Carl Linnaeus or Carl von Linné, as was his true name after his ennoblement in 1757, was born in May 1707. He is well known for his work in formalizing a hierarchical system of classification of animals and plants into species, genera, orders, classes, and kingdoms, which still forms the basis for the classification of the biodiversity. He indeed also set rules for a system of binomial nomenclature and a third effort was his initiative to systematically find, diagnose and record biodiversity around the world. Linnaeus was active in several fields within and beyond what we now call biology.

He undertook his own field expeditions although only in his native Sweden, and he was diligent in producing stylish narratives that are still worth reading. However, he surrounded himself with capable students and established far-reaching networks of correspondents and through these he obtained access to animals and plants from around the world. Reptiles and amphibians during Linnaeus’s time were particularly poorly known and their diversity under-appreciated, but they nonetheless received their due attention in Linnaeus’s studies, descriptions and teaching.

For the year of commemoration of Linnaeus’s 300-year birthday, which by and large received a lot of attention internationally, we felt it desirable to organize a symposium to recognize Linnaeus’s scientific contribution to herpetology. Such an arrangement was eventually implemented on July 14, 2007 in St. Louis, Missouri, USA in conjunction with the annual Joint Meeting of Ichthyologists and Herpetologists.

Requests for presentations went out in February 2006 and resulted in ten people signing up (some with joint authors). Together with a key-note presentation of Linnaeus’s biography these filled a half day symposium.

A display and presentations of some original literature written by Carl Linnaeus and his disciples on herpetological subjects were on show during the meeting. An audience of approximately 250 people attended the symposium as listeners and there were lively discussions with the presenters.

The idea of a proceedings volume came up soon after the symposium closing. Eventually two of the presenters were unable to provide written contributions but one author who was not present at the symposium has been included with a contribution in the proceedings. For one of the contributions, the precise subject that was presented at the symposium has been incorporated into a more comprehensive paper of Linnaeus’s contribution to herpetology at large.

The contributions include treatments that are historical, bibliographical, biographical, taxonomic, geographic, iconographic and philosophical in their approaches and, as such, give a broad view of Linnaeus and his contributions to herpetology.

It is our hope that this volume will encourage students and others to pursue further research on the Linnaean contributions to herpetology. Thus we view this symposium volume as merely a starting point for further explorations of this field.

Our thanks are due to the Herpetologist’s League, which hosted and generously sponsored the symposium. All contributions in this volume have been peer-reviewed and we offer our sincere thanks to the reviewers.
as well as the contributors themselves. We also thank Christopher J. Bell, the editor of Bibliotheca Herpetologica for shepherding the papers through to their final stage after a long delay not of his making. Finally, we dedicate this volume to one of the symposium participants, Dr. Ernest A. Liner of Houma, Louisiana, USA. Ernie, who was a friend to all who knew him and particularly to members of the International Society for the History and Bibliography of Herpetology, passed away at the age of 85 on September 23, 2010. He will be missed.

Lund and Villanova November 13, 2011

Richard Wahlgren  Aaron M. Bauer

Organizers of The Herpetological Legacy of Linnaeus in St. Louis, Missouri, USA in July 14, 2007 in conjunction with the annual Joint Meeting of Ichthyologists and Herpetologists.


About the Cover

The cover montage has as its centerpiece an image of Carl Linnaeus (1707–1778) from a color printed stipple engraving (11.4 × 8.7 cm filled oval fringe) dated October 16, 1802 made by John Chapman after an oil painting (56 × 46 cm) by Alexander Roslin (1718–1793) from 1775. The engraving appeared in A genuine and universal System of Natural History 1794-1810, a publication attributed to Ebenezar Sibly (vol. 1–3), and John Wilkes (vol. 4–14).

INTRODUCTION

In the composition of an overview of Linnaeus’s contributions to herpetology, I have chosen to primarily describe his various achievements chronologically. His involvement in this field has mainly been based on his publications, but there are other sources, such as his correspondence (much of it is published), his students’ annotations that have been published and to a certain extent what is left of collections he worked with. Linnaeus carried out several journeys in Sweden and one to Holland that usually resulted in published narratives. His diaries during these expeditions have been published posthumously with annotations. The observations, annotations and contemplations of herpetological issues in these field studies hence form an important part of the present essay. The literature in English on Linnaeus’s life and contributions to science as a whole is lavish, e.g. Blunt and Stearn (1971) and Goerke (1973), two primary sources that I have used in this essay for his life history at large, so I provide only a skeleton of Linnaeus’s biography, but hopefully sufficient for any reader to gather the basics of his life and career.

The Gregorian calendar was introduced in Sweden on February 17, 1753. The earlier calendar dates were based on the Julian calendar. I have adjusted the dates used by Linnaeus, notably for his field observations, by adding the 11 days difference and marking them “n.s.” (i.e. “new style”).

Linnaeus did not write anything in English; he used Latin or Swedish depending on the avenue of publication. Linnaeus’s own text or passages that were originally written in Swedish or Latin are here reproduced in English. Any text available from previously translated English sources I have used critically and sometimes revised, as translators have not always been observant to the scientific significance of precise details.

Linnaeus did not separate reptiles and amphibians into two different classes. Instead he used...
the term “Amphibia” to denote both the amphibians and the reptiles and established two orders: “Serpentia” for the limbless Amphibia and “Reptilia” for the Amphibia with legs. He also introduced the 3rd order “Nantes” for cartilaginous and some other fish, which I will not deal with in this essay. It was an antagonist to Linnaeus, Jacob Theodor Klein (1685–1759), who in 1755 coined the Latin term *Herpetologiae* to include any serpentoid animals (e.g. snakes, amphisbaenians, and worms; Johnson et al. 1984). Herpetology today embraces reptiles and amphibians.

**LINNAEUS’S YOUTH AND UNIVERSITY LIFE**

Carl Linnaeus (Fig. 1) was born on May 23, 1707 (n.s.) in the village Råshult, situated in the south part of the province of Småland in southern Sweden. When Carl was two years old his family moved to a larger house in nearby Stenbrohult, where his father served as minister from 1709. He was the first child of five and the inspiration for his given name most likely came from the popular reigning monarch Carl XII (1682–1718). His father adopted the name Linnaeus from the lime or linden tree (*Tilia cordata*), called “lind” in Swedish and “linn” in the provincial dialect. This is the standard name employed in English, but after Carl Linnaeus was ennobled in 1761 he adopted the name von Linné. A curious mix of German and French components, this name was employed retroactively in Swedish (and occasionally elsewhere) to 1757.

When Linnaeus was seven years old he was sent to Växjö, 50 km away, for schooling in preparation for priesthood, as it was a family tradition and the only occupation his mother would approve for her oldest son. However, Linnaeus showed little interest in theological subjects, and, probably for that reason, no brilliance. The teachers recommended to his father that the boy would probably develop much better as a craftsman, such as a shoemaker or tailor. However, one of the senior masters at the grammar school and a physician, Dr. Johan Rothman, had observed the young man’s interests in botany and natural history in general. Rothman recommended that Carl’s parents allow him to study medicine, which was the usual discipline for a naturalist. In August 1727 Carl enrolled at Lund University. He found a sponsor in his professor of medicine, Kilian Stobaeus (1690–1742), who took the new student to his house as a son with lodging and meals. Linnaeus eventually got access to Stobaeus’s extensive library and could accompany his professor on sick calls. However, the academic tutoring was inadequate and he left for Uppsala University after a year. In Uppsala times were hard, especially for a poor student, but Linnaeus’s brilliance was soon unearthed. The dean, Professor Olof Celsius the Elder (1670–1756), who possessed a strong interest in botany, provided Linnaeus with free lodging. From the beginning of 1730 Linnaeus lectured in botany and served as a very popular guide in the botanical garden. He tutored the children of Professor Olof Rudbeck the Younger (1660–1740), famous for his bird studies, and had access to his rich library. It was in Uppsala he first met the slightly older student from the north of Sweden, Petrus Arędzi (1705–1735), who shared his interest in natural history, and had a similar kind of ingenuity. They even divided the specialties among them so that, in a nutshell, Arędzi should focus on the fishes and the amphibians (including reptiles) whereas Linnaeus should restrict his attention to botany and the other animals.

**LINNAEUS’S TOURS TO THE PROVINCES OF LAPPLAND AND DALARNA**

Olof Rudbeck had undertaken an exploratory journey to Lapland (Lapland) in northern Sweden, an unusual expedition for his time, which had inspired Linnaeus to plan for a similar tour. He applied for money at the Royal
Society of Science in Uppsala and pointed out the opportunity of unusual discoveries and observations of this remote and unexplored part of the country. On May 23, 1732 (n.s.), at the age of 25 he started his five-months-long journey on horseback and on foot. He made careful records for the report to his sponsor, but also for a separate publication. However, his diary was not published until almost a century later as an English translation (Linnaeus 1811). An annotated Swedish edition was compiled by Bertil Gullander (Linnaeus 1969). While the herpetological observations are trivial, this diary contains the first records made by Linnaeus. In Lycksele he met a woman who complained that she had three frogs in her stomach (this was a common kind of belief of the period) which she claimed to have acquired as frogspawn when drinking water earlier in the spring. Linnaeus recommended tar as a cure but she had grumbled that she could not retain it. When describing the feeding habits of the reindeer he declared that they can eat frogs, snakes and even lemmings, which they run after so intensely that they can’t find the way back to the herd. When he reached the high mountain areas in Norway, he briefly stated that there are “no fleas, snakes and bedbugs” there.

An interest in mineralogy emerged in Lapland, and in December 1733 he made a short journey to the province of Dalarna (Dalecarlia) especially to investigate the copper mine at Falun, then the largest in the world. There he met the provincial Governor, who would be the benefactor for another expedition into Dalarna as far as Norway; that six-week-long trip was made with a small group of students during the summer 1734. The narrative was not published until 1889 (in Swedish). A new edition with detailed annotations with Arvid Hj. Uggla as the supervising editor was published in 1953 (Linnaeus 1953). An English edition translated by Andrew Casson came out in 2007 (Linnaeus 2007a). The company set off on July 14 (n.s.) from Falun. They stayed at the Älvdalen parsonage for a few days and used the time for excursions and observations.

Linnaeus wrote with an annotation in the left margin “vipera vera” (the “true viper”):

When we returned we found a quarter long [20 cm] snake, its back was with a linea longitude. Dentate, fusca [a dark line with indentations lengthwise], besides this the whole snake was gray apart from blackish spots just opposite each tag on the entwined line. The belly was brown with a black spot at the tip of each scale. Gula [The throat] was pallida [pale] and labium superius, secundum marginem white [the upper lip white at the edge]. Iris oculorum ignea, cum pupilla perpendicular nigra [The iris colored as fire, the pupil vertical and black].

This was obviously an adder, Vipera berus (L., 1758).

In Älvdalen they “went out fishing and for a long time tried in vain to observe a 4-footed fish that was said to run up the trees, one that we thought to be Salamandra aquatica.” On August 26 (n.s.), the company on their way back had reached Floda (now Dala-Floda) and Linnaeus reported that carps and “skrot-abborar” are said to occur there (Sw. abborrar...
are perches and the Sw. prefix skrot, or skratt, is probably a dialectal word for a demon). He commented further on this species within parenthesis: “Salamandra aqvatica or the fish that is for long said to leap in the trees when he is on the fish hook.” In local folklore it was considered to be a fish, but Linnaeus postulated an amphibian affinity even without having seen it. Sven Nilsson (1787–1883) in his classic Scandinavisk herpetologi (1842:108) assumed it referred to the great crested newt, Triturus cristatus (Laurenti, 1768), whereas Ingvar Svanberg (2005) strongly advocated it to be the smooth newt, Lissotriton vulgaris (L., 1758), because the dialectical name is more sympatric with its distribution in northern Sweden. However, Mattias Sterner (2005:14) considered it the male of the great crested newt, which in the breeding season has a definite appearance of a perch at first glance and the actual northern distribution of this species is not yet fully investigated. Personally I consider it even doubtful that the two newts were differentiated in the local folklore.

Once back in Falun, a well-off man offered Linnaeus financial aid to accompany his son, Claes Sohlberg (1711–1773), to Holland to study for a few years. This would be a great opportunity for young Linnaeus to finish his studies of medicine as well, because due to a royal decree in 1688 the Swedish universities stopped bestowing the M.D. degree in medicine (Goerke 1973:5). During the first four decades in the 18th century the university in Leiden, Holland, became popular place for Swedish medical students to study, and the university at Harderwijk, Holland, to graduate from. A doctor degree could actually be acquired promptly and at low cost if the manuscript to the dissertation was ready (Holmstedt et al. 1998). It was in 1734 during the Christmas celebrations he met Sara Elisabeth (Lisa) Moraea (1717–1806) to whom he was engaged in January the following year and made an agreement with her parents about a three year absence before they would marry (Goerke 1973).

HAMBURG AND THE HYDRA

Linnaeus and Claes Sohlberg left for Holland in early spring 1735, although the pledged money by the latter’s father was subtly withdrawn. They made several stops on their way and stayed in Hamburg in northern Germany for three weeks. Linnaeus had made himself known to the intellectual community by having his visit announced in a local periodical dealing with scholarly matters, Hamburgische Berichte both beforehand and during his stay. Once there, he sometimes made a show by dressing in a Lapp outfit with the ritual drum that he had acquired on his Lapland tour and he also sang his own praises with a collection of insects plus several scientific manuscripts that he had plans to publish when he reached Holland. It was in Hamburg he was shown the stuffed hydra or seven-headed serpent, which Albertus Seba (1665–1736), although he had not seen it himself, had described as a genuine natural specimen and reproduced it from a sketch in his imposing Thesaurus of natural history, volume one (1734:158–160, pl. 102) the year before. The hydra had been looted in 1648 from an altar in Prague and was now for sale at a substantial price. The body was a foot long and the tail as much. Linnaeus found that the skin was taken from snakes, the jaws and feet from a weasel, and the teeth “were not naturæ, but artis miraculum.” The hydra has its roots from the Greek mythology and as a fabulous animal it has appeared in the natural history literature, for example in Jonstonus 1653:38–39, plate 11, with reference to Conrad Gesner (1516–1565). Arvid Hj. Uggl (1946) has given a detailed story on Linnaeus’s encounter with the Hamburg hydra.

From Hamburg Linnaeus and Sohlberg proceeded down the Elbe on May 28, 1735 (n.s.) and arrived in Amsterdam after a 16-day voyage. Linnaeus wrote in his diary that was compiled and published by A. Hj. Uggl (Linnaeus 1953; in Swedish):
The frogs croaked very loudly 3 to 4 times louder than in Sweden, had its own sound. Some sang so beautifully that you felt newborn, and banished all disagreeable thoughts, others so mournfully that one almost dies of melancholy.

**HOLLAND AND SYSTEMA NATURAE**

Linnaeus had already written, in Latin, his thesis in medicine, “A new hypothesis as to the cause of intermittent fevers”. Linnaeus’s theory was that they resulted from living on a clay soil (Blunt and Stearn 1971). Once in Harderwijk, it took just a week to have it printed, defend it in a formal disputation, and receive the doctor degree, which happened on June 23, 1735 (n.s.). Within a week, on the day he returned to Amsterdam, he moved to Leiden to meet more scholarly people and to visit the renowned botanical gardens. Among the many influential individuals he met was the botanist and physician Johan Frederik Gronovius (1690–1762). Linnaeus had many book-length manuscripts ready, including the one that would be so fundamental to the natural science, *Systema Naturae* (hereafter *SN*). Gronovius came from a wealthy family of scholars and together with a Scottish doctor Isaac Lawson (?–1747) he realized its importance and they offered to pay for the printing. It was given to the printer in Leiden on June 30, 1735. *SN* was in Latin and the first book that Linnaeus published (Linnaeus 1735). There are several facsimile editions but Engel-Leideboer and Engel (1964) have also provided translation of essential parts. The ‘natural bodies’ were divided into three kingdoms, namely: stones, vegetables and animals. Linnaeus classified taxa in a hierarchical system of classes, orders, genera, and species, a system still in use although many more levels have been added. Linnaeus wanted each of the kingdoms to appear on one page but because the known animal kingdom at that time was already heaving, the size of the book had to be a giant folio (53x42 cm). The size in itself, and the many tables, caused problems for the printer in Leiden and it was not finished until December 9. The book consists of only eleven printed pages on seven leaves. Each table of the three kingdoms is preceded by a chapter “Observationes.” Linnaeus established among other matters that zoology is the noblest part of the natural history, that most of what was so far published on animals consisted of fabulous stories and imperfect illustrations, and that the only authors dealing with acceptable systematics were Francis Willoughby (1635–1672) and John Ray (1627–1705). Linnaeus was not the first to devise a system for a methodical arrangement of nature but earlier methods lacked consistency and were difficult to use in practice. Nonetheless, the success of *SN* could also be explained by talented marketing efforts by Linnaeus and his Dutch network.

The table with the orders, genera and species for the animal kingdom contains six numbered classes; these are I *Quadrupedia*, II *Aves*, III *Amphibia*, IV *Pisces*, V *Insecta* and VI *Vermes*. Each class occupies one column in the table, but the Amphibia section is shorter than the others. Linnaeus identified four genera, *Testudo*, *Rana*, *Lacerta*, and *Anguis*, with altogether 27 “species”, here marked by me in quotes to indicate his possible concept of a species in a collective sense, because he must have realized that there were more than 27 types of “amphibia” on earth, especially because he had on June 4 seen Albert Seba’s extensive zoological collections and his *Thesaurus* volumes 1 and 2 (Engel 1936). Beneath the Amphibia column Linnaeus noted:

> The Creator in his benignity has not wanted to continue any further the Class of Amphibians; for, if it should enjoy itself in as many Genera as the other Classes of Animals, or if those things were true that the Tetralogists have fabricated about Dragons, Basilisks, and such monsters, the human genus would hardly be able to inhabit the earth. 

[Translation from Latin by Engel-Leideboer and Engel 1964.]
The remaining space in the column is filled with observations on “Paradoxa”, being mythical animals or phenomena in Nature that according to Linnaeus lacked natural foundations (Fig. 2). Three of the ten listed paradoxes have herpetological connotations.

Linnaeus wrote that the seven-headed serpent, which he had inspected a few weeks earlier, had similarities with the dragon in the Book of Revelation and he concluded:

Nature, always invariable, has never in a natural way shaped several heads on one body. Fraud and artifice, we have easily revealed from the teeth of the carnivorous weasel instead of the teeth of Amphibians [as defined in SN I].

It is obvious that Linnaeus had read about the paradox frog, *Pseudis paradoxa* (L., 1758), in *Metamorphosibus Insectorum Surinamensium* (1719:71, pl. 71) by Sibylla Merian (1647–1717) and in Albert Seba’s *Thesaurus* (1734:125–126, pl. 78), that the tadpole, which at a stage is three to four times larger than the adult frog, develops to a fish:

The Frog-Fish, or the metamorphosis of *Rana* into Fish, is very paradoxical, as Nature would not admit the change of one Genus into another one of a different Class.

Linnaeus properly included the flying dragon from East India as a species, “*Draco volans*”, among the *Lacerta*. To the mystifying “Draco” that often appeared as a natural curiosity sometimes fabricated from a ray fish Linnaeus made these comments:

Draco with a serpent body, two feet and two wings like a bat is *Lacerta alata* [=winged lizard] or a *Ray* artificially shaped as monster and dried.

Linnaeus published in 1736 a broadside with the title *Methodus* that explained his method for the descriptions of natural objects. The broadside has the same size as *SN I* and was apparently furnished with the copies of the *SN I* that remained in stock when the *Methodus* was printed. Karl P. Schmidt (1952) stressed the importance of the document, even for modern practice, for adequate description of newly discriminated species of plants, animals, or minerals. He undertook to translate it for the first time into English. It contains nothing special about herpetology but it provides a good representation of Linnaeus’s structured method of defining names, theory, genus, and species. (Fig. 3)

In August 1735, on recommendation of Gronovius and Hermann Boerhaave (1668–1738), an influential professor of medicine, botany and chemistry at Leiden, Linnaeus was made superintendent of the botanical and zoological garden in Hartekamp belonging to a wealthy banker and patron of culture, George Clifford (1685–1760) (Goerke 1973:28). Linnaeus spent three years at this country place between Haarlem and Leiden with some periods of absence for travels and services for other people. During this period he had a striking output of books from manuscripts that he had produced either in Sweden or in Holland. Most of those were on botanical systematics, but he also edited *Ichthyologia* (Artedi 1738), a treatise on the systematics of fishes from the manuscript of his Swedish friend and colleague Peter Artedi, who had drowned in Amsterdam in August 1735.

**LINNAEUS IN STOCKHOLM 1738 TO 1741 WORKING AS A PHYSICIAN**

During the summer in 1738 Linnaeus left Holland for Paris and then sailed directly to Sweden from France. Linnaeus demonstrated in letters that he wanted to continue his scientific works as a botanist, but there was no vacant professorship in Sweden. Instead, he set up a medical practice in Stockholm, which normally was not a worthwhile business at the time, but Linnaeus succeeded and
within a year he was appointed Physician to the Admiralty.

In May 1739, Linnaeus participated in founding the Swedish Academy of Sciences which was based in Stockholm (a discussion of the early history and contributions to herpetology of the Royal Swedish Academy of Sciences has earlier been provided by me (Wahlgren 1999). In June 1739 he married Sara Lisa in Falun.

Besides serving as a physician he published the 2nd edition of Systema Naturae in Stockholm in 1740 (SNII). The format was changed thoroughly, produced as a very small quarto with 84 pages. The text for the class Amphibia is similar to SNI, but now occupying one full page. This time he established two orders: Ordo 1 Reptilia, Pedes quattuor containing the sequentially numbered genera 79 Testudo, 80 Rana, and 81 Lacerta, and Ordo 2 Serpentina, Pedes nulli containing the single genus 82 Angvis. For some species he added the Swedish vernacular names. He removed the species Rana Carolina and Lacerta Senembi Mrg. The latter was referred in SNI to Georgius Marcgravius (1648) Historiae rerum naturalium Brasiliae libri octo. In later editions of SN Linnaeus brought it up again as a synonym for Lacerta Iguana, the green iguana, now Iguana iguana (L., 1758). Rana Carolina never emerged again.

The family's first child, Carl, was born in Falun in January 1741. On May 5, Linnaeus was appointed professor in botany at Uppsala University, but it would take about half a year before the installation and when he gave his first lectures.

**FIGURE 2. Systema Naturae I – Amphibia and Paradoxa.** Amphibia, comprised of both amphibians and reptiles, formed Class III of Regnum animale in Carl Linnaeus Systema naturae 1735. Paradoxa was comprised of mythical animals or phenomena in nature that according to Linnaeus lacked natural foundations.
FIGURE 3. *Methodus*, a broadside that Linnaeus published in 1736 in which he explained his method for the descriptions of natural objects. It has the same size as *Systema Naturae* I (1735).
JOURNEY TO THE BALTIC ISLANDS ÖLAND AND GOTLAND

In January 1741 the Swedish parliament invited Linnaeus to undertake a journey to the Swedish islands Öland and Gotland in the Baltic Sea. The purpose was primarily economic, with goals of identifying natural resources such as new material for dyeing, clay for porcelain and tobacco pipes, and finding plants for pharmaceutical purposes, but also to identify what belongs to *historiam naturalem patriæ*. Recording of observations was fundamental and the diary now belongs to the Linnean Society of London. The narrative was not published until October 1745 (Linnaeus 1745a). The text is in Swedish, but Marie Åsberg and William T. Stearn (Linnaeus 1973; 2007b) have provided English translations.

He set off from Stockholm in May 26, 1741 (n.s.) on a land route with a group of six students and officers, and returned on September 8 via Stenbrohult, the place in Småland where he spent his childhood and his father still lived. Linnaeus was indeed also a botanist, and he wanted to study the plants during the flowering season, which is quite short in Sweden. The group therefore had to rush through the itinerary in order to see as much of the blooming flora as could be possible. On the fourth day, after leaving Nyköping, they found a grass snake (*Natrix natrix* [L., 1758]) and Linnaeus described it quite precisely but at this stage he did not count the scales:

Snakes are neither in Sweden nor abroad at any point sufficiently well described. Therefore, in order to illustrate *historiam naturalem patriæ* we will make descriptions of them. Here we found a *Coluber*, which hence was noted: gray body with ovate scales, on its back more narrow, with a raised *linea*, in the same color except a few which are blackish at the tip, so that his back looked slightly mottled. The underside was covered with scales as large as the belly or half of the body. These are black, lighter at the sides, closer to the head even more. The head black with several sutures. The jaws with black transverse stripes. Nostrils small. Around the ears black with large white patch. The teeth in two rows on each side and are of equal size. The tongue is composed of two black strings. This one makes no harmful bites and is of the Grass snake genus.

In another five days the group had reached Vetlanda in the heart of Småland and they came upon the second snake, which was the European adder, *Vipera berus* (L., 1758):

An adder lay on the road . . . , he was big and gray, his buck with what resembled a dark thorny band, between which thorns a blue spot was observed along the body, the head was separated from the dark back by a blue *anguulus acutus*, whose *fibra superior* was at the edge with white spots. In the mouth, on either side, toward the tip, and in the upper jaw was a large fang, which could be both retracted and expanded like a cat’s claw, which revealed that this snake belongs to the genus that causes harmful, indeed often fatal wounds.

A month later, on Öland, in a limestone quarry they found a common toad (*Bufo bufo* [L., 1758]) under a stone, which Linnaeus described morphologically with accuracy, similar to the snakes. Just a few days later, on July 1 (n.s.), while waiting for a boat to bring the group to Gotland they surveyed the area and could report on the grass snake (*Natrix natrix*), which he described morphologically with little additions to the previous individual’s characters and a *Rana temporaria Charl. onom.* 24. The Latin name can be misleading as this happened before he introduced the binominal nomenclature.

*Rana temporaria Charl. onom.* 24 was caught and described; its hind feet had 6 toes, which were somewhat webbed, the first smallest, the second in order longer, the second last longest. The fore-feet or hands had 4 toes, well divided, of which the 2nd and 4th were shorter. The back was flat, separated from the sides by a raised line, which ran from the point of the head toward the eyebrows, afterwards to the
tail. She was completely gray with black elongated stripes and warts on the back; the thighs were even paler with black transverse stripes.

[Walter Charleton (1619–1707) was an English writer who published on theology, natural history, and antiquities.]

Linnaeus eventually listed this individual in the SNX (1758) under *Rana temporaria* L., 1758, the common frog. However, this species does not occur on Öland or even in the immediate neighboring mainland. They had either found a moor frog, *Rana arvalis* Nilsson, 1841, or an agile frog, *Rana dalmatina* Bonaparte, 1840, but regrettably Linnaeus did not recognize it as a separate species from *Rana temporaria*, as the three taxa are morphologically quite similar.

The group continued to Gotland but Linnaeus reported nothing of observed reptiles and amphibians on this island. Back on the mainland, in Orraryd 32 km south of Växjö, on August 13 (n.s.), Linnaeus acted as a physician and treated a woman, who had been bitten by a snake. He wrote:

Stung by a snake was a woman, for which I promptly prescribed olive oil to be taken in large quantities and this frequently, but a few days later I heard that this, by the English so appraised medicament, had no effect whatsoever, although the woman was bitten by a gray snake (*Vipera*) only 6 hours earlier, before she began to take the oil. The Medici and the Pharmacists then should be concerned to procure for our pharmacies radicem *Senegae* from Virginia.

Linnaeus will later report in more detail about this North American remedy for the snakebite (Linnaeus and Kiernander1749) with reference to John Tennent (who had published a paper on snakebites in 1738).

When dealing with harmful snakes, Linnaeus continued the text about the “äsping”:

Äsping, a kind of red snake, said to be small and thick, but moreover very quick to deliver deadly bites, was told to be often seen in this part of the country. Whoever hereafter sees them does well in describing a non-described animal; then he should be careful to count the scales between the chin and the tail on the underside.

The vernacular name äsping is still used in some parts of Sweden for small reddish-brownish adders, *Vipera berus* (L., 1758), which usually are females. In 1749 he will describe it formally from four specimens that he eventually obtained.

On August 13 (n.s.) Linnaeus also reported about a limbless lizard, or slow-worm, *Anguis fragilis*, L., 1758:

The slow-worm is a snake so stanch that she breaks to pieces, as soon as you hit on her. Her belly is black, the sides purple, the back grayish with a dark linea, which on both sides separates the back from the sides. The people believed that this snake bites only at mid-day, but the teeth seem to make him innocent.

On their way toward Stockholm, 66 km from Växjö, they observed another individual. Linnaeus demonstrated here that he did not believe in unfounded folklore, but he fully appreciated the value of well-nursed livestock.

A slow-worm (koppar-orm) was seen at the road similar to the last one (August 2) [August 13 (n.s.)] but with a black spot at the top of the head. The farm-girls used to pat the snake on his back with the flat hand three times, on the supposition that the cattle subsequently will fare well and become well-groomed when they in turn were patted with the hand of the maids. The ancient *rei rusticæ autores* [the authors on agriculture] knew the same trick, though they did not prepare the hand with snakes before.
PROFESSOR IN UPPSALA, THE DISSERTATIONS AND THE DESCRIPTIONS OF THREE EXTENSIVE DONATIONS

The Linnaeus family moved in October 1741 to the official residence in Uppsala adjacent to the academic botanical garden.

During a period from 1744 to 1750, when Linnaeus had been established as the professor in botany for some years and being responsible for the Academic Natural History Museum, six donations containing zoological specimens were made to the museum. Linnaeus examined these and for four of them he made catalogues. Three of the collections not only contained amphibians and reptiles, but in fact these animals made up all or the bulk of them. The catalogues were published in Latin as academic dissertations and defended by a student, sometimes called the respondent, who probably influenced the contents to some degree, but it is quite clear that Linnaeus is the leading author. Linnaeus considered the theses maintained by students under his guidance as his own work (Smit 1979). Out of the 186 dissertations written during Linnaeus’s professorship at Uppsala University (1741–1773), about 30 were devoted to zoological issues. At least eight of them deal with herpetological matters and these theses are discussed in this paper. The academic procedure associated with the Linnaean dissertations is provided by Torbjörn Lindell in the present volume. In the citations I have here treated the dissertations as produced by Linnaeus and the respondents jointly, but with Linnaeus as the first and leading author and holder of any conceptions and opinions.

The three collections are still to a large extent preserved at the Uppsala University Museum of Evolution. They have been examined by several persons after Linnaeus. Carl Peter Thunberg (1743–1828), successor of Linnaeus’s professorship from 1784, listed the materials in order of the several donations (Thunberg 1787a, b). Einar Lönnerg (1865–1942) in his catalogue of the Uppsala University Linnaean collection (1896) identified the types. Ossian Olofsson (1886–1973) has left a manuscript “The Linnaean collections” at the museum in which he reviewed the type status (Olofsson 1915) of the specimens. Holm (1957) published the most complex account of the collection. Wallin (2001) compiled the most recent list of the Linnaean collection of the museum in Uppsala but based much of the type status on Olofsson and Holm.

Count Carl Gyllenborg (1679–1746), who was chancellor of Uppsala University, made the first donation in two installments, in 1744 and 1745, which contained various preserved animals or parts of animals, including amphibians and reptiles, as well as plants. A script copy of the first inventory of this donation made in 1744 exists in London at the Linnean Society of London (Holm 1957). Linnaeus and Barthold Rudolph Hast (1724–1784) as a respondent described the herpetological material in a dissertation, Amphibia Gyllenborgiana (1745). Precise descriptions are made of nine snakes, eight lizards, one crocodilian, four turtles, and two amphibians, altogether 24 species numbered sequentially, most originating from South America and Europe. Linnaeus explained for the first time how to distinguish snakes by counting ventral and subcaudal scales, because, he claimed, other characteristics such as color and size vary between individuals while the scale counts are stable. Most specimens in the collection are still extant and 13 specimens have been assigned type status according to Wallin (2001).

The Crown Prince Adolf Fredrik made a donation in 1745 of natural curiosities to the Academy of Uppsala. Adolf Fredrik was crowned King in 1751. The collection consisted of 87 specimens in “bottles” of Spiritus vini, predominantly amphibians and reptiles (Löwegren 1952). The Prince continued to be a passionate collector of natural history.
curiosities even after this donation. Thunberg has stated that the donation consisted of duplicates of his collection (Löwegren 1952). Nothing is recorded of the provenance of the animals, but Löwegren assumed that they were purchased in Holland. Linnaeus and the respondent Laurentius (Lars) Balk (1726–1790) described the collection in Museum Adolpho-Fridericianum (1746), a thesis that was defended in the spring of that year. Linnaeus described 64 species that are sequentially numbered, of which 30 are amphibians and reptiles, namely, one turtle, three amphibians, 11 lizards, and 15 snakes, coming from both the old and the new World. Two engravings accompany the dissertation, one depicting a Chinese pheasant and the other showing five fish species and an anolis lizard with erected dewlap. Linnaeus referred to this dissertation as Museum Principis. Wallin (2001) indicated that approximately twelve surviving specimens have type status.

The animal collection that Linnaeus described in the thesis Surinamensia Grilliana (Linnaeus and Sundius 1748) originated largely from Dutch Guyana in South America. The thesis, written in Latin, was defended by Peter Sundius (1725–1786). In the foreword is mentioned that the animals were collected by the plantation owner Pater Gerret with his son from Surinam and that they were given to Mr. Claes Grill (1705–1767), who was a leading Swedish entrepreneur and head of the Swedish East India Company and had a great interest in natural sciences. Grill thereafter submitted the collection to the Museum Upsaliense. Linnaeus described 24 animals from the collection of which 17, numbered 3–19, comprised Amphibia; No 25 was a snake from Turkey given by another donor. Linnaeus emphasized that the Grill collection contained a new snake genus named Cecilia, which was described and the specimen nicely depicted in an engraving (168x266 mm). According to Wallin (2001), the type specimen, Caecilia tentaculata L., 1758, is extant in the museum. The collection also included a rattlesnake, which was described with the words “Crotalophorus scutis abdominalibus CLXXII, scutis caudalibus XXI, paribusque squamarum III”, which is likely to be Crotalus durissus (L., 1758). The specimen is now lost (Wallin 2001). In an appendix he described a snake that had been donated separately and came from Turkey (a country then larger than it is today), which is also depicted in the engraving. He will later name it Coluber ammodytes (Vipera ammodytes [L., 1758]). The Grill family originated from Italy, where the name meant “grasshopper.” The inclusion of the grasshopper “Gryllus thorace…” in the engraving was probably a way of honoring the donor.

THE SWEDISH FAUNA ON RECORD – FAUNA SVECICA

In 1745 Linnaeus published his book Flora Svecica (Linnaeus 1745b) that presented the Swedish plant life arranged systematically, and in 1746 he published a catalogue of the known natural animals occurring in Sweden, Fauna Svecica (Linnaeus 1746), both written in Latin. In Fauna Svecica, Linnaeus treated 44 mammals (beginning with Homines – man), 205 birds, 13 reptiles and amphibians, 76 fishes (including six cetaceans), 932 insects and spiders and 87 “Vermes”, comprising mainly all other invertebrates, a total of 1,357 species (Nybelin 1946). The class Amphibia appearing on the pages 94–97 and 387 (an appendix) is divided into the two orders, “Reptilia” and “Serpentia”. For each species he gave first a description of the salient features with a dozen words. For the snakes, he stated only the numbers of the abdominal and caudal scales, a method first explained in Amphibia Gyllenborgiana (Linnaeus 1745b). Linnaeus listed bibliographic references or synonyms with an index of authors and their publications at the introduction. Linnaeus must have disregarded many important references that indeed are listed under other groups by listing
only three references under Amphibia: Bart. Rudolph Hast 1745 (Linnaeus and Hast 1745), Joh. Paulus Wurffbainius 1683 (Wurffbain 1683), and Christ. Franc. Paullinus 1686 (Paullini 1686).

For the first frog, as an example, “Rana minibus tetractylis fissis, plantis hexadactylis palmatis, pollice longiore” (Rana temporaria L., 1758), Linnaeus listed nine authors and their publications, including his own “It. œl” (i.e. the narrative of his journey to Öland in the Baltic Sea; Linnaeus 1745a). For each species, he mentioned habitats and distribution in Sweden and its vernacular names. A detailed morphological description in smaller letters followed. He listed four species of each of the genera Rana, Lacerta and Anguis (the last being the snake äsping still wanting), in all 12 species. Linnaeus did not differentiate between lizards and newts, or between snakes and the limbless lizard, and he distinguished two species of the adder, Vipera berus (L., 1758), and three of the smooth newt, Lissotriton vulgaris (L., 1758). Sven Nilsson (1842) in his early comprehensive account of the Swedish herpetofauna included 17 species. The Swedish fauna currently comprises 19 recognized reptiles and amphibians (Gislén and Kauri 1959). The agile frog Rana dalmatina Bonaparte, 1840 was found for the first time in 1907 in Öland; the pool frog Pelophylax (Rana) lessonae (Camerano, 1842) was reported in Sweden by Sten Forselius (1962). Two large engravings depicting mainly birds are included in Fauna Svecica. Linnaeus set the symbols ♂ and ♀ respectively for male and female, a Linnaean invention (Dal 1996). The word “fauna” used here was also coined by Linnaeus as a match to “flora”, being derived from the feminine counterpart to the Roman forest god of antiquity, Faunus. Fauna Svecica was published with two different title pages, both dated 1746, one in Stockholm, Sweden, and one in Leiden, the Netherlands. A second edition of Fauna Svecica was published 15 years later (Linnaeus 1761).

