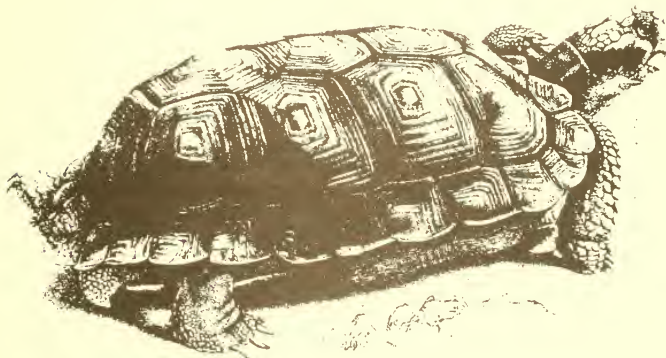


A NOMENCLATURAL HISTORY OF TORTOISES
(FAMILY TESTUDINIDAE)



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Introduction

Prerequisite to most revisionary studies is an examination of the nomenclatural history of the taxa under study. This is often a grueling task, but is rarely published. Thus, each subsequent revisor must repeat the task of gathering all the references together and extracting the pertinent information. The following idiosyncratic review summarizes my view on the nomenclatural history of tortoises (family Testudinidae).

Most, but not all, of the synonyms noted by Wermuth and Mertens (1977) are discussed below. The generic names in brackets are the currently used names (Loveridge and Williams, 1957; Auffenberg, 1974) or my recently recommended usage (Crumly, 1983, 1984b, 1984c). I have chosen not to detail the nomenclatural history of the Indian Ocean tortoises or the Galapagos tortoises (= *Geochelone elephantopus* complex of Crumly, 1984c) because their histories are too complex and because many biological questions need to be considered in order to interpret their histories. Detailed historical discussions of the tortoises of the Indian Ocean islands and the Galapagos can be found elsewhere (Van Denburgh, 1914; Slevin, 1959; Bour, 1984). Furthermore, the nomenclatural history of entirely extinct groups of tortoises (e.g. *Stylomys*, *Cylindraspis*) are not discussed.

1750-1800

Linnaeus (1758) proposed eleven turtle binomials in his 10th edition of *Systema Naturae*; two of these are now in the family Testudinidae. Both tortoises had been recognized earlier. He referred to Edwards's (1751, p. 204) figure in the description of *Testudo graeca*, and his description of *Testudo* [= *Psammobates*] *geometricus* referred to several earlier publications. *T. graeca* was characterized by elephantine feet with 4 toes on the pes. *Psammobates geometricus* was distinguished by the slightly conical carapacial scutes and the radiating shell pattern. Wallin (1977) demonstrated that Linnaeus based his description of *P. geometricus* on a specimen of *Geochelone elegans* as well as other descriptions. To preserve common usage, Hoogmoed and Crumly (1984) selected a lectotype one of the earlier descriptions (= syntypes) employed by Linnaeus. In the 12th edition of *Systema Naturae*, Linnaeus (1766) recognized *Testudo* [= *Geochelone*] *denticulata* by its eroded carapacial marginal (now known to be more prominent in *Geochelone carbonaria*, fide Williams, 1960) and the elephantine feet.

Carsten Niebuhr edited Petrus Forskål's notes on his Middle Eastern travels (Forskål, 1775). These notes included Arabic names for all the animals he saw and the description of *Testudo terrestris* [= *T. graeca terrestris*] plus some life history and distributional notes. Forskål felt that Arabic names would assist others in future fieldwork; however, if "Libanon" had not been mentioned there would have been no means of recognizing *T. g. terrestris*; it is the only tortoise living here. Miller's description (1780) of *Testudo* [= *Geochelone*] *sulcata* is based solely on an illustration. The illustration itself is unlabeled. However, Miller's index of illustrations, which includes the name *T. sulcata*, enabled Loveridge and Williams (1957) to verify his authorship. Carl Peter Thunberg, a Linnaeus correspondent and collector coined *Testudo* [= *Homopus*] *areolata* (Thunberg, 1787). He noted the flattened mid-dorsal region of the carapace, the large imbricate scales of the forearm, and the depressed carapacial areolae. Two years later, Gmelin (1789), in Linnaeus's 13th edition of *Systema Naturae*, named *Testudo hermanni*. Gmelin noted two especially distinctive features: 1) The "caudae apice unguiculato" [an apical tail spine] and 2) "marginis scutella 24" [24 marginal scutes indicating a divided supracaudal].

Schoepff's beautifully illustrated volume (1792b) included descriptions of two new species, *Testudo marginata* and *Testudo* [= *Geochelone*] *elegans*. The marginated tortoise was delineated by its expanded and flared posterior carapacial margin. The shell pattern and less conical carapacial scutes distinguished *Testudo* [= *Geochelone*] *elegans* from *P. geometricus*. With the close of the 18th century, seven of the approximately 40 living species of testudinid were recognized.

