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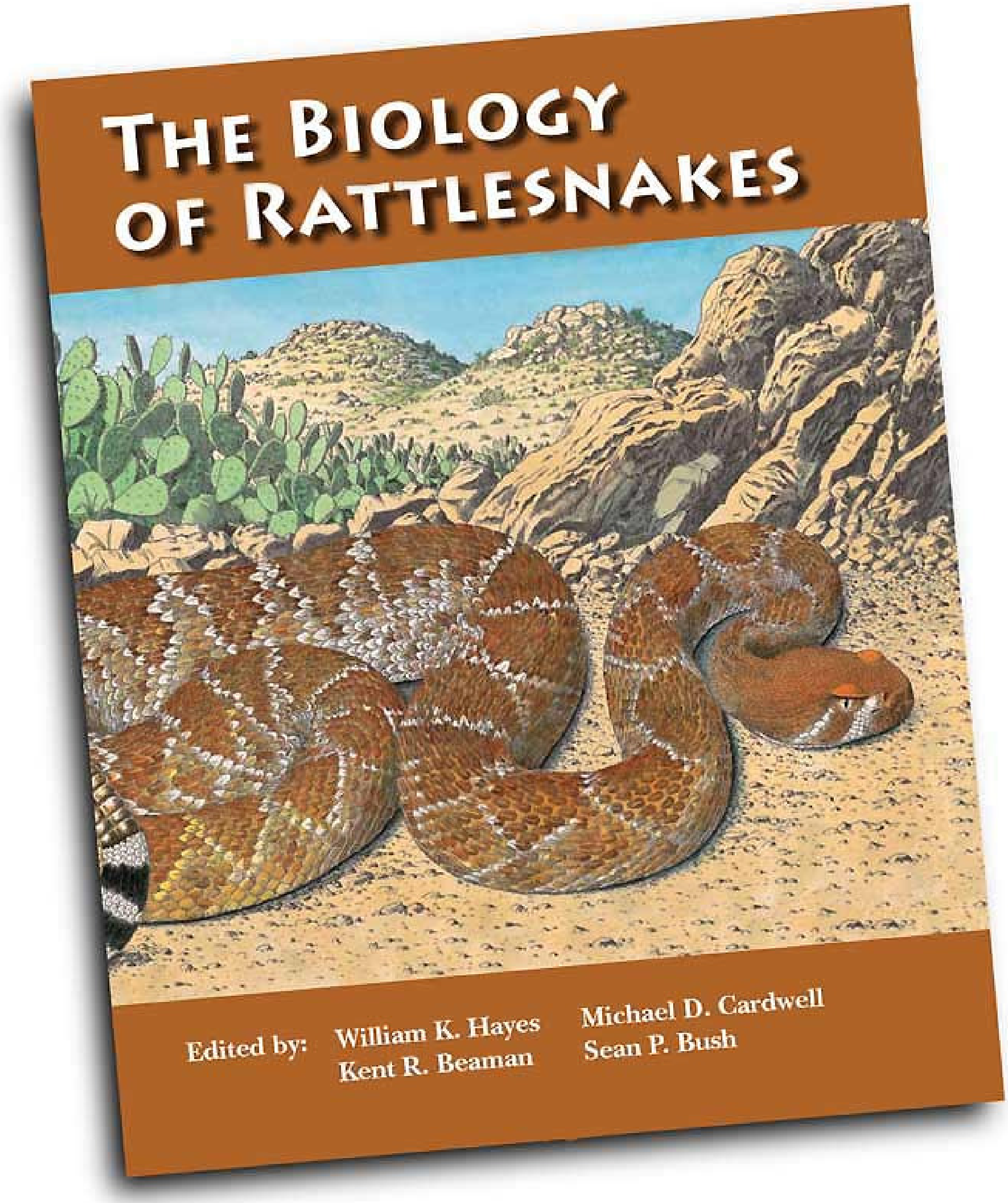

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# Rattlesnakes: Research Trends and Annotated Checklist

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**Abstract.**—The remarkable diversity, widespread distribution, and unique adaptations of rattlesnakes testify to their success. The charismatic nature of this group has inspired intense fascination and substantial scientific research. Indeed, rattlesnakes appear to be the most-studied group of snakes (at the generic level), due largely to their presence in North America and the toxic venom they produce. The majority of studies have focused on their venom, but organismal-level research, particularly in ecology, has increased dramatically in recent decades. Two large species yielding substantial venom quantities (*Crotalus atrox* and *C. durissus*) have been the primary focus of venom research, whereas a smaller-bodied but geographically widespread species complex (*C. viridis*/*oreganus*) has been preferred for studies of behavior and ecology. Research in systematics has also increased, with new species and subspecies described in recent years. Currently, 37 species and 80 taxonomic forms (species + subspecies) of rattlesnakes are recognized from the genera *Crotalus* and *Sistrurus*. From the checklist provided herein, 18 species and 30 named taxa reside in North America north of Mexico, two species and two taxa live in Central America from Belize to Panama, and one species and eight taxa occur in South America. Mexico boasts the highest richness, with 31 species and 58 named taxa. These numbers will vary among authorities and no doubt change with intensified study and further refinement of concepts and methods in systematics.

