



A taxonomic bibliography of the South American snakes of the *Crotalus durissus* complex (Serpentes, Viperidae)

PAULO E. VANZOLINI and MYRIAM E.V. CALLEFFO

¹Museu de Zoologia, Universidade de São Paulo, Cx. Postal 42694, 04299-970 São Paulo, SP, Brasil

²Instituto Butantan, Laboratório de Herpetologia, São Paulo, SP, Brasil

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contributed by PAULO E. VANZOLINI

ABSTRACT

A survey is made of the taxonomic literature on South American rattlesnakes (genus *Crotalus*, family Viperidae). Two main areas are emphasized: the attribution of the names proposed in the eighteenth century by Linnaeus and Laurenti, and the current scheme of division in subspecies.

The attribution of names is examined based on the original descriptions and on relevant previous and contemporary literature. The presently adopted scheme, proposed by Klauber (1941, 1972) is found not entirely satisfactory, but reasonable enough – besides being hallowed by use.

The scheme of geographical differentiation, intrinsically important and with broad practical implications (differentiation of the venom) is found to be the culmination of a long series of deficient analyses, and in urgent need of proper investigation.

Key words: *Crotalus durissus*, Viperidae, geographical differentiation, differentiation of the venom.

INTRODUCTION

The assemblage of forms currently known as the subspecies of *Crotalus durissus* embodies some of the most interesting problems in Neotropical herpetology. They constitute a set of closely related parapatric forms, whose mutual relations and mechanisms of speciation, never yet properly studied, are conceivably of great theoretical interest. Additionally, on the practical side, geographical differentiation has been demonstrated in the chemistry of the venom, a fact of far-reaching and urgent medical as well as zoological implications. In contradistinction with these attractive features, studies on the group have been few and undistinguished. The

old literature is confused and confusing: it has been analyzed at several reprises by Klauber (q.v.i.), who proposed a sensible, if rather uninspired scheme, generally adopted. Geographical differentiation, obvious and intense, was deplorably dealt with by Hoge (1966), whose cursory work has been accepted in the literature without evaluation, culminating in the thorough but uncritical compilation by McCranie (1993).

The very extensive range of the group and the relatively large size of the individual snakes raise considerable logistic problems to a comprehensive revision. We have undertaken a piecemeal review of the Brazilian forms, using mostly the materials at hand in our institutions and aiming initially at a formal traditional taxonomic treatment, to be followed, if feasible, by investigations in more depth

Correspondence to: P.E. Vanzolini
E-mail: vanzo@usp.br

of the evolutionary aspects. Thus the present review of papers of systematic or distributional importance.

We have organized the matter in four sections: (i) a history of the systematic concepts in what they refer to South America; (ii) papers that contain precise geographic information, listed in Appendix 1; and (iii) papers that, although mentioning South American rattlers, contain no information useful in the present context, so denoted in the References. There is one additional section on chromatism, and a concise gazetteer.

A HISTORY OF CONCEPTS AND NAMES

Usually, the review of old literature is evocative and pleasant. Not here: the literature on South American *Crotalus* is very uneven and uncommonly unrewarding. Rattlesnakes are charismatic animals, surrounded by legend, and from early times attracted the attention of travelers of diverse scientific competence, who tended to write copiously on them. These, mostly naive, travel reports constitute the raw materials of practically all the early literature (Curran 1935). Specimens, with or without locality data, were surprisingly rare in collections, and sparingly reported upon.

Linnaeus (1758: 214) diagnosed the genus *Crotalus* as snakes having (widened) ventral scales, small or large (actually divided or undivided) subcaudals, and a terminal rattle, or crepitaculum. He included three species, all three marked with the “Mars sign”, ♂, that at the time already signified in the general literature “male”, but that in the context of the *Systema Naturae* indicated instead that the species had poison fangs (Linnaeus 1758: 194-195). For each species Linnaeus gave scale counts (ventrals and subcaudals), country of origin (“habitat”) and, in two cases, summary notes on color pattern. He also included bibliographic references, to his own pre-*Systema* work and to contemporary authors. The species were:

1. *Crotalus horridus*, 167 ventrals + 25 subcaudals, from “America”. References are given to Linnaeus’s own “Mus. Ad. Fr.”, better known as Mu-

seum Regis, to Bradley (1721), and to Seba (1734-1765). Additional notes referred to its venomousness, to its eating birds and squirrels on trees, to its being predated upon by hogs and to the existence of a natural antidote (“senega”, or milkwort, root, a *Polygala*). All these are well-known parts of North American folklore, early reported in Europe by Kalm (1752).

2. *C. dryinas*, 165 + 30 scales, from “America”, with a laconic note on color pattern, and a reference to *Amoenitates Academicæ* 1: 217 (Linnaeus 1749). This is a mistaken reference: the page mentioned is part of a botanical dissertation on “*Peloria*”. However, in the same *Amoenitates*, in the chapter entitled *Museum Principis*, p. 578, n° 24, is described an “*Anguis (Crotalophorus) scutis abdominalibus CLXV, caudalibus XXX*”, which is certainly *C. dryinas*. Eight references are made to the literature. Five are useless to us: Ray (1693), Seba (1734-1765), Jonstone (1650-1653), Nieremberg (1635) and Olearius (1674). Three other citations are potentially useful, to Marcgrave (1648), Piso (1648) and Hernandez (1651) – but in fact they are contradictory. The former two would point to northeastern Brasil, the latter to Mexico. One juvenile (“barely 2 feet long”) was available, gray with yellowish dorsal spots; no doubt a faded specimen.

3. *C. durissus*, with 172 + 24 scales, was referred to Kalm (1752, 1753), to Gronovius (1763-1764) and to the *Amoenitates* 1: 500. This last citation is again a mistake: the page mentioned (part of the thesis *Surinamensia Grilliana*) contains reference to one *Amphisbaena* and to *Anilius scytale*, not to *Crotalus*. Instead, on page 510 of the same *Surinamensia Grilliana* there is a “*Crotalophorus scutis abdominalibus CLXXII, scutis caudalibus XXI, paribusque squamarum III*”, which is certainly *C. durissus*. References in the *Amoenitates* are to Jonstone (1650-1653), to Nieremberg (1635), to Olearius (1674) to vol. 1, part 1, of the “*Museum Imperiale Petropolitans*” (1742), and to Vincent (1726). None of them is of any present use. Additionally, Swedish scientists who reviewed surviving Linnean herpetologi-

cal types (Lönnerberg 1896, Andersson 1900, Holm 1957) make it clear that no rattlesnake type is extant.

It is evident that Linnaeus recognized three species of rattlesnakes, based on actual specimens, but that his understanding of these was confused and did not go beyond the generic level. It is a conspicuous fact in the history of the knowledge about rattlesnakes that their being large venomous snakes sporting a rattle did for a long time overshadow more systematic information. In the case of the Linnaean names it is impossible to restore the original concepts. Short of squarely dismissing them (to us the best alternative, but too late now), the solution is to find an acceptable compromise – which was attempted, without much success, by Klauber (1941 q.v.i.).

Houttuyn (1764), in his adaptation of the Linnaean system, discusses briefly Linnaeus's concept of the genus and embarks on a discussion of the literature. The accounts of North and South American species, and even of supposedly Oriental ones, and especially of their emotional impact, are always treated jointly, as of a single entity. This is an interesting point in the history of Herpetology as a scientific discipline, but is confusing in the present context of assigning names to the South American forms. In this regard Houttuyn faithfully follows Linnaeus: he presents one figure of a rattlesnake (pl. 54: 1), copied from Seba, from the "East Indies", showing no color pattern and numbering some 42 segments to the rattle. It does not seem recognizable.

Linnaeus (1766: 372), in the twelfth edition of the *Systema*, adds two new species, *miliarius* (now *Sistrurus*) and *mutus* (now *Lachesis*). As to the species previously described, he adds new citations from Seba and leaves the rest unchanged.

Vosmaer (1767, 1768), the curator of the zoological cabinet of Stadtholder William V of Holland at The Hague, has a very interesting article that, curiously enough, never attracted proper attention. Besides experiments with the venom, he discusses (1768: 12) six specimens from Surinam

– three of them, he says, depicted by Seba (1735: pl. 45, fig. 4). (Incidentally this, a precise and reliable locality, is unusual for a Seba plate). Vosmaer comments on the Linnaean device of characterizing snake species by counts of ventral and subcaudal scales, and attempts to identify his own specimens by this means. He finds them in agreement with Linnaeus's *horridus*. This was the beginning of the pre-Klauberian tradition of applying *horridus* to South American snakes. This was not such an unreasonable construction, especially given the information on Seba's specimens. Klauber's purely pragmatic proposal (see below) was in fact motivated by the lack of positive data on the Linnaean types and on the strength of North American tradition. Klauber (1956), incidentally, does not cite Vosmaer.

Vosmaer's specimens were certainly taken to Paris with the remainder of the Stadtholder's museum, plundered by the French army in 1795 (Pieters 1980); apparently there is no trace left of them. Anyway, as Vosmaer did not innovate in nomenclature, the interest of his paper resides in the early and perceptive attempt to use numerical methods in taxonomy. As to Seba's collections, they were dispersed (Boeseman 1970); some specimens were later tracked (e.g. Thomas 1892), but no rattlesnake.

As a curious and obliquely informative note, Vosmaer (1768: 6) informs that rattlesnakes were called "boicinginga" in Surinam. This could hardly be so. The term ("snake that makes noise") is of the Tupí-Guaraní language, which was never spoken in northern South America – not even near Surinam. The citation indicates instead that Vosmaer was acquainted with Piso or Marcgrave, or both, although he does not quote them.

Laurenti (1768) includes in his genus *Caudisona* (explicitly a new name for *Crotalus*) five species:

1. *Caudisona terrifica*, sp.n., based on Seba (II: 95: 1), which had already served as partial basis for Linnaeus's *C. horridus*.
2. *C. durissus*, a Linnaean name maintained without reference to Linnaeus and based instead on Catesby

(1731-1743), and so on a North American snake.

3. *C. gronovii*, sp.n., based on Gronovius's (1754-1756) *Museum Ichthyologicum*, p. 45, a citation already used by Linnaeus for *C. durissus*.
4. *C. dryinas*, for which he literally repeats Linnaeus, including the wrong citation of the *Amoenitates Academicæ*.
5. *C. orientalis*, based on Seba (II: 96: 1 and II: 95: 3), both citations already used by Linnaeus for *C. dryinas*.

Fermin (1769: 218) was the second author to report on undoubtedly South American *Crotalus*, in the case also from Surinam. He does not use a Latin name, and repeats the usual comments on the rattle and the poison.

Boddaert (1783: 16), in a paper with an avowed systematic intention, accepts three species of *Crotalus*: (i) *C. horridus* L., (ii) *C. durissus* L. (of which he states having seen one specimen), and (iii) *C. exalbidus*, a new name for *C. dryinas*, explicitly cited from the *Systema Naturæ* and respective Seba references.