1800-1850

Shaw's description (1802) of *Testudo* [= *Geochelone*] *radiata* was the first new tortoise named in the 19th century. He relied heavily on Grew's earlier description (1681, *Musaeum Regalis Societatis*). Shaw recognized that this species was not synonymous with *T.* [= *Psammobates*] *geometrica*. By virtue of its larger size and flattened, rather than conical, carapacial scutes, it was distinct from the earlier known *T. geometrica*. In France, Daudin published the second volume of *Histoire Naturelle des Reptiles* (1802) and described *Testudo* [= *Gopherus*] *polyphemus* and *Testudo luteola* [= *Psammobates geometricus*]. *Testudo* [= *Gopherus*] *polyphemus* was distinguished by its small scales, flattened forelimbs and ash-gray color. The description of *T. luteola* notes the many similarities shared with *P. geometrica* but distinguished it by less elevated conical carapacial scutes.

Subsequently (Loveridge & Williams 1957; Müller, 1939), the heights of carapacial scutes have been shown to be extremely variable.

The parade of new names for tortoises continued with August Schweigger's (1812) famous *Prodromus monographiae Cheloniorum*. The *Prodromus* included three new tortoises, *Testudo* [= *Kinixys*] *erosa*, *Testudo* [= *Chersina*] *angulata* and *Testudo* [= *Geochelone*] *gigantea*. *Testudo erosa* was distinguished by shell shape and its denticulate margin. The number of marginal scutes and the elongation of the anterior periphery of the shell was also mentioned, but not the unique carapacial hinge. Schweigger used the type locality from Shaw's earlier description (1802) of *T. denticulata* (preoccupied by *T. denticulata* Linnaeus, 1766); the locality, "America septentrionali," was in error. *T. angulata* was distinguished by shell shape, shell color, and narrow anterior marginals. Because eleven plastral scutes were mentioned the presence of a single gular scute can be inferred. The provenance of this species was unknown to Schweigger, who had examined two living specimens at the Paris museum. The description of *T. gigantea* is quite difficult to interpret; over the years it has come to refer to the tortoise now living on the island of Aldabra. However, three very different positions have been articulated (Bour, 1982b, 1984b; Crumly, 1986; Pritchard, 1986).

In 1820, Kuhl named *Testudo* [= *Psammobates*] *oculifera* and characterized it by its color pattern and did not compare it to any other species. In the same year, Merrem authored his *Versuch eines Systems der Amphibien* (1820). He introduced a new generic name, *Chersine*, for all tortoises. This name subsumed many turtles besides testudinids (for example, *Kinosternon scorpioides*, *Clemmys muhlenbergi*). In part, this name has been considered a synonym of *Testudo*.

Four years later, Spix (1824) named *Testudo* [= *Geochelone*] *carbonaria*, and three species now considered synonyms of *G. denticulata*, i. e., *Testudo hercules*, *T. sculpta* and *T. cagado*. Hoogmoed and Gruber (1983) discovered that, except for 4 specimens of *T. sculpta* in the Zoologische Sammlung des Bayerischen Staates (= ZSM) collections (ZSM 2753/0 a, b, c and 2738/0), Spix's tortoise types had been destroyed near the end of World War II. Spix used color, elevated conical carapacial scutes and eroded lateral shell margins in his description of *T. carbonaria*.

In 1827, a banner year for new tortoise taxa, four species and 2 genera were described. Richard Harlan (1827) named *Testudo* [= *Geochelone*] *elephantopus* based on its reflected anterior shell margin and absent terminal tail spine. Thomas Bell (1827) named three new species and two new genera. Bell distinguished *Pyxis arachnoides*, a new species and genus, from other tortoises on the basis of its unique anterior plastral hinge. He coined *Kinixys* for those tortoises with posteriorly mobile carapacial lobe and recognized two species, *Kinixys castenea* and *K. homeana*. *K. castenea* was later synonymized with *K. erosa* by Gray (1831b). Bell did not mention and was apparently unaware of Schweigger's (1812) earlier description of *T.* [= *Kinixys*] *erosa*.

In the following year, Bell (1828) named three more taxa: *Testudo* [= *Psammobates*] *tentoria*, *Testudo* [= *Geochelone*] *pardalis* and *Testudo actinoides*. *Testudo actinoides* was synonymized with *Testudo* [= *Geochelone*] *elegans* by Boulenger (1889). *T. tentorius* was distinguished from other tortoises on the basis of conical carapace scutes, a radiating carapacial color pattern and unequal sized anterior marginals. This last trait was not mentioned by earlier workers, and apparently Bell considered it a very significant diagnostic character. Bell diagnosed *T.* [= *Geochelone*] *pardalis* by the light-golden yellow colored carapace with black flecks, the superior location of the pleural areolae, and the equal sized anterior marginals, emphasizing the pleural areolae trait.

John Edward Gray's *Cataphracta* volume of the *Synopsis Reptilium* appeared in 1831; he named two new taxa. *Kinixys belliana* was described in the *Additions and Corrections* chapter and was distinguished from other *Kinixys* species by the shape of the carapace, cervical scute and shell margin. He believed that this new species was intermediate between *K. erosa* and *K. denticulata* (?= *Testudo denticulata* Shaw 1802). During this same year, Gray (1831a) coined *Chersina* (not the same as Merrem's *Chersine* of 1820) for *Testudo angulata* Schweigger. He noted eleven plastral scutes (from which I infer that there was a single gular scute) as the distinguishing feature of this South African species.