## Introduction

The remarkable diversity, widespread distribution, and unique adaptations of rattlesnakes attest to their success. Because of these qualities—in particular the signature rattle and highly toxic venom—many scientists, hobbyists, and lay people share an intense fascination for these snakes. Like other animals having significant public appeal, rattlesnakes must be regarded as a "charismatic" species (Simberloff, 1998). The 2005 symposium that led to this volume, with 105 papers presented and approximately 300 attendees, reflected the amount of attention this group attracts.

In this chapter, we seek to accomplish two goals in providing a meaningful background for the chapters that follow. First, we review the recent trends in research on rattlesnakes, seeking to understand what has motivated the studies. Second, we provide an annotated checklist of the rattlesnakes, which we have constructed from the most recently available literature. How many recognized species and subspecies exist in the different regions of the Americas?

## Recent Trends in Rattlesnake Research

To better understand what motivates researchers to study rattlesnakes, we asked several questions regarding recent trends in rattlesnake research. First, how well studied are rattlesnakes compared to other snake taxa, and why have rattlesnakes proven to be popular research subjects? Second, how have studies of rattlesnakes varied among different disciplines, and has research in some areas of inquiry increased disproportionately to others? We suspected that the number of studies at the organismal level (e.g., evolution, behavior, ecology) has increased to a greater extent than studies at the suborganismal level (e.g., morphology, physiology, venom). Third, what rattlesnake species in particular have been favored for research, and what shifts in preferred study species have occurred over the past several decades?

To answer these questions, we conducted literature searches in October 2007 using Science Citation Index Expanded (1970-present) at Web of Science (ISI Web of Knowledge, Thomson Scientific, Philadelphia, Pennsylvania, USA). This search method suffers from inherent biases and limitations, some related to the database and others to changing science. We found, for example, occasional overlap between decades (e.g., a 2000 publication listed as 1999, or vice versa) and changes in the content searched for key words (i.e., from titles and key words in the 1970s and 1980s to also include words in the text and literature cited in the 1990s and 2000s). The citations occasionally included papers presented at meetings, some of which were published subsequently and cited again. Many studies involved multiple species, and taxonomic changes affected searches when species were assigned to new genera (e.g., *Vipera russellii* to *Daboia russellii*). Changes in word usage for titles, abstracts, and keywords were also likely. In spite of these problems, we assumed that bias and other problems would be equal across the species and disciplines compared, yielding a signal-to-noise ratio adequate for answering our questions.

*Comparisons to other snake genera*.—To compare the frequency of publications among different snake taxa and

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**Table 1.** Mean number of citations per year during the past four decades that mentioned various snake genera, and the factor of increase from the 1970s to the 2000s. Numbers in parentheses indicate proportion of citations per decade including the term "venom." Results are based on searches of Science Citation Index Expanded at ISI Web of Knowledge.

| Genera | 1970-1979 | 1980-1989 | 1990-1999 | 2000-2006 | Increase |
|---|---|---|---|---|---|
| Non-venomous genera | | | | | |
| *Elaphe* | 3.4 | 4.5 | 14.0 | 20.4 | 6.0x |
| *Natrix/Nerodia* | 9.1 | 13.3 | 20.1 | 27.6 | 3.0x |
| *Thamnophis* | 8.9 | 14.3 | 32.5 | 49.9 | 5.6x |
| Venomous genera | | | | | |
| *Agkistrodon* | 5.9 (64) | 12.6 (70) | 38.0 (80) | 53.1 (83) | 9.0x |
| excluding venom | 2.1 | 3.8 | 7.5 | 9.0 | 4.3x |
| *Bothrops* | 6.3 (71) | 13.6 (68) | 58.2 (83) | 91.3 (85) | 14.5x |
| excluding venom | 1.8 | 4.4 | 9.7 | 13.3 | 7.4x |
| *Crotalus* | 16.5 (56) | 30.2 (55) | 73.3 (68) | 78.9 (61) | 4.8x |
| excluding venom | 7.2 | 13.6 | 23.8 | 30.9 | 4.3x |
| *Crotalus/Sistrurus* | 16.7 (56) | 31.0 (54) | 74.5 (67) | 82.0 (59) | 4.9x |
| excluding venom | 7.4 | 14.4 | 24.9 | 33.6 | 4.5x |
| *Naja* | 22.9 (65) | 23.9 (59) | 61.6 (75) | 51.0 (76) | 2.2x |
| excluding venom | 8.0 | 9.7 | 15.5 | 12.0 | 1.5x |
| *Trimeresurus* | 5.1 (86) | 9.6 (71) | 37.1 (87) | 44.0 (81) | 8.6x |
| excluding venom | 0.7 | 2.8 | 5.0 | 8.4 | 12.0x |
| *Vipera* | 13.7 (58) | 16.2 (44) | 34.5 (50) | 40.7 (49) | 3.0x |
| excluding venom | 5.7 | 9.1 | 17.3 | 20.9 | 3.7x |

