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An Annotated List of Modern Turtle Terminal Taxa with Comments on Areas of Taxonomic Instability and Recent Change

TURTLE TAXONOMY WORKING GROUP*

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ABSTRACT. – We compiled a list of the named terminal taxa for the world's modern turtle fauna that would summarize recent changes in turtle nomenclature. We provide an annotated list of 465 currently recognized modern terminal taxa (319 species plus 146 additional subspecies) in a hierarchical framework. In order to be as objective as possible we strive to uncritically record the most recent assignment of terminal taxa. For higher-level changes, we show competing schemes equally without endorsing any arrangement. In both cases (terminals and higher taxa) we direct readers to the systematic works that discuss taxonomic revisions. We anticipate that this annotated list will be a useful resource for everyone interested in turtles and their nomenclature. In addition to clarifying some issues or points of confusion, this list should also provide an impetus for future work aimed at clarifying and resolving areas of taxonomic disagreement and/or uncertainty.

KEY WORDS. – Reptilia; Testudines; turtle; tortoise; taxonomy; nomenclature; genera; species; subspecies; synonymization

Turtles, perhaps more than any other reptile group, have been the subject of numerous comprehensive lists (e.g., Wermuth and Mertens, 1977; Iverson, 1992; David, 1994; Iverson et al., 2001a; Joyce et al., 2004; Fritz and Havas, 2006, 2007; also see Pritchard, 1990, and Adler, 2007, for historical reviews). But despite their relatively modest extant diversity, turtle nomenclature is in a constant state of flux and, in places, wrought with differing opinions and directly conflicting arrangements. Consequently, it is impossible to compile a comprehensive list that is not already partially obsolete (or disagreed upon) by the time it is published. We took on the challenge of compiling a list of the named terminal taxa for the world's modern turtle fauna that would summarize some of this recent dynamism in turtle nomenclature. We decided to use Iverson's 1992 checklist of recognized turtle taxa as a starting point, since it was published in hardcopy form and widely disseminated and accepted (e.g., as opposed to starting from the Iverson et al. 2001a web-based checklist), and we agreed on a general format, using a hierarchical, *mostly* rank-free list.

As the title of this work implies, this list attempts to serve two functions. First, it is a list of all currently recognized named terminal taxa for modern turtles. This aspect is meant to be comprehensive as of November 2007 for extant or recently extinct turtle taxa (using the IUCN and CREO criteria of 1500 AD as the cutoff date for recent extinctions, see annotation number 1 below). This comes to a total of 465 modern turtle taxa, comprised of 319 species and 146 additional subspecies (see Table 1). By 'currently recognized' we simply mean those terminals that have not been explicitly refuted or synonymized. In order to be

as objective as possible we accepted the most recent changes relatively uncritically and direct readers to the systematic works that discuss these terminals. However, our one criterion for accepting a proposed change was that it be accompanied by data or at least arguments explaining the taxonomic revision. Consequently, some species lists published with major ad hoc revisions (e.g., from the herpetoculturist and web-based literature) were not incorporated.

The second aspect of this list highlights areas of instability or recent change, especially at the genus level, but also some higher-level categories. In contrast to the terminal list, we do not always accept the most recently proposed changes. Instead, we try to highlight these areas of instability and direct readers to the papers that discuss these controversies, and make no specific recommendations as to which terminology should be used. For a discussion of higher-level phylogenetic relationships, including consensus supertrees and unresolved controversies, see Iverson et al. (2007, this volume) for details.

In addition, we document those taxa that have been described as new or resurrected since Iverson (1992), plus those taxa still recognized as distinct by Iverson (1992) or other subsequent authors, that have subsequently been synonymized under current names for various reasons. In many cases those synonymizations have been well supported by morphologic or genetic analysis, but some have not. These recently synonymized taxa, in addition to the many previously synonymized taxa documented in Iverson (1992) and Fritz and Havas (2006, 2007), represent a wealth of potential diversity at lower levels of distinctiveness (e.g., possible Evolutionarily Significant Units or Management Units) or possibly valid terminal taxa simply in need of more detailed analysis.

Our list is not a complete historical review of all taxonomic changes to turtles, but does aim to be complete for the time since Iverson (1992). Moreover, it should not be taken as our opinion on the validity of any particular name. We fully expect that some of the terminals listed here will be synonymized based on future work while some excluded names will later be considered valid.

The format of this list is an indented hierarchy (by phylogeny) of turtle clades with modern terminal taxa. See Krenz et al. (2005) and Parham et al. (2006a) for the phylogeny used to create this hierarchy. The major levels of the hierarchy are listed phylogenetically with lower levels (equivalent to families, subfamilies, genera, species, and subspecies) listed alphabetically. Terminal taxa (species or subspecies) are in bold. Nominotypical subspecific terminals are implied, but not listed separately. Competing genera are generally listed in the order that they were most recently proposed, so the sequence should not be used to infer preference for any name. Because we sometimes list multiple genera for several terminals we abandon the convention of placing authorities of transferred species names in parentheses. Comments on areas of instability or recent change or synonymizations are indicated by superscript numbers that refer to the annotations below, while terminal taxa that have gone extinct within modern times (since 1500 AD) are indicated by a (†).

We anticipate that this annotated list will be a useful resource for everyone interested in turtles and their nomenclature. In addition to clarifying some issues or points of confusion, this list should also provide an impetus for future work aimed at clarifying and resolving areas of taxonomic disagreement and/or uncertainty.

