prolonged occipital blotches but rarely exceeding the line of the quadrate-mandibular articulation. Postcephalic stripes usually absent; when present never larger than occipital blotch length. Postocular stripe very defined with a medium width of three scales extends from the eye to the line of the labial fissure. Absence of melanism in the head. Supralabials evenly pigmented or with large dark markings (covering more than 50% of the supralabial surface) more conspicuous in the anterior half of the mouth; the largest marking is exactly under the eye. Sometimes these marks occupy the totality of the anterior supralabials or all the supralabials, resulting in an entire mouth or with the darker anterior half. Dorsolateral blotches in the trunk 16 to 33 (modes 21 and 22); usually the last dorsolateral blotches of the trunk are vertically divided to the middle. Dorsolateral blotch in the middle trunk with 1 to 6 scales in the superior margin (mode 3), 3 to 8 arrays of scales in the height of the principal part (mode 5), 3 to 7 scales in the lower margin of the principal part (mode 4), 8 to 12 arrays of scales in the total height (mode 10), 3 to 9 scales in the total width (mode 5), 0 to 7 scales separate this blotch of the anterior blotch and 0 to 6 scales separate it of the posterior blotch (mode 3 in both cases). Ground coloration varying from the clear brown to the dark brown-olive. Dorsolateral blotches are dark brown or black and can present white margins.

Individual variation - Occurrence of specimens with the whole body of discolored aspect (significantly clear pigmentation) was attributed to this species.

Geographic distribution (Figure 3) - This species occurs in Paraguay, Bolivia, Peru and

Brazil, in the States of Amazonas (isolated population in the fields of Humaitá), Rondônia, Mato Grosso, Mato Grosso do Sul, Tocantins, Goiás and São Paulo. Recently one specimen was registered in the Province of Salta, Argentina (Avila and Moreta 1995), but this individual was not examined in the present work.

*Bothrops neuwiedi* Wagler, 1824
(Figures 1B, 11, 14)

*Bothrops neuwiedi* Wagler, 1824: 56, pl. 22 (fig. 1).
*Bothrops neuwiedii* Wagler, 1830: 174.
*Bothrops urutu* Lacerda, 1884: 11, pl. 3.
*Bothrops atrox meridionalis* Müller, 1885: 699.
*Bothrops neuwiedii bahiensis* Amaral, 1925: 57, pl. 14 (fig. 1), pl. 15 (fig. 1).
*Bothrops neuwiedii goyazensis* Amaral, 1925: 58, pl. 14 (fig. 3), pl. 15 (fig. 3).
*Bothrops neuwiedii minasensis* Amaral, 1925: 59, pl. 14 (fig. 4), pl. 15 (fig. 4).
*Bothrops neuwiedii paranaensis* Amaral, 1925: 61, pl. 14 (fig. 7), pl. 16 (fig. 7).
*Bothrops neuwiedii fluminensis* Amaral, 1933b [1932]: 97, fig. 1.
*Bothrops neuwiedii urutu* Amaral, 1937 [1936]: 160.
*Bothrops neuwiedi meridionalis* Hoge, 1966 [1965]: 128.
*Bothrops neuwiedi paranaensis* Hoge, 1966 [1965]: 128.
*Bothrops neuwiedi urutu* Hoge, 1966 [1965]: 129.
*Bothrops neuwiedi goyazensis* Peters and Orejas-Miranda, 1970: 50.

Lectotype - ZSM 2348/0, adult male. Type-locality: Province of Bahia (current State of Bahia): Brazil. Lectotype designated by Hoogmoed and Gruber (1983). This specimen was collected by Johann Baptist von Spix, during an expedition in Brazil from 1817 to 1820 (Vanzolini 1996).

Diagnosis - More than half or all the supralabials of intense dark pigmentation with large round white spots. Dorsolateral blotches of well-defined contour, still more enhanced by white margins that detach them from the ground coloration. Prolonged occipital blotches, usually surpassing the quadrate-mandibular articulation and fusing to the first pair of dorsolateral blotches of the trunk forming the somewhat short postcephalic stripes. Head without melanism. Postocular stripe very marked and keels always with the same coloration of the dorsal scales. Blotches between two consecutive dorsolateral blotches are present. Two arrays of scales between the subocular and the 4$^{th}$ supralabial. Dorsolateral blotches of the trunk with triangular or semi-lunar format from 17 to 27 (modes 19 and 21).

Description - Blunt rostral, in contact with internasals, nasals and first pair of supralabials. Internasals and canthals of the same size, in contact, a little larger than scales that separate the nasals, that are a little larger than dorsals of the rest of the head. Canthals usually separate from the big and ovoid supraoculars for one scale. Second supralabial separated from prelacunal. Intersupraocular rows 5 to 12 (mode 9); 21 to 30 scales in the sagital line beginning after internasals and ending at the level of the rictal region (modes 24 and 25); two arrays of scales between the subocular and the 4$^{th}$ supralabial; supralabials 6 to 11 (mode 8); infralabials 7 to 13 (mode 11). Dorsals in the beginning of the trunk 21 to 32 (modes 25 and 28); 22 to 29 dorsals in the half of the trunk (mode 25); 161 to 188 ventrals for females; 152 to 186 ventrals for males; 31 to 51 subcaudals for females; 39 to 56 subcaudals for males. Keel coloration equal to the color of dorsal scales. Borders of the dorsolateral blotches with very defined contour, detaching them of the ground color. Blotches between two consecutive dorsaloteral blotches always present. Prolonged occipital blotches exceed the line of the quadrate-mandibular articulation, fusing to the first pair of dorsolateral blotches of the trunk and originating postcephalic stripes.

Nevertheless, these stripes usually are not larger than occipital blotches. Postocular stripe very defined with a medium width of three scales extends from the eye to the line of the labial fissure. Absence of melanism in the head. All the supralabials, or at least more than half, with great round white spots on intense dark ground. Dorsolateral blotches in the trunk 16 to 27 (modes 19 and 21). Dorsolateral blotch from middle trunk with 1 to 5 scales in the superior margin (mode 2), 3 to 9 arrays of scales in the height of the principal part (mode 6), 3 to 7 scales in the lower margin of the principal part (modes 4 and 5), 7 to 14 arrays of scales in the total height (mode 10), 3 to 9 scales in the total width (mode 6), 0 to 7 scales separate this blotch of the anterior blotch and 1 to 6 scales separate it of the posterior blotch (mode 3 in both cases). Ground coloration varying from brown to dark brown. Dorsolateral blotches dark brown or black with white margins very marked.

Individual variation - The format of the white spots in the supralabials can vary, but are always large spots on intense dark brown or black bottom. The occipital blotches also present different formats, but are usually prolonged tending to form short postcephalic stripes.

Geographic distribution (Figure 3) - This species only occurs in Brazil, in the States of Bahia, Goiás, Minas Gerais, Rio de Janeiro, São Paulo, Paraná and Santa Catarina. It is possible that this species reaches the northern State of Rio Grande do Sul.

*Bothrops pauloensis* Amaral, 1925, status nov.
(Figures 1C, 15A-B)

*Bothrops neuwiedii pauloensis* Amaral, 1925: 59, pl. 14 (fig. 5), pl. 16 (fig. 5).

*Bothrops neuwiedi pauloensis* Hoge, 1966 [1965]: 128.

Holotype - IBSP 3013, adult male. Type-locality: Leme: São Paulo: Brazil. Specimen collected on September 1922 by J. S. Queiroz.

Diagnosis - Postocular stripe well marked, which frequently expands around the labial fissure, developing a melanism on the sides of head. All the supralabials with uniform pigmentation, without conspicuous spots. Oblique occipital blotches rarely surpass quadrate-mandibular articulation, consequently postcephalic stripes are absent. Borders of the dorsolateral blotches with variable contour: diffuse or well marked. Blotches between two consecutive dorsolateral blotches usually absent. Keels with the same coloration of the dorsal scales. Ground coloration extremely varied, but the cream tone with the black dorsolateral blotches are more common. Dorsolateral blotches of the trunk from 11 to 25 (modes 15 and 17) with variable formats and relatively distant from each other.

Description - Blunt rostral, in contact with internasals, nasals and first pair of supralabials. Internasals and canthals of the same size, in contact, a little larger than scales that separate the nasals, which are a little larger than dorsals of the rest of the head. Canthals usually separate from the large and ovoid supraoculars for one scale. Second supralabial separated from prelacunal. Intersupraocular rows 5 to 11 (modes 7 and 9); 21 to 30 scales in the sagital line beginning after internasals and ending at the level of the rictal region (modes 24 and 25); 1 or 2 arrays of scales between the subocular and the 4$^{th}$ supralabial; supralabials 6 to 11 (mode 8); infralabials 7 to 13 (mode 11). Dorsals in the beginning of the trunk 21 to 29 (mode 25); 21 to 29 dorsals in the half of the trunk (mode 25); 163 to 187 ventrals for females; 161 to 184 ventrals for males; 33 to 53 subcaudals for females; 42 to 56 subcaudals for males. Keel coloration equal to that of dorsal scales. Borders of the dorsolateral blotches of well-defined contour or not. Blotches between two consecutive dorsolateral blotches usually absent. Oblique occipital blotches rarely exceeding the line of the quadrate-mandibular articulation. Postcephalic stripes absent. Postocular stripe well defined with a medium width of three scales extends around labial fissure, developing a more melanic head. Supralabials evenly pigmented. Dorsolateral blotches in the trunk 11 to 25 (modes 15 and 17). Dorsolateral blotch from middle trunk with 1 to 6 scales in the superior margin (mode 3), 3 to 8 arrays of scales in the height of the principal part (mode 5), 2 to 7 scales in the lower margin of the principal part (mode 4), 3 to 12 arrays of scales in the total height (modes 9 and 10), 3 to 9 scales in the total width (mode 6), 2 to 10 scales separate this blotch of the anterior blotch and 2 to 12 scales separate it from the posterior blotch (mode 4 in both cases). Ground coloration can be very variable (brown tonalities, gray and red), but the cream bottom with black blotches can be considered characteristic. Borders of the dorsolateral blotches can present white margins.

Individual variation - As before registered, the coloration is very variable. Three specimens (IBSP 57081-83) collected in the same locality, Parque Nacional de Emas, GO presented completely different coloration patterns.

Geographic distribution (Figure 3) – This species occurs in Brazil, being registered in States of Minas Gerais, Goiás, Mato Grosso, Mato Grosso do Sul and São Paulo. Janzen (2006) registered this species in Bolivia.

*Bothrops pubescens* (Cope, 1870), status nov.
(Figures 1G, 15I-J)

*Trigonocephalus* (*Bothrops*) *pubescens* Cope, 1870 [1869]: 157.

*Bothrops neuwiedii riograndensis* Amaral, 1925: 61, pl. 14 (fig. 8), pl. 16 (fig. 8).

*Bothrops neuwiedii pubescens* Hoge, 1959 [1957/58]: 84.

*Bothrops neuwiedi pubescens* Hoge, 1966 [1965]: 128.

Type-material - as the holotype of *Trigonocephalus* (*Bothrops*) *pubescens* Cope, 1870 was not found (McDiarmid *et al*. 1999), we suggest the designation of a lectotype.