years, we quantified the number of citations that mentioned rattlesnakes and other select genera for each of the past four decades. In the basic search option, we entered the genera names and Boolean operator "*Crotalus* OR *Sistrurus*" to locate all citations having one or both terms in article titles, keywords, or abstracts. We conducted the search within the following time periods: 1970-1979, 1980-1989, 1990-1999, and 2000-2006. For comparison to other taxa, we repeated these searches using eight other geographically widespread, well studied, but otherwise arbitrarily selected genera, including three non-venomous (rat snakes, *Elaphe*; water snakes, *Natrix/Nerodia*; garter snakes, *Thamnophis*) and five venomous (the vipers *Agkistrodon*, *Bothrops*, *Trimeresurus*, and *Vipera*; and cobras, *Naja*). We also conducted searches for many additional genera from 2000-2006 to ensure that the most frequently studied taxa were included in our final comparisons. Several genera names were confounded by homonymous biochemical abbreviations (*Boa*) or computer languages (*Python*), but relative level of study could still be inferred. Because so many citations for the venomous taxa (*Crotalus/Sistrurus*, *Vipera*, and *Naja*) involved studies of venom, we repeated the searches for these taxa while excluding citations having the term "venom" (e.g., "*Vipera* NOT venom"). Because the most recent decade included just 7 yr (2000-2006), we standardized research per decade as the number of citations per year during each of the four time periods.

The results, shown in Table 1, confirmed the popularity of rattlesnakes as research subjects. Apart from the 1970s, when cobras received more attention, and the most recent decade, when *Bothrops* became favored, our searches suggest that rattlesnakes of the genus *Crotalus* have been studied more frequently than members of any other snake genus. No doubt, their availability to researchers in North America has contributed to their frequent study. However, the majority of studies involving venomous taxa have focused on properties of the venom rather than the snake itself. When searches excluded the term "venom," rattlesnakes were studied less than garter snakes (*Thamnophis*), which serve as popular models for a wide range of research questions (e.g., Burghardt, 2002; Shine et al., 2005). Based on the search parameters, the proportion of citations including "venom" was greater for *Agkistrodon* (64-83% for the four decades), *Bothrops* (68-85%), and *Naja* (59-76%) than for *Crotalus/Sistrurus* (56-67%) and *Vipera* (44-58%). Clearly, rattlesnakes and other venomous taxa attract much more attention from researchers because they possess venom. Even so, rattlesnakes draw considerable attention for reasons other than their venom, which we explore in further detail in the next section.

Although the number of publications increased substantially across the decades—nearly five-fold for rattlesnakes between the 1970s and 2000s—citations during the latter two decades are inflated, as a substantial proportion of "hits" involved papers mentioning but not directly studying these genera. The genera with the largest increase in interest were *Agkistrodon* (nine-fold), *Bothrops* (14.5-fold), and *Trimeresurus* (8.6-fold). Increases for *Agkistrodon* and *Bothrops* reflect growing interest in the venom of these snakes, whereas *Trimeresurus* is attracting remarkable interest in-

**Table 2.** Mean number of citations per year involving rattlesnakes (*Crotalus* and *Sistrurus*) within two suborganismal- and three organismal-level disciplines, and the factor of increase from the 1970s to the 2000s. Numbers in parentheses indicate proportion of all citations per decade primarily focused on venom. Results are based on searches of Science Citation Index Expanded at ISI Web of Knowledge.

| Disciplines | 1970-1979 | 1980-1989 | 1990-1999 | 2000-2006 | Increase |
|---|---|---|---|---|---|
| Suborganismal-level | 14.8 | 24.7 | 39.2 | 43.8 | 3.0x |
| Morphology/physiology | 2.2 | 2.7 | 4.4 | 8.9 | 4.0x |
| Venom | 12.6 (77%) | 22.0 (73%) | 34.8 (75%) | 34.9 (57%) | 2.8x |
| Organismal-level | 1.5 | 5.5 | 7.4 | 17.0 | 11.3x |
| Evolution/systematics | 0.5 | 0.7 | 1.4 | 4.9 | 9.8x |
| Behavior | 0.9 | 2.9 | 3.5 | 4.7 | 5.2x |
| Ecology/conservation | 0.1 | 1.9 | 2.5 | 7.4 | 74.0x |
| Total | 16.3 | 30.2 | 46.6 | 60.8 | 3.7x |

dependent of its venom. Our search parameters suggest that *Bothrops* may have now supplanted *Crotalus* as the most studied snake genus. However, a more focused examination of the papers may be necessary to confirm this; again, many hits for the latter decades involved mere mention of the genera rather than focused study.

*Comparisons among disciplines*.—To compare the frequency of publications on rattlesnakes among different disciplines, we similarly quantified the number of citations for each of the past four decades. Because keywords had limited utility for designating disciplines in the 1970s and 1980s, we visually examined all hits for "*Crotalus* OR *Sistrurus*" within each decade and used our best judgment to assign each citation to the most relevant discipline. We arbitrarily settled on two suborganismal-level disciplines (morphology/physiology and venom biochemistry) and three organismal-level disciplines (evolution/systematics, behavior, and ecology/conservation). Again, a number of citations in the 1990s and 2000s were disregarded because they did not involve direct study of rattlesnakes. We also concede that distinctions between disciplines have become increasingly obscured, impeding our ability to categorize publications.