Table 1. How many modern turtle species are there?
This table, modified and expanded from Adler (2007), records the number of modern turtle species, additional subspecies, and total taxa (species plus subspecies) listed as distinct by various authorities progressively through the years. As we have continued to discover and investigate more of the world's turtle populations, and applied increasingly refined morphologic and genetic characters and criteria for recognizing and documenting chelonian diversity, the number of distinct turtle species and total taxa have grown dramatically. Of the currently recognized turtle taxa, 6 species plus 3 additional subspecies (9 total taxa) have gone extinct since 1500 AD, leaving us currently with 313 living turtle species, 143 additional living subspecies, and 456 living turtle taxa (species and subspecies).

Authority	Species	Additional Subspecies	Total Taxa
Linnaeus, 1758	11	0	11
Linnaeus, 1766	15	0	15
Schneider, 1783-92	20	0	20
Gmelin, 1789	33	0	33
Schoepff, 1792-1801	55	0	55
Daudin, 1801	58	0	58
Schweigger, 1812	78	0	78
Duméril and Bibron, 1835	121	0	121
Fitzinger, 1835	122	0	122
Gray, 1844	136	0	136
Gray, 1856b	154	0	154
Gray, 1873c	209	0	209
Boulenger, 1889	212	0	212
Siebenrock, 1909	232	33	265
Rust et al., 1934	252	45	297
Mertens and Wermuth, 1955	211	121	332
Wermuth and Mertens, 1961	212	112	324
Pritchard, 1967	232	95	327
Wermuth and Mertens, 1977	219	121	340
Pritchard, 1979	237	115	352
Iverson, 1986	246	115	361
Ernst and Barbour, 1989	257	125	382
Iverson, 1992	257	139	396
David, 1994	273	137	410
Fritz and Havas, 2006	313	148	461
Fritz and Havas, 2007	313	147	460
Present checklist	319	146	465

CHECKLIST OF MODERN TURTLE TAXA[1]

Testudines
- Cryptodira
  - Chelydridae
    - *Chelydra*[2]
      - ***acutirostris*** Peters 1862
      - ***rossignonii*** Bocourt 1868
      - ***serpentina*** Linnaeus 1758
        - ***osceola*** Stejneger 1918
    - *Macrochelys* [formerly *Macroclemys*][3]
      - ***temminckii*** Troost 1835
  - Chelonioidea
    - Cheloniidae
      - *Caretta*
        - ***caretta*** Linnaeus 1758
      - *Chelonia*
        - ***mydas*** Linnaeus 1758[4]
      - *Eretmochelys*
        - ***imbricata*** Linnaeus 1766
          - ***bissa*** Rüppell 1835[5]
      - *Lepidochelys*
        - ***kempii*** Garman 1880
        - ***olivacea*** Eschscholtz 1829
      - *Natator*
        - ***depressus*** Garman 1880
    - Dermochelyidae
      - *Dermochelys*
        - ***coriacea*** Vandelli 1761
  - Kinosternoidea
    - Dermatemydidae
      - *Dermatemys*
        - ***mawii*** Gray 1847
    - Kinosternidae
      - Kinosterninae
        - *Kinosternon*
          - ***acutum*** Gray 1831b
          - ***alamosae*** Berry and Legler 1980
          - ***angustipons*** Legler 1965
          - ***arizonense*** Gilmore 1922[6]
          - ***baurii*** Garman 1891
          - ***chimalhuaca*** Berry, Seidel, and Iverson 1996[7]
          - ***creaseri*** Hartweg 1934
          - ***dunni*** Schmidt 1947
          - ***durangoense*** Iverson 1979[6]
          - ***flavescens*** Agassiz 1857[6]
          - ***herrerai*** Stejneger 1925
          - ***hirtipes*** Wagler 1833
            - ***chapalaense*** Iverson 1981
            - ***magdalense*** Iverson 1981
            - ***megacephalum*** Iverson 1981 (†)
            - ***murrayi*** Glass and Hartweg 1951
            - ***tarascense*** Iverson 1981
          - ***integrum*** Le Conte 1854
          - ***leucostomum*** Duméril and Bibron 1851
            - ***postinguinale*** Cope 1887
            - ***oaxacae*** Berry and Iverson 1980
          - ***scorpioides*** Linnaeus 1766[8]
            - ***abaxillare*** Baur 1925
            - ***albogulare*** Duméril and Bocourt 1870
            - ***cruentatum*** Duméril and Bibron 1851
          - ***sonoriense*** Le Conte 1854
            - ***longifemorale*** Iverson 1981
          - ***subrubrum*** Bonnaterre 1789
            - ***hippocrepis*** Gray 1856a
            - ***steindachneri*** Siebenrock 1906b
        - *Sternotherus* [formerly in *Kinosternon*][9]
          - ***carinatus*** Gray 1856a
          - ***depressus*** Tinkle and Webb 1955[10]
          - ***minor*** Agassiz 1857
            - ***peltifer*** Smith and Glass 1947
          - ***odoratus*** Latreille 1801
      - Staurotypinae
        - *Claudius*
          - ***angustatus*** Cope 1865
        - *Staurotypus*
          - ***salvinii*** Gray 1864b
          - ***triporcatus*** Wiegmann 1828
- Testudinoidea
  - Emydidae
    - Deirochelyinae
      - *Chrysemys*
        - ***picta*** Schneider 1783[11]
          - ***bellii*** Gray 1830
          - ***dorsalis*** Agassiz 1857[11]
          - ***marginata*** Agassiz 1857
      - *Deirochelys*
        - ***reticularia*** Latreille 1801
          - ***chrysea*** Schwartz 1956
          - ***miaria*** Schwartz 1956
      - *Graptemys*
        - ***barbouri*** Carr and Marchand 1942
        - ***caglei*** Haynes and McKown 1974
        - ***ernsti*** Lovich and McCoy 1992
        - ***flavimaculata*** Cagle 1954
        - ***geographica*** LeSueur 1817
        - ***gibbonsi*** Lovich and McCoy 1992
        - ***nigrinoda*** Cagle 1954
          - ***delticola*** Folkerts and Mount 1969
        - ***oculifera*** Baur 1890
        - ***ouachitensis*** Cagle 1953
          - ***sabinensis*** Cagle 1953[12]
        - ***pseudogeographica*** Gray 1831b
          - ***kohnii*** Baur 1890
        - ***pulchra*** Baur 1893c
        - ***versa*** Stejneger 1925
      - *Malaclemys*
        - ***terrapin*** Schoepff 1793
          - ***centrata*** Latreille 1801
          - ***littoralis*** Hay 1904
          - ***macrospilota*** Hay 1904