Lectotype - MZUSP 5874, adult male. Type-locality: Pozo Hondo, Tambores: Departamento de Tacuarembó: Uruguay. Specimen collected in 1952 by F. Achaval and C. Prigioni.

Diagnosis - More than half or all the clear supralabials with dark markings (covering less than 50% of the supralabial surface) not very intense triangular format always in the suture between two supralabials. Dorsolateral blotches of well-defined contour, outstanding gray-ground coloration, still more for the presence of white margins in the principal parts of the dorsolateral blotches. Short postcephalic stripes can be present. Pair of occipital blotches with different formats, but the arrangement usually resembles two opposed arrows pointing to the head sides (“< >”). Melanism in the head absent. Postocular stripe very marked and keels always with the same coloration of the dorsal scales. Dorsolateral blotches in the trunk from 19 to 30 (mode 21) with triangular to trapezoid format and relatively close to each other.

Description - Blunt rostral, in contact with internasals, nasals and first pair of supralabials. Internasals and canthals of the same size, in contact, a little larger than scales that separate the nasals, that are a little larger than dorsals of the rest of the head. Canthals usually separated from the large and ovoid supraoculars for one scale. Second supralabial separated from prelacunal. Intersupraocular rows 5 to 11 (mode 8); 21 to 30 scales in the sagital line beginning after internasals and ending at the level of the rictal region (mode 25); usually two arrays of scales between the subocular and the 4$^{th}$ supralabial; supralabials 6 to 11 (mode 8); infralabials 7 to 13 (mode 11). Dorsals in the beginning of the trunk 21 to 30 (mode 25); 22 to 29 dorsals in the half of the trunk (mode 25); 169 to 188 ventrals for females; 164 to 181 ventrals for males; 37 to 49 subcaudals for females; 43 to 53 subcaudals for males. Keel coloration equal to the color of dorsal scales. Borders of the dorsolateral blotches of well defined contour, detaching them from the ground color. Blotches between two consecutive dorsolateral blotches usually present. Prolonged occipital blotches exceed the line of the quadrate-mandibular articulation, fusing to the first pair of dorsolateral blotches of the trunk originating postcephalic stripes. Nevertheless, these stripes usually are not larger than occipital blotches. Postocular stripe well defined with a medium width of three scales extends from the eye to the line of the labial fissure. Absence of melanism in the head. All the supralabials, or at least more than half, with dark spots (covering less than 50% of the supralabial surface) not very intense triangular format always in the suture between two supralabials. Dorsolateral blotches in the trunk 19 to 30 (mode 21). Dorsolateral blotches from mid-trunk with 1 to 5 scales in the superior margin (modes 2 and 3), 4 to 12 arrays of scales in the height of the principal part (mode 6), 3 to 6 scales in the lower margin of the principal part (mode 4), 6 to 12 arrays of scales in the total height (mode 10), 4 to 9 scales in the total width (mode 5), 0 to 5 scales separate this blotch of the anterior and posterior blotches (mode 3 in both cases). Ground coloration varies from the brown-gray to the dark brown. Dorsolateral blotches dark brown or black. The principal parts of the dorsolateral blotches with white margins well-defined.

Individual and geographic variation - Vaz-Ferreira and Sierra-de-Soriano (1960) described the color variation of drawing patterns and of pholidosis of 11 specimens of this species in the collection from Departamento de Zoologia de Vertebrados of Faculdad de Humanidades y Ciencias de Montevidéo, Uruguay. Vieira and Alves (1975) redescribed this species (as subspecies), including the pholidosis variations, morphometry, coloration and blotches drawing patterns. They separated three groups with base in coloration: a) brown-gray specimens from São Francisco de Paula, Viamão, Guaíba, Porto Alegre, Encruzilhada do Sul and Santa Maria, RS; b) gray specimens from Boçoroca and Rosário do Sul, RS and c) dark gray specimens from Livramento, RS and Uruguay. Even so, certain individual variations were verified in group "a", with specimens of brown coloration (Porto Alegre and Viamão, RS) and others of gray coloration (Santa Maria, RS). The variation in the ventral region among males and females from Porto Alegre (Lema *et al*. 1984) was not verified in the present work.

Geographic distribution (Figure 3) - This species occurs in Uruguay, in the Departamentos of Artigas, Rivera, Tacuarembó, Cerro Largo, Treinta y Tres, Lavalleja, Maldonado, Canelones, Rocha and San José (Vieira and Alves 1975, Achaval *et al*. 1976,) and in the southern Brazil, in the State of Rio Grande do Sul.

## Description of the new species

*Bothrops marmoratus* sp. nov.
(Figures 1D, 12 and 13)

Holotype – IBSP 55055, adult female from Ipameri (17°43'S, 48°09'W), State of Goiás, Brazil, collected on June, 29th 1993 by Flávio Rodrigues Alves.

Paratypes – Seventeen specimens: IBSP 33236, adult male, IBSP 33347, adult female, and IBSP 33894, adult female, all collected on April 23, 1971 by José Borges in Ipameri (17°43'S, 48°09'W), State of Goiás, Brazil; IBSP 55056, adult male, collected on 29 June 1993 by Flávio Rodrigues Alves in Ipameri (17°43'S, 48°09'W), State of Goiás, Brazil; IBSP 32268, adult female, and IBSP 32271, adult male, all collected on June 11, 1971 by Léo Roberto Barbosa Moraes in Cristalândia (10°36'S, 49°11'W), State of Tocantins, Brazil; IBSP 41264, adult female collected on July 1, 1977 by José Mariano de Mello Barbosa in Porto Nacional (10°42'S, 48°25'W), State of Tocantins, Brazil; IBSP 44310, adult female collected on March 29th, 1982 by José Olimpo de Oliveira in Gurupi (11°43'S, 49°04'W), State of Tocantins, Brazil; IBSP 56075, adult male collected on January 22nd, 1996, IBSP 56947, adult male collected on March 26th, 1997, and IBSP 57015, adult female, collected on May 6th, 1996 by A. M. Fonseca in Medeiros

(19°59'S, 46°13'W), State of Minas Gerais, Brazil; IBSP 55027, adult female, IBSP 55028, adult female, IBSP 55029, adult male, IBSP 55030, adult male, IBSP 55031, adult female, IBSP 55032, adult female, all collected on June 15th, 1993 by Forest Police in Patos de Minas (18°35'S, 46°32'W), State of Minas Gerais, Brazil.

Diagnosis – The new species is distinguished from the 22 species of *Bothrops* by having a prelacunal not fused to the second supralabial (list in Campbell and Lamar 2004). On the other hand, it shares with fourteen other *Bothrops* species, the prelacunal separated from the second supralabial. Of these fourteen species of *Bothrops*, eight do not belong to the complex *B. neuwiedi*. *B. marmoratus* is distinguished from *B. alternatus* by having 5–9 intersupraoculars (vs. 8–13), 21–26 midbody dorsal scale rows (vs. usually 27–33 in *B. alternatus*), and by lacking a distinctive dorsal pattern of bold, headphone-shaped markings. It differs from *B. ammodytoides* by not having a canthus rostralis that is characteristically curved upward, and a distinctly raised snout. *Bothrops marmoratus* differs from *B. cotiara* and *B. fonsecai* by not showing conspicuous dark brown occipital stripes extending forward to the snout where they converge, forming a distinctive spear-shaped mark on the top of the head, as well as by having a venter brighter than these two species. It differs from *B. erythromelas* by having higher counts of midbody dorsal scale rows, ventrals, and subcaudals (19–21, 139–158 and 32–42, in *B. erythromelas* respectively). It can be distinguished from *B. itapetiningae* by the higher number of ventrals, and subcaudals (157-182, and 32-50 in *B. marmoratus* vs. 144–160, and 26–38 in *B. itapetiningae*), from *B. jonathani* by having 21-26 midbody dorsal scale rows (vs. 30-33), and from *Bothrops pictus* by not showing dorsal blotches arranged mostly on the middorsum, fusing into a zigzag stripe (Campbell and Lamar 2004).

The other six remaining *Bothrops* species, together with *B. marmoratus*, belong to the *B. neuwiedi* complex. In general, they have 4-12 intersupraoculars, 1-2 rows of small scales between the subocular and fourth supralabial, prelacunal separated from second supralabial, 7-10 supralabials (usually 8-9), 9-13 infralabials (usually 10-11), 21-29 midbody dorsal scale rows, 157-187 ventrals in males, 158-189 ventrals in females, 39-61 divided subcaudals in males, 34-55 in females; often the top of the head with a blotch between the canthals, one pair close to supraoculars, and another pair in the occipital-temporal region; triangular to trapezoidal dorsolateral blotches that alternate or are opposite one another mid-dorsally; between two consecutive dorsolateral blotches there may or may not be one spot or blotch; the base of each dorsolateral blotch has a pair of oval or round blotches, that tend to form a lateral series of blotches typical in the complex; a series of brown or gray paraventral spots may be present; supralabials with some type of ornamentation in color; bronze or bright gold iris, dark pinkish gray tongue; white tail tip in juveniles; white or yellow venter with gray specks scattered throughout, that may form transverse markings throughout the scale sutures; lobes of hemipenis are moderately attenuated, with 28-35 medium to large spines in each one (Campbell and Lamar 2004). Therefore, *Bothrops marmoratus* may be distinguished from other species of the *B. neuwiedi* complex mainly through qualitative characteristics (Table 1, Figure 1). *Bothrops lutzi* has dark brown or brown supralabials with small vertically elongated white blotches more conspicuous on the posterior half of the mouth, and white keels in many dorsal scales (Figure 1A). *Bothrops neuwiedi* has dorsolateral blotches with well-defined, white-edged borders, short postcephalic stripes; most supralabials black or dark brown with large, round white blotches (Figure 1B). *Bothrops pauloensis* has a melanic head, supralabials not finely stippled; posteriormost pair of occipital blotches generally ellipsoidal (Figure 1C). *Bothrops mattogrossensis* has dorsolateral blotches with well-defined borders, supralabials generally creamish-white with large dark brown blotches that cover most of the supralabials from the anterior half of the mouth; largest blotch is beneath the eye (Figure 1E). *Bothrops diporus* has postcephalic stripes (much) larger than the occipital blotches; supralabials generally creamish-white with large dark brown blotches that cover most of supralabials throughout the anterior half of the mouth; largest blotch directly under the eye (Figure 1F). In *Bothrops pubescens* more than half to all supralabials creamish-white with small, triangular dark blotches (covering less than half of the supralabial surface); dark blotches not very conspicuous, lying throughout the suture between two supralabials (Figure 1G).