The results, summarized in Table 2, reveal three obvious trends. First, the number of citations for rattlesnakes increased steadily among successive decades for all disciplines. The nearly four-fold increase for all citations combined between the 1970s and 2000s should be more realistic than the nearly five-fold increase in Table 1 because we screened references in this analysis. Second, the majority of citations involved research on venom (73-77% in the first three decades), as expected from the prior analysis, though the proportion waned substantially in the most recent decade (57%). Third, the number of citations within organismal-level disciplines increased dramatically between the 1970s and 2000s compared to the sub-organismal disciplines. This was especially true for citations involving ecology and conservation, which had an exceptional 74-fold increase. There has also been a recent proliferation of systematics studies (see Checklist below). The development and refinement of molecular analyses and phylogenetic theory has inspired much of the systematics work.

Thus, we conclude that there has been a profound shift in research interest involving rattlesnakes. The dramatic increase in ecological studies parallels that noted for snakes in general, as the representation of snakes in ecological studies, once substantially lagging, now equals that of other advanced vertebrates (Shine and Bonnet, 2000). Several reasons proposed by Shine and Bonnet (2000) for the renewed emphasis on snakes include: advances in technology, such as the use of radiotransmitters; the void in knowledge of less popular or difficult-to-study subjects; plasticity in a number of ecological traits; the inspiration of early workers; and changing social attitudes toward snakes. We suspect the latter reason carries considerable weight, as snakes recently have become dominant fixtures in nature television programming. The contents of this volume certainly reflect a strong interest in ecological studies. We regard this trend in rattlesnakes and snakes in general as encouraging, particularly given the recent decline in interest in natural history studies of amphibians and reptiles (McCallum and McCallum, 2006).

Despite its novelty, the rattlesnake's rattle has received scant attention. From the searches, we located just one publication in the 1980s that focused on the rattle, six in the 1990s, and three in the 2000s. Approximately half the studies examined morphological and physiological properties, and the other half considered behavioral and ecological attributes. Some of this work is conveniently summarized in three other chapters: Moon and Rabatsky (this volume) examine the biomechanical properties of sound production; Rabatsky (this volume) explores hypotheses for the rattle's evolution; and Owings and Coss (this volume) discuss the role of sound production in the cloak-and-dagger interactions between snake predator and rodent prey.

*Comparisons among rattlesnake species*.—To evaluate the preferred species studied by researchers and changes over time, we arbitrarily selected 10 species of what we assumed would be among the most studied. We then exam-

**Table 3.** Mean number of citations per year for select rattlesnake species studied at the suborganismal (venom only) and organismal (behavior and ecology/conservation only) levels during two different decades. Results are based on searches of Science Citation Index Expanded at ISI Web of Knowledge.

| | Venom | | Behavior and Ecology/Conservation | |
|---|---|---|---|---|
| **Species** | **1970-1979** | **2000-2006** | **1970-1979** | **2000-2006** |
| *Crotalus adamanteus* | 1.5 | 2.3 | 0 | 0.4 |
| *Crotalus atrox* | 2.6 | 16.6 | 0.2 | 2.6 |
| *Crotalus cerastes* | 0.0 | 0 | 0.3 | 0.1 |
| *Crotalus durissus* | 1.1 | 19.7 | 0 | 0.4 |
| *Crotalus horridus* | 0.1 | 1.1 | 0.2 | 2.1 |
| *Crotalus molossus* | 0 | 1.1 | 0 | 0.6 |
| *Crotalus scutulatus* | 0.7 | 1.7 | 0 | 0.1 |
| *Crotalus viridis/oreganus* | 1.9 | 4.9 | 0.7 | 3.0 |
| *Sistrurus catenatus* | 0 | 0.4 | 0.1 | 1.9 |
| *Sistrurus miliarius* | 0 | 0.7 | 0.1 | 0.7 |

ined the frequency with which each of these species was cited during the 1970s and the 2000s, and apportioned citations to either the suborganismal (venom only) or organismal (behavior and ecology/conservation) level, using our best judgment.

