



The Development of Systematic Reviews of the Turtles of the World

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Turtles are one of nature's most immediately recognizable life forms. They are an ancient group of vertebrates with a rich fossil history whose natural limits have long been recognized by naturalists. Indeed, the monophyly of this order has never been seriously questioned. The use of turtles and their eggs as food and for medicinal and ceremonial purposes has made them of importance to mankind since prehistoric times. As such, chelonians figured prominently in the earliest museum collections, all of them privately owned, including that of the Italian physician and encyclopedist of nature, Ulisse Aldrovandi of Bologna, in the late 16th century and the collections amassed in Amsterdam by the wealthy pharmacist and amateur naturalist, Albertus Seba, early in the 18th century. The first books devoted exclusively to turtles were on their anatomy. Giovanni Caldesi, physician to the last grand duke of Tuscany, and Christoph Gottwald, a physician and collector of natural history curiosities in Danzig, published their treatises on chelonian morphology in 1687 and 1781, respectively, the latter being issued eight decades after Gottwald's death. Neither author, however, provided a comprehensive review of the world's turtles.

The First Systematic Lists of Turtles

The first systematic lists of living turtles that presumed to be globally representative were those of the Swedish botanist, Carl Linnaeus. In the first edition of his epochal series, "Systema Naturæ," published in Leiden in 1735 as a folio of 13 pages, he listed four species, including terrestrial, freshwater, and marine forms. He defined turtles as amphibians having four legs, a tail, and that most defining characteristic—*testa munitum*—a protective shell. In his tenth edition of 1758, the cornerstone of modern animal systematics, he enumerated 11 species, all placed in his genus *Testudo*. By 1766, in the 12th and his last edition, the number had grown to 15 species. The list included sea turtles and taxa from Africa, Asia, Europe, and North and South America. Still later, the turtle book "Chelonographia" (1782), by the German physician and amateur naturalist, J. J. Walbaum, contained a competent and detailed description of a half dozen species from various parts of the world, but it did not include a comprehensive list of known species.

The First Complete Review of Turtles

The first author to provide what could reasonably be called a complete review of the turtles of the world was the German philologist and naturalist, Johann Gottlob Schneider. His book, "Allgemeine Naturgeschichte der Schildkröten" (1783, with two short supplements in 1787 and 1789), contains an extensive historical review of turtles plus a 68-page systematic section in which he recognized 20 species (including the supplements), all of them in a single genus (*Testudo*), and including four marine species. Schneider also described three distinctive new taxa—today known as *Apalone ferox*, *Chelus fimbriata*, and *Chrysemys picta*—in this book.

For the next 30 years, all comprehensive reviews of the living turtles of the world, whether they were parts of larger works or separate treatises that dealt exclusively with turtles, classified all chelonians into a single

genus—*Testudo*. This includes Count de Lacepède's review (1788), which lists 23 species, including two softshells and six marine species; J. F. Gmelin's edition of Linnaeus's "Systema Naturæ" (1789) with 33 species; Johann D. Schoepff's never-completed book on turtles (1792–1801) which lists 54 or 55 species; Georg Adolph Suckow (1798), 45 species; C. S. Sonnini and P.-A. Latreille (1801), 38 species; F.-M. Daudin (1801), 58 species; and the first comprehensive review of turtles in English, written by George Shaw (1802), with 48 species. None of these authors provided a natural arrangement of turtles. Nevertheless, some natural groups of turtles were beginning to be recognized with the proposals of several new genera by Parisian naturalists, although none of these names was generally adopted until later: *Chelonia* (Alexandre Brongniart, 1800); *Chelus* and *Emys* (Constant Duméril, 1806); and *Amyda* and *Trionyx* (Étienne Geoffroy Saint-Hilaire, 1809).