Peter Simon Pallas (1831) named *Testudo ibera* [= *T. graeca ibera*], in the third volume of a posthumously published three volume set. The original date of publication for this third volume has been variously cited: 1814 by Wermuth (1958), Darevsky and Mertens (1973), and Wermuth and Mertens (1961, 1977), and 1827 by Mertens (1946). Neither is correct. In Pallas's *Zoographica Rosso-Asiatica*, the description of *Testudo ibera* is species number 14 on page 18, thus 1814. Zaunick (1925) noted that the third volume of the set was published in 1831

when the printing plates, which had been lost for two decades, were found. Pallas's description is accurate, mentioning the number of scutes on the shell, the number of toes on the manus and pes, and the color and shape of the shell; however, without his figure, *T. ibera* could not be recognized as a subspecies of *T. graeca*.

Perhaps the most colorful contributor to tortoise nomenclature was Constantine Samuel Rafinesque. In 1832, he began publishing *The Atlantic Journal and Friend of Knowledge*, which ceased publication two years later, after, among other things, making an enemy of Richard Harlan (Rafinesque, 1836:333). In this publication, Rafinesque (1832) provided an extremely brief description of *Gopherus*, specifically referring to the flattened nails of the manus.

The second volume of Duméril and Bibron's encyclopedic *Erpetologie Generale* (1835) contained descriptions of *Testudo* [= *Geochelone*] *nigrita* and a new genus *Homopus*. *T. nigrita* was characterized as black with a crescent-shaped anterior carapacial edge, a single supracaudal, slightly imbricate scales on the forearm, and no cervical. *Homopus* was characterized by four digits on all limbs, ungulate feet and a solid carapace without a hinge. *T. areolata* and *T. signatus* were referred to *Homopus*; however, *H. signatus* usually has five toes on the manus.

In 1835, Fitzinger coined many of the generic and subgeneric names employed today. *Geochelone*, for example, was proposed by Fitzinger. *Cylindraspis*, the name for the extinct tortoises from Mauritius, Rodrigues and the Mascarenes, was delineated from other *Geochelone* by its single gular scute, which is only present in some *Cylindraspis*, and by another ambiguous character, lateral shell margin arcuate. *Chelonoidis* and *Psammobates* were also differentiated by ambiguous characters. Both *Cylindraspis* and *Chelonoidis* were proposed as subgenera of *Geochelone*, whereas *Psammobates* was considered a subgenus of *Testudo*.

From 1838 to 1849 (see Waterhouse, 1880, for publication dates), Andrew Smith published pieces of his *Illustrations of the Zoology of South Africa*.... In the 1839 installment, he illustrated and described two tortoises: *Testudo verroxii* [= *Psammobates tentorius verroxii*] and *Testudo semiserrata* [= *Psammobates oculifer*]; both defined primarily by coloration and shell shape. In 1840, Schlegel and Müller described two new species, *Testudo* [= *Manouria*] *emys* and *Testudo* [= *Indotestudo*] *forstenii*. A good illustration was provided for *T. emys*, but *T. forstenii* was described only in the text of a footnote. Nevertheless, the written descriptions of both species are accurate, matching well the surviving types (Hoogmoed and Crumly, 1984). Four years later, Gray (1844) named *Testudo horsfieldii* from an "India, Afghanistan" [sic] juvenile. Gray's description did not include features sufficient to diagnose this species. He noted blunt hip spines, long gular scutes, large anal scutes and an oblong shell. Although well done for its time, Gray's descriptions make Schlegel and Müller's contribution all the more impressive.

1850-1900

Duméril, Bibron and Duméril (1851) proposed the substitute name *Testudo* [= *Manouria*] *emydoides* for *Testudo emys* Schlegel and Müller. The Dumérils' description emphasized cervical shape, the shape and number of marginal scutes, the scales covering the limbs, and hip and tail spines. Twelve plastral scutes were noted; although they did not mention whether the pectoral scutes met medially or were separated by humero-abdominal contact. Because they did not mention the unusual condition in *Manouria emys* [ssp. *emys*], it seems likely that the pectoral scutes did meet on the midline. Because 25 marginals were noted, it is probable that the supracaudal was split. Another synonym of *Geochelone emys* was proposed a year later by Gray (1852), who provided a new genus name *Manouria* for his species, *M. fusca*. *Manouria* was characterized by a divided supracaudal, pectoral scutes not meeting on the midline and centrally located carapacial areolae. Gray believed that *Manouria* was an emydid but noted many similarities shared with testudinids. He characterized *Manouria fusca* using shell color, recurved anterior and posterior shell margin, and projecting gular region.

In 1853, Edward Blyth recognized two new species: *Testudo phayeri* [= *Manouria emys phayeri*] and *Testudo* [= *Indotestudo*] *elongata*. *Testudo phayeri* was distinguished by its flat carapace, double supracaudal, unusual limb scalation and color. This name has been considered a synonym of *G. emys*, although the color is somewhat different from previously described *G. emys*. Roger Bour (pers. comm.) and I consider *T. phayeri* the senior synonym of *G. nutapundi* Nutaphand (1979). It seems likely that *Manouria emys* comprises two subspecies intergrading along a north-south cline. *T. elongata* was recognized by its elongated carapace and characteristic coloration. But, Blyth did not notice that the humero-pectoral sulcus transversely crosses the entoplastron, a feature that I consider diagnostic for *Indotestudo*.

