Lizard Pollinator Mediates Positive Interactions Between Plant Species

Previous studies of indirect relationships between species have focused primarily on predator-prey and competitive interactions. However, indirect interactions can also be an important factor in mutualistic relationships. In this study, the authors tested whether the declining, endemic Trochetia blackburniana plant benefits from proximity to the endemic Pandanus plant in Le Pétrin, Mauritius. This positive interaction is thought to be mediated by the blue-tailed day gecko, Phelsuma cepediana, which moves between Pandanus thickets, the gecko’s preferred microhabitat, and T. blackburniana, where it feeds on nectar and pollinates the plants. By comparing T. blackburniana plants growing close to (< 10 m) with those growing away from Pandanus (> 20 m), the authors confirmed that gecko visitation to T. blackburniana was related to its proximity to Pandanus plants. Also, by fitting a generalized linear mixed-model, the authors demonstrated that the number of fertilized fruits on the T. blackburniana plants was also positively related to proximity to Pandanus thickets, but results from a previous study show that these differences are unrelated to variation in soil quality. Finally, an experiment was conducted in which geckos were excluded from some T. blackburniana branches. This resulted in fewer fertilized fruits relative to branches on the same plant from which geckos were not excluded. The authors highlight the importance of considering these types of indirect, positive interactions in both plant and lizard conservation.


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FIG. 1. Photograph of Reptile Building at National Zoological Park shortly after completion in 1931. Credit: National Zoological Park Photo Archives.

this impressive building remains one of the most beautiful reptile facilities in the world (Figs. 1–4). Ewing (1990) published a report called “An Architectural History of the National Zoological Park.” According to Ewing, the architecture exemplifies the Italian Byzanto-Romanesque ecclesiastical style and the main cathedrals in Ancona and Verona, built in Romanesque style in Northern Italy, provided the idea for Harris’ design. “... The brick structure was assembled in a building-block fashion, accumulating to form several ranges. Rising from a low asymmetrical level, the tower culminated in an octagonal drum and lantern ... articulated with round windows encircled by alternating red and white marble blocks ... the arch of the pedimented porch displayed small alternating curved blocks of little creatures: toads, turtles, lizards, etc. Under the cornice along the entire facade the arched corbels culminated in roughly-hewn abstracted reptiles. These terracotta figures served as subtle gargoyles, continuing the correlations with the cathedral model.” Unfortunately, the original elevated porch leading to the entrance has been removed but the porch columns supported by turtles remain. The massive wooden entrance doors with essonite/gold leaf panels depicting many extinct and extant


FIG. 3. Mosaic of Stegosaurus above doorway of visitor entrance to reptile building at Smithsonian Institution’s National Zoological Park. Credit: photograph by Dennis Desmond in 2004.

FIG. 4. Carved rock tortoise supporting column at entrance to reptile building at Smithsonian Institution’s National Zoological Park. Credit: photograph by Dennis Desmond in 2004.
The modules improved visitors' feelings about reptiles. Intellectually, they communicated new ideas, especially about internal anatomy, communication, and feeding.

During the past seventy-five years, reptile buildings and accompanying exhibits throughout the world were often designed by architects and zoo administrators who had little experience with living herps, public education, or who paid scant attention to the concept of exciting and aesthetically-pleasing presentations. Educational and interactive exhibits were an afterthought; visitors were subjected to row after row of uninspiring and unimaginative displays, hardly an enriching experience. One problem was the lack of input from the biological staff. Until the 1960s, amphibians and reptiles were rarely kept in appropriate social situations and little attention was paid to behavioral or environmental cues; social stressors among conspecifics such as competition or aggression were barely considered. Fortunately, zoo biologists have now become aware of these deficiencies and have worked to remedy them.

HISTORY OF THE COLLECTION

In the late 1920s and early 1930s, a number of interesting herps were represented in the NZP collection: Komodo Dragons, Sumatran Cobras, King Cobras, Boa Constrictors, Gila Monsters and Bearded Lizards, Zaire Toads, many rattlesnakes, Radiated Tortoises, Gould’s Monitor, and other lizards (Figs. 5, 6). In the Annual Reports of NZP beginning in 1931, one can see the enormous variety of specimens in the collection, such as tuataras.