The First Scientific Monograph on Turtles

The first truly scientific account of turtles was provided by a German physician and naturalist, August Friedrich Schweigger. He, like Schoepff before him, had studied with J. C. D. Schreber, who had been one of Linnaeus's doctoral students. Schweigger later conducted research at the Muséum d'Histoire Naturelle in Paris with Georges Cuvier, Constant Duméril, and Étienne Geoffroy Saint-Hilaire and thus had available to him what was then the largest preserved collection of turtles in the world. In Schweigger's monograph, published in two parts in 1812 under the title "Prodromus Monographiae Cheloniorum," he listed 78 species (24 of them new) in six genera: *Chelonia*, *Chelydra* (new), *Chelys*, *Emys*, *Testudo*, and *Trionyx*. Furthermore, he attempted to subdivide some genera into natural groups. In *Emys*, for example, he separated those species having a hinged or moveable plastron from the rest. His list included six species of sea turtles and seven of softshells.

Multiplication of Genera

With this foundation, the classification of turtles progressed rapidly. During the two decades following Schweigger's monograph, 21 currently-recognized genera were named: *Caretta* (C. S. Rafinesque, 1814), *Dermochelys* (Henri de Blainville, 1816), *Terrapene* (Blasius Merrem, 1820), *Kinosternon* (J. B. von Spix, 1824), *Sternotherus* (John E. Gray, 1825), *Chelodina* (Leopold Fitzinger, 1826), *Kinixys* and *Pyxis* (Thomas Bell, 1827), *Clemmys* (Ferdinand von Ritgen, 1828), *Hydromedusa*, *Pelomedusa*, *Pelusios*, *Phrynops*, *Platemys*, *Podocnemis*, *Rhinemys*, and *Staurotypus* (J. G. Wagler, 1830), *Chersina* and *Platysternon* (John E. Gray, 1831), and *Apalone* and *Gopherus* (C. S. Rafinesque, 1832). The comprehensive reviews of turtles during this period include those of Blasius Merrem (1820) who listed 62 species in four genera and J. G. Wagler (1830) with 48 species in 21 genera. The large increase in the number of genera recognized by Wagler, a German naturalist, in his book "Natürliches System der Amphibien" (1830), was criticized by some of his contemporaries. Thomas Bell, the English dental surgeon and author of the magnificently illustrated but never-completed "Monograph of the Testudinata" (1832–1835 [–1836?]), caustically remarked that Wagler had used an "... unnecessary and unnatural multiplication of genera, founded on very trifling distinctions" To the contrary, 20 of the 21 generic entities used by Wagler are recognized today. Wagler also attempted to organize his genera into natural groups and thus subdivided turtles into three family-like tribes: *Testudines oiacopodes* (sea turtles), *T. steganopodes* (freshwater turtles), and *T. tylopodes* (land tortoises).

Organization of Turtles into Families

In 1835, two radically different classifications of turtles were published. Two herpetologists at the museum in Paris, Constant Duméril and his chief assistant and essential collaborator, Gabriel Bibron, in volume 2 of their monumental "Erpétologie Générale," organized a total of 121 species of turtles into a natural classification of 22 genera and, following Wagler's discovery, recognized the division between cryptodires and pleurodires. They also named the genera *Homopus* and *Peltocephalus* in the "Erpétologie Générale." Duméril and Bibron formally subdivided turtles into four families, to which they applied only vernacular names: Chersites or Tortues Terrestres (tortoises), Élodites or Tortues Paludines (freshwater and land turtles), Potamites or Tortues

Fluviales (softshell turtles), and Thalassites or Tortues Marines (seaturtles). From the time of Cuvier, French naturalists not only had the advantage of having the largest collection of specimens in alcohol, but also a large number of skeletons and knowledge of the soft anatomy based upon their own dissections. On the other hand, the contemporary Austrian zoologist, Leopold Fitzinger, restricted his study to external characteristics and organized turtles in a haphazard manner in which quite unrelated species were often grouped together. He recognized 122 living species in 10 genera. His paper, however, is remembered mainly because of his division of genera into subgeneric categories. Thus, Fitzinger became credited with several genera of turtles because six of his 37 subgenera were later raised to generic status: *Chelonoidis*, *Geochelone*, *Pelodiscus*, *Psammobates*, and *Rhinoclemmys*. The last species in his sixth genus, *Cylindraspis*, became extinct about 1830.