John Leconte (1854) described *Teleopus luxatus*, a synonym of *Geochelone emys*. LeConte noted a split supracaudal scute and described in great detail the vertebral and marginal scutes. He also noted the tricuspid upper jaw and bicuspid lower jaw and further remarked that this species shared features with both testudinids and emyids.

Louis Agassiz published *Contributions to the Natural History of the United States of America* in 1857. A great proportion of this work (Parts II & III of three parts) dealt with turtles. Therein, Agassiz named and allocated two species to a new genus *Xerobates* [= *Gopherus*]. It was diagnosed by a median premaxillary ridge, broad flattened unguligrade forelimbs, and a broad head covered with mostly small scales. *Xerobates carolinus* [= *polyphemus*] was not characterized, but distribution and life history notes were included. *X. berlandieri* was described and distinguished by light yellow color in the middle of and rimming some carapacial scutes, by divergent gulars, and by small size as suggested by retained granular areolae of the shell. The syntypes of *Xerobates berlandieri* (two specimens bearing the same number, USNM 60) are a juvenile and a hatchling, which explains the presence of granular areolae. These areolae are worn smooth in adults.

Six years passed before any more currently valid names for tortoise species were proposed. Blyth (1863) then named *Testudo* [= *Geochelone*] *platynota* based on its large size, flat back, less numerous radiations on the carapacial scutes, and broader and lower carapacial shape. John Edward Gray (1863) "provisionally" named *Kinixys spekii* from an "imperfect" specimen from central Africa. The oblong shell, areolar color and lack of a carapacial hinge were used by Gray to characterize this form. Loveridge and Williams (1957) tentatively synonymized *K. spekii* with *K. belliana*; this decision was later reversed by Broadley (1982). John G. Cooper (1863) described *Xerobates* [= *Gopherus*] *agassizii* in honor of Alexander Agassiz. Cooper inadequately distinguished *X. agassizii* from other *Xerobates* by shell shape and color. Four years later, Grandidier (1867) named a tortoise from Madagascar, *Testudo* [= *Acinixys*] *planicauda*. He characterized this species on the basis of color, a single supracaudal, a small nuchal, and a uniquely flattened tail.

One of the few studies to deal specifically with the cranial osteology of land tortoises appeared in 1869. In this work, John Gray described two taxa, *Testudo* (*Scapia*) *falconeri* [= *Manouria emys*] and *Peltastes* (an invalid genus including five species now allocated to at least three genera). Gray's characterization of *T. falconeri* detailed cranial structures that are not diagnostic, but the accompanying figure clearly illustrated features unique to *M. emys*; broad skull arches, a deep lower jaw, a narrow but long skull and the absence of an interdigitating surangular process. Gray further noted the similarities between *Manouria fusca*, another synonym of *M. emys*, and *T. falconeri*. The interruption of the alveolar surface by enlarged internal narial openings and slight prominences at the labial maxillo-premaxillary suture characterized *Peltastes* Gray (1869). Of the five species allocated to *Peltastes* by Gray, only *P. [= Indotestudo] elongata* was well characterized.

A year later, Gray (1870a) named *Testudo* [= *Geochelone*] *chilensis* with only a very sketchy description, which wrongly contended that a nuchal plate [= cervical scute] is present. A plate of the presumed type is presented by Gray, and the cervical scute is absent on the illustrated specimen. In that same year, Gray (1870b) published another even shorter note that reviewed previous papers concerning the synonymy of *T. chilensis*. Also in 1870, Sclater noted that *T. chilensis* does not occur in Chile and that this species had been known to previous students. Fueling the fires of mutual dislike, he suggested a substitute name, *Testudo argentina*, which was never adopted. Gray published his *Appendix* to his earlier catalogue of British Museum turtles in 1872 and created another synonym of *Geochelone*, *Centrochelys* (type species *Geochelone sulcata*), defined by an absent cervical and large hip spines.

Following Gray's flurry of activity, Günther (1875) briefly reported on giant land tortoises in the British Museum and named three new taxa from the Galapagos, *Testudo ephippium*, *Testudo microphyes* and *Testudo vicina*. Günther's descriptions are very good and include data on shells, skulls and limbs. Unfortunately, the lack of good locality data for referred material diminishes the utility of Günther's descriptions. In fact, he incorrectly identified the island of origin for both *Geochelone ephippium* and *Geochelone microphyes*, whereas he was unable to discover an exact island of origin to *Geochelone vicina*. Two years later, Günther's monograph (1877) on British Museum giant tortoises appeared. Therein, he named *Testudo* [= *Geochelone*] *abingdonii*. This monograph is second only to Van Denburgh's (1914) classic study and exceeded even Van Denburgh in the quality illustration and in his discussion of non-shell material. Günther (1877) thought the skulls and other post-cranial non-shell material could be identified to species. My studies of the cranial osteology of Galapagos tortoises (Crumly, 1984a) have not supported Günther's contention. Later, Günther (1882) described *Geoemyda* [= *Manouria*] *impressa* from an 11 inch shell and noted its concave carapacial scutes. Günther's outstanding illustrations of the type over-shadow the remainder of his description.