The Zoo collection was utilized in 1932 for a classic scientific study on brooding behavior in pythons by Frances G. Benedict, Director of the Nutrition Laboratory at the Carnegie Institution of Washington. He observed an incubating female African Rock Python (Python sebae) on exhibit and made detailed environmental and body temperature readings during one entire day.

Captive crocodilians can be exceedingly dangerous, especially if their exhibits are poorly designed without shift cages. In the late 1950s, the solarium housed a Nile Crocodile (Crocodylus niloticus) and an American Crocodile (Crocodylus acutus) in the same enclosure. The middle enclosure housed an aggressive and agile Saltwater Crocodile (Crocodylus porosus) called “Biggie” by the staff, and the end enclosure featured a group of 5–7-foot long American Alligators (Alligator mississippiensis). Because there were no shift cages, keepers had to work around the crocodilians. The Nile and American crocodiles were extremely aggressive, attacking the keepers constantly. Two keepers were always in attendance, one to clean and the other to fend off the reptiles. Holding them off with a broom and shovel worked for the most part but cleaning these enclosures was a constant strain on the staff.

“Biggie” was acquired in the 1930s and lived over 40 years at the zoo where it attained a length of over 14 feet. When the crocodilian was weighed and measured in 1932, its size was modest: 150 lbs and six feet total length. One of us (WAX) was responsible for cleaning its enclosure during the late 1950s and early 1960s, a very dangerous task indeed, for the procedure was to actually enter its domain. On one occasion, “Biggie” was lying in the emptied pool and WAX was on the surrounding land, picking up some leaves. “Biggie” spun around and charged with mouth agape and WAX had to leap over the recurved bars. Unfortunately,
unidentified, some venomous, often loose in the box or with their port, such as one sent by Wesley Dickinson from India (see Murphy unannounced large shipments regularly arrived at the local air-

belly and tossed its head in a violent slashing motion which evis-

remain closed during feeding, due to concern about public sensi-

python" and continued on to finish his task. His horrified parents

minutes before to the zoo. When the child asked where the keeper

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wicker basket, the child recognized his pet "Fluffy," donated just

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were rarely considered. We could not sex our animals accurately

rians and reptiles alive and plans to accumulate breeding groups

wildlife conservation. Most efforts centered on keeping amphib-

were new to the collection.

On Easter Sunday in 1983, a teenaged boy who liked snakes waited until the building closed, broke the glass of the Gaboon Viper (*Bitis gabonica*) exhibit, put two adult snakes into a plastic garbage bag, flung the bag over his shoulder and caught a bus to take them home. He was bitten through the bag on the shoulder while departing the bus and rushed to the hospital. He survived the ordeal after antivenin therapy was undertaken but recovery was protracted. Later, some well-meaning citizens, including Smithsonian Secretary S. Dillon Ripley’s wife, suggested that he be hired at the Zoo since he liked snakes but this recommendation was not adopted. Several others sent get-well cards to Mr. and Mrs. Gaboon Viper.

Play behavior in reptiles is rarely reported. At NZP, an adult Nile Softshell Turtle (*Trionyx triunguis*) collected by William Mann in Liberia, played with a variety of objects: pushing a basketball with its snout, swimming through a hoop, and biting and pulling a hose (Burghardt et al. 1996). One of the captive-hatched Komodo Dragons (*Varanus komodoensis*) named Kraken interacted in the most unexpected way with humans and objects (see Burghardt et al. 2002; Murphy and Walsh 2006 for details).

When we entered the zoo profession (WAX in the late-1950s, JBM in the mid-1960s), there was little discussion in zoos about conservation. Most efforts centered on keeping amphibians and reptiles alive and plans to accumulate breeding groups were rarely considered. We could not sex our animals accurately and if successful reproduction occurred, it was a major event. Virtually all zoo collections at that time were composed of herps from the wild; captive-bred amphibians and reptiles were mostly unavailable. Now that captive breeding has been relatively successful (although long-term breeding programs producing multiple generations are still somewhat rare), zoos tend to get their new ani-

the cuff on his pants was caught on one of the pointed tips. As WAX tried to free his cuff while balanced on the top of the bars, his hand fell off to one side. The reptile redirected the attack toward the dangling hand rather than the foot and just missed a tasty snack when WAX was able to pull his hand away, extricate his leg from the bars, and fall into the next enclosure.