A COMMISSIONED TOUR TO THE WESTERN REGIONS OF SWEDEN

Upon request by the Parliament five years earlier, Linnaeus undertook during the summer of 1746 a study tour to “Wästergötland” (Västergötland, the western part of southern Sweden) to document observations on the antiquities, physics, economy, manufacturing, medicine, customs, and traditions. He was accompanied by a student as a secretary, Eric Gustaf Lidbeck (1724–1803), who in 1756 became professor of natural history at Lund University. They started on June 23 (n.s.) and returned on August 22. Linnaeus’s narrative, in Swedish, was published the year after (Linnaeus 1747). On Ålleberg (a 330 meter mountain plateau near Falköping) they found frogs and Linnaeus wrote:

Frogs (Faun. 250.) [Fauna Svecica 1746, no. 250] of a large quantity jumped on the rock hill on the north side, which was so steep that we ourselves not without the greatest difficulty and danger could get up; we wondered all the more how these miserable wretches could work their way as far up and what they wanted so high, which otherwise, always seek the depth.

It was the animal he later would name Rana temporaria L., 1758, the common frog.

At a shipyard outside Göteborg (Gothenburg) they found a snake that Linnaeus could determine to be the harmless Natrix (Latin for water snake; Natrix natrix [L., 1758]).

In Uddevalla they found several toads (Bufo bufo [L., 1758]) close to the stinking plants hedge woundwort, Stachys sylvatica, and baneberry, Actaea spicata. Linnaeus was puzzled why the toads seemed to have a liking of odorous herbs. He wrote:

Toads (Faun. 253) [Fauna Svecica 1746, no. 253] reside in shady places, particularly at the roots of the rock, where this stinking Stachys
489, and the stinking Actaea 431 grow. I do not know what pleasure these ugly animals find in ill-smelling herbs, and I have seen, how the Toads intruded into the houses, when Stachys foetida are brought inside; in Ukraine, too, where Cotula foetida 703 is more common than elsewhere, there are so many Toads that they occur everywhere near the houses; but as soon as Cotula vanishes in the countries also the Toads disappear.

Stachys foetida is probably also S. sylvatica and Cotula foetida is mayweed chamomile, Anthemis cotula. The figures in Linnaeus’s text refer to record numbers in Flora Svecica (Linnaeus 1745b). He continued:

I set my dog on a large Toad, he bit her, but trembled and shook his mouth pretty badly afterwards and it was obvious, that it harmed him. Nor could he later be persuaded to try again, so it is possible what LISTER ¹ says is true that if one seizes the animal with forceps, then she pisses from each wart a white juice, which damages and poisons.

[¹Dr Martin Lister (c. 1638–1712), vice-president of the Royal Society and court physician, is best known as England’s first arachnologist and conchologist.]

In Persberg, near Filipstad, they found toadlets of what Linnaeus thought was a new species, which he carefully described. They were similar to what he had described in Fauna Svecica (Linnaeus 1746) as no. 253, which later would become Bufo bufo (L., 1758) with reference, among others, to the Öland journey (Linnaeus 1745a). This species jumped differently and its forefeet had four toes and its hind feet had five. In SNX (Linnaeus 1758) he would name it Rana Rubeta, a species with no present allocation but probably is Bufo bufo.
TABLE 1. The orders, genera and number of species of Class III Amphibia (excluding the order Nantes) that Linnaeus listed in the five editions of *Systema Naturae* that he wrote. The genera are here arranged alphabetically per the spelling in the 6th edition. The total number of species in this class is listed in the bottom row.

<table>
<thead>
<tr>
<th>1st ed. 1735</th>
<th>2nd ed. 1740</th>
<th>6th ed. 1748</th>
<th>10th ed. 1758</th>
<th>12th ed. 1766</th>
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<tr>
<td><strong>Serpentia</strong></td>
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<td>10 Lacerta</td>
<td>9 Lacerta</td>
<td>20 Lacerta</td>
<td>43 Lacerta</td>
<td>48 Lacerta</td>
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<tr>
<td>4 Rana</td>
<td>3 Rana</td>
<td>8 Rana</td>
<td>17 Rana</td>
<td>17 Rana</td>
</tr>
</tbody>
</table>
| Classis tertiary [Class 3] Amphibia.

This is the shortest of all Classes naturales, so we should praise the all-wise Creator, as this Genus is the ugliest, cruelest and most poisonous, it would have done the other Genera too much harm if they were many.

The turtle can live headless for eight days; also frogs live as long though you take from them the heart, lungs and all that they have inside.

A person can drink without harm snake poison taken from the blisters.

When someone is bitten by a poisonous snake, nothing is more important than expeditious measures. All the serpent bites are not cured in the same way, but for the most general, we want to provide cures. The peasants of the countryside submerge the injured limb in the soil, which is quite right as the nasty matter is then extracted, but it is slow. The customary way is to bind up around the leg or the bitten place so it swells and the blood may not come up in the body; then cut around the bitten leg several punctures and apply the sucking horn until it is believed that the evil matter and all the infested blood are removed. Then you slice a snake or frog and put it on as well as the lard from the very snake.

Genus 87 Amphisbaena. Occurring in Greece, Egypt, Brazil and East and West Indies. … The old saying that there are snakes with two heads and that they command the body one at a time, but such monstrous animals with more than one head nature knows nothing about, nor are those existing in tota rerum natura.

Genus 89 Coluber, Sp: 6, 7, 17 are all *Viperae*. With these are always shown Signum Martis ♂, which means that they have quite sharp teeth.

Genus 92 Draco. Bontius ¹ calls him Dracunculus alatus. … He lives in the East Indies in the trees, but is probably rare and flies only at midday when the heat is most intense. He is ¹ One Coluber described in 1771 is included here.
not larger than an ordinary lizard. … A dragon exists in Hamburg, which fooled all Curious observers in the World, until Archiater Linnaeus came, when he found him to be artificially made and he ranks amongst the foremost art piece: He has the teeth of Mustela [weasels] and is made of many snake skins and has 7 heads made of Mustela. … On the dragon are maybe as many stories as there are old women, but all equally false for no dragon exists in the world than this small one, having neither treasures to rest on nor fire in the tail for lighting.

[1 Linnaeus (1758) refers to Jacobus Bontius (1592–1631) who featured “Lacertus volans” in 1658 Historiae naturalis & medicæ Indiæ Orientalis. Elzevirios, Amstelaedami (Amsterdam), p. 59 (not 57 as given by Linnaeus in 1758). Bontius was a Dutch physician and naturalist who resided in Batavia (now Jakarta) in Java for many years.]

Linnaeus’s lectures in the Uppsala gardens, at the University, and on the excursions are legendary. In a letter written in March 1754 to his friend the physician Abraham Bäck (1713–1795) living in Stockholm Linnaeus (1910:266–267) wrote (in Latin):

Privately I lecture on Amphibians for such a magnificent audience, the space is barely adequate, and this to the indignation of my envious friends and resentment of my enemies.

TWO DISSERTATIONS ON TREATMENT OF EFFECTS OF SNAKEBITES

In the spring of 1749 Linnaeus was the first preses (chairman heading the examination) and author to two dissertations addressing herbal antidotes against snakebites that were discovered in India/Sri Lanka and North America. Like the other Linnaean dissertations they are written in Latin. My summaries here are from abstracts of the dissertations in the Swedish twice-weekly magazine Lärda Tidningar (Scholarly Newspapers) that the industrious publisher Lars Salvius (1706–1773) started in 1745 in Stockholm. New publications from Sweden and abroad were announced and reviewed in the magazine. Lärda Tidningar is now a scarce publication but conveniently all reviews of Linnaeus’s publications as well as short notices relating to the learned professor were brought together and reprinted in 2007 by Ove Hagelin, director of The Hagström Medico-Historical Library, Stockholm. Although there is no clear evidence, it is deemed that Linnaeus himself wrote at least most of the reviews of his own publications (Hagelin 2007).

The dissertation Lignum colubrinum (Linnaeus and Darelius 1749) was defended in March by Johan Anders Darelius (1718–1780). He was in 1773 raised to nobility and took the name af Darelli. The opening part in the review of the dissertation contains the following passages:

In the East Indies there is a snake called Naja or Cobra de Capella, which is the most venomous of them all. // There is also a little sore marten, known as Quirpele or Mongoose. … Now, when it happens that this Mongoose encounters a Naja, and it is not better than the Mongoose is wounded by the poisonous arrows of the Naja, then the Mongoose must die unless he can get an Antidote; therefore once he is bitten he runs onto the ground to take any herb and to seek Antidotes. As soon as he gets hold of it, he takes courage and again attacks his enemy, without fear of its venom.

Several authors described and named as Lignum Colubrinum (snake wood) many different plants that they believed the mongooses used as antidote. Linnaeus had examined the characteristics of the various plants with this name and could identify the correct antidote as a tree from Ceylon (Sri Lanka).

The next dissertation, Radix senega (Linnaeus and Kiernander 1749) was defended a few weeks later by Jonas Andersson Kiernander (1721–1778). The opening part in the review of the dissertation in Lärda Tidningar contains the following passages:

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In America exists a common snake, which is called Rattle snake or [in Swedish] Skaller-orm, because he has on the tail a rattle, which the Creator seems to have put there like an alarm clock to warn people from this snake’s bite, which is so dreadful, that a person dies within a few hours while she is coughing blood and the flesh falls off the bones. Yes, the bite is so venomous that, if the snake in the strike gets into a large blood vessel, the Patient often dies within 2, or no more than 5 minutes; this is before any cure can be applied. The people of Virginia and in particular in our Swedish Nation at Philadelphia have with endless Experiments suffered this effect.

The Native Americans have, from the arrival of the Christians in America, had a Powder made from a root that they used against the said horrible bites, specifically when the snake did not hit any major artery; which Powder is always found to be Specific and infallible if it is applied promptly; even, as the bite has always been deadly when this antidote was not available. But the natives were in no way induced to reveal to the Europeans of what kind of plant the root was, until Rewards were introduced by the British and thus it was discovered that she is an herb, called Senega.

It was the Scotsman John Tennent, physician in Virginia, who became aware it was the root from a plant Polygala Senega. The dissertation includes an overview of snake venoms and of the genus Crotalophorus (rattlesnakes) with its two species, one earlier described in Surinamenis Grilliana (Linnaeus and Sundius 1748) and the other in Museum Adolpho-Fridericianum (Linnaeus and Balk 1746).

Torbjörn Lindell provides in the present volume a more comprehensive account of the two dissertations Lignum colubrinum and Radix senega.

The Swedish Parliament commissioned Linnaeus in 1748 to carry out a journey through Skåne (Scania), the southernmost Swedish province. His task was similar to the previous expeditions, in short to discover natural resources that could be used to improve the Swedish economy. As usual he commented on many aspects of nature, geology, people, antiquities, etc. Linnaeus was now 42 years old and an internationally recognized scientist in his mid-career. The narrative, authored by Linnaeus, was published in 1751 in Swedish (Linnaeus 1751). The diary, which is now in the Linnean Society of London, was compiled and annotated by Bertil Gullander (Linnaeus 1975) and it contains valuable additional information. A few herpetological observations were reported.

He set off in the second week of May 1749 (n.s.) from Uppsala, this time in a coach together with a secretary, his student Olof Söderberg (1728–1758). Linnaeus typically was observant of amphibians and reptiles. His first observation was on June 8 (n.s.) at the east coast of Skåne in Ravlunda where he commented that snakes are relatively rare, a somewhat odd remark, because he did not report that snakes should be other than scarce in any of his narratives. At the same place, he wrote on June 9 (n.s.):

The frogs sang in the evening, however, they had another sound than our common Swedish frogs. They were said to play until midsummer, when ours [common frogs] play as soon as the ice is gone.

This is most probably the European tree frog, Hyla arborea (L., 1758), a species restricted in Sweden to southeastern Skåne. He will later describe it in SNX (Linnaeus 1758) without reference to this observation. Presumably he never collected any specimens. The day after,
in Andrarum, he heard the fire-bellied toad, *Bombina bombina* (L., 1761):

The farmers call this kind of frog, barley frogs, because, when they begin to be heard, it is the right time to sow the barley.

Linnaeus described the fire-bellied toad in *Fauna Svecica* (Linnaeus 1746), but only with an obscure reference to Johan Leche (1704–1764; professor of medicine and bird specialist in Turku, Finland). Linnaeus did not include it in *SN*, but described it again as *Rana Bombina* in the second edition of *Fauna Svecica* (Linnaeus 1761) with reference to *It. Scan.*, thus signifying this journey.

In Skanör, located on the southwestern cape of Sweden, he found “Lacerta *cauda verticillata*”, giving reference to “Fn 1352”, i.e. *Fauna Svecica* (Linnaeus 1746:387). Linnaeus conflated the two *Lacerta* lizards in Sweden, *Lacerta agilis* L., 1758 and *Zootoca* (*Lacerta*) *vivipara* (Jacquin, 1787). In the 2nd edition of *Fauna Svecica* (Linnaeus 1761:103) he described the proper *Lacerta agilis* (α) with two varieties: β “*Lacertus viridis*” (being very rare) and γ “*Lacertus dorso punctis albis duplici serie*” (observed in Lapland and in Uppsala); with the latter he meant what is now *Zootoca* (*Lacerta*) *vivipara* (Nilsson 1842:25–26). However, in *SNXII* (1766) he dropped the γ-variety.

On the return route through the province of Småland he received news that one specimen of the snake Äsping, which he had advertised for in the travel account published in 1745 (Linnaeus 1745a) and in *Fauna Svecica* (Linnaeus 1746), had been caught in Angelstad for him and it could be obtained from a Reverend Ulmgren. Later, although it is unclear exactly when, another two were obtained from a schoolmaster named Kallenberg in Nötbeck (now most likely Nottebäck). From the diary it can be understood that Linnaeus spent some time and effort in obtaining the specimens, so it is clear that describing this poorly known snake species was essential to him. Linnaeus briefly portrayed the snake collected by Ulmgren as hissing louder than other snakes do, that it is fiercer, and that the snake will be described in more detail from the preserved specimen.

On August 24 (n.s.) they were back in Uppsala. The tour had been successfully accomplished and they had on the whole been lucky with the weather. This was the last of the longer tours that Linnaeus embarked on during his lifetime.

**A NEW SNAKE DESCRIBED – ÄSPING**

The Swedish Academy of Sciences was founded in 1739 by Linnaeus and five other individuals, most of them aristocrats. The first issue of its quarterly *Handlingar* (Transactions) was printed in the third quarter of 1739. Linnaeus made frequent contributions to the flora and fauna in the Transactions. The Swedish language was a nucleus of the Academy, which therefore was used in all writings and publications.

Linnaeus had in earlier years advertised to obtain individuals of the snake Äsping. On the journey to Skåne in 1749 he had obtained three specimens from Småland and he possessed another, albeit, what he expressed, doubtful specimen, from Uppsala. On his return he prepared an account on the Äsping for the Transactions. In a letter (Linnaeus 1910) to his friend Abraham Bäck in Stockholm on October 24, 1749 (n.s.) he lamented that he was not able to find an artist in Uppsala to illustrate the snake. So he must have sent the preserved specimen to the editor for him to arrange for the illustration in Stockholm (although there is no documentation of this detail). The paper with title Äsping appeared in the fourth issue of the Transactions of that year (Linnaeus 1749a). He began the article pitying the snakes that have no legs to escape any predator but, at the same time, admiring...
the Creator who had invented a system that science would in due course call mimicry:

Anyone enemy, whom the Creator himself has fortified, may not be pleasant encountering. The Creator has on the other hand been so merciful telling the snakes, not to act in offence; thus you never observe a snake chasing man, but only defending himself, when one gets too close to him.

I halt for admiration, when I carefully reflect on this arrangement by the Creator, in particular when I notice that the Master of Nature has not supplied every snake with arms, instead may often a snake, which is most dangerous, dress as one without arms, as well as an unarmed, on the contrary, may carry the armor of the equipped.

He reiterated what he had said in the dissertation Amphibia Gyllenborgiana:

A few years back, when His Majesty and Advisor to the King, Count Carl Gyllenborg bequeathed to me the beautiful collections of Indian animals, which now Upsala Academy is proudly in possession of, I received the opportunity to examine the snakes; I then learned that the broad scales on the belly and the small scales under the tail were just the only marks, through which the Creator characterized the snakes. I then arranged all the snakes I had in the Museo, after this given reason, which can be seen in Syst. Natur, 6, p. 34.

He described the Åsping in great detail and stated that it resembles a young adder. Drawings on plate VI depict the snake from above and below. Linnaeus finished the description

But getting to the true characteristics, it consists of broad scales that run from the chin to the tail or the vent, which amount to 150, but under the tail are 34 divided scales.

When I for the first time saw this snake I was in doubt whether it could be a Viper or common Adder, in particular as the Viper has 145 scales under the belly and 36 under the tail, which together make 181 scales while the Aesping’s scales together make 184. But as all these [four] snakes agree in the minute scales, the spot on the tail, and other small details in the scales on the head, I am certain that it is a true species, which by Naturalists should be called

\[ \text{COLUBER scutis abdominalibus 150, squamis caudalibus 34.} \]

Its distribution, he continued, is mostly and predominantly the province of Småland. It would be some five years before he would use the binominal system for the first time. Linnaeus eventually called this species \text{Coluber cherssea} in \text{SNX} (Linnaeus 1758:218; now \text{Vipera berus} [L., 1758]). An abbreviated English translation of that paper was provided by Wahlgren (1999).

The very specimen of the four that Linnaeus sent to the Royal Swedish Academy of Sciences in Stockholm was kept in their collections, which later were transferred to the Swedish Museum of Natural History. The Linnaean type material of the three \text{Vipera} species of \text{Coluber berus}, \text{Coluber cherssea} and \text{Coluber prester}, all currently in the synonymy of \text{Vipera berus}, were surveyed by Krecsák and Wahlgren (2008). The specimen sent to Stockholm and depicted in Linnaeus’s paper was during the course of the survey found in the main collection, identified as a Linnaean specimen and designated the lectotype of \text{Coluber cherssea}, now \text{Vipera berus} (L., 1758).

**THE DISSERTATIONS IN A NEW FORMAT – AMOEINITATES ACADEMICÆ VOL. 1**

Linnaeus published the dissertations collectively as a new edition under his own name in \text{Amoinitates Academicæ} (Academic Amusements), first published in 1749 (\text{AA1}; Linnaeus 1749b). The first volume was actually edited by Petrus Camper (1722–1789) and
ON DISTINGUISHING MARKS BETWEEN SNAKES – A CONTRIBUTION IN THE ROYAL SWEDISH ACADEMY OF SCIENCES TRANSACTIONS

Linnaeus’s method of diagnosing snakes was to count the scales under the belly and under the tail. The adder, common in Sweden, was therefore diagnosed in Fauna Svecica I (Linnaeus 1746:97) as “Scutis abdominalibus CXLIV, squamis caudæ XXXIX”[Abdominal shields 144, tail-scales 39]. A person had sent in to the Royal Swedish Academy of Sciences a typical adder found in Stockholm having 153 belly shields and 32 tail-scales. Linnaeus therefore adjusted his theory (Linnaeus 1752), and explained:

…what is added or taken off of the number of the belly shields, the same is shortened or increased in equal proportion in the scales under the tail.

In this case there is a difference of two scales

…which is not of any fundament, as the first scale under the chin, the last on the tail, and the scale by the opening, can hardly be determined, so that the sum ought to be accurately the same.

Linnaeus therefore pronounced the snake to be the common adder and not a new species. We know today that the sum of the number of abdominal and caudal plates may vary between individuals, but scale counts are still significant morphological characterizations of snake species and sexes. A full English translation of Linnaeus’s contribution was provided by Wahlgren (1999).

MUSEUM SÆÆ RÆÆ MÆTIS ADOLPHI FRIDERICI REGIS – A MAGNUM OPUS

King Adolf Fredrik (1710–1771) with his wife Queen Lovisa Ulrika (1720–1782) occupied the royal throne of Sweden from 1751. The royal couple followed the fashion of the aristocracy of those times to keep personal cabinets of natural and artificial curiosities. The king kept his collection at his palace at Ulriksdal while the queen kept hers at the palace at Drottningholm, both located in the vicinity of Stockholm. They invited Linnaeus to arrange the collections. Linnaeus, starting in 1751 made several visits to the palaces up until 1755 (Lovén 1887). His first published work about the collections, Museum SæÆ RÆÆ MÆtis Adolphi Friderici Regis (Linnaeus 1754), dealt with the animals belonging to the king, most
of which consisted of animals in alcohol, such as reptiles and fish. Linnaeus focused only on some animals and did not make a complete description of the collection. He consistently used a binominal nomenclature here for the first time in a zoological work. The book, a large folio measuring 51 by 35 cm, was lavishly illustrated with 33 uncolored plates, 23 of them depicting serpentoid animals made by Olof von Dalin (1708–1763) and Jean Eric Rehn (1717–1793), and engraved by Jacob Gillberg (1724–1793) (Löwegren 1952:316). Of the 318 animals described 90 were of the orders Reptilia and Serpentia (12 amphibians, 50 snakes, 25 lizards, 2 turtles, and 1 crocodile). Except for SN I this is by size the largest single volume that Linnaeus ever produced (Dal 1996). The text is in Latin and Swedish.

The main part of the collection of the king was in 1801 transferred to the Royal Swedish Academy of Sciences. Its collections formed in turn in 1828 the Swedish Natural History Museum in Stockholm (NRM). A great part of the many Linnaean type specimens in NRM stems from this collection. The French author, Pierre-Joseph Bonnaterre (1751–1804) meticulously copied 39 of the snakes from the engravings in Linnaeus’s work for his Ophiologie (1790) (Krecsák 2006). The account of the collection of the queen, all of non-herpetological naturalia, followed ten years later (Linnaeus 1764a) in a more modest volume without illustrations. A second part of the Adolf Fredrik collection (Linnaeus 1764b) with 21 herpetological species described (16 snakes, 2 each of lizards and amphibians, and 1 turtle) is bound with it, but with independent pagination; the pages with the herpetological part (Amphibia Reptilia, Amphibia Serpentia) being 35–48.

Natura pelagi, a dissertation on oceanic animals

Linnaeus continued his intense publishing work after the voluminous Museum SæÆ RÆ M:Æ Adolphi Friderici Regis I was finished, but for four years only one title touched on reptiles or amphibians. This was Natura pelagi (Linnaeus and Hager 1757), a dissertation with J. H. Hager (17??–1770) as defendant. The animals in the “deep hole sea” are described from the study of the latest travel accounts. The class Amphibia is treated on half a page only and three species are described. Testudo Midas (Testudo mydas L., 1758) was taken from the 1757 narrative of the Linnaean apostle Pehr Osbeck (1723–1805) but the other two, Squali and Lophius histrionius, also referring to Osbeck, are fishes in the group Nantes, an order of fish that Linnaeus arranged systematically for the first time in Amphibia in SNX (Linnaeus 1758).

Systema naturae – the tenth edition

Linnaeus had earlier written three editions of Systema Naturae (1735, 1740, and 1748) and other authors had provided another six; a listing of the editions was provided by Soulsby (1933). In 1758, Linnaeus published the 10th edition (SNX), his 4th, which eventually would mark the starting point of zoological nomenclature. The International Code of Zoological Nomenclature fixed its publication date to January 1, 1758. A second volume was botanical and is not as important because an earlier botanical treatise, Linnaeus’s (1753) Species plantarum is considered the starting point for the nomenclature of higher plants.

In Lärda Tidningar, issue number 13 on February 13, 1758, there is a detailed essay on the SNX that Linnaeus probably wrote himself. Linnaeus was known for habitually
praising himself although this time it is indeed anonymously:

Mr. Archiatri and Knight published the first edition of Systema Naturae in Leiden, 1736 [sic] by which he also won a general standing and esteem of the learned world. This book has within 20 years, now for the 10th time been published.

In the comments on the section Amphibia at least a touch of his fascination with snakes is noticeable:

The Amphibians, which include the many strange and exceptional animals, which generally represent the largest number in Natural Curiosity Cabinets are gathered here with their characteristics marked out, so no one can with any critical usefulness behold such Cabinets without this manual. Among these are such a number of Snakes with distinctive rings and features, that a reader might well get vertigo when he considers what abundance the warm countries suffer from these visitors.

The increase of amphibians and reptile species from 65 in the 6th edition to now 182 is notable (Table 1). Kitchell and Dundee (1994) provided an annotated English translation of the herpetological section of SNX which is also available as a pdf on the Internet.

The introduction part of the third class of the animals contains interesting passages, which disclose Linnaeus’s true opinion about reptiles and amphibians, his correct interpretations, as well as misjudgment of phenomena in nature such as some fish species (Nantes) being Amphibians.

Class III.

Amphibians.

These most terrible and vile animals are distinguished by their unilocular and single chambered heart, arbitrary lungs, and divided penis.

Most amphibians are rough, with a cold body, a ghastly color, cartilaginous skeleton, foul skin, fierce face, a meditative gaze, a foul odor, a harsh call, a squalid habitat, and terrible venom. Their Author has not, therefore, done much boasting on their account.

A polymorphous nature has bestowed a double life on most of these Amphibians: granting that some undergo Metamorphosis and others cast off their old age. Some are born from Eggs, whereas others bear naked young. Some live variously in dry or wet, whereas others hibernate half the year. Some overcome their prey with effort and cunning, whereas others lure the same prey to their jaws as if by magic.

REPTILES. Footed and have flat-nude ears without ear lobes. They pursue various lives depending on their structure. Testudines [the turtles] are protected by their shell. Dracones [the gliding lizards] fly on Wings, whereas Lacertæ [the lizards] flee on feet, and Ranæ [the frogs] are hidden by Location. Nor do they all lack Venom, for example the Toad, Salamander, and Gecko.

SERPENTES. Footless and, lacking Ears, are deaf. Lungs separate them from the Fish, as do Eggs in a chain and a divided penis. In short, the resemblance of the serpents with the lizards and that of the lizards with the frogs is so great as to admit no boundaries. Nature the savior has armed these creatures, cast onto the bare ground, ignorant of the use of limbs, and exposed to every harm, with weaponry bristling with dreadful venom, each unto its own kind. These Weapons are very like teeth, but they are located on the outside edge of the upper jaw and can be extended and retracted at will. They are equipped with a sack of poison which they inject into the blood through a wound— the cause of dire results though in other respects it is inert. And thus these Catonians have a poisonous bite and threaten death with the tooth; the cups lack death surely according to Redi. He who was in charge armed (♂) only a tenth of the species, but lest those who were deprived of the weapons the others possessed should be miserable and rage too much, he wished them to be similar in shape so that all of them, of dubious identification, would be feared by all. But man’s Benefactor gave to the people of India the Mongoose along with the
Ophiorhiza, to the Americans the Pig along with Senega and to the Europeans the Stork along with the Olive.

Should one wish a diagnosis for these, let him take it from the presence or absence of feet and from abdominal and caudal Scutes. But lest the number, taken from one and added to another, should confuse, it is useful to have each one numbered (Act. Stockh. 1752, p. 206.). The Length should be given to and from the anus and in some cases it should be by color. Be careful, however, lest the tail, once cut off, has been regenerated.

NANTES the aquatic finned ones (Chondropterygios, or the so-called cartilaginous Fishes). A class of amphibians that have arbitrary Lungs, although it is true that they are not to be seen [the lungs are pectinate, finned like those of fish but are joined to an arcate, cylindrical, bulbous passageway, lacking a bony rod, unlike that of a fish, except in external appearance]. They do not breathe with free, but with joined gills. The males lie upon the females with a divided penis! The eggs are in a chain with young, the skin is foul, the bones and the rest are cartilaginous. Nor are they entirely unschooled in Venom, as witness Pastinaca [the sting ray] and Torpedine [the electric ray].

AMPHIBIOLOGI are the smallest of them all, but none are true. Seba has collected and delineated a tremendous number of them unknown to himself, but he multiplied them and described them but minimally. Catesby sketched a few serpents more beautifully than he made notes about them. [Translation from Latin by Kitchell and Dundee 1994; italics, name of genera and use of initial capital letters here adjusted after the original text.]

A MONOGRAPH ON SNAKES AND SNAKE BITES – DE MORSURA SERPENTUM

De morsura serpentum (Linnaeus and Acrel 1762) (Fig. 4), “On Snakebites”, is one of Linnaeus’s few academic dissertations devoted entirely to zoology although technically it is a medical treatise, Disputatio medica. It solely deals with snakes and their toxins. It was defended under Linnaeus’s presidium on June 16, 1762 and the respondent was Johan Gustav Acrel (1741–1801), who became a physician and from 1788 was professor in Stockholm.

The slim booklet is in small quarto with 20 pages. Some of the copies include a rather tiny illustration, about 60 mm in height and 70 mm in width, engraved and attractively framed with an ornament (Fig. 5). It depicts the skull of a solenoglyph snake and has finely engraved figure labels ‘a’ to ‘h’ with captions printed further down the page. It is named Vipera vulgaris, but Linnaeus has no such name in SNX. It translates “Common viper” and could indicate that Linnaeus didn’t know the origin. However, Fredric Hasselquist (1722–1752), a Linnaean apostle who traveled in the Middle East had, at his premature
death in Smyrna (now Izmir), his manuscript ready for the narrative in which he not only described his journeys but also included an extensive zoological and botanical systematic part (see Adler p. 39 in the present volume). His collections and manuscripts were bought by Lovisa Ulrika, the Queen of Sweden, and the manuscript was compiled and published by Linnaeus in 1757. Hasselquist told how he on July 3, 1750 purchased from a female snake charmer “4 different kinds [of snakes]; these I described and preserved in aqva vitæ. These are *Vipera vulgaris*, …” The name is not repeated in Hasselquist’s systematic part, but still not being binominal, the authors described the same snake as *Coluber (Vipera) scutis abdominalibus 118, squamis caudalibus 40, cauda aculeate*. In SNX it became *Coluber Vipera (Cerastes vipera [L., 1758]).* Thus, it is possible that the species from which the skull was taken is a *Cerastes vipera*.

Svenska Linnésällskapet (The Swedish Linnaean Society), established in 1917, started in 1921 the publication of a series with translations of the Linnaean dissertations from Latin to Swedish. So far 78 accounts have been published. *De Morsura Serpentum*, no. 47, was published in 1965 with a reissue in 2006. The translation was made by Ejnar Haglund (1905–1991) with the notes and conclusion written by Telemak Fredbärj (1895–1975). The thesis was included in *Amoenitates Acadamicæ* volume 6 (Linnaeus 1763) and translated into English (Linnaeus 1781).

The thesis is divided into seven chapters each with a headline.

**Introduction**

Linnaeus begins with the observation that anything taken in excessive quantities can be considered a poison, but also makes a more strict characterization of poison as a substance that when it is applied to the human body internally or externally, even in small doses, produces dramatic effects, which are disastrous for the health and life. He then examines the origins of toxins that appear in each of nature’s three kingdoms. In the mineral kingdom there are arsenic and other metal compounds, in the plant kingdom a number of toxic genera and species and in the animal kingdom snakes, frogs and toads, and “all other concealed.”

**Amphibia**

The chapter begins with a description of the amphibian class, which includes disapproving wording:

For almost all of mankind as well as for other animate beings the *serpents* appear, because of their poison and other unexplained features, which would thwart our ingenuity, so horrific that they instill fear even in the most daring, if they unexpectedly slither towards him. … In the *amphibian* class animals occur, equipped...
with more than peculiar features, which do not exist in other animals. Most of them live both on land and in water, and most spend half the year in death-like winter dormancy. Their breathing is very different from birds and mammals, for they inhale the air without a corresponding exhalation, at least not a noticeable one. Their body is by nature rigid and abounding in cold blood. They are equipped with double penis, as far as I know does not exist in other animals, other than possible in some insects. With its hissing sound, terrible countenance and its stinking smell they offend our senses. Some of them lay eggs, others give birth to live young, and like the crayfish to the result of the cartilaginous skeleton each spring take off their old skins, whereby no specific limit is set for their growth and size. …

The author then discusses the prey capture methods by snakes with an example from a Boas Javanensis that swallowed a whole buffalo. About the native adder, Vipera berus (L., 1758), he writes:

Our Colubri Beri also occur with expanded bodies and seen through dissection they had swallowed a frog or a mouse or, as we observed, 7 still undigested nestlings.

Tela Serpentum
(The Weapons of the Snakes)

“No scientific issue has been the subject to more different opinions than that of snake venom” Linnaeus begins. He tells that some believe that the venom comes from the tail; others think it comes from the black forked tongue but most have the erroneous opinion that the harm derives from the very fangs, but that all these theories are monstrous fabrications and contradicting all careful observations. About the jaw apparatus he says:

Inside the poisonous snake’s lips sits at the tip of the upper jaw a little bone, which the snake can move back and forth. This bone is attached to two or three fangs, larger than all other teeth. The snake can move the fangs with help of the little bone similar to the cat with its claws: erect them when he is provoked and hide them when he goes to rest after the bite. These fangs, which common folk call Dentes majores serpentum have been valiantly described by Tyson. Act. Angl. p. 144 in Anatome Crotali [Edward Tyson (1683) Vipera caudisconsa Americana, or The Anatomy of a Rattle-Snake. Philos. Transact. (Royal Soc.), No. 144.]: …Each fang is surrounded by a small bladder, equipped with glands, so that at a pressure on the glands a fluid seeps out and can be seen from the very tip of the fang.

Virus (Poison)

In the past it was thought that anger is inflamed from the dark bile, a view that probably lacks all likelihood, but nevertheless without hesitation it is invoked in this context. For, by virtue of this, by the Gods uncertain hypothesis, the origin of the snake’s venom has been deduced. Namely, it was envisioned that some unknown duct, which would directly lead the bile from the gallbladder to the snake’s mouth, from which the bite would float into the wound, and then the deadly symptoms were caused. But let us leave the ancient delusions and glance at the far truer observations, gained from more recent time earnest naturalists.

Linnaeus gives references to Francesco Redi (1626–1697) who conducted several experiments with vipers and their poison. Linnaeus relates the divergent views between Redi and Moys Charas (1619–1698) and the debate a century earlier (see Knoefel 1988). Linnaeus dismisses Charas’s opinion that the poison is generated by a flare-up of natural spirits, and thus snakebites were not fatal, unless the snake had been teased. English surgeons have, Linnaeus says, injected medicine diluted in alcohol in the blood, with some medical success, but that the patients usually died. Linnaeus does a matching with snake venom and milk, man’s first nourishment, which also leads to death when applied in the veins. In the same way as a little yeast can ferment large dough, the entire blood mass can be destroyed by snake venom injected to the blood, but how, Linnaeus dares not say.
**Puncturae symptomata**  
(*Snake* bite symptoms)

In this chapter, the author aims to account for the various genera and species and the different toxins. Linnaeus first depicts the typical symptoms following the bite of the native adders, *Vipera berus* (L., 1758), which he refers to as “BERI nostri”, our Beri. He then describes the snakes found in the classical literature: “HÆMORRHOUS, DIPSAS, and ASPIS, the latter of three different types *Phytas*, *Chersea*, and *Chelidonia.*” Linnaeus refers to the results of the tests conducted by Cleopatra’s physicians on persons sentenced to death. Aspis produced the gentlest death and this is according to Linnaeus probably the serpent that the queen used for her demise.

He refers to SNX (1758) in which the poisonous snakes, “in addition to if not all the rattlesnakes”, are listed (under the genus *Coluber*): *Vipera*, *Berus*, *Leberinus*, *Naja*, *Dipsas*, *Atropos*, *Chersea*, *Severus*, *Atrox*, *Mysterizans*, *Leberis*, *Prester*, *Stolatus*, *Niveus*, *Ammodytes*, *Aspis*, *Lacteus*, *Corallinus*. Actually, Linnaeus did not list in SNX “Prester”, i.e. *Coluber prester* L., 1761 (*Vipera berus* [L., 1758]), but all the others were indeed labeled poisonous along with three rattlesnakes. Of these, most now belong in the family Viperidae, two in Elapidae (*Naja naja* and *N. nivea*), five in Colubridae, and two have not been allocated (*C. Leberis* and *C. Dipsas*). He particularly mentions *Naja* that can attack people with a bite so intense that the victims die in less than an hour with symptoms of flesh that falls off from the bones and dissolves to a sticky stinking mass.