Testudo kleinmanni was described by Lortet in 1883. His description emphasized shell color. Vaillant (1885) described *Testudo* [= *Geochelone*] *yniphora* on the basis of its not quite unique single gular scute (also found in *Chersina angulata* and *Geochelone vosmaeri*). Vaillant also noted that the carapacial pattern was similar to *Geochelone radiata*. Fernand Lataste described *Homopus nogueyi* [= *Kinixys belliana nogueyi*] in 1886. Despite Lataste's good description, he incorrectly assigned *nogueyi* to the genus *Homopus*. The small size of the type specimens and the inadequate comparative material probably contributed to Lataste's error. Because of the smallness of Lataste's specimens, they would not show the diagnostic feature, i.e., the carapacial hinge of *Kinixys*.

In 1886, Boulenger named three taxa all now included within *Psammobates tentorius*. Loveridge and Williams (1957) considered *Testudo fiski* and *Testudo smithi* synonyms of *Psammobates tentorius verroxii*, whereas Boulenger's *T. trimeni* was considered to be a valid subspecies of *Psammobates tentorius*. Cervical scute size and shape, hip spine presence or absence, relative plastral scute length and shell color figured prominently in Boulenger's descriptions and good plates were included. Boulenger (1888) later described another species of small South African tortoise, *Homopus femoralis*. Boulenger noted large hip spines, large prefrontal and frontal head scales, the absence of median lingual triturating ridge on the lower jaw, and five claws on the manus (unlike the four-clawed condition in *H. arelatus* and *H. signatus*). In the following year, Baur (1889) discussed some nomenclatural problems in earlier works. As a consequence of his discussion, he proposed the names *Testudo* [= *Geochelone*] *guentheri* and *T.* [= *Geochelone*] *galapagoensis*. Unfortunately, nowhere did Baur discuss the morphological bases of his decisions.

1900-1950

At the beginning of twentieth century, Rothschild named three new species from Galapagos in five short notes. In the first of these, Rothschild (1901) described *Testudo* [= *Geochelone*] *becki* on the basis of the characteristic flaring of the anterior carapace margin also found in other saddlebacked tortises. In his next two notes, Rothschild (1902a, 1902b) corrected some understandable mistakes concerning Harlan's (1827) type of *Testudo elephantopus*. In another paper, Rothschild (1902c) described *Testudo wallacei*, which has since been shown to be an invalid, probably introduced, form (MacFarland et al. 1974a). Rothschild's final note (1903) concerned the tortoise species that now lives on Isla Santa Cruz (Indefatigable), which he named *T.* [= *Geochelone*] *porteri* (Fritts, pers. comm., believes this name is a junior synonym of *T.* [= *Geochelone*] *nigritia*).

Frederick Siebenrock (1902) proposed the name *Acinixys* for Alfred Grandidier's *Testudo planicauda* and compared it to *Kinixys* and the then unwieldy genus *Testudo*. Siebenrock (1903) later named *Testudo* [= *Malacochersus*] *torneri* and noted its flattened and leathery shell, but considered it an abnormality. In the following year, Siebenrock's description (1904b) of *Testudo boettgeri* [= *Psammobates tentorius verroxii*] indicates his confusion with the astounding variation in some tortoise species. Also in 1903, Boulenger described *Testudo pseudemys* [= *Manouria impressa*]. He used two features to distinguish *T. pseudemys* from similar species (*M. emys* and *M. impressa*). The length of the anterolateral vertebral sulci supposedly distinguished *T. pseudemys* from *M. impressa*. However, this feature is quite variable and insufficiently delineated *T. pseudemys* from *M. impressa*. The narrow skull arches of *T. pseudemys* distinguished it from *M. emys*, which has broad skull arches. The skull of *T. pseudemys* was unknown to Boulenger but has since been shown to be *M. impressa*.

In 1906, Deurden named a new species of South African tortoise, *Homopus boulengeri*. Deurden noted the higher number of marginal scutes (12 or 13, rarely 11), a small cervical scute, large imbricate forearm scales, and large hip spines, and several other features. Deurden also characterized the other species of *Homopus*, but wrongly included two taxa whose type specimens were juvenile *Kinixys* (*H. darlingi* Boulenger, 1902 and *H. nogueyi* Lataste, 1886). Deurden (1907) more completely described the species of *Homopus* in the following year in a paper specifically concerned with color pattern. Boulenger (1907) described *Testudo* [= *Indotestudo*] *travancorica*. Although he didn't make special note of the fact, he noted that the cervical scute was absent, unlike the condition in *Indotestudo elongata*. Boulenger (1907) included two excellent plates with his description; both showed the similarities with *Indotestudo elongata*. Boulenger made no mention of the earlier described species *Testudo* [= *Indotestudo*] *forstenii* Schlegel and Müller, 1840. Hoogmoed and Crumly (1984) showed that *Indotestudo forstenii* was the senior synonym of *I. travancorica* (Boulenger, 1907). Van Denburgh (1907) named four new tortoise species from Galapagos. All of his "diagnoses" were actually characterizations that relied mostly on shell ratios. However, both of the saddlebacked species described (*Testudo* [= *Geochelone*] *phantasticus* and *Testudo* [= *Geochelone*] *hoodensis*) were noted to have a throat marked with yellow. The throats of the other two species (*T.* [= *Geochelone*] *darwinii* and *T.* [= *Geochelone*] *chathamensis*) were noted to be black.