Weigel (1783) repeats Linnaeus and Laurenti.

Daubenton (1784) is an encyclopaedic dictionary. The relevant entries in the present context are: (i) "boiquira" (p. 593), a Marcgrave name, to become important in the literature; (ii) "serpent à sonette" (p. 678); and (iii) "teuthlaco" (p. 685), a name from Hernandez (1651), applied to *C. durissus*, strictly from the literature.

Gmelin (1789: 1080-1081), in his "thirteenth" edition of the *Systema Naturæ*, includes five species of *Crotalus*, the same as Linnaeus (1766). He has, however, some changes in the literature he cites: (i) Michaelis (1785) is added to *C. horridus*; (ii) Laurenti (1768), Boddaert (1783) and Weigel (1783) to the appropriate species, and Vosmaer (1767) to *C. durissus*. He questions the generic assignment of *C. mutus*.

Of these additions, Michaelis (1785) is no doubt the most interesting. It deals with the subjects of relevance at the time, length and thickness

of individual snakes, temperament, venom and bite (especially for us, the search for an antidote) in a professional and level-headed way. Unfortunately, it is all on northeastern North American snakes.

Lacépède (1789: 130, 408 seq.) includes five species of rattlesnakes; the proposed scientific names are given on a "table méthodique" (p. 130), individual treatments later. Given the great homogeneity of the genus, Lacépède describes in detail only the "boiquira", *Crotalus boiquira*, new name for Linnaeus's *C. horridus*. The distribution is given as extending from the Straits of Magellan (Tierra del Fuego) to Lake Champlain (in the northeastern U.S. near the Canadian border). In accordance with this broad distribution, Lacépède's comments are drawn from a variety of authors, from Marcgrave and Piso, who dealt with northeastern Brasil, through Hernandez on Mexico to Catesby and Kalm, on the United States. Considering the highly heterogeneous quality of Lacépède's information, this new name of his, *Crotalus boiquira*, could be taken seriously only if the specimen in Paris were extant. It is not (Thireau 1991). In fact, Duméril and Duméril (1851) refer no rattlesnakes in the Paris collection.

Besides (mis-)naming the "boiquira", Lacépède included in *Crotalus* three Linnaean species, *durissus*, *dryinas* and *miliarius*, and proposed a fully new one, *C. piscivorus*, currently valid in the genus *Agkistrodon*.

Bonnaterre (1790a, b) should be taken in conjunction with Daubenton (1784), to which he adds nothing.

The citation of Andrada (1791) is only a bibliographical curiosity aimed at Brasilians. José Bonifácio de Andrada e Silva, the "patriarch" of Brazilian independence, is known for his scientific activities in the field of mineralogy (Figueiroa 1997). This is the first reference we find to zoological interests. The paper deals superficially with envenomation, and is not relevant, but contains an intriguing phrase, unexplainable to this day: "The author reduces to fewer than 21 the total number of poisonous snakes".

Donndorff (1798), another paraphrase of Linnaeus (in fact of Gmelin, i.e., of the "thirteenth"

edition), maintains *miliarius*, *horridus*, *durissus*, *dryinas* and *mutus*, which latter species he speculates might be a *Boa*, and cites a wealth of eighteenth century literature, fortunately irrelevant in the present context. He cites, curiously enough, *Crotalus piscivorus* Lacépède, as “Neuere Gattungen” (“recent genera”).

Suckow (1798: 149), as many authors of the time, followed Lacépède, further adding two varieties: one, after Vosmaer (1768), unnamed, to *C. durissus*, and another, *C. orientalis* Laurenti, 1768, to *C. dryinas*.

Latreille (1801a,b) has a long chapter on rattlesnakes. He comments on the current confusion and adds to it. After the usual generalities on the rattle and the venom, he treats systematically eight species, of which four are described as new, reportedly with types in the Paris Museum: (i) *C. rhombifer* (p. 197), no type locality given; (ii) *C. immaculatus* (p. 201), after a figure of Seba, attributed to the East Indies; (iii) *C. simus* (p. 202, also after Seba, allegedly from Ceylon; and (iv) *C. atricaudatus*, from the United States, collected by Bosc. The type locality cited for the latter is “Carolina”, accepted by Klauber (1956). If there were interest in further refinement, the locality might be corrected to the neighborhood of Wilmington, North Carolina, where Bosc was for a time French consul (Aulard 1907). In his “additions” at the end of the text Latreille (1801: 313) restricts both *C. durissus* and *C. horridus* to North America, based on specimens collected by Ambroise Palisot de Beauvois during his exile in Philadelphia. He removes from *Crotalus* the species *mutus* and *piscivorus*.

Thireau (1991), in his most useful paper on old French rattlesnake types and notable specimens, remarks that he was unable to locate any Latreille specimen. He follows Hoge and Romano-Hoge (1981a, b) in assigning *simus* to the synonymy of *C.d. durissus*, and McCranie (1980 – in fact, Schmidt 1953) in assigning *rhombifer* to that of *adamanteus*.

Daudin (1802) has a very good survey of eighteenth century literature, and seems to be the first author to state that no species of *Crotalus* occurs on

both Americas. In his volume 5 Daudin (1802: 47-75) includes a text by Palisot de Beauvois on North American rattlesnakes, especially on their temperament, on hibernation and on the treatment of bites. His handling of the species, however, is less discerning; for instance, in spite of all the information to the contrary already available, he considers the number of rattle segments a valid systematic character. He accepts three Linnean species, *durissus* and *miliarius* in North America, *horridus* (the “boiquira”) in South America. *C. simus* and *C. rhombifer*, both of Latreille, are accepted at face value, and a new name is proposed, *C. strepitans* for *C. immaculatus* Latreille.

Thireau (1991) remarks that there is no extant type of Daudin’s *strepitans*. This is not surprising, since the name was expressly intended as a replacement for *immaculatus*. Thireau follows Klauber (1972) in assigning this name to the synonymy of *C. durissus terrificus*, which is in fact meaningless, as Klauber’s *terrificus* is a complex mix.

Bechstein (1802) mixes straight translation of Lacépède into German with updatings. His treatment is in general uncritical: he simply lists, without comment, *C. boiquira*, *C. dryinas*, *C. durissus*, *C. miliarius* and *C. piscivorus*.

Shaw (1802) accepts four species, three (*horridus*, *durissus* and *miliarius*) from North America, and one, *dryinas*, from an unspecified American region.

Hermann (1804) describes as new *Crotalus tessellatus*, no locality, said to differ (no details given) from *C. horridus* in color pattern and number of scales (151 + 21). Oppel (1810, 1811a, b) revises the work of earlier authors, and finds Linnaeus’s and Laurenti’s schemes good at the generic level.

Humboldt (1813) brings the first meaningful contribution to the study of South American rattlers. Two species are described, from the same locality, Cumaná in Venezuela. *Crotalus cumanensis* and *C. loefflingii* are said to differ in details of color pattern, body shape and tooth shape; they are currently considered synonyms. Humboldt briefly diagnoses the species he considered valid (*horridus*,

durissus and *rhubifer*) on the basis of scale counts and color pattern. In spite of his misapprehensions, Humboldt's paper is the first one that can be called professional, but was overlooked in the literature. Venezuelan rattlesnakes were included in the melting pot of the old names (*horridus* and *durissus*) until Boulenger (1896) placed them under *terrificus*, a position next adopted by Milá de la Roca (1932) and others, explicitly under the influence of Amaral. It was only J.A. Peters (1967) who, in a critique of Roze (1966), re-established *cumanensis*, which remains valid. Pérez-Santos and Moreno (1988) unexplainably attribute the species to Hoge (1966).

Cuvier (1817) did not aim at completeness in his treatment of genera, just at exemplification. With regard to *Crotalus* he clarifies (p. 78) that the name *horridus* should be applied to a North American species, *durissus* to a South American one; no further explanation is given. Exactly the same treatment is given in the succeeding editions of the Règne Animal (Cuvier 1829, Duvernoy 1842, Guérin-Méneville 1829-1844). The figure in the "disciples" edition is quite convincing for a South American specimen. Schinz (1822) in his translation is faithful to the original.

Goldfuss (1820), as noted in Vanzolini (1977: 23) is a mere compilation, without further meaning. The same may be said of Hemprich (1820).

Merrem (1820), is a very important book, but contributes nothing to the issue. He accepts five species: *miliaris* (from Carolina), *durissus* (Mexico and South America), *atricaudatus* (North America), *dryinas* (North America) and *rhubifer* ("America"). His only novelty is the synonymy of *C. tessellatus* Hermann, 1804, with *C. rhombifer* sensu Daudin, in whose synonymy he also includes *C. horridus* L.

Wied (1821: 170), in his *Reise*, has the first post-Linnaean mention of a Brazilian rattlesnake. He remarks on meeting the species (which he called *C. horridus* L.) in Angicos, Bahia, and has brief notes on its ecology and distribution in the open formations of the area. In his additions to the *Reise*, Wied (1850: 124) mentions a rattlesnake, but only

as a pretext to briefly discuss popular beliefs on venomous snakes.

Fleming (1822: 294) keeps Laurenti's genus *Caudisona* for *C. horrida* ("boiquira") and *Crotalus* for *C. miliaris* ("millet"). His work had no repercussion.

Lichtenstein (1822: 249) comments on Marcgrave's illustration; he uses the name *C. horridus* but does not enter into the systematics.

Schinz (1822), in spite of being, as the title of the book implies, a sequel to Cuvier, contains much additional matter (Vanzolini 1977: 28) – but not on *Crotalus*.

Bory de Saint-Vincent (1824) summarizes uncritically earlier literature.

Wagler's (1824) contribution, the description of *Crotalus cascavella*, however, was and for quite some time continued to be, the best. It is comprised of two complementary (non-overlapping) texts, one in French, on rattlesnake generalities, mostly North American, and the other a Latin description of the new form. The latter is terse and to the point. It mentions the shape of the head and of the body scales, and contains a short but quite adequate description of the color pattern. The accompanying plate is excellent – it is a form that can be confidently identified, the first since Linnaeus started the confusion. It is true it has not a definite type locality ("non rarus in campis provinciae Bahiae"), but the ecological connotations and the very explicit itinerary of the expedition (Vanzolini 1981a) that collected the specimen make up for the deficiency. The type has been lost (Hoogmoed and Gruber 1983), but the loss is not serious.

Kaup (1825) immediately after sank *C. cascavella* ("ist rhombifer Daud"), to which Wagler (in Boie 1827) promptly retorted. However, in his synoptic *Natürliches System*, Wagler (1830: 176) accepts only two species of rattlesnake, *horridus* L. (with which he explicitly synonymizes his own *cascavella*) and *atricaudatus*, which he attributes to Daudin. No geographic indication is given. Jan (1859: 275) likewise laconically says "*Crotalus cascavella* = *Crotalus horridus*".