- ***pileata*** Wied 1865
- ***rhizophorarum*** Fowler 1906
- ***tequesta*** Schwartz 1955

Pseudemys
- ***alabamensis*** Baur 1893a
- ***concinna*** Le Conte 1830[13]
  - ***floridana*** Le Conte 1830[14]
  - ***suwanniensis*** Carr 1937[15]
- ***gorzugi*** Ward 1984[16]
- ***nelsoni*** Carr 1938a
- ***peninsularis*** Carr 1938b[17]
- ***rubriventris*** Le Conte 1830
- ***texana*** Baur 1893a

Trachemys[18]
- ***adiutrix*** Vanzolini 1995
- ***callirostris*** Gray 1856b[18]
  - ***chichiriviche*** Pritchard and Trebbau 1984[19]
- ***decorata*** Barbour and Carr 1940
- ***decussata*** Gray 1830
  - ***angusta*** Barbour and Carr 1940
- ***dorbigni*** Duméril and Bibron 1835[18,20]
- ***emolli*** Legler 1990[18]
- ***gaigeae*** Hartweg 1939[18]
  - ***hartwegi*** Legler 1990[19]
- ***nebulosa*** Van Denburgh 1895[18]
  - ***hiltoni*** Carr 1942[19]
- ***ornata*** Gray 1830[18]
- ***scripta*** Schoepff 1792
  - ***elegans*** Wied 1839
  - ***troostii*** Holbrook 1836
- ***stejnegeri*** Schmidt 1928
  - ***malonei*** Barbour and Carr 1938
  - ***vicina*** Barbour and Carr 1940
- ***taylori*** Legler 1960[18]
- ***terrapen*** Bonnaterre 1789
- ***venusta*** Gray 1856b[18]
  - ***cataspila*** Günther 1885[19]
  - ***grayi*** Bocourt 1868[19]
- ***yaquia*** Legler and Webb 1970[18]

Emydinae

Clemmys
- ***guttata*** Schneider 1792

Emys or *Actinemys*
- ***marmorata*** Baird and Girard 1852 [formerly in *Clemmys*][21,22]

Emys or *Emydoidea*[21]
- ***blandingii*** Holbrook 1838

Emys[21]
- ***orbicularis*** Linnaeus 1758
  - ***capolongoi*** Fritz 1995
  - ***colchica*** Fritz 1994
  - ***eiselti*** Fritz, Baran, Budak, and Amthauer 1998
  - ***fritzjuergenobsti*** Fritz 1993
  - ***galloitalica*** Fritz 1995
  - ***hellenica*** Valenciennes 1832
  - ***hispanica*** Fritz, Keller, and Budde 1996
  - ***iberica*** Eichwald 1831[23]
  - ***ingauna*** Jesu, Piombo, Salvidio, Lamagni, Ortale, and Genta 2004
  - ***lanzai*** Fritz 1995
  - ***luteofusca*** Fritz 1989
  - ***occidentalis*** Fritz 1993
  - ***persica*** Eichwald 1831[24]
- ***trinacris*** Fritz, Fattizzo, Guicking, Tripepi, Pennisi, Lenk, Joger, and Wink 2005

Glyptemys [formerly in *Clemmys*][21]
- ***insculpta*** Le Conte 1830
- ***muhlenbergii*** Schoepff 1801

Terrapene
- ***carolina*** Linnaeus 1758
  - ***bauri*** Taylor 1895
  - ***major*** Agassiz 1857
  - ***mexicana*** Gray 1849[25]
  - ***triunguis*** Agassiz 1857
  - ***yucatana*** Boulenger 1895[25]
- ***coahuila*** Schmidt and Owens 1944
- ***nelsoni*** Stejneger 1925
  - ***klauberi*** Bogert 1943
- ***ornata*** Agassiz 1857
  - ***luteola*** Smith and Ramsey 1952

Platysternidae[26]

Platysternon
- ***megacephalum*** Gray 1831c[27]
  - ***peguense*** Gray 1870b
  - ***shiui*** Ernst and McCord 1987

Testudinoidae or Testuguria[28]

Bataguridae or Geoemydidae[29]

Batagur[30]
- ***baska*** Gray 1830[31]
- ***borneoensis*** Schlegel and Müller 1844 [formerly in *Callagur*][30]
- ***dhongoka*** Gray 1832 [formerly in *Kachuga*][30]
- ***kachuga*** Gray 1831a [formerly in *Kachuga*][30]
- ***trivittata*** Duméril and Bibron 1835 [formerly in *Kachuga*][30]

Cuora[32,33]
- ***amboinensis*** Daudin 1801
  - ***couro*** Schweigger 1812
  - ***kamaroma*** Rummler and Fritz 1991
  - ***lineata*** McCord and Philippen 1998
- ***aurocapitata*** Luo and Zong 1988
- ***flavomarginata*** Gray 1863d
  - ***evelynae*** Ernst and Lovich 1990
  - ***sinensis*** Hsü 1930[34]
- ***galbinifrons*** Bourret 1939b[35]
  - ***bourreti*** Obst and Reimann 1994
  - ***picturata*** Lehr, Fritz, and Obst 1998