**Medela (Cures)**

Linnaeus explains that the foremost among treatments is to remove as soon as possible the poison from the affected area. This can be done most easily by sucking, but the person that sucks must have a gum that is not attacked by scurvy. One can with a knife broaden the wound and try to draw the poison with the help of a pumpkin (*Cucurbita*). Olive oil is particularly used in Europe; the patient should drink a large quantity. Linnaeus, however, shows a hesitation for its healing powers. The antidote, which is mainly used in America, is powdered “Radix *Senega*”, as well as other American drugs, such as Eryngium fœtidum, aquaticum, etc. The author, however, chooses to ignore them because our knowledge of them is less certain. With regard to Asia, it is *Ophiorrhiza mungos*, which is the famous antidote against the “colubri Najæ”. The use of Strychnos colubrini appears to be, if not completely worthless, of uncertain effect.

The author concludes the chapter by mentioning the snake stone, “*Lapis Serpentum*, Pedra de Cobras di capello” and states that Redi has made many attempts to show any effects with it without success: “Many have told me that the stone is artificial and does not consist of anything else than burnt deer antler, Cornu cerviustum.”

**Excantatio (Snake charming)**

Linnaeus concludes the thesis with a short chapter that deals with snake charming. He says that according to Ovidius, Plinius and other authors from ancient times, the Psylli in Libya could handle the most venomous snakes and they treated snakebites by sucking out the venom. Linnaeus refers to Fredric Hasselquist (1757:70) who has witnessed the snake charmers’ art but that the charmers did not want to reveal the magic of their talent. The dissertation finishes with the prese, Linnaeus, appearing in third person but with a hope expressed jointly:

Mr. JACQUIN [Nic. Jos. von Jacquin (1727–1817)], who returned from West India, said in a letter to Mr. PRÆSES [Linnaeus] that he has acquired the art of snake charming for gold. If this means chewing his *Aristolochia anguicida*, or any other method, is so far unknown to us but we hope that Mr. Jacquin is about to publish this secret, which all inquisitives along with us beg for.
Linnaeus often told in letters about his current projects to friends and colleagues. The available correspondence is accessible on the Internet under the title *The Linnaean Correspondence* with summaries in English and a few with complete translations and some with scans of the originals (http://linnaeus.c18.net). From these letters or summaries I have been able to record the background to Linnaeus’s description of the greater siren. It all started in a correspondence by letters in the mid-1750s with Alexander Garden (1730–1791), a Scottish/American doctor of medicine living in South Carolina in North America. Garden sent various collected specimens of animals and plants to Linnaeus. He enclosed in a letter dated May 18, 1765, a small specimen of an animal and wrote (original in Latin):

. . . I have sent you the characters of a very extraordinary animal, which I have never seen till lately, though they are common here. I have likewise sent to you two specimens of it, though they are much less than the one from which I made out the characters, which was between two and three feet in length. I have sent it to Mr. Ellis for the museum. It happens to be a middle link between the *Lacerta* and *Muræna*, having some things in common with both, and yet differing from both. [Alexander Garden to Carl Linnaeus, 18 May 1765, *The Linnaean correspondence*, linnaeus.c18.net, letter L3591 (consulted 18 October 2010). Also in Smith (1821).]

Linnaeus responded on December 27, 1765, saying about the specimen that it seemed to be a larva of a lizard, if it is not a very special genus that could be named *Sirene* [Carl Linnaeus to Alexander Garden, 27 December 1765, *The Linnaean correspondence*, linnaeus.c18.net, letter L3682 (consulted 18 October 2010)]. He could not determine if it was a larva or a full-grown individual. However, it had two feet with nails, and it could produce a sound. In a letter to his close friend Abraham Bäck on January 1, 1766 Linnaeus wrote (original in Swedish):

A Siren has been sent to me from America; but a species that is small … she has only 2 arms and hands; no feet. the rear part is like an eel. She has both gills (Branchias) like fish, and lungs 2 like the perfect animals. [Carl Linnaeus to Abraham Bäck, 1 January 1766, *The Linnaean correspondence*, linnaeus.c18.net, letter L3704 (consulted 18 October 2010).]

Linnaeus wrote on January 24, 1766, to Johan Andreas Murray (1740–1791), a Swedish professor of medicine and botany living in Göttingen, Germany (original in Swedish):

Now I amuse myself with an animal that is like a Siren and has come from America. has only 2 front feet with arms and hands, no hind feet, but looks like an eel. has both lungs and branchias. sings like a bird. I plan to write about
In another letter to Bäck on February 11, 1766, he wrote:

Now our draftsman is working on the illustration of the Siren. … The dissertation I am done with. [Carl Linnaeus to Abraham Bäck, 11 February 1766, The Linnaean correspondence, linnaeus.c18.net, letter L3719 (consulted 18 October 2010).]

The dissertation (Linnaeus and Österdam 1766) was printed for hearing on June 21, 1766, with Linnaeus in presidium and Abraham Österdam (1745–1776) in defense (Fig. 6). Österdam attended Uppsala University in 1764–1766 and was appointed Royal Life Surgeon in 1775.

The dissertation was reviewed in Swedish in Lärda Tidningar, No. 5:203–204 (see Hagelin 2007), probably written by Linnaeus himself. The review has provided me with some keys to the contents of the dissertation which is in Latin. The first two chapters deal, according to the review, with the mythical Siren, the third on the differences between the orders in the Animal kingdom, the fourth on strange animals of our time, and the fifth on characters of fishes. The description of the siren is made in the sixth chapter with reference to Dr. Garden. This text is a translation from the review:

In § 7. is shown to us how the animal diverges from the general characterizations in the Animal kingdom; in lack of hair and feathers it can be neither Mammal nor Bird; among Amphibia it cannot be assigned to any of the known divisions, neither to the Reptilia, which have four feet and no gills; nor to the Snakes, that are without feet, fins and gills; nor to Nantes, which all have fins. In view of this, Author shows the necessity of establishing a new Ordo in Reptilia, with two feet, lungs and gills. Many would think this animal is simply a larva of Lacerta Iguana or another, but both claws and its sound deny this, which can be seen of § 8. In the end, the animal is described as Siren Lacertina, of which our Auctor has done a beautiful copper engraving.

A copper engraving accompanies the dissertation (Fig. 7) in which the siren is depicted with a mermaid named Siren Bartholini that a Danish author Thomas Bartholin in 1664 had illustrated based on a hand and a rib sent from Brazil and then called it Homo marinus (Broberg 1975). The conclusion part of the text in the dissertation is modified in Amoenitates Acadamicæ, volume 7 (Linnaeus 1769) and with a new and larger illustration of Siren lacertina. A systematic part is listing the siren as

FIGURE 7. The illustration of Siren lacertina, Linnaeus & Österdam 1766. Linnaeus received the specimen from Dr. Garden in North Carolina in North America. Linnaeus could see similarities with the mermaid that Thomas Bartholin had reported in 1664 based on a hand and a rib sent from Brazil.
The greater siren (*Siren lacertina* L., 1766) is a valid species; Linnaeus and Österdam jointly should be the authors of the description and not Öterdam alone, as have been suggested by Dubois (1989–1990). The type specimen is extant in the Uppsala University Museum of Evolution.

**SYSTEMA NATURAE – THE TWELFTH EDITION**

*Systema Naturae* in the 12th edition, *SNXII*, with an appendix in *Mantissa plantarum altera* (Linnaeus 1766, 1767, 1771) was compiled by Linnaeus; this being the last of the five editions of *SN* that he was personally responsible for. It is a much-expanded version of the *SNX* edition, although the increase in number of Amphibia species is less remarkable. The numbers of herpetological taxa in all five editions are shown in Table 1. Linnaeus actually dropped three species from *SNX*: *Rana variegata*, *Rana Hyla*, and *Lacerta hispida* without leaving what I can find any reason for the omissions. In both *SNX* and *SNXII* there is for Amphibia a table of all genera preceding the listings, which are named *Characters amphibiorum* in *SNX* and *Generum Characteres* in *SNXII*. He changed within the order Reptilia the arrangement of numbering and listing of the genera. These are in *SNX*: 103 *Testudo*, 104 *Draco*, 105 *Lacerta*, and 106 *Rana*. In *SNXII* they are: 119 *Testudo*, 120 *Rana*, 121 *Draco*, and 122 *Lacerta*. The number of the Genera follows a series that was expanded in *SNXII*, but I cannot see any explanation for the move of *Rana*.

The Sirens he placed in a new order *Meantes* with the single genus and species *Siren Lacertina*. It is included in an Addendum to part 2 of the first volume that was published in 1767. In the *Mantissa plantarum altera appendix* (1771) Linnaeus included *Coluber crotalinus*, a snake in “Museo Regio” with no current allocation.

**DELICIAE NATURAE**

In December 1772 Linnaeus held his last oration, *Deliciae naturae* (Nature’s delights) to mark his departure from the presidency of the University. It was a brilliant oration held in Latin by the now elderly Linnaeus. His students required a translation into Swedish (Linnaeus 1773). In one chapter of the oration he compared the animals with an infantry, the mammals are the foot soldiers clothed in furs, the birds the cavalry beautifully dressed in dyed down. Linnaeus demonstrated that he retained his aversion against the animals of the class Amphibia. They constituted “an unsightly, hideous naked mob, with no uniforms, inadequately armed except some who got terrifying poisoned darts. They stick to the ground; a few are seamen.” The fishes and insects, in turn, he described generally in positive terms. However, Vermes are also quite depressingly portrayed as small, sluggish mariners with no attire.

**THE LAST YEARS**

Linnaeus was now an old man. He had his first stroke in 1774, when he was lecturing to private pupils, and the second in 1776. Short periods of physical revitalization did not prevent the trend of gradually failing health. In 1775 he was still teaching students, though more often than not they could hardly understand a word he said. On 22 June 1775 he presided, for what proved to be the last time, at a disputation. Linnaeus died on 10 January 1778 at eight o’clock in the morning in his home in Uppsala. The funeral took place on 22 January at the Uppsala Cathedral, where he is buried (Blunt and Stearn 1971). Linnaeus’s library and specimens went to his son Carl, now having the professorship after his father. However,
after his premature death in 1783 they were returned to Linnaeus’s widow. She in turn sold all books, specimens and correspondence the following year privately to a James Edward Smith in England. Eventually all ended up in The Linnean Society of London, where they still remain except for the mineral collection that had been sold (Blunt and Stearn 1971).

However, Linnaean zoological materials that belonged to the Academy of Uppsala, such as the donations catalogued by Linnaeus were not included in the sale and largely remain in the museum.

ACKNOWLEDGMENTS

Torbjörn Lindell has been an enduring partner for discussing problematic Linnaean issues and proposing academic sources. Lindell also read and commented on a draft of the paper, as did two anonymous reviewers. Lars Fröberg at the Botanical Museum of Lund University assisted in identifying pre-Linnaean plants. Ralph Tramontano assisted with the English style and grammar. Last but not least I thank the Herpetologists’ League for support of the Linnaean Tercentenary Symposium at the Joint Meeting of Ichthyologists and Herpetologists in St. Louis, Missouri.

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Herpetological Exploration in the 18th Century: Spanning the Globe with Linnaeus’s Students

Kraig Adler

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Abstract. Carl Linnaeus’s travels as an explorer were limited to the Scandinavian provinces. He had opportunities to visit places that were more exotic, but arranged instead to send his young male pupils. During the period 1742 to 1778, his students who went exploring—collectively called “Linnaeus’s Apostles”—visited six continents and one even closely approached Antarctica. Of the 17 who went overseas, eight died in the effort. Those of particular herpetological interest were Pehr Kalm (Russia, Ukraine, and northeastern North America), Fredric Hasselquist and Pehr Forsskål (Egypt and Near East), Pehr Osbeck (Java and China), Daniel Rolander (Suriname), Anders Sparrman (China, Cape Colony, Senegal, and a circumnavigation with Captain James Cook that included New Zealand, the South Pacific, and within the Antarctic Circle), and Carl Peter Thunberg (Cape Colony, Java, Japan, and Ceylon) who eventually succeeded to Linnaeus’s chair at Uppsala University. Most of these expeditions were primarily botanical, but numerous specimens of amphibians and reptiles were collected that served as types for many new species. These collections contributed significantly to the first global reviews of the world’s herpetofauna in the last two editions of “Systema Naturæ” prepared by Linnaeus himself.

Key words. Carl Linnaeus, Apostles, Global exploration, Pehr Kalm, Fredric Hasselquist, Pehr Osbeck, Daniel Rolander, Pehr Forsskål, Anders Sparrman, Carl Peter Thunberg.

CARL LINNAEUS AS A TEACHER

Carl Linnaeus’s (1707–1778) role as a teacher and motivator of students has long been overshadowed by his brilliance as a systematic biologist and as developer of the universal system of binomial Latin nomenclature for plants and animals. But he was also perhaps the greatest teacher of naturalists in the 18th century and, as this essay will detail, he established the first comprehensive scientific team—all of them his former students—to explore the world for its natural treasures. As his reputation as a teacher grew outside of Sweden, he attracted students from other places including England, central and northern Europe, and even from America. Several came from Russia including a nobleman from Siberia sent by the czar to study with Linnaeus.

A total of 331 pupils are known to have studied with Linnaeus at Uppsala University, located in Uppsala just north of Stockholm in eastern Sweden. This number includes all students referred to as such by Linnaeus himself or by his colleagues or his other pupils. A phenomenal 186 dissertations were completed under Linnaeus’s supervision (Sandermann Olsen, 1997). Most of these students became physicians or other professionals, but many became natural scientists. It was the custom at Swedish universities in the 18th Century that the professor provided the material to be studied for the dissertation, wrote it, and was responsible for its scientific content (Stearn, 1966). However, the student, or respondent, defended the dissertation under the chairmanship (in Latin, praeses, guard or protector) of the professor, showed his mastery by discussing it, and paid for its publication. Thus, the professor, in this instance Linnaeus, was the intellectual author and writer of the dissertation. In a few
instances, the dissertations were completed by his students in a more independent fashion, as will be noted below.

Linnaeus conducted extensive local field trips for students at Uppsala University, members of the nobility, and the townspeople. These usually were held twice a week, sometimes with as many as 300 persons and often accompanied by a small band of musicians. Linnaeus always marched at the lead. The participants were required to dress in standard attire and the group was divided according to specific duties (bird hunters, plant gatherers, etc.). These outings typically began at seven o’clock in the morning and would last up to 12 hours. Through these communions with nature and by his classroom lectures, Linnaeus inspired his students in their academic work and exhorted them to travel and explore.

**LINNAEUS’S TRAVELS AND HIS “APOSTLES”**

A small subset of Linnaeus’s students—all of them men and numbering 17 or so—went on to explore the world overseas under Linnaeus’s instructions in search of nature’s productions. These have generally been referred to as “Linnaeus’s Apostles,” a term Linnaeus himself once applied to them. A series entitled “The Linnaeus Apostles” has been issued in eight volumes under the general editorship of Lars Hansen (2007–2010).

This paper focuses on those apostles who, as part of their exploration, became a virtual network of herpetological collectors. Their specimens contributed significantly to the 10th and 12th editions of Linnaeus’s “Systema Naturæ” and to our knowledge of the world’s herpetofauna in the 18th Century. Linnaeus’s students visited nearly every continent, although Antarctica was only approached aboard ship (Figure 1).
Linnaeus himself was a far more modest traveler. During 1732, he visited Lapland in northern Scandinavia and two years later Dalarna in central Sweden. He lived in Holland from June 1735 to June 1738 during which period he also traveled to Paris and London. In 1738, he declined opportunities to visit Dutch colonies in South America and southern Africa. Linnaeus did visit the Swedish Baltic islands of Öland and Gotland in 1741 and made his last two trips to southern Scandinavia (Västergötland and Skåne) in 1746 and 1749, respectively. He never left Sweden for the remaining 29 years of his life. Instead, his students traveled, mostly by sea and as far as China and Japan, trips that could take as much as six to eight months excluding time ashore at way stations (Figure 2). One student even made a complete circumnavigation of the southern oceans. As Linnaeus once said to a departing apostle (in translation): “I avoid long voyages. Now you are on your own. You’ll manage well.”

Unlike many European nation-states, Sweden, then also encompassing Finland and parts of Norway, did not have overseas colonies to supply the raw materials from which to manufacture finished products to sell. Thus, one national mission was to discover exotic plants that could be naturalized in Sweden and help support its economy. Linnaeus was a central figure in this effort and his desire to send students abroad, supported by governmental or commercial interests, was as much about helping his nation’s economy as it was to undertake the exploration, systematization, and naming of the natural world.

Among his students who went overseas, eight died while abroad. Seven of the 17 figured prominently as collectors, and four even as describers, of amphibians and reptiles. Several of them published in the primary Swedish scientific periodical of the day, Kongliga Svenska Vetenskaps Akademiens Handlingar (the title varies slightly over the years; for a detailed review of the herpetological articles in this serial, see Wahlgren, 1999 [2000]). The remainder of this paper provides brief synopses of their lives, travels, and herpetological work. These are presented in chronological order according to the dates of their travels.

**Pehr Kalm (1716–1779)**

Kalm (Figure 3A) was born in Ångermanland, on the Gulf of Bothnia in northeastern Sweden, of Finnish parents. (Finland was then part of Sweden, until 1809 when it was incorporated into the Russian Empire.) He studied with Linnaeus at Uppsala University during 1740–1742 and then traveled to Russia and Ukraine in 1742–1746 before becoming a professor at Åbo Academy in Finland. During 1748–1751, Kalm went to England for six months, then to eastern North America including French
Canada and the British colonies of New Jersey, New York, and Pennsylvania. His primary assignment was to obtain mulberry trees on which to grow silkworm moths to establish a silk industry in Sweden, but he also made observations and natural history collections. Linnaeus’s instructions specifically asked him (in translation) “[to make] observations on Birds and Fishes, on Snakes and Insects.” Kalm’s base of operations was the Swedish-Finnish community of Raccoon (now Swedesboro), New Jersey, where he served as substitute pastor at Trinity Church. Among other accomplishments, he produced the first detailed technical description of Niagara Falls in western New York.

Kalm collected the specimens on which Linnaeus based five new species of snakes. Three of them—Coluber constrictor, Nerodia sipedon, and Thamnophis sirtalis—are recognized today and are among the most widespread and well-known species on the North American continent (Table 1). Coluber constrictor is the type of its genus, on which the family name Colubridae is based. Klauber (1948) tentatively allocated the two other Kalm species named by Linnaeus (see Table 1, footnote 3). Most of Kalm’s collecting, however, was botanical. Of some 700 North American plants described by Linnaeus, 60 were based on specimens collected by Kalm.

The name Rana halecina has often been attributed to Kalm for the species now known as R. pipiens, the Northern Leopard Frog (Pace, 1974). Although Kalm made numerous references to American frogs in his travel book, nowhere in it did he use the epithet halecina. In fact, Linnaeus himself (1766) introduced this name in his synonymy of R. ocellata, following a reference to Kalm’s book. Kalm had reported that Swedish immigrants in New Jersey called these frogs “silhopptåssor,” or herring-hopper, in allusion to the fact that their breeding calls are heard in the spring during the herring-catching season (haleco is Latin for herring). Coincidentally, Johann C. D. von Schreber, another of Linnaeus’s students and the describer of R. pipiens, based his name in part on Kalm’s description of what Kalm mistakenly thought was this frog’s bird-like peeping call, which he apparently got mixed up with that of the Spring Peeper, Pseudacris crucifer. For further details about Kalm’s frogs, see Garman (1888).

Kalm returned to his professorship in Åbo where, nearly 30 years later, he died at the age of 63. He published a report in Swedish on his American journey, “En Resa til Norra America” (1753–1761, in three volumes), which was translated into German (1754–1764), English (1770–1771), Dutch (1772), and French (1768). He also published a series of three papers on the Timber Rattlesnake (Crotalus horridus) and the native medicines used to cure its bites (1752–1753; English version 1758; for commentary, see Larsen, 1957).

The New Jersey Chorus Frog (Pseudacris kalmii), recently raised to species status (Lemmon et al., 2007), is the only amphibian or reptile named for him. Better known is Mountain Laurel, a flowering ericaceous tree found throughout eastern United States and named Kalmia latifolia by Linnaeus in 1753 from Kalm’s specimens.

Fredric Hasselquist (1722–1752)

Hasselquist was born in Törnevalla Parish, Östergötland County, southwest of Stockholm, and attended Uppsala during 1741–1749. His dissertation under Linnaeus’s supervision, completed in 1747, was one of the few conducted relatively independently (Staffleu, 1971). He received a medical degree in 1749. Influenced by Linnaeus’s oft-repeated lament that the natural history of the Holy Land was so poorly known, Hasselquist resolved to explore Palestine and, in preparation, he studied Arabic. In 1749, Hasselquist obtained free passage aboard the Swedish Levant Company’s ship Ulrica to Smyrna (now Izmir, Turkey); he then traveled to northern Egypt, Syria,
Palestine, and Cyprus. At the age of 30 he died near Smyrna from tuberculosis that had been contracted earlier in Sweden. Hasselquist had developed large debts in Smyrna, and creditors seized his collections and notes. Agents for Queen Louisa Ulrica (in Swedish, Lovisa Ulrika) redeemed them, and these materials were sent to Sweden for study by Linnaeus who later edited Hasselquist’s book, “Iter Palæstinum eller Resa til Heliga Landet” (1757).

In his book, Hasselquist recorded the Nile Crocodile (*Crocodylus niloticus*) and noted its propensity to swallow stones to aid in digestion. He also remarked on 13 species of lizards and snakes, which led to descriptions of eight new species by Linnaeus in the 10th edition of his “Systema Naturæ” (1758) and another one in the 12th (1766); Linnaeus used other Hasselquist specimens as types for five additional new species (Table 1). Another species discovered by Hasselquist was named by a later Linnaeus apostle, Pehr Forsskål (see Table 1).

Hasselquist’s book, having been published in 1757, is considered to be pre-Linnaean
TABLE 1. Species of amphibians and reptiles described by Linnaeus based on specimens collected, at least in part, by his apostles and other species described by them.

<table>
<thead>
<tr>
<th>Original Name</th>
<th>Current Name</th>
<th>Collector / Source</th>
</tr>
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<tbody>
<tr>
<td>Linnaeus</td>
<td></td>
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</tr>
<tr>
<td><em>Lacerta crocodilus</em> Linnaeus 1758: 200</td>
<td><em>Crocodylus niloticus</em> Laurenti 1768</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Lacerta stellio</em> Linnaeus 1758: 202</td>
<td><em>Laudakia stellio</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Lacerta angulata</em> Linnaeus 1758: 204</td>
<td><em>Alopoglossus angulatus</em> (Linnaeus 1758)</td>
<td>Rolander</td>
</tr>
<tr>
<td><em>Lacerta chamaeleon</em> Linnaeus 1758: 204</td>
<td><em>Chamaeleo chamaeleon</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Lacerta gecko</em> Linnaeus 1758: 205</td>
<td><em>Gekko gecko</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Lacerta stincus</em> Linnaeus 1758: 205</td>
<td><em>Scincus scincus</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Rana typhonia</em> Linnaeus 1758: 211</td>
<td><em>Trachycephalus typhonius</em> (Linnaeus 1758)</td>
<td>Rolander</td>
</tr>
<tr>
<td><em>Boa canina</em> Linnaeus 1758: 215</td>
<td><em>Corallus caninus</em> (Linnaeus 1758)</td>
<td>Rolander</td>
</tr>
<tr>
<td><em>Coluber vipera</em> Linnaeus 1758: 216</td>
<td><em>Cerastes vipera</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Coluber leberis</em> Linnaeus 1758: 216</td>
<td><em>?Storera occiptomaculata</em> (Storer, 1839)</td>
<td>Kalm</td>
</tr>
<tr>
<td><em>Coluber constrictor</em> Linnaeus 1758: 216</td>
<td><em>Coluber constrictor</em> Linnaeus 1758</td>
<td>Kalm</td>
</tr>
<tr>
<td><em>Coluber cerastes</em> Linnaeus 1758: 217</td>
<td><em>Cerastes cerastes</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Coluber lebetinus</em> Linnaeus 1758: 218</td>
<td><em>Macroviadrus lebetina</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Coluber sipedon</em> Linnaeus 1758: 219</td>
<td><em>Nerodia sipedon</em> (Linnaeus 1758)</td>
<td>Kalm</td>
</tr>
<tr>
<td><em>Coluber sirtalis</em> Linnaeus 1758: 222</td>
<td><em>Thamnophis sirtalis</em> (Linnaeus 1758)</td>
<td>Kalm</td>
</tr>
<tr>
<td><em>Coluber ovivorus</em> Linnaeus 1758: 223</td>
<td><em>?Pantherophis gloydi</em> (Conant, 1940)</td>
<td>Kalm</td>
</tr>
<tr>
<td><em>Coluber situla</em> Linnaeus 1758: 223</td>
<td><em>Zamenis situla</em> (Linnaeus 1758)</td>
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<tr>
<td><em>Coluber tyria</em> Linnaeus 1758: 224</td>
<td><em>?Hemorrhoidum nummifer</em> (Reuss 1834)</td>
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<tr>
<td><em>Coluber jugularis</em> Linnaeus 1758: 225</td>
<td><em>Dolichophis jugularis</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Coluber haje</em> Linnaeus 1758: 225</td>
<td><em>Naja haje</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Anguis colubrina</em> Linnaeus 1758: 228</td>
<td><em>Eryx colubrinus</em> (Linnaeus 1758)</td>
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</tr>
<tr>
<td><em>Anguis jactulus</em> Linnaeus 1758: 228</td>
<td><em>Eryx jactulus</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Anguis cerastes</em> Linnaeus 1758: 228</td>
<td><em>Eryx jactulus</em> (Linnaeus 1758)</td>
<td>Hasselquist</td>
</tr>
<tr>
<td><em>Lacerta nilotica</em> Linnaeus 1766: 369</td>
<td><em>Varanus niloticus</em> (Linnaeus 1766)</td>
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Osbeck

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<tr>
<td><em>Lacerta chinensis</em> Osbeck 1765: 175, 366</td>
<td><em>?Hemidactylus bowringii</em> (Gray 1845)</td>
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<tr>
<td><em>Rana chinensis</em> Osbeck 1765: 244</td>
<td><em>?Hoplobatrachus rugulosa</em> (Wiegmann 1834)</td>
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Forsskål

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<td><em>Testudo terrestris</em> Forsskål 1775: VIII, 12</td>
<td><em>Testudo graeca terrestris</em> Forsskål 1775</td>
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<tr>
<td><em>Lacerta ocellata</em> Forsskål 1775: VIII, 13</td>
<td><em>Chalcides ocellatus</em> (Forsskål 1775)</td>
<td>Forsskål</td>
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<tr>
<td><em>Lacerta aegyptia</em> Forsskål 1775: VIII, 13</td>
<td><em>Uromastyx aegyptius</em> (Forsskål 1775)</td>
<td>Forsskål</td>
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<tr>
<td><em>Coluber dhara</em> Forsskål 1775: VIII, 14</td>
<td><em>Telescopus dhara</em> (Forsskål 1775)</td>
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<td><em>Coluber schokari</em></td>
<td><em>Psammophis schokari</em> (Forsskål 1775)</td>
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<tr>
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<td><em>Trionyx triunguis</em> (Forsskål 1775)</td>
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<tr>
<td><em>Lacerta harbai</em></td>
<td><em>?Uromastyx aegyptius</em> (Forsskål 1775)</td>
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**Sparrman**

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<td><em>Pachydactylus geitje</em> (Sparrman 1778)</td>
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<td><em>Lacerta sputator</em></td>
<td><em>Sphaerodactylus sputator</em> (Sparrman 1784)</td>
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<td><em>Lacerta bimaculata</em></td>
<td><em>Anolis bimaculatus</em> (Sparrman 1784)</td>
<td>Acrelius / De Geer</td>
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<tr>
<td><em>Coluber ferruginosus</em></td>
<td><em>Coronella austriaca</em> Laurenti 1768</td>
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**Thunberg**

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<td><em>Lacerta japonica</em></td>
<td><em>Onychodactylus japonicus</em> (Houttuyn 1782)</td>
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<tr>
<td><em>Lacerta lateralis</em></td>
<td>“A” <em>Chalcides ocellatus</em> (Forsskål 1775)</td>
<td>Thunberg</td>
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<tr>
<td><em>Lacerta lateralis</em></td>
<td>“B” <em>Not allocated</em> (Vesterås)</td>
<td>Vesterås</td>
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<tr>
<td><em>Lacerta abdominalis</em></td>
<td><em>?Chamaesaura aenea</em> (Fitzinger 1843)</td>
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<tr>
<td><em>Testudo japonica</em></td>
<td><em>Chelonia mydas japonica</em> (Thunberg 1787)</td>
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<tr>
<td><em>Testudo rostrata</em></td>
<td><em>Pelodiscus sinensis</em> (Wiegmann 1834)</td>
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</tr>
<tr>
<td><em>Testudo areolata</em></td>
<td><em>Homopus areolata</em> (Thunberg 1787)</td>
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<tr>
<td><em>Coluber strigilis</em></td>
<td><em>Thamnodynastes strigilis</em> (Thunberg 1787)</td>
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<td><em>Amphisbaena reticulata</em></td>
<td><em>Blanus cinereus</em> (Vandelli 1797)</td>
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<td><em>Boa variegata</em></td>
<td><em>Candoia carinata</em> (Schneider 1801)</td>
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<tr>
<td><em>Emys discolor</em></td>
<td><em>Platemys platycephala</em> (Schneider 1792)</td>
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</tr>
</tbody>
</table>

1 Linnaeus’s concept of *Gekko gecko* was a composite based on specimens from several localities, including some collected by Hasselquist. According to Anderson (1896), Hasselquist’s specimens are referable to *Ptyodactylus hasselquistii*.

2 Linnaeus’s name *Rana typhonia* has long been allocated to the Neotropical toad, “*Bufo* typhonius.” However, the recent translation and publication of Rolander’s diary (Hansen, 2008) made it possible to identify *R. typhonia* Linnaeus 1758 as an older synonym of *R. venulosa* Laurenti 1768 (see Lavilla et al., 2010).

3 Klauber (1948) believed that *Coluber leberis* was a *Storeria*, most likely *S. occipitomaculata*. He tentatively allocated *C. ovivorus* to *Elaphe vulpina* (now *Pantherophis vulpinus*), but because he noted Kalm’s field work in the Lake Ontario region the correct allocation today would be *P. gloydi*.

4 There is no indication in Thunberg 1787a that he was aware of Houttuyn’s prior description of this salamander. Thus, Thunberg apparently intended his name as new.
for taxonomic purposes. The translations into German (1762), English (1766), French (1769), and Dutch (1771) would seem to make his new names nomenclaturally available, but the International Commission on Zoological Nomenclature declared (Opinion 57, 1914) the German edition rejected for nomenclatural purposes (Heming, 1958) and, by implication, names introduced in the other translations would similarly be unavailable.

It has long been assumed that Linnaeus devised the Latin names for animals and plants in Hasselquist (1757). In the introduction to Hasselquist’s book, Linnaeus states (in translation): “I have . . . added names [italics in original] to plants and animals . . . ,” referring to Hasselquist’s own original manuscript. However, it should be noted that Hasselquist had earlier published ten articles about his collections in the journal, *Acta Societatis Regiae Scientiarum Upsaliensis* (1751). In these he described and named four new species of reptiles, which he called *Vipera aegypti*, *Coluber cornutus*, *Anguis cerastes*, and *Lacerta scincus* (not *stincus*, as Linnaeus wrongly wrote it in the 10th edition of “Systema Naturæ” and created a century of confusion in the proper spelling of this name). None of the four herpetological papers is dated, but they appear consecutively in the *Acta* and immediately following them is a final paper by Hasselquist that is dated “Smirnæ 1749,” his first year in the field, so it appears that at least these herpetological names originated with Hasselquist and not with Linnaeus, the latter’s claim notwithstanding.

Hasselquist was immortalized by the name of the Fan-footed Gecko (*Ptyodactylus hasselquistii*), the first specimens of which he collected (see Table 1, footnote 1).

**Pehr Osbeck (1723–1805)**

Osbeck (Figure 3B), who was born in a small settlement called Oset, in Hålanda Parish, Västergötland County, southwestern Sweden, studied with Linnaeus at Uppsala during 1745–1750, and then shipped out to China in 1750 as a chaplain aboard a Swedish East India Trading Company vessel, the *Prince Charles*. The ship anchored for four and one-half months in the Pearl River (Zhu Jiang), just downstream from Canton (Guangzhou) in southern China. This permitted Osbeck to go ashore to make large collections, mostly botanical but also including herpetological ones, as noted in his book, “Dagbok öfwer en Ostindisk Resa” (1757). Although he introduced Latin names for a frog (*Rana chinensis*) and a lizard (*Lacerta chinensis*), the book is pre-Linnaean, but translations into German (1765; revised and completed by Osbeck himself) and English (1771; translated by Johann Reinhold Forster who added a list of the fauna and flora of China) make the names nomenclaturally available (Table 1). However, the descriptions are not referable to known species with any certainty and the names, therefore, have been regarded as *nomina dubia* and are not generally used (Zhao and Adler, 1993).

On Osbeck’s return to Sweden in 1752, he became vicar of Hasslöv and Växtorp parishes in southern Sweden. He died in Hasslöv at the age of 82.

**Daniel Rolander (1725–1793)**

Born in southern Sweden at Hälleberga Parish in Småland Province, Rolander studied at Uppsala during 1744–1754, specializing in insects. It was Rolander who, in 1750, discovered the chemical defensive sprays of bombardier beetles (Eisner et al., 2001). During 1755–1756, Rolander collected in the Dutch colony of Suriname, or Dutch Guiana, in northern South America. Among these collections were the types of three Linnaean herpetological taxa: a gymnophthalmid lizard, *Alopoglossus angulatus*; a tree boa, *Corallus caninus*; and a hylid frog, *Trachycephalus typhonius* (Table 1).
On Rolander’s return from Suriname in 1757, he became director of the botanical gardens at Seraphimer Hospital in Stockholm for a few years, but eventually died a pauper in Lund at the age of 68. His journal, “Diarium Surinamicum,” was never published in book form, but exists as a manuscript in the Danish Botanical Library in Copenhagen. Recently, it was translated into English and published by the IK Foundation (Hansen, 2008). This translation has made it possible to better identify Rolander’s specimens (see Table 1, footnote 2).

Pehr Forsskål (1732–1763)

Forsskål (Figure 3C) was born in Helsingfors (or Helsinki), in Swedish Finland. The Latin spelling of his name is Petrus Forskal, but the Swedish spelling—Forsskål—was officially adopted by the International Botanical Congress in 1975 (see Friis and Thulin, 1984). He first attended Uppsala University at the astonishingly young age of ten and, after a hiatus of three years during which he studied Arabic and other oriental languages in Göttingen, he completed his studies in Uppsala in 1756–1760. At that time the government of Frederick V, king of Denmark and Norway, was planning a scientific expedition to the Near East, the Royal Danish Arabia Expedition, the first ever to Arabia, and Linnaeus highly recommended Forsskål to the king because of his abilities in oriental languages and natural history. In 1761, Forsskål joined the expedition aboard the Gronland and sailed to the Near East (Egypt, Suez, the Red Sea, and southern Arabia). He obtained numerous marine organisms in the Mediterranean Sea and was apparently the first to collect pelagic species using a plankton net. He died of malaria in Jerîm, Arabia (now Jarim, in central Yemen), at the age of 31.

Only one of the original party of six, Carsten Niebuhr, a surveyor and geographer, survived the journey and he edited Forsskål’s notes into a book, “Descriptiones Animalium . . . quæ in Itinere Orientali” (1775; an atlas of 43 plates, none herpetological, was issued in 1776 under Niebuhr’s editorship). No translations were issued. Niebuhr published his own book, in German, about the group’s travels in Arabia (1772–1837, in four volumes, with later translations into Dutch, English, and French).

In Forsskål’s book, 13 species of reptiles are discussed, of which six named by him are recognized today (Table 1). Among Forsskål’s new taxa was the Nile Softshell (Trionyx tringuis), type of the genus on which the turtle family name, Trionychidae, is based. One other, the Egyptian Dabb Lizard (Uromastyx aegyptius), had been named in Hasselquist’s book (1757) and, oddly, was overlooked by Linnaeus in his last two editions of “Systema Naturæ” (1758, 1766). Thus, it was properly named in Forsskål’s book, although he clearly derived his information and even the Latin name from Hasselquist.