Gray (1825) for the first time proposed a separate genus for the rattlesnakes with large regular scutes on the top of the head. He called it *Crotalophorus*, unfortunately a homonym of *Crotalophorus* Houttuyn, 1764, itself a strict synonym of *Crotalus* Linnaeus, 1758. A valid name was proposed only in 1883 (*Sistrurus* Garman), but the concept was firmly established, and from now on we need not to occupy ourselves with this purely North American entity.

Wied (1825), in the Beiträge, has a very good description of northeastern Brazilian *Crotalus*, and sensible notes on distribution and systematics. It is not clear, however, on which materials he relied. In his works there is no mention of actual specimens, and there is no rattlesnake in what remains of his collection at the American Museum of Natural History. However, his description is detailed and accurate, and accompanied by obviously original measurements.

Fitzinger (1826 a) lists three species: *C. horridus* L. ("America, Brasilia"), *C. catesbaei* Hemprich ("America septentrionali") and *Caudisona miliaris* (L.) ("America septentrionali"). It should be noted that, although Hemprich (1820: 125) in fact mentions the name *catesbaei*, he presents no description or identifying citation. In his next paper (Fitzinger, 1826b), he is acidly critical of Wagler (1824): he was apparently very annoyed at a book published in Germany containing texts in French, as well as at the use of Latin, a dead language, in a scientific paper. His conclusion, based on a consideration of scale counts and color pattern, was that three species of rattlesnakes were valid: *Crotalus catesbaei* Hemprich and *Caudisona miliaris* (L.) in North America, and *Crotalus horridus* L. in South America. With the latter he synonymized *C. cascavella* Wagler, *C. horridus* sensu Wied, *C. dryinas* L., *C. immaculatus* Latreille, *C. strepitans* Daudin, *C. simus* Daudin and (in part, no further details) *C. durissus* L. Such extensive lumping is certainly strange coming from Fitzinger, beyond doubt the most extreme splitter in the history of systematic herpetology. Wagler (1827) replied angrily to the

criticism, but did not specifically mention *Crotalus*.

Friedrich Boie (Boie 1827), under the pretext of commenting on Merrem's system, presented in the Isis von Oken a précis of his brother Heinrich's own classification. With regard to *Crotalus*, he lists, with practically no comments, *miliarius*, *durissus* (*cascavella* being a synonym), *atricaudatus*, *dryinas* and *rhomبifer*, besides two North American species newly described by Say, *C. confluentus* and *C. tergeminus*.

Schinz (1835: 164 seq., pl. 74) lists as valid only two species, *C. miliarius* and *C. horridus* L., the latter including, as synonyms, *C. rhombifer* sensu Daudin, *C. "tessellatus"* Hermann, *C. cascavella* "Spix", *C. atricaudatus* sensu Daudin, and, with doubt, *C. orientalis* Laurenti. He also includes in the synonymy vernacular "boiquira" (Marcgrave 1648) and "boicinga" (Piso 1648). He has color plates of the two forms he accepts, with no indication of source. His *horridus* is certainly not based on a South American specimen; the plate reminds one rather of North American *C. horridus*.

Schlegel (1837) published two very important books, summarizing his outlook on herpetology and the contents of the rich contemporary Dutch collections. In the Abbildungen (Schlegel 1837-1843), a book with a pronounced Asian bias, he mentions few crotalines and no *Crotalus*. In the Essay sur la physiologie des serpens he includes (p. 555 seq., pl. XX) four species: *C. horridus* from South America, *C. durissus*, from North America, *C. miliarius* and at, this late date, *C. mutus*. The figures are very good-looking, but those of the cephalic scutellation of *C. horridus* and *C. durissus* do not seem to correspond to current ideas about these forms.

Filippi (1840) has no contribution. The collection he reports upon (Pavia) sounds interesting, as part of it is said to come from Seba's cabinet (loc.cit.: 3), but the paper does not mention rattlesnakes.

The "disciples" edition of Cuvier's Règne Animal (Duvernoy 1842) is, as already said, a faithful reproduction of the previous editions, first and second, and adds nothing. The figure (plate 33: 1) is of a very young specimen.

Gray (1842) is an attempt at a broad synthesis of an insufficiently known group. Among the thirty species of crotalines he recognizes there are two inclusive ones, containing, among others, the South American species. For present purposes the paper is irrelevant.

Fitzinger (1843), dealing with snakes at the generic level, divides Linnaeus's genus *Crotalus* in two. For *C. miliarius*, adequately described by Linnaeus in the 12th edition, but attributed by Fitzinger to himself, he assigns the genus *Caudisona*, erected by Laurenti (1768) for *terrifica*. For the remaining species he maintains *Crotalus*, with three subgenera: *Crotalus* L., for *horridus* L., *Uropsophus* Wagler, for *triseriatus* Wagler, and *Urocrotalon*, new, for *durissus* L. At the time there was not yet a clear distinction between systematics and nomenclature, and Fitzinger signified within a parenthesis (in the case of *Crotalus*) that Linnaeus had proposed the name but not quite ("non stricte in eodem sensu") the concept.

Tschudi (1845, 1846) has the earliest reference to *Crotalus* in Peru. He follows Schlegel's scheme, using (1846: 17) the name *horridus* (sensu Daudin) to include *horridus* sensu Wied and *cas-cavella* Wagler; apparently (p. 63) he saw specimens, but his data on distribution ("montañas des nördlichen Theile") is at variance with current information, which limits *Crotalus* to southern Peru (see Appendix 1).

Berthold (1846: 25), also an explicit Schlegel follower, cites two species: *horridus* (Surinam) and *durissus* (Carolina).

Troschel (1848) has notes, from Richard Schomburgk, on the distribution of *Crotalus* (*horridus*, sensu Schlegel) in the Guianan savannas and along the coast. He refers for the first time to the presence of rattlesnakes up to 6000 feet (ca 1800 m).

Gray (1849), in the first British Museum snake catalogue, separates *Crotalus* from *Uropsophus* by some minor details of head scutellation. He does in both genera a considerable amount of lumping, but, as there is no discussion, the point is irrelevant to us.

Le Conte (1853) discusses two names, *horridus*

and *terrificus*. He attributes both to North American species; we find his account confusing. He seems to call *Crotalus terrificus* the southern "Oak Ridge Rattle Snake", the present *C. adamanteus*. Consequently, *C. durissus* would be the "Pine Barrens Rattle Snake", presently *C. h. horridus*. Cope (1859) refers favorably to this article by Le Conte. We differ. To get an idea of his competence, one needs only to note that Le Conte (1853: 416) called Laurenti an "illustrious Italian"; the title of Laurenti's Synopsin begins: "Josephi Nicolai Laurenti austriaci viennensis...". Another curious point in Le Conte's paper, which we haven't seen cited since is (l.c.: 417-418): "The male is generally to be distinguished by a black spot behind the occiput".

By this time the history of North American rattlers was beginning to be better known (a good summary is in Baird and Girard 1853), but Duméril, Bibron and Duméril (1854), the emblematic Herpetology of the time, still adhered to the scheme of South America *horridus* and North American *durissus*, with the addition of *rhombifer* Latreille as a junior synonym of, yet preferable to, *adamanteus* Palisot de Beauvois, 1799. This scheme was still used in Paris in 1861 (A. Duméril 1861: 439).

Guichenot (1855), in his report on the herpetological results of Castelnau's expedition to Brasil and Bolivia, mentions one specimen of rattlesnake ("*C. horridus*"), from "la province de Chiquitos au Pérou". This is a bad anachronism. Chiquitos had always been a part of Bolivia, which in 1776 had been transferred from the viceroyalty of Peru to that of Buenos Aires, and become an independent country in 1825, a fact well known to Castelnau (1851, 1852, 1866), who labeled his maps "Republica de Bolivia".

Cope (1859) remarks on the prevailing nomenclatural confusion; he adopts Le Conte's (1853) scheme. However, his concept of *durissus* is broader than Le Conte's, including explicitly one Mexican and one Surinamese specimens. All in all his treatment is quite sensible.

Bates (1864: 295) has the first mention of rattlesnakes in patches of open formations in Amazo-

nia, specifically in Parintins (then Villa Nova) and Santarém. Unfortunately, he collected no specimens – at least none is mentioned in the British Museum Catalogue (Boulenger 1896: 575).

Cope (1867), commenting on a large collection from Arizona, has a key to the genus *Caudisona*, which to him included all rattlers, with the exception of the species now in *Sistrurus*, and of *Crotalus lepidus*, for which he erected the new genus *Aploaspis*. The two main characters Cope used in rattlesnake systematics were the scalation of the top of the snout and the shape of the rattle (acuminate vs parallelogrammic). Cope (1884) himself corrected the name to *Haploaspis*. Two other generic names had been proposed for North American *Crotalus*, but not generally adopted: *Crotalinus* Rafinesque, 1818 (type *cyanurus* = *horridus*) and *Aechmophrys* Coues, 1875 (type *cerastes*).

Jan and Sordelli (1874) present excellent plates of specimens with approximate localities. According to then prevailing ideas, their *durissus* is no doubt North American *horridus*; their plate of *horridus* (livraison 46, plate 3, fig. 1) is the best rendition of South American *durissus* so far.

W. Peters (1877: 459) uses *C. durissus* for a Venezuelan (Calabozo, estado Guárico) rattlesnake. So does Ernst (1877) referring to Venezuela in general.

Garman (1883), in a paper that started as a list of the snakes of Kentucky and ended by comprising all of America north of Tehuantepec, cites *durissus* as extending from Brasil to Mexico. He proposes, without calling attention to the novelty, the new genus *Sistrurus*, including *catenatus* (plus one variety) and *miliarius* (plus two varieties).

Lacerda (1884) is the first Brazilian zoologist to write on rattlesnakes; he uses the name *horridus*. It is interesting to note that he remarked on the abundance of rattlers in Marajó and Roraima (then Rio Branco); this went unnoticed for a long time.

Cope (1887: 59) has a short but extremely important paper on *Crotalus* from Chapada dos Guimarães, north of Cuiabá. He synonymizes *C. cascavella* Wagler with *C. terrificus* Laurenti, and de-

scribes its color pattern as: ‘‘a brown snake with brown dorsal rhombs with narrow yellowish borders’’, in which it would differ from *C. durissus* (= *C. horridus* sensu Duméril and Bibron), a ‘‘yellow snake with brown dorsal rhombs which have yellow centers, the brown being little more than a border’’. (It will be remembered that *C. horridus* was the name preferred by Duméril and Bibron for the South American rattlesnakes in general). Cope was the first to make a meaningful, accurate and sensible statement about rattlesnake color pattern; this in 1887.