- ***mccordi*** Ernst 1988
- ***mouhotii*** Gray 1862 [formerly in *Pyxidea*][32]
  - ***obsti*** Fritz, Andreas, and Lehr 1998
- ***pani*** Song 1984
- ***trifasciata*** Bell 1825[36]
- ***yunnanensis*** Boulenger 1906[37]
- ***zhoui*** Zhao 1990

Cyclemys[38]
- ***atripons*** Iverson and McCord 1997
- ***dentata*** Gray 1831b
- ***oldhamii*** Gray 1863d
- ***pulchristriata*** Fritz, Gaulke, and Lehr 1997
- ***shanensis*** Annandale 1918
  - ***tcheponensis*** Bourret 1939a

Geoclemys
- ***hamiltonii*** Gray 1830

Geoemyda[39]
- ***japonica*** Fan 1931
- ***spengleri*** Gmelin 1789

Hardella
- ***thurjii*** Gray 1831b[40]

Heosemys
- ***annandalii*** Boulenger 1903 [formerly in *Hieremys*][41]
- ***depressa*** Anderson 1875
- ***grandis*** Gray 1860b
- ***spinosa*** Gray 1830

Leucocephalon
- ***yuwonoi*** McCord, Iverson, and Boeadi 1995 [formerly in *Geoemyda* or *Heosemys*][42]

Malayemys
- ***macrocephala*** Gray 1859[43]
- ***subtrijuga*** Schlegel and Müller 1844

Mauremys[33,44]
- ***annamensis*** Siebenrock 1903a [formerly in *Annamemys*][44]
- ***caspica*** Gmelin 1774
  - ***siebenrocki*** Wischuf and Fritz 1997
  - ***ventrimaculata*** Wischuf and Fritz 1996
- ***japonica*** Temminck and Schlegel 1835
- ***leprosa*** Schweigger 1812[45]
  - ***saharica*** Schleich 1996
- ***mutica*** Cantor 1842
  - ***kami*** Yasukawa, Ota, and Iverson 1996
- ***nigricans*** Gray 1834 [formerly in *Chinemys*][44]
- ***reevesii*** Gray 1831b [formerly in *Chinemys*][44,46]
- ***rivulata*** Valenciennes 1833
- ***sinensis*** Gray 1834 [formerly in *Ocadia*][44]

Melanochelys
- ***tricarinata*** Blyth 1856
- ***trijuga*** Schweigger 1812
  - ***coronata*** Anderson 1879
  - ***edeniana*** Theobald 1876[47]
  - ***indopeninsularis*** Annandale 1913
  - ***parkeri*** Deraniyagala 1939
  - ***thermalis*** Lesson 1830

Morenia
- ***ocellata*** Duméril and Bibron 1835
- ***petersi*** Anderson 1879

Notochelys
- ***platynota*** Gray 1834

Orlitia
- ***borneensis*** Gray 1873a

Pangshura [formerly in *Kachuga*][48]
- ***smithii*** Gray 1863e
  - ***pallidipes*** Moll 1987
- ***sylhetensis*** Jerdon 1870
- ***tecta*** Gray 1830
- ***tentoria*** Gray 1834[49]
  - ***circumdata*** Mertens 1969
  - ***flaviventer*** Günther 1864[49]

Rhinoclemmys
- ***annulata*** Gray 1860a
- ***areolata*** Duméril and Bibron 1851
- ***diademata*** Mertens 1954
- ***funerea*** Cope 1876
- ***melanosterna*** Gray 1861
- ***nasuta*** Boulenger 1902
- ***pulcherrima*** Gray 1856b
  - ***incisa*** Bocourt 1868
  - ***manni*** Dunn 1930
  - ***rogerbarbouri*** Ernst 1978
- ***punctularia*** Daudin 1801
  - ***flammigera*** Paolillo 1985
- ***rubida*** Cope 1870
  - ***perixantha*** Mosimann and Rabb 1953

Sacalia[33]
- ***bealei*** Gray 1831b
- ***quadriocellata*** Siebenrock 1903a

Siebenrockiella
- ***crassicollis*** Gray 1830
- ***leytensis*** Taylor 1920 [formerly in *Heosemys*][50]

Vijayachelys
- ***silvatica*** Henderson 1912 [formerly in *Geoemyda*][51]

Testudinidae

Aldabrachelys or *Dipsochelys* [formerly in *Geochelone*][52,53]
- ***arnoldi*** Bour 1982[54]
- ***daudinii*** Duméril and Bibron 1835 (†)
- ***dussumieri*** Gray 1831b[55]
- ***hololissa*** Günther 1877

Astrochelys [formerly in *Geochelone*][52]
- ***radiata*** Shaw 1802

Astrochelys or *Angonoka* [formerly in *Geochelone*][52]
- ***yniphora*** Vaillant 1885a[56]

Chelonoidis [formerly in *Geochelone*][52]
- ***carbonaria*** Spix 1824
- ***chilensis*** Gray 1870a[57]
- ***denticulata*** Linnaeus 1766
- ***nigra*** Quoy and Gaimard 1824[58]