Description of holotype – An adult female preserved in ethanol with 520 mm SVL; tail non-prehensile with length of 65 mm; HL 28.50 mm; maximum head width 16.35 mm; rostral scute 3.85 mm wide and 3.90 mm high; snout width or nostril-nostril distance 5.00 mm; left eye-snout distance 8.15 mm; left eye-nostril distance 6.05 mm; diameter of left eye 4.15 mm; left eye-pit distance 2.95 mm; left internasal length 2.95 mm; left internasal width 1.40 mm; left canthal length 3.15 mm; left canthal width 1.75 mm; left supraocular length 5.35 mm; left supraocular width 2.80 mm; nasals completely divided anterior and posterior to nostril; loreal single in contact with canthal; 6/6 prefoveals between posterior nasal and prelacunal; prelacunal separated from second supralabial in both sides by 2/2 subfoveals; 2/2 postfoveals anterior to 2/2 preoculars; upper preocular very large, lower distinctly small and elongated; 1/1 subocular separated from the fourth supralabial by one row of small scales; 2/2 small postoculars identical in size; 7/7 supralabials; 8/10 infralabials, first pair in contact posteriorly; mental triangular nearly as long as wide; first genial elongated in contact with three first infralabials; posterior genial small and indistinct from proximal gulars; 7 gulars between genials and first ventral; 6 rows of gulars separating first ventral from infralabials; 1/1 internasals; 1/1 canthals; two rows of intercanthals, the first with 3 shields, and the second with 4 shields separated from the first by one smaller shield; 7 intersupraoculars rows; 22 dorsal cephalic scales in the sagital line beginning after internasals and ending at the level of the rictal region; 24/23/18 dorsal scale rows; 168 ventrals; cloacal scute single; 44 divided subcaudals; 4 small scales on each side of the cloaca; tail spine 4 times longer than adjacent subcaudals; dorsal scales covering anterior half of tail spine; dorsal scales twice as long as the width and strongly keeled; paraventral row of scales 1.8 times wider than adjacent dorsal

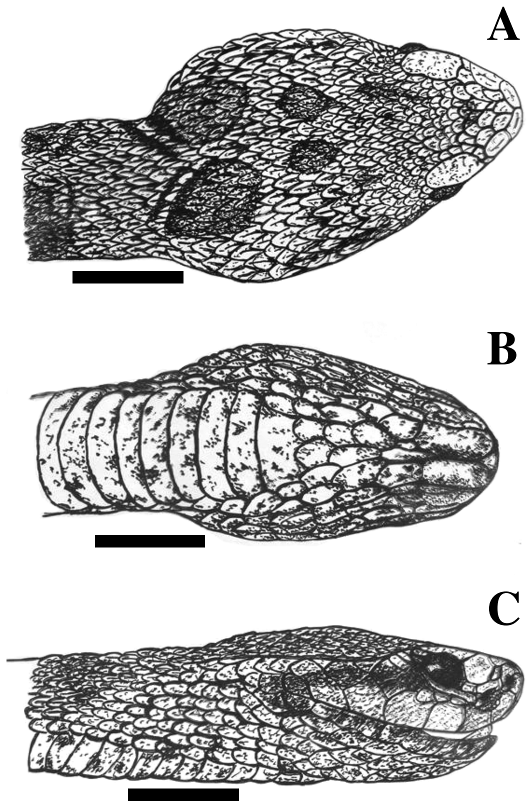


**Figure 16** - Head of the holotype (IB 55055 ♀) of *Bothrops marmoratus* sp. nov in dorsal (A), ventral (B), and lateral (C) views. Bar = 10 mm.

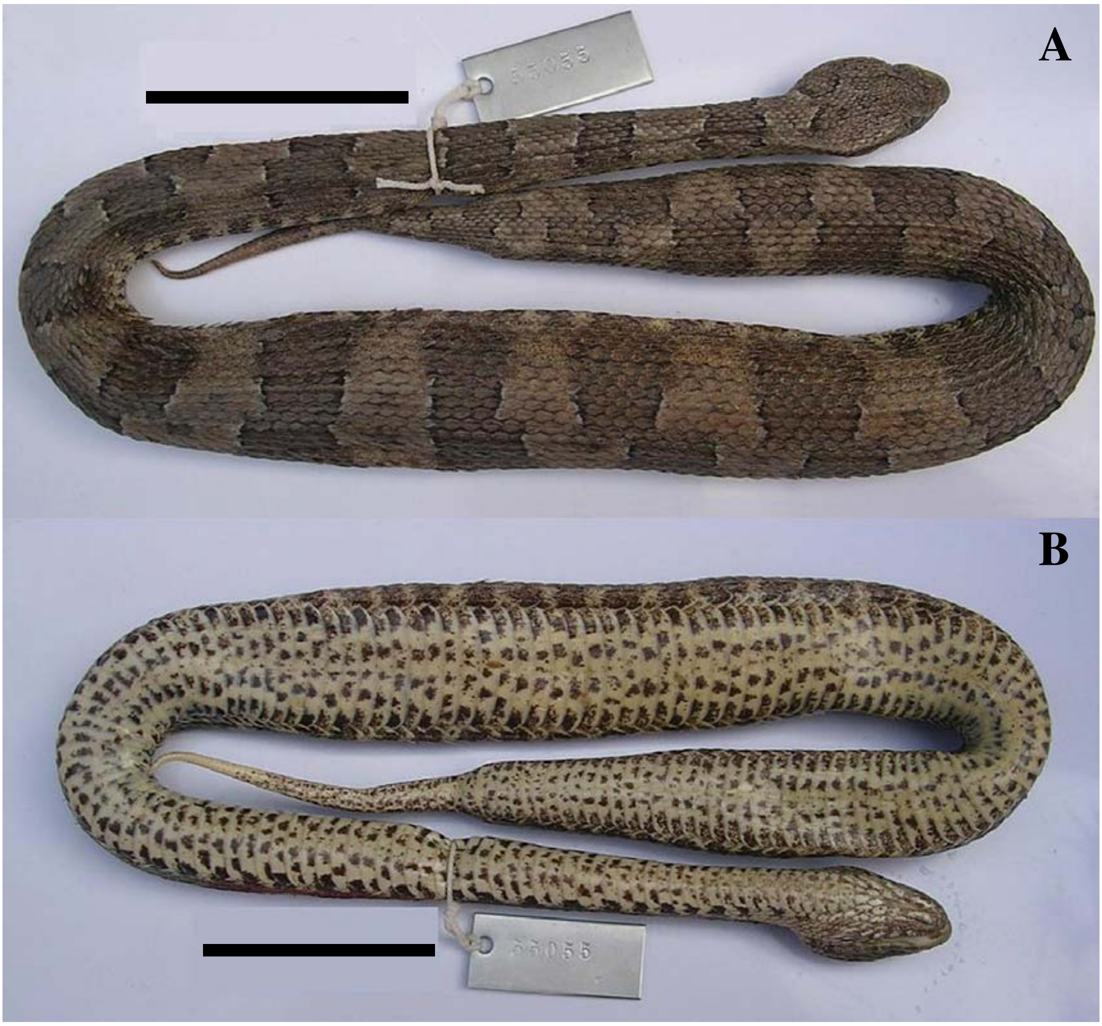


**Figure 17** - Dorsal (A) and ventral (B) views of the holotype (IB 55055 ♀) of *Bothrops marmoratus* sp. nov. Bar = 50 mm.

scales, weakly keeled, mainly on posterior portion of the body; parasubcaudals strongly keeled; posterior cephalic dorsal scales strongly keeled and longer than wide; anterior cephalic scales and intercanthals rounded and weakly keeled; internasals, canthals, and supraoculars smooth; temporal scales enlarged and smooth connecting with the last supralabials; temporal scales become progressively smaller and keeled towards the top of head (Figure 16).

The ground color (in preservative) is olive brown on the dorsal surface of the body and head; the 16/17 trapezoidal dorsolateral blotches are dark brown with ill-defined borders, and weakly white-edged. The small spots between consecutive dorsolateral blotches are inconspicuous, and the pairs of spots under the dorsolateral blotches have diffuse borders, giving the aspect of transverse saddles to the whole dorsolateral blotches. Dorsolateral blotches begin middorsally opposite one another becoming alternate on the posterior half of the body (Figure 17). Dark brown paraventral spots. Keels with the same color as dorsal scales. Pair of occipital blotches with round format, white posterior edge, and not fused anteriorly, nor elongated forming dorsal postcephalic stripes. Inconspicuous postorbital stripe. Supralabials stippled without conspicuous blotches. Iris-bronze tongue dark pinkish-gray. Ventrals cream speckled with dark brown dots that fuse to form transverse markings, especially near paraventrals (Figure 17).

Variation (n = 65, Table 1) – A medium sized terrestrial snake, SVL between 500-600 mm, occasionally reaching 800 mm in total length, with canthus rostralis moderately straight, snout not elevated, 5-9 intersupraoculars (usually 7), 1-2 rows of small scales between the subocular and fourth supralabial, 8-9 supralabials (rarely 7 or 10), prelacunal separated from second supralabial, 9-13 infralabials (usually 10-11), 21-26 midbody dorsal scale rows (usually 23), 157-181 ventrals in males, 158-182 ventrals in females, 41-50 divided subcaudals in males, 37-47 in females. Dark blotches on the top of the head arranged more or less symmetrically, often with a blotch between the canthals, one pair close to the supraoculars, and a pair in the occipital-temporal area. The posteriormost pair of supracephalic blotches is usually rounded and are rarely fused anteriorly, nor elongated onto the neck in a stripe-like fashion. The keels of the dorsal scales are brown to dark brown and generally have the same color as the background. The borders of the dark spots or blotches are ill defined and weakly white-edged. The postorbital stripe is also slightly marked. The canthus may be dark gray with dark spots. All supralabials are stippled without conspicuous blotches. The stippled aspect of supralabials extends throughout the body. This characteristic and the diffuse borders of the body blotches contribute to the marbled aspect of this species. The iris is bronze or bright gold, and the tongue is dark pinkish gray. The body has 15–27 dorsolateral blotches that may be strongly trapezoidal in shape, eventually connecting middorsally. The spaces between two consecutive dorsolateral blotches may be marked with one diffuse spot or blotch. The apices of dorsolateral blotches have a middorsal position. Each dorsolateral blotch presents in the base one pair of smaller oval or round blotches, tending to form a lateral series of blotches typical in the complex. Generally, it is difficult to distinguish between the pair of spots or blotches from base of each dorsolateral blotch, and the entire conjunct (dorsolateral blotch and its pair of basal spots or blotches) resembles a trapezoidal transverse saddle. The color of these dorsolateral blotches is darker than the ground color. A series of brown or gray paraventral spots may be present. The tail tip is white only in juveniles. The venter is white or yellow speckled with a profusion of gray dots; these dots may fuse to form transverse markings mainly on the lateral edges of the ventrals, throughout the scale sutures.

Also in preservative, the paratypes IBSP 33236 and IBSP 55056 are very similar in color to the holotype, but the ground color is gray. Nevertheless, the scattered ventral color markings of IBSP 33236 form complete transverse dark brown markings in all the ventrals. Paratypes IBSP 33347 and IBSP 33894 have the same color pattern with pale brown old scales with darker blotches, and ventral markings paler than other specimens from the type-series. In natural settings, the dorsal ground color of the head and body is highly variable, including tonalities of cream, pale brown, dark brown, rosy, orange, and gray. The wide variation of color also occurs among individuals in a single locality, as seen in specimens from Palmas, in the State of Tocantins, illustrated in Campbell and Lamar (2004). The anomalous specimen IBSP 57257 from the type-locality is another example of the extreme variation of the species with such intense melanism that the dorsolateral blotches are invisible.