This point in our history of systematic reviews of turtles brings us to the most prolific and sometimes overzealous author of new genera and species—John E. Gray, founder of the zoological collections at the British Museum. His taxonomic scope was very broad, but chelonians were one of his principal interests throughout his long life. He named no less than 93 genera of turtles of which 35 are recognized today (fully one-third of the genera of living chelonians), and he authored some of the most distinctive genera of turtles. In addition to the three noted earlier, he erected *Batagur*, *Chitra*, *Chrysemys*, *Cuora*, *Dermatemys*, *Elseya*, *Geoemyda*, *Kachuga*, *Macrochelys*, *Mauremys*, *Pseudemys*, and 21 others. Among the 313 species recognized today, he named 55 of them (18%). Gray published several lists of the turtles of the world, including a catalogue based on those in the British Museum (1844), with 42 genera and 136 species arrayed into five families: Cheloniidae, Chelydidae, Emydidae, Testudinidae, and Trionychidae, as he spelled them.

The First Modern Summaries of Turtles

Less than 50 years later, the British Museum possessed the largest herpetological collection and the most representative collection of turtles. A classification comprising 48 genera and 212 species grouped in 11 families was presented in George A. Boulenger's "Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History)" (1889). This book, by the world's leading systematic herpetologist of the day, is the first modern summary of living turtles. It included keys to genera and species as well as numerous illustrations of shells and skulls. Boulenger recognized the families Carettochelydidae, Chelonidae, Chelydidae, Chelydridae, Cinosternidae, Dermatemydidae, Pelomedusidae, Platysternidae, Sphargidae, Testudinidae, and Trionychidae, but did not accept the Emydidae as distinct from the Testudinidae. In a contemporary account (1890), the Russian herpetologist, Alexander Strauch, produced a more conservative arrangement of turtles in which he listed only 32 genera and 206 species in just five families.

The next catalogue of turtles, and the first of the 20th century, was authored by Friedrich Siebenrock, a zoologist and anatomist at the museum in Vienna and a specialist on turtles. His un-illustrated summary, "Synopsis der rezenten Schildkröten" (1909), published 20 years after Boulenger's book, enumerates 57 genera and 232 species in 11 families. Siebenrock's species list is 20 entries longer than Boulenger's, but a comparison of the totals alone would be deceptive. Siebenrock includes 36 species described since Boulenger's catalogue and, thus, he relegated 16 species recognized by Boulenger to synonymy. Moreover, Siebenrock corrected the major error in Boulenger's higher classification of turtles when he transferred *Claudius* and *Staurotypus* from the family Dermatemydidae to the Kinosternidae. An update of Siebenrock's list was published in 1934 by an amateur German herpetologist and terrarist, Hans-Theodor Rust, with the assistance of two senior German herpetologists, Robert Mertens and Lorenz Müller. This article was published in two parts, with the systematic list in part 2. All newly described species were included and the species total became 252 in 67 genera. With the intervention of World War II, this was to be the last list of the world's turtles for more than 20 years.