At NZP, live food was used until the 1960s. When one of the keepers was seen by a mother and child carrying a rabbit in a wicker basket, the child recognized his pet “Fluffy,” donated just minutes before to the zoo. When the child asked where the keeper was taking his rabbit, the latter said, “I am going to feed him to the python” and continued on to finish his task. His horrified parents wrote a seething letter to Director Theodore H. Reed, who immediately banned the use of live food during public hours. Although offering dead prey is now common in zoos, some reptile buildings remain closed during feeding, due to concern about public sensitivities. NZP feeds only dead vertebrate prey and stays open.

Many years ago, NZP herp keepers also fed dead animals from the collection to reptiles. Head keeper Lee Schmeltz acquired a carcass of a muntjac that recently died in the collection and fed it to the Komodo Dragon. The dragon seized the muntjac by the belly and tossed its head in a violent slashing motion which eviscerated the deer, and splashed the glass front of the enclosure. Someone reported the incident to higher authorities and Schmeltz was warned never to let it happen again (C. Wemmer, pers. comm.).

NZP is the national zoo of the United States, so governmental employees, Smithsonian scientists, and military personnel, particularly the Naval Medical Research Unit-S.E. Asia (NAMRU) and the Army Medical Research Unit-North Africa (AMRU), often sent amphibians and reptiles to the Zoo. During the 1960s, unannounced large shipments regularly arrived at the local airport, such as one sent by Wesley Dickinson from India (see Murphy and Jacques 2006). The animals in these shipments were mostly unidentified, some venomous, often loose in the box or with their cloth bags unmarked; unpacking these shipments, although exci-
mals from other zoos rather than the wild. Today there are many cooperative breeding programs in zoos. The downside of these collaborative programs is that we now rarely see something new in zoos; there is not room or resources for a diverse collection with many new species.

Today, the NZP collection is stable, many of the specimens bred in captivity, with ca. 63 species of reptiles totaling nearly 350 specimens and 15 species of amphibians numbering nearly 140 animals. The collection includes Cuban Crocodiles, Gharials, highly-endangered Cayman Island Iguanas (Fig. 5), Aldabra and Radiated Tortoises, an adult Japanese Giant Salamander, large constrictors and a variety of amphibians such as breeding colonies of a number of poison dart frogs (Dendrobates) and Panamanian Golden Frogs (Atelopus zeteki). Komodo Dragons reproduced at NZP in 1992 for the first time in any zoo in the Western Hemisphere (Fig. 6). Reproduction over multiple generations has been accomplished in several taxa: Emerald Tree Boas (Corallus canina), Green Tree Pythons (Morelia viridis), Brazilian Rainbow Boas (Epicrates cenchria), African Rufous-beaked Snake (Rhamphophis oxyrhynchus rostratus), Chinese Water Dragons (Physignathus cocincinus), and Madagascan Giant Day Geckos (Phelsuma madagascariensis).

PEOPLE

Like a notorious keeper at London a century earlier, WAX and a fellow keeper at NZP held contests to see who could handle pitvipers (rattlesnakes, copperheads, moccasins, bamboo vipers) without getting bitten. Their reasoning, hardly justifiable and certainly illogical, was this practice was acceptable as a displacement activity to relieve the stress of battling crocodilians. The snakes chosen to be handled all resided on the same row of exhibit cages. Each day before the building opened, these foolhardy caretakers would take turns, starting at the first exhibit cage and working their way down the line. The process was simple: when the serpent was in a resting coil, the contestants would slide hands beneath the coils, lift gently from the substrate for a few seconds, then replace the reptile in its original resting place. The contest ended after the entire group of exhibits holding venomous snakes was sampled or one of the participants lost courage. Miraculously, no one was bitten so none of the snakebite recommendations in Footnote #7 could be tried but had this practice been discovered by their bosses, repercussions would have probably been more unpleasant than a bite.