Distribution, habitat and natural history – *B. marmoratus* sp. nov. is found in the States of Goiás, Tocantins, and western Minas Gerais, Brazil (Figure 3). This distribution coincides entirely with the nuclear area of Cerrado in Central Brazil (Ab'Saber 1977). Although this morphoclimatic domain is critically endangered (Myers *et al.* 2000), *B. marmoratus* sp. nov. seems to be abundant in its area of occurence, as indicated by a wide variety of specimens examined (Appendix I). Considering the difficulty of correctly identifying forms of the *B. neuwiedi* complex until now, natural history data for *Bothrops marmoratus* may already exist, although mixed up with that of other species of this complex. The venom of this species, for example, presents unique properties among *Bothrops* venoms (M. F. D. Furtado, personal communication).

Etymology – the specific epithet is a reference to the marbled aspect of the body pigmentation of this species. We suggest the common name "Marbled lancehead" for the new species.

## Final considerations

As was observed in the species of *Tropidurus* of the *torquatus* group (Rodrigues 1987), despite the wide overlap among the geographic distributions of different species of the *B. neuwiedi* complex, sympatry was a rare event. In addition, the numbers are relatively similar: sympatric species of *Tropidurus* were present in 32 of approximately 300 localities (Rodrigues 1987), and there was sympatry between different species of the *B. neuwiedi* complex in 25 of the 360 localities of the present study. *Bothrops marmoratus*, for example, occurred sympatrically with *B. pauloensis* at Araguari-MG, with *B. neuwiedi* at Ipameri-GO, and with *B. neuwiedi* and *B. lutzi* in Brasília-DF. However, some differences are evident. Firstly, in none of the sympatry cases of the *neuwiedi* group is it possible to say whether the species are syntopic; therefore, species can present significant ecological differences. Second, snakes are not common and locally abundant animals such as the lizards of the genus *Tropidurus*, in which a few hours of collection can generate a considerable number of specimens. Therefore, the lack of records of some species in certain areas may reflect insufficient collecting effort. This obviously depends on the area. The State of São Paulo, for example, is very well sampled due to the location of the Instituto Butantan. Ten of the 25 cases of sympatry were registered in this State. Consequently, the rarity of registration of this group in the western half of the State indicates real absence.

Within the context of the morphoclimatic domains of Ab´Saber (1977), snakes of the *B. neuwiedi* complex are restricted to open areas of cis-andean South America, south of the Amazon, except for the Caatingas, domain of *B. erythromelas*. The group does not inhabit the Amazon nor the Atlantic Forests, although it occurs in enclaves of open areas within these domains. Two types of geographic distribution were identified in the species of this complex: species with widespread distributions occurring across different habitats but with isolated populations in the peripheries of their occurrence areas (*B. diporus, B. lutzi, B. mattogrossensis, B. neuwiedi,* and *B. pauloensis*) and species with distributions restricted to ecologically homogeneous regions (*B. marmoratus* and *B. pubescens*). *Bothrops lutzi, B. marmoratus,* and *B. pauloensis* are predominantly associated with the Cerrado domain but *B. marmoratus* is the only one exclusively restricted to this habitat. *Bothrops diporus* and *B. mattogrossensis* are more associated with the Chaco domain, but do not occur exclusively there. *B. neuwiedi* was registered in mountainous areas, mainly throughout the Serra do Espinhaço, State of Minas Gerais. *B. pubescens* was predominant in the Pampas Grassland from Rio Grande do Sul and Uruguay. Of the morphoclimatic domains (Ab´Saber 1977), the Cerrados have

**Identification key for species of the *Bothrops neuwiedi* complex:**

1. a) Dorsolateral blotches with diffuse borders (Figures 2A and 2D) .......................................... 2
b) Dorsolateral blotches with well-defined borders (Figures 2B-C, 2E-G) ................................ 4

2. a) Supralabials without conspicuous blotches (Figures 2C-D), intersupraoculars of same size, keels with the same color as dorsal scales, one or two rows of scales between the subocular and the 4th supralabial. ................................................................................................................ 3
b) Supralabials with small white blotches elongated vertically, usually more conspicuous on the posterior half of the mouth (Figure 2A), central intersupraoculars fused or larger than adjacent ones, some dorsal scales with white keels, a single row of scales between subocular and the 4th supralabial. .......................................................................................................................*lutzi*

3. a) Postorbital stripe extends from behind the eye to the angle of the jaw, curving slightly downward at its terminus, making the sides of head uniformly dark; supralabials not stippled, oblique or ellipsoid occipital blotches without white edge in posterior borders, body without marbled aspect (Figure 2C) ........................................................................................ *pauloensis*
b) Postorbital stripe not conspicuous, sides of head clear; supralabials stippled, occipital blotches rounded and white-edged posteriorly, body with marbled aspect (Figure 2D)........... *marmoratus*

4. a) More than half of supralabials (usually all) with blotches (Figures 2B, 2G) .......................... 5
b) Supralabials with large dark brown blotches restricted to anterior half of mouth, the largest blotch under the eye (Figures 2E-F), or supralabials without blotches (Figure 2C) ................... 6

5. a) Supralabials very dark with large round white blotches, dorsum with brown or dark brown ground color, occipital blotches of varied shapes, but rarely as described below (Figure 2B) *neuwiedi*
b) Supralabials creamish-white with small dark brown triangular blotches (covering less than half of supralabial surface), always situated throughout the suture between two supralabials, dorsum with gray-brown or dark brown ground color, pair of occipital blotches with an arrangement that resembles two opposed arrows pointing to the head sides (“< >”) (Figure 2G) ........... *pubescens*

6. a) Supralabials without blotches (Figure 2C) ................................................................... 7
b) Supralabials with large dark blotches (covering more than half of supralabial surface) more conspicuous on the anterior half of mouth, the largest blotch is directly beneath the eye (Figures 2E-F) ...................................................................................................................... 8

7. a) Postorbital stripe extends around the labial fissure, becoming more melanic on the sides of the head (Figure 2C) ........................................................................................... *pauloensis*
b) Postorbital stripe finishes at the level of the labial fissure, head without lateral melanism (Figures 2E-F) ..................................................................................................... 8

8. a) Usually with elongated dorsal postcephalic stripes resulting from the occipital blotches fused to the first pair of dorsolateral blotches of the body (Figure 2F), posterior dorsolateral blotches of the trunk (anterior to cloacal scute) without vertical division, 5-7 scales forming the basis of the dorsolateral blotch from midbody ......................................................................... *diporus*
b) Elongated dorsal postcephalic stripes absent (Figure 2E), posterior dorsolateral blotches of the trunk (anterior to cloacal scute) vertically mid-divided, 4-5 scales forming the basis of the dorsolateral blotch from midbody ....................................................................... *mattogrossensis*

greater diversity of species within the *B. neuwiedi* complex. Five of the seven species are widespread (*B. lutzi, B. marmoratus* and *B. pauloensis*) or partially distributed (*B. mattogrossensis* and *B. neuwiedi*) in this domain. Data on the biology for some these species (Valdujo *et al*. 2002, Hartmann *et al*. 2005, Monteiro *et al*. 2006) corroborate the preference of this group for open areas.

Morphologically, the *neuwiedi* group displays ample individual, ontogenetic, sexual and geographic variation (Xavier 2001, Silva 2000, 2004). Qualitative characteristics, however, diagnosed seven different taxa that were considered full species. A similarity analysis (UPGMA) defined two morphological groups: 1) *B. lutzi, B. pauloensis* and *B. marmoratus* and 2) *B. diporus, B. mattogrossensis, B. neuwiedi* and *B. pubescens* (Silva 2000). It is possible that some individuals of different species intergrade (Silva 2000), but this does not invalidate the evolutionary unit of each determined lineage, according to the vision of the evolutionary species concept (Wiley 1978, 1981). The preliminary nature of this hypothesis is only an initial contribution to the study of this complex. Mainly in the case of highly variable and historically recent groups, the analysis of only external morphological characteristics may not be sufficient for definitive species delimitation. The short time for speciation impedes the fixation of evolutionary innovations, increasing the profusion of polymorphisms. In these situations, a more refined study, such as DNA analysis, is critical,. On the other hand, we believe that a study based on morphological data of a wide variety of specimens, a more cost-effective appoach, is an appropriate beginning for understanding this group.

Below we present an identification key for the species of the *B. neuwiedi* complex. An identification key for the entire genus *Bothrops* is available in Campbell and Lamar (2004).

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## **Appendix I** - Specimens examined

*Bothrops diporus* - ARGENTINA: *Cordoba*: Argüello: IBSP 5319 (paratype of *Bothrops neuwiedii meridionalis* Amaral, 1930c). *Chaco*: Charata: IBSP 5317 (paratype of *Bothrops neuwiedii meridionalis* Amaral, 1930c). *Formosa*: Km 151: IBSP 5318 (paratype of *Bothrops neuwiedii meridionalis* Amaral, 1930c). *Salta*: Embarcación: IBSP 5316 (holotype of *Bothrops neuwiedii meridionalis* Amaral, 1930c). *Santiago del Estero*: Km 644: IBSP 5320 (paratype of *Bothrops neuwiedii meridionalis* Amaral, 1930c). *Tucumán*: Villa Alberdi: IBSP 5321 (paratype of *Bothrops neuwiedii meridionalis* Amaral, 1930c). BRAZIL: *Paraná*: Cascavel: IBSP 24441, IBSP 24592, IBSP 24732, IBSP 29197-98, IBSP 42474, IBSP 42711; Foz do Iguaçu: IBSP 20342-43, IBSP 20350, IBSP 20354, IBSP 22924, IBSP 24503, IBSP 24940-45, IBSP 25337, IBSP 25600, IBSP 25655, IBSP 25808-15, IBSP 26002-03, IBSP 26045, IBSP 26171, IBSP 26239, IBSP 26323, IBSP 26475, IBSP 26477, IBSP 26640, IBSP 26655, IBSP 26766-67, IBSP 27032-34, IBSP 27061-78, IBSP 27319, IBSP 27531-33, IBSP 27540, IBSP 30734, IBSP 30790, IBSP 32562, IBSP 33128, IBSP 43782, IBSP 43832, IBSP 44144, IBSP 44970, IBSP 45018, IBSP 45174-76, IBSP 45288-89, IBSP 45302, IBSP 45463, IBSP 45502, IBSP 45540-42, IBSP 45602-05, IBSP 46003, IBSP 46040, IBSP 46106, IBSP 46192, IBSP 46215, IBSP 49471, IBSP 49472-73, IBSP 51062, IBSP 51074, IBSP 51250, IBSP 51869, IBSP 52967, IBSP 53017-19, IBSP 55263; Maringá: IBSP 21694; Primeiro de Maio: IBSP 30826. *Rio Grande do Sul*: Braga: IBSP 26164-65, IBSP 27148, IBSP 28517, IBSP 32047, IBSP 32316, IBSP 33795, IBSP 45979; Carazinho: IBSP 24170, IBSP 52836-37; Cruz Alta: IBSP 18133; Getúlio Vargas: IBSP 55603-04; Giruá: IBSP 16411; Ijuí: IBSP 11430-31, IBSP 22972-73; Mata: IBSP 22814; Santa Bárbara do Sul: IBSP 16751-52; Santa Cruz do Sul: IBSP 15303-20; Santiago: IBSP 49470; Santo Ângelo: IBSP 8749-50, IBSP 11281-82; Tigre: IBSP 32314; Tucunduva: IBSP 56461-62; Tuparendi: IBSP 57299. *Santa Catarina*: Campo Erê: IBSP 29766; Chapecó: IBSP 51448-54, IBSP 53021; Itapiranga: IBSP 26537, IBSP 26662-63, IBSP 27137-44; Porto União: IBSP 13000. *São Paulo*: Bernardino de Campos: IBSP 27351.