Modern Checklists of Turtles

The next checklist of turtles was authored by Robert Mertens, a herpetologist at the museum in Frankfurt am Main, and his compatriot and protégé at the museum in Berlin, Heinz Wermuth, who specialized on turtles and crocodylians. This critical list, entitled "Die rezenten Schildkröten, Krokodile und Brückenechsen" (1955) is un-illustrated and lacks keys, but it provides partial synonymies for species as well as distributions for all living species and subspecies. It became the basis for all later lists. Mertens and Wermuth include 211 species



Plate 1. Authors of early systematic works on turtles. **A:** Carl Linnaeus (1707–1778). **B:** Johann Julius Walbaum (1724–1799). **C:** Johann Gottlob Schneider (1750–1822). **D:** Bernard Germain Étienne, Count de Lacepède (1756–1825). **E:** Johann David Schoepff (1752–1800). **F:** August Friedrich Schweigger (1783–1821). **G:** Blasius Merrem (1761–1824). **H:** Johann Georg Wagler (1800–1832). **I:** Thomas Bell (1792–1880).



Plate 2. Authors of early and recent systematic works on turtles. **A:** André Marie Constant Duméril (1774–1860). **B:** Marie Gabriel Bibron (1805–1848). **C:** Leopold Joseph Fitzinger (1802–1884). **D:** John Edward Gray (1800–1875). **E:** George Albert Boulenger (1858–1937). **F:** Alexander Alexandrovich Strauch (1832–1893). **G:** Friedrich Siebenrock (1853–1925). **H:** Hans-Theodor Rust (1905–1950). **I:** Robert Friedrich Wilhelm Mertens (1894–1975).



Plate 3. Authors of recent systematic works on turtles. **A:** Heinz Wermuth (1918–2002). **B:** Fritz Jürgen Obst (1939–). **C:** Peter Charles Howard Pritchard (1943–). **D:** John Burton Iverson, III (1949–). **E:** Carl Henry Ernst (1938–). **F:** Roger William Barbour (1919–1993). **G:** Frederic Wayne King (1936–). **H:** Russell Lewis Burke (1959–). **I:** Patrick André Raymond David (1959–).

Table 1. Changes in the number of taxa of living turtles from Linnaeus (1735) to Fritz and Havaš (2007).

Author, Date	Families	Genera	Species
Linnaeus, 1735	–	1	4
Linnaeus, 1758	–	1	11
Linnaeus, 1766	–	1	15
Schneider, 1783–1789	–	1	20
Lacepède, 1788	–	1	23
Gmelin, 1789	–	1	33
Schoepff, 1792–1801	–	1	54 or 55
Suckow, 1798	–	1	45
Sonnini and Latreille, 1801	–	1	38
Daudin, 1801	–	1	58
Shaw, 1802	–	1	48
Schweigger, 1812	–	6	78
Merrem, 1820	–	4	62
Wagler, 1830	–	21	48
Duméril and Bibron, 1835	4	22	121
Fitzinger, 1835	3	10	122
Gray, 1844	5	42	136
Boulenger, 1889	11	48	212
Strauch, 1890	5	32	206
Siebenrock, 1909	11	57	232
Rust, 1934	11	67	252
Mertens and Wermuth, 1955	12 (1)	66	211
Wermuth and Mertens, 1961	12	65	212
Pritchard, 1967 (2)	12	67	232
Iverson, 1986	12	80	242
Müller, 1987	12	67 (3)	226
Ernst and Barbour, 1989	12	86	257
King and Burke, 1989	13 (4)	89	250
Iverson, 1992	12	87	257
David, 1994	13 (5)	90	273
Obst in Wermuth and Mertens, 1996	12	73	271
Fritz and Havaš, 2007	14 (6)	97	313

- (1) Mertens and Wermuth (1955) recognized the Emydidae as a family.
- (2) The totals for Pritchard (1979) are not entered in this table because the numbers given in his text and those given in his two appendices do not agree.
- (3) Müller's (1987) classification at the generic level is unclear. Although he recognizes subgenera for three genera within the families Emydidae (*Clemmys*, *Geoemyda*) and Testudinidae (*Testudo*), in his species accounts he treats subgeneric names as genera. For example, *Sacalia* is named as a subgenus within the genus *Clemmys*, yet he uses the species name *Sacalia bealei*. If all of his subgeneric names were counted as genera, the total number of genera would be 82.
- (4) King and Burke (1989) recognize the Staurotypidae as a family.
- (5) David (1994) recognizes the Bataguridae as a family.
- (6) Fritz and Havaš (2007) recognize the Geoemydidae (senior synonym of Bataguridae) and the Podocnemididae as families.