Over the years, Roy Jennier, Charlie Braxton, Jack Armstrong, Lester Ratliff, Lee Schmeltz, Cecelia Chang, Russell Morrison, Mike Johnson, William Xanten, Sam Davis, Bob Davis, Tom Keefer, Roger Rossco, Charles Courits, and Rob Lewis worked as keepers in the department. The first woman keeper ever hired at NZP was Brenda Hall in the early 1970s, who wrote a paper on tegu lizards (Tupinambis tequixin). Today, women outnumber men in the Animal Department. Before curatorial positions were established at NZP, Mario (Jack) DePrato was the Head Keeper. Now retired, the first herpetological curator was Jaren Horsley, who was elevated to General Curator (Fig. 7). His replacement was Dale Marcellini, whose research interests were primarily directed toward public education and visitor behavior, as well as gekkonid and iguanid ethology (Fig. 8). Louis (Trooper) Walsh retired from the zoo as Biologist/Museum Specialist and is best known for his work with Komodo Dragons and boid snakes. Biologist Béla Demeter published a number of papers on Malagasy geckos. Michael Davenport is the current curator who focuses on the captive breeding of crocodilians. In addition to Davenport and Demeter, the current staff is Janis Gerrits, Sean Henderson, and Robin Saunders. After retiring from the Dallas Zoo, one of us (JBM) is now a research associate at the Zoo.

Jonathan Ballou is the Population Manager at NZP's Department of Conservation Biology; he has published many papers and several books on the proper management of captive populations.

Long-term investigation of essential dietary ingredients for captive and wild reptiles by Mary Allen and Olav Ofstedal includes evaluating the diets of desert tortoises. The evolution, expansion and sophistication of herpetological medicine and the understanding of emergent diseases has contributed to significant advances. Recently, the pathogenic chytrid fungus attacking captive and wild amphibians was isolated and described by former NZP pathologist Donald Nichols.

John (Jack) Frazier has studied chelonians since 1979 as a Smithsonian research associate. His major focus centers on the conservation of marine turtles and he has published widely in this area. In addition, his earlier studies have included behavioral and ecological aspects of the Aldabrachelys and the Star Tortoise, and recently a sortie into nomenclatural never-never land (see Frazier 2006).

The Smithsonian Institution offers stipends for limited periods to outside investigators, mostly from the academic community, to do research at the Zoo. Using this program, Marcellini brought in an impressive series of herpetologists. Eliezer Frankenberg (The Hebrew University of Jerusalem) focused on animal communication, lizard ecology and reproductive biology. Thomas Jensen (Virginia Polytechnic Institute and State University) studied lizard ethology and visitor behavior, beginning in the 1980s. Paul Weldon (Texas A & M University) was a research associate at the Zoo from January 1991 to January 1993, working closely with zoo personnel on a variety of studies, such as collecting and analyzing glandular materials from reptiles in zoos. Now living in Baltimore, he currently...
holds the same appointment at the Zoo’s Conservation and Research Center in Front Royal, Virginia. Eric Wikramanayake from Sri Lanka was a research associate at the Zoo, specializing in field studies on varanid lizards. He is now a senior conservation biologist for World Wildlife Fund-US in Southeast Asia.

PROGRAMS

Christen Wemmer, retired Director of the NZP Conservation and Research Center (CRC) in Front Royal, Virginia, and his associates were instrumental in creating Zoo Biology Training Courses held in many developing countries throughout the world (see Wemmer et al. 1990 for description). The program and all written materials were developed by the staff at the Zoo, beginning in 1987. These courses included a herpetological component and focused on captive management. Zoo herpetologists, including JBM, were participants in these various training courses. In 1997, Wemmer, George Zug from the US National Museum of Natural History, and JBM traveled to Myanmar (Burma) to teach a workshop on herpetology to local wildlife biologists. The course provided an introductory treatment of amphibian and reptile biology, including a field component for sampling populations. This herpetofaunal survey continues to this day.

The American Association of Zoos and Aquariums hosted a Wildlife Conservation and Management Committee (WCMC) workshop on the conservation and captive management of Komodo Dragons, held at Tamin Safari in Bogor, Indonesia in 1995, which included a presentation by Trooper Walsh on the husbandry of these lizards. Three years later, the Thoiry Komodo Dragon Symposium was held at the Thoiry Zoological Park in France. The program was created by Walsh and Colomba de La Panouse, who invited the world’s leading experts involved with field research and conservation, laboratory studies, and zoo conservation/education initiatives, to present their findings and write chapters for a comprehensive book on dragons. The research presented by several of the attendees was supported financially by grants from NZP’s “Komodo Dragon Conservation Fund.” Four years later, the book entitled Komodo Dragons: Biology and Conservation appeared.

There have been several herp initiatives at CRC: metapopulation analysis of the Eastern Newt (Notophthalmus viridescens) in northern Virginia, including sampling the CRC population; drift fence survey of indigenous species; Box Turtle (Terrapene carolina) study; and northern Virginia frog study guide written by Joseph Mitchell for the education program at CRC.