Anders Sparrman (1748–1820)

Sparrman (Figure 3D), the most widely traveled of Linnaeus’s pupils, was born in the village of Tensta, located 25 km north of Uppsala, Sweden, and attended Uppsala University in 1757–1765. In 1765, at the age of 17, he traveled to China as a ship’s surgeon aboard a vessel captained by his cousin. He returned to Uppsala to complete his studies during 1768–1770. His dissertation under Linnaeus was one of the few to be written relatively independently (Stafleu, 1971). In 1772, Sparrman traveled aboard the Swedish East India Company’s ship Stockholm to Cape Colony at the southern tip of southern Africa, as tutor to the Swedish consul’s children. The colony was then operated by the Dutch East India Company as a way station to its activities in the East Indies and the Far East.

Later that year, however, he joined two British ships, Resolution and Adventure, commanded by Captain James Cook on Cook’s second circumnavigation and the first ever in an easterly direction. Sparrman was hired to assist
the two German naturalists on board, Johann Reinhold Forster, and his son, Johann Georg Forster. The elder Forster had been corresponding with Linnaeus and doubtless learned of Sparrman from him. The ships first headed toward Antarctica as far south as 71° 10’ and thus crossed the Antarctic Circle and, amidst ice bergs, came very near the ice shelf, the first expedition to do so (Figure 1), then meandered around New Zealand, Fiji, Tahiti, again to New Zealand and then, southwest of the southern tip of South America, crossed the Antarctic Circle twice again, before returning Sparrman to Cape Colony in 1775. Sparrman was insistent to stay at the very rear of the ship when, after approaching Antarctica, it finally turned about to head north. Long thereafter, he boasted that he had been at the southernmost point ever reached by a human! He published several popular books on his time in Cape Colony and his round the world voyage with Cook in Swedish (1783, 1802, 1818), with German (1784), English (1785), Dutch (1787), and French (1787) translations of the 1783 book.

Sparrman was the most zoological of Linnaeus’s apostles and described several new species of reptiles, among them three lizards from the West Indies and South Africa that are recognized today (Table 1). In 1795 he named a snake from southern Sweden, *Coluber ferruginosus*, a synonym of *Coronella australica*, the Smooth Snake, as the northern European populations are not recognized nomenclaturally.

In 1777, Sparrman became curator of natural history and pharmacy at the Swedish Royal Academy of Sciences in Stockholm until his retirement in 1797. He made only one further expedition overseas, to Senegal in western Africa in 1787–1788, in an abortive attempt to send Swedish settlers there. He died in Stockholm of a wasting disease at the age of 72.

**Carl Peter Thunberg (1743–1828)**

The most famous of Linnaeus’s students, Thunberg (Figure 3E) was born in Jönköping, Småland, in southern Sweden, and eventually became Linnaeus’s worthy successor at Uppsala University. He took his *medicus candidatus* degree with Linnaeus in 1769 and then went to Paris to study surgery and to Amsterdam for natural history. He aspired to explore Japan, which Linnaeus had urged him to do, but at that time the country was closed to all foreigners but Dutch and Chinese traders. He therefore studied the Dutch language in order to pass as Dutch and during 1772–1775 made collections in Dutch Cape Colony in southern Africa with his former fellow student at Uppsala, Anders Sparrman, among others. There, he further burnished his knowledge of the Dutch language.

In 1775, Thunberg sailed to Japan via Java (then also Dutch and where he collected for half a year) aboard the *Stavenisse*, with a crew of 110 men and 34 slaves, and spent 16 months during 1775–1776 on the artificial island of Decima (measuring only 75 by 120 meters) in Nagasaki harbor where the foreign merchants were required to live. He served as the company’s surgeon, but was occasionally allowed ashore by the Japanese to botanize. He also obtained other specimens by bribing his Japanese translators to collect for him. In mid-1776, he accompanied the Dutch company’s director on a 1000-km, 50-day journey, mostly on foot, to pay homage to the shogun in Edo (now Tokyo), during which trip he collected along the way. Thunberg thus found the first hynobiid salamander, *Onychodactylus japonicus*, which he called *Lacerta japonica*, in the Hakone Mountains, near Mt. Fuji southwest of Edo (Stejneger, 1907). The first describer of this species, which has digits bearing keratinized, claw-like tips, was Martinus Houttuyn, a Dutch physician-naturalist and developer of a private natural history museum in Amsterdam who had helped finance Thunberg’s trip to Japan. Thunberg returned to Europe via Java and Dutch Ceylon. He published a summary
of his voyage in Swedish, “Resa uti Europa, Africa, Asia förrättad åren 1770–1779” (1788–1793, in four volumes), with German (1792–1794), English (1793–1795), and French (1794) translations.

After spending 1778–1779 in Holland and England, Thunberg returned to Sweden in 1779, but Linnaeus had already died in 1778 and was succeeded by his son. Thunberg became a professor at Upsala in 1781 and, on the early death of Linnaeus’s son in 1783, finally took his master’s chair the following year. Thunberg continued Linnaeus’s tradition of training students in the natural sciences and of describing collections of plants and animals from all parts of the world. Among his student dissertations, all written by Thunberg in the then-prevailing tradition, were several reports on collections of amphibians and reptiles; these student respondents were Fredric Wilhelm Radloff, 1787; Lars Magnus Holmer, 1787; Andreas Kjeller, 1823; and Mauritz Kahn, 1823.

In these and separate papers, Thunberg authored several new species of reptiles from Africa, East Indies, Europe, Japan, and South America (Table 1). Two of his new names were overlooked for many years and more recent names have become established for these species. Testudo rostrata, named by Thunberg in 1787, is the well-known softshell, Pelodiscus sinensis, of East Asia (Zhao and Adler, 1993). Another, Amphisbaena reticulata, also named by Thunberg in 1787, is today synonymized with Blanus cinereus of the Iberian Peninsula and North Africa (Gans, 1967; Gans, however, incorrectly credited the name reticulata to Thunberg’s student, Holmer). Thunberg’s Boa variegata, based on specimens from the East Indies and published in 1807, is a senior synonym of the South Pacific ground boa, Candoia carinata (for details, see Bauer and Wahlgren, 2000). Schweigger (1812) credited the name Emys discolor to Thunberg, based on a drawing sent to him by Thunberg, but today the name is a synonym of Platemys platycephala, a South American sideneck. Blasius Merrem named one turtle for Thunberg, Caretta thunbergii, but it is now synonymized with Thunberg’s own Chelonia mydas japonica.

Thunberg also wrote, as dissertations, a long series on animals and plants described in the Bible (1825–1829; the two herpetological and one ichthyological parts were published together in 1827 and reported on materials collected by Fredric Hasselquist, a fellow apostle, during his travels in the Holy Land). The student respondents for these herpetological dissertations were Erik Henrik Eriksson and Carl Jacob Wettergren. The number of dissertations Thunberg supervised—294—exceeded even that of the illustrious Linnaeus. He died at his home in Tunaberg, near Uppsala, at the age of 84.

**DISCUSSION**

This paper summarizes only the herpetological activities of Linnaeus’s apostles, which were but a minor portion of their biological scope. In fact, the major focus of all of these voyages and expeditions was botanical. Collectively, these former pupils amassed enormous natural history collections from all parts of the globe for Linnaeus and his other students to study and for Linnaeus to systematize, describe, name, and incorporate into the editions of his major works, “Species Plantarum” and “Systema Naturæ.” By inspiring so many of his students to explore and collect and by his arrangements for their trips, Linnaeus’s influence was extraordinary and perhaps even unparalleled. Indeed, the only comparable plans for continental natural history surveys—in the Russian Empire and in North America—both had massive governmental support, yet Linnaeus’s individual effort was more globally comprehensive.

In the late 1760s and 1770s, the government of Empress Catherine II in Saint Petersburg appointed Peter Simon Pallas, a German naturalist and explorer, to organize a series
of scientific surveys—collectively called the “Physical Expeditions”—to explore the rapidly expanding Russian Empire (Adler, 2007). The team of astronomers and six naturalists composed of Pallas and, coincidentally, two of Linnaeus’s former pupils, Johan Peter Falck (see Figure 1) and Ivan Ivanovich Lepechin, as well as numerous support personnel including military escorts and staff. The naturalists would sometimes travel together and sometimes separately, in order to cover more territory, from the Caucasus and the Caspian Sea to the Ural Mountains and throughout Siberia to eastern Mongolia.

The other effort was that of the United States government to survey the natural history of North America, especially the newly acquired lands in the American West and also Russian Alaska that was purchased in 1867. During the 1850s and 1860s, Spencer Fullerton Baird, a vertebrate naturalist and director of the fledgling national museum in Washington, arranged to have naturalists or surgeon-naturalists appointed to army posts; to surveys of various river basins, mountain ranges, and border areas; and to a dozen topographical surveys formed to explore possible routes for the new continental railroads, the “Pacific Railroad Surveys” (Adler, 1979).

Massive collections were made in both Russia and the United States and numerous reports were published, but the collections made by Linnaeus’s apostles from 1742 to 1778 were equally important and global in scope. They were also demonstrably the more dangerous to make, given that fully forty-seven percent of Linnaeus’s former pupils died while on their overseas travels. But as Linnaeus once wrote to Thunberg, “He who wants to gain something great must also venture high.” Indeed, the apostles provided essential collections on which Carl Linnaeus wrote the first scientific summaries of the plants and animals of the world.

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REFERENCES


INTRODUCTION

In the 10th edition of *Systema Naturae* Linnaeus (1758) described 182 species of amphibians and reptiles. The majority of these (150; 82%) had been described or illustrated elsewhere prior to this. Many of these “pre-Linnaean” (i.e., prior to the official start of binominal nomenclature as recognized by the International Commission on Zoological Nomenclature) names were, in fact, Linnaean – noted by Linnaeus in earlier editions of *Systema Naturae*, *Fauna Svecica* (1746), the theses published as part of the *Amenititates Academicae*, Volume 1 (1749), the published catalogue of the Museum Adolphi Friderici (1754), Hasselquists’s *Iter Palestinum* (1757, with new species described by Linnaeus), Linnaeus’s “Travels,” or in his papers published in scientific periodicals. In total 72 species were based entirely on material examined by Linnaeus and/or described by him and his students in theses or other published works (see Smit 1979 and Adler 1989 for the contribution of Linnaeus to the dissertations of his students). Thus, 110 species descriptions referred to one or more earlier non-Linnaean sources. Forty-one works by 37 different authors, exclusive of Linnaeus and his students, spanning two centuries (1547–1756) were cited in the synonymies of the herpetological species described in the 10th edition of *Systema Naturae*. These include 25 authors whose works appeared in Latin (or in dual language texts, one of which was Latin, or in simultaneous published editions in multiple languages, one of which was Latin), six in English (including one with a dual French text), two each in French and German, and one each in Italian and Spanish (Table 1). Linnaeus’s abilities in language were limited to Swedish and Latin (Lindroth 1979; Skuncke 2008), although it must be assumed that, like many modern herpetologists, he could muddle through works in other languages when necessary.

Linnaean Names and Pre-Linnaean Sources in Herpetology

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Abstract. One hundred ten of 182 species of amphibians and reptiles described in *Systema Naturae X* were based, at least in part, on Linnaeus’s indications to older literature and specimens described and/or figured therein. Such specimens cited in pre-Linnaean sources have the status of holotypes or syntypes and are often important for resolving difficult taxonomic and nomenclatural issues. Twenty-three of Linnaeus’s herpetological species were based solely on literature indications of pre-1758 works not authored by Linnaeus or his students. The 13 authors cited by Linnaeus for these 23 names are briefly profiled and the status of each of the names and its associated type(s) are considered. Albertus Seba was the most frequently cited of Linnaeus’s sources, followed by Laurentius Theodorus Gronovius. Although only one “pre-Linnaean” Linnaean type of this sort is demonstrably extant, designation of lectotypes from among the available secondary syntypes of Linnaeus can and has provided stability to current usage of well established names. A previous neotype designation for *Anguis reticulata* is considered invalid and a lectotype is chosen for this taxon.

Keywords: Linnaeus, *Systema Naturae*, Albertus Seba, zoological nomenclature, lectotype, nomenclatural stability.

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Among the authors referenced by Linnaeus (1758), Seba, with 81 citations, is the most cited, followed by Gronovius (34), Ray (17), Aldrovandi (12), Gessner (8), Catesby and Bradley (both 7), and Jonstonus and Olearius (both 6). All other authors were cited for four or fewer taxa (Table 1). Many of the indications were for just a few well-known taxa that had been often mentioned in the pre-Linnaean literature: e.g., *Testudo mydas* = *Chelonia mydas*, *Lacerta crocodilus* = *Caiman crocodilus*, *Lacerta chamaeleon* = *Chamaeleo chamaeleon*, *Lacerta igvana* = *Iguana iguana*. Indeed, seven sources were cited by Linnaeus exclusively for one or more of these species. The titles and editions of the works cited by Linnaeus have been summarized by Wheeler (1979) and Dundee (1994). The AnimalBase website (www.animalbase.uni-goettingen.de) likewise lists and provides links to digitized versions of the literature used by Linnaeus. Further comments on the particular editions of the works consulted by Linnaeus are here provided as footnotes to Table 1.

At least some of these pre-Linnaean sources are of nomenclatural relevance. Under the *International Code of Zoological Nomenclature* (ICZN 1999) new names published before 1931 must be accompanied by a description, definition, or an *indication* [italics mine] – “a bibliographic reference to a previously published description even if the description or definition is contained in a work published before 1758” (Article 12.2.1). Further, “syntypes may include … specimens … which form the bases of previously published descriptions or illustrations upon which the author founded the new nominal species-group taxon” (Article 73.2.1). Thus, the specimens described and/or illustrated in the earlier works indicated by Linnaeus are to be considered as type specimens (syntypes if among multiple specimens cited, holotypes if the sole specimen associated with the name proposed). Although the type status of material from such indicated works is routinely ignored by many systematists, it may have bearing on taxonomic and nomenclatural issues. The value of these provisions of the *Code* for providing stability to herpetological names has been discussed by Dubois and Ohler (1995 “1994”, 1997a “1996”, 1997b “1996”).

In some instances Linnaean specimens represented by extant type material in Stockholm or Uppsala are non-conspecific with those syntypes in such indicated works. Moravec et al. (2006) demonstrated that the specimens illustrated and described by Seba (1734) and Aldrovandi (1637) and allocated to the scincid lizard species *Lacerta aurata* = *Trachylepis aurata* by Linnaeus (1758) are, in fact, assignable to other genera or families. Consequently they designated one of Linnaeus’s own specimens that is consistent with the existing application of the name as the lectotype of the species, thus stabilizing current usage of the name. In this example, the action of Moravec et al. (2006) stabilized the *de facto* nomenclatural situation. However, instability linked to Linnaean types themselves can also be rectified through reference to indicated syntypes (secondary syntypes *sensu* Dubois and Ohler 1997a “1996”). For example, Dubois and Ohler (1997b “1996”) detailed such a case with the example of *Rana arborea* = *Hyla arborea*. Another case in point involves the identity of several widely used scincid lizard names. Mausfeld et al. (2002), based on phylogenetic data, advocated the subdivision of the widespread scincid genus *Mabuya*. They identified *Euprepis* Wagler, 1830 as the oldest available name for the clade comprising African members of this group. From the species assigned by Wagler (1830) to *Euprepis*, they selected *Lacerta punctata* Linnaeus, 1758 as the type species. Based on Andersson (1900) the two type specimens that originated from the Swedish King Adolf Fredrik (1710–1771) (now NRM 135) cited by Linnaeus are referable to the common South African species until recently universally called *Mabuya homalocephala* (Wiegmann, 1828) (e.g., Branch 1998). Acceptance of *Euprepis punctatus* as the valid name of
this taxon would have had two unfortunate consequences for nomenclatural stability; not only would it destabilize an established name for the African species, but it would also affect a common Asian species of skink — *Lacerta punctata* Linnaeus, 1758 has also been considered to be referable to the species widely known as *Lygosoma punctatum* (Bauer et al. 2003). If the name *Lacerta punctata* were to be associated with the African skink, then *Lygosoma interpunctatum* (Gmelin, 1789), a name that has not been used as valid for more than 200 years would be the next available name for the Asian taxon. However, in addition to the two syntypes of *Lacerta punctata* preserved in Stockholm, Linnaeus (1758) also cited two figures from Seba (1735), thus making the specimens illustrated part of the syntype series. Although these specimens have not been traced, this has no bearing on their status as types. Based both on the illustrations provided by Seba (1735) and his description, it may be assumed that these specimens represent the species currently known as *Lygosoma punctatum*. Because Mausfeld et al. (2002) did not designate a lectotype for *Lacerta punctata*, Bauer (2003) selected one of the Seba specimens as lectotype, linking the name *Lacerta punctata* to the Asian skink and stabilizing the usage of the commonly employed specific epithets for both species involved.

The examples of *Rana arborea*, *Lacerta aurata* and *L. punctata* are just three of the 83 species in *Systema Naturae* that were based on Linnaean material (primary syntypes) plus indicated sources (secondary syntypes). Descriptions of four other such taxa — *Rana ocellata*, *Boa hipnale*, *Boa murina*, and *Anguis meleagris* — are without any reference to Linnaeus’s earlier works, and list only the works of others in synonymy. These species were treated in the second volume of the catalogue of the Museum Regis Adolphi Friderici (Linnaeus 1764a). This work was completed at the same time as the first volume, published in 1754, but owing to financial difficulties it was not published until a decade later (Andersson 1899); thus, no explicit reference to specimens in this portion appears in the 10th edition of *Systema Naturae* (although ‘Mus. Ad. Frid. 2’ was cited, without page reference, in the accounts for *Coluber Padera*, *Coluber viridissimus*, and *Anguis laticauda*). Nonetheless, Linnaeus clearly had access to specimens of these species prior to 1758 and his descriptions in *Systema Naturae* certainly were based, in part, on Swedish types. Putative types in Stockholm, however, survive only for *Rana ocellata* (Andersson 1900; Heyer et al. 2006) and *Boa murina* (Andersson 1899; McDiamid et al. 1999), although in the case of the frog, neither the Linnaean specimen, nor the paralectotype figured by Browne (1756) and indicated by Linnaeus, are conspecific with the species currently known as *Leptodactylus ocellatus* (Heyer et al. 2006).

Another 23 species described in *Systema Naturae*, many from the Americas, were previously described or illustrated only in “non-Linnaean” works (Table 1). These have no type specimens in Swedish collections and Linnaeus’s knowledge of them would have relied heavily or solely on secondary syntypes described and/or illustrated in previously published sources. In the remainder of this paper I will briefly introduce these authors and their works and summarize the status of their specimens which, by indication, serve as types linked to names proposed by Linnaeus (1758).

**PRE-LINNAEAN AUTHORS**

The works of 13 different authors were indicated by Linnaeus (1758) as sources for herpetological descriptions for which there are no primary syntypes. These authors (and the number of species for which they are cited) are: Seba (10), Gronovius (6), Ray (4), Edwards (3), Catesby (3), Browne (2), Gessner (2), Scheuchzer (2), Grew (1), Worm (1), Feuillée (1), Hernández (1), and Rösel
von Rosenhof (1). Detailed biographies exist for most of these and Adler (1989, 2007) has provided concise accounts for those who made significant herpetological contributions. I here provide only skeletal biographic for these authors, arranged chronologically.

**Francisco Hernández** [de Toledo] (1514-1587). Hernández was a Spanish medical doctor who became the personal physician to King Philip II. Already known for his study of medicinal plants, he was sent in 1571 on a mission to Mexico where he traveled the country for seven years, collecting plants and other natural history objects and interviewing local people about their potential uses. His findings were published posthumously in 1615 in Spanish, but the 1651 Latin version, *Rerum Medicarum Novae Hispaniae Thesaurus* or *Nova Plantarum, Animalium et Mineralium Mexicanorum Historia* is the edition to which Linnaeus (1758) had access and referred.

**Conrad Gessner** [= Gesner = Gesnerus; see Adler 1989] (1516-1565). Gessner’s *Historia Animalia* was the first printed encyclopedic treatment of the animal kingdom and was illustrated throughout by woodcuts. Largely a compiler and organizer of existing information, Gessner’s herpetological descriptions were based on even earlier sources as well as personal observations. Linnaeus drew on two of the volumes, *Quadrupedibus Oviparis* (1586 and subsequent editions) and *De Piscium et Aquatilium Animantium Natura* (1554 and later editions), chiefly in reference to European species (see Table 1, footnote 3).

**Ole Worm** (1588-1654). Worm was a Danish physician and antiquary who was broadly trained at intellectual centers across Europe. In addition to his medical activities he generated scholarly writings on Scandinavian runes, and on numerous topics in natural history (Randsborg 1994). He possessed a large and diverse private cabinet of curiosities that he described and interpreted in his most well-known work, *Museum Wormianum* (1655), which was cited by Linnaeus (1758). Worm’s collection was purchased after his death and became part of the Royal Danish Kunstkammer.

**John Ray** (1627-1705). Ray was an English botanist and zoologist who made fundamental contributions to the systematics of both animals and plants, establishing the first modern system of classification based on the whole structure of organisms (Adler 2007). Ray’s contributions laid the foundations for Linnaeus’s later work and were frequently cited by him. His herpetological contributions appeared in his *Synopsis Methodica Animalium Quadrupedum et Serpentium Generis* (1693).

**Neimiah Grew** (1641-1712). Grew was an English botanist and physician who was a member and later secretary of the Royal Society, as well as editor of its *Proceedings*. His writings were chiefly botanical, but spanned many aspects of science (Lefanu 1971). His chief zoological contribution, and that cited by Linnaeus (1758) was his 1681 *Musaeum Regalis Societatis*.

**Louis Feuillée** [= Feuillet] 1660-1732. Feuillée was a French astronomer, geographer, physicist, and naturalist who was instrumental in mapping the coastline of South America (Howgego 2003). Although he returned to Europe with botanical specimens, he does not appear to have collected zoological material in any systematic fashion. His *Journal des Observations Physiques, Mathematiques et Botaniques* (1714-1725) contains little of herpetological relevance, although the single taxon for which Linnaeus (1758) cited him (*Lacerta caudiverbera*, see below) is among the most enigmatic of all Linnaean names.

**Albertus Seba** (1665-1736). The Dutch pharmacist Seba amassed two of the greatest private collections of natural history specimens ever assembled. The first was sold to Peter the Great of Russia in 1716 (not 1717 as often reported; Driessen-van het Reve 2006). The
second, which was visited by Linnaeus during his stay in the Netherlands (Boerman 1979), formed the basis for Seba’s *Thesaurus* (1734-1765), one of the largest and most attractive and valuable of all published works in natural history (Holthius 1969; Bauer 2002). Seba’s illustrations served as the basis for more of Linnaeus’s descriptions than any other “pre-Linnaean” author. Although many of the illustrations are unambiguously referable to known taxa, others are unidentifiable. The specimens illustrated in the Thesaurus were dispersed in 1752 when Seba’s collection was auctioned by his heirs (Engel 1961). The majority was purchased by dealers acting on behalf of private buyers. Ultimately specimens reached national collections as nobles and wealthy citizens donated or sold their cabinets to royal or other state-sponsored museums. Seba specimens are known to be present in collections in St. Petersburg, Amsterdam, London, Leiden, and Paris (Boeseman 1970; Juriev 1981; Thireau et al. 1998). However, perhaps the largest group of Seba specimens may be present in Berlin. These specimens came from the collection of Graf von Borcke zu Hueth, donated to the Zoological Museum in 1818 (Merrem 1821). Von Borcke had in turn purchased the collection from Janssen in Düsseldorf, who had obtained it from natural history dealers following the auction of Seba’s collection (Boeseman 1970). Approximately 100 specimens from von Borcke are still present in Berlin and these are currently being investigated for their ties to Seba (Bauer and Günther, in prep.).

**Johann Jakob Scheuchzer** (1672-1733). Scheuchzer was a Swiss naturalist, historian, and physician who made contributions in many fields and maintained an extensive network of correspondents and specimen trading partners across Europe (Fischer 1973). His masterwork was the *Physica Sacra*, or “Copper Bible,” a huge illustrated work of more than 750 plates, published over five years (1731-1735), that depicted the natural history of the Bible (Müsch 2000). Rather incongruously, however, 24 of the plates depict 67 “snakes” (amphisbaenians are included) from the herpetological collection of the Linck family in Leipzig (Seifert 1934; Beyrich 1994; Budig 1999b).

**Mark Catesby** (1683-1749). Catesby was an English naturalist who explored the southern colonies of British North America as well as Spanish Florida and the Bahamas during two extensive trips (1712-1719 and 1722-1726) (Adler 2007). He recorded his observations in *The Natural History of Carolina, Florida, and the Bahama Islands* (1729-1747 and subsequent editions), for which he etched the 220 folio-sized plates himself. Linnaeus drew heavily on Catesby’s work for American species, including amphibians and reptiles.

**George Edwards** (1694-1773). Edwards was an English ornithologist and librarian of the Royal College of Physicians in London. His *Natural History of Birds* (1743-1751) and later works established him as a world leader in the study of birds and he was a regular correspondent of Linnaeus as well as a frequently cited source for vertebrates in *Systema Naturae* (Mason 1992).

**August Johann Rösel von Rosenhof** (1705-1759). Although best known as an entomologist, Rösel produced one of the most sumptuous and often copied herpetological works of all time, *Historia Naturalis Ranarum Nostratium* (1753-1758), with dual Latin/German text and 24 hand colored plates and an equal number of uncolored key plates. A planned companion volume on lizards (including salamanders) was never completed (Leydig 1886; Adler 1989; Köhler 2005), but the associated plates have recently been published (Niekisch 2009). Rösel’s natural history observations were exact and detailed and the quality and accuracy of his illustrations remained unsurpassed for more than a century.

**Patrick Browne** (1720-1790). Browne was an Irish physician and botanist who traveled
widely in the West Indies and ultimately settled in Jamaica. He carried on a correspondence with Linnaeus and his *A Civil and Natural History of Jamaica* (1756, 1789) was often cited in *Systema Naturae* (Nelson 1997).

**Laurentius Theodorus Gronovius** (1730-1777). Gronovius was a Dutch lawyer, naturalist, and collector from a prominent family of German origin. His herpetological contributions were incidental to his strong interest in ichthyology, to which he made contributions in the field of preservation techniques, as well as systematics. Linnaeus’s (1758) herpetological indications to Gronovius refer to the herpetological portion of his *Museum Ichthyologicum* (1754, 1756). He was a regular correspondent of Linnaeus. The bulk of his extant ichthyological collection is in the Natural History Museum (London) (Wheeler 1958).

**LINNAEAN NAMES BASED EXCLUSIVELY ON SECONDARY SYNTYPES**

The 23 herpetological names from *Systema Naturae X* that are based on indicated non-Linnaean works only (or, for which there is no direct evidence of material examined by Linnaeus himself), refer to a diversity of taxa, including some of the most well-known species of amphibians and reptiles. Some have been the topic of extensive nomenclatural debate, whereas others have not previously been considered in any detail. I have attempted to clarify the identity of the type specimens of each of these taxa and have summarized previous considerations of the status of these names and their associated types. Names are discussed in the order in which they appear in *Systema Naturae*. Literature sources indicated by Linnaeus (1758) are noted in square brackets after each name.

*Testudo caretta* [Ray, Gronovius, Catesby, Browne] = *Caretta caretta* (Linnaeus, 1758) *fide* Fritz and Havaš (2007): King & Burke (1989) indicated that no type had been designated and Wallin (1985) stated that the name was based entirely on literary sources for which there were no surviving specimens, a view first expressed by Parker (1939). Catesby’s plate 39 and Gronovius’s specimen(s) both explicitly reference particular specimens and at least these animals must be considered as syntypes. Although Gronovius’s fish collection ultimately was obtained by the British Museum of Natural History (now The Natural History Museum, London) (Wheeler 1958), the fate of the herpetological portion of the collection is uncertain.

*Testudo orbicularis* [Ray] = *Emys orbicularis* (Linnaeus, 1758) *fide* Fritz and Havaš (2007): King & Burke (1989) considered the type “unknown” and Iverson (1992) referred to it as “not located.” Ray’s (1693) comments do not explicitly refer to specific individuals. Any such specimens that may have been seen by Ray cannot be identified and are certainly not extant. Fritz (1992, 1994), recognized this and designated a neotype for the species, necessitated by the need to stabilize the status of the nominotypical form of this polytypic species.

*Testudo pusilla* [Ray, Worm, Grew] = *Testudo graeca* Linnaeus, 1758 *fide* Fritz and Havaš (2007): As this name has long been regarded as a junior synonym of *T. graeca*, there has been little effort to identify the type specimens. Ray’s (1693) reference is not to a specific, identifiable individual, but both Worm (1655) and Grew’s (1681) references are to particular specimens and these, now lost or unlocated, must be regarded as syntypes. Grew mentioned three specimens of “chequered shell from Virginia,” one of which was figured. Worm’s reference appeared on p. 317 of his book, not p. 313 as given by Linnaeus (1758).

## TABLE 1. Authors of works cited by Linnaeus in the synonymies\(^1\) of the herpetological section of *Systema Naturae X* and the taxa for which indications are provided. Taxa based entirely upon secondary sources (i.e., for which there are no Linnaean type specimens or citations to earlier Linnaean works) are indicated in bold and are discussed more fully in this paper.

<table>
<thead>
<tr>
<th>Author and Dates of Work Cited</th>
<th>Language</th>
<th>Citations by Linnaeus</th>
<th>Taxa Cited</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aldrovandii (1613?; 1637 or 1645; 1640)(^2)</td>
<td>Latin</td>
<td>12</td>
<td><em>Testudo mydas, Lacerta crocodilus, L. agilis, L. chamaeleon, L. salamandra, L. aurata, L. chalcides, Rana temporaria, Coluber ammodytes, C. berus, C. chesrea, Anguis fragilis</em></td>
</tr>
<tr>
<td>Gessner (1586; 1558, 1604 or 1620)(^3)</td>
<td>Latin</td>
<td>8</td>
<td><em>Testudo mydas, Lacerta crocodilus, L. salamandra, L. aquatica, Rana bufo, R. temporaria, R. hyla, R. arborea</em></td>
</tr>
<tr>
<td>Catesby (1734-1743 or 1754)(^4)</td>
<td>English/French</td>
<td>7</td>
<td><em>Testudo caretta, Lacerta crocodilus, L. igvana, L. bullaris, L. fasciata, Coluber nebulatus, C. mycterizans</em></td>
</tr>
<tr>
<td>Bradley (1721)</td>
<td>English</td>
<td>7</td>
<td><em>Testudo mydas, Draco volans, Rana pipa, R. bufo, R. temporaria, Crotalus horridus, C. ahaetulla</em></td>
</tr>
<tr>
<td>Johnstonus (1650 or 1657)(^5)</td>
<td>Latin</td>
<td>6</td>
<td><em>Lacerta crocodilus, L. chamaeleon, L. salamandra, L. igvana, Rana bufo, R. temporaria</em></td>
</tr>
</tbody>
</table>
### TABLE 1. Continued ...

<table>
<thead>
<tr>
<th>Author and Dates of Work Cited</th>
<th>Language</th>
<th>Citations by Linnaeus</th>
<th>Taxa Cited</th>
</tr>
</thead>
<tbody>
<tr>
<td>Olearius (1674)</td>
<td>German</td>
<td>6</td>
<td>Testudo mydas, Lacerta crocodilus, L. chamaeleon, L. salamandra, L. stincus, L. igvana</td>
</tr>
<tr>
<td>Bellonius (1553, 1605)'</td>
<td>Latin</td>
<td>4</td>
<td>Lacerta crocodilus, L. chamaeleon, Coluber ammodytes, C. cerastes</td>
</tr>
<tr>
<td>Bontius (1658)'</td>
<td>Latin</td>
<td>4</td>
<td>Draco volans, Lacerta crocodilus, L. gecko, L. igvana</td>
</tr>
<tr>
<td>Edwards (1751)</td>
<td>English</td>
<td>4</td>
<td>Testudo graeca, T. carolina, Lacerta turcica, L. ameiva</td>
</tr>
<tr>
<td>Worm (1655)</td>
<td>Latin</td>
<td>4</td>
<td>Testudo geometrica, T. pusilla, Lacerta ameiva, L. igvana</td>
</tr>
<tr>
<td>Maregrave (1658)'</td>
<td>Latin</td>
<td>3</td>
<td>Testudo mydas, Lacerta crocodilus, L. igvana</td>
</tr>
<tr>
<td>Browne (1756)</td>
<td>English</td>
<td>3</td>
<td>Testudo caretta, Rana ocellata, Anguis lumbricalis</td>
</tr>
<tr>
<td>Grew (1681)</td>
<td>English</td>
<td>3</td>
<td>Testudo mydas, T. geometrica, T. pusilla</td>
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<td>Sloane (1725)</td>
<td>English</td>
<td>3</td>
<td>Lacerta crocodilus, L. ameiva, L. igvana</td>
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<tr>
<td>Besler [Besler and Besler] (1716)</td>
<td>Latin</td>
<td>3</td>
<td>Lacerta crocodilus, L. chamaeleon, L. stincus</td>
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<td>Clusius (1605)'</td>
<td>Latin</td>
<td>2</td>
<td>Lacerta ameiva, L. igvana</td>
</tr>
<tr>
<td>Merian (1719)'</td>
<td>Latin</td>
<td>2</td>
<td>Lacerta crocodilus, Rana paradoxa</td>
</tr>
<tr>
<td>Scheuchzer (1735)</td>
<td>Latin/</td>
<td>2</td>
<td>Boa scytale, Anguis reticulata</td>
</tr>
<tr>
<td>Vallisnieri (1733)</td>
<td>Italian</td>
<td>2</td>
<td>Lacerta crocodilus, Rana pipa</td>
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<tr>
<td>Columna (1606)'</td>
<td>Latin</td>
<td>1</td>
<td>Lacerta chalcides</td>
</tr>
<tr>
<td>Feuillé (1714)</td>
<td>French</td>
<td>1</td>
<td>Lacerta caudiverbera</td>
</tr>
<tr>
<td>Hernández (1651)</td>
<td>Latin</td>
<td>1</td>
<td>Lacerta orbicularis</td>
</tr>
<tr>
<td>Jacobaeus (1696)</td>
<td>Latin</td>
<td>1</td>
<td>Lacerta igvana</td>
</tr>
<tr>
<td>Kaempfer (1712)</td>
<td>Latin</td>
<td>1</td>
<td>Coluber naja</td>
</tr>
<tr>
<td>Bonanni (1709)</td>
<td>Latin</td>
<td>1</td>
<td>Lacerta chamaeleon</td>
</tr>
<tr>
<td>Matthioli (1570)</td>
<td>Latin</td>
<td>1</td>
<td>Lacerta salamandra</td>
</tr>
<tr>
<td>Nieremberg (1635)</td>
<td>Latin</td>
<td>1</td>
<td>Lacerta igvana</td>
</tr>
<tr>
<td>Oviedo y Valdés (1526 or 1535 or 1547)</td>
<td>Spanish</td>
<td>1</td>
<td>Lacerta igvana</td>
</tr>
<tr>
<td>Piso (1658)'</td>
<td>Latin</td>
<td>1</td>
<td>Testudo geometrica</td>
</tr>
<tr>
<td>Redi (1675)</td>
<td>Latin</td>
<td>1</td>
<td>Lacerta igvana</td>
</tr>
<tr>
<td>Roessel von Rosenhof (1754)</td>
<td>Latin/</td>
<td>1</td>
<td>Rana esculenta</td>
</tr>
<tr>
<td>Tournefort (1717)</td>
<td>French</td>
<td>1</td>
<td>Lacerta stellio</td>
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<tr>
<td>Valentini (1704)</td>
<td>German</td>
<td>1</td>
<td>Lacerta chamaeleon</td>
</tr>
<tr>
<td>Vincent (1725)</td>
<td>Latin</td>
<td>1</td>
<td>Rana pipa</td>
</tr>
</tbody>
</table>

1A 41st reference and 38th author, Lémery (1716) is also cited by Linnaeus (1758) for Anguis fragilis, but not in the synonymy. In the synonymy of Testudo caretta, yet another author — Rochefort (1658) — is indirectly cited as reference is made to Catesby’s reference to this work.
TABLE 1. Continued ...

2 Because of the multiple editions of Aldrovandi’s work, there is a confusion regarding the dating of the particular versions used by Linnaeus. Dundee (1994) suggests that Linnaeus’s reference to “Ald. aquat.” refers to the 1613 edition of the volume dealing with fish and whales, but notes that there is a non-correspondence of at least one page citation. Both Dundee (1994) and Moravec et al. (2006) cite 1637 as the date of the edition of “Ald. quad.” but AnimalBase (www.animalbase.uni-goettingen.de) cites the 1645 edition of this work as that used by Linnaeus.