abingdonii Günther 1877
becki Rothschild 1901
chathamensis Van Denburgh 1907[59]
darwini Van Denburgh 1907
duncanensis Garman 1917[60]
hoodensis Van Denburgh 1907
(nigra Quoy and Gaimard 1824) (†)[61]
phantastica Van Denburgh 1907 (†)[62]
porteri Rothschild 1903[63]
vicina Günther 1875[64]
petersi Freiberg 1973[57]
Chersina
angulata Schweigger 1812
Cylindraspis
indica Schneider 1783 (†)[65]
inepta Günther 1873 (†)
peltastes Duméril and Bibron 1835 (†)
triserrata Günther 1873 (†)
vosmaeri Suckow 1798 (†)[66]
Geochelone[52]
elegans Schoepff 1795
platynota Blyth 1863
Geochelone or *Centrochelys*[52]
sulcata Miller 1779
Gopherus
agassizii Cooper 1863
berlandieri Agassiz 1857
flavomarginatus Legler 1959
polyphemus Daudin 1801
Homopus[67]
areolatus Thunberg 1787
boulengeri Duerden 1906
femoralis Boulenger 1888a
signatus Gmelin 1789
cafer Daudin 1801
solus Branch 2007[67]
Indotestudo
elongata Blyth 1853
forstenii Schlegel and Müller 1844
travancorica Boulenger 1907[68]
Kinixys
belliana Gray 1830[69]
domerguei Vuillemin 1972
nogueyi Lataste 1886
zombensis Hewitt 1931
erosa Schweigger 1812
homeana Bell 1827
lobatsiana Power 1927
natalensis Hewitt 1935
spekii Gray 1863c
Malacochersus
tornieri Siebenrock 1903b
Manouria
emys Schlegel and Müller 1844
phayrei Blyth 1853
impressa Günther 1882
Psammobates
geometricus Linnaeus 1758
oculifer Kuhl 1820
tentorius Bell 1828
trimeni Boulenger 1886
verroxii Smith 1839
Pyxis
arachnoides Bell 1827[70]
brygooi Vuillemin and Domergue 1972
oblonga Gray 1869
planicauda Grandidier 1867
Stigmochelys or *Psammobates* [formerly in *Geochelone*][52]
pardalis Bell 1828[71]
babcocki Loveridge 1935
Testudo[72]
graeca Linnaeus 1758[73]
armeniaca Chkhikvadze and Bakradze 1991
buxtoni Boulenger 1921
cyrenaica Pieh and Perälä 2002
ibera Pallas 1814
lamberti Pieh and Perälä 2004
marokkensis Pieh and Perälä 2004
nabeulensis Highfield 1990
soussensis Pieh 2001
terrestris Forsskål 1775
zarudnyi Nikolsky 1896
kleinmanni Lortet 1883[74]
marginata Schoepff 1793[75]
Testudo or *Agrionemys*[72]
hermanni Gmelin 1789[76]
boettgeri Mojsisovics 1889
horsfieldii Gray 1844[77]
kazachstanica Chkhikvadze 1988[77]
rustamovi Chkhikvadze, Amiranashvili, and Ataev 1990[77]

Trionychia
Carettochelyidae
Carettochelys
insculpta Ramsay 1886
canni Wells 2002a[78]
Trionychidae
Cyclanorbinae
Cyclanorbis
elegans Gray 1869
senegalensis Duméril and Bibron 1835
Cycloderma
aubryi Duméril 1856
frenatum Peters 1854
Lissemys
punctata Bonnaterre 1789
andersoni Webb 1980
scutata Peters 1868
Trionychinae
Amyda
cartilaginea Boddaert 1770
Apalone

ferox Schneider 1783
mutica LeSueur 1827
calvata Webb 1959
spinifera LeSueur 1827
aspera Agassiz 1857
atra Webb and Legler 1960[79]
emoryi Agassiz 1857
guadalupensis Webb 1962
hartwegi Conant and Goin 1948
pallida Webb 1962
Aspideretes or *Nilssonia*[80]
gangetica Cuvier 1825
hurum Gray 1830
leithii Gray 1872
nigricans Anderson 1875[81]
Chitra
chitra Nutaphand 1986
javanensis McCord and Pritchard 2003
indica Gray 1830
vandijki McCord and Pritchard 2003
Dogania
subplana Geoffroy Saint-Hilaire 1809
Nilssonia[80]
formosa Gray 1869
Palea
steindachneri Siebenrock 1906a
Pelochelys
bibroni Owen 1853
cantorii Gray 1864a
signifera Webb 2003
Pelodiscus[82]
axenaria Zhou, Zhang, and Fang 1991
maackii Brandt 1857
parviformis Tang 1997
sinensis Wiegmann 1835
Rafetus
euphraticus Daudin 1801
swinhoei Gray 1873b[83]
Trionyx
triunguis Forsskål 1775

Pleurodira
Chelidae
Acanthochelys
macrocephala Rhodin, Mittermeier, and McMorris 1984[84]
pallidipectoris Freiberg 1945
radiolata Mikan 1820
spixii Duméril and Bibron 1835
Chelodina[85]
canni McCord and Thomson 2002[86]
gunaleni McCord and Joseph-Ouni 2007
longicollis Shaw 1794
mccordi Rhodin 1994b
roteensis McCord, Joseph-Ouni, and Hagen 2007a[87]
novaeguineae Boulenger 1888b
oblonga Gray 1841[88]
pritchardi Rhodin 1994a
reimanni Philippen and Grossmann 1990
steindachneri Siebenrock 1914[85]
timorensis McCord, Joseph-Ouni, and Hagen 2007b[89]
Chelodina or *Macrochelodina*[85]
burrungandjii Thomson, Kennett, and Georges 2000
expansa Gray 1857
kuchlingi Cann 1997d[90]
parkeri Rhodin and Mittermeier 1976
rugosa Ogilby 1890[91]
Chelus
fimbriata Schneider 1783
Elseya[92]
albagula Thomson, Georges, and Limpus 2006
branderhorsti Ouwens 1914[93]
dentata Gray 1863a
irwini Cann 1997c
jukesi Wells 2007b[94]
lavarackorum White and Archer 1994
novaeguineae Meyer 1874
schultzei Vogt 1911[95]
stirlingi Wells 2007b[96]
Elseya or *Wollumbinia*[92]
bellii Gray 1844[97]
georgesi Cann 1997a
latisternum Gray 1867
purvisi Wells and Wellington 1985
Elusor
macrurus Cann and Legler 1994
Emydura
australis Gray 1841
macquarii Gray 1830[98]
binjing Cann 1998
dharra Cann 1998
dharuk Cann 1998
emmotti Cann, McCord, and Joseph-Ouni 2003
gunabarra Cann 1998
krefftii Gray 1871
nigra McCord, Cann, and Joseph-Ouni 2003
signata Ahl 1932
subglobosa Krefft 1876
worrelli Wells and Wellington 1985[99]
tanybaraga Cann 1997b
victoriae Gray 1842
Hydromedusa
maximiliani Mikan 1825
tectifera Cope 1870
Phrynops[100]
geoffroanus Schweigger 1812
hilarii Duméril and Bibron 1835
tuberosus Peters 1870
williamsi Rhodin and Mittermeier 1983