In the reptile building, several dozen volunteers serve as instructors, teaching zoo visitors about amphibians and reptiles. As an example, these interpreters explained the research that was being done on play behavior in Komodo Dragons.

SUMMARY

Retired curator Dale Marcellini (1994) summarized the challenges that zoo herpetologists face when managing zoo collections, “Conservation is one of the main goals of zoo reptile houses, and yet curators act in ways which may be harmful to the conservation of species in the wild. Collections are composed largely of exotic, rare, and wild-caught species. Only rarely are breeding programs done on a long-term basis. When breeding is successful, reintroduction into the wild is almost never done. Zoo herpetologists must begin to act more responsibly in the way collections are managed, and more emphasis needs to be placed on conservation education.”

In the same volume, Robert J. Wiese and Michael Hutchins (1994) enumerate additional responsibilities, “There is much work to be done if we are to assist even a fraction of the species currently at risk. Through the successful use of captive-breeding and reintroduction programs in conjunction with strategic collection planning, scientific research, in situ conservation efforts, and public education, professionally managed zoos and aquariums can play a significant role in amphibian and reptilian conservation.”

In our view, the results have been mixed! On the plus side, the dramatic improvements of husbandry protocols have led to better lives for captive herps—no longer are “snake dens” ordered every year from suppliers to replace losses as was the case occasionally in the past. Zoos and aquariums are involved in many in situ and ex situ conservation projects. We are concerned, however, that herpetological collections and buildings are viewed as a relict from the past; as a result, there has been a significant decline in new facilities, emphasis, and financial support. Instead, many zoo administrators build elaborate and costly zoogeographic mixed exhibits housing mostly mammals and birds.

One can track the paradigm shift over seventy-five years at NZP in the literature citations below as the staff gradually became more aware of the enormity of the threat to a diverse and interesting natural world, and began taking steps to intervene by adjusting their programs and research focus.

Acknowledgments.—We dedicate this contribution to veterinarian and retired NZP director Theodore H. Reed, who was at the helm from 1956 until 1983. Reed inherited a facility where major building construction and preventive maintenance had been halted for over twenty years due to inadequate funding. Under his leadership, NZP was reborn with increased appropriations, construction of a number of new buildings and revitalized exhibits. He established the first education department in a zoo in the United States and created the first research positions (Department of Zoological Research) with the hiring of the late John Eisenberg. The acquisition of the Conservation and Research Center (CRC) in Front Royal, Virginia, comprising more than 1200 hectares, was the culmination of a dream and years of intense work by Dr. Reed and Assistant Director John Perry.

Judith Block, Béla Demeter, Jack Frazier, Devra Kleiman, Karl Krantz, Dale Marcellini, Robin Saunders, Trooper Walsh, Christen Wemmer, and Judy White read early drafts of the manuscript and made helpful suggestions. We thank Ed Bronikowski, Jessie Cohen, Michael Davenport, Dennis Desmond, Mark Grisham, Polly Lasker, Steven Monfort, John Moriarty, Mandy Murphy, J’nie Woosley, and William Xanten III for various courtesies.

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1907:785-794) that dead prey would be taken by many different species and would

FOOTNOTES

1 “John Earley was the last of the concrete pioneers. Others before him had dis-

covered how to produce the ‘magic powder’—portland cement—how to mix it with stone and sand to make concrete, and how to use concrete as a structural material. But Earley was the first to control the exterior appearance of concrete in an important way and to impart brilliant permanent color to the surface. His contri-

bution was unique: he was the man who made concrete beautiful.”


2 “One of the most interesting and one of the most fascinating additions of recent years to zooological exhibits is the modern reptile house. Both the animal and the vegetable world are represented in it. It is a whole world of forests, dusky swamps, barren deserts, and tangled jungles brought from North and South and East and West and crowded under one roof. And under the roof, caged among giant palms, hinging bushrope, and drooping resurrection ferns, there squirm and coil the most 

mysterious and uncanny and merciless of all of God’s creatures, housed according to the most advanced ideas of animal science, with all the surroundings peculiar to the wild and natural state of each. This novelty of showing the animals, and the modern facilities for feeding them as once they fed themselves, for studying reptile diseases, and even for operating with the surgeon’s knife, have practically revolutionized the snake house of old into the marvelous reptile house of to-day.”