*Bothrops lutzi* - BRAZIL: *Bahia*: Barreiras: IBSP 49634-35, IBSP 51553-54, IBSP 51686; Camaçari: IBSP 959, UFBA 985-86; Cocos: IBSP 44518-24, IBSP 49650, IBSP 51427; Dias d'Ávila: UFBA 1191; Guanambi: IBSP 53591; Santa Maria, Rio Corrente: AL 5.337 (holotype of *Lachesis lutzi* Miranda-Ribeiro, 1915); São Desidério: IBSP 55674. *Distrito Federal*: Brasília: IBSP 49492-97. *Goiás*: Mambaí: IBSP 49505, IBSP 51455-60, IBSP 51471, IBSP 52890-91. *Minas Gerais*: Januária: IBSP 43693. *Pernambuco*: Petrolina: IBSP 49804. *Piauí*: Fazenda Grande, margem direita do Rio Gurguéia: IBSP 1672 (holotype of *Bothrops neuwiedii piauhyensis* Amaral, 1925), IBSP 1673 (paratype of *Bothrops iglesiasi* Amaral, 1923); Regeneração: IBSP 551-60 (paratypes of *Bothrops iglesiasi* Amaral, 1923), IBSP 561 (holotype of *Bothrops iglesiasi* Amaral, 1923), IBSP 562 (paratype of *Bothrops iglesiasi* Amaral, 1923), IBSP 563 (paratype of *Bothrops iglesiasi* Amaral, 1923), IBSP 565-68 (paratypes of *Bothrops iglesiasi* Amaral, 1923), IBSP 3100 (paratype of *Bothrops iglesiasi* Amaral, 1923); Rio Piauí: IBSP 51555; Teresina: IBSP 1285 (paratype of *Bothrops iglesiasi* Amaral, 1923), IBSP 51412; Uruçuí: IBSP 53871-72, IBSP 54499; Valença: MZUSP 5854-5859. *São Paulo*: Americana: IBSP 50499, IBSP 50691, IBSP 52839.

*Bothrops marmoratus* sp. nov. - BRAZIL: *Distrito Federal*: Barragem de Paranoá: IBSP 19465; Brasília: IBSP 20431-32, IBSP 20610, IBSP 21590, IBSP 22765, IBSP 26224, IBSP 26262, IBSP 33604, IBSP 34490, IBSP 41516, IBSP 45728, IBSP 48932-34, IBSP 58238-39; *Goiás*: Alto Paraíso, em Veadeiros: IBSP 24147, IBSP 56105, IBSP 56511; Bucania, km 58 da Rod. Uruaçu-Niquelândia: IBSP 56085; Corumbá de Goiás: IBSP 51414, IBSP 51996; Fazenda São João, Córrego Águas Claras, Alto Sucuriú: IBSP 23326; Luziânia: IBSP 24604-05; Minaçu (UHE Serra da Mesa): IBSP 56864-71, IBSP 57151-58; Niquelândia: IBSP 44502; Planaltina de Goiás: IBSP 56826; Uruaçu: IBSP 43891. *Minas Gerais*: Araguari: IBSP 57060; Corinto: IBSP 31243; Ibiá: IBSP 29104; João Pinheiro: IBSP 56260, IBSP 56805; Lassance: IBSP 599; São Francisco: IBSP 51137. *Tocantins*: Gurupi: IBSP 44310; Porto Nacional: IBSP 41264.

*Bothrops mattogrossensis* - BOLIVIA: *Santa Cruz*: Santa Cruz de La Sierra: IBSP 31369-74, IBSP 33284, IBSP 41345, IBSP 41349; Sara: Buenavista: MZUSP 6478 (paratype of *Bothrops neuwiedii boliviana* Amaral, 1927); *Velasco*: Santo Ignacio de Velasco:: IBSP 19750, IBSP 25045, IBSP 26099, IBSP 26228. BRAZIL: *Amazonas*: Humaitá: IBSP 40880-81, IBSP 40889, IBSP 40892. *Goiás*: Buriti Alegre: IBSP 5242; Campinas: IBSP 4451-52, IBSP 5179. *Mato Grosso*: Cáceres: IBSP 22986, IBSP 23849, IBSP 23998, IBSP 24108-09, IBSP 24114, IBSP 24135; Cuiabá: IBSP 20885, IBSP 24634-35, IBSP 25049, IBSP 26008, IBSP 26144-46, IBSP 26326-27, IBSP 28040-42, IBSP 32745, IBSP 33032, IBSP 33217, IBSP 33319, IBSP 53516, IBSP 56641, IBSP 57064-78; Fazenda Santa Edwiges: MZUSP 10972; Marlinópolis (Maloca Feia), em Villa Bela:

IBSP 24232-33; Porto Esperidião, Fazenda Paiquerê: IBSP 54843; São Simão: IBSP 56642-43, IBSP 56799. *Mato Grosso do Sul*: Agachi: IBSP 7720, IBSP 14358, IBSP 21125, IBSP 41517, IBSP 42690, IBSP 43109, IBSP 43111, IBSP 46171; Albuquerque, P. Caraguatá: IBSP 4653-54, IBSP 4661, IBSP 4666, IBSP 4673, IBSP 4685, IBSP 4687-88, IBSP 4692-715, IBSP 4724-29, IBSP 4773, IBSP 4877-900, IBSP 23526, IBSP 24113; Aquidauana: IBSP 4417, IBSP 5219, IBSP 5360, IBSP 6119, IBSP 6299, IBSP 11597, IBSP 11600, IBSP 11602, IBSP 11824, IBSP 11846, IBSP 11928, IBSP 13591-92, IBSP 13848-50, IBSP 16835, IBSP 16975-76, IBSP 17031, IBSP 18598, IBSP 18610, IBSP 18916, IBSP 19019, IBSP 19390, IBSP 19759-62, IBSP 20512-13, IBSP 29103, IBSP 32320, IBSP 33041, IBSP 33260, IBSP 33595, MZUSP 10108; Arapuá: IBSP 6310; Bodoquena: IBSP 18691, IBSP 19098; Campo Grande: IBSP 6086, IBSP 13688, IBSP 14216-17, IBSP 24107; Carandazal: IBSP 15483; Coimbra: IBSP 26290, IBSP 26457, IBSP 26719, IBSP 32850, IBSP 32853; CorumbáCORUMBÁ: IBSP 4441, IBSP 4443, IBSP 4867, IBSP 4940-41, IBSP 4964-67, IBSP 5118, IBSP 5206, IBSP 5326, IBSP 5723, IBSP 5728, IBSP 5759-61, IBSP 5846, IBSP 5854, IBSP 5877, IBSP 5883, IBSP 5900, IBSP 5943, IBSP 5973, IBSP 6046, IBSP 6505-06, IBSP 10245, IBSP 11868-70, IBSP 11876, IBSP 12263, IBSP 12264, IBSP 15597-601, IBSP 19077, IBSP 31089, IBSP 31094, IBSP 33089, IBSP 53644, IBSP 55594, IBSP 55673; Coxim: IBSP 6682; Fazenda Bom Jesus do Taquari, margem do Rio Taquari (Pantanal): IBSP 23893-94, IBSP 23993-95, IBSP 25377, IBSP 26246-47, IBSP 27440; Fazenda Cruzeiro, Aquidauana: MZUSP 4436; Ferreiros: IBSP 15161; Guaicurus: IBSP 12994; Guavira: IBSP 17861; Guia Lopes: IBSP 11402, IBSP 11963-64, IBSP 12433, IBSP 15474; Miranda: IBSP 3011 (holotype of *Bothrops neuwiedii mattogrossensis* Amaral, 1925), IBSP 6159, IBSP 6331, IBSP 6430-31, IBSP 24488-89, IBSP 24602, IBSP 27524-26; Miranda Estância: MZUSP 8827; Nhecolândia: IBSP 5497, IBSP 5510, IBSP 5524, IBSP 5527, IBSP 5605, IBSP 6507-08, IBSP 6519, IBSP 6928, IBSP 7527, IBSP 8525; Ponta Porã: IBSP 13322, IBSP 16456, IBSP 16655, IBSP 55389; Porto Esperança: IBSP 3092, IBSP 4672, IBSP 4838-39, IBSP 4858, IBSP 5293-94, IBSP 6613, IBSP 6615, IBSP 12548, IBSP 12609-10, IBSP 12613-26, IBSP 12628-31, IBSP 12637-40, IBSP 12642-70, IBSP 13902, IBSP 24663; Porto Murtinho: IBSP 13821, IBSP 19764-67, IBSP 26173-74, IBSP 26720-21, IBSP 29746, IBSP 55675; Rio Branco: IBSP 5170; Rio Negro: IBSP 24157, IBSP 24393-94; Senador Vitorino: IBSP 5178; Taunay: IBSP 5383, IBSP 5595, IBSP 5618, IBSP 5698, IBSP 5878, IBSP 5981, IBSP 6155-56, IBSP 6271, IBSP 7712, IBSP 12671, IBSP 14369, IBSP 14977, IBSP 28636, IBSP 28638; Xavantina: IBSP 25660. *Rondônia*: Vilhena: IBSP 22686. *São Paulo*: Araçatuba: IBSP 18624, IBSP 20521-22; Cascalho: IBSP 6606, IBSP 6614; Jaú: IBSP 6572. *Tocantins*: Ilha do Bananal: IBSP 20392, IBSP 26252; Santa Isabel, Ilha do Bananal: IBSP 12047. PARAGUAY: *Alto Paraná*: Hernandarias, Corpus Christ: IBSP 29972, IBSP 29975; Baía de Assunção: IBSP 10093-94. *Amambay*: Pedro Juan Caballero: IBSP 40047, IBSP 40634, IBSP 40635-43.