3 Dundee (1994) cites the 1586 edition of De Quadrupedibus Oviparis as that used by Linnaeus. As noted in the account of Rana hyla, it is ambiguous as to which edition of De Piscium et Aquatilium Animantium Natura Linnaeus cited, AnimalBase (www.animalbase.uni-goettingen.de) cites the 1558 Zürich edition, but Myers and Stothers (2006) indicate the editions of 1604 or 1620 as most likely.


5 AnimalBase (www.animalbase.uni-goettingen.de) cites the Frankfurt am Main edition of 1650, whereas Dundee (1994) cites the Amsterdam edition of 1657. Both editions were probably in Linnaeus’s library (pers. comm., R. Wahlgren, 23 March 2008).

6 Dundee (1994) specifically mentioned the Antwerp edition of Bellonius (1605), but indicated that Linnaeus had used an interpretive edition of Belon’s work, Clusius (1605). In contrast, J.L. Heller (in Dundee 1994) stated that the actual edition consulted by Linnaeus was a 1609 French translation, of which no bibliographic trace appears to exist and AnimalBase gives Bellonius (1554) as the corresponding work for Linnaeus’s “Bellon. itin.” However, as the 1605 Antwerp edition was owned by Linnaeus himself (Linnean Society of London 1925), it seems likely that this was the version he consulted.

7 The works of Bontius, Margrave, and Piso cited by Linnaeus (1758) were all published as part of a single revised volume under Piso’s name in 1658. According to Rookmaaker (1998) this is the version of Bontius consulted by Linnaeus. However, Bontius’s work was published separately in 1642 and an earlier edition of Margrave and Piso appeared in 1648 (see Dundee 1994).

8 Dundee (1994) gave 1705 as the date of Merian’s work on Suriname. However, the work was printed in several editions and that containing the references to Lacerta crocodilus and Rana paradoxa appeared for the first time in 1719.

9 AnimalBase (www.animalbase.uni-goettingen.de) gives the edition used by Linnaeus as 1616. Dundee (1994) was uncertain of the year of this work, but noted that the 1606 edition was the earliest. Linnaeus’s page citation of Columna is consistent with the 1616 edition; I was unable to examine the 1606 edition.

10 AnimalBase (www.animalbase.uni-goettingen.de) gives the probable edition used by Linnaeus as 1535 or 1526. Dundee (1994) cites the 1547 edition.
204) was the type of this species. Bour (1987 “1986”) explicitly referred to this specimen, now lost, as the holotype and reprinted Edwards’ figure.

Testudo Carolina [Edwards] = Terrapene carolina (Linnaeus, 1758) fide Fritz and Havaš (2007): King & Burke (1989) considered the type “unknown” and Iverson (1992) referred to it as “not located.” Edwards (1751), in the only work indicated by Linnaeus, figured a specimen on plate 205 (Fig. 1) and the individual described and pictured should be considered as the holotype of the species, but this does not appear to have been explicitly noted in the literature. Like Edwards’ other herpetological specimens, the whereabouts of this specimen are unknown.

Lacerta caudiverbera [Feuillée, Seba] [see below for a discussion of identity]: This taxon has been the basis for much speculation. Feuillée (1714) and Seba (1735) each illustrated an animal indicated by Linnaeus (1758) in his description. In the former instance it was supposed to have originated from Chile and in the latter from Arabia. Russell and Bauer (1988) and Bauer and Russell (1989) considered the identity of these two animals, reproducing the original illustrations and accompanying text and providing synonymies for each. In each instance these animals, and thus Lacerta caudiverbera, had been considered by at least some authors to be a member of the Malagasy gekkonid genus Uroplatus. However, Boulenger (1885) considered both to be mythical. At least Feuillée’s “salamandre aquatique et noire du Chili,” however, was clearly based on a real specimen observed by the author (see Bauer and Russell 1989), although the accompanying illustration does not match this description particularly well. Although they considered it possible that an anuran larva might be implied, Bauer and Russell (1989) thought it most likely that Feuillée’s (1714) text referred to some sort of iguanian, perhaps a Basiliscus. Although neither this, nor any other iguanian bearing a resemblance to Feuillée’s animal occurs in the region of Concepcion, Chile, where Feuillée claimed to have caught and observed the specimen, it is possible that he did examine B. basiliscus during the period he spent in northern South America (1704-
1706) (Howgego 2003). Bauer and Russell (1989) considered Seba’s (1735) description to be at least partly consistent with *Uromastyx* sp. However, the accompanying illustration (pl. 62, fig. 9) is highly fanciful and unlike Seba’s other lizard representations, some of which are quite recognizable, does not seem to have been based on a real specimen. This is explained by Seba’s (1735:109) comment that he had sent the only specimen he had ever seen to Peter the Great as part of the sale of his first collection (see also Driessen-van het Reve 2006). Thus, *Lacerta caudiverbera* appears to be composite, with its two identifiable syntypes being a specimen collected by Feuillée (here posited to be *Basiliscus basiliscus*, probably from coastal Venezuela) and another (probably *Uromastyx* sp.) from Seba’s first natural history cabinet and subsequently in the Kunstkammer of Peter the Great of Russia. Feuillée (1714) makes it clear that his specimen was not preserved or returned to France with him. Peter the Great’s collection of Seba material appears to have mostly been lost or destroyed over the last 290 years, but at least one specimen, a headless anaconda (*Eunectes murinus*) is still present and on display in the Zoological Institute of the Russian Academy of Sciences in St. Petersburg (Driessen-van het Reve 2006).

Myers (1962) and Donoso-Barros and Cei (1962), however, associated the Feuillée-based name *Caudiverbera peruviana* Laurenti, 1768 (and, by extension, *Lacerta caudiverbera* Linnaeus, 1758 in part) with the larva of the Chilean calyptocephalellid (formerly leptodactylid) frog *Calyptocephalella gayi* (Duméril and Bibron, 1841). On this basis Myers (1962) argued that the correct name for this frog was *Caudiverbera caudiverbera*. Myers and Stothers (2006), however, considered that Feuillée’s (1714) drawing and description were a composite of a Chilean tadpole and one or more unknown lizards and as such the descriptions based thereon constitute hypothetical concepts, excluded from the provisions of zoological nomenclature, under the International Code of Zoological Nomenclature (ICZN 1999: Art. 1.3.1). These authors, therefore, reinstated *Calyptocephalella gayi* as the proper name for the Chilean frog in question, an action followed by Frost (2007). Myers and Stothers (2006) considered the status of *Caudiverbera aegyptiaca* Laurenti, 1768, based on Seba’s (1735) plate to be “an enigma.”

*Lacerta scutata* [Seba] = *Lyriocephalus scutatus* (Linnaeus, 1758) *fide* Smith (1935): Smith (1935) acknowledged that the description was based on the specimen figured by Seba (1734) on pl. 109, fig. 3. This specimen, currently unlocated, is therefore the holotype.

*Lacerta orbicularis* [Hernández, Ray, Seba] = *Phrynosoma orbiculare* (Linnaeus, 1758) *fide* Smith and Taylor (1950): Smith and Taylor (1950) considered the type of this species to be “presumably the unnumbered figure in Hernández [1651].” The specimens indicated from Seba (1734), p. 134, pl. 83, figs. 1-2 were not mentioned by Smith and Taylor (1950), but must also be considered syntypes. It is not possible to associate any particular specimens with Ray’s mention of this lizard, which itself is based on Hernández.

*Lacerta aquatica* [Gessner, Seba, Gronovius] = *Lissotriton vulgaris* (Linnaeus, 1758) *fide* Frost (2007): Linnaeus’s indication to Gessner is to text on page 31 and does not refer to one or more specific individuals. The identifiable syntypes are thus the specimen(s) in the museum of Gronovius (1756), and the individual illustrated by Seba (1735) in figure 7 of plate 12 and discussed on page 15, none of which are confirmed as extant.

*Lacerta basiliscus* [Seba] = *Basiliscus basiliscus* (Linnaeus, 1758) *fide* Lang (1989): Linnaeus (1758) clearly referred to a single illustration in Seba (1734) in his description of the taxon. This specimen is thus the holotype. The same specimen was discussed by Daudin (1802), who used it as the type for *Basiliscus*...
mitratus, and subsequently by Duméril and Bibron (1837). It was confirmed as originating from Seba’s collection and verified to be present in Paris by Duméril (1851), Guibé (1954), and Brygoo (1989), who provided the registration number MNHN 780. These authors, however, had not recognized that the type of B. mitratus Daudin, 1802 was also the type of B. basiliscus Linnaeus, 1758. This was noted, however, by Taylor (1956), Lang (1989), and Thireau et al. (1998). This specimen is one of 12 Seba specimens that are probable Linnaean types from Seba’s collection that have thus far been located in Paris (Thireau et al. 1998), but the only one for which Seba was the sole source. The Seba specimens in Paris were obtained as a result of the confiscation of the Stathouder (Prince of Orange) collection by the French Republic in 1794 (Thireau et al. 1998; Bauer 2002; Daszkiewicz and Bauer 2003).

**Lacerta strumosa** [Seba] = *Anolis lineatus* Daudin, 1802 *fide* Savage and Guyer (1991): This name was considered unassignable to any particular known species by Brown (1908). According to Savage and Guyer (1991), the holotype of *Anolis lineatus* Daudin, 1802 is a specimen (MNHN 795) originating from Seba’s collection and is the animal illustrated in Seba (1735, pl. 20, fig. 4) and thus also the holotype of *L. strumosa* Linnaeus, 1758. Savage and Guyer (1991) argued that the younger name *A. lineatus* should be retained for the species in question because the epithet *strumosa* had not been used as a valid name in more than 175 years and that its adoption would severely disrupt stability. Under Article 23.9 of the present edition of the *International Code for Zoological Nomenclature* (ICZN 1999), the older name would be considered a *nomen oblitum* and the younger a *nomen protectum.* Duméril (1851) actually indicated “origine inconnue: du Cab. De Séba?” and Guibé (1954) noted only “origine inconnue.” Neither of these authors nor Brygoo (1989), explicitly linked MNHN 795 to the name *Lacerta strumosa.* Holm (1957) mentioned a dry specimen of *Lacerta strumosa* (Nr. 55) in Uppsala that was, according to Thunberg, originally from the Museum Gustavi Adolphi. Wallin (2001) also referred to an extant stuffed preparation of this taxon from the Gustav IV Adolf collection (#286), presumably the same individual. This collection was donated to the University of Uppsala by King Gustav IV Adolf during the period of Thunberg’s tenure there, long after Linnaeus’s death. The material mostly originated from the collection of Gustav Adolf’s grandmother, Queen Lovisa Ulrika, which had been studied by Linnaeus, but the donation also included a smaller number of vertebrates from the collections which originally had been kept at the castle of Ulriksdal and which were the property of King Adolf Fredrik (Holm 1957). The dry specimen of *Lacerta strumosa* could be one of these specimens. The majority of the king’s collection had earlier been transferred to the Swedish Academy of Sciences in Stockholm (Holm 1957). The king’s collection had been studied by Linnaeus, who did not explicitly list *Lacerta strumosa* among the selection of animals in the two published catalogues (Linnaeus 1754, 1764a). The catalogue of the queen’s collection was not published until 1764 (Linnaeus 1764b), but the manuscript was completed and referred to by Linnaeus in the 10th edition of *Systema Naturae* (Wallin 2001), although no vertebrate specimens from the Museum Ludovicae Ulricae were noted by Linnaeus (1758). As Linnaeus did not list the specimen in any of these collections there is no direct evidence that Linnaeus actually saw or studied the extant specimen in Uppsala; therefore, I believe it should not be considered as part of the type series.

**Lacerta turcica** [Edwards] = *Hemidactylus turcicus* (Linnaeus, 1758) *fide* Kluge (2001): McCoy (1970) indicated “Holotype unknown.” Linnaeus’s sole indication is to Edwards (1751), thus the holotype is the specimen figured on plate 204 of this work, just beneath the holotype of *Testudo graeca.* Although Edwards (1751) clearly thought the animal was a salamander, the figure is suffi-
cient to confirm the specimen’s identity as this common Mediterranean gecko.

*Lacerta anguina* [Seba] = *Chamaesaura anguina* (Linnaeus, 1758)* fide* Wermuth (1969): There appears to be no explicit mention of the status of the types (two specimens figured by Seba 1735, pl. 68, figs. 6-7) of this species. However, the holotype of *Seps monodactylus* Daudin, 1802 (syn. *Chamaesaura anguina*), was stated by Lacépède (1803) to have been derived from the Statthouder collection, which was confiscated from the Netherlands. This collection, in turn, included numerous specimens derived from Seba’s collection (Thireau et al. 1998; Bauer 2002; Daszkiewicz and Bauer 2003), thus it is possible that the holotype of *S. monodactylus* was one of the Linnaean syntypes. Unfortunately, however, the specimen, which was figured both by Daudin (1802) and Lacépède (1803), was not among the specimens recorded by Duméril (1851) and appears to be lost (Brygoo 1985).

*Lacerta bullaris* [Catesby] = *Anolis garmani* Stejneger, 1899 *fide* Russell and Bauer (1991): Linnaeus’s description is based solely on a specimen of *Lacerta viridis jamaicensis* illustrated in plate 66 of Catesby (1743). Stejneger (1899) was unconvinced of the applicability of the name *L. bullaris* to the “great crested *Anolis* of Jamaica” but argued that the name then in use, *Anolis edwardsii* Merrem, 1820 was certainly not applicable for this species. As a result he proposed the name *A. garmani*. Although subsequent authors likewise considered the identity of Catesby’s anole, and thus Linnaeus’s *L. bullaris*, as questionable (Brown 1908; Smith et al. 1963), Stimson and Underwood (1983) argued that the combination of illustrated features and described habits were sufficient to recognize the species intended as *A. garmani*. They further argued, contrary to Smith et al. (1963) that the name should not be considered a *nomen oblitum* and that stability would not be disrupted by recognizing the priority of *Lacerta bullaris* over *Anolis garmani*. Savage and Guyer (1991), however, argued for the retention of *A. gar-

*manii* because the epithet *bullaris* had not been used as a valid name in over a century (except by Stimson and Underwood 1983) and that its adoption would severely disrupt stability.

*Lacerta fasciata* [Catesby] = *Plestiodon fasciatus* (Linnaeus, 1758)* fide* Smith (2005): Taylor (1935) acknowledged that Linnaeus’s description was based on Catesby’s *Lacerta cauda caerulea*, illustrated on plate 67 in Volume 2. Taylor (1935) also mentioned Linnaeus’s reference to Petiver’s *Gazophylacti* (1702-1709), but he is mistaken as this work is not referenced in the herpetological portion of the 10th edition of *Systema Naturae*. Catesby’s specimen is thus the holotype of this taxon. Taylor (1935) also reproduced Catesby’s figure and reviewed the then convoluted nomenclatural history of *P. fasciatus* and similar forms.

*Rana hyla* [Gessner] = *Rana temporaria* Linnaeus, 1758 *fide* Frost (2007): Dubois and Ohler (1997b “1996”) designated the specimen of *Rana gibbosa* figured by Gessner [= Gesner = Gesnerus] in *De Piscium et Aquatilium Animantium Natura* (and reproduced by them) as the lectotype of this taxon. Linnaeus’s specific reference to page 809 indicates that either the second (1604) or third (1620) edition of the work was his reference, but the same illustration was used in the first edition of *De Quadrupedibus Oviparis* (1554) as well (see Myers and Stothers 2006). In this instance referral to the indicated work also resulted in a correction of the synonymy of this form from *Hyla arborea* (with which it had long been associated; see comments in Myers and Stothers 2006) to *Rana temporaria*, although Linnaeus (1766) subsequently listed the Gessner reference in the synonymy of *Rana esculenta* and omitted *R. hyla* from the 12th edition of *Systema Naturae*. Laurenti (1768) based his *Rana campanisona*, long regarded by many as a synonym of *Alytes obstetricans* Laurenti, 1768 (see Frost 2007) on the same source and it is thus an objective junior synonym of *R. hyla* (Myers and Stothers 2006).
Rana marina [Seba] = Rhinella marina (Linnaeus, 1758) *fide* Frost (2007): The holotype is the specimen illustrated by Seba (1734, pl. 76, fig. 1) according to Frost (2007). Thunberg (1787) recorded a single specimen of this species in the Alström-Linné collection in Uppsala (Holm 1957) that might have had status as a type. Although it was subsequently reported as being lost (Lönnberg 1896), Wallin (2001) indicated that the specimen had been mislabeled by Thunberg and this it is actually referable to Rana catesbeiana. I consider it highly unlikely that this specimen was included by Linnaeus in his concept of Rana marina, therefore Seba’s specimen is indeed correctly identified as the holotype.

Rana esculenta [Rösel von Rosenhof] = Pelophylax klepton esculenta = Pelophylax lessonae X Pelophylax ridibundus hybridogen *fide* Frost (2007): Dubois and Ohler (1995 “1994”) designated the specimen of Rana viridis aquatica illustrated by Rösel von Rosenhof (1758; pl. 13, upper figure) as the lectotype of this taxon. Other specimens of this species figured by Rösel von Rosenhof are paralectotypes. Dubois and Ohler (1995 “1994”) cited the Rösel name as Rana viridis aquaticae, but it actually appears as Rana viridis aquatica or, in the genitive, Ranae viridis aquaticae, as in the title of the chapter in which this frog is discussed “Ranae viridis aquaticae proprietates, coitus, generation ….” A specimen from the Alström-Linné collection and identified by Linnaeus as Rana esculenta (Lönnberg 1896; Holm 1957) that was redetermined by Thunberg as Rana arvalis (Lönnberg 1896; Wallin 2001) may or may not have also been a syntype (and now a paralectotype). The whereabouts of Rösel’s original material is unknown and no specimens illustrated in his work have ever been identified. Rösel’s figured amphibians have also served as types for a number of species described by Laurenti (1768). Although generally cited as 1758, the different chapters of the book appeared over a series of years, with the Wasserfrosch (Rana viridis aquatica) in 1754 (Niekisch 2007).

Boa scytale [Scheuchzer, Gronovius] = Eunectes murinus (Linnaeus, 1758) *fide* McDiarmid et al. (1999): Stimson (1969) noted that the types were not traced. McDiarmid et al. (1999) listed the types only as “Gron. Mus.” However, according to Smith and Gloyd (1963), the identification of B. scytale as E. murinus is based on Linnaeus’s own description, not on his indications, which include both Gronovius’s specimen (1756:55) and a specimen illustrated by Scheuchzer (1735) as figure 1 on plate 737 (identified by Linck 1783 as Coluber aesculapiii; nos. 483-484 in the Linck catalogue). These were identified by Duméril and Bibron (1844) as representing the species now called Scaphiodontophis venustissimus (Wied, 1821). Smith and Gloyd (1963) consequently restricted the application of the name Boa scytale to the anaconda. However, it appears that Linnaeus had no specimens at hand and used only Scheuchzer’s (1735) plate and Gronovius’s (1756) description (itself partly based on Scheuchzer) as the basis for his name. This is supported by the fact that Linnaeus quoted Gronovius’s ventral and subcaudal scale counts. Linnaeus (1766) later, however, must have obtained additional material as his revised and expanded description in the 12th edition of Systema Naturae includes a new subcaudal count and differs so significantly from that of 1758 as to be unrecognizable as the same species. He further has added the information “constringit & deglutit Capras, Oves &c.” Thus, there were two syntypes associated with the name Boa scytale. The whereabouts of Gronovius’s specimen is unknown. Scheuchzer’s illustration, like all of the naturalistic snake illustrations appearing on 24 of the 760 plates in the Physica Sacra, was based on a specimen in the collection of the Linck family, three generations of apothecaries in Leipzig. Material in this collection dates back to at least to the 1670 founding of the collection by Heinrich Linck, although it is probable that most of the herpetological material was amassed by Johann Heinrich Linck the elder (1674-1734). The widow of J.H. Linck the younger (1734-1807) sold the
collection, which was ultimately purchased by Fürst Otto Victor I von Schönburg-Waldenburg (1785–1859) in 1839, although not before some material (including herpetological specimens) deteriorated and was destroyed or was sold piecemeal (Seifert 1934; Mohr 1940; Beyrich 1994). The collection was combined with other natural history purchases, but a reorganization of the collections in the 1930s attempted to identify parts of the original Linck collection, many of which remain intact today in the Heimatmuseum und Naturkabineett Waldenburg (Mohr 1940; Budig 1999a). At least some of the specimens illustrated by Scheuchzer are still extant (Bauer and Wahlgren, in prep.), but the syntype of *B. scytale* is not among them. A specimen unambiguously referable to *Eunectes murinus* was figured by Scheuchzer (plate 606A — “Coluber Indicus putorius gryseo-luteus”) and is also now lost.

*Coluber arges* [Seba] = *Nomen dubium* fide McDiarmid et al. (1999): Although long associated with Australian pythons (e.g., Loveridge 1934; Stimson 1969) McDiarmid et al. (1999) list this species as a *nomen dubium* in the synonymy of *Morelia spilota* (Lacépède, 1804). Boulenger (1893) believed that Seba’s illustration, upon which the Linnaean name is based, was not based on a specimen, and he regarded it as a “mythical species.” McDowell (1975) likewise, considered the illustration to represent a mythical snake, or perhaps a poorly rendered subadult *Crotaphopeltis hotamboeia*. Cogger et al. (1983) determined that the name was not applicable to an Australian species and noted that Seba’s plate predated the discovery of eastern Australia by Europeans by 35 years. Linnaeus (1766) corrected the specific epithet to *argus*.

*Anguis lumbricalis* [Seba, Browne, Gronovius] = *Typhlops lumbricalis* fide McDiarmid et al. (1999): Hahn (1980) stated that the holotype had not been traced. McDiarmid et al. (1999) provided the following information: “TYPES(S): Holotype: “Gron. Mus. 2. p. 554. n. 7 [sic].” Based on pl. 86 (fig. 2) in Seba, 1734, Loc. Nat. Thes. Desc. Icon. Exp. 1:178 pp.[137].” However, Linnaeus indicated three sources for the description of this taxon: text page 137 and plate 86, figure 2 from Seba (1734), “Gron. Mus. 2. p. 52. n. 3” and text page 460 and plate 44, figure 1 from Browne (1756). Thus there were three syntypes rather than a single holotype as indicated by McDiarmid et al. (1999).

*Anguis reticulata* [Scheuchzer, Gronovius] = *Typhlops reticulatus* fide McDiarmid et al. (1999): Dixon and Hendricks (1979) stated “Holotype. — None designated (Linnaeus’ 1758 reference to Scheuchzer’s (1735-1738) [sic!] figure suggests that this represents the iconotype” and then designated a neotype for the taxon (RMNH 7660). In fact, as correctly noted by McDiarmid et al. (1999), Linnaeus cited both a Gronovius specimen, and Scheuchzer’s illustration (pl. 747, fig. 4). Thus, there were originally two syntypes. As noted above, Scheuchzer’s material was part of the Link collection, now in Waldenburg. The syntype of *Anguis reticulata*, however, does not seem to be among the surviving specimens from Scheuchzer’s time (Bauer and Wahlgren, in prep). Nonetheless, Scheuchzer’s illustration clearly show’s the diagnostic pale snout and pale tail ring of this species. Dixon and Hendricks (1979) outlined the taxonomic confusion surrounding *Typhlops reticulatus*. All of this, however, is related to the fact that the details of the specimen described by Gronovius (1756) are inconsistent with this or any other New World typhlopidae. Indeed, these authors expressed the belief that Gronovius’s specimen was probably an amphibiaenian.

Of course, the problem of composite type series is widespread and not unique to *Anguis reticulata*. Selection of the specimen illustrated by Scheuchzer as a lectotype would have solved this problem without the need for the designation of a neotype. Indeed, the neotype designation of Dixon and Hendricks (1979) fails to address several of the qualifying conditions for the designation of a neotype (ICZN 1999, Art. 75.3), and the confusion regarding the identity of New
World typhlopids appears to be a function of Gronovius’s (1756) description as indicated by Linnaeus. On this basis I consider the neotype designation of Dixon and Hendricks (1979) to be invalid and their neotype, thus, has no name-bearing status. Rather, I here designate the specimen illustrated as figure 4 of plate 747 of Scheuchzer (Fig. 2; Linck collection specimen number 608; Linck 1783) as the lectotype of *Anguis reticulata* in accordance with the *International Code of Zoological Nomenclature* (ICZN 1999, Art. 74.4). The taxonomic purpose of this designation is to fix the name *Anguis reticulata* (now *Typhlops reticulatus*) to the only one of the two original syntypes that is fully consistent with the current use of the name (*fide* Dixon and Hendricks 1979). This action also follows Recommendation 74B, the preference for an illustrated syntype to be designated as the lectotype.

*Anguis eryx* [Gronovius] = *Anguis fragilis* Linnaeus, 1758 *fide* Boulenger (1885): Linnaeus’s indication makes it clear that a single specimen from the Gronovius collection is the holotype of *A. eryx*. It is possible that this name represents a North American *Ophisaurus*, rather than *Anguis*, but as the whereabouts of this specimen are unknown this cannot be verified.

**DISCUSSION**

A review of the Linnaean (1758) names based entirely on secondary sources reveals that 11 were originally based on a single holotype (although there are several ambiguous cases, e.g. *Lacerta strumosa*). Another 11 were based on two or more syntypes and one, *Testudo orbicularis*, was based on Ray’s (1693) general concept of the species and cannot be associated with any identifiable individual specimen(s). In this last instance a neotype has subsequently been designated (Fritz 1994). In the cases of two anurans — *Rana hyla* and *R. esculenta* — the identity and status of types has been considered in detail and lectotypes have been selected from among the available syntypes (Dubois and Ohler 1997b “1996”). In the present paper the neotype designation for *Anguis reticulata* (Dixon and Hendricks 1979) is considered invalid and a lectotype is selected from among the two identifiable syntypes.

For some names the identity of associated type specimens has been considered in detail. This has not guaranteed the correct identification of the types in all cases, however, and many modern authors have ignored one or more clearly identifiable syntypes. In other instances...
no explicit statements regarding types has ever been made. Although some of these refer to names currently placed in the synonymy of others, names such as *Testudo Carolina* that apply to well known valid species also fall into this category. Several other cases have been addressed, but are contentious, for example, *Lacerta bullaris* and *L. strumosa*. The case of *Lacerta caudiverbera* is especially problematic. Past authors have considered the name to be invalid — referring to a mythical or chimeric concept (Boulenger 1885; Myers and Stothers 2006), or to be attributable to a frog (Myers 1962) or one of several types of lizards (Bauer and Russell 1989).

At present, only one secondary syntype specimen associated with a Linnaean name published in *Systema Naturae X* appears to have been located. This specimen, the holotype of *Lacerta basiliscus*, has been identified in the Paris Museum’s holdings of material ultimately deriving from the collection of Albertus Seba, Linnaeus’s most frequently cited herpetological source. Additional types may yet be identified as ongoing work in major European herpetological collections, particularly Paris and Berlin, holds the potential of locating more of Seba’s material (Thireau et al. 1998; Bauer and Günther, in prep.). Research in the small collection in Waldenburg, Germany (Bauer and Wahlgren, in prep.) has revealed the survival of other specimens illustrated by Scheuchzer (1735). To date neither specimen cited by Linnaeus (1758) has been identified, but further work may yet reveal their presence.

As noted by Dubois and Ohler (1995 “1994”, 1997a “1996”, 1997b “1996”), even when no longer extant, the existence of secondary syntypes of Linnaean or other old names in herpetology often provides solutions to taxonomic and nomenclatural problems. Surprisingly, many such problems still exist among Linnaeus’s herpetological names. In this paper I have attempted to highlight the current state of knowledge with respect to the names based solely on indications to pre-Linnaean literature and, where possible, have corrected errors. However, much remains to be done, both in regard to the critical assessment of the identified types and the designation of lectotypes (when warranted), and to the review of the much more numerous cases in which names in *Systema Naturae X* are based on a combination of both primary and secondary syntypes.

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LINNAEAN NAMES AND PRE-LINNAEAN SOURCES IN HERPETOLOGY


LINNAEAN NAMES AND PRE-LINNAEAN SOURCES IN HERPETOLOGY


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LINNAEAN NAMES AND PRE-LINNAEAN SOURCES IN HERPETOLOGY


**Lignum colubrinum and Radix senega - Two Dissertations on Snakebite Treatments Published by Linnaeus in 1749**

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**Abstract.** The academic dissertation was a very important form of publication to Linnaeus. He was the preses on 186 such dissertations. A general description of this kind of imprint is given together with an account of the academic procedure connected to the dissertations.

In 1747 Linnaeus published his *Flora Zeylanica* which was based on plants collected during the period 1670-1677 by the Dutch botanist Paul Hermann. In Hermann’s collection Linnaeus found a plant which he recognized as the true “snakewood” — “Lignum colubrinum” — which resulted in an academic dissertation with the same name. There had been a lot of confusion about which plant this concept was really referring to. In *Lignum colubrinum* Linnaeus gave a survey of previous authors on the subject and finally stated that the true species is *Ophiorrhiza mungos*, a member of the family Rubiaceae. An anecdote about how the mongoose uses the plant if it is bitten by a cobra is also given. Linnaeus published in 1749 in *Materia medica* a beautiful copper engraving illustrating *Ophiorrhiza mungos* together with a cobra.

In *Radix senega* Linnaeus referred to the Scottish physician John Tennent who had travelled in North America in 1735. Tennant had received information from the Native Americans about a root, referred to as “Radix senega”, which was said to be an efficient antidote against the venom of the rattlesnake. Linnaeus stated that the concept “Radix senega” involves at least one species of the genus *Polygala*. The dissertation is subdivided into different chapters which include descriptions of snakes in general and especially the rattlesnake, the plant genus *Polygala*, the drug and how to use and prepare it and, finally, different substitutes. A copper engraving with the plant and the root is also included in the dissertation.

**INTRODUCTION**

As many as 187 of Linnaeus’s works are published in the form of an academic dissertation, 186 with him as the chairman/preses and one with him as the respondent. Because this kind of publication obviously was very important to Linnaeus and because the dissertations from the 18th century have very little in common with an academic thesis written today, a description of that kind of publication is given here.

**THE ACADEMIC DISSERTATION AT THE SWEDISH UNIVERSITIES DURING THE 18TH CENTURY**

The academic dissertation was developed early on the European continent and was used as a form of publication at the Swedish universities from their beginning. The title-leaf always has two names, the name of the chairman/preses and the respondent respectively (Fig. 1 and Fig. 2). Some of the dissertations are illustrated with copper engravings (Fig. 3) or wood-cuts.
There were two kinds of dissertations, “pro exercitio” and “pro gradu”. The former preceded the latter which gave the highest academic degree and thus may be compared with a Ph.D. thesis today. A major difference compared with today was that the dissertation only rarely was written by the respondent. Instead it was usually written by the preses who almost always was one of the professors within the faculty. The aim of this seemingly odd procedure was twofold. The first purpose was to check the respondent’s knowledge in Latin. The manuscript was not handed over to the respondent in a complete version so he had to develop the language and also pay for the printing which gave the preses/professor a good opportunity to publish results from his own research at no cost at all. However, frequently the dissertation only included facts which were previously published (Lindell 2007).

The second purpose was to check the respondent’s ability to present logical arguments at the oral defense where the respondent had to defend the thesis against the author himself (Lindell 2007)! One or two official opponents were also present. This procedure was not altered in Sweden until 1852 when it was clearly stated that the thesis must be written by the respondent and reflect his own research.

To Linnaeus the dissertations gave a good opportunity to publish observations within a wide range of subjects covering the fields of natural history and medicine, subjects which were limited and well-defined. A few of the dissertations included herpetological observations, two of which, Lignum colubrinum and Radix senega both published in 1749, dealt with snakebite treatments. The dissertations were written in Latin and have never been translated into any other language. However, Linnaeus himself anonymously gave extensive and, not surprisingly, positive reviews of them in Swedish in Lärda Tidningar (Linnaeus 1749a, 1749c), a Swedish periodical which contained news mainly from the universities.

Both of the dissertations are “pro gradu”. Because the design of the dissertation with two names on the title-leaf has caused problems because authorship sometimes has been attributed to the respondent it must be clearly emphasized here that all of the Linnaean dissertations dealing with herpetology are works by Linnaeus himself. There are a few of the Linnaean dissertations where the respondents obviously have had some influence on the content but there is no dissertation where the respondent should be considered as the sole author (Heller 1983). However, since the respondent, due to the academic procedure described above, has had some influence on the final version of the first edition of a dissertation it should be referred to as a joint product of Linnaeus and the respondent (Heller 1983, Stearn 1957). From this it is also understood
that Linnaeus was justified in issuing the amended dissertations under his own name in the *Amonenitites academicae* (Stearn 1957).

All dissertations were originally printed in small editions and are consequently very rare on the market. However, as have been stated above Linnaeus collected the dissertations and published them together in several volumes under the title *Amonenitites academicae*. Several editions of the *Amonenitites academicae* have been published (Linnaeus 1751, 1752, 1762, 1764, 1787). However, the text of the dissertations published in the *Amonenitites academicae* cannot automatically be used instead of the text of the original dissertation since Linnaeus frequently made additions and corrections to the original text. Once a dissertation was published in the *Amonenitites academicae* Linnaeus always cited the latter.


The plants collected on Ceylon in 1670–1677 by the Dutch botanist Paul Hermann were lost for some time before they were rediscovered in the possession of a pharmacist in Copenhagen named Günther. Because Günther wanted to know which plants were included in the collection he sent it to Linnaeus who became very enthusiastic because he understood that this must be the plants collected by Hermann. According to his autobiographical notes (Linnaeus 1823) Linnaeus spent days and nights on this difficult work examining plants which had been dry for such a long time. Linnaeus said that “it took him a year to soften and open up all these flowers which had been dry for almost a century and then describe them”. Based on that collection Linnaeus finally published his *Flora Zeylanica* (Linnaeus 1747).

In the collection he recognized a plant which obviously was the plant referred to as “snakewood” — “Lignum colubrinum”. This finding was a good subject for a dissertation since there was some confusion about the plant to which this name was actually referring. Several substitutes for the original antidote had been used with little or no effect. Referring to several authors especially de Orta (1593), Fragoso (1601), Kaempfer (1712), Grim (1677), Acosta (1593) and Hermann (1726a and b) Linnaeus gave in the dissertation a survey of the different species to which the name had been given and finally stated that a member of the family Rubiaceae, *Ophiorrhiza mungos*, is the species that had the properties to treat snake bite. He described the plant and how to use and prepare the drug and also included an anecdote telling how the mongoose uses the root of this species if it is bitten by a cobra: if the mongoose is bitten she (Linnaeus referred to the mongoose as something feminine) immediately, according to Linnaeus, interrupts the attack on the cobra and runs away to seek for the plant. If the mongoose finds the plant she will eat it and soon recover.

*Lignum colubrinum* (Linnaeus & Darelius 1749)
The dissertation is printed in quarto and consists of 22 pages. A beautiful copper engraving of Ophiorrhiza together with a cobra (Fig. 4) is surprisingly not included in the dissertation but appears instead in Materia medica (Linnaeus 1749b), a book by Linnaeus which was published soon after the dissertation was defended. Apart from the frontispiece this is the only illustration in Materia medica. The illustration was probably originally meant to be included in the dissertation but either because it was delayed or that Linnaeus wanted it to be published in a more widespread work it was instead included in his Materia medica.

Today the concept “snake-wood”, or “Lignum colubrinum”, usually refers to Strychnos colubrina L., a member of the family Loganiaceae, which is a tree with a thick and often curved trunk. This species was mentioned by de Orta (1593) as one of the species given the label “Lignum colubrinum” and was frequently sold by pharmacists as an antidote to snake bite. As Linnaeus concluded in the dissertation, this species is not effective against snake bites but because it includes powerful substances such as strychnine Strychnos colubrina is used for other medical purposes.

The respondent of Lignum colubrinum was Johan Anders Darelius (1718–1780) who later published a few works in medicine and became physician to Queen Lovisa Ulrica in 1754. He was raised to nobility in 1773 and took the name af Darelli (Sandermann Olsen 1997). However, his successful career had a poor start because Darelius is famous for being the respondent on the “pro exercitio”–dissertation Decades binae thesium medicarum with Johan Gottschalk Wallerius as chairman/preses (Wallerius & Darelius 1741). Wallerius became Sweden’s first professor in chemistry but in 1741 he was one of Linnaeus’s competitors for one of the chairs in medicine at Uppsala University. Wallerius, as author of the Decades, took the opportunity to attack and discredit Linnaeus in the dissertation. That caused tumult when the dissertation was de-
fended and the records from the university tell that the room was filled with destroyed copies of the dissertation (which consequently now is very rare)! Darelius was of course not responsible for the content of this dissertation, and obviously Linnaeus did not hesitate to accept Darelius for a dissertation “pro gradu” in spite of the fierce attacks on Linnaeus in Darelius’s dissertation “pro exercitio”.