Lidith de Jeude (1887) described, from the Dutch Caribbean island of Aruba, *Crotalus horridus* var. *unicolor*, later to become the focus of much discussion.

Cope (1892: 694) firmly established *durissus* in South America and distinguished between it and *terrificus* in a good key (p. 688). Cope (1895) has the first figure of the hemipenis of a South American specimen.

Boulenger, in his Catalogue (1896: 572 seq.) deviates from the usual high level of his syntheses. He was, in fact, frequently inexperienced on North American snakes (Battersby 1971), and this is quite evident in his treatment of *Crotalus*. He lumps under *terrificus* (and in this he was much followed) such disparate forms as *basiliscus* and *molossus*; on the other hand, he presciently subdivides *terrificus* in two varieties, with and without neck stripes, anticipating Amaral’s (1926a, b, c, d) varieties and the present subspecies.

Ditmars (1905) described from Guatemala another form, *C. pulvis*, remarkable for being patternless. This was also fated to be the focus of controversy; we will return to it when discussing albinism.

Mocquard (1909) in the Mission Scientifique au Mexique, places (as everybody did, following Cope) *durissus* and *terrificus* next to each other. His geography, however, is fanciful: both forms would reach Arizona, New Mexico and Texas to the north.

Vital Brazil (Brazil 1911, 1914) inaugurates the era of Instituto Butantan publishing on Brazilian snakes. He uses the name *terrificus*, and has no

zoological contribution.

Rodolpho von Ihering (1911), then at the Museu Paulista (now Museu de Zoologia, Universidade de São Paulo), published a semi-popular work on the snakes of Brasil: he also adopts the name *terrificus* and describes the color pattern of specimens from the state of S. Paulo.

Ducke (1913) has definite data on the occurrence of rattlesnakes in disjunct spots of open vegetation (“campos”) in Amazonia.

Werner (1922), who explicitly followed Cope, also grouped together in a key *durissus* and *terrificus*, as having on top of the snout three pairs of scutes meeting on the midline, four scale rows (the circumorbital circles included) between the eye and the lip, and cervical stripes. They would differ in color pattern, though, *durissus* being yellow, with yellow-centered dark dorsal rhombs, *terrificus* brown, with darker, light-edged rhombs. This is precisely Cope’s (1887) scheme. In the list that follows the key Werner gives scale counts and measurements for *terrificus*; *durissus* is unfortunately (if characteristically) omitted.

Amaral (1926c), in reference to chromatic variation in Brazilian snakes, proposes two varieties of *Crotalus terrificus*: (i) *collirhombeatus*, with a design of irregular rhombs on the neck, and (ii) *collilineatus*, with longitudinal cervical stripes. He took no nomenclatural steps: he neither designated hypodigms, nor type localities, nor even mentioned individual specimens. He gave only broad geographical data on the distribution of the varieties: *collirhombeatus* had so far been found in the Brazilian states of Piauí, Ceará and part of Bahia, while *collilineatus* had been found in the “central and Southern-oriental parts of the country”, namely the states of Minas Gerais, Rio de Janeiro, S. Paulo, Mato Grosso, Paraná and Rio Grande do Sul, as well as, probably, in Argentina and Paraguay. Later, Hoge (1966) proposed that *collilineatus* be considered a subspecies of *C. durissus*, designating a lectotype from “the state of Mato Grosso”. The other variety, *collirhombeatus*, would also be a subspecies of *durissus*, but a junior synonym of *cascavella* Wa-

gler. We shall return to this question.

The International Commission on Zoological Nomenclature (henceforth ICZN, 1926: 3) placed (Opinion 92), *Crotalus* L., 1758, type *horridus* L., 1758, together with eight other genera of reptiles, in the Official List of Generic Names.

Amaral’s next paper (1929a, b) is an awkward one to criticize: it is entirely composed of wild statements and unsupported conclusions. In the text, and in a key to the species of *Crotalus*, *durissus* is explicitly called a subspecies of *terrificus*. In a footnote (p. 5) he says about *durissus*: “This corresponds to *Crotalus durissus* specimen γ referred to by Linné in Syst. Nat. XIII edit.: ... 1788... and described as a separate species by Cope in 1864 and 1866”. The thirteenth edition of the Systema Naturae was published in 1789, not 1788, by Gmelin, not by Linnaeus (who died in 1778). The two papers in which Cope, according to Amaral, would have described *C. durissus* as a separate species, are not on Amaral’s (1929a, b) list of references. In a footnote he cites a 1864 paper by Cope (Proceedings of the Academy of Natural Sciences of Philadelphia), in which *C. durissus* is not mentioned. In no other paper by Cope can we find a reference to a description of *C. durissus* as a new species.

Additionally, *C. durissus*, originally described in 1758, ten years before *C. terrificus*, could not be a subspecies of the latter. Klauber (1936) corrected this mistake. Amaral (1937: 161) did not take kindly to Klauber’s correction. In a footnote to the second edition of his checklist of the snakes of Brasil he refers to *C. durissus* as nomenclatorially unavailable and proposes the name *Crotalus terrificus copeanus* to replace it. Gloyd (1940: 123) included this name in the synonymy of *C. durissus*, and thus conveniently killed it for nomenclatural purposes.

In his next paper Amaral (1938) makes still more extravagant statements. He initially states (p. 221) that the varieties described in 1926, *collirhombeatus* and *collilineatus*, were exactly that, color varieties of a subspecies (“race”), *Crotalus terrificus terrificus*. On the same page, however, he says that, given the difference in color of the

venoms (respectively yellowish and whitish), correlated with (unspecified) “important chemical differences”, the two varieties should be considered as good “physiological species”. This well illustrates the syndrome of mental confusion that followed these names from the inception – to continue following them in the future.

Gloyd (1940) is the first treatment with a proper professional outlook. The bibliographical review is careful and lucid, and the descriptions are as good as possible with contemporary resources. All the South American populations continued lumped under the name *C. durissus terrificus*; the data on distribution are, however, precarious.

Klauber (1941) was the decisive paper on the application of Linnaean names to the rattlesnakes recognized in his 1936 scheme. Among the taxa recognized, Klauber selected seven forms, based on geographical accessibility in Linnaeus’s time.

Klauber’s premises were: (i) that the “scale counts (and sexes) as given by Linnaeus are accurate and were made by the same methods as those used today”; (ii) that the scale counts included in Klauber’s samples represented the areas from which Linnaeus’s specimens were derived, so that the statistical tests would not be affected by intrasubspecific trends or clines.

The statistical tests used were: (i) for each scale count and modern taxon a value of t (Student’s) was calculated for the difference between the Linnaean count and the mean of the respective Klauber sample; (ii) the values of the probabilities for all the tests relating to each modern taxon were combined according to Fisher (1938: § 21.1; 1946: 99).

This procedure is theoretically justifiable, but its discriminatory power is low – especially in the case of rattlesnakes, which show little inter-specific variability in scale counts.

The results of the statistical tests were further examined by Klauber under the light of some additional information contained in the literature references cited by Linnaeus in the *Systema Naturae* (not, though, in the *Amoenitates Academicae*).

The final results were:

Linnaeus’s *C. horridus* corresponds to *C. h. horridus* sensu Klauber / Linnaeus’s *C. dryinas* corresponds to *C. durissus terrificus* / Linnaeus’s *C. durissus* corresponds to *C. d. durissus*.

This is far from a flawless scheme. Klauber himself called attention to some problems. For instance, *dryinas*, a name ten years older than *terrificus*, should have been preferred. It was not (Klauber, 1941: 93) because “*dryinas*, not having been used for a long time, should be neglected, although we can come nearer to a positive identification of this specimen than either of the others”. On the other hand (p. 92), “while the chances seem rather remote that the Linnaean type of *horridus* could have come from the United States, it may be best to continue the name *horridus* as the specific name of the timber rattlesnake, for we cannot prove absolutely that such an identification is inaccurate.” At best a Scotch verdict.

A further criticism that can be leveled at Klauber’s paper refers to the scantiness of his database. His data on North American snakes were probably sufficient, but in the case of South America, where he recognized one single subspecies, *C. d. terrificus*, he had (Klauber, 1941: 86) 18 specimens, representing an area (Klauber, 1936: 250, fig. 25) of nearly 14 million square kilometers, where geographical differentiation, if not yet known, could be confidently predicted.

Finally, Klauber (e.g. Klauber, 1948: 1) was not aware that the “Mars” symbol (♂) did not mean in the *Systema Naturae* a male specimen, but, among other things, the presence of poison fangs (“tela”), as explicitly stated by Linnaeus (1758: 195). In the case of sexually dimorphic characters this makes a difference.

In this same paper Klauber (1941) describes a new species of *Crotalus* of the *durissus* group, *C. vegrandis*, from Uracoa (estado Monagas, Venezuela). This is a very distinctive species, but Klauber (loc. cit.: 334) states that “it is entirely possible that this may ultimately prove to be a subspecies of *durissus*, intergrading through a stunted race that seems to be present on Mt. Roraima.” (Its is hard for us to

figure how a Central American population would intergrade with a northeastern Venezuelan one in Mt. Roraima).

The Roraima rattlesnake, of whose existence Klauber was apprised (pers. comm.) by his friend C. M. Bogert (American Museum of Natural History), would be later described as *C. durissus ruruima* Hoge, 1966.

In his paper on the application of Linnaean names to North American snakes, Klauber (1948) quietly introduced a novelty in the nomenclature of rattlesnakes. These are not the subject of any part of the paper, but, citing “by example” (l.c.: 2) *Crotalus dryinas* (which spelling he had consistently used before), Klauber corrects it, without comment, to *dryinus*, possibly under the impression that this was better Latin, in conformity with the ICZN (1999). The correction is, in fact, uncalled for. Article 11 (b) (ii) and (iii) legislates that Greek, properly transliterated, is an acceptable language (the same as Algonquian), and Appendix B prescribes, with numerous examples, how to go about the transliteration. Accordingly, *Crotalus dryinas* is nomenclatorially unimpeachable – as, of course, well realized by Linnaeus, who knew Latin.

Smith and Taylor (1950: 348) restricted the type locality of *C. durissus* to Jalapa, Veracruz, Mexico. The numerous restrictions of type localities in this paper were made wholesale, without reference to any historical or taxonomic analysis; that of *C. durissus* was adequately criticized by Klauber (1956: 31, footnote 5).

Ruiz (1952) is a first, and somewhat feeble, attempt at discriminating the crotaline genera by means of cranial characters (the maxillo-palatal ensemble). This line of research was very competently resumed by Brattstrom (1964) whose conclusion, in what concerns us here, is in agreement with previous opinion: two taxa (to Brattstrom subgenera) should be recognized, *Crotalus* and *Sistrurus*.