The results, summarized in Table 3, illustrate some interesting patterns. First, *Crotalus atrox* has attracted more attention from researchers than other species. We suspect that this taxon, historically, has been the most studied snake species in the world, resulting largely from the snake's relative abundance across a large range in North America, making it readily accessible to researchers. Commercial round-ups have no doubt been a source for many study subjects, although venom extracted from snakes at round-ups has *not* been a significant source of venom used by either antivenom producers or researchers. Perhaps most important, this species has provided substantial quantities of venom for study because of its large body size. Indeed, the vast majority of publications (93% in the 1970s, 86% in the 2000s) involving this species have focused on properties of its venom. Second, citations from the current decade suggest that *C. durissus* has recently displaced *C. atrox* as the most studied rattlesnake species. This close relative of *C. atrox* similarly has a large distribution, through much of South America, and also attains a large body size; its venom has been the near-exclusive topic of research (100% of studies in the 1970s, 98% in the 2000s). Compared to these two large species, the comparatively inadequate attention paid to *C. adamanteus*, which also attains a large size and has a reasonably large distribution, seems surprising. Third, *C. viridis/oreganus*, a smaller-bodied species complex, has been the preferred subject of behavioral and ecological studies, though *C. atrox*, *C. horridus*, and *S. catenatus* have also received significant attention this current decade. The popularity and utility of *C. viridis/oreganus* for such studies has likely stemmed from three qualities: 1) its broad distribution through much of the Great Plains and western region of North America; 2) its proclivity for denning communally, whereby large numbers of snakes can be collected by researchers during spring and fall near the entrances to hibernacula; and 3) the geographic locations of researchers who have conducted productive behavioral and ecological studies on this group (e.g., David Chiszar and Hobart Smith, University of Colorado; Michael Douglas, formerly at Colorado State University; David Duvall, formerly at University of Wyoming; Patrick Gregory, University of Victoria, British Columbia; Kenneth Kardong, Washington State University; Stephen Mackessy, University of Northern Colorado; and Donald Owings and Richard Coss, University of California, Davis).

Finally, whereas venom has featured prominently in studies of genus *Crotalus*, researchers have been far less interested in the venom of genus *Sistrurus*, as evidenced in both the number and emphasis of publications. In terms of emphasis, of the eight *Crotalus* species considered here, 85% of the citations in the 1970s and 84% in the 2000s focused on their venom. By comparison, neither of the two citations for *Sistrurus* from the 1970s considered venom, and only 7% of those in the 2000s focused on venom. The relatively small body size and corresponding low venom yield of *Sistrurus* species have probably contributed to this disparity. Recent behavioral and ecological interest in *S. catenatus* has resulted largely from its threatened status (Szymanski, 1998; see also http://www.massasauga.ca and http://www.brocku.ca/massasauga).

*Conclusions*.—Collectively, our literature searches revealed that rattlesnakes have long held the fascination of researchers, and will continue to do so well into the future. Although venom has been a primary focus of interest, studies at the organismal level (e.g., behavior, ecology) have increased markedly in recently years. As study subjects, rattlesnakes have greatly enriched our understanding not just of snakes in general, but also in many other disciplines, as the chapters in this volume will testify.

**Table 4**. Number of species and total taxonomic forms (species + subspecies) of rattlesnakes recognized within each of four geopolitical regions.[a] Numbers endemic to each region are indicated parenthetically.

| Region | Species | Species + Subspecies |
|---|---|---|
| North America north of Mexico | 18 (5) | 30 (14) |
| Mexico | 31 (16) | 58 (40) |
| Central America (Belize to Panama) | 2 (0) | 2 (0) |
| South America south of Panama | 1 (1) | 8 (8) |
| Total | 37 | 80 |

[a] Excluded: *Crotalus tortugensis*, *C. durissus maricelae*, *C. d. cascavella*, *C. d. collilineatus*, *C. viridis nuntius* (see text).

## Annotated Checklist of the Rattlesnakes

In the two-and-a-half centuries since Carl Linnaeus first described a rattlesnake in his tenth installment of *Systema Naturae* (1758), the classification of rattlesnakes has experienced few periods of stability. In 1940, Howard K. Gloyd published the first comprehensive review of rattlesnake classification and biology in *The Rattlesnakes, Genera* Sistrurus *and* Crotalus*: A Study in Zoogeography and Evolution*. At that time, 26 species and 29 taxonomic forms (species + subspecies) were recognized. In 1956, Laurence M. Klauber published his two-volume *magnum opus*, *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*, in which he recognized 29 species and 65 taxa. In the second edition (Klauber, 1972), these totals were increased to 31 species and 70 taxa.

The following checklist provides the scientific and generally accepted common names for each recognized taxon of rattlesnake. Because a consensus is lacking regarding rattlesnake taxonomy, we have structured the following checklist to represent the most broadly accepted views. Nomenclature follows Crother (2000, 2008) and Crother et al. (2003) for North America north of Mexico and Campbell and Lamar (2004) for Central and South America. Departures from these sources include four taxa supported by detailed molecular and/or morphological data sets, with *C. culminatus* and *C. tzabcan* elevated to species (Wüster et al., 2005), *C. stephensi* elevated to species (Douglas et al., 2007; Meik, this volume), and *C. tortugensis* synonomized with *C. atrox* (Castoe et al., 2007). A recently described species is also included (*C. ericsmithi*), only the third distinctly new species discovered in the last half-century (Campbell and Flores-Villela, 2008). Although recent studies cast doubt on the historic recognition of two monophyletic genera, *Sistrurus* and *Crotalus* (summarized in Crother 2000, 2008), these are retained, with the taxon *ravus* included within *Crotalus* (Murphy et al., 2002). Common names were adopted from Crother (2000, 2008), Crother et al. (2003), Campbell and Flores-Villela (2008), and several internet sources. We provide comments that reflect on relatively recent changes and hypotheses.