In 1913, Annandale, the superintendent of the Indian Museum, named *Testudo* [= *Indotestudo*] *parallelus* from Chaiabassa, Chota Nagpur. The specific name alludes to the parallel sides of the shell; other characters noted by Annandale included gular, pectoral and humeral proportions. However, Annandale admitted that he was unable to obtain additional specimens besides the holotype. *Testudo parallelus* has been considered a synonym of *I. elongata*.

During the same year that the British Museum shifted its collections to methyl alcohol and abandoned wine spirits, George Boulenger continued his described two species of tortoises: *Testudo buxtoni* [= *T. graeca ibera*] (1920a) and *Testudo loveridgii* [= *Malacochersus tornieri*] (1920b). *Testudo buxtoni* was distinguished from what Boulenger considered its closest relatives (*T. graeca ibera* and *T. graeca zarudnyi*) by narrower pectoral scutes and a divided supracaudal scute; however, both the features are extremely variable in *Testudo graeca*. *Testudo loveridgii* was based on a series of six individuals; these individuals had divided supracaudal scutes. Arthur Loveridge (1923) reported on a collection of East African reptiles described and recognized *Testudo proceratae*, differentiated from Boulenger's *Testudo loveridgii* by its narrower, less flattened shell and its isolated distribution. Mertens et al. (1934) and Mertens and Wermuth (1955) recognized *T. proceratae* as a distinct species and *T. loveridgii* a junior synonym of *M. tornieri*. Both species were declared synonyms of *M. tornieri* by Loveridge and Williams (1957).

In 1929, Lindholm published a classification of turtles without supporting data. Therein, he recognized five genera (*Testudo*, *Kinixys*, *Homopus*, *Pyxis* and *Acinixys*) of tortoises and delineated four new subgenera of *Testudo* (*Pampatestudo* [= *Chelonoidis*], *Indotestudo*, *Malacochersus* and *Goniochersus* [= *Chersina*]). DeSola (1930) named a Galapagos species, *Testudo* [= *Geochelone*] *vandenburghi*, based on Van Denburgh's description (1914).

In the early 1930's, John Hewitt described over a dozen new species and subspecies of tortoises, as well as three new genera. Loveridge and Williams (1957) considered most of Hewitt's names to be junior synonyms of other older names. For example, *Pseudomopus* and *Neotestudo* were described in 1931 by Hewitt. *Pseudomopus* was distinguished from *Homopus* by its small inguinal scute and five toes of the manus. *Neotestudo* was proposed for *Chersina angulata*, in order to remove this unique species from *Testudo*, at that time a large polyphyletic taxon. Hewitt (1931) also named two new subspecies of *Kinixys belliana* and three new species of *Kinixys*, all synonyms of *Kinixys belliana*. In 1933, Hewitt named nine new subspecies of *Chersinella* [= *Psammobates*] *tentorius*. Eight of these subspecies are junior synonyms of *Psammobates tentorius tentorius*, fide Loveridge and Williams (1957). Hewitt (1933) proposed *Megachersine* [= *Geochelone*] for the species *Geochelone pardalis* and *Geochelone elegans* and *Chersinella* for the *geometrica* group of *Testudo*. Hewitt's generic descriptions relied on head scale variation. His new subspecies were based largely on small samples and used variable shell color and scale patterns.

During his tenure as a Guggenheim Fellow, Loveridge collected a large number of reptiles and amphibians from East Africa for the Museum of Comparative Zoology collections at Harvard University. His collection contained fourteen new taxa, including a new race of *Geochelone pardalis*. In 1935, Loveridge distinguished this race from the nominate form by its proportionally more vaulted shell and named it *Testudo* [= *Geochelone*] *pardalis babcocki*. Grieg and Burdett (1976) suggested that the characters that distinguish the two subspecies of *G. pardalis* vary too much to warrant subspecific recognition.

In a book on the fauna of Palestine, Friederich Bodenheimer described *Testudo floweri* [= *T. graeca terrestris*]. His single sentence description, one of the shortest of the 20th century, is nevertheless sufficient: "The tiny variety found in the Negeb ..." (Bodenheimer, 1935). Hewitt described *Kinixys natalensis* in 1935 and noted that the supracaudal scute is sometimes split. Loveridge and Williams (1957) considered *K. natalensis* a junior synonym of *K. b. belliana*. Broadley (1982) resurrected *K. natalensis* on the basis of pectoral scute proportions and a divided suprapygial.

1950-Present

In his cervical vertebrae article Williams (1950a) suggested *Bellemys* as a substitute name for *Pyxis*. A subsequent decision of the ICSN (Direction #32 of 1956) reversed Williams recommendation and *Pyxis* has been retained. Heinz Wermuth, two years later (1952), named a new subspecies, *Testudo hermanni robertmertensi* in a review of *T. hermanni* from southern Europe. He distinguished this new subspecies on the basis of color pattern, particularly of the plastron, and overall shell proportions.