**Radix senega**
*(Linnaeus & Kiernander 1749)*

In *Radix senega* Linnaeus referred to the Scottish physician John Tennent who had travelled in North America in 1735. Tennant had received information from the Native Americans how to use a root which was said to be very efficient against the venom of the rattlesnake but was also considered to be a good remedy against severe fevers. Linnaeus previously discussed this root in 1743 in a university programme (Linnaeus 1743) and returned to the subject in the dissertation *Hortus Upsaliensis* (Linnaeus & Nauclér 1745). He stated that the root of at least one species of the genus *Polygala* are included under the name “Radix senega” and argued that because this genus also is common in Europe it is likely that European species also include the antidote.

The dissertation is printed in quarto and consists of 32 pages and one engraved plate. The content is subdivided into eleven chapters, the last one being just an epilogue:

Chapter one consists of a short description of snakes in general, their behaviour and if they are venomous. The second chapter focuses on the rattlesnake and its venom and in the third chapter the plant genus *Polygala* of the family Polygalaceae is described together with the 18 species of the genus then recognized. Chapter four consists of a detailed description with references to the plate of the 11th species from the previous chapter which is called “Senega” (today *Polygala senega* L.) and in chapter five a detailed description of the root of “Senega” is given together with an analysis of its chemical composition. The sixth chapter provides...
description of how the drug affects the human body and the seventh gives a review of the different diseases which were treated with the drug such as severe fevers, rheumatism, gout, asthma and an endemic disease in Virginia called “Marasma virginicus”. Different methods of preparing the drug are given in chapter eight and the ninth chapter focus on how to take and use the drug. In the tenth chapter different substitutes are described – it is said that physicians in Paris obtained equally good results with *Polygala vulgaris*, a common European species. *Solanum dulcamara*, a member of the family Solanaceae that is quite common in Sweden, is here suggested to be used against the venom of Swedish snakes (*Vipera berus*).

Today this drug is primarily used to cure catarrhs of the respiratory tract. Pehr Kalm, a Linnaeus Apostle, raised doubts about the efficiency of “Radix senega” against the venom of snakes and related in a letter to Linnaeus a story about a Native American who, in the presence of many witnesses, was killed by a rattlesnake when he was bitten on the thumb during an attempt to show the efficiency of the antidote. However, Linnaeus himself really believed that the drug could serve as an antidote against the venom of snakes and returned to the subject several years later in his dissertation *De morsura serpentum* (Linnaeus & Acrel 1762). In this dissertation Linnaeus described how he, at a farm close to Uppsala, successfully had cured a maid-servant with “Radix senega” when she had been bitten by a snake, obviously the common European adder (*Vipera berus*). Linnaeus was also responsible for the introduction of the drug in the first edition of the Swedish pharmacopoeia.

The name of the respondent was Jonas Kiernander (1721–1778) who also became a physician but a less famous one compared to Darelius. He did not publish anything after *Radix senega* and worked as a physician in the province of Västergötland before he moved to Stockholm where during his last years he had a private practice (Sandermann Olsen 1997).

**DISCUSSION**

Linnaeus’s contributions to herpetological classification and nomenclature are significant and of the utmost importance. However, when he didn’t have to include the entire kingdom Animalia in a work and freely could select a subject, he rarely wrote about herpetology. His 186 dissertations clearly reflect this. Some dissertations have a herpetological connection but, apart from descriptions found in three dissertations in which Linnaeus describes zoological collections made by others (Linnaeus & Balk 1746, Linnaeus & Hast 1745 and Linnaeus & Sundius 1748), only *Siren lacertina* (Linnaeus & Österdam 1766) focuses exclusively on the animal itself. In *Radix senega* and *Lignum colubrinum* the focus is on the venom, different antidotes and the used plants rather than on the animals. The reason for this was obviously given by Linnaeus himself in his famous and last oration *Deliciae naturae* (Linnaeus 1773) held in 1772 when Linnaeus for the last time was Rector Magnificus at Uppsala University. In this oration Linnaeus used several metaphors and compared different groups within his three kingdoms with human characteristics, activities and occupations. In the part dealing with the class Amphibia Linnaeus expressed the following opinion: “An ugly, horrible, naked mob . . .”! It is not far-fetched to conclude that Linnaeus did not very much appreciate the animals included in “Classis III. Amphibia”.

**ACKNOWLEDGEMENTS**

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Linnaean Names in South American Herpetology

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Abstract. In the 10th edition (1758) of Systema Naturae, Linnaeus named 76 amphibians and reptiles known to occur in South America (1 caecilian, 6 anurans, 2 amphisbaenians, 15 lizards, 47 snakes, 1 crocodilian, 3 turtles); two additional snakes and two turtles were named in the 12th edition (1766). Of these, 64 are recognized at the species level today; one of his lizards (Lacerta caudiverbera) turned out to be a mythical creature. Moreover, he named 13 of his snakes twice. Although many of Linnaeus’s names were based on illustrations in Seba’s “Thesaurus” (1734–1735), most are represented by type specimens in the Swedish Museum of Natural History in Stockholm and in the Museum of Evolution, Zoology Section in Uppsala. Although Linnaeus gave the provenance of his types and Seba’s illustrations as a variety of general terms (e.g., America, Asia, Indies), the majority of the specimens apparently originated in the Guianas, and probably more specifically Surinam, where all but a few exceptions occur today.

Keywords: Amphibians, reptiles, mythical creature, Guianan Region in South America.

INTRODUCTION

Four decades have passed since I visited the Swedish Museum of Natural History in Stockholm. During my visit, Greta Vestergren kindly showed me some Linnaean types in the collection. It was quite a thrill to hold specimens that Linnaeus once had examined and described. Now I have an opportunity to write about those specimens that fascinated me those many years ago. Herein I summarize those South American taxa named by Linnaeus, give their present taxonomic status, and provide comments as necessary. Also, I provide copies of illustrations of many of the types and color photographs of living examples of the same species.

SOUTH AMERICAN AMPHIBIANS AND REPTILES NAMED BY LINNAEUS

In the 10th edition of the Systema Naturae Linnaeus named 68 species of amphibians and reptiles from specimens collected in South America—one caecilian, six anurans, two amphisbaenians, 14 lizards, 44 snakes, and one crocodilian. Two more turtles and two more snakes were named in the 12th edition on 1766. Of all of these Linnaean names, 54 are taxa that are recognized today; he named 13 species of snakes twice (Appendix). Moreover, his name Lacerta Caudiverbera, is based on an illustration in Seba (1735) that is either mythical or a representation based on the features of two or more actual species (Russell and Bauer 1988; C. W. Myers and Stothers 2006).

Most of Linnaeus’s South American herpetological taxa are based on specimens that were donated to the Uppsala Academy collections or were in the collection of King Adolf Fredrik. Linnaeus examined all these collections and published catalogues of them as students’ dissertations and the royal collection as two books. Linnaeus also had access to the rich holdings of Charles De Geer at Leufsta, but no catalogue was ever printed of this collection. Linnaeus listed several synonyms of the taxa he described; either he had examined the relevant specimens himself or based his synonymies on the literature. Albertus Seba’s “Thesaurus”
(1734–1735) is the most frequently cited source. Other sources occur more sporadically and include among South American reptiles and amphibians Johannes Jacob Scheuchzer’s “Physicae Sacrae” (band IV 1735), L. T. Gronovius (1756) “Musei Ichthyologicii”, Mark Catesby (1731–1747) “The Natural History of Carolina” and Patrick Browne (1756) “Civil and Natural History of Jamaica”.

In reviewing Linnaean names of amphibians and reptiles in South America, I have relied considerably upon the translation of the amphibian and reptile section in the *Systema Naturae* 1758 by Kitchell and Dundee (1994). Also, I have examined the plates in Seba (1734 and 1735, see also 2001/2005) that illustrate types of many of Linnaeus’s taxa. I have not included all of Linnaeus’s syntypes from secondary sources in the Appendix, but I have listed Seba, whenever Linnaeus quoted his illustrations. The provenance of most Linnaean names is very general and for many, completely erroneous. Of the 80 names of South American taxa proposed by Linnaeus, 61 were designated as having originated from the new world—America (23), Indies (21), Surinam (6), Guinea (= Guyana) (1), South America (2), and Virginia (2). However, nine species were said to have come from Asia, three from Africa, and one each from Ceylon (= Sri Lanka), Spain, Ternate (Moluccas), and southern regions. None of the non-marine South American taxa named by Linnaeus is known to occur in Africa, Asia, the Moluccas, or Spain, and all of them occur in South America. Consequently, the provenance of specimens on which these names were based must be some place in South America. As noted by Kitchell and Dundee (1994), the term *Indiis*, which refers to the West Indies, is a common error of Linnaeus. Most species so designated occur in South America.

The most specific location in South America given by Linnaeus is Surinam. At the time of Linnaeus’s writing, Surinam was a Dutch colony. The port of Paramaribo was an important shipping center of tropical woods and other commodities from South America to Europe, especially to Amsterdam, the home of Albertus Seba. Paramaribo also was visited by persons collecting for Linnaeus.

Examination of the distributions of the South American taxa named by Linnaeus reveals that all of the recognized species (with two exceptions) occur in the lowlands of the Guianan Region in northeastern South America. Many of these species (e.g., *Hypsiboas boans*, *Rhinella marina*, *Amphisbaena fuliginosa*, *Ameiva ameiva*, *Liophis cobella*, *Chironius fuscus*,

**FIGURE 1.** Type specimen of *Caecilia tentaculata.*
and Caiman crocodilus) are abundant in the vicinity of Paramaribo. Consequently, the “best guess” for the origin of Linnaean taxa is the vicinity of Paramaribo, Surinam. Hoogmoed (1973) restricted the type localities of seven of Linnaeus’s species of lizards [Lacerta Ameiva (Ameiva ameiva), L. azurea (Uracentron azureum), L. Iguana (Iguana iguana), L. lemniscata (Cnemidophorus lemniscatus), L. Plica (Plica plica), L. superciliosa (Uranoscodon superciliosa), and L. Umbra (Plica umbra)] and the two species of amphisbaenians (Amphisbaena alba and Amphisbaena fuliginosa) to the confluence of the Cottica River and Perica Creek, Surinam; two species of lizards [L. bicarinata (Neusticurus bicarinatus) and L. marmorata (Polychrus marmoratus) were restricted to the vicinity of Paramaribo, Surinam. The exceptions are Lacerta Basiliscus (Basiliscus basiliscus), which has most of its distribution in lower Central America and barely enters northwestern South America, and L. Teguixin (Tipinambis teguixin), which does not occur in coastal Surinam.

The Amphibians

Of course, the organisms that we know today as amphibians and reptiles were all placed in the Class Amphibia by Linnaeus (1758), who considered them to be “the most terrible and vile animals.” Laurenti (1768) replaced the Linnaean name Class Amphibia with Reptilia, and Blainville (1816) separated Amphibia and Reptilia into two classes (see Lescure and David, 2008).

Linnaeus obviously did not realize that the caecilian that he named Caecilia tentaculata was not a “reptile.” He associated it with limbless lizards (Anguis fragilis), two amphisbaenians (Amphisbaena alba and A. fuliginosa), two typhlopid snakes (Anguis lumbricalis and A. reticulatus), and an aniliid snake (Anilius scytale) in the Order Serpentes. The type specimen of Caecilia tentaculata is broken and faded (Fig. 1).

Linnaeus placed all anurans in the genus Rana. Six of these are readily associated with species that occur in the Guiana Region, and the type specimens or illustrations on which the names were based are like recent specimens (Figs. 2 and 3).
In the case of *Rana boans* Andersson (1900:17) stated that an unnumbered specimen in the Swedish Museum of Natural History in Stockholm is the holotype. However, Duellman (1977:39) noted that the type specimen actually is No. 27 in the Museum of Evolution, Zoology Section, Uppsala.

The sixth frog species is *Rana typhonia*, a name that has had a frenetic history. Linnaeus listed *Rana typhonia* as being without provenance although he noted that Rolander who visited Surinam 1755–56 described it in his journal: “This noise-making frog, which is called *Rana typhonica* (Albert Seba, Locupletissimi rerum naturalium thesauri accurate descriptio, vol. 1, p. 114, tab. 71, fig. 3, 4) is about the size of *Rana aquatica*. It is brown above, yellow below. Its body covered with raised, convex, uneven spots; the same sort of spots are seen on the ducts through which it secretes the milky fluid that coats its body, so that a frog that appeared brown becomes in an instant very white. *Palmae tetradactyae, fissae; plantae pentadactyae, subpal-matae: digitorum apices rotundati, planisculi.* The American Indians use them for food.” (Hansen, 2008:1434).

Throughout most of the 19th and 20th centuries, this name was applied to a South American toad, *Bufo typhonius*. Hoogmoed (1986) suggested that the name had been misapplied to the South American toad, to which he (Hoogmoed, 1989) applied the name *Bufo margaritifer* (Laurenti, 1768). Contrary to Rolander’s mentioning this toad in his journal of his travels in Surinam, Frost (2010) treated *Rana typhonia* Linnaeus as a *nomen oblitum* in the synonymy of the Indian ranid *Hoplobatrachus tigerinus* Daudin, 1802! It should be noted that Frost’s (2010) synonymy of that taxon contains many names that have
been applied to this South American toad but
never to the Asian Hoplobatrachus tigerinus. 
During a thorough investigation of Rolander’s 
notes, and all associated literature, Lavilla et 
al. (2010b) discovered the holotype of Rana 
typhonia and presented a precise description 
of the specimen (No. 134 in the Museum of 
Evolution, Zoology Section in Uppsala), 
which clearly is a specimen of the hylid frog 
commonly known as Phrynohyas venulosa (= 
Trachycephalus venulosus fide Faivovich et al. 
[2005]). Thus, it now seems to be conclusive 
that the Linnaean name Rana typhonia applies 
to a hylid frog, Trachycephalus typhonius. 
Also, based on Rolander’s notes, they placed 
the type locality as Paramaribo, Surinam.

In two of the South American species of an-
urans, Linnaeus had specimens revealing the 
life history. Although he does not mention 
them in his text, the type specimens of Rana 
paradoxa include a gigantic tadpole, a meta-
morphosing young individual, and an adult 
(Fig. 4); presumably he was aware of the 
unusual size relationship of the tadpole and 
adult because of his selection of the specific 
name paradoxa for this species. Linnaeus in 
SN I (1735) listed beneath AMPHIBIA 10 
PARADOXA, the 2nd being [transl. from 
Latin:] “The Frog-Fish, or the metamorphosis 
of Rana into a Fish is very paradoxical, …” In 
SN VI (1748:36) he listed under ‘93. Lacerta’ 
2. Rana-Pisces. In SN X (1758:212) he refers 
under Rana paradoxa to SN (1748). Thus, it 
is apparently not the size of the larva as such 
but the phenomenon of a frog turning to a fish 
that inspired the name R. paradoxa (Richard 
Wahlgren, pers. comm.). Moreover, there are 
several specimens in the collection, some add-
ed after Linnaeus; therefore, no specific holo-
type can be assigned.

The second species is now known as Pipa 
pipa. According to Wahlgren (pers. comm.), 
the preserved specimen in Uppsala clearly is 
a syntype of Rana pipa; it is an adult female 
with numerous hatching eggs imbedded in the 
dorsal skin (Fig. 4). In the account of Rana 
pipa, Linnaeus (1758:210) stated: “It hatches 
its young by laying them on its back” (transla-
tion from Kitchell and Dundee [1994]).

The frog named Rana ocellata by Linnaeus 
has long been associated with South America; 
the name was based on descriptions and fig-
ures in Browne (1756). Lavilla et al. (2010a) 
thoroughly reviewed the pertinent literature 
and selected as the lectotype the individual 
described by Browne (1756) under the name 
Rana maxima compressa miscella, which re-
stricts the type locality to Jamaica. This is a
common species known only from Jamaica, where it has been known for decades as *Hyla brunnea* Gosse, 1851. According to Lavilla et al. (2010a), the current name for the Jamaican frog is *Osteopilus ocellatus*, whereas the South American frog formerly known as *Leptodactylus ocellatus* (Linnaeus) now has the scientific name *Leptodactylus latrans* (Steffen, 1815).

**The Reptiles**

Linnaeus (1758) defined *Amphisbaena* as having rings on the body and tail. He diagnosed the two species by coloration—variegated with white and black in *A. fuliginosa* and totally white in *A. alba*.

As noted by Hoogmoed (1973), most of Linnaeus’s descriptions of lizards are readily associated with existing type specimens or illustrations in Seba (1734–1735). Some of the type specimens are in excellent condition and can be compared with modern specimens (Figs. 5 and 6).

Linnaeus’s *Lacerta Crocodilus* is the crocodilian, *Caiman crocodilus*, which is illustrated in Seba (1734, Volume 1, Plates 103 and 104). In his description, he noted that it “lays one hundred

**FIGURE 5.** One of the syntypes of Linnaeus’s *Lacerta Umbra* and a photograph of a living individual (KU 204982).

**FIGURE 6.** Seba’s illustration (Volume 1, Plate 85) that is a syntype for the Linnaean name *Lacerta Ameiva* and photograph of a living individual of *Ameiva ameiva* (KU 204966).
eggs, and...when the young hatch, the mother calls them forth onto her back...” (translation by Kitchell and Dundee, 1994).

Linnaeus’s *Lacerta Caudiverbera* has been a taxonomic enigma for more than two centuries. Linnaeus (1758) stated that he based the name on an illustration in Seba (1735, Volume II, Plate 62, figure 9), but there is no figure 9 on that plate. In 1766 Linnaeus corrected the citation to Volume II, Plate 103, figure 2, which is an illustration of a lizard similar to the illustration in Feuillée (1714). Laurenti (1768) erected a generic name, *Caudiverbera* based on the same illustration. Although Boulenger (1885:236) suggested that the “species” was mythical, G. S. Myers (1962) considered the name to be applicable to the tadpoles of the large Chilean frog, which he determined should be known as *Caudiverbera caudiverbera*. Upon carefully examining the pertinent pre-Linnaean literature, C. W. Myers and Stothers (2006:256) concluded that “Feuillée’s drawing and description represent a composite creature—an amphibian-reptilian hybrid created out of an imagination based on his remembrances of a large Chilean tadpole and the lizards mentioned in the creature’s description.” Thus, they concluded that such a hypothetical concept is excluded from the provisions of zoological nomenclature and is an unavailable name.

Linnaeus grouped all limbless reptiles, as well as caecilians, in Serpentes, wherein he recognized six genera—*Amphisbaena, Anguis, Boa, Caecilia, Coluber*, and *Crotalus*. The definitions of the genera are generalized, but in some cases particular attributes were noted; for example, among other characters of the genus *Crotalus* is a rattle at the end of its tail. However, in 1766 Linnaeus recognized similarities between the bushmaster and *Crotalus* and named the species *Crotalus mutus*, in recognition of the absence of a rattle. On the other hand he placed the large pit viper *Bothrops atrox* in his genus *Coluber*, wherein he also placed other vipers (e.g., *Cerastes* and *Vipera*). Obviously, Linnaeus’s *Coluber* was a “catch-all;” it also included snakes now placed in Elapidae. However, he used the Mars sign to accurately denote the front fanged snakes. Although some names were based on illustrations in Seba (1734–1735), Linnaeus had specimens of many kinds of reptiles and
amphibians available (Andersson, 1899, 1900; Lönnerberg 1896). The type specimens of many of these still are in remarkably good condition and can easily be associated with presently recognized species (Figs 7–9).

Among the Linnaean taxa, 13 presently recognized species were assigned two or more names by Linnaeus. Thus, Boa Enydris and Boa Hortulana are Corallus hortulanus. Coluber Æsculapii and Coluber agilis are Erythrolamprus aesculapii, and so on (see Appendix).

In the 10th edition of the Systema Naturae Linnaeus named no turtles definitely from South America. Two sea turtles—Testudo (= Chelonia) mydas and Testudo (= Caretta) caretta—are based on illustrations and descriptions in Seba (1734) and Browne (1756), respectively. Most likely Testudo caretta was from Jamaica, and Testudo mydas may have come from anywhere in warm oceanic waters. Although Testudo (= Chelydra) serpentina occurs in northwestern South America, it is most likely that Linnaeus based his description on one from southeastern United States. In the 12th edition of the Systema Naturae Linnaeus named two South American species—Testudo (= Geo- chelone) denticulata and Testudo (= Kinosternon) scorpioides. The former was stated as living in Virginia!

Thus, in summary, Linnaeus provided names for 63 species of amphibians and reptiles now known to occur in South America. Most of the taxa that he named are conspicuous species in the northeastern part of the continent, especially in Surinam, the likely source of most of the specimens on which his names are based. However, two of the species do not occur there.

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helpful suggestions. Images of the type specimens of Linnaeus were provided by the Swedish Museum of Natural History in Stockholm. John E. Simmons kindly loaned a reprint (2001) with the plates of Seba’s “Thesaurus.” Images of living amphibians and reptile are from the KU Herpetology Archives (KUDA), Natural History Museum, University of Kansas.

FIGURE 9. Type specimen of Linnaeus’s Coluber Ahaetulla and a photograph of a living individual of Leptophis ahaetulla (KU 220194). [The holotype is probably in Uppsala]

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with their descriptions in English and French. To which, are added observations on the air, soil, and waters: with remarks upon agriculture, grain, pulse, roots, &c. To the whole, is prefixed a new and correct map of the countries treated of. Vol. 2. Histoire naturelle de la Caroline, la Floride, & les Isles Bahama: contenant les desseins des oiseaux, animaux, poissons, serpents, insectes, & plantes. Et en particulier, des arbres des forets, arbrisseaux, & autres plantes, qui n’ont point été decrits, jusques à present par les auteurs, ou peu exactement dessinés. Avec leur descriptions en francois et en anglois. A quoi on a adjouté, des observations sur l’air, le sol, & les eaux, aves des remarques sur l’agriculture, les grains, les legumes, les racines, &c. Le tout est precedé d’une carte nouvelle & exacte des païs dont ils s’agist. Tome II and appendix (1734–1735, 1743, 1747). Pages 1–100, [1–6], I–XLIV, 1–20, [1], plates 1–120, 1 map. London: Innys & Manby.


Myers, C. W., and R. B. Stothers. 2006. The myth of Hylas revisited: the frog name *Hyla* and other commentary on *Specimen medicum* (1768) of J. N. Laurenti, the “father” of herpetology. *Archives of Natural History* 33:241–266.


The Swedish botanist, Carolus Linnaeus, originator of binomial nomenclature, published his monumental tenth edition of *Systema Nature* (1758), which became the cornerstone for the Latin nomenclature applied to animals. In the twelfth edition (1766), the last written by Linnaeus himself, he produced an expanded version of the tenth in which he added many new taxa. His new classification organized animals into classes that were further subdivided into genera and then into species. Later workers further subdivided some species into subspecies.

This review considers all Linnaean taxa of amphibians and reptiles that are distributed (either naturally or by introduction) in four geographic regions: the United States and Canada; Mexico; Central America; and the Caribbean including Trinidad and Tobago. This review is meant to complement similar papers on other geographic regions in this volume. The United States and Canada have 32 species named by Linnaeus of which 27 are still recognized (plus 11 introduced species with Linnaean names). The comparable numbers for Mexico are 15 named and 14 recognized (1 introduced); Central America 32 and 27 (1); Caribbean, Trinidad, and Tobago 37 and 36 (4). Three names have been suppressed by action of the International Commission on Zoological Nomenclature or are unidentifiable. Some taxa were named more than once and some are included in more than one of the four geographic regions utilized in this paper.

A special note must be made concerning the marine Leatherback Sea Turtle, *Dermochelys coriacea*, which was long credited to Linnaeus (1766). Recently, it has been shown that this species was actually described by Vandelli (1761), in a published letter addressed to Linnaeus. Vandelli proposed a binomial name for this species (*Testudo coriacea*) and included a description, a drawing, and collection locality, and he noted where the type specimen was deposited. The type has now been re-located (Bour and Dubois, 1983 [1984]).

The order of taxa in each geographic category is: frogs, salamanders, caecilians, lizards, snakes, crocodiles, and turtles. The literature cited at the end of this paper covers the titles used in compiling this paper and is not meant to be exhaustive.
### UNITED STATES AND CANADA

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**Linnaeus’s capitalization of certain specific epithets is seemingly haphazard, but in fact follows a very specific rule, as noted by Myers and Sothers (2006, p. 253, caption to figure 4). Linnaeus capitalized the initial letter of species names used as nouns in apposition.

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**Introduced Linnaeus’s Name Current Nomenclature**

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### MEXICO

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### CENTRAL AMERICA

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## CARIBBEAN (INCLUDING TRINIDAD AND TOBAGO)

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ACKNOWLEDGEMENTS

Thanks are extended to Kraig Adler, Aaron M. Bauer, Brian Crother, William E. Duellman, Darrel Frost, Kenneth Krysko, and Richard Wahlgren for looking over my rough draft or for other courtesies.

REFERENCES


Myers, C. W., and R. B. Sothers. 2006. The myth of Hylas revisited: the frog name *Hyla* and other commentary on *Specimen Medicum* (1768) of J. N. Laurenti, the “Father of Herpetology.” Archives of Natural History, 33: 241–266.


Looking East: Carolus Linnaeus and His Herpetological Species from Asia

Indraneil Das

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Abstract. Linnaean names based on material from Asia, indicated as from “Oriente”, “Indiis” or extralimital areas, are reviewed. This material, representing 31 species names and 29 recognizable biological species, can be restricted geographically to one of three regions—Sri Lanka, southern Malay Peninsula, or Java—although it is conceivable that some of these could have been collected from adjacent regions where these species co-occur. A number of specimens purported to be from the region have been shown by subsequent authors to be extralimital. The presumed points of origin are along trade routes in the East, where seventeenth century maritime trade (spices, timber, textiles) took place, and the vast majority of species are abundant, lowland species of such areas.

Keywords: Linnaeus, “Oriente”, “Indiis”, Asia, amphibians, reptiles.

INTRODUCTION

“By the mid eighteenth century, the physiognomy of collections had changed. The millenarianist zeal to make the invisible visible by means of the curio cabinet had been transformed by a new spirit that held collections up to empirical and experimental investigations. New procedures required living and dead plants, minerals, fossils, shells, animal specimens, machines, and scientific instruments, and these were the objects that came to fill museum shelves. A new ideology of encyclopedism placed stock in displaying the expanse of natural and artificial productions, whose utility derived from their importance to human education, culture, and wellbeing.” (Pyenson & Sheets-Pyenson 1999:128)

Interest in the East, which was often to be their future empires, figured prominently in state policies of major European nations during the Age of Reason (the eighteenth century), thus named for no small measure on account of Carolus Linnaeus (1707–1778). In the wake of Portugal and Spain, other naval powers of Europe, Sweden attempted to navigate the eastern shores, the intention initially, not empire building, but commerce. The British were to eventually steal a march over the others, through the English East India Company (see Keay 1991), but the French and Dutch were not far behind. Sweden, fatherland for Linnaeus, was not quite in the same league as the aforementioned nations, in merchant marine (Müller 2009), but trade with eastern nations was of vital interest in furthering relations with them. Indeed, the Swedish East India Company (“Svenska Ostindiska Companiet”, or SOIC), founded in 1731, given a Royal Charter, and working as a monopoly enterprise until 1813 (Benner 2003), had strong trading links with both China and India. The SOIC supported several Linnaean apostles, one being Olof Torén (1718–1753), pastor of Hope that traversed the eastern seas to Canton (equivalent to the city of Guangzhou, in southern China) in 1748–1749, and subsequently Göthe Leijon, which traveled to the same destination, via Surat, on India’s west coast (Franks 2005). As expected of his background, Torén collected along these voyages, and made material available to Linnaeus (Nyberg 2009).
In 1746, Linnaeus was a professor at Uppsala University, and wrote to the Royal Swedish Academy of Sciences, “Nature has arranged itself in such a way that each country produces something especially useful; the task of economics is to collect [plants] from other places and cultivate [at home] such things that don’t want to grow [here] but can grow [here]” (Koerner 1999). In an age where scientific research had to be strongly justified (Sweden’s economy was devastated following the Great Northern War, 1700–1721), Linnaeus perhaps adopted this stance to further the work then taking place at Uppsala (and perhaps also at Lund). By this time, the once obscure professor of natural history at Uppsala had already laid, in a botanical work entitled “Genera Plantarum” (Linnaeus 1737), a method for the unambiguous classification of both plants and animals in the future, that was to gain widespread cosmopolitan acceptance. As a result, economic botany, the focus of seventeenth century research, was replaced with, among at least the learned, with collecting thereby fuelling the desire for scientific enquiry (Whittle 1997).

ASIAN HERPETOFAUNA OF LINNAEAN WORKS

Linnaeus’s concept of Asia included not only contemporary Asia but also the eastern bank of the River Nile in Egypt, following the perception of the time (see Wissowa, 1896), and sometime included parts of Libya (Brandstaetter, 1996).

A total of 10 herpetofaunal generic names were established by Linnaeus (1758) for the world’s “Amphibia” (his concept included amphibians, reptiles, plus, oddly, cartilaginous fish). One of these—the spectacular Draco—is exclusively Asian. Also noteworthy is its recognition in a genus placed apart from Lacerta, to which Linnaeus included representatives from the Caudata, Crocodylia and Squamata (Schmidtler 2010). In total, 23 species names are associated with biological species that originate from Asia; additional species known from the region and described by Linnaeus (1758, 1766) are those that are widely distributed (e.g., marine turtles) or that occur in peripheral western regions of Asia (squamates). Table 1 lists 30 Linnaean species, inclusive of taxa belonging to the latter category.

The first Linnaean publication to present the adopted method of zoological description of “Genera Plantarum” (Linnaeus 1737), and covering 24 species of amphibians and reptiles, is “Amphibia Gyllenborgiana” (Fig. 1), published in 1745. It was based on the natural history collections of Count Carl Gyllenborg (1679–1746), then Chancellor of the University of Uppsala, that had been presented in 1744 to the University, and served as the basis for a thesis defended on 18 June 1745 by Barthold Rudolph Hast (1724–1784), a student of Linnaeus. The authorship of the work deserves comment. Of the 186 academic dissertations defended by the students of Linnaeus between 1743 and 1776, as many as 185 were authored by Linnaeus himself, as was the practice in eighteenth century Sweden (Smit 1979). Doctoral students typically expounded and defended the contents of the theses, and in the case of “Amphibia Gyllenborgiana”, although Hast is indicated as the author on the title page, the authorship for the work should be attributed to Linnaeus. Count Gyllenborg himself was a diplomat and politician, and apart from his numerous works on statecraft and poetry, collected objects of natural history, as was the fashion of the day for the landed gentry. The sole southeast Asian reptile represented in this otherwise predominantly North American collection is Draco volans Linnaeus, 1758, and suggestive of early trade with Java. The specimen was stuffed, with patagial pigmentation visible when examined by Lönnberg (1896). A second Asian squamate from this collection is the gekkonid lizard, Lacerta Gecko Linnaeus 1758 (current name: Gekko gecko), a syntype of which is extant in the Uppsala University Museum of
Table 1. Chronological list of names of Asian taxa of amphibians and reptiles cited in Linnaean works, their current names and remarks on nomenclature and type specimens. The original orthographies have been retained. Species of extralimital provenance, but known to reach the limits of the region as defined here marked with asterisk. Pre-Linnaean works cross-referenced in Bauer (2011).

<table>
<thead>
<tr>
<th>Linnaean Name</th>
<th>Current Name</th>
<th>Remarks/References</th>
</tr>
</thead>
<tbody>
<tr>
<td>*1. Testudo Mydas</td>
<td>Chelonia mydas (Linnaeus, 1758)</td>
<td>Material examined from &quot;Grön. mus.:&quot; location of herpetological material from this collection at present unknown (Bauer, 2011).</td>
</tr>
<tr>
<td>3. Draco volans</td>
<td>Draco volans (Linnaeus, 1758)</td>
<td>&quot;Asia&quot; Java</td>
</tr>
<tr>
<td>4. Lacerta Monitor</td>
<td>Lyriocephalus scutatus (Linnaeus, 1758)</td>
<td>&quot;Asia&quot; Java</td>
</tr>
<tr>
<td>5. Lacerta scutata</td>
<td>Homodactylus nudicollis (Linnaeus, 1758)</td>
<td>&quot;Asia&quot; Java</td>
</tr>
<tr>
<td>6. Lacerta scutata</td>
<td>Calotes calotes (Linnaeus, 1758)</td>
<td>&quot;Asia: Zeylona&quot; (= Asia: Sri Lanka)</td>
</tr>
<tr>
<td>7. Lacerta Colostus</td>
<td>Calotes colostus (Linnaeus, 1758)</td>
<td>&quot;Asia: Zeylona&quot; (= Asia: Sri Lanka)</td>
</tr>
<tr>
<td>8. Lacerta aurata</td>
<td>Trachylepis aurata (Linnaeus, 1758)</td>
<td>&quot;Asia: Zeylona&quot; (= Asia: Sri Lanka)</td>
</tr>
</tbody>
</table>

**Remarks**: Types: NRM 19, NRM 26, and NRM 231 (syntypes). Material examined from "Grön. mus.:" location of herpetological material from this collection at present unknown (Bauer, 2011). Pre-Linnaean works cross-referenced in Bauer (2011).
<table>
<thead>
<tr>
<th>No.</th>
<th>Species Name</th>
<th>Authority (Year)</th>
<th>Status</th>
<th>Regions</th>
<th>Specimens</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.</td>
<td>Lygosoma punctata</td>
<td>Linnaeus, 1758</td>
<td>Lacerta punctata</td>
<td>Asia (&quot;Ceylon&quot;) in Seba, 1735</td>
<td>Specimen illustrated in Seba 1735, Pl. 2, Fig. 9, based on material from Museum Adolphi Fredrici, currently NRM 135 (Kullander 2001), designated lectotype by Bauer (2002)</td>
<td>ex-Museum Adolphi Fredrici</td>
</tr>
<tr>
<td>11.</td>
<td>Oligodon calamarius</td>
<td>Linnaeus, 1758</td>
<td>Coluber Calamarius</td>
<td>Sri Lanka (&quot;America&quot;)</td>
<td>NRM 62 (holotype; fide Kullander 2001)</td>
<td>Untraced (fide Andersson 1900); ex-Museum Adolphi Fredrici</td>
</tr>
<tr>
<td>12.</td>
<td>Homalopsis buccata</td>
<td>Linnaeus, 1758</td>
<td>Coluber buccatus</td>
<td>South and southeast Asia (&quot;Indiac&quot;)</td>
<td>Specimen reportedly from &quot;Hasselqvist&quot; (= Fredric Hasselquist, 1722–1752, a Linnaean disciple, who collected in Turkey, Palestine, Cyprus, and Egypt)</td>
<td>Kullander 2001</td>
</tr>
<tr>
<td>13.</td>
<td>Macrovipera lebetina</td>
<td>Linnaeus, 1758</td>
<td>Coluber Lebetinus</td>
<td>Western Asia (&quot;Indiac&quot;)</td>
<td>NRM (holotype; fide McDiarmid et al. 1999); type unlocated (Kullander 2001)</td>
<td>ex-Museum Adolphi Fredrici and other collections</td>
</tr>
<tr>
<td>15.</td>
<td>Xenochrophis vittatus</td>
<td>Linnaeus, 1758</td>
<td>Coluber Vittatus</td>
<td>Singapore, Sumatra, Pulau, Surabaya, and Java (&quot;Indiac&quot;)</td>
<td>Untraced (Kullander 2001)</td>
<td>Kullander 2001</td>
</tr>
<tr>
<td>16.</td>
<td>Lycodon aulicus</td>
<td>Linnaeus, 1758</td>
<td>Coluber Aulicus</td>
<td>South Asia (&quot;America&quot;)</td>
<td>South Asia (&quot;America&quot;)</td>
<td>Ex-Museum Adolphi Fredrici; ex-Museum Adolphi Fredrici and other collections</td>
</tr>
<tr>
<td>17.</td>
<td>Xenochrophis nigricollis</td>
<td>Linnaeus, 1758</td>
<td>Coluber Vittatus</td>
<td>&quot;In Indias&quot;</td>
<td>Untraced</td>
<td>&quot;America&quot;</td>
</tr>
<tr>
<td>18.</td>
<td>Uropeltis nigripunctata</td>
<td>Linnaeus, 1758</td>
<td>Coluber Nigripunctatus</td>
<td>&quot;In Indias&quot;</td>
<td>Untraced</td>
<td>&quot;In Indias&quot;</td>
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</tbody>
</table>

Bauer (2003) revisited the problem and showed that NHRM syntypes refer to *Mabuya cf. homalocephala*, an African species.
<table>
<thead>
<tr>
<th>Linnaean Name</th>
<th>Current Name</th>
<th>Type Locality</th>
<th>Current Known Distribution</th>
<th>Types</th>
<th>Remarks/References</th>
</tr>
</thead>
<tbody>
<tr>
<td>*20. Coluber candidus</td>
<td>Bungarus candidus</td>
<td>“in Indiis”</td>
<td>Indo-China, Malay Peninsula, Sumatra, Java, and Bali</td>
<td>NRM 89 (holotype; fide Kullander 2001)</td>
<td>ex-Museum Adolphi Fredrici</td>
</tr>
<tr>
<td>Linnaeus, 1758 (p.223)</td>
<td>(Linnaeus, 1758)</td>
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<tr>
<td>21. Coluber Pelias</td>
<td>Chrysopelea pelias</td>
<td>“in Indiis”</td>
<td>Southeast Asia</td>
<td>Untraced</td>
<td>Specimen from “Mus. De Geer”</td>
</tr>
<tr>
<td>Linnaeus, 1758 (p.224)</td>
<td>(Linnaeus, 1758)</td>
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<tr>
<td>Linnaeus, 1758 (p.225)</td>
<td>(Linnaeus, 1758)</td>
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<tr>
<td>23. Coluber mucosus</td>
<td>Ptyas mucosa</td>
<td>“in Indiis”</td>
<td>South and southeast Asia</td>
<td>NRM 26 and 61 (suspected to be syntypes; fide Kullander 2001)</td>
<td>ex-Museum Adolphi Fredrici</td>
</tr>
<tr>
<td>Linnaeus, 1758 (p.226)</td>
<td>(Linnaeus, 1758)</td>
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<tr>
<td>Linnaeus, 1758 (p.226)</td>
<td>Link, 1807</td>
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<tr>
<td>25. Anguis maculata</td>
<td>Cylindrophis maculatus</td>
<td>“America”</td>
<td>Sri Lanka</td>
<td>NRM 14 (three syntypes; fide Kullander 2001)</td>
<td>ex-Museum Adolphi Fredrici</td>
</tr>
<tr>
<td>Linnaeus, 1758 (p.228)</td>
<td>(Linnaeus, 1758)</td>
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<tr>
<td>Linnaeus, 1758 (p.229)</td>
<td>(Linnaeus, 1758)</td>
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<tr>
<td>*27. Testudo imbricata</td>
<td>Eremochelys imbricata</td>
<td>“Mari Americano, Asiatico”</td>
<td>Cosmopolitan</td>
<td>UUZM 130 suspected to be the holotype (Smith and Smith 1979), although Wallin (1985) indicated that no type existed</td>
<td>Linnaeus referred to text including “Gron. zooph.” (= Gronovius, 1756); see Bauer (2011)</td>
</tr>
<tr>
<td>Linnaeus, 1766 (p:350)</td>
<td>(Linnaeus, 1766)</td>
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<tr>
<td>28. Draco praepos</td>
<td>Draco volans</td>
<td>“America”</td>
<td>Java</td>
<td>Untraced</td>
<td>Based on Seba (1734:160; Pl.102; Fig.2)</td>
</tr>
<tr>
<td>Linnaeus, 1766 (p.358)</td>
<td>(Linnaeus, 1758)</td>
<td></td>
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<tr>
<td>29. Anguis quadrupes</td>
<td>Lygosoma quadrupes</td>
<td>“Java”</td>
<td>Indo-China, Sumatra, and Java</td>
<td>Not designated</td>
<td>Not specified</td>
</tr>
<tr>
<td>Linnaeus, 1766 (p.390)</td>
<td>(Linnaeus, 1766)</td>
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<tr>
<td>*30. Anguis platura</td>
<td>Pelamis platura</td>
<td>Type locality not specified</td>
<td>Pacific and Indian Oceans</td>
<td>Untraced</td>
<td>ex-“Mus. Fr. Ziervogel Pharmac. Holmes” (see text for details)</td>
</tr>
<tr>
<td>Linnaeus, 1766 (p.391)</td>
<td>(Linnaeus, 1766)</td>
<td></td>
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</tbody>
</table>
Evolution, Uppsala (UUZM 17). *Gekko gecko* is widespread in eastern Asia and mainland southeast Asia, with only localized populations in insular areas, and given the activity of Swedish maritime trade, is likely to have been collected originally in eastern China.