Table 4 provides a list of species and taxonomic forms (species + subspecies) recognized within each of four geopolitical regions. These regions are abbreviated in the checklist to indicate where each taxon occurs: NA = North America north of Mexico; MX = Mexico; CA = Central America from Belize to Panama; and SA = South America south of Panama. Currently, 37 species and 80 taxa are recognized. The remarkable taxonomic richness in Mexico, which hosts 84% of the recognized species and 73% of the named taxa, presumably reflects the likely origin of rattlesnakes in this geopolitical region (reviewed by Place and Abramson, 2004). The relative paucity of species in Central and South America corresponds to the relatively recent history of rattlesnakes in these geopolitical regions (Wüster et al., 2002, 2005; Quijada-Mascareñas and Wüster, 2006). The numbers given here and in Table 4 will vary among authorities and no doubt change with intensified study and further refinement of concepts and methods in systematics.

***Crotalus adamanteus*** Palisot de Beauvois, 1799—Eastern Diamond-backed Rattlesnake [NA]
***Crotalus aquilus*** Klauber, 1952—Queretaran Dusky Rattlesnake [MX]
***Crotalus atrox*** Baird and Girard, 1853—Western Diamond-backed Rattlesnake [NA, MX]
(***Crotalus tortugensis*** Van Denburgh and Slevin, 1921)—Tortuga Island Rattlesnake [MX] (placed in synonymy with *C. atrox* by Castoe et al., 2007).
***Crotalus basiliscus*** Cope, 1864—Mexican West Coast Rattlesnake [MX]
***Crotalus catalinensis*** Cliff, 1954—Santa Catalina Island Rattleless Rattlesnake [MX]
***Crotalus cerastes*** Hallowell, 1854—Sidewinder [NA, MX] (subspecies designations are questionable; see Douglas et al., 2006).
***C. c. cerastes*** Hallowell, 1854—Mohave Desert Sidewinder [NA]
***C. c. cercobombus*** Savage and Cliff, 1953—Sonoran Sidewinder [NA, MX]
***C. c. laterorepens*** Klauber, 1944—Colorado Desert Sidewinder [NA, MX]

***Crotalus cerberus*** (Coues, 1875)—Arizona Black Rattlesnake [NA] (see Pook et al., 2000, Ashton and de Queiroz, 2001, and Douglas et al., 2002, for comments on this taxon).

***Crotalus culminatus*** Klauber, 1952—Northwestern Neotropical Rattlesnake [MX] (formerly *C. durissus culminatus*; elevated to species by Wüster et al., 2005).

***Crotalus durissus*** Linnaeus, 1758—South American Rattlesnake [SA] (see Campbell and Lamar, 2004, Savage et al., 2005, and Wüster et al., 2005, for comments on this taxon).

***C. d. cumanensis*** Humboldt, *in* Humboldt and Bonpland, 1813—Venezuelan Rattlesnake [SA]

***C. d. durissus*** Amaral, 1929—Cascabel Rattlesnake [SA]

***C. d. marajoensis*** Hoge, 1966 [dated 1965]—Marajoan Rattlesnake [SA]

(***C. d. maricelae*** García-Pérez, 1995)—*Nomen nudem* [SA] (see Esqueda et al., 2001)

***C. d. ruruima*** Hoge, 1966 [dated 1965]—Mount Roriama Rattlesnake [SA]

***C. d. terrificus*** Laurenti, 1768—South American Rattlesnake [SA]

(***C. d. cascavella*** Wagler, 1824)—Northeastern Brazilian Rattlesnake (placed in synonymy with *C. d. terrificus* by Wüster et al., 2005).

(***C. d. collilineatus*** Amaral, 1926)—Central Brazilian Rattlesnake (placed in synonymy with *C. d. terrificus* by Wüster et al., 2005).

***C. d. trigonicus*** Harris and Simmons, 1978 [dated 1976/1977]—Rupunini Rattlesnake [SA]

***C. d. unicolor*** Lidth de Juede, 1887—Aruba Island Rattlesnake [SA]

***C. d. vegrandis*** Klauber, 1941—Uracoan Rattlesnake [SA]

***Crotalus enyo*** Cope, 1861—Baja Rattlesnake [MX] (each subspecies referred to as a "pattern class" by Grismer, 2002).

***C. e. cerralvensis*** Cliff, 1954—Cerralvo Island Rattlesnake [MX]

***C. e. enyo*** Lowe and Norris, 1954—Lower California Rattlesnake [MX]

***C. e. furvus*** Lowe and Norris, 1954—Rosario Rattlesnake [MX]

***Crotalus ericsmithi*** Campbell and Flores-Villela, 2008—Guerreran Long-tailed Rattlesnake [MX]

***Crotalus horridus*** Linnaeus, 1758—Timber Rattlesnake [NA] (mtDNA haplotypes identified by Clark et al., 2003, and morphological analysis by Allsteadt et al., 2006, did not support formal recognition of subspecies within *C. horridus*; see also Crother, 2000).