— A. W. Rolker in Treasury of Snake Lore (1956)

3 In the paper files on Komodo Dragons in the Reptile House there is an interesting entry attributed to Raymond L. Ditmars. Back in ~1934 when the first dragon arrived at NZP Ditmars was contacted and asked what he thought the lizards would eat and how often they should be fed. He replied, “Offer lobster, fish, octopus, horse meat, cattle organs, fresh killed rats and mice, deer meat, and pig... offered three times a day.” It is fascinating that the then “world authority” on reptiles would provide such guess work about how much food was appropriate, showing how little was really known about the biology of these animals at the time.

4 Raymond L. Ditmars (1933) described crocodilians in this way: “Such is the average crocodile—an active, vicious and, above all, treacherous brute. When the keepers of the reptile house in the New York Zoological Park clean out the big pool for crocodilians, they actually walk over the backs of some of the big ‘gators, so tame are these. They never become unduly familiar with the crocodilians, finding it necessary to pen the latter behind heavy barred gates—and in the process the men are often chased from the enclosure.”

5 Saltwater Crocodiles have acute vision. At Zoo Atlanta, a large individual located and consumed mealworms tossed into its pool. At NZP a mixed exhibit of birds and crocodilians was attempted. A large Asian Jay was released into the solarium where it flew several times from one end to the other. When it passed overhead on its final journey, “Biggie” exploded from the water and caught the bird in mid-air—over a meter above the surface.

6 The feeding of live food to snakes has always been controversial among some sectors of the public. It was an issue so inflammatory in London over a century ago that it was discussed in Parliament. For many years, live mice, rabbits, birds, frogs and other prey had been fed to snakes at the London Zoo but little public outcry ensued; in fact, the feeding demonstrations were enthusiastically viewed by the visitors. In 1869, however, the climate began to change, fueled in part by newspaper campaigns in London to elicit reader responses as to whether the practice should continue. A few selected sentences quoted in Blunt (1976) should put the contro-

versy in proper perspective: “... that a rabbit should be shut up in a cage with a snake without any chance of his life, deprived of the means of escape allotted to him by nature, and subject to the exquisite torture of terror prolonged by factitious circumstances and enhanced by despair” or “... trembling rabbits devoured by a serpent?-a monster reptile maintained and thus feasted for the pleasure of the En-

English—for their children ...” To deal with continuing public pressure, P. Chalmers Mitchell, Secretary of the Society from 1902 to 1935, and curator of mammals Reginald I. Pocock presented dead prey to snakes at the Zoo to determine whether this practice was a viable alternative. They documented (Proc. Zool. Soc. London 1907:785–794) that dead prey would be taken by many different species and would
The classification of taxa has always been an area of debate among systematists—empirically, methodologically, and philosophically. Arguably, the single most important change over the past forty years is the widespread recognition that a classification system is only useful when it functions as a storage and retrieval system of phylogenetic information. Although the type of information to be stored has largely been agreed upon (i.e., propinquity of descent and monophyly), debate continues on the method of this system (e.g., PhyloCode: Cantino and de Queiroz 2003; contra Keller et al. 2003; Nixon et al. 2003). Regardless, the role of classification as a subsystem of the science of systematics is clear, and it is separate from that of nomenclature, although both are subsystems of taxonomy (de Queiroz 2006). Taxonomy is informed by phylogenetics, and this information is used in the naming of biodiversity (nomenclature) and in the organization of the named groups (classification). All systems of classification and nomenclature that are based on evolutionary hypotheses (phylogeny) provide ranks and names for only monophyletic groups. It is from this framework that we address recently proposed changes to the taxonomy of the Colubroidea in North America (NA; Table 1).

One of the largest groups of squamates, the Colubroidea, was recently found to contain a number of families and subfamilies that were determined to be para- or polyphyletic (Kelly et al. 2003; Lawson et al. 2005). The “traditional” classification, with four families and 15 subfamilies, has remained in this state at least since Dowling and Duellman (1978; although five of the aforementioned subfamilies were used as tribes in that work). Virtually all of these subfamily names (except Pseudoxyrhophiinae), even those used as tribes in Dowling and Duellman (1978), long predate that publication (Table 2). To rectify this disconnection between phylogeny and taxonomy, establish consistency with phylogenetic hypotheses generated from a large number of morphological and molecular studies (see references in Lawson et al. 2005), and make...