In Laurent's (1956) survey of herpetofauna of the great lakes region of central Africa, he described a new subspecies, *Kinixys belliana mertensi*. This report was soon followed by the most influential paper on African testudinids, Loveridge's and Williams' monograph on African cryptodires (1957). Their classification was a departure from earlier classifications (e.g., Mertens and Wermuth, 1955) which included most tortoises in the single large genus *Testudo*. Instead, they recognized the so-called Ethiopian endemics (*Chersina* and *Psammobates*), elevated *Geochelone* to generic level, and severely restricted the genus *Testudo* to include only north African, Mediterranean and southwest Asian tortoises with a prootic concealed in dorsal view, a posterior plastral hinge, and "supranasal" scales. In addition, subgenera were proposed for *Testudo kleinmanni* (subgenus *Pseudotestudo*) and *Geochelone gigantea* (subgenus *Aldabrachelys*). Loveridge disclaimed responsibility for these radical changes in classification in a footnote. He believed the changes would be overturned by future study; however, I have corroborated (Crumly, 1984c) most of the changes suggested by Loveridge and Williams (1957).

Wermuth (1958) usefully reviewed the nomenclature and status of *Testudo graeca* subspecies. He also corrected some nomenclatural errors and noted that *Testudo terrestris* Forskål, 1775 (as a subspecies of *T. graeca*) is the senior synonym of *Testudo floweri* Bodenheimer 1935. Legler's (1959) description of *Gopherus flavomarginatus* followed a year later. He distinguished it from other *Gopherus* on the basis of a longer intergular and a shorter interhumeral sulcus, and a broad head. Khozatsky and Mlynarski (1966) suggested that *Testudo horsfieldii* be allocated to a new genus *Agriemys*. They noted that *T. horsfieldii* had only four toes on the manus and that the deeply "V"-shaped humeral pectoral sulcus laterally (but not medially) overlaps the entoplastron. My cladistic results (Crumly, 1984b, 1984c) and Kirsch's (pers. comm.) breeding experiments do not support the recognition of a separate genus for *Testudo horsfieldii*.

In the late sixties and early seventies, Simone Vuillemin published several papers on Malagasian tortoises (1968 [with L. Rabodomihamina], 1972 [with C. Domergue], 1972a, and 1972b). Three new species were named in the latter three papers. Unfortunately, Vuillemin apparently lacked sufficient comparative material, because all three of his new taxa were clearly recognized as synonyms of earlier named species by both Obst (1978) and Bour (1979a, 1981). *Pyxis brygooi* Vuillemin & Domergue (1972) was considered a synonym of *Pyxis arachnoides* by Obst and was afforded subspecific rank (*P. arachnoides brygooi*) by Bour (1981), because it lacks an anteriorly mobil plastral lobe. *Testudo morondavaensis* Vuillemin (1972a), based on an immature specimen, was rightly synonymized with *Acinixys planicanda* by both Bour and Obst. And *Madakinixys domerguei* Vuillemin (1972b), which was distinguished by dubious vertebral characters, was synonymized with *Kinixys belliana* by Obst (1978) and Bour (1979a).

Freiberg (1973) named two new species from southern South America, based on insufficient comparative material of *Geochelone chilensis*. The new species were named in honor of Dr. James A. Peters (*Geochelone petersi*) and Dr. Roberto Donoso-Barros (*Geochelone donosobarrosi*) and were distinguished by size, color, shape and thickness of the shell. *G. petersi*, a northern form of *G. chilensis*, has a smaller elongated, thick and light colored shell; whereas *G. donosobarrosi*, a southern form of *G. chilensis*, has a large and dark-colored oval, but very thin shell. Marlow and Patton (1982) uncritically accepted Freiberg's names, but also showed that the three populations were very closely related. My reasons for considering Freiberg's species as synonyms of *Geochelone chilensis* are discussed in elsewhere (Crumly, 1984c). In short, Freiberg failed to note sexual dimorphism and latitudinal clinal variation within *G. chilensis*, which could account for the variation he noted.

The most active student of land tortoise evolution in the past few years has been Roger Bour of the Muséum National d'Histoire Naturelle in Paris. His interest has been regional and limited to Madagascar and the islands of the Indian Ocean. Some of his papers have been reviews of the confusing nomenclatural history (1978, 1982b, 1984a) of Malagasian testudinids. His most significant contribution has been to the systematics of *Pyxis*, an endemic tortoise genus of the Malagasy Republic (1979a, 1981, 1982a). In these papers, he recognized two subspecies of *Pyxis arachnoides* and named a third that was later considered a synonym of an earlier name (Bour 1982a). Thus, the trivial names recommended by Bour (1981, 1982a) are: *Pyxis arachnoides arachnoides* Bell, 1827; *P. a. brygooi* Vuillemin and Domergue, 1972; and *P. a. oblonga* Gray, 1869. In these same papers, Bour recommended that *Acinixys* be considered a subgenus of *Pyxis*, citing *P. a. brygooi* as an intermediate between *Acinixys* and other *Pyxis*. For reasons presented elsewhere, I (Crumly, 1984c) prefer to retain *Pyxis* and *Acinixys* as separate genera.