***Crotalus intermedius*** Troschel, *in* Müller, 1865—Mexican Small-headed Rattlesnake [MX]

***C. i. gloydi*** Davis and Dixon, 1957—Oaxacan Small-headed Rattlesnake [MX]

***C. i. intermedius*** Klauber, 1952—Totalcan Small-headed Rattlesnake [MX]

***C. i. omiltemanus*** Klauber, 1952—Omilteman Small-headed Rattlesnake [MX]

***Crotalus lannomi*** Tanner, 1966—Autlán Long-tailed Rattlesnake [MX]

***Crotalus lepidus*** (Kennicott, 1861)—Rock Rattlesnake [NA, MX]

***C. l. klauberi*** Gloyd, 1936a—Banded Rock Rattlesnake [NA, MX]

***C. l. lepidus*** (Kennicott, 1861)—Mottled Rock Rattlesnake [NA, MX]

***C. l. maculosus*** Tanner, Dixon and Harris, 1972—Durango Rock Rattlesnake [MX]

***C. l. morulus*** Klauber, 1952—Tamaulipan Rock Rattlesnake [MX]

***Crotalus mitchellii*** (Cope, 1861)—Speckled Rattlesnake [NA, MX] (Douglas et al., 2006, presented mtDNA evidence suggesting that this may be a species complex).

***C. m. angelensis*** Klauber, 1963—Angel de la Guarda Rattlesnake [MX] (elevated to species by Grismer, 1999, 2002).

***C. m. mitchellii*** Cope, *in* Yarrow, *in* Wheeler, 1875—San Lucan Speckled Rattlesnake [MX] (referred to as a "pattern class" by Grismer, 2002).

***C. m. muertensis*** Klauber, 1949—El Muerto Island Rattlesnake [MX] (elevated to species by Grismer, 1999, 2002).

***C. m. pyrrhus*** (Cope, 1867)—Southwestern Speckled Rattlesnake [NA, MX] (referred to as a "pattern class" by Grismer, 2002).

***Crotalus molossus*** Baird and Girard, 1853—Black-tailed Rattlesnake [NA, MX] (Wüster et al., 2005, suggested that this taxon represents a species complex).

***C. m. estebanensis*** Klauber, 1949—San Esteban Island Rattlesnake [MX] (elevated to species by Grismer, 1999, 2002).

***C. m. molossus*** Baird and Girard, 1853—Northern Black-tailed Rattlesnake [NA, MX]

***C. m. nigrescens*** Gloyd, 1936b—Mexican Black-tailed Rattlesnake [MX]

***C. m. oaxacus*** Gloyd, 1948—Oaxacan Black-tailed Rattlesnake [MX]

***Crotalus oreganus*** Holbrook, 1840—Western Rattlesnake [NA, MX] (see Pook et al., 2000, Ashton and de Queiroz, 2001, and Douglas et al., 2002, for comments on this taxon).

***C. o. abyssus*** Klauber, 1930—Grand Canyon Rattlesnake [NA]

***C. o. caliginus*** Klauber, 1949—Coronado Island Rattlesnake [MX] (elevated to species by Grismer, 2001, but placed in synonymy with *C. o. helleri* by Douglas et al., 2002).

***C. o. concolor*** Woodbury, 1929—Midget Faded Rattlesnake [NA]

***C. o. helleri*** Meek, 1905—Southern Pacific Rattlesnake [NA, MX]

***C. o. lutosus*** Klauber, 1930—Great Basin Rattlesnake [NA]

***C. o. oreganus*** Holbrook, 1840—Northern Pacific Rattlesnake [NA]

***Crotalus polystictus*** Cope, 1865—Mexican Lance-headed Rattlesnake [MX]

***Crotalus pricei*** Van Denburgh, 1895—Twin-spotted Rattlesnake [NA, MX] (Crother, 2000, 2008, suggested that the taxonomic status of the allopatric subspecies needs reevaluation).

***C. p. miquihuanus*** Gloyd, 1940—Eastern Twin-spotted Rattlesnake [MX]

***C. p. pricei*** Van Denburgh, 1895—Western Twin-spotted Rattlesnake [NA, MX]

***Crotalus pusillus*** Klauber, 1952—Tancitaran Dusky Rattlesnake [MX]

***Crotalus ravus*** Cope, 1865—Mexican Pygmy Rattlesnake [MX] (reassigned from *Sistrurus* to *Crotalus* by Murphy et al., 2002).

***C. r. brunneus*** Harris and Simmons, 1978—Oaxacan Pygmy Rattlesnake [MX]

***C. r. exiguus*** Campbell and Armstrong, 1979—Guerreran Pygmy Rattlesnake [MX]

***C. r. ravus*** Harris and Simmons, 1978—Central Plateau Pygmy Rattlesnake [MX]

***Crotalus ruber*** Cope, 1892—Red Diamond Rattlesnake [NA, MX] (mtDNA sequences analyzed by Douglas et al., 2006, offered no support for formal recognition of subspecies, though *C. r. lorenzoensis* was not included in the study).