A majority of Linnaean names were derived from Museum Adolphi Friderici, the natural history collection maintained by the King of Sweden, Adolf Fredrik (1710–1771), and abbreviated as “Mus. Ad. Fr.” in Linnaean works (i.e., Vol. 1: Linnaeus 1754, in folio; Vol. 2: Linnaeus 1764, in octavo). This collection was kept in the Ulriksdal Castle, north of Stockholm, and consisted of mostly alcoholic specimens (numbering about 1,100 jars). A parallel collection was maintained by the Queen, Lovisa Ulrika (1720–1782), at the Drottningholm Castle, and comprised mostly of dry specimens of shells, coral and insects, especially butterflies (Holm 1957; Kullander 2001). In citing the names (and material) from Museum Adolphi Friderici, the descriptions of Linnaeus (1758) typically contained references to the volume and for most, page numbers as well, while the latter edition (1766) provided both volume and page numbers. This is important, in view of the fact that the second volume of contents from Museum Adolphi Friderici was completed by 1754 but published only in 1764 (Kottelat and Persat 2005). Provenance for most of the material in this collection remains unclear, and some ichthyological types were presumably obtained during the voyages of the SOIC, along the India-China route (see Ng and Kottelat 2008).

Sri Lankan representatives from Linnaean material include: *Anguis maculata* Linnaeus, 1758 (current name: *Cylindrophis maculatus*), a lowland endemic, as well as *Coluber Calamarius* Linnaeus, 1758 (current name: *Oligodon calamarius*). Two species from this collection co-occur in Sri Lanka as well as peninsular Indian and the Indian and Asian mainland, respectively, the agamid *Lacerta Calotes* Linnaeus, 1758 (current name: *Calotes calotes*). *Coluber vittatus* (current name: *Xenochrophis vittatus*) represented in this collection at the time of Linnaeus (but not found by Andersson 1900) represents a Malayan element, and known to be restricted to the southern Malay Peninsula. *Coluber buccatus* (current name: *Homalopsis buccata*), material of which was not found by Andersson (1900), is now known to have a broad distribution, from the Himalayan foothills to south-east Asia. The caecilian, *Caecilia glutinosa* Linnaeus, 1758 (current name: *Icthyophis glutinosus*) is also from this collection, and indicated as from “Indiis”; the species is an endemic of Sri Lanka.

Another source of specimens available to Linnaeus was the private collection of the Dutch industrialist and amateur entomologist, Baron Charles de Geer (family name typically written as De Geer; 1720–1778). De Geer’s major work was entomological
in scope (“Mémoires pour servir à l’histoire des insectes”, in eight volumes, published between 1752 and 1778,) and he was an elected member of the Royal Swedish Academy of Sciences. His estate home and library remain extant at Leufsta bruk, now Lövstabruk (see Tancin 2007). Andersson (1900) reported that specimens from this collection remain unlabelled, but given that only holotypes are represented, they are easily recognized as Linnaean types. The south Asian pythonid snake, *Coluber Molurus* Linnaeus, 1758 (current name: *Python molurus*) was based on a specimen from “Mus. De Geer” and is extant at the Naturhistoriska Riksmuseet, Stockholm (NRM 5).

A third collection that was open to Linnaeus was that of Jonas Alströmer (1685–1761), who was a pioneer of agriculture, as well as shipbroker and proprietor of a wool factory and a sugar refinery. He was one of the founders of the Royal Swedish Academy of Sciences (in 1739), and was knighted in 1748. A biography of Jonas Alströmer can be found in Leche et al. (1904). An Asian taxon from the collection is *Coluber buccatus* Linnaeus, 1758 (current name: *Homalopsis buccata*), reportedly from “in Indiis”, the holotype is currently untraced (Andersson 1900; Kullander 2001). A second colubrid from this collection is *Coluber mycterizans* Linnaeus, 1758 (current name: *Ahaetulla mycterizans*), based on NRM 81–82 (two syntypes; Kullander 2001), reported as from “America”, and is a lowland species from the Malay Peninsula, Sumatra and Java.

The fourth and last collection to be discussed here is that of Friederich Ziervogel (1727–1782), who kept a personal collection that was donated in 1789–92 to the University of Uppsala. Ziervogel is known to have purchased specimens from the Royal collection (Wallin 2001), but little else if known about the man or his collections, except that he was Apothecary Royal, in charge of packing the collections of King Adolf Fredrik (Thunberg 1816), accompanied Linnaeus on his Öland and Gotland journeys and presented a collection of books and objects of natural history to the Royal Society of Sciences in Uppsala (Sandermann Olsen 1997). *Anguis platatura* Linnaeus, 1766 (current name: *Pelamis plataura*) is catalogued in Linnaeus (1766) as from “Mus. Fr. Ziervogel Pharmac. Holmes” (hence, the specimen should have been examined by Linnaeus at least 23 years before the donation).

Analysis of names used within the same work (e.g., “Amphibia Gyllenborgiana”; Linnaeus 1745), or over time, by Linnaeus himself (see below) sometimes show differences in either spelling, orthography or the names themselves: for example, in 1754, *Anguis* was spelled *Angvis*, for *Anguis Scytale* Linnaeus, 1758, *Anguis maculata* Linnaeus, 1758 and *Anguis bipes* Linnaeus, 1758. The use of “v” was Old Latin, dating to the early to middle Roman Republic, the names in the 1758 work may have been an attempt to use more recent (= contemporary) Latin (late Republic onwards). Other more serious differences in names include *Lacerta tigrina* Linnaeus, 1754, which became *Lacerta monitor* Linnaeus, 1758, and *Lacerta Chamaeleo* Linnaeus, 1754, which was written as *Lacerta Chamaeleon* Linnaeus, 1758.

A number of names based on Asian specimens were indicated to have been collected elsewhere: *Rana typhonia* Linnaeus, 1758, *Coluber stolatus* Linnaeus, 1758, *Coluber Calamarius* Linnaeus, 1758, *Anguis maculata* Linnaeus, 1758, *Coluber vittatus* Linnaeus, 1758, and *Coluber mycterizans* Linnaeus, 1758, were all listed from “America”. Several names that apply to Indian and southeast Asian species, such as *Caecilia glutinosa* Linnaeus, 1758, *Lacerta Monitor* Linnaeus, 1758, *Coluber mucosus* Linnaeus, 1758, *Coluber buccatus* Linnaeus, 1758, *Coluber Molurus* Linnaeus, 1758, *Coluber candidus* Linnaeus, 1758, and *Coluber Pelias* Linnaeus, 1758, were reported as from “Indiis” (referring to either the East or the West Indian Archipelagos). The problem with erroneous data has been serious for
the last two and half millennia, and stems no doubt from unknown provenance of specimens received in collections at the time, and the lack of labels bearing data (documented, most famously, for the De Geer collection).

A number of herpetological taxa in Linnaean works that are mentioned as having originated from “Oriente” or “Indiis” have been found to be extralimital to the region. Among the more familiar and spectacular taxa are *Coluber Ammodytes* Linnaeus, 1758 (current name: *Vipera ammodytes*; type locality: “Oriente”; known distribution: Europe and adjacent parts of west Asia) and *Coluber atrox* Linnaeus, 1758 (current name: *Bothrops atrox*; type locality: “Asia”; known distribution: South America and Trinidad). Given the unknown provenance or collector of a majority of specimens in the collection, the provenance of types of certain presumably rare or poorly known species continue to remain unknown. For a number of types, the use of “Indiis” as a type locality (e.g., *Boa constrictor* Linnaeus, 1758 and *Testudo scabra* Linnaeus, 1758) has led some authorities to assume erroneously that these came from India, because an indication of a western origin (sometimes even the West Indies; Kitchell and Dundee 1994) is possible. Nonetheless, a number of Linnaean names, herpetological and others, continue to be wrongly applied (see Rhodin and Carr 2009). From pre-Linnaean times to about the middle of the Victorian Period (the late nineteenth century) a number of species have been described on the basis of paintings in published works. At least part of the reason for wrong allocation of names may be attributed to the indifference to morphological/coloration details of specimens by draftsmen, engravers, colorists, and even naturalists of the time. This may be due to the lack of accuracy in available techniques and vagaries of hand-operated printing presses. These inadequate representations were compounded by a general lack of knowledge of the morphology of poorly-known tropical organisms that were inadequately preserved when they arrived in European collections. It was a long time before “accurate observations of nature become accepted as a worthwhile goal in its own right” (Dance 1978). Because a number of Linnaean names were based on previously published (= pre-Linnaean) works (e.g., Aldrovandi 1637; Seba 1734, 1735; Gronovius 1756), problems resulting from historical interpretations of Linnaean names continue to trouble contemporary taxonomy (see Moravec et al. 2006; Bauer 2012).

In all, 23 names of Asian taxa were described by Linnaeus, representing 21 biological species (Table 1). Three localities—southern Malay Peninsula, Sri Lanka and Java—could be the sources for all Asian taxa described by Linnaeus, and may indicate their importance to trade routes with Europe at the time. Some of the taxa concerned occur in adjacent areas (e.g., peninsular India, southeast Asia beyond Java, etc), and conceivably were taken elsewhere. A majority of the species are abundant, lowland taxa that may have been collected near ports, for sale to sailors, or collected by naturalists during short furloughs during voyages of the SOIC. A few (e.g., *Lyriocephalus scutatus*, *Ahaetulla mycterizans*) are rare at present, and their presence in early eighteenth century collections may reflect former abundance.

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Observation and Distillation—Preservation, Depiction, and the Perception of Nature

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Abstract. Although Linnaeus was opposed to the use of illustrations in species descriptions, \textit{Systema Naturae} includes many references to illustrations that have enabled systematists to identify species that Linnaeus described. Illustrations of specimens in early museum catalogs and printed books also provide clues to how organisms were preserved. Illustrating a specimen is a process of abstraction and distillation, beginning with a drawing based on observation of an animal by the illustrator or the graphic interpretation of someone else’s observations. The illustration can then be transferred to a wood block, copperplate, or lithographic stone and reproduced repeatedly. The impetus to produce illustrations of biological species came from both scientific necessity and aesthetic appreciation. Between the 16th and 18th centuries the accuracy of illustrations increased, corresponding to advances in preservation technology. Preservation produces physical changes in the form and color of specimens. The earliest preservation technology was dehydration, later enhanced by chemicals. Fluid preservation, introduced in 1662, was limited by the expense of alcohol and containers. In the late 1700s, improved taxidermy techniques were developed. Advances in preservation technology are reflected in contemporary illustrations of preserved specimens. While making a visual record of a specimen the illustrator recorded the specimen’s condition; these illustrations can be used to interpret preservation technology and storage conditions that altered the organism and the perception and understanding of the organism.

Keywords. Illustration, preservation, printing.

DEPICTION AND PERCEPTION

Modern systematic collections of natural history specimens evolved from the cabinets of curiosities of Renaissance Europe. The collections in these early cabinets were assembled in an attempt to find order in the chaos of nature (Findlen 1994, Mauriès 2002). By the mid-16th century, unfamiliar species brought to Europe from expeditions to the New World were confounding the existing systems of order and the dominant classification scheme, the scala natura of Aristotle (de Asúa and French 2005). Specimens of these unknown species were described and often illustrated by the owners of the collections that made up the cabinets of curiosities. An examination of illustrated and pictorial catalogs of collections can tell us much about early knowledge of biodiversity and the state of the specimens that were reaching Europe (Barbero Richart 1999, de Asúa and French 2005, Schultze 1994).

Many early graphic depictions of exotic animals from the New World were not based on direct examination of specimens, but were extrapolations from known European species, embellished by descriptions from travelers. No matter how the specimens were described
or preserved (Table 1), the perception and interpretation of what they were was both constrained and influenced by the European artists’ prior knowledge and cultural framework (de Asúa and French 2005, Findlen 1994). A reverse example of this phenomenon can be seen in New World adaptations of Old World conventions, such as the 16th century painting, “La Última Cena” (The Last Supper) that hangs in the Cathedral of Cuzco, Peru (Angles Vargas 1999). The painting is the work of native artist Marcos Zapata and shows Jesus and his disciples feasting on a roasted guinea pig (Figure 1), a New World species.

Some of the creatures that showed up in the pre-Linnaean scientific works were not based on specimens of real animals, but were interpretations of the mythological creatures described in earlier bestiaries. A commonly depicted animal was the hydra, which had no clear link to any living creature. Nevertheless, the tradition of accepting the hydra as a living creature was so strong that Albertus Seba (1665–1736) included an illustration of one (Figure 2a) in his catalog (Müsch 2001). The Seba illustration was based on a preserved specimen that had once belonged to Count Königsmark, who acquired it in 1648 after the Battle of Prague, but it bears a strong resemblance to previous depictions of the hydra such as the hydra in Prodigiorum ac ostentorum chronicon, published in 1557 (Figure 2b). When Carl Linnaeus (1707–1778) saw the preserved specimen in Hamburg in 1735 that had been used by Seba’s artist, he denounced it at once as a fake made from snake skins and the jaws and feet of several weasels (Blunt 2001). Linnaeus argued that God had never put more than one head on any created body, and so presumed that monks had manufactured the hydra as a representation of an apocalyptic beast (Blunt 2001:90).

Dragons depicted in the bestiaries could easily have been interpretations of the very real lizard

FIGURE 1. La Última Cena, Marcos Zapata (ca. 1750), Cathedral de Cuzco, Perú.

FIGURE 2. Hydra: (a) hydra from Seba’s Thesaurus (1734); (b) hydra from Prodigiorum ac ostentorum chronicon (1557).
genus, *Draco* (Figure 3) (Barbero Richart 1999). Flying lizards were one of the most prized specimens in a cabinet of curiosities (George 1985). The *Draco*-like dragon was often depicted without hind limbs. This may have been because specimens lost their hind legs during preparation or shipment or because only partial specimens were preserved—the skin and spread wings of a *Draco* are easier to dehydrate than an entire, intact lizard. Limbs missing from preserved specimens were not unprecedented—for years Europeans thought that the bird of paradise did not have legs because the first specimens shipped to Europe arrived without them (Barbero Richart 1999).

On 13 May 1572, a live and somewhat fearsome dragon was discovered near Bologna, Italy. Despite the fact that the appearance of the beast was widely seen as a troublesome omen, it was sent to one of the leading scholars and collectors of the day, Ulisse Aldrovandi (1522–1605), who quickly put the “monstrous dragon” or *Dragone mostroficato* on exhibit in his museum and reported that “an infinite number of gentlemen came to my house to see it” (Findlen 1994:17). Aldrovandi went on to write an authoritative book about dragons that included an image of the captured creature (Figure 4a). The illustration created for Aldrovandi was surely as accurate a representation of the dragon specimen as could have been made. The fact that Aldrovandi’s dragon does not have hind legs may reflect the characteristics of the real specimen or the artist may have been following the established convention of picturing dragons with only forelegs. The 1553 image of a “dragonel” or young dragon from Pierre Belon (1515–1564) (Figure 4b) is an earlier example of this custom. The way that Aldrovandi interpreted the dragon set a new standard. Previously, dragons had been thought to be portents of some diabolical catastrophe, but Aldrovandi insisted that the dragon was simply “…a natural phenomenon, devoid of metaphysical implications but rich in anatomical meaning” (Findlen 1994:22). The fact that we know as much about Aldrovandi’s dragon as we do is, in large part, thanks to the illustration of it that was reproduced as a woodblock print (also known as woodcut) in his catalogs and then copied endlessly by others. As a great...
### TABLE 1. Development of preservation technology for natural history specimens.

<table>
<thead>
<tr>
<th>Date</th>
<th>Development</th>
<th>Comments</th>
</tr>
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<tbody>
<tr>
<td>ca. 8000 BC</td>
<td>Mummification by stretching dehydrated skin over bone and wood frame (coastal Peru and Chile).</td>
<td>Oldest purpose-made animal mummies are from coastal Peru (Arriaza 1995).</td>
</tr>
<tr>
<td>ca. 5000 BC</td>
<td>Dehydration with natron (sodium chloride and sodium bicarbonate) and treatment with oils and resins (Egypt).</td>
<td>Egyptian animal mummies date to ca. 5000 BC (El Mahdy 1989). Dehydration causes distortion of tissues, loss of color, darkening of tissues due to combination of oxidation, and use of salts, spices, and resins.</td>
</tr>
<tr>
<td>5th century</td>
<td>Preservation in brine solution.</td>
<td>Reported by Herodotus (Greene 1987)</td>
</tr>
<tr>
<td>ca. 1000</td>
<td>Preservation in sealed containers of vinegar, honey, oil, or brine.</td>
<td>Bolnest 1672, Ransome 1937, Reid 1994, Shephard 2000</td>
</tr>
<tr>
<td>ca. 1550</td>
<td>Dehydration followed by varnishing.</td>
<td>Findlen 1994</td>
</tr>
<tr>
<td>1555</td>
<td>Embalming with salt preparations.</td>
<td>Pierre Belon (Farber 1977)</td>
</tr>
<tr>
<td>1560-1624</td>
<td>Plants dried in press and attached to paper.</td>
<td>Schmitz et al. 2007</td>
</tr>
<tr>
<td>1662</td>
<td>Preservation in spirit of wine (ethyl alcohol &gt;50%).</td>
<td>Presented before the Royal Society of London by William Croone (Croune) (Birch 1968, Cole 1944, Simmons 2002). Preservation in alcohol causes color changes due to shrinkage, loss of soluble pigments, and oxidation.</td>
</tr>
<tr>
<td>Mid-1600s</td>
<td>Development of taxidermy.</td>
<td>Progression from stuffing skins without forms to stretching tanned skins over body forms to allow for more realistic shapes (Farber 1997).</td>
</tr>
<tr>
<td>1695</td>
<td>Skins dried, stuffed with oakum or tow mixed with pitch or tar, dried in the sun; submerged in beverage alcohol, such as arrack, rum, or brandy (ca. 10 to 50% ethyl alcohol); preserved in sea water.</td>
<td>Recommended by James Petiver (ca. 1660–1718) and others (Farber 1977, Stearns 1953).</td>
</tr>
<tr>
<td>ca. 1700</td>
<td>Injection with colored wax or mercury.</td>
<td>Developed by Frederick Ruysch (1638–1731) (Cole 1921, Whitehead 1970).</td>
</tr>
<tr>
<td>ca. 1740</td>
<td>Inside of skin rubbed with arsenical soap (mixture of soap and arsenic powder).</td>
<td>Developed by French taxidermists, introduced in the US by Charles Willson Peale (Farber 1977).</td>
</tr>
<tr>
<td>1748</td>
<td>Guts removed, skin wrapped to protect feathers, submerged in brandy. Small birds inserted whole in glass jars or wooden barrels.</td>
<td>Réaumur 1748</td>
</tr>
<tr>
<td>1748</td>
<td>Birds soaked in brandy for 8d to 6 wks, then packed in chaff or straw in a box.</td>
<td>Réaumur 1748</td>
</tr>
<tr>
<td>1748</td>
<td>Bird gutted, embalmed with aromatic spices.</td>
<td>Réaumur 1748</td>
</tr>
<tr>
<td>1748</td>
<td>Bird gutted, dried in oven.</td>
<td>Réaumur 1748</td>
</tr>
</tbody>
</table>
naturalist of another generation, Baron Cuvier (1769–1832) put it, “One must say that without the art of the printer, natural history and anatomy, as they exist today, would not be possible” (quoted in Rifkin and Ackerman 2006:271).

The amphisbaena was another mythical animal that was described by Pliny and depicted in medieval bestiaries as a reptile with two heads (Payne 1990). Although several species of amphisbaena were known from Spain and northwest Africa, the characteristics of the mythical creature were readily matched with real specimens of amphisbaenians arriving from the New World, as seen in an illustration in Johannes Faber’s *Rerum medicarum Novae Hispaniae thesaurus* (1651) (Figure 5). The woodcut published by Faber had its origin in a manuscript compiled by Francisco Hernández (c. 1514–1587) between 1571 and 1577 that was later acquired by Nardo Antonio Recchi (d.1595), who passed it along to his nephew, Marco Antonio Petilo (dates unknown), who in turn allowed Federico Cesi (1585–1630) access to some of the illustrations; Cesi in

<table>
<thead>
<tr>
<th>Date</th>
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<tbody>
<tr>
<td>Mid-1700s</td>
<td>Use of mercuric chloride as pesticide.</td>
<td>Mercuric chloride (corrosive sublimate) causes darkening of specimens.</td>
</tr>
<tr>
<td>1753</td>
<td>Sugar added to alcohol.</td>
<td>Holm 1957</td>
</tr>
<tr>
<td>ca. 1769</td>
<td>Snakes coiled in cylindrical containers in alcohol preservative.</td>
<td>Bancroft 1769</td>
</tr>
<tr>
<td>1770</td>
<td>Preservation of bird skins (1) with varnish of turpentine and camphor; (2) dry mix of corrosive sublimate, saltpeter, alum, sulfur, musk, pepper, and ground tobacco; (3) as above but also stuffed with tansy, wormwood, hops, and tobacco, with artificial breastbone and eyes.</td>
<td>Kuckahn 1771</td>
</tr>
<tr>
<td>1774</td>
<td>Preservation of dry skins by chemical removal of fats, use of tanning solution and soapy pomade.</td>
<td>Farber 1977</td>
</tr>
<tr>
<td>1800</td>
<td>Arsenical soap (arsenic, soap, tartar salt, camphor, and powdered lime).</td>
<td>Bécoeur’s formula, first published by Dufresne (1800).</td>
</tr>
<tr>
<td>ca. 1820</td>
<td>Preparation of bird specimens as study skins; lead tags attached to specimens, specimens stored in drawers with camphor.</td>
<td>Recommended study skins over taxidermy mounts to save space (Allen 1994).</td>
</tr>
<tr>
<td>1825</td>
<td>Specimens soaked in alcohol with corrosive sublimate (mercuric chloride), then dried.</td>
<td>Waterton 1825</td>
</tr>
<tr>
<td>1830</td>
<td>Use of aqueous salt solution; oil of turpentine; acid solution; ammonia solution; or “metallic, alkaline, or earthy salt” added to alcohol solution.</td>
<td>Parsons 1831</td>
</tr>
<tr>
<td>1840</td>
<td>Aluminum sulfate, alum, or nitre and salt added to alcohol solution.</td>
<td>Gannal and Harlan 1840</td>
</tr>
<tr>
<td>1893</td>
<td>First use of formaldehyde fixation.</td>
<td>Blum 1893</td>
</tr>
</tbody>
</table>
It was Linnaeus who brought the first real order to the chaos of known and unknown species. Linnaeus believed that species should be described in just a few words at most (Schmitz et al. 2007). Even though he did not think much of illustrations—he referred to them as “icons” (Freedberg 2002:6)—Linnaeus based many of his species descriptions on published illustrations of animals he had never seen, alive or preserved. Other authors, however, including Aldrovandi and John Ray (1627–1705), treasured illustrations as much as the specimens themselves as having unique epistemological status (Grindle 2005). Aldrovandi’s collections included 11,000 animal specimens, 8,000 tempera illustrations, and countless woodblock prints (de Asúa and French 2005); Ray’s collections included numerous illustrations, many prepared on commission (Grindle 2005).

In Linnaeus’ time, it is worth noting, botanical illustration was much more accurate than the illustrations of animals (Dance 1978, Pavord 2005, Pinault 1991). Botany was more standardized, not hampered as much by mythology, and plant specimens were more easily preserved than other living organisms. The practice of pressing plants and arranging herbaria has been carried out since the early 16th century (the oldest known extant herbarium was established by Luca Ghini (1490–1556) in 1532) (Schmitz et al. 2007). Many of the animal species Linnaeus named were based on the illustrated catalog published by Seba (Blunt 2001, Müsch 2001). A famous portrait by Jan Mauritius Quinkhard (1688–1772) shows Seba with row upon row of fluid preserved specimens behind him, holding a snake in a jar in one hand, while pointing to shells, loose drawings, and an opened copy of his printed catalog with his other hand, making clear the connection between the living organism, the preserved specimen, the materials of the artist, and how the species was subsequently interpreted (Figure 6). As one author put it, “…the plant or animal in question underwent a considerable abstraction and distillation on its way to becoming a scientific illustration” (Müsch 2001:16). Linnaeus cited specimens depicted in Seba’s *Thesaurus* no less than 284 times (Willmann and Rust 2001).

The catalogs of Konrad Gesner (1516–1565; sometimes spelled Gessner), Aldrovandi, and Seba marked the acceptance of the fact that pictures convey authentic information about nature (Dickenson 1998). These illustrations played a leading role in disseminating knowledge throughout Europe because drawing, like writing, was a means of widely broadcasted communication. It has been said that printing provides an “exactly repeatable visual statement” (William M. Ivins, quoted in Blum 1993:8). Another scholar noted “It may even be true that no single factor has influenced scientific illustration as much as the convention of rectangular paper” (Blum 1993:3). What is often overlooked is that the illustrations used to study and prepare the learned treatises, reproduced as woodblocks and copper engravings, became a distinct pictorial genre all by themselves. These works were produced with two different audiences in mind—natural historians, and collectors of fine art (Müsch 2001, Rifkin and Ackerman 2006). The illustrations served both for scientific instruction and aesthetic appreciation because neither audience alone could support the production of these expensive, lavishly illustrated books. Gesner’s *Historia animalium*, for example,
contained more than 4,000 woodblock prints (Müsch 2001); John Ray was forced to publish his master work, *Historia plantarum* (1686–1704) with no illustrations in its 3000 pages of text due to the expense of engravings (Desmond 2003). By the 18th century, many of the large and generously illustrated natural history books were issued in parts to allow subscribers to pay in installments, and to allow the publishers to spread their costs over a longer period of time (Desmond 2003).

Paper was not made in Europe until the 1100’s (Table 2), and remained expensive and difficult to obtain until the 1400s. From the Renaissance onward artists made drawings on paper using a variety of materials, including black and red chalks, charcoal, pen & ink, washes, and watercolors. As a greater variety of fine grades of paper became available, artists were able to produce more nuanced drawings than had previously been possible, drawings more finely detailed and sophisticated.

Carving woodblocks and engraving copper-plates was a laborious and tedious task. In some cases, the artists themselves prepared the blocks and plates, but more commonly this task was handed off to specialized artisans (Dance 1978). Images were frequently reused, both due to the expense of making a new block or plate and because of their popularity.

Hand-coloring of the black and white printed illustrations added value to the work, particularly among collectors of fine art, but it was very expensive and the colors were not necessarily accurate (Knight 1977). For example, in order to get his *Thesaurus* published, Seba had to put up a third of the money while his two joint publishers put up the other two-thirds (Müsch 2001). Purchasers of the book (most by subscription) had to hire their own artists to add color to the plates. At least one artist, named J. Fortuyn (dates unknown), specialized in coloring the Seba plates and signed his work (Müsch 2001). Maria Sybilla Merian (1647–1717) and her daughters colored a few copies of her books, but the majority of the color work was completed by other artists (Reitsma 2008). Copies of Merian’s work from Surinam in the Royal Library at Windsor Castle have watercolor applied over faintly etched outlines on velum and paper, presumably colored by Merian’s own hand (Owens 2007).

An example of the impact of the printing process and image reproduction is the well-known drawing of the “boilerplate rhino” of Dürer (Quammen 2000)—in 1515, Albrecht Dürer (1471–1528) made a drawing of a rhinoceros based on a description and a sketch, possibly by a Moravian artist named Valentim Ferdnandes (?–1519) (Bedini 1997, Dickenson 1998) who had access to the animal before it died (Dürer himself never saw his subject). The rhinoceros in question, a specimen of *Rhinoceros unicornis*, the Indian rhinoceros (Figure 7), had arrived at Lisbon on 20 May, 1515 as a gift to King Manuel I (1469–1521) from Sultan Muzafar II (dates unknown) of
TABLE 2. Development of illustration and replication technology for natural history illustrations in Europe.

<table>
<thead>
<tr>
<th>Date</th>
<th>Development</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>ca. 3000 BC</td>
<td>Papyrus paper and lamp-black based ink</td>
<td>Papyrus reeds (<em>Cyperus papyrus</em>) were split, the pith cut into strips about 40 cm long, and laid across each other at right angles, then hammered together, and dried under pressure. The sheets were polished with a smooth stone, then glued together to form a roll. Egyptian ink was made from lamp-black and gum; pens and were made from rushes (Derry and Williams 1961).</td>
</tr>
<tr>
<td>ca. 250 BC</td>
<td>Parchment and vellum</td>
<td>Un-tanned leather from cattle, sheep, or goats; vellum is made from the skin of a young calf or kid. Skins are washed, soaked in lime, stretched and dried, shaved thin with a knife, then smoothed.</td>
</tr>
<tr>
<td>ca 100 BC</td>
<td>Paper</td>
<td>Papermaking began in China with pressed and dried randomly interwoven mats of plant fibers.</td>
</tr>
<tr>
<td>1266</td>
<td>First Spanish paper mill</td>
<td>Papermaking reached the Arab world after the defeat of the Chinese at the Battle of Talas in 751 AD.</td>
</tr>
<tr>
<td>Prior to 1400</td>
<td>Woodblock</td>
<td>Relief printing technique (unwanted wood cut away on plank side of a block of hard wood, traditionally pear, apple, or sycamore; ink applied to uncut surface; image transferred to paper, fabric, etc.) that produces a mirror image of the original illustration (Dance 1978). Oldest known woodblock print is from China in A.D. 868 (Ross et al. 1990).</td>
</tr>
<tr>
<td>ca. 1400</td>
<td>Oil-based ink</td>
<td>Oil based ink spreads more evenly over the printing surface than water-based ink and produces cleaner lines (Derry and Williams 1961).</td>
</tr>
<tr>
<td>ca. 1430</td>
<td>Intaglio</td>
<td>Gravure printing technique (image incised into metal plate, usually copper or zinc; incised area filled with ink that is transferred under pressure onto paper) to produce a mirror image of the original illustration (Ross et al. 1990).</td>
</tr>
<tr>
<td>ca. 1439</td>
<td>Printing press</td>
<td>Mechanical device to apply pressure on inked surface resting on a medium (paper). The printing press combined woodblock and movable type to eventually replace most versions of block printing. First system assembled by Johann Gutenberg (Derry and Williams 1961). The printing press accelerated the printing process and allowed for the production of more copies more quickly and economically than previous methods.</td>
</tr>
<tr>
<td>15th century</td>
<td>Copperplate engraving</td>
<td>Engraved copper plates allowed more delicate shading and lines than woodblock; produced a mirror image of the original illustration. Copper plates were expensive to execute but did not last as long as woodblocks in the printing process (Müsch 2001, Rifkin and Ackerman 2006, Willmann and Rust 2001).</td>
</tr>
<tr>
<td>1500s</td>
<td>Illustrations in printed books</td>
<td>Published illustrations became increasingly realistic (Müsch 2001).</td>
</tr>
<tr>
<td>1508</td>
<td>Chiaroscuro woodcut</td>
<td>Multiple-block color printing technique developed in Germany (Ross et al. 1990).</td>
</tr>
<tr>
<td>Mid- to late-17th century</td>
<td>Mezzotint</td>
<td>Variant of intaglio; copper plate worked with rocker tool and emery cloth to burnish design into roughened surface (Dance 1978, Rifkin and Ackerman 2006).</td>
</tr>
</tbody>
</table>
TABLE 2. Continued . . .

<table>
<thead>
<tr>
<th>Date</th>
<th>Development</th>
<th>Comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>Late 1760s</td>
<td>Aquatint</td>
<td>Variant of intaglio; copper plate treated with varnish and etched with acid to cover large areas of illustration with tone (so that image appears grey) without time-consuming cross-hatching (Dance 1978).</td>
</tr>
<tr>
<td>Late 1700s</td>
<td>Woodblock on end grain</td>
<td>Thomas Bewick and other craftsmen began using end grain of wood (cut across the trunk instead of along the trunk like a plank) and cutting image into the wood with gravers instead of knives to make sharper, more durable images (Ross et al. 1990, Uglow 2006).</td>
</tr>
<tr>
<td>Late 18th century</td>
<td>Lithography</td>
<td>Planographic printing technique. Image is drawn or painted onto smooth surface of limestone slab with oily medium; medium creates hydrophobic regions that accept ink; untreated areas remain hydrophilic; ink transferred under pressure to paper. Produces a mirror image of illustration on stone. Artists were able to create illustrations directly on the limestone slab (Dance 1978). Lithography greatly reduced the cost of printing illustrations (Rifkin and Ackerman 2006).</td>
</tr>
<tr>
<td>Early 19th century</td>
<td>Color printing</td>
<td>Multicolored lithographic prints replaced hand coloring; developed in France (Dance 1978).</td>
</tr>
</tbody>
</table>

Gujarat in Western India. Dürer based his rhinoceros on the familiar armor of a German knight of his era, and changed the angle of the horn to look more dangerous, matching the menacing look on the beast’s face. Dürer probably would have made a much more accurate drawing given the opportunity because he was a good observer of animals who corrected himself when confronted with new information. For example, Dürer’s 1490 woodblock of Saint Jerome (Figure 8a) included a lion with proportions that were too small and thin and with a small head, but after he later saw a live lion at a zoo in Belgium, his subsequent lion drawings (e.g, Figure 8b, dated 1511) depicted creatures that were “vastly more leonine” (Quammen 2000:208).  