Hoge (1953: 269), in a paper on albinism in rattlesnakes, took Amaral’s side against Klauber in the matter of the specific name of the South American rattler: “Klauber’s statement that *terrificus* is

a subspecies of *durissus* is not accepted by Amaral. We agree with Amaral, especially since Klauber’s systematic arrangement would further complicate things, as in a large number of papers on the venom of the South American rattler it has been called *terrificus terrificus*.” (Our translation from the German). In fact, the only difference between the names adopted by Amaral and by Klauber resides in the position of the epithets (*terrificus durissus* and *durissus terrificus*), neither of which is suppressed; Hoge’s argument seems weak to defend a serious breach of the law of priority. Exactly the same position, based on equally lame arguments, was maintained by Sandner-Montilla (1983, 1985).

Gonçalves (1956) published a paper entitled “*Crotalus terrificus crotaminicus*, biological subspecies”. It deals with the geographical distribution of crotamin, a toxic protein discovered by Gonçalves and Vieira (1950) in the venom of Brazilian *Crotalus*.

Gonçalves and Vieira (1950) had analyzed pools of venom from “northern, central and southern Brasil.” Considering that Brasil extends from 0430N to 3345S (over 4,000 km), it seems to us insufficient geographical specification. It was, nevertheless, an intriguing clue, confirming and extending earlier observations of Vellard (1941, 1943), and Vellard and Huidobro (1941) – and most certainly in need of strenuous pursuance. Gonçalves’s (1956) paper offers no better geographical information; three localities are mentioned from which venoms containing crotamin were obtained, Morro Agudo, Franca and Ituverava, but it is not made clear where in Brasil these places were (they are in the state of S. Paulo, see Appendix 1). Of the elements nomenclatorially indispensable to the recognition of a new taxon, none was offered: no specimens are mentioned, much less a hypodigm. It seems clear that the authors had at hand only pools of dried venom; the subspecies proposed has no nomenclatorial status. It is a sign of the low esteem in which systematics is held in Brasil that such a travesty of a scientific paper was published in the Annals of the Brazilian Academy of Sciences.

It is an interesting sidelight that Gonçalves

(1956: 365) explicitly makes the point that the presence of crotamin was in no way related to the color of the venom, contrary to previous belief and to later findings of Schenberg (1959, 1960). Schenberg repeated Gonçalves's work on a much larger scale (530 snakes), and mapped for the state of S. Paulo localities showing venom containing crotamin only, which he considered to come from "genetically pure" snakes, and not containing the toxin, which he took to come from "hybrid" snakes. Unfortunately Schenberg's papers do not include the primary data; we looked for them, but were informed at Instituto Butantan that upon his death his laboratory had been closed and his materials and notes dispersed and lost.

Barrio (1961) criticized Gonçalves's paper, and came to the very sensible conclusion that there is no reason to erect "biological" subspecies.

Klauber (1956) is the magnum opus, in which he synthesizes his lifelong bibliographic, laboratory and field work on rattlesnakes, "their habits, life histories and influence on mankind." It is understandably more closely and extensively concerned with the North American forms; the information on South America is found in:

1. The checklist (p. 27-51), followed by distribution maps and photographs of live specimens. In accordance with his previous work and to some extent with the availability of materials, Klauber accepts two South American subspecies of *durissus*, *C. d. terrificus* (Laurenti, 1768) and *C. d. vegrandis* Klauber, 1941. He accepts a Panamanian gap between Central American *durissus* and South American *terrificus*, and synonymizes both Humboldt's species with the latter. His concept of *terrificus* is too inclusive; he states, however (p. 32, footnote 5): "I have no doubt that, when sufficient materials become available for study, at least three South American subspecies of *durissus* (besides *vegrandis*) will be recognized: *C. durissus cumanensis* Humboldt, 1833 in the north; *C. durissus cascavella* Wagler, 1824, in the Brazilian "bulge"; and *C. durissus terrificus* Laurenti, 1768, in the south. These further

subdivisions will be useful in venom studies. I did not make these segregations in this book because I was unable to secure sufficient material wherewith to determine accurately either the territorial limits or character distinctions that would be necessary to define the three subspecies".

2. Klauber's (1956: fig. 25) map of the distribution of *terrificus* is not very good, especially in what concerns Peru and Bolivia.

3. In the key (p. 117), the differences in color pattern among the forms that Klauber recognized are adequately described and represented by excellent photographs.

4. From the South American viewpoint, the weakest part of the book is the "Table of Character Variations" (following p. 124). In it the 14 million square kilometers of South America occupied by *Crotalus* are subsumed in one line (*terrificus*), without mention of the number of specimens examined. To us, this voids the scheme of any usefulness.

Allen and Neill (1957) have a very interesting paper on the rattlesnakes of the Guyanan savannas. Their locality was McTurk's Homestead, in the Rupununi. They were informed by local people that there were there two species of rattler, a savanna and a bush one. They give measurements and scale counts of six specimens of the savanna form, and compare it with *terrificus* sensu Gloyd, not very usefully, as the latter is itself a complex composite.

The savanna form was described as new by Harris and Simmons (1978a), under the name *Crotalus durissus trigonicus*. It was synonymized by Abuys (1987) with *C. durissus dryinus*, and later, following a lead of Cunha and Nascimento (1980), with *C. durissus ruruima* by Rubio (1998). We have examined a paratype (Univ. Florida 16159) and agree with Rubio.

Hoge and Lancini (1962) record for Venezuela *C. d. terrificus* and *C. d. vegrandis*, but do not recognize *C. d. cumanensis*. Neither does Lancini (1962) in his list of the snakes of Curupao.

Hoge (1966) is a fundamental article, in which

several far-reaching decisions are taken, but that throughout lacks clarity and organization. *Crotalus durissus* L. is accepted as the specific name for the Neotropical rattlesnake. *Crotalus vegrandis* Klauber, 1941, is re-established at specific status. Four subspecies (*C. d. durissus* L., 1758; *C. d. culminatus* Klauber, 1952; *C. d. totonacus* Gloyd and Kauffeld, 1940; and *C. d. tzabcan* Klauber, 1952) are confined to Mexico and Central America and will be not further mentioned here. As to the South American forms:

C. d. cascavella Wagler, 1824. A neotype is designated, Instituto Butantan (IB) 23400 from Mina Caraíba, Bahia, Brasil, "near Spix itinerary". The coordinates are 0950, 3952, in fact near the route of the Spix-Martius expedition (Vanzolini 1981a). At the time (1966) the designation of a neotype was not necessary, as there were yet no news of the disappearance of Wagler's type, which became known through Hoogmoed and Gruber (1983). The plate (Hoge 1966: pl. 12) illustrating the neotype disagrees with Wagler's original one, which shows definite diamonds on the cervical region, while the figure of the neotype has longitudinal stripes.

Hoge (l. c.) places *C. terrificus collirhombeatus* Amaral, 1926, in the synonymy of *cascavella*. This would need a consideration of nomenclatural aspects, but these are best left for the next subspecies.

C. d. collilineatus "Amaral, 1926". Hoge (1966: 139) says: "Since Amaral's concept of *collilineatus* includes at least two subspecies, a type specimen must be selected in accordance with international rules of nomenclature between the three ones figured in Amaral's description. By present selection, in agreement with Dr. A. do Amaral, we select IBH n° 2180, from State Mato Grosso as lectotype of *Crotalus durissus collilineatus* Amaral".

Although the specimens listed by Amaral (1926) were not explicitly and formally designated as syntypes, they may be reasonably taken to be so under the Code (ICZN, 1999), and become eligible for choice as a lectotype (Art. 72.i.i).

The next point to consider is the elevation to

subspecific rank of names originally proposed as infrasubspecific varieties. The Code permits such an elevation, of course under some stipulations. First comes the matter of availability under Art. 45.6.4.1: in the present case, the names were explicitly proposed as varieties, and were used in 1966 (before 1985) as the valid names of subspecies, and thus fulfil the requirements.

As to authorship, Art. 10.2 prescribes that "if an author uses a name previously published at infrasubspecific rank, in a way that makes it available for a species or subspecies, that author thereby establishes it as a new name and it takes his or her authorship Art. 45.5.1 (see also Articles 23.3.4 and 50.3.1)".

Finally, as to date of priority, Art. 23.3.4 prescribes "The Principle of Priority does not apply to names applied to infrasubspecific entities... If a new name which had been published for an entity later established for a species or subspecies (see Articles 10.2, 45.5 and 45.6), then the Principle of priority applies from the date the name becomes available as a result of that establishment".

All this leads to the conclusion that *Crotalus durissus collilineatus* Hoge, 1966, and *Crotalus durissus collirhombeatus* Hoge, 1966, are nomenclatorially valid subspecies.

Hoge's (1966) treatment of the systematics of *C. durissus* is uneven and highly unsatisfactory from several viewpoints. In a later section we shall deal with the characterization of the subspecies. Here we begin by saying that geographical distributions are too summarily treated, and that there is practically no mention of intergradation, of course a fundamental feature of subspecific variation.

For *cascavella* very little information is given (not even the sex of the neotype). The geographic distribution is cited incorrectly as "the dry 'caatinga' areas of States Maranhão, Ceará, Piauí, Pernambuco, Alagoas, Rio Grande do Norte and Bahia": there are no caatingas in Maranhão; they prevail in the other states mentioned, but rattlesnakes are by no means limited to them; they occur in all open formations.

Another point concerns the chosen type locality of *collilineatus*. It is vague, “state Mato Grosso”, at the time with an area of over 1.2 million square kilometers. For a subspecies (geographical race) it seems too much imprecision.

There are further questions yet to be raised. About *Crotalus durissus terrificus*, Hoge (1966: 147) says: “We retain the name of *terrificus* for the extreme Southern population for following reasons: 1) This population fits best *Crotalus durissus terrificus* “sensu” Klauber 1956. 2) Most of medical and biochemical research on South American Rattlers was done with venoms from the South, and always *terrificus* was associated with this research, used either as a specific or subspecific name.” He proceeds to designate IB 22997, from “Julio Castilho, Município Taquarí, State Rio Grande do Sul” as neotype. There are two mistakes here. The actual spelling is “Julio de Castilhos”, coordinates 2919, 5340. This locality is the seat of its own município; the município of Taquarí (2948, 5151) is almost 200 kilometers away (Lema 1994: 28).

Several remarks must be made about Hoge’s course. First, it would seem preferable to have fitted the solution to Laurenti’s original concept, rather than to Klauber’s – which was later, nomenclatorially not binding, taxonomically imprecise and in fact never justified or defended, but simply presumed. Second, it cannot be said that “most of” medical or biochemical research was done on Rio Grande do Sul snakes. The bulk of the materials used in such research was in fact from S. Paulo, but geographical origin was never taken into account, not even routinely recorded. Specimens were taken from the communal snake pit, and venoms pooled.