*Bothrops neuwiedi* - BRAZIL: ZSM 2348/0 (lectotype of *Bothrops Neuwiedi* Wagler, 1824). *Bahia*: Itiúba: IBSP 3012 (holotype of *Bothrops neuwiedii bahiensis* Amaral, 1925); Vitória da Conquista: CZGB-UESB 3794, CZGB-UESB 3910, CZGB-UESB 6531, CZGB-UESB 8073, CZGB-UESB 8509. *Goiás*: Campinas: IBSP 4677, IBSP 5264; Ipameri: IBSP 3016 (holotype of *Bothrops neuwiedii goyazensis* Amaral, 1925), IBSP 23449; *Minas Gerais*: Alfenas: IBSP 6089, IBSP 56390, IBSP 56524; Antônio Carlos: IBSP 21240, IBSP 22770, IBSP 23743, IBSP 24057; Antônio Justiniano: IBSP 3015 (holotype of *Bothrops neuwiedii minasensis* Amaral, 1925); Arantes: IBSP 6669; Bambuí: IBSP 53986; Barão de Cocais: IBSP 31554; Barbacena: IBSP 12265, IBSP 21682; Barra Feliz, Serra do Caraça: IBSP 17303, IBSP 17951, IBSP 18943, IBSP 19054, IBSP 19089, IBSP 24110; Belo Horizonte: IBSP 1599, IBSP 1614, IBSP 1617, IBSP 1632; Bocaina de Aiuruoca: IBSP 55320, IBSP 55742, IBSP 57059; Boqueirão: IBSP 11957; Caldas: IBSP 6014-15, IBSP 6844, IBSP 18953, IBSP 19046, IBSP 19081; Camanducaia: IBSP 6468, IBSP 16132-34, IBSP 24549, IBSP 24597, IBSP 24693-96, IBSP 24748-49, IBSP 24751, IBSP 27175, IBSP 33579, IBSP 43024, IBSP 46522, IBSP 56108, IBSP 56560, IBSP 57061; Campanha: IBSP 632-33, IBSP 6517, IBSP 15246-47; Caneleiras: IBSP 4430, IBSP 6534, IBSP 7763-64, IBSP 16449, IBSP 21203; Carandaí: IBSP 5254, IBSP 6569, IBSP 6796, IBSP 21181-82; Carrancas: IBSP 16928; Congonhas do Campo: IBSP 12242, IBSP 15149, IBSP 15260; Conselheiro Lafaiete: IBSP 23703-04; Conselheiro Mata: MZUSP 8120; Datas: MZUSP 8121; Diamantina (2 km ao S de): MZUSP 7559; Engenheiro Dolabela: IBSP 26895, IBSP 28398; Grão Mogol: IBSP 56519; Itacolomi: IBSP 4717; Itutinga: IBSP 52750; Jacutinga: IBSP 53517; João Aires (estação): IBSP 27291; Juiz de Fora: IBSP 46288; Lagoa Dourada (em Carandaí): IBSP 19030, IBSP 19035, IBSP 21132, IBSP 21248, IBSP 21836; Lagoa Santa: MNRJ 1315-16; Lavras: IBSP 23443; Liberdade: MNRJ 4949; Luminárias: IBSP 6317, IBSP 6752; Mariana: IBSP 4716, IBSP 6192, IBSP 6679, MZUSP 1469-72, MZUSP 1474; Monte Verde: IBSP 47184-85, IBSP 51984-85; Ouro Fino: IBSP 6610, IBSP 56052-54, IBSP 56074, IBSP 57277; Pacaú: IBSP 975; Parque Nacional da Serra da Canastra (Rolador): MZUSP 7580; Pedra do Sino: IBSP 11603-06, IBSP 28549-56; Pedra Menina: MZUSP 9044, MZUSP 9604; Pedro Leopoldo: IBSP 17386; Poços de Caldas: IBSP 3356, IBSP 6743-45, IBSP 7718-19, IBSP 9747, IBSP 14998, IBSP 15254-55, IBSP 15347, IBSP 16447-48, IBSP 17819-23, IBSP 18149, IBSP 18338, IBSP 18774, IBSP 19012-13, IBSP 19033, IBSP 19041, IBSP 19053, IBSP 19066, IBSP 19086, IBSP 20803, IBSP 21361-63; Prata: IBSP 56806-11; Queluzita: IBSP 17554; Rodrigo Silva: IBSP 15671, IBSP 15776; Santa Bárbara: IBSP 12546, IBSP 16472-73, IBSP 19732-33, IBSP 20345-46, IBSP 27169, IBSP 28047; Santa Rita: IBSP 4830; Santa Rita da Extrema: IBSP 6467, IBSP 6730, IBSP 6798, IBSP 6877; São Gotardo: IBSP 51280; Serra do Caraça (Parque do Caraça): IBSP 25121, IBSP 52968, MZUSP 5249; Serra do Cipó: MZUSP 7516, MZUSP 7567; Três Pontas: IBSP 46490; Tripuí: IBSP 10974, IBSP 13964, IBSP 15473; Varginha: IBSP 7778. *Paraná*: Arapongas: IBSP 18385; Araucária: IBSP 4459, IBSP 4477, IBSP 4539, IBSP 4627, IBSP 4977-78, IBSP 6024, IBSP 6063, IBSP 6212-19, IBSP 6230-34, IBSP 6274-75, IBSP 6305, IBSP 6747-48, IBSP 11168-70, IBSP 11231-35, IBSP 11285, IBSP 14987, IBSP 14989, IBSP 14992, IBSP 16224-25, IBSP 18047, IBSP 18080, IBSP 18148, IBSP 18340, IBSP 18412, IBSP 18629, IBSP 18692, IBSP 18762, IBSP 18782, IBSP 18862, IBSP 19000, IBSP 19018, IBSP 19045, IBSP 20974, IBSP 20986, IBSP 33611; Campo Largo da Piedade: IBSP 6025-28, IBSP 6736-37, IBSP 11107-08; Castro: IBSP 3014 (holotype of *Bothrops neuwiedii paranaensis* Amaral, 1925), IBSP 4338, IBSP 5174, IBSP 6321, IBSP 6509, IBSP 6687-88; Curitiba: IBSP 2687, IBSP 11227-28, IBSP 13981, IBSP 19729, IBSP 21044, IBSP 21050, IBSP 21133; Jaguariaíva: IBSP 6570, IBSP 56058-62; Joaquim Murtinho: IBSP 4689, IBSP 5239; Júlio de Castilhos: IBSP 7005; Piraí: IBSP 5168, IBSP 6726-27, IBSP 14999, IBSP 28911; Piraquara: IBSP 18145, IBSP 18153, IBSP 18252-54, IBSP 18260, IBSP 18277, IBSP 18280, IBSP 18283, IBSP 18398, IBSP 18411, IBSP 18465, IBSP 18544, IBSP 18855, IBSP 19042; Ponta Grossa: IBSP 21214; Rolândia: IBSP 16217-18, IBSP 16470-71; São José dos Pinhais: IBSP 4432-33, IBSP 4822; Tamandaré: IBSP 6609, IBSP 12335, IBSP 12269; Teixeira Soares: IBSP 6746; Telêmaco Borba: IBSP 57276; Tibagi: IBSP 53518; Tronco: IBSP 2718. *Rio de Janeiro*: Barão de São José: IBSP 6154 (paratype of *Bothrops neuwiedii fluminensis*, Amaral, 1933b), IBSP 6263, IBSP 6402 (paratype of *Bothrops neuwiedii fluminensis*, Amaral, 1933b), IBSP 7424 (paratype of *Bothrops neuwiedii fluminensis*, Amaral, 1933b), IBSP 7602-04 (paratypes of *Bothrops neuwiedii fluminensis*, Amaral, 1933b), IBSP 8419; Barcelos: IBSP 7806 (holotype of *Bothrops neuwiedii fluminensis*, Amaral, 1933b), IBSP 7869-70, IBSP 8766, IBSP 9680, IBSP 9792, IBSP 11095, IBSP 11269; Itacuruçá: MZUSP 3095; Saturnino Braga: IBSP 9841. *Santa Catarina*: Campos Novos: IBSP 46001, IBSP 46108, IBSP 46217, IBSP 47671; Ipoméia: IBSP 12471; *São Paulo*: Andrade: IBSP 6301, IBSP 6381; Angatuba: IBSP 55555, MZUSP 4917; Bandeirantes: IBSP 6035, IBSP 6090; Birigui: IBSP 9858; Botucatu: IBSP 53520; Buri: IBSP 6161, IBSP 18921; Cotia: IBSP 56639; Cunha: IBSP 51249; Dona Catarina: IBSP 19017, IBSP 33167; Engenheiro Hermillo: IBSP 4442, IBSP 6160, IBSP 6280, IBSP 6302-03, IBSP 6466, IBSP 6520, IBSP 9994, IBSP 11087, IBSP 11166-67, IBSP 11406-07, IBSP 16409-10, IBSP 17406, IBSP 18079, IBSP 18261-62, IBSP 18276, IBSP 18294, IBSP 18339, IBSP 18341, IBSP 18414-15, IBSP 18420, IBSP 18857, IBSP 18905, IBSP 18940, IBSP 19024; Faxina: IBSP 4845, IBSP 6141, IBSP 6465, IBSP 6475, IBSP 6607, IBSP 6839, IBSP 6888, IBSP 28052; George Oetterer: IBSP 11750; Guaíra: IBSP 4484; Guaratinguetá: IBSP 24643, IBSP 25981, IBSP 28259; Itapetininga: IBSP 4292, IBSP 6434, IBSP 6473-74, IBSP 6631-32, IBSP 7893, IBSP 11608, IBSP 18082, IBSP 18146-47, IBSP 18946, IBSP 21137, IBSP 22820, IBSP 31923, IBSP 31935, MZUSP 4767; Itu: IBSP 21062, IBSP 51425, IBSP 54566, IBSP 56946, IBSP 57016; Jundiaí: IBSP 55930; Juriti: IBSP 16259-60; Km 81 da Via Raposo Tavares: IBSP 21268; Mairinque: IBSP 24329, IBSP 53970, IBSP 57278; Moreiras: IBSP 17969, IBSP 18963; Peixoto Gomide: IBSP 12306, IBSP 15576; Pirapitingui: IBSP 6190-91; Prata: IBSP 576, IBSP 3591, IBSP 4720, IBSP 8438; Rancho Villela: IBSP 28547; Ribeirão Preto: IBSP 53521; Rocinha: IBSP 11884; Salto de Itu: IBSP 19037, IBSP 56950; Salto de Pirapora: IBSP 55322-23; São José do Barreiro (Serra da Bocaina, 1600 m): IBSP 29240; São José dos Campos: IBSP 31427; São Miguel Arcanjo: IBSP 26222; Sorocaba: IBSP 4821, IBSP 4828, IBSP 4831, IBSP 4857, IBSP 6157, IBSP 6162, IBSP 6256, IBSP 6286-88, IBSP 6833-34, IBSP 55986; Tombadouro: IBSP 3263; Vargem: IBSP 11943, IBSP 17399-400, IBSP 17945, IBSP 18150.