Batrachemys or *Mesoclemmys*[100]
dahli Zangerl and Medem 1958
heliostemma McCord, Joseph-Ouni, and Lamar 2001[101]
nasuta Schweigger 1812
raniceps Gray 1856b
tuberculata Luederwaldt 1926
zuliae Pritchard and Trebbau 1984
Mesoclemmys[100]
gibba Schweigger 1812
perplexa Bour and Zaher 2005
Mesoclemmys or *Bufocephala*[100]
vanderhaegei Bour 1973
Mesoclemmys or *Ranacephala*[100]
hogei Mertens 1967
Phrynops or *Rhinemys*[100]
rufipes Spix 1824
Platemys
platycephala Schneider 1792
melanonota Ernst 1984
Pseudemydura
umbrina Siebenrock 1901
Rheodytes
leukops Legler and Cann 1980

Pelomedusidae
Pelomedusa
subrufa Bonnaterre 1789[102]
Pelusios
adansonii Schweigger 1812
bechuanicus FitzSimons 1932
broadleyi Bour 1986
carinatus Laurent 1956
castaneus Schweigger 1812
castanoides Hewitt 1931
intergularis Bour 1983
chapini Laurent 1965
cupulatta Bour and Maran 2003
gabonensis Duméril 1856
marani Bour 2000
nanus Laurent 1956
niger Duméril and Bibron 1835
rhodesianus Hewitt 1927
seychellensis Siebenrock 1906c (†)[103]
sinuatus Smith 1838
subniger Bonnaterre 1789
parietalis Bour 1983
upembae Broadley 1981
williamsi Laurent 1965
laurenti Bour 1984
lutescens Laurent 1965

Podocnemididae or Podocnemidae[104]
Erymnochelys
madagascariensis Grandidier 1867
Peltocephalus
dumerilianus Schweigger 1812
Podocnemis
erythrocephala Spix 1824
expansa Schweigger 1812
lewyana Duméril 1852
sextuberculata Cornalia 1849
unifilis Troschel 1848[105]
vogli Müller 1935

ANNOTATIONS

1. Both IUCN (The World Conservation Union, http://www.iucnredlist.org) and CREO (Committee on Recently Extinct Organisms, http://creo.amnh.org) have designated 1500 AD as their official cutoff date for determining what constitutes a recently extinct species, and we follow their criteria in our checklist.
2. *Chelydra*: Phillips et al. (1996) elevated *acutirostris* and *rossignoni* to full species status and retained the subspecies *osceola*. See Shaffer et al. (in press) for a complete review.
3. *Macrochelys* [formerly *Macroclemys*]: Although *Macroclemys* has been the most commonly used name, Webb (1995) showed that *Macrochelys* is the oldest available name.
4. *Chelonia mydas*: Bowen et al. (1992) showed that recognition of the taxon *agassizii* Bocourt 1868 renders *mydas* paraphyletic, and *agassizii* is no longer generally recognized as either a distinct species or subspecies. See Parham and Zug (1996) and Karl and Bowen (1999) for a complete review.
5. *Eretmochelys imbricata*: Fritz and Havas (2006, 2007) did not list *bissa* as a valid taxon, but no argumentation for this opinion was given. Genetic data (Okayama et al., 1999) have suggested significant separation of Atlantic from Pacific stocks.
6. *Kinosternon* species: Serb et al. (2001) elevated two former subspecies of *flavescens* (*arizonense* and *durangoense*) to full species status.
7. *Kinosternon chimalhuaca*: This new species name appeared prematurely and erroneously first in the hobbyist literature, with the full original description published a few months later (Berry et al., 1996, 1997).
8. *Kinosternon scorpioides scorpioides*: Includes the previously recognized subspecies *seriei* Freiberg 1936 and *carajasensis* Cunha 1970 in synonymy (Cabrera and Colantonio, 1997).
9. *Sternotherus*: This genus was included as a junior synonym of *Kinosternon* by Iverson (1992) and David (1994) based on work by Seidel et al. (1986) and Iverson (1991). However, this view was never widely accepted, and Iverson (1998) showed that the species referred to either *Sternotherus* or *Kinosternon* formed reciprocally monophyletic clades and recommended that both genera be used.