It might also be inquired what the probability was of Laurenti referring, however obliquely, to a Rio Grande do Sul snake. His description is explicitly based on a figure from Seba’s collection, whose localities are well known to be fanciful – but see remark on Vosmaer (1768) above – but decidedly do not include southern Brasil. In fact it is highly doubtful that any specimens from Rio Grande do Sul had reached Europe before 1800. By that

time 42 South American nominal species of serpents had been described by five authors: Linnaeus (31), Laurenti (6), Sentzen (2), Scopoli (2) and Lacépède (1); not one was listed as from Rio Grande do Sul. Of these, five are presently known to occur in the state, but are so widely distributed in South America and so abundant everywhere that nothing can be guessed about a putative type locality: *Boa constrictor*, *Liophis miliaris*, *Philodryas viridissimus*, *Tantilla melanocephala*, and *Crotalus terrificus*. The six species described by Laurenti were *Caudisona terrifica*, *Siphlophis cervinus* and four synonyms of *Boa constrictor*: *Constrictor rex serpentum*, *C. aruspex*, *C. formosissimum* and *C. diviniloquus*. There is nothing here pointing at Rio Grande do Sul; *S. cervinus* does not even occur there.

Crotalus dryinas Linnaeus, 1758, unnecessarily, as said, emended to *dryinus*, and left out of the scheme by Klauber (1956), was revived by Hoge (1966: 142) as subspecies *dryinus* of *durissus* L.

In spite of its material flaws, Hoge’s (1966) paper should not be prima facie dismissed. Butantan herpetologists handle literally thousands of live snakes, and this certainly educates the eye to significant peculiarities of color pattern that, in the finished research, may turn out to be poorly expressed or even omitted, but are nonetheless real. The case of the varieties/subspecies *collilineatus* and *collirhombatus* is typical. It is obviously indispensable to perform on South American *Crotalus* a proper analysis of geographical differentiation, starting with color pattern.

This paper by Hoge was the last conceptual contribution to the understanding of the systematics of South American *Crotalus*. Subsequent authors adopted the scheme; differences are to be noted only on the characterization of the subspecies, which is one of our next themes.

CHARACTERIZATION OF THE SUBSPECIES

In the 1966 paper Hoge considers seven South American subspecies, *cascavella*, *collilineatus*, *cumanensis*, *dryinus*, *marajoensis*, *ruruima* and *terrificus*. His data on the morphological characters (color pat-

tern and scale counts) are unevenly dispersed among the individual topics. Three subspecies, the two new ones, *ruruima* and *marajoensis*, and *terrificus*, of which, as said, a neotype is designated, are formally diagnosed and described. The meristic characters of those are cited as ranges for the sexes, without indication of the size of the samples; in the case of the new forms that is presumably that of the hypodigms. In the case of *terrificus* it is impossible to guess, but, given the large number of localities represented on the maps, a sizable sample must have been available. Color patterns are described only for the new subspecies, without mention of variation; it is probable that they are modal accounts. There are brief pairwise comparisons of *collilineatus* vs. *cascavella*, *terrificus* and *dryinus* vs. *durissus*, and *marajoensis* and *ruruima* vs. *terrificus*. The plates, which include all forms, are not adequate substitutes for good descriptions, but to some extent they clarify the abbreviated differential diagnoses. All in all, Hoge's treatment does not allow for unambiguous identification of the subspecies. This is not helped by the summary geographical treatment.

The accounts of distributions are indeed very sketchy: instead, there are maps for all subspecies. The localities are not identified on the maps, and it is impossible to retrieve from them the coordinates. This is particularly unfortunate in the case of Map VIII, which is said to include intergradation between *cascavella* and *terrificus*. As mentioned, it is not possible to retrieve coordinates from the maps, but a consideration of state borders as depicted places the "intergrade" localities some 750 km to the north of the nearest *terrificus* locality. There is no geographical support for Hoge's scheme.

The best representation of the Butantan concepts of rattlesnake subspecies is to be found in Grantsau (1991), who has outstanding paintings and photographs of *C. d. cascavella*, *collilineatus* and *terrificus*.

Peters and Orejas-Miranda (1970: v, 74-75; see 1986) present a key to the forms of *Crotalus* that occur south of the Mexico-Guatemala border and give it a four star (maximum) rating for reliability. In

fact, the key is entirely based on Hoge (1966) and, in spite of being more systematically constructed and more clearly written, suffers from the same flaws as its model.

Harris and Simmons (1972a, b) present a combination of Hoge (1966) and Peters and Orejas-Miranda (1970; see 1986); they bring no novelties. Hoge and Romano (1973) is again based on Peters and Orejas-Miranda, with figures from Hoge (1966), the latter poorly reproduced. The same scheme is used by Hoge and Romano-Hoge (1981a, b) for the five subspecies they recognize in Brasil, including *trigonicus* Harris and Simmons, 1978, that they consider might occur in Roraima.

Finally, McCranie (1993) sums up the available literature. With regard to color pattern he also follows Peters and Orejas-Miranda. He is the first author to systematically present scale counts for all the forms recognized (those in Hoge, 1966), but he calls attention to the fact that, being culled from a very uneven literature, these should be taken with caution. His map is also a distillation from the literature, likewise to be taken with caution. This closes this part of the survey. It is fair to say that no clear scheme exists of the geographical differentiation of *C. durissus* in South America. No significant addition has so far been made to Hoge's 1966 scheme, which, as discussed, is rather superficial and methodical.

RECENTLY DESCRIBED SPECIES

After Hoge (1966), two species of rattlesnakes were described, both from Venezuela.

Crotalus pifanorum Sandner-Montilla, 1980, from southern Guárico, was said to differ from *cumanensis* principally in dorsal pattern: comparative drawings are presented, but are very crude. Differences in scale counts are mentioned but not specified. Lancini and Kornacker (1989: 295) found the species' status "debatable" until more specimens became available. Campbell and Lamar (1989: 344) thought it could not be distinguished at the time, and tentatively considered it a synonym of *cumanensis* or an intergrade (with what they did not spec-

ify). However, in an undergraduate thesis, Perez-Bidó (1992) compared *pifanorum* and *cumanensis* as to karyotype, protein electrophoresis and microdermatoglyphics, and concluded that they were good species. This thesis was later formally published (Perez, Rada de M. and Bello de L. 1997): in neither version is there mention of the number or geographical provenance of the specimens compared, but the data seem substantial enough. A good formal treatment of this form seems highly desirable.

Crotalus maricelae Garcia-Pérez, 1995, was described from the Andes of Mérida. It was diagnosed with basis on a character of cephalic scutellation (4-5 prefrontals) and on color pattern. McDiarmid, Campbell and Touré (1999: 283) say that it is a synonym, but do not elaborate the point.

A NOTE ON CHROMATISM

Deviant color patterns, often called “aberrations”, are fairly frequent in snakes. In *Crotalus* by far the most common deviation, one that has taken taxonomic relevance, is albinism, on which there is a sizable literature, especially on the North American species (Gloyd 1935a, 1958, Hensley 1959, Nickerson and Mays 1968, Klauber 1972, Gilboa and Dowling 1974, Dyrkacz 1981). On the South American forms there is also abundant information (Amaral 1926 b, 1926 c, 1933a, Prado and Barros 1940, 1941, Renault and Schreiber 1951, Hoge 1953c, Miranda, Tio-Vallejo and Grisolia 1985, Bérnils, Moura-Leite and Ajuz 1990, Sazima and DiBernardo 1992).

Albinism in such cases is due to a loss-of-function mutation of the tyrosinase gene and exhibits considerable phenotypic heterogeneity (Bechtel 1978, Gilbert 2000). In fact, the literature shows that pure albinos are relatively rare, some kind of a “ghost pattern” of dorsal rhombs over a gray background being predominantly found. This has led some authors (e.g. Klauber, Ditmars), unaware of the genetic aspects of the problem, to deny that such shadowy specimens were albinos; for them only complete (“pure”) albinos would count. The tail

is frequently, but not always, darker than the body. Albino snakes are found of diverse sizes, and presumably ages, tending to support Sazima and DiBernardo’s (1992) contention that predation on nocturnal albinos should not be too severe.

The first mention of an albinistic rattlesnake is by van Lidth de Jeude (1887: 133). In a collection of reptiles from Aruba, Netherlands Antilles, he found one rattler with “no streaks behind the eye, nor any marking whatever. It is on the back of a uniform gray color, somewhat lighter on the ventrals; the very short tail is darker than the body, and its lower part of a bluish black color.” The specimen was made the type of a new variety, *unicolor*, of *Crotalus horridus*, as said a current name for the South American rattler in the nineteenth century. A further specimen (no locality) in the Leiden collection fully agreed with the Aruba snake in color and scutellation. Two additional Aruba specimens, kept alive in the Zoo, are also mentioned: one in full agreement with the type, the other showing “on the back a trace of lozenge-shaped spots.” The word “albino” is nowhere mentioned.

Meek (1910), commenting on a collection from the Leeward islands, records, without comment, one *Crotalus terrificus* from Aruba. The specimen is in the Field Museum; we have inquired, and it is ordinary *unicolor*.

Ditmars (1905) described a new species from Nicaragua, *Crotalus pulvis*. The type measured 635 + 55 mm; the dorsal background was bluish-gray (“pumice stone”) and there was practically no pattern. However, after shedding, a pattern of indistinct diamonds could be seen. Ditmars (l.c.) states explicitly that “the possibility of albinism... has been fully considered, and is believed to have no bearing upon the case”.

Amaral (1926a: 8), in a paper on chromatism of coral snakes, states, without comment, that *C. pulvis* was a synonym of *C. terrificus*. In a following paper (Amaral, 1926b), on albinism in rattlesnakes, Amaral confirms his opinion and gives a description and a (bad) photograph of the type of *pulvis*.

The matter was retaken by Gloyd (1936), who

states that the two forms are ‘‘not true albinos’’. He declared *unicolor* a good species and *pulvis* a straight synonym – in spite of the geographical incongruity, which he noted and for which he proposed a rather naive hypothesis (an analogy with the distribution of a *Leptodeira*).

Hoge (1966), who accepted Gloyd’s proposition, tried to solve the geographical problem by supposing the locality of *pulvis* to be in error. This is a gratuitous supposition. As said, albinos are not uncommon among rattlesnakes, at least another specimen being known from Nicaragua (Villa and Rivas, 1971).

Kauffeld and Gloyd (1939) stressed again that ‘‘The possibility that the Aruba specimens are aberrant *durissus* no longer seems plausible.’’ The exact meaning of ‘‘aberrant *durissus*’’ is not discussed.

Amaral (1944) emphasized the lack of pholidotic differential characters between *unicolor* and continental *terrificus*, and concluded that ‘‘the representatives of *terrificus* in the island of Aruba (coast of Venezuela) would represent a ‘‘population’’ with a tendency to melanism and perhaps to dwarfism, soon to become extinct’’.