After Dürer produced woodblocks of his drawing of the rhinoceros, the image (Figure 9a) was quickly disseminated throughout Europe. Dürer had the choice of using woodblock or copperplate (Table 2). Copperplate could produce finer lines and shading, but woodblock could be printed on the same page as text and the blocks were more durable than plates (one of Thomas Bewick’s (1753–1828) woodblocks was used to make more than 900,000 impressions) (Rifkin and Ackerman 2006, Ross et al. 1990). Text was set as a series of reversed letters (when printed they would be readable). Likewise, the image on the face of the woodblock would be reversed when printed. The woodblock Dürer carved of his rhino was used in at least nine editions of the print, and continued in use long after Dürer’s death, until the block had cracks and holes in it. Dürer’s rhino illustration took on an iconoclastic role which it held for more than two centuries. When Dürer’s woodblock

FIGURE 7. Indian rhinoceros, with armor-like skin.
was copied by Gesner, the resulting image of the rhino was reversed (Figure 9b). The copy from Gesner made by Matthäus Merian the Younger (1621–1687) in 1658 (Figure 9c) reversed the rhino again, made it more detailed, and reinstated the landscape seen in Dürer’s print. The rhino was considered a formidable creature and appropriate for personal emblems emphasizing personality, so the basic traits of the Dürer rhino are clearly seen in a simplified version from 1612 (Figure 9d). Aldrovandi copied the Dürer rhino from Gesner for use in his *De animalibus exanguis*, and later Edward Topsell (c1572–1625) copied Dürer’s rhino again in his *History of four-footed beasts* (1607) even though live rhinos had been seen in Europe by that time. By contrast, the 1766 illustration of the rhinoceros used by Buffon (1707–1788) was based on a live animal (Figure 10).

**FIGURE 8.** Depictions of the lion by Albrecht Dürer: (a) St. Jerome in his Study (1490); (b) St. Jerome in his Cell (1511).

**PRESERVATION**

The fate of the dragon specimen that Aldrovandi had in hand when the illustration was made is unknown. Certainly such a marvel would have been preserved carefully, but unfortunately the best preservation technology of the time was inadequate to the task. We know from contemporary descriptions that the early collections were filled with rare and valuable specimens, most dried and fragile, many coated in varnish. For example, a description of Francesco Calzolari’s (1521–1600) cabinet of curiosities in 1584 noted “how many dried terrestrial and aquatic animals” were on exhibit, and the same can be seen in a woodblock of Imperato’s museum in 1549 (Figure 11). New techniques were developed as museums evolved. The quality of the specimens reaching Europe in the 15th and 16th centuries was limited by the available preservation
technology and the constraints of travel (Table 1). Often, only parts of specimens survived the journey, such as a dried skin, a shell, or a mummified foot. The earliest preservation techniques included dehydration, and preservation in brine or vinegar. For example, about 1541, Roger Barlow (d. 1554) described how a bird was preserved: “…after it was dead we toke of the skynne, the heade, fete and feath- ers as nie as we coulde, and stuffed it with drie mosse and put it in a coffer…” (Taylor 1932:161). Preservation in ethyl alcohol became common after 1662 (Simmons 2002), and improved taxidermy techniques were employed beginning in the 17th century (Farber 1977). In 1748, the known techniques for preserving specimens were summarized (Reámur 1748) as:

1. Remove the skin and wash it, then stuff the skin and dry it, without using any preservatives.
2. Put the whole specimen in spirit of wine (alcohol).
3. Empty the body cavity and embalm the specimen, using spices, salt, alum, or lime.
4. Gut the specimen then dry it in the oven (the author recommended immediately after the bread is baked).
Preservation technologies employed during any time period frequently can be ascertained by examination of a contemporary illustration of a specimen (Simmons and Snider 2010). In the depictions of crocodiles in Figure 12a–c, we see evidence of direct observation plus cultural influence and a bit of artistic license. The Gesner crocodile in combat with a hippopotamus (Figure 12a) is clearly not based on knowledge of a live specimen, but reflects the way mythical creatures were depicted in the bestiaries (Willmann and Rust 2001). The drawing of a crocodile in Figure 12b was made by Father Louis Plumier (1646–1704) in the late 1600s on one of his trips to investigate “everything Nature produced…that was most rare and curious” (Pinault 1991:69). It is clearly based on direct observation of a specimen but then manipulated to fit on the size of paper used by Plumier. The depiction from Seba of a hatching crocodile (Figure 12c) is based on a specimen preserved in alcohol that we examined in the Museum Adolphi Friderici collection of the Naturhistoriska Riksmuseet in Stockholm (Figure 12d)—the emerging crocodile is somewhat stylized and a suture through the corner of the mouth securing the specimen in the egg is not depicted in the illustration. The cultural influence on artists was so strong that for the 1798 edition of Tableau élémentaire de l’Histoire naturelle des animaux, Cuvier also chose a representation of a crocodile (Figure 12e) based on the descriptions of crocodiles in medieval bestiaries (Payne 1990), one wielding its tale in an impossibly threatening manner, rather than one based on contemporary knowledge of crocodile behavior and examination of specimens.

As noted by Dance (1978), the copper engravings of a black-throated diver and a lizard from Ole Worm’s (1588–1655) Museum Wormianum in 1655 (Figure 13) were based on dehydrated specimens with no attempt to depict them in lifelike poses. By contrast, Maria Sibylla Merian’s illustration of the metamorphosis of the frog (Figure 14) was based on live animals that she observed, sketched, and painted (on vellum) in Suriname in 1699–1701 and on specimens she brought back to Europe, both dried and preserved in brandy (Desmond 2003, Owens 2007, Reitsma 2008, Todd 2007). Nevertheless, Merian’s images were arranged on the page for artistic appeal (Pinault 1991, Todd 2007). Most of her paintings were intended for art collectors rather than for replication. While line drawings could be reproduced on woodblocks or copperplates, no printing methods were available during Merian’s lifetime that could adequately reproduce the look of her paintings (the printed black and white images had to be hand colored).

The set of turtle illustrations published by Matthäus Merian the Younger in his Theatrum universale omnium in 1650 (Figure 15) seems to have been made by an artist who had access to the carapaces and perhaps one complete...
animal—note that the similarity of the head and limbs carried through all the specimens illustrated. The topmost “turtle” is identified as a *tatu*, which is actually the common name of a species of armadillo. Armadillos were frequently grouped with turtles because both had shells. The dried shells of armadillos, a New World animal with no Old World analog, were popular items in the cabinets of curiosities. The inaccurate depiction of the prancing armadillo in Gesner’s *Historia animalium* from 1551 (Figure 16a) was common until live specimens began to reach European artists. Gesner’s illustration of an armadillo was based on a crude drawing and a shell sent to

FIGURE 12. Crocodiles: (a) from Gesner’s *Nomenclator Aquatilium Animantium* (1560); (b) field sketch by Father Luis Plumier (late 1600s); (c) crocodile from Seba’s *Thesaurus*; (d) crocodile specimen used as basis of image in Seba’s *Thesaurus* (1734); (e) from Cuvier (1798).


FIGURE 14. Metamorphosis of the frog (ca 1700) painted by Maria-Sybilla Merian.
him from a colleague in Paris (de Asúa and French 2005). Figure 16b is a photograph of an armadillo specimen studied by Linnaeus; Figure 16c is a color illustration from Seba that is based on the same specimen (note the indentation in the shell, which we observed was caused by the convex bottom of the container the specimen is stored in when we examined the specimen in the Naturhistoriska Riksmuseet in Stockholm).

The illustration of the Suriname toad, *Pipa pipa* (Figure 17a) was based on fluid preserved specimens, quite probably including a specimen (shown in the photograph, Figure 17b) in the Museum Adolphi Friderici collection. Figure 17c shows *Pipa* specimens in jars with unusually ornamented lids. The jarred specimens are illustrated as preserved specimens rather than in lifelike poses.

The horned frog, *Ceratophrys*, was another species that confounded artists. The Seba illustration (Figure 18a) was based on a preserved specimen (Figure 18b), now in the Museum Adolphi Friderici collection. The 1802 illustration from Shaw’s *Zoology* (Figure 18c) was made from the Seba illustration—note that the image is reversed and it repeats the errors made in the shape of the eye, the digits, and the mouth.

The iguana depicted in Seba’s *Thesaurus* (Figure 19a) has an exaggerated tail curled in
FIGURE 17. Suriname toad, *Pipa pipa*: (a) from Seba’s *Thesaurus* (1734); (b) specimen in Museum Adolphi Friderici collection (Naturhistoriska Riksmuseet, Stockholm); (c) depiction of Suriname toad specimen preserved in alcohol from Ruysch’s *Opera Omnia* (1721).

FIGURE 18. The horned frog, *Ceratophrys ornate*: (a) from Seba’s *Thesaurus* (1734); (b) specimen from the Museum Adolphi Friderici collection (Naturhistoriska Riksmuseet, Stockholm); (c) illustration from Shaw’s *Zoology* (1802).
an unnatural position. Because of the accuracy of most of the animal’s features, it is reasonable to assume that the illustration was based on a well-preserved specimen but arranged for aesthetic appeal on the page. By contrast, Louis Feuillée’s (1660–1732) field sketch of a West Indian iguana (Figure 19b) shows the straight lines used as part of measuring system to ensure proper dimensions, although the illustration was adapted to fit within the format of the paper.

The depiction of the entwined vipers in Figure 20a may have been based on observations of mating or territorial interactions of live snakes. More typically, snakes were shown positioned in unnatural, awkward coils (Figure 20b). This may have been for aesthetic effect, in order to show both dorsal and ventral patterns and colors, or to show the length of the snake. It has been suggested that these illustrations are of specimens that had been coiled in round containers when preserved (Adler 2000). Prior to about 1800 most snake specimens were not coiled when preserved—glass containers were very expensive, difficult to seal, and prone to breakage so specimens of were usually preserved in wooden casks. We have examined pre-1800 snake specimens in the Museum Boorhave in Leiden and the Naturhistoriska
Riksmuseet in Stockholm and found that very few of them show evidence of having been coiled up the sides of cylindrical containers when preserved. A review of preservation instructions (for example, Anonymous 1831, Baird 1852, Bean 1881, Reámur 1748, and Walker 1811) reveals that wooden casks and barrels were recommended until the late 1880s for preserving specimens in fluid. However, a contemporary account of how one collector preserved snakes in the field can be found in the 1769 book published by Edward Bancroft (1744–1821) about his travels in Guiana:

“The method which I use in preserving these Animals, may perhaps not be unworthy of a communication. When the Snake is killed, it must first be washed clean, and freed from all filth and nastiness; then it is to be put into a glass of a proper size, the tail first, and afterwards the rest of the body, winding it in spiral ascending circles, and disposing the back, which is always the most beautiful, outwardly. A thread, connected to a small glass bead, is, by the help of a needle, to be passed thro’ the upper jaw from within outwardly, and

FIGURE 21. Snakes: (a) illustration of cobra with hood extended from Seba’s *Thesaurus* (1734); (b) preserved cobra specimen with hood artificially extended from Museum Adolphi Friderici collection (Naturhistoriska Riksmuseet, Stockholm).

FIGURE 22. Snakes: (a) color change from green to blue due to loss of alcohol soluble pigments and tissue shrinkage in specimen of “Boa canina” (= *Corallus caninus*) from Museum Adolphi Friderici collection (Naturhistoriska Riksmuseet, Stockholm); (b) illustration of specimen in 20a showing color change from green to blue from Seba’s *Thesaurus* (1734).
then thro’ the cork of the bottle where it must be fastened: by this means the head will be drawn into a natural posture, and the mouth kept open by the bead, whereby the teeth, &c. will be discovered: the glass is then to be filled with rum, and the cork sealed down, to prevent its exhalation. A label, containing the name and properties of the Snake, is then to be affixed to the wax over the cork; and in this manner the Snake will make a beautiful appearance, and may be thus preserved a great number of years; nor will the spirits impair or change the lustre of its colours” (Bancroft 1769:218–220).

Figure 20c shows the sort of preserved specimen artists typically had to work with at the time. In Figure 21a, two cobras are shown with their hoods extended, significantly similar to the preserved cobra specimen with hood artificially extended in Figure 21b. The preserved snake (Figure 22a), which was green in life, has turned blue as a result of a combination of the loss of alcohol-soluble pigments and tissue shrinkage, a common preservation-induced color shift in green reptiles and amphibians. Artists drawing from preserved specimens, and unfamiliar with the living organisms, had to either guess how the specimens had looked in life or depict the color changes caused by preservation. The illustration of a snake (Figure 22b) shows the color of the preserved specimen as its color begins to shift from green to blue. The blue snake in Figure 20b may have been drawn from a preserved specimen that had lost its green color completely.

As more species were collected and cabinets grew in popularity, both the scientific and the aesthetic value of prints and drawings of organisms comprising these collections increased. Advances in preservation technology that allowed for better prepared specimens to reach European scientists and artists equaled the demand for greater accuracy in illustration and reproduction. The heightened sophistication of drawings, paintings, and prints not only recorded a pictorial description of a specimen but also chronicled the advancements in preservation technology.

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Reamur, R.A.F. 1748. Diverse means for preserving from corruption dead birds, intended to be sent to remote countries, so that they may arrive there in good condition. Some of the same means may be employed for preserving quadrupeds, reptiles, fishes and insects. Philosophical Transactions of the Royal Society of London 45:304–320.


INTRODUCTION

In this paper, I will present a brief overview of general approaches to biological nomenclature, from Linnaeus to the present, including a controversial new approach called phylogenetic nomenclature and an alternative code based on it, commonly known as the PhyloCode. Both in the popular press and in the scientific literature, the PhyloCode is often characterized as a challenge to the “Linnaean System.” For this reason, describing and indeed endorsing this approach in a symposium celebrating the legacy of Linnaeus may seem out of place. However, I will argue that contrary to common characterizations, phylogenetic nomenclature and the PhyloCode represent, in at least one very important respect, a return to the nomenclatural practices of Linnaeus and other early taxonomists.

To make this case, I will first describe nomenclature as practiced by Linnaeus and other early taxonomists. I will then describe the rank-based approach to nomenclature that emerged in the century after Linnaeus and came to form the basis of the current Zoological Code. And finally, I will describe the recently proposed phylogenetic approach to nomenclature that underlies the PhyloCode. In each case, I will discuss (using herpetological examples) the relationships between taxon names, on the one hand, and taxa versus categorical ranks, on the other, for the purpose of comparing...
the three approaches. I should also note that I have published the main ideas presented in this paper previously (de Queiroz, 2005) and have agreed to revisit them here at the request of the symposium organizers.

LINNAEAN NOMENCLATURE

I will use the term “Linnaean nomenclature” to refer to the general approach to nomenclature practiced by Linnaeus. This general approach should not be confused with the taxon names used by Linnaeus, which is Linnaean nomenclature in a different sense. More importantly, it should not be equated with nomenclature as currently practiced, as I will explain below. I should also clarify that when I refer to Linnaean nomenclature, I am really referring to nomenclature not only as it was practiced by Linnaeus but also as it was practiced by late 18th and early 19th Century naturalists generally—specifically, to nomenclature as it was practiced after the use of categorical ranks became widespread (following Linnaeus) but before the alternative rank-based approach emerged in the mid 19th Century.

Most readers will be familiar with the so-called Linnaean hierarchy, the series of taxonomic categories or categorical ranks instituted by Linnaeus and elaborated upon by subsequent taxonomists. Linnaeus himself used only five ranks consistently: kingdom, class, order, genus, and species (variety was used only in some cases). Subsequent taxonomists added both primary ranks, such as phylum and family, as well as secondary ranks formed by adding rank-modifying prefixes to the primary ranks, resulting in ranks such as subclass, infraorder, and superfamily. Most readers will also know that these categorical ranks were, and still are, used to help indicate position in the taxonomic hierarchy—that is, which groups are nested and which are mutually exclusive.

Relationships between Taxon Names, Taxa, and Categorical Ranks under Linnaean Nomenclature

Although Linnaeus and other early naturalists used ranks to convey taxonomic (hierarchical) relationships, they did not use ranks for nomenclatural purposes. As a consequence, taxon names were more closely associated with taxa than they were with ranks. The evidence supporting this proposition concerns how changes in the assignments of taxa to different ranks affected the names of those taxa, and the relevant cases are those in which different authors recognized the same taxon but assigned that taxon to different categorical ranks. Ideally, these would be examples of how Linnaeus applied names to taxa that had been recognized by previous authors but assigned those taxa to different categorical ranks. However, most authors prior to Linnaeus did not make extensive use of categorical ranks; that was one of Linnaeus’s innovations. Therefore, the relevant comparisons are those involving taxa that were recognized both by Linnaeus and by subsequent authors who assigned those taxa to different categorical ranks. In keeping with the theme of the symposium and the taxonomic emphasis of this journal, I will use herpetological examples.

The first concerns the taxon that Linnaeus, in some of the early editions of his Systema Naturae (e.g., Linnaeus, 1735, 1740, 1748) recognized for a group composed of turtles, frogs, lizards, crocodylians, salamanders, and snakes. Linnaeus ranked this taxon as a class, and he named it Amphibia. Later, Merrem (1820) recognized the same taxon but assigned it to a higher categorical rank. Although Merrem did not state the exact rank of Amphibia, that rank can be inferred to have been above the rank of class, given that the two primary subgroups of Amphibia (Pholidota and Batrachia) were ranked as classes. The relevant point is that Merrem used the same name used by Linnaeus,
Amphibia, despite assigning the group to a different categorical rank.

In later editions of the *Systema Naturae* (1758, 1766–8), Linnaeus recognized a taxon of a somewhat different composition as Amphibia, adding various (mostly cartilaginous) “fishes” to the original set of organisms and again ranking it as a class. Later, Scopoli (1777) recognized the same taxon but assigned it to the rank of tribe. Despite the difference in rank, Scopoli used the same name, Amphibia, for this taxon.

To cite a final example, Linnaeus (1748, 1758, 1766–8) recognized a group composed of lizards, crocodylians, salamanders, frogs, and turtles (but not snakes or any fishes) as a subgroup of Amphibia. He ranked this taxon as an order and called it by the names Reptilia and Reptiles. Scopoli (1777) once again recognized the same taxon, but ranked it as a division rather than an order. Despite this difference in rank, he used the same name, Reptilia. Most other late 18th and early 19th Century authors who used the name Reptilia or Reptiles (e.g., Laurenti, 1768; Daudin, 1802–1803; Lamarck, 1809) applied that name to a more inclusive taxon corresponding in composition to the one that Linnaeus (e.g., 1735, 1748; see also Linnaeus and Gmelin, 1788) called Amphibia, ranking it as a class. The fact that these other authors ranked Reptilia as a class, while Linnaeus ranked it as an order, did not prevent them from using the same name.

These examples illustrate that among Linnaeus and his immediate followers, different authors often recognized the same taxa (groups) but assigned them to different categorical ranks, and that when they did this, they often used the same names. This situation constitutes evidence that taxon names were more closely associated with taxa than they were with categorical ranks—a point that should become clearer when we consider an alternative approach to nomenclature that emerged during the century after Linnaeus.

**RANK-BASED NOMENCLATURE**

I will use the term “rank-based nomenclature” for an approach to nomenclature based on categorical ranks. Under this approach, taxon names are linked to particular ranks, and rank assignment is therefore necessary for the application of those names. The rank-based approach emerged during the middle of the 19th Century, becoming well established roughly 100 years after the publication of the tenth edition of Linnaeus’ *Systema Naturae* (1758). It is important to recognize that although this approach is based on the taxonomic ranks introduced by Linnaeus, it differs significantly from the nomenclatural approach adopted by Linnaeus and his immediate followers. The rank-based approach underlies the current nomenclatural codes, including the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature [ICZN], 1999), which are therefore more appropriately designated “rank-based” rather than “Linnaean.”

The rank-based approach is used for all names whose application is most closely governed by the rank-based codes. In zoology, this means all names associated with the ranks from subspecies to superfamily (i.e., names in the species, genus, and family groups). It is most obvious, however, for the subset of those names from subtribe to superfamily, which are formed using standardized rank-specific or rank-signifying suffixes. Table 1 is a list of the standardized, rank-signifying endings used in zoology. It is important to note that standardized, rank-signifying endings were not used by Linnaeus and other 18th and early 19th Century naturalists. For example, some of the names of taxa that Linnaeus ranked as classes ended in -ia, others in -es, and still others in -a. In addition, these same endings were also used for the names of taxa ranked as orders. In short, particular endings were not used exclusively and universally in association with particular categorical ranks, the way they are today. The
standardized, rank-signifying endings were introduced sometime during the early middle of the 19th Century. I have not researched their history thoroughly, but consistent use of the -idae ending for zoological taxa ranked as families can be found as early as 1825 in a paper by the herpetologist J. E. Gray, and this practice was endorsed as a general rule as early as 1835 by W. Swainson. It was also adopted by some of the important precursors of the modern rank-based codes, such as the Stricklandian code in zoology (Strickland et al., 1843). Most importantly, it was adopted by the original international codes of both botanical and zoological nomenclature and all of their subsequent revisions.

The use of standardized, rank-signifying endings implies a method of definition (i.e., of specifying the reference of a taxon name so that it can be applied in the context of alternative taxonomic proposals) that is strongly tied to the taxonomic ranks. Although this definitional method is not stated explicitly in the rank-based codes, it can nevertheless be inferred from the manner in which names are applied in rank-based nomenclature. The method takes the following form: [taxon name] = the taxon assigned to the rank of [rank name] that includes [name of type]. For example, the taxon name Iguanidae is implicitly defined as the taxon assigned to the rank of family that includes the genus Iguana. Although this definitional method is most apparent in the case of names with standardized, rank-signifying suffixes—it that is, to names associated with ranks from supergenus to subspecies.

**Relationships between Taxon Names, Taxa, and Categorical Ranks under Rank-based Nomenclature**

The adoption of rank-based nomenclature led to a significant change in the relationships between taxon names, on the one hand, and taxa versus ranks, on the other. As demonstrated above, earlier nomenclatural practices granted more importance to the associations of taxon names with taxa, rather than ranks. In contrast, the rank-based approach reversed the relative importance of those associations. Greater importance was effectively placed on the associations of names with ranks, rather than with taxa. This situation is evident from the way that rank-based nomenclature works, as illustrated in the example in Figure 1.

Suppose we have three taxa, an inclusive group named Acrodonta, ranked as a suborder, and two subgroups named Agamidae and Chamaeleonidae, ranked as families (Fig. 1a). Now suppose that later the same taxa are assigned to different ranks: the inclusive group is demoted in rank from suborder to family and its subgroups are lowered in rank from family to subfamily (Fig. 1b). Under rank-based nomenclature, such a change in ranks would require changing the names of the three taxa to reflect the new ranks. For example, the taxon originally

**TABLE (1).** The Standardized Rank-signifying Endings used by the Rank-based Zoological Code (ICZN, 1999, Art. 29.2). Note that the rank-based approach applies to names associated with all ranks from subspecies to superfamily in zoology, not only to those with standard rank-signifying endings.

<table>
<thead>
<tr>
<th>Categorical Rank</th>
<th>Ending</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superfamily</td>
<td>-oidea</td>
<td>Iguanoidea</td>
</tr>
<tr>
<td>Family</td>
<td>-idae</td>
<td>Iguanida</td>
</tr>
<tr>
<td>Subfamily</td>
<td>-inae</td>
<td>Iguanina</td>
</tr>
<tr>
<td>Tribe</td>
<td>-ini</td>
<td>Iguanini</td>
</tr>
<tr>
<td>Subtribe</td>
<td>-ina</td>
<td>Iguanina</td>
</tr>
</tbody>
</table>

Kevin de Queiroz
named *Chamaeleonidae* (with a *d*) would have to change its name to *Chamaeleoninae* (with an *n*), to reflect its new rank of subfamily. The change would be more severe in the case of the inclusive taxon, which would have to change from *Acrodonata* to *Chamaeleonidae*. In addition to the taxa changing their names, the names would also change their references. For example, the name *Chamaeleonidae*, which originally applied to one of the two less inclusive taxa, would have to be applied to the more inclusive taxon under the new ranks.

This example illustrates that under rank-based nomenclature, taxon names are more closely associated with categorical ranks than they are with taxa. When the ranks of taxa are changed, taxon names retain their associations with the original ranks, rather than retaining their associations with the original taxa. This situation implies that the rank-based system effectively treats the rank of a taxon as though it is more important to the concept of that taxon than are ideas about properties such as composition, diagnostic characters, or phylogenetic relationships. It is therefore inconsistent with the widespread opinion among biologists that the rank of a taxon is less significant than are those other properties.

### Non-rank-based Contemporary Nomenclature

Oddly, not all of contemporary nomenclature is rank-based. At least some contemporary names are applied in a manner that is more similar to the manner in which Linnaeus and other early naturalists applied them. In both botany and zoology, the application of certain names is not based on ranks, and those names, like those of 18th Century biology, are more closely associated with taxa than with ranks. In zoology, this is true for names above the rank of superfamily, which have neither standardized, rank-signifying suffixes nor implicit rank-based definitions. Consider the case of “*Lacertilia*” (lizards, now known to be a paraphyletic group), *Serpentes* (snakes, which render lizards paraphyletic when treated as a mutually exclusive taxon), and *Squamata*, a more inclusive group containing both “*Lacertilia*” and *Serpentes*. Before the paraphyletic “*Lacertilia*” was abandoned (in truth, this process has not yet been completed), some authors ranked these three taxa as two suborders within an order (e.g., Romer, 1956, 1966; Kuhn, 1966; Carroll, 1988), while others ranked them as two orders within a superorder.
However, because all of these ranks are above the level of superfamily, application of the names was not based on ranks but on composition and diagnostic characters. As a consequence, the taxa retained the same names regardless of which ranking scheme was adopted.

**PHYLOGENETIC NOMENCLATURE**

The term “phylogenetic nomenclature” has been applied to a nomenclatural approach based on evolutionary principles. This approach ties taxon names to explicitly phylogenetic concepts of taxa using methods that describe taxa in terms of common ancestry and descent. Phylogenetic nomenclature is a relatively new approach that was first proposed in the late 20th Century. Given the theme of the symposium and the taxonomic focus of this journal, it is worth noting that this approach was first proposed by herpetologists (e.g., Gauthier et al., 1988; Estes et al., 1988; de Queiroz and Gauthier, 1990, 1992, 1994). In any case, the methods of phylogenetic nomenclature are inherently tree-based in that they require phylogenetic trees (or some analogous method for describing or representing phylogenetic relationships) for their application. Phylogenetic nomenclature forms the basis of the draft Phylogenetic Code or PhyloCode (Cantino and de Queiroz, 2010), a nomenclatural code currently under development that represents an alternative to the rank-based codes such as the Zoological Code (ICZN, 1999).

**Similarities to Rank-based Nomenclature**

Before discussing the relationships between names, taxa, and ranks in phylogenetic nomenclature, I want to describe a few general things about this approach, which may be unfamiliar to some readers. Importantly, phylogenetic nomenclature shares several basic goals and methods with rank-based nomenclature. For example, both approaches have the same fundamental goals of promoting nomenclatural clarity and stability, to the extent that doing so does not interfere with the representation of new taxonomic conclusions. Both approaches accomplish this goal by providing unambiguous methods for applying names to taxa and for selecting a single accepted name for each taxon as well as a single accepted referent taxon for each name. Neither approach infringes upon the judgment of taxonomists with respect to inferring the composition of taxa or to assigning taxonomic ranks (contrary to a widely held misconception, phylogenetic nomenclature does *not* prohibit the use of ranks). Furthermore, both approaches use precedence, a clear order of preference, to determine the accepted name of a taxon when synonyms or homonyms exist. Both use priority, the earliest date of publication, as the primary criterion for establishing precedence. And both phylogenetic and rank-based approaches allow a later-established name to be conserved over an earlier-established one—that is, for priority to be set aside—if using the earlier name contradicts the fundamental goal of promoting nomenclatural stability and continuity.

**Differences from Rank-based Nomenclature**

The main difference between phylogenetic and rank-based nomenclature concerns the methods for applying names to taxa under the alternative systems. As described above, rank-based nomenclature uses implicit definitions that are stated in terms of taxonomic ranks. In contrast, phylogenetic nomenclature uses explicit definitions that are stated in terms of ancestry and descent, or their products, clades. Figure 2 illustrates the three most general kinds of phylogenetic definitions—termed *node-based*, *branch-based*, and *apomorphy-based*—and how they relate to the components of phylogenetic trees. For example, in the case of a node-based definition, a taxon
name is defined as referring to the clade originating with the most recent common ancestor of two or more specified species or organisms (labeled A and B in Fig. 2, where the definition is stated in an alternative, more economical, form). As should be evident from this description, the methods of phylogenetic nomenclature are based on trees. In this respect, phylogenetic nomenclature is part of a general trend in biology towards more explicitly tree-based methods (e.g., O’Hara, 1988; Donoghue, 1989; Harvey et al., 1995).

**FIGURE 2.** Three General Types of Phylogenetic Definitions. A node-based definition (a) associates a name with the clade originating with the last common ancestor of two or more specified species or organisms (A and B in this example). A branch-based definition (b) associates a name with the clade originating with the first ancestor of one (or more) specified species or organisms (A) that is not an ancestor of one or more other specified species or organisms (C). An apomorphy-based definition (c) associates a name with the clade originating with the first ancestor of a specified species or organism (A) to evolve a specified derived character state (X). Arrows point to the node (a), branch (b), and apomorphy (c) specified by the three definitions.

An example is given in Figure 3, which uses the same taxa, names, and ranks as the example illustrating the effect of changes in rank under rank-based nomenclature (Fig. 1). In this example, the original names (Fig. 3a) have been defined hypothetically using phylogenetic definitions employing species included within the named taxa as reference points (which are called *specifiers* in the terminology of phylogenetic nomenclature and function roughly analogously to the name-bearing types of rank-based nomenclature). The two diagrams (Fig. 3a and 3b) indicate changes in ranks without any changes in ideas about phylogenetic relationships. In one case, the two taxa (clades) are ranked as a suborder and two families (Fig. 3a); in the other, as a family and two subfamilies (Fig. 3b). If the stated definitions are applied in the context of these two ranking schemes, the same names are applied to the same clades. This is to be expected given that the application of names under phylogenetic nomenclature depends on
phylogenetic relationships, not on ranks, and the tree topologies are identical. The important point is that the names retain their associations with the same taxa, not with the same ranks.

Thus, when only ranks change, and ideas about more significant biological properties (e.g., phylogenetic relationships, hypothesized composition) do not, names in phylogenetic nomenclature remain associated with the same taxa. In this important respect, phylogenetic nomenclature is like Linnaean nomenclature, but unlike rank-based nomenclature. In other words, both phylogenetic nomenclature and nomenclature as it was practiced in the time of Linnaeus grant more importance to the associations of taxon names with taxa, rather than with ranks, which is exactly opposite to the situation in rank-based nomenclature.

Changing Ideas about Phylogenetic Relationships

In the example presented in the previous section, ideas about phylogenetic relationships were held constant. If ideas about phylogenetic relationships change, then the composition of the taxon to which a particular name is applied can also change. This is the case regardless of whether names are governed by rank-based or phylogenetic nomenclature. Under phylogenetic nomenclature, however, such changes occur in ways that make more sense with respect to the associations between names and taxa (Figure 4).

For example, suppose that the taxon Agamidae was found to be paraphyletic relative to Chamaeleonidae—that Agama was found to share a more recent common ancestor with Brookesia and Chamaeleo than with Leiolepis.
FIGURE 4. The Effect of Changes in Hypotheses about Phylogenetic Relationships under Rank-based (a) and Phylogenetic (b) Nomenclature. In both diagrams, grey dashed lines indicate that Agama was inferred to share a more recent common ancestor with Leiolepis than with Brookesia and Chamaeleo under an earlier phylogenetic hypothesis, while black solid lines indicate that Agama is inferred to be more closely related to Brookesia and Chamaeleo than to Leiolepis under a later hypothesis. Under rank-based nomenclature (a), one way to eliminate the paraphyletic taxon Agamidae (grey) would be to unite the two families into a single family, which would be called Chamaeleonidae according to the principle of priority. This action causes both taxa that are still considered monophyletic to change their names. Under phylogenetic nomenclature (b), using the same definitions as in Figure 3, the name Agamidae would become a synonym of Acrodonta. Although precedence has not been established for these two names, if Acrodonta had precedence, then neither of the taxa with the same hypothesized composition would change their names. Even if Agamidae had precedence, that name would make more sense as the name of the inclusive clade than would Chamaeleonidae given that the new phylogenetic hypothesis implies that Chamaeleonidae is derived from within Agamidae rather than the reverse.

(Fig. 4). Given the principle that scientific names are to be given only to monophyletic (as opposed to paraphyletic) taxa, a possible solution under rank-based nomenclature is to unite (lump) the two original families, Agamidae and Chamaeleonidae, into a single family (Fig. 4a). If this were to be done, then the names Agamidae and Chamaeleonidae would become synonyms, because both names would then refer to the same taxon. The official name of that taxon would be Chamaeleonidae, because that name has priority (i.e., a family-group name based on the genus Chamaeleo was published before a family-group name based on the genus Agama). This outcome makes little sense given that 1) the inclusive group already has a name, Acrodonta, 2) the smaller group to which the name Chamaeleonidae was previously applied is still thought to be monophyletic but now must be given a new name, and 3) the new phylogenetic hypothesis implies (under the original ranking scheme) that Chamaeleonidae is derived from within Agamidae, but the name change implies the opposite (in that all former agamids would now be considered subgroups of Chamaeleonidae).

Phylogenetic nomenclature handles the same situation in a way that makes more sense with respect to the references of names (Fig. 4b). Using the same definitions adopted in Figure 3 in the context of the new phylogenetic hypothesis, the names Agamidae and Acrodonta (rather than Agamidae and Chamaeleonidae) both apply to the inclusive clade and therefore become synonyms. Although precedence of Acrodonta versus Agamidae has not been established (because the PhyloCode is not yet in operation), either name makes more
sense as the name of the inclusive clade than does Chamaeleonidae—Acrodonta because it was previously applied to that clade, and Agamidae because the new phylogenetic hypothesis implies that the composition formerly associated with that name referred to a paraphyletic group originating with the same ancestor (i.e., that chamaeleonids are derived from within Agamidae). In addition, the name Chamaeleonidae is applied to the same clade to which it had been applied previously. Phylogenetic nomenclature thus preserves the associations between names and taxa better than does rank-based nomenclature not only in cases in which only ranks change but also in cases in which both hypothesized relationships and ranks change.

CONCLUSIONS

Phylogenetic nomenclature is a new approach that connects taxon names to evolutionary concepts of taxa by specifying the references of names in terms of common ancestry relationships. As a consequence, taxon names are more strongly tied to taxon concepts than to categorical ranks. In this respect, phylogenetic nomenclature resembles nomenclature as practiced by Linnaeus and other early naturalists but differs from the rank-based approach to nomenclature that underlies the current codes. Of course, phylogenetic nomenclature also differs in one very important respect from nomenclature as practiced by Linnaeus and other 18th Century naturalists. Those early naturalists practiced nomenclature in the context of a non-evolutionary world-view, and consequently, their taxon concepts were also non-evolutionary. In contrast, taxon concepts in phylogenetic nomenclature are explicitly evolutionary. Phylogenetic nomenclature thus combines both Linnaean and modern components. On the one hand, it embodies the wisdom of Linnaeus and his immediate successors, who treated ranks merely as devices for representing hierarchical relationships that had no bearing on the application or spelling of taxon names. On the other hand, it embraces the most important theoretical development in biology since the time of Linnaeus—the principle of evolution (common descent)—which it uses to specify the referents of taxon names in accord with modern concepts of taxa. Thus, rather than representing a challenge to the Linnaean approach to biological nomenclature, phylogenetic nomenclature represents Linnaean wisdom updated with evolutionary principles. It therefore extends the legacy of Linnaeus and provides a fitting tribute on the tercentenary of his birth.

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REFERENCES


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