10. *Sternotherus depressus*: Whereas some earlier authors had placed this taxon as a subspecies of *minor*, Walker et al. (1998) showed that *depressus* was genetically distinct from *minor*.
11. *Chrysemys picta dorsalis*: This subspecies of *Chrysemys picta* was elevated to full species status by Starkey et al. (2003), who recognized two distinct genetic lineages: *C. dorsalis* and *C. picta*. They did not find genetic support for the other subspecies of *C. picta* (*belli*, *marginata*) but did not recommend that they be abandoned. Fritz and Havas (2006, 2007) argued that full specific status of *dorsalis* was not fully demonstrated and retained it and the other two taxa as subspecies of *C. picta*, agreeing also with Ernst et al. (2006).
12. *Graptemys ouachitensis sabinensis*: Based on molecular and morphologic data, Stephens and Wiens (2003) suggested that *sabinensis* may not be closely related to *ouachitensis*. However, statistical support for this was weak, and they did not discuss or recommend a taxonomic change. Further study of this complex may warrant the elevation of the sympatric taxon *sabinensis* to full species status.
13. *Pseudemys concinna concinna*: Includes the previously recognized subspecies *hieroglyphica* Holbrook 1836, *mobilensis* Holbrook 1838, and *metteri* Ward 1984 in synonymy (Seidel, 1994).
14. *Pseudemys concinna floridana*: This taxon was previously considered a separate species, but was designated a subspecies of *concinna* by Seidel (1994). Jackson (1995) argued for the retention of *floridana* as a full species, but Seidel (1995) rejected this argument.
15. *Pseudemys concinna suwanniensis*: Previously considered a subspecies of *concinna*, Seidel (1994) argued for the elevation of this taxon to full species status, but Jackson (1995) argued for its subspecific status.
16. *Pseudemys gorzugi*: This taxon was previously considered a subspecies of *concinna*, but was elevated to species status by Ernst (1990) without argumentation, but then supported through analysis by Seidel (1994).
17. *Pseudemys peninsularis*: This taxon was previously considered a subspecies of *floridana*, but was elevated to species status by Seidel (1994). Jackson (1995) argued for the retention of *peninsularis* as a subspecies of *floridana*, but Seidel (1995) reaffirmed his recognition.
18. *Trachemys* species: Seidel (2002) recommended elevating nine Mesoamerican taxa, previously recognized as subspecies of *Trachemys scripta*, to species rank.
19. *Trachemys* subspecies: Seidel (2002) also recommended reassigning five taxa, previously subspecies of *scripta*, to subspecies of his various elevated *Trachemys* species.
20. *Trachemys dorbigni*: Includes the previously recognized subspecies *brasiliensis* Freiberg 1969 in synonymy, based on morphologic work (del Barco and Larriera, 1993).
21. *Emydoidea* and the turtles formerly known as *Clemmys*: The four traditional species of *Clemmys* (*guttata* [type], *insculpta*, *muhlenbergii*, and *marmorata*) do not form a monophyletic group with respect to the two monotypic genera *Emys orbicularis* and *Emydoidea blandingii* in phylogenies based on DNA data (Bickham et al., 1996; Burke et al., 1996; Lenk et al. 1999; Feldman and Parham, 2002). While there is a general agreement that *insculpta* and *muhlenbergii* are sister-species and should be placed in the genus *Glyptemys* (Holman and Fritz, 2001; Parham and Feldman, 2002), there are two schemes presented for *marmorata* and *blandingii*. Holman and Fritz (2001) recommended that *marmorata* be placed in the monotypic genus *Actinemys*, retaining both *Emys orbicularis* and *Emydoidea blandingii* as additional monotypic genera. Other authors (Bickham et al., 1996; Feldman and Parham, 2002; Parham and Feldman, 2002) recommended that *marmorata* and *blandingii* be placed into an expanded *Emys*, a scheme favored in the most recent analysis of variation in *marmorata* (Spinks and Shaffer, 2005).
22. *Emys* or *Actinemys marmorata*: Previously, two subspecies were distinguished, including *pallida* Seeliger 1945, but genetic analysis by Spinks and Shaffer (2005) demonstrated that the typical and previously recognized subspecies *pallida* were within the same phylogeographic clade and so *pallida* should not be considered valid.
23. *Emys orbicularis iberica*: Includes the recently described subspecies *kurae* Fritz 1994 in synonymy (Fritz, 1998).
24. *Emys orbicularis persica*: Includes the recently described subspecies *orientalis* Fritz 1994 in synonymy (Fritz, 1998).
25. Mexican *Terrapene carolina*: Stephens and Wiens (2003) suggested that Mexican subspecies of *T. carolina* may warrant full species status. While this convention has also been adopted previously (Smith et al., 1996), almost all other workers recognize these as subspecies.
26. Platysternidae: Krenz et al. (2005) confirmed that nuDNA placed *Platysternon* solidly within the Testudinoidea, and Parham et al. (2006a) supported this finding with mtDNA.
27. *Platysternon megacephalum*: Ernst and Laemmerzahl (2002) synonymized two subspecies of *megacephalum* (*vogeli* Wermuth 1969 and *tristernalis* Schleich and Gruber 1984) with the nominate subspecies.
28. Testudinoidae or Testuguria: Shaffer et al. (1997) coined the name 'Testudinoidae' for the clade that united Testudinidae with Bataguridae/Geoemydidae. Joyce et al. (2004) listed Testudinoidae as an undesirable derivative of *Testudo* being to similar to both 'Testudinidae' and 'Testudinoidea.' In that same paper, the authors coined the new clade name 'Testuguria' for that same clade (while neglecting to list Testudinoidae as an objective senior synonym). Parham et al. (2006a) explicitly argued for the use of Testuguria over Testudinoidae.
29. Bataguridae or Geoemydidae: Both names are being used to refer to this group of predominantly Asian testudinoids. McDowell (1964) used the name Batagurinae for this group (as a subfamily) which was

changed to Bataguridae (as a family) by Gaffney and Meylan (1988). Bour and Dubois (1986) showed that Geoemydidae has priority, and David (1994), Spinks et al. (2004) and others have embraced this view. However, this approach was questioned by Joyce et al. (2004) who, working in a rank-free phylogenetic taxonomy framework, recommended the continued use of Bataguridae. In the interest of reconciling phylogenetic nomenclature with traditional Linnaean rules of priority, Parham et al. (2006a) endorsed a phylogenetic codification of Geoemydidae.