*Bothrops pauloensis* - BRAZIL: *Distrito Federal*: Brasília: IBSP 43182, IBSP 44011, IBSP 45638; Taguatinga: IBSP 53142. *Goiás*: Anápolis: IBSP 16757, IBSP 54327; Campinas: IBSP 4651, IBSP 6797; Campo Alegre de Goiás: IBSP 47362, IBSP 56535; Catalão (Via Araguari): IBSP 32186, IBSP 32190, IBSP 32768, IBSP 32775, IBSP 32781, IBSP 32785, IBSP 32788-90, IBSP 53515; Goiânia: IBSP 33008-10, IBSP 33029, IBSP 33031, IBSP 33125-27, IBSP 33156, IBSP 33158, IBSP 33161, IBSP 33262, IBSP 33479, IBSP 33534; Jataí: MZUSP 3779-81; Parque Nacional de Emas: IBSP 57081-83, IBSP 58206-22; Santa Rita do

AraguaiaSANTA RITA DO ARAGUAIA: MZUSP 9914-15, MZUSP 9940. *Mato Grosso*: Alto Araguaia: MZUSP 9926, MZUSP 9928, MZUSP 9937, MZUSP 10805; Barra do Garças: IBSP 37574, IBSP 37578; Base Camp: MZUSP 5397; Chapada dos Guimarães: IBSP 24557-58, IBSP 42252; Colônia Indígena de São Marcos: IBSP 33883, IBSP 34337, IBSP 43181, IBSP 43183; Cuiabá: IBSP 24619-20; Diamantino: IBSP 26261; Guiratinga: IBSP 16874. *Mato Grosso do Sul*: Aparecida do Taboado: IBSP 41491; Aquidauana: IBSP 11598-99, IBSP 11601, IBSP 32072, IBSP 32092; Arapuá: IBSP 6279, IBSP 6307, IBSP 6311, IBSP 15297; Bela Vista: IBSP 16633; Bodoquena: IBSP 17038-39; Cabeceira do Apa: IBSP 19718-20, IBSP 19724; Campo Grande: IBSP 6054, IBSP 14993, IBSP 18858; Coxim: IBSP 41496; Guavira: IBSP 14599, IBSP 15298; Guia Lopes da Laguna: MZUSP 10212-13; Itaum: IBSP 17764, IBSP 18549; Jaraguari (Quinta do Socego): MZUSP 10233; Jupiá: IBSP 21372, IBSP 22036; Maracaju: IBSP 18081, IBSP 19834, IBSP 19856, IBSP 21255-56; Nioaque: IBSP 20884, MZUSP 10220; Paranaíba: IBSP 46126-27, IBSP 46129, IBSP 46131, IBSP 46135-36, IBSP 46138-39; Ponta Porã: IBSP 13321, IBSP 16459-61, IBSP 16491, IBSP 16725, IBSP 16829-31, IBSP 17629, IBSP 17718, IBSP 17763, IBSP 18545, IBSP 18593, IBSP 19747, IBSP 19824, IBSP 19883-84, IBSP 22317, IBSP 28063-64; Senador Vitorino: IBSP 5177; Sidrolândia (Fazenda Santa Olinda): MZUSP 10202; Terenos: IBSP 12336, IBSP 15579-80; Três Lagoas: IBSP 17765, IBSP 44623, IBSP 53659. *Minas Gerais*: Araguari: IBSP 56520, IBSP 56527-34, IBSP 56536; Itaipu (estação): IBSP 25185-86; Prata: IBSP 53679, IBSP 56949; Santa Juliana: IBSP 15325; São Sebastião do Paraíso: IBSP 18286; Uberaba: IBSP 46998, IBSP 56942-44; Uberlândia: IBSP 5217, IBSP 6078, IBSP 6153, IBSP 6518, IBSP 27534; Uruburetama: IBSP 15256-58; Vazante: IBSP 52805; Zelândia: IBSP 29982, IBSP 30203. *São Paulo*: Agudos: IBSP 6753; Altinópolis: IBSP 18162, IBSP 18734, IBSP 18852, IBSP 18856, IBSP 18925, IBSP 19055, IBSP 19073, IBSP 19097, IBSP 19162; Américo Brasiliense: IBSP 18158; Analândia: IBSP 18475, IBSP 56945; Andrade: IBSP 6322, IBSP 6382-83, IBSP 6472; Araraquara: IBSP 4485, IBSP 23459, IBSP 53509; Artur Nogueira: IBSP 6384; Assis: IBSP 21324, IBSP 21325, IBSP 21326; Avaré: IBSP 6152, IBSP 18157, IBSP 19014, IBSP 20997, IBSP 58240-41, MZUSP 4738; Barra Bonita: IBSP 53508; Barra Grande (povoado de Avaré): IBSP 21170-73, IBSP 21196-97, IBSP 23408; Boa Esperança: IBSP 1296, IBSP 6670; Bofete: IBSP 53514, IBSP 56311; Borebi: IBSP 6272; Botucatu: IBSP 15394, IBSP 44486, IBSP 56948, IBSP 57063, MZUSP 1918, MZUSP 1990-92, MZUSP 2009-10, MZUSP 2221-33, MZUSP 2652-55, MZUSP 3982-83, MZUSP 5281; Brotas: IBSP 6318-19; Buri: IBSP 4563, IBSP 6571; Cabrália: IBSP 6281; Cajuru: IBSP 6754; Campo Alegre: IBSP 11286; Cerqueira César: IBSP 6386, IBSP 6393, IBSP 29202, IBSP 46100; Cerrado: IBSP 5401; Córrego Fundo: IBSP 16285; Corumbataí: IBSP 583, IBSP 8442; Descalvado: IBSP 18282, IBSP 18615-16, IBSP 19056-57, IBSP 53510; Emas: MZUSP 3669; Engenheiro Coelho: IBSP 6428; Engenheiro Hermillo: IBSP 5201; Espírito Santo do Pinhal: IBSP 56525; Faxina: IBSP 1193; Franca: IBSP 56437; Guaíra: IBSP 5228; Guatapará: IBSP 6173, IBSP 6228-29; Itapetininga: IBSP 6304; Itaquerê: IBSP 6469-70; Itatiba: IBSP 32040, IBSP 32293; Itatinga: IBSP 6680, IBSP 6684-85; Itirapina: IBSP 44479, IBSP 56313; Itobi: IBSP 459, IBSP 4461, IBSP 6429; Jataí: IBSP 3104; Joá: IBSP 6273, IBSP 6875; Lagoa Branca: IBSP 18289, IBSP 18981, IBSP 19072, IBSP 19113-14; Leme: IBSP 3013 (holotype of *Bothrops neuwiedii pauloensis* Amaral, 1925); Lobo: IBSP 6300; Macedônia: IBSP 6059, IBSP 6320; Matão: IBSP 4718, IBSP 4996, IBSP 6380, IBSP 21158-66; Mococa: IBSP 4758, IBSP 7858; Mogi-Guaçu: IBSP 17995; Monjolinho: IBSP 13194; Morro Agudo: IBSP 56051; Motuca: IBSP 6385, IBSP 6735; Nova Granada: IBSP 22632; Nova Louzã: IBSP 6432-33; Palmeiras: IBSP 6827, IBSP 9027; Palmital: IBSP 6728-29; Paranapanema: IBSP 56312; Porangaba: IBSP 5887, IBSP 11607; Ressaca: IBSP 6608, IBSP 6671, IBSP 6835, IBSP 6895-97; Restinga: IBSP 575, IBSP 6828, IBSP 6882; Ribeirão Preto: IBSP 53511-12, IBSP 54732; Rubião Júnior: IBSP 6829, IBSP 18947; Santa Cruz da Conceição: IBSP 24883; Santa Elisa: IBSP 5795, IBSP 6140; Santa Rosa do Viterbo: IBSP 52545, IBSP 57062; São Carlos: IBSP 21119-22, IBSP 48342, IBSP 56433; São João da Boa Vista: IBSP 18284; São Joaquim da Barra: IBSP 13869, IBSP 15265-69; São Simão: IBSP 56097; Sapezal: IBSP 15404; Serrana: IBSP 6881; Sorocaba: IBSP 53513; Tambaú: IBSP 18735, IBSP 56443; Timbira: IBSP 6379; Toledo: IBSP 6683, IBSP 6686; Trabiju: IBSP 6285; Tujuguaba: IBSP 6391-92; Visconde do Rio Claro: IBSP 6681, IBSP 6843; Vitória: IBSP 6779.

*Bothrops pubescens* - BRAZIL: *Rio Grande do Sul*: Bagé: IBSP 19745; Cachoeira do Sul: IBSP 26944-45, IBSP 27454, IBSP 27621, IBSP 28635, IBSP 28907, IBSP 28972, IBSP 28974, IBSP 32313, IBSP 32358, IBSP 32361, IBSP 32416, IBSP 32480, IBSP 32509, IBSP 32758, IBSP 32767; Canguçu: IBSP 20851-54; Capela: IBSP 5186-87, IBSP 5203, IBSP 5220-21, IBSP 5606, IBSP 5823, IBSP 5889, IBSP 6013, IBSP 6016-18, IBSP 6139, IBSP 6142-43, IBSP 6174, IBSP 7004 (fêmea prenhe); Cerro Chato: IBSP 23437, IBSP 23448, IBSP 24112, IBSP 24130, IBSP 24654, IBSP 24656, IBSP 24753-54;

Encruzilhada do Sul: IBSP 28248-50; Ijuí: IBSP 6831, IBSP 6876; Itaqui: MZUSP 1476 (holotype of *Bothrops neuwiedii riograndensis* Amaral, 1925); Jaguari: IBSP 16474, IBSP 27324-26, IBSP 28773-74, IBSP 29891, IBSP 30937, IBSP 31291; Monte Alegre: IBSP 20899; Pelotas: IBSP 12432, IBSP 12484-85, IBSP 12487-89, IBSP 25640, IBSP 28534-35, IBSP 28537-38, IBSP 28914, IBSP 29250, IBSP 29322, IBSP 29890, IBSP 32283-84; Porto Alegre: IBSP 5244, IBSP 6630, IBSP 6832, IBSP 22499, IBSP 22681, IBSP 22731, IBSP 44277, IBSP 44544, IBSP 46057, IBSP 47670; Restinga Seca: IBSP 6894, IBSP 7241, IBSP 7765, IBSP 27099, IBSP 49392; São Gabriel: IBSP 34168, IBSP 34173. URUGUAY: *Maldonado*: Cerro Pan de Azucar, Piriapolis: IBSP 46077, IBSP 46220; Clemente, Instituto Universitário de Biologia: IBSP 46358; *Tacuarembó*: Pozo Hondo, Tambores: MZUSP 5874.

## Appendix II

Contributions of each variable analyzed to the first three principal components for males and females of seven patterns (A-G) of the *Bothrops neuwiedi* complex. The five largest contributions of each component are emphasized with asterisk. PCA statistics: VA = variance explained by the components; % = percent of total variance explained by the components. Variables: IR = intersupraocular rows; V = ventrals; SC = subcaudals; D1 = initial dorsals; SSS1 = scales between subocular and 4th supralabial counted in anterior level under the eye; DB = number of dorsolateral blotches throughout body; SHB = shape of the dorsolateral blotch from middle trunk; RDB = rows of dorsal scales that form the principal part of dorsolateral blotch from middle trunk; NDB = number of dorsal scales in the smallest distance between the dorsolateral blotch from middle trunk and the anterior blotch; KC = keels with the same color as dorsal scales; BI = blotches in the interspaces between two consecutive dorsolateral blotches; BB = border of dorsolateral blotches; DPS = dorsal postcephalic stripes; M = melanic head; OS = ornamentation of supralabials; EOS = extension of the ornamentation of supralabials.