Klauber (1972: 200) finally states that ‘‘it is generally agreed that albinism has little or no effect on evolution; light-colored species are not derived from an albino ancestry. Thus, the Aruba rattlesnake (*C. unicolor*), a conspicuously light species allied to the Neotropical rattlesnake (*C. durissus*) is in no way a result of albinism’’.

The matter seems to us rather simple. The Aruba population has a fixed allele for albinism; it is prevented by its insular situation from intergrading (exchanging genes) with adjacent populations. There is good reason to consider it a good species. The type of *C. pulvis* is beyond doubt an albino *C.d. durissus*.

LOCALITIES

Published information on geographical distribution can be of two sorts: specific, i.e., referring to definite individual localities, that can be reasonably rep-

resented by geographical coordinates with little uncertainty, and generic, referring to a country, to a major subdivision (state, province or department) or still to a given ecological or political sub-unit of such a subdivision.

During the preparation of this bibliography several facts early became evident regarding the raw materials for distributional analyses. In spite of the widespread preoccupation with subspecies, there are very few geographically oriented surveys; country and regional lists seldom include specific localities and still more rarely proper documentation. On the other hand, precise indications are often found in non-taxonomic papers (notes on ecology, venoms, chromatism, teratology, and such). Since our aim was to revise as much as possible of the total South American literature, regardless of intention of ulterior publication, we thought it useful to prepare a list of documented localities (Appendix 1). In the literature, they are usually not accompanied by geographical coordinates: those we supply ourselves, and acknowledge the responsibility. Our main source are the gazetteers for individual countries issued by the U.S. Central Intelligence Agency (CIA) under the nom-de-plume ‘‘U.S. Board on Geographical Names’’ and published by the Office of Geography, Department of the Interior. Failing this most reliable and thorough source, it becomes a matter of consulting scattered and frequently obscure literature and, as a last resort, of inconveniencing colleagues unlucky enough to be in the proper country, or collection. A sizable proportion of published South American localities needed extra investigation; we do not include the search details in this paper, but of course our files are open to colleagues.

Accessorily (Appendix 2) we present a list of the generic localities found in the literature.

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There is no need to stress the difficulties met in assembling this bibliography, which spans over three hundred years and involves faunas outside the ordinary scope of South American herpetology. Our first

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RESUMO

Fez-se um levantamento da literatura taxonômica sobre cascavéis sul americanas (gênero *Crotalus*, família Viperidae). Duas áreas mereceram especial atenção: a atribuição dos nomes propostos no século XVIII por Lineu e Laurenti, e o esquema correntemente adotado de diferenciação subespecífica.

A atribuição de nomes é examinada com base nas descrições originais e na literatura anterior e contemporânea relevante. O esquema atualmente adotado, proposto inicialmente por Klauber (1941, 1972) é considerado não inteiramente satisfatório, mas suficientemente razoável, além de consagrado pelo uso.

O esquema de diferenciação geográfica, importante em si mesmo e por suas conseqüências práticas (diferenciação geográfica do veneno) é considerado como a culminação de uma longa série de análises deficientes, e em urgente necessidade de investigação adequada.

Palavras-chave: *Crotalus durissus*, Viperidae, diferenciação geográfica, diferenciação do veneno.

APPENDIX I

South American localities of *Crotalus*.

Locality	Coordinates	Authority
COLOMBIA		
Atlantico		
Barranquilla	1100 N, 7449	Nicéforo 1942
Km 6 Barranquilla – Puerto Colombia	1100 N, 7452	Dugand 1975
Puerto Colombia	1059 N, 7459	Gloyd 1940
Cesar		
Bolivar	1021 N, 7409	Ruthven 1922
San Sebastian (de Rábago)	1034 N, 7336	Ruthven 1922, Gloyd 1940 ³ , Nicéforo 1942
Cundinamarca		
Tocaima	0428 N, 7438	Nicéforo 1942
La Guajira		
Rio Hacha	1133 N, 7255	Brongersma 1940
Magdalena		
Bonda	1114 N, 7408	Griffin 1916
Cacagualito	1115 N, 7352	Griffin 1916, Gloyd 1940, Nicéforo 1942
Rio Frio	1054 N, 7411	Amaral 1928, Gloyd 1940
Meta		
Villavicencio	0409 N, 7337	Nicéforo 1930, 1933, 1942
Tolima		
Honda	0512 N, 7445	Nicéforo 1942
Valle del Cauca		
Tenerife	0344 N, 7607	Nicéforo 1942
VENEZUELA		
Aragua		
Las Mercedes	1008 N, 6714	Marcuzzi 1950, Roze 1966
Bolivar		
Arabupu	0506 N, 6044	Roze 1966
Cerro Cariman Paru	0429 N, 6109	Hoge & Romano 1969, Hoge & Romano-Hoge 1981a,b
Cuquenán	0511 N, 6049	Roze 1966
Danto Manchado camp 1	0724 N, 6254	Gorzula & Señaris 1998
camp 2	0724 N, 6254	Gorzula & Señaris 1998
El Diamante	0716 N, 6227	Gorzula & Señaris 1998
El Manteco	0727 N, 6232	Gorzula & Señaris 1998
Hato El Paraiso	0731 N, 6231	Gorzula & Señaris 1998
Hato Kamariapo	0720 N, 6226	Gorzula & Señaris 1998

APPENDIX I (continuation)

Locality	Coordinates	Authority
Hato La Vergareña	0650 N, 6334	Gorzula & Señaris 1998
Parupa	0531 N, 6337	Gorzula & Señaris 1998
Paulo	0506 N, 6048	Gloyd 1940, Hoge 1966, Roze 1966
Hato Terekey	0729 N, 6232	Gorzula & Señaris 1998
Upata	0801 N, 6224	Gorzula & Señaris 1998
Carabobo		
Borburata	1031 N, 6758	Roze 1952, Hoge 1966
Distrito Federal		
Baruta	1026 N, 6653	Alemán 1952
Camuri Chico	1037 N, 6652	Roze 1953, 1966
Caracas	1030 N, 6655	Boettger 1898, Roze 1966, Tello 1968
Catía La Mar	1036 N, 6702	Roze 1966
El Cementerio	1039 N, 6656	Marcuzzi 1950, Roze 1966
El Junquito	1028 N, 6705	Marcuzzi 1950, Roze 1966
El Valle	1027 N, 6655	Marcuzzi 1950, Roze 1966
Macanao	1026 N, 6702	Marcuzzi 1950
Tacagua	1032 N, 6659	Roze 1966
Falcón		
Pauji	1049 N, 6936	Shreve 1947
Riecito	1055 N, 6844	Shreve 1947, Roze 1966
Cerro Santa Ana	1150 N, 6958	Bisbal 1990
Guárico		
Calabozo	0856 N, 6726	Peters 1877
Espino	0834 N, 6601	Marcuzzi 1950, Roze 1966
San Juan de Paya	0932 N, 6714	Roze 1966
type locality of <i>C. pifanorum</i>	0759 N, 6544	Sandner-Montilla 1980
Lara		
Las Brujitas	1024 N, 6924	Garcia-Perez 1995
Merida		
Egido	0833 N, 7114	Vellard 1941
Muchachay	0829 N, 7110	Garcia-Perez 1995
Miranda		
Curupao	1030 N, 6639	Lancini 1962
Las Mercedes	1026 N, 6653	Marcuzzi 1950
Ocumare del Tuy	1007 N, 6646	Roze 1966
Pico Naiguatá	1033 N, 6646	Gloyd 1940
Santa Lucia	1018 N, 6640	Gloyd 1940, Marcuzzi 1950
Turgua	1023 N, 6646	Marcuzzi 1950
Monagas		
Caripito	1007 N, 6303	Beebe 1946
San Antonio de Maturin	1007 N, 6343	Gloyd 1940
Temblador	0859 N, 6244	Roze 1966
Sucre		
Laguna Campoma	1031 N, 6326	Roze 1966
Puerto de Hierro	1038 N, 6205	Roze 1966
Tunapuy	1034 N, 6307	Gorzula & Señaris 1998

APPENDIX I (continuation)

Locality	Coordinates	Authority
Trujillo		
Rio Burbusay	0931 N, 7016	Vellard 1941
Carache	0938 N, 7014	Garcia-Perez 1995
Zulia		
Maracaibo	1040 N, 7137	F. Müller 1892
Lower Rio Negro	0935 N, 7212	Alemán 1953
GUYANA		
Kartabo	0622 N, 5840	Beebe 1946
Laluni	0622 N, 5751	Hoevers 1967
McTurk's Homestead	0345 N, 5915	Allen & Neill 1957
Torani River ¹	0546 N, 5741	Gloyd 1940
SURINAM		
Matappica Beach	0557 N, 5454	Abuys 1987
Zanderij	0527 N, 5517	Hoge 1964
FRENCH GUIANA		
Canal Magnan	0543 N, 5344	Gasc & Rodrigues 1980
BRASIL		
Amazonas		
Parintins	0237, 5644	Bates 1864
Bahia		
Angicos	1513, 4110	Wied 1821
Mina Caraíba	0950, 3952	Hoge 1966
Salvador	1300, 3830	Wucherer 1861, 1863, 1867
Ceará		
Aroeira	0402, 3824	Gomes 1918
Juatama (formerly Floriano Peixoto)	0505, 3902	Gomes 1918
Quixadá	0458, 3902	Gomes 1918
São Vicente	0324, 4016	Gomes 1918
Uruquê	0509, 3910	Gomes 1918
Ceará/Rio Grande do Norte		
Chapada do Apodí	0510, 3745	Lima-Verde 1974, 1976
Mato Grosso		
Barracão Queimado	1345, 5943	Silva 1993
Chapada dos Guimarães	1526, 5545	Cope 1887, Gloyd 1940 ²
Mato Verde	1113, 5040	Hoge 1953b
Vila Bela da Santíssima Trindade	1501, 5957	Amaral 1926
Xavantina	1440, 5221	Hoge 1953b
Mato Grosso do Sul		
Arapuá	2048, 5202	Amaral 1925a
Campo Grande	2027, 5438	Amaral 1925a
Carandazal	1948, 5711	Amaral 1925a
Corumbá	1900, 5739	Amaral 1925a
Guaicurus	2004, 5646	Amaral 1925a
Miranda	2015, 5622	Koslowsky 1898a, Amaral 1925a
Porto Esperança	1936, 5727	Amaral 1925a
Urucum	1910, 5739	Peracca 1904

APPENDIX I (continuation)