Bour has also addressed the taxonomy of Indian Ocean tortoises in several papers. In 1982b, Bour rejected *T. gigantea* Schweigger, 1812, as the proper name for the tortoise species now inhabiting Aldabra and substituted *T.*

elephantina Duméril and Bibron, 1835. He believed that this required the rejection of *Aldabrachelys* Loveridge and Williams, 1957, and a new generic name. Thus, Bour coined *Dipsochelys*. However, there is an available generic name for tortoises with an elongated external narial opening: *Megalochelys* Falconer and Cautley, 1835 (type species *M. atlas*). I prefer to retain the specific epithet *gigantea* for three reasons: 1) an enormous amount of recent ecological research has used the name, 2) abandonment of *gigantea* requires the acceptance of an uncertain interpretation of Schweigger's (1812) description, and 3) *elephantina*, the next available name, is very much like *elephantopus* and would increase the opportunity for orthographic errors (see Crumly, 1986). Still another interpretation of Schweigger's original description is presented by Pritchard (1986); he suggests that Schweigger actually described a specimen of *Geochelone denticulata*.

Broadley (1982) reviewed the savannah *Kinixys*, some of which were subsumed into *Kinixys belliana* by Loveridge and Williams (1957). Broadley reinstated two names synonymized by Loveridge and Williams: *Kinixys natalensis* (Hewitt, 1935) and *Kinixys belliana spekii* (Gray, 1863). *K. natalensis* was distinguished from other *Kinixys* by gular scute proportions, a tricuspid beak and a divided suprapygal. *Kinixys belliana spekii* was distinguished from other *K. belliana* by carapacial and gular proportions, a unicuspid beak and coloration.

Bramble (1982) restricted *Gopherus* by removing two of the primitive species and placing them in his new genus *Scaptochelys*. Although *Gopherus* (sensu lato) is exceptionally well defined, *Scaptochelys* is based on shared primitive characters (Crumly, 1984b, 1984c). Furthermore, *Scaptochelys*, containing *Gopherus agassizii* and *G. berlandieri* as well as some fossil species, is a junior subjective synonym of *Xerobates* Agassiz 1857 (type species *Xerobates berlandieri* designated by Brown 1908) (Bour and Dubois, 1984; Crumly, 1985).

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SYSTEMATIC LIST

The following is a list of the names used for tortoises taken mostly from the taxonomic index of Wermuth and Mertens (1977). The names discussed in the text are indicated with an asterisk. Names not mentioned by Wermuth and Mertens were usually those not yet published and are indicated by a double asterisk.

abingdonii*		boulengeri*	Chersinella*
Acinixys*	babcocki*	brygooi*	Chersobius
actinoides*	becki*	burnesii	Chersus
agassizii*	Bellemys*	buxtoni	chilensis*
Agriemys*	belliana*		Cinixys
Aldabrachelys*	belli	cagado*	Cinnothorax
angulata*	bergeri*	calcarata	coui
arachnoides*	berlandieri*	campanulata	Cylindraspis*
areolatus*	bettai	caouana	
argentina*	bicaudalis	carbonaria*	darlingi*
armata	biguttata	castanea*	darwini*
Astrochelys	bipunctata	Centrochelys*	daudini*
atlas**	boettgeri*	chathamensis*	denticulata*
	boiei	Chersina*	depressa

desertorum	Kinixys*	Pyxoides*
Dipsochelys**	kleinmanni*	
domerguei**		racovitzai
donosobarrosi**	leithii*	radiata*
	lobatsiana*	robertmertensi*
elegans*	loveridgii**	
elephantina*	lutcola*	Scapia**
Elephantopus	luxatus*	Scaptochelys**
elephantopus*		seimundi
elongata*	macrophyes*	semiserrata*
emydoides*	madagascariensis*	senegalensis
emys*	Madakinixys*	signata*
erosa*	Manouria*	signatus*
	marginata*	smithii*
falconeri*	mauritanica*	spekii*
fiski*	Megachersine*	stellata*
flavomarginatus*	Megalochelys*	Stigmochelys
floweri*	megalopus*	strauchi
forstenii*	mertensi*	sulcata*
fusca*	microphyes*	
	morondavaensis**	tabulata*
galapagoensis*		Teleopus*
Geochelone*	natalensis*	tentoria*
geometrica*	Neotestudo*	tentorius*
geometricus*	nigra	terrestris*
gigantea*	nigrita*	Testudinella
Goniocbersus*	nigriventris	Testudo*
Gopher	nogueyi*	tornieri*
gopher		travancorica*
Gopherus*	oblonga**	trimeni*
graeca*	oculifer*	typica
graja		
grica	pallida	vandenburghi*
gricoides	Pampatestudo*	verroxii*
guentheri*	parallelus**	vicina*
	pardalis*	
hercules*	Peltastes*	wallacei*
hololissa	Peltonia	
homeana*	petersi*	Xerobates*
Homopus*	phantastica*	
hoodensis*	phayeri*	yniphora*
horsfieldii*	planata	youngi*
hyniphora	planicauda*	
hypselonota	planiceps	zarudnyi*
	platynota*	zohalfa
ibera*	polyphemus*	zombensis
iberia	ponderosa	zuluensis
impressa*	procterae*	
Indotestudo*	pseudemys*	
	Pseudomopus*	
karuella	Pseudotestudo*	
karuica	Pyxis*	