in 66 genera. Their major innovation was the re-recognition of the subfamily Emydinae of previous authors as a distinct family, which became the first step in the further subdivision of the Testudinidae *sensu lato*. A major revision and enlargement of this list was published in 1961 by these same authors, but with the order of their names reversed, in a book entitled “Schildkröten, Krokodile, Brückenechsen.” The number of genera and species remained virtually unchanged, but this treatise included keys to families, genera, species, and subspecies as well as illustrations of most turtles (some combination of the entire animal, carapace, plastron, and skull). This classic text was reprinted in 1996 with an afterword by the surviving author, Wermuth, and an extensive supplement by Fritz Jürgen Obst, a reptile specialist at the museum in Dresden.

In the supplement, Obst provides an update to the nomenclature over the 35-year interval and he gives in tabular form a direct comparison between the taxonomy used by Wermuth and Mertens in 1961 and those used in several, but not all, subsequent reviews of the world’s turtles. These include the color iconographies of turtles by Peter C. H. Pritchard (1967, 1979); the *Das Tierreich* checklist of turtles by Wermuth and Mertens (1977), which made the first attempt at complete synonymies for species and genera; Obst’s own color-illustrated volume on turtle biology (1985; English edition 1986); John B. Iverson’s checklists (1986; revised edition 1992), which contain detailed distribution maps of turtles showing localities for most museum specimens; a synoptic checklist by Gerhard Müller (1987) intended primarily for terrarists; “Turtles of the World” by Carl H. Ernst and Roger Barbour (1989), with keys to genera and species and photographs, many in color, of each species; a list with detailed geographic information compiled by F. Wayne King and Russell L. Burke (1989) as a standard reference on turtle nomenclature for use by CITES and other conservation organizations; and, finally, the checklist produced by Patrick David (1994) that contains detailed commentary by several systematists (Roger Bour, James Buskirk, John Iverson, and Peter Pritchard) and a complete bibliography cross referenced to species. Taken together, these several recent works on turtles provide a large and diverse body of information on chelonians that in its scope and detail is unavailable for any other order of amphibians or reptiles.

In Obst’s supplement to the 1996 edition of Wermuth and Mertens, all newly described genera, species, and subspecies are listed and referenced to the literature. If one simply adds the newly described taxa to the 1961 numbers, the Obst list brings the totals to 271 species and 73 genera in 12 families. These numbers may be directly compared to those of the present list by Uwe Fritz and Peter Havaš that contains 313 species and 97 genera in 14 families. Their species total takes into account the subtraction of five Asian “species” that have turned out to be hybrids between pairs of previously known species, but also the addition of seven species of giant tortoises that were exterminated in historic times. The increase in the number of families by two reflects the partition of the Emydidae into two families (Emydidae *sensu stricto* and Geoemydidae) and the Pelomedusidae into two others (Pelomedusidae *sensu stricto* and Podocnemididae).

The Future

New species will continue to be discovered, especially in the Indo-Australian region and Southeast Asia, as well as in Africa and South America and perhaps elsewhere. And the higher classification of turtles will be further refined. Although molecular studies of particular groups of species have been undertaken, there is as yet no comprehensive molecular phylogeny for all turtles, a “Chelonian Tree of Life,” which is a critical need. These academic efforts, however, are not without broader societal implications. In the face of unrelenting human pressure on turtles and their habitats and with many species on the brink of extinction, it has never been more urgent to produce a complete and natural taxonomy, in order to develop a more rational conservation effort. This will require the highest level of cooperation among scientists, amateurs, conservationists, politicians, and an informed public.

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