Locality	Coordinates	Authority
Minas Gerais		
Alfenas	2126, 4557	Sazima & Di Bernardo 1992
Djalma Dutra	2004, 4501	Renault & Schreiber 1951
Lagoa Santa	1938, 4353	Warming 1892, Jensen 1900
Monte Cristo	2121, 4625	Amaral 1933
Ouro Fino	2217, 4623	Carrillo de Espinoza 1983
Santa Rita da Extrema	2252, 4639	Gloyd 1940
Uberlândia	1855, 4815	Brites & Bauab 1989
Pará		
Condeixa	0054, 4836	Nascimento et al. 1991
Serra do Ererê	0153, 5411	De Witte 1930
Lago Mariapixí	0155, 5616	Ducke 1913
Santarém	0225, 5448	Bates 1864
Paraná		
Campo Mourão	2403, 5222	Bernils, Moura-Leite & Ajuz 1990
Japira	2348, 5009	Hoge 1953c
Piraí do Sul	2431, 4957	Gloyd 1940
Vila Velha	2513, 5000	Bernils & Moura-Leite 1990
Pernambuco		
Carnaubeira	0818, 3845	Cordeiro & Hoge 1974, Vanzolini et al. 1980
Exu	0731, 3943	Vitt & Vangilder 1983
Jaboatão	0807, 3501	Cordeiro & Hoge 1974
Ouricuri	0753, 4005	Miranda & Miranda 1982
Recife	0802, 3453	Cordeiro & Hoge 1974
Tapacurá	0800, 3503	Morais & Morais 1987
Rio de Janeiro		
Niterói	2255, 4305	Gloyd 1940
Rio Grande do Sul		
Ilha Barba Negra	3028, 5109	Lema 1994
Cazuza Ferreira	2857, 5040	Araujo & Perazzolo 1974
Julio de Castilhos	2919, 5340	Hoge 1966
Pelotas	3145, 5220	Magalhães 1922, 1925, P. Müller 1971a
Porto Alegre	3000, 5110	Lema et al. 1980
Rio Pardo	2958, 5222	Hensel 1868
Santa Cruz do Sul	2943, 5226	Hensel 1868
Santana da Boa Vista	3052, 5307	Lema 1994
Santana do Livramento	3053, 5531	Lema 1994
São Marcos	2858, 5104	Lema 1994
Viamão	3005, 5102	Lema et al. 1980
Rondonia		
Vilhena	1242, 6006	Silva 1993
Roraima		
Boa Vista	0249 N, 6040	Hoge & Romano 1969
Colônia Coronel Motta	0318 N, 6102	Cunha & Nascimento 1980
Limão, Rio Cotingo	0356 N, 6030	Gloyd 1940

APPENDIX I (continuation)

Locality	Coordinates	Authority
Ilha de Maracá São Paulo	0325 N, 6140	O'Shea 1989
Água Vermelha	2154, 4753	Belluomini & Autuori 1983
Araçatuba	2112, 5025	Amaral 1926c, 1933, Santos & Germano 1996
Rio Feio	2202, 4929	Ihering 1911
Franca	2033, 4724	Ihering 1911, Gonçalves 1956
Helvetia	2304, 4710	Gloyd 1940
Ilha Solteira	2023, 5121	Hoge et al. 1975
Ipauçu	2303, 4957	Amaral 1933
Ituverava	2020, 4748	Gonçalves 1956
Itu	2317, 4718	Amaral 1926a
Jurucê (formerly Sarandy)	2105, 4745	Amaral 1926b
Limeira	2234, 4956	Amaral 1934
Martinho Prado	2119, 4809	Gloyd 1940
Morro Agudo	2044, 4804	Gonçalves 1956
Palmar	2040, 4834	Prado & Barros, 1940, 1941
Piracicaba	2242, 4738	Ihering 1911
Piraju	2312, 4923	Gloyd 1940
São José do Rio Pardo	2136, 4654	Amaral 1926a
São José dos Campos	2311, 4553	Boulenger 1896
São Paulo	2332, 4637	Ihering 1911, Gloyd 1940
São Roque Tocantins	2342, 4708	Amaral 1926a
Barra do São Domingos	1243, 4746	Amaral 1935
Cana Brava	1247, 4653	Amaral 1935
BRASIL / PARAGUAY		
Represa de Itaipu	2526, 5435	Dure-Rodas 1995
PERU		
Puno		
Sandia (provincia)	1350, 6920	Schmidt & Walker 1943
San Juan del Oro	1412, 6910	Carrillo de Espinoza 1983
BOLIVIA		
Santa Cruz		
Buenavista	1727, 6340	Gloyd 1940
La Florida	1435, 6050	Fugler & De la Riva 1990, De la Riva, Castroviejo & Cabot 1992
Parque Nacional Noel Kempff Mercado	1419, 6055	Harvey et al. 1998
Piray	1829, 6351	Gloyd 1940
Santa Cruz de la Sierra	1748, 6310	Griffin 1916, Fugler & De la Riva 1990
Vallegrande	1829, 6406	Fugler & De la Riva 1990
PARAGUAY		
Alto Paraguay		
Rio Apa	2205, 5800	Peracca 1895
Fortin Teniente Martinez Amambay	2100, 5946	Aquino et al. 1996
Parque Nacional Cerro Corá	2238, 5601	Aquino et al. 1996

APPENDIX I (continuation)

Locality	Coordinates	Authority
Boquerón		
Filadelfia	2221, 6002	Aquino et al. 1996
Cañendiyú		
Curuguaty	2427, 5538	Aquino et al. 1996
Reserva Biológica Mbaracayu	2425, 5526	Aquino et al. 1996
Central		
Asunción	2519, 5741	Boulenger 1894
Chaco		
Parque Nacional Defensores del Chaco	22038, 5952	Aquino et al. 1996
Concepción		
Estancia Centurión	2215, 5735	Aquino et al. 1996
Guairá		
Independencia	2543, 5615	Gloyd 1940
Nueva Asunción		
Km 530 Ruta 9	2206, 6029	Aquino et al. 1996
km 605 Ruta 9	2139,6105	Aquino et al. 1996
Parque Nacional Teniente Enciso	2113, 6149	Aquino et al. 1996
Paraguarí		
Parque Nacional Ybycui	2614, 5703	Aquino et al. 1996
Presidente Hayes		
Estancia Juan de Zalazar	2304, 5913	Aquino et al. 1996
Km 150 Ruta 9 (Transchaco)	2413, 5807	Aquino et al. 1996
Km 344 Ruta 9 (Transchaco)	2315, 5916	Aquino et al. 1996
Ruta 9 (Transchaco) at Rio Verde	2311, 5914	Scott & Lovett 1975
San Pedro		
Colonia Rio Verde	2350, 5608	Aquino et al. 1996
ARGENTINA		
Chaco		
Resistencia	2727, 5900	Peracca 1895, Berg 1898
Tres Palmas	2644, 5959	Berg 1898
Cordoba		
Rio Primero	3120, 6337	Foote & MacMahon 1977
Entre Rios		
Puerto Algarrobo	3038, 5935	Freiberg 1939, Vuoto 1995
Formosa		
Reserva El Bagual	2611, 5857	Yanosky 1989
Mendoza		
General Alvear	3458, 6742	Sage & Capredoni 1971
Misiones		
Aristobulo del Valle	2706, 3450	Giraud & Abranson 1994
Monte Carlo	2634, 5447	Freiberg 1939
Oberá	2729, 5507	Cei 1993
Parque Nacional del Iguazu	2543, 5425	Montanelli & Acosta 1991, Acosta et al. 1994

APPENDIX I (continuation)

Locality	Coordinates	Authority
San Juan		
Guayaguas	3149, 6712	Cei & Castro 1978a,b
Marayes	3129, 6720	Cei & Castro 1978a,b
San Luis		
La Botija	3213, 6636	Sage & Capredoni 1971
Las Tres Cañadas	3413, 6635	Sage & Capredoni 1971
Nahuel Mapa	3447, 6611	Sage & Capredoni 1971
San Francisco del Monte (de Oro)	3336, 6608	Sage & Capredoni 1971
San Luis	3318, 6622	Sage & Capredoni 1971
Zanjitas	3348, 6636	Sage & Capredoni 1971
Santiago del Estero		
Guardia Escolta	2900, 6208	Miranda et al. 1985
Pozo Herrado		Abalos & Nader 1967
URUGUAY		
Maldonado		
Pan de Azucar	3450, 5508	Lema 1994

¹In Gloyd (1940), as elsewhere in the literature, misspelled “Toroni Road”. I owe the correction to Dr. Greg Schneider, University of Michigan Museum of Zoology. ²Gloyd (1940) has this locality misspelled “Chapadão” and placed in the state of S. Paulo. I owe the correction to Dr. Ned S. Gilmore, Academy of Natural Sciences of Philadelphia. ³Gloyd (1940) has this locality as San Sebastian, “Monagas, Venezuela”. I owe the correction to Drs. James Hanken and José Rosado, Museum of Comparative Zoology.

APPENDIX II

Generic localities of South American *Crotalus*

ARGENTINA

General

Cope 1899

Di Tada & Abalos 1976

Cei 1986

Williams & Francini 1991

Chaco

Gallardo 1979

Bucher 1980

Córdoba

Weyenbergh 1876

Mendoza

Burmeister 1861

Misiones

Gallardo 1986

Martinez, Martinez & Montanelli 1992

Santiago del Estero

Esteso & Urtubey 1983

“Distrito chaqueño”

Leynaud & Bucher 1999

BOLIVIA

La Paz

“Caupolicam” = Provincia Franz Tamayo

Boulenger 1896

Santa Cruz

Provincia Chiquitos

Guichenot 1855

Provincia Sara

Griffin 1916

“Distrito chaqueño”

Leynaud & Bucher 1999

BRASIL

- Amapá
Hoge 1967
- Bahia
Gunther 1861
Wucherer 1861, 1863
- Mato Grosso
Chapada dos Guimarães
Cope 1887
- Pará
Ilha de Marajó
Lacerda 1884
Yuki & Santos 1996
- Pernambuco
Boulenger 1896
- Rio Grande do Sul
General
Hensel 1868
Boulenger 1886
Boettger 1898
Greater Porto Alegre
Fundação Zoo-botânica 1976
- Roraima
Lacerda 1884

COLOMBIA

- General
Perez-Santos & Moreno 1988

GUIANAS

- General
Hoogmoed 1979

FRENCH GUIANA

- General
Chippaux 1986
Starace 1998
- “Savannes côtières”
Lescure 1986

GUYANA

- General
Quelch 1898
Beebe 1919
Parker 1935

PARAGUAY

- General
Schenkel 1901
Bertoni 1913, 1913a
Amaral 1925b

Canese 1966

- Alto Paraná
Bertoni 1939
“Districto chaqueño”
Leynaud & Bucher 1999

PERU

- Madre de Dios
Carrillo de Espinoza & Icochea 1995

SURINAM

- Kappler 1885

URUGUAY

- General
Devincenzi 1925, 1929, 1939
Achaval & Olmos 1997
- Artigas
Vaz-Ferreira & Sierra de Soriano 1960
- Tacuarembó
Devincenzi 1925

VENEZUELA

- General
Ernst 1877

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