***C. r. exsul*** Garman, 1884—Cedros Island Rattlesnake [MX] (placed in synonymy with *C. ruber*; see Beaman and Dugan, 2007).

***C. r. lorenzoensis*** Van Denburgh, 1920—San Lorenzo Island Rattlesnake [MX] (elevated to species by Grismer, 1999, 2002).

***C. r. lucasensis*** Schmidt, 1922—San Lucan Rattlesnake [MX] (referred to as a “pattern class” by Grismer, 2002).

***C. r. ruber*** Klauber, 1949—Red Diamond Rattlesnake [NA, MX]

***Crotalus scutulatus*** (Kennicott, 1861)—Mohave Rattlesnake [NA, MX] (the spelling of the common name was changed recently from “Mojave” to “Mohave,” as summarized by Crother et al., 2003, and Crother, 2008).

***C. s. salvini*** Günther, 1895—Huamantlan Rattlesnake [MX]

***C. s. scutulatus*** (Kennicott, 1861)—Northern Mohave Rattlesnake [NA, MX]

***Crotalus simus*** Latreille, 1801—Middle American Rattlesnake [MX, CA] (elevated to species from the *C. durissus* complex by Campbell and Lamar, 2004; supported, but also found to be polyphyletic, by Wüster et al., 2005; see also Savage et al., 2005).

***Crotalus stejnegeri*** Dunn, 1919—Sinaloan Long-tailed Rattlesnake [MX]

***Crotalus stephensi*** Klauber, 1930—Panamint Rattlesnake [NA] (formerly *C. mitchellii stephensi*; elevated to species by Douglas et al., 2007, and Meik, this volume).

***Crotalus tancitarensis*** Alvarado-Diaz and Campbell, 2004—Tancitaran Cross-banded Rattlesnake [MX]

***Crotalus tigris*** Kennicott, 1859 [*in* Baird, *in* Emory, 1859]—Tiger Rattlesnake [NA, MX]

***Crotalus totonacus*** Gloyd and Kauffeld, 1940—Totonacan Rattlesnake [MX] (formerly *C. durissus totonacus*; elevated to species by Campbell and Lamar, 2004, and supported by Wüster et al., 2005).

***Crotalus transversus*** Taylor, 1944—Ajuscan Cross-banded Rattlesnake [MX]

***Crotalus triseriatus*** Wagler, 1830—Dusky Rattlesnake [MX]

***C. t. armstrongi*** Campbell, 1979—Mexican Dusky Rattlesnake [MX]

***C. t. triseriatus*** Wagler, 1830—Western Dusky Rattlesnake [MX]

***Crotalus tzabcan*** Klauber, 1952—Yucatan Neotropical Rattlesnake [MX, CA] (formerly *C. durissus tzabcan*; elevated to species by Wüster et al., 2005).

***Crotalus viridis*** (Rafinesque, 1818)—Prairie Rattlesnake [NA, MX] (see Pook et al., 2000, Ashton and de Queiroz, 2001, and Douglas et al., 2002, for comments on this taxon).

(***C. v. nuntius*** Klauber, 1935)—Hopi Rattlesnake [NA] (placed in synonymy with *C.* v. *viridis* by Douglas et al., 2002).

(***C. v. viridis*** [Rafinesque, 1818])—Prairie Rattlesnake [NA, MX]

***Crotalus willardi*** Meek, 1905—Ridge-nosed Rattlesnake [NA, MX]

***C. w. amabilis*** Anderson, 1962—Del Nido Ridge-nosed Rattlesnake [MX]

***C. w. meridionalis*** Klauber, 1949—Southern Ridge-nosed Rattlesnake [MX]

***C. w. obscurus*** Harris and Simmons, 1976—New Mexico Ridge-nosed Rattlesnake [NA, MX]

***C. w. silus*** Klauber, 1949—Western Chihuahuan Ridge-nosed Rattlesnake [MX]

***C. w. willardi*** Meek, 1905—Arizona Ridge-nosed Rattlesnake [NA, MX]

***Sistrurus catenatus*** (Rafinesque, 1818)—Massasauga [NA, MX] (see Holycross et al., 2008, for comments on nomenclature; Crother, 2000, 2008, suggested that the subspecies represent arbitrary delimitations of continuous morphological and ecological variation).

***S. c. catenatus*** (Rafinesque, 1818)—Eastern Massasauga [NA]

***S. c. edwardsii*** (Baird and Girard, 1853)—Desert Massasauga [NA, MX]

***S. c. tergeminus*** (Say, 1823)—Western Massasauga [NA]

***Sistrurus miliarius*** (Linnaeus, 1766)—Pygmy Rattlesnake [NA]

***S. m. barbouri*** Gloyd, 1935—Dusky Pygmy Rattlesnake [NA]

***S. m. miliarius*** (Linnaeus, 1766)—Carolina Pygmy Rattlesnake [NA]

***S. m. streckeri*** Gloyd, 1935—Western Pygmy Rattlesnake [NA]

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