| PCA statistics/ variables analyzed | PATTERNS A+C+D | | | | | |
|---|---|---|---|---|---|---|
| | Males | | | Females | | |
| | Comp. 1 | Comp. 2 | Comp. 3 | Comp. 1 | Comp. 2 | Comp. 3 |
| **VA** | 6.3 | 1.7 | 1.4 | 5.4 | 2.1 | 1.2 |
| **%** | 39.5 | 10.4 | 8.8 | 33.9 | 12.6 | 7.4 |
| **KC** | -0.860* | 0.423 | -0.159 | -0.684* | 0.572* | 0.064 |
| **OS** | -0.844* | 0.438* | -0.153 | -0.718* | 0.609* | 0.079 |
| **EOS** | -0.844* | 0.438* | -0.153 | -0.693* | 0.617* | 0.093 |
| **DB** | -0.829* | -0.015 | 0.177 | -0.788* | -0.049 | 0.100 |
| **M** | -0.791* | 0.282 | -0.299 | 0.853* | 0.221 | -0.155 |
| **BB** | -0.703 | -0.425* | 0.010 | -0.653 | -0.319 | 0.068 |
| **IR** | 0.667 | 0.265 | 0.345 | 0.583 | 0.360 | 0.379* |
| **SC** | 0.583 | 0.065 | -0.375* | 0.546 | 0.364 | -0.066 |
| **V** | 0.578 | 0.161 | -0.449* | 0.593 | 0.426* | 0.141 |
| **SSS1** | 0.544 | -0.023 | 0.064 | 0.474 | -0.059 | 0.311* |
| **D1** | 0.528 | 0.266 | 0.426* | 0.517 | 0.232 | 0.455* |
| **NDB** | 0.519 | 0.097 | -0.513* | 0.635 | 0.123 | -0.279* |
| **SHB** | 0.342 | 0.677* | 0.278 | 0.333 | 0.054 | -0.018 |
| **RDB** | 0.330 | 0.092 | 0.478* | -0.025 | -0.421* | 0.277 |
| **DPS** | -0.084 | 0.054 | 0.006 | -0.030 | -0.271 | 0.712* |
| **BI** | 0.393 | -0.443* | -0.006 | 0.428 | -0.111 | -0.045 |

| PCA statistics/ variables analyzed | PATTERNS B+C+D | | | | | |
|---|---|---|---|---|---|---|
| | Males | | | Females | | |
| | Comp. 1 | Comp. 2 | Comp. 3 | Comp. 1 | Comp. 2 | Comp. 3 |
| **VA** | 5.3 | 2.3 | 1.2 | 5.4 | 2.5 | 1.0 |
| **%** | 35.6 | 15.1 | 7.8 | 38.4 | 17.7 | 7.3 |
| **OS** | 0.937* | 0.030 | -0.033 | 0.953* | 0.048 | -0.014 |
| **DPS** | 0.839* | 0.021 | 0.009 | 0.875* | 0.005 | -0.141 |
| **BI** | -0.835* | 0.012 | 0.003 | -0.861* | 0.055 | 0.006 |
| **RDB** | 0.799* | 0.109 | 0.010 | 0.612 | -0.020 | 0.325* |
| **M** | -0.736* | 0.462 | 0.191 | -0.753* | 0.515* | -0.144 |
| **BB** | -0.602 | -0.533* | -0.183 | -0.641* | -0.499* | 0.152 |
| **IR** | 0.584 | 0.463 | 0.074 | 0.462 | 0.565* | 0.081 |
| **D1** | 0.552 | 0.287 | -0.066 | 0.586 | 0.420 | 0.010 |
| **DB** | 0.510 | -0.551* | -0.435* | 0.591 | -0.403 | 0.439* |
| **V** | -0.159 | 0.645* | -0.455* | -0.064 | 0.727* | 0.241* |
| **SC** | -0.026 | 0.614* | -0.350* | -0.021 | 0.626* | 0.357* |
| **NDB** | -0.499 | 0.512* | 0.179 | -0.619 | 0.453 | -0.030 |
| **EOS** | 0.109 | -0.105 | 0.595* | - | - | - |
| **SHB** | 0.483 | 0.088 | 0.427* | 0.480 | 0.055 | -0.666* |
| **SSS1** | 0.315 | 0.297 | -0.000 | 0.299 | 0.410 | -0.155 |

| PCA statistics/ variables analyzed | PATTERNS C+D+E | | | | | |
|---|---|---|---|---|---|---|
| | Males | | | Females | | |
| | Comp. 1 | Comp. 2 | Comp. 3 | Comp. 1 | Comp. 2 | Comp. 3 |
| **VA** | 5.2 | 2.1 | 1.3 | 5.2 | 1.9 | 1.4 |
| **%** | 34.9 | 13.7 | 8.9 | 34.4 | 12.5 | 9.4 |
| **OS** | 0.958* | 0.120 | -0.038 | 0.957* | 0.138 | -0.073 |
| **EOS** | 0.958* | 0.120 | -0.038 | 0.957* | 0.138 | -0.073 |
| **BI** | -0.837* | -0.106 | -0.020 | -0.874* | -0.056 | 0.085 |
| **M** | -0.791* | 0.393 | -0.168 | -0.823* | 0.351 | 0.087 |
| **DB** | 0.732* | -0.351 | 0.133 | 0.652 | -0.304 | 0.388* |
| **SC** | 0.562 | 0.411 | -0.344 | 0.360 | 0.547* | -0.100 |
| **NDB** | -0.547 | 0.359 | -0.391* | -0.608 | 0.376* | -0.155 |
| **BB** | -0.535 | -0.622* | 0.088 | -0.674* | -0.531* | -0.005 |
| **IR** | -0.517 | 0.447* | 0.304 | -0.510 | 0.376* | 0.421* |
| **V** | 0.242 | 0.515* | -0.506* | 0.267 | 0.680* | 0.098 |
| **SHB** | 0.245 | 0.422* | 0.482* | 0.231 | 0.096 | 0.388* |
| **RDB** | 0.329 | 0.297 | 0.473* | 0.242 | -0.172 | 0.377 |
| **D1** | -0.266 | 0.379 | 0.369* | -0.195 | 0.415* | 0.523* |
| **SSS1** | -0.232 | 0.419* | 0.252 | -0.053 | 0.246 | -0.607* |
| **DPS** | 0.146 | -0.096 | 0.093 | 0.181 | -0.159 | 0.272 |

| PCA statistics/ variables analyzed | PATTERNS A+B+E | | | | | |
|---|---|---|---|---|---|---|
| | Males | | | Females | | |
| | Comp. 1 | Comp. 2 | Comp. 3 | Comp. 1 | Comp. 2 | Comp. 3 |
| **VA** | 5.4 | 2.9 | 1.3 | 4.4 | 2.6 | 1.6 |
| **%** | 34.1 | 18.0 | 8.0 | 29.5 | 17.4 | 10.9 |
| **EOS** | -0.929* | -0.036 | 0.012 | 0.932* | -0.087 | 0.098 |
| **IR** | 0.792* | 0.244 | 0.130 | -0.749* | -0.254 | 0.005 |
| **D1** | 0.723* | 0.186 | 0.075 | -0.726* | -0.042 | 0.031 |
| **DPS** | 0.723* | 0.425 | -0.122 | -0.853* | -0.193 | -0.040 |
| **KC** | -0.702* | 0.619* | 0.188 | 0.408 | -0.781* | -0.017 |
| **BB** | -0.700 | 0.607* | 0.193 | 0.439 | -0.828* | -0.021 |
| **RDB** | 0.697 | 0.144 | -0.031 | -0.579 | 0.066 | 0.228* |
| **OS** | -0.624 | -0.684* | -0.171 | 0.803* | 0.485 | 0.098 |
| **SSS1** | 0.597 | -0.000 | 0.208 | -0.044 | 0.149 | -0.681* |
| **DB** | -0.567 | 0.196 | -0.291* | 0.095 | 0.027 | 0.868* |
| **SC** | 0.039 | -0.792* | 0.031 | 0.241 | 0.536* | -0.016 |
| **V** | 0.070 | -0.676* | 0.370* | 0.146 | 0.580* | 0.105 |
| **NDB** | 0.122 | -0.192 | 0.787* | 0.113 | 0.140 | -0.540 |
| **BI** | -0.370 | 0.358 | 0.333* | 0.329 | -0.549* | -0.005 |
| **M** | -0.255 | 0.216 | 0.287* | - | - | - |
| **SHB** | 0.398 | 0.163 | -0.232 | -0.436 | 0.044 | 0.210* |

| PCA statistics/ variables analyzed | PATTERNS E+F+G | | | | | |
|---|---|---|---|---|---|---|
| | Males | | | Females | | |
| | Comp. 1 | Comp. 2 | Comp. 3 | Comp. 1 | Comp. 2 | Comp. 3 |
| **VA** | 2.8 | 1.6 | 1.2 | 2.8 | 1.6 | 1.3 |
| **%** | 23.3 | 13.7 | 10.1 | 21.7 | 12.1 | 9.7 |
| **DPS** | 0.841* | 0.092 | 0.058 | 0.814* | -0.282 | -0.030 |
| **IR** | 0.598* | -0.342* | -0.173 | 0.644* | 0.064 | -0.045 |
| **SHB** | 0.588* | 0.243 | 0.121 | 0.527* | -0.446* | 0.043 |
| **SSS1** | 0.530* | -0.121 | -0.219 | 0.490 | 0.179 | 0.204 |
| **SC** | -0.211 | 0.656* | -0.027 | -0.462 | -0.066 | 0.308* |
| **OS** | -0.441 | -0.604* | 0.062 | -0.129 | 0.790* | -0.136 |
| **EOS** | -0.473 | 0.538* | 0.304* | -0.539* | -0.508* | 0.260* |
| **NDB** | -0.206 | 0.249 | -0.692* | -0.370 | 0.062 | -0.695* |
| **D1** | 0.449 | -0.172 | 0.478* | 0.461 | 0.007 | -0.150 |
| **V** | 0.275 | 0.379* | 0.397* | 0.137 | -0.095 | 0.339* |
| **DB** | -0.485* | -0.300 | 0.382* | 0.073 | 0.552* | 0.623 |
| **RDB** | 0.293 | 0.181 | -0.056 | 0.559* | 0.218 | -0.122 |

| PCA statistics/ variables analyzed | PATTERNS B+F+G | | | | | |
|---|---|---|---|---|---|---|
| | Males | | | Females | | |
| | Comp. 1 | Comp. 2 | Comp. 3 | Comp. 1 | Comp. 2 | Comp. 3 |
| **VA** | 2.5 | 2.0 | 1.5 | 2.2 | 2.0 | 1.4 |
| **%** | 19.6 | 15.1 | 11.9 | 18.6 | 16.9 | 11.5 |
| **IR** | -0.720* | 0.185 | 0.098 | -0.600* | -0.161 | 0.344 |
| **OS** | 0.691* | -0.459* | 0.065 | 0.696* | 0.513* | -0.065 |
| **EOS** | 0.684* | 0.319 | -0.176 | 0.712* | -0.417 | 0.148 |
| **D1** | -0.562* | 0.211 | -0.176 | -0.486 | -0.226 | 0.445* |
| **RDB** | -0.511* | 0.344 | -0.139 | 0.007 | 0.196 | 0.348* |
| **DPS** | 0.264 | 0.699* | -0.329 | 0.316* | -0.773* | 0.148 |
| **DB** | 0.029 | -0.622* | 0.111 | 0.176 | 0.487* | 0.271 |
| **SC** | 0.309 | 0.511* | 0.407* | 0.250 | 0.184 | 0.371 |
| **BI** | -0.092 | 0.212 | 0.606* | - | - | - |
| **V** | 0.449 | 0.364* | 0.546* | 0.560* | 0.172 | 0.505* |
| **NDB** | -0.248 | 0.059 | 0.504* | -0.228 | 0.455* | 0.109 |
| **SHB** | 0.223 | 0.361 | -0.357* | 0.270 | -0.600* | -0.050 |
| **SSS1** | -0.153 | 0.046 | 0.340 | -0.107 | -0.121 | 0.643* |