30. *Batagur*: Praschag et al. (2007b) and Le et al. (2007) demonstrated that species of *Kachuga* were genetically paraphyletic with respect to those referred to *Batagur* and *Callagur* and recommended that only one genus be recognized, and the name *Batagur* has priority.
31. *Batagur baska*: The subspecies *ranongensis* Nutaphand 1979 is not well differentiated and has been synonymized under *baska* by Fritz and Havas (2006, 2007), but no specific morphologic or genetic analysis has yet been performed to formally evaluate the status of this taxon.
32. *Cuora*: Phylogenies based on DNA data (Honda et al., 2002a; Stuart and Parham, 2004; Parham et al., 2004; Spinks et al., 2004) have shown that continued recognition of the genus *Pyxidea* for *mouhotii* would render *Cuora* paraphyletic. All of these studies recommended expanding *Cuora* to include *mouhotii*. Other schemes for *Cuora* have not been published in the recent scientific literature, though there has been some use of *Cistoclemmys* for *flavomarginata* and *galbinifrons* (e.g., Zhao et al., 1997; Zhao, 1997; Yasukawa and Ota, 1999).
33. Hybrid species: The validity of six taxa of *Cuora*, *Mauremys* [including *Ocadia*], and *Sacalia* recently described from pet trade specimens has been refuted by genetic studies that have shown them to be based on hybrids (Parham et al., 2001; Wink et al., 2001; Spinks et al., 2004; Stuart and Parham, 2004, 2007). The taxa shown to be hybrids are: *Cuora galbinifrons serrata* Iverson and McCord 1992b, *Mauremys iversoni* Pritchard and McCord 1991, *Mauremys pritchardi* McCord 1997, *Ocadia glyphistoma* McCord and Iverson 1994, *Ocadia philippeni* McCord and Iverson 1992, and *Sacalia pseudocellata* Iverson and McCord 1992a.
34. *Cuora flavomarginata sinensis*: Some authors recognize this taxon as a valid subspecies (McCord and Iverson, 1991; Fong et al., 2002) while others synonymize it with *flavomarginata* (Yasukawa and Ota, 1999; Fritz and Havas, 2006, 2007).
35. *Cuora galbinifrons*: The taxa *bourreti* and *picturata*, originally described as subspecies of *Cuora galbinifrons*, were elevated to species rank by Stuart and Parham (2004) based on concordance of morphological with molecular differentiation. Fritz et al. (2006c) returned *bourreti* to subspecies rank based on osteological characters shown by market specimens, and suggested that *picturata* warrants the same ranking; Fritz and Havas (2006, 2007) subsequently listed *picturata* at subspecies rank based on morphologically intermediate pet trade specimens. Includes the previously recognized *hainanensis* Li 1958 in synonymy (Zong and Pan, 1989; Iverson and McCord, 1992b).
36. *Cuora trifasciata*: Blanck et al. (2006) recommended that *Cuora trifasciata* be split into two species (including their newly named species *cyclornata* and its new subspecies *meieri*) based on paraphyletic mtDNA haplotypes and morphological differences. Spinks and Shaffer (2007) showed that *trifasciata* as traditionally recognized is monophyletic based on nuDNA and therefore recommended that *cyclornata* should not be recognized, pending additional study.
37. *Cuora yunnanensis*: This species has been listed as extinct by the IUCN since 2000 (www.iucnredlist.org), based on several decades of not finding any surviving animals despite intensive searches. Recently, a pair of animals representing this species were found in markets (Zhou and Zhao, 2004; Zhou, 2005), with subsequent confirmation through genetic analysis (He et al., 2007).
38. *Cyclemys*: Iverson (1992) recognized two taxa of *Cyclemys* (*dentata* and *tcheponensis*). Later, *atripons* and *pulchristriata* were described and *oldhamii* was resurrected (Iverson and McCord, 1997; Fritz et al., 1997). Genetic analysis by Guicking et al. (2002) also supported the validity of *shanensis*.
39. *Geoemyda*: Yasukawa et al. (1992) elevated *japonica* to species status (previously considered a subspecies of *spengleri*).
40. *Hardella thurjii*: Praschag et al. (2007b) found no genetic or morphologic evidence for continued recognition of the subspecies *indi* Gray 1870b, and synonymized it under *thurjii*.
41. *Heosemys annandalii* [formerly in *Hieremys*]: Spinks et al. (2004) showed that *annandalii* was nested among species of *Heosemys*. Diesmos et al. (2005) formally moved *annandalii* into *Heosemys*.
42. *Leucocephalon yuwonoi* [formerly in *Geoemyda* or *Heosemys*]: Originally described as a species of *Geoemyda* (McCord et al., 1995), Fritz and Obst (1996) placed *yuwonoi* in *Heosemys*. McCord et al. (2000) showed that *yuwonoi* was not closely related to the type species of *Geoemyda* or *Heosemys*, but instead sister to *Notochelys platynota*, and erected a new genus, *Leucocephalon*, for *yuwonoi*.
43. *Malayemys macrocephala*: Brophy (2004) proposed the recognition of this species as distinct from *subtrijuga* based on morphological grounds.
44. *Mauremys* [including species formerly in *Annamemys*, *Chinemys*, or *Ocadia*]: Iverson and McCord (1994) included *annamensis* under an expanded *Mauremys*. Subsequent phylogenies based on DNA data (Honda et al., 2002b; Barth et al., 2004; Feldman and Parham, 2004; Spinks et al., 2004) showed that the genera *Ocadia* and *Chinemys* rendered *Mauremys* paraphyletic. Based on these results, some authors (Feldman and

Parham, 2004; Spinks et al., 2004) recommended synonymizing *Ocadia* and *Chinemys* under *Mauremys*. Barth et al. (2004) presented this same scheme as well as one that would retain *Chinemys* and *Ocadia* and further divide *Mauremys* into the genera *Cathaiemys* and *Emmenia*. Barth et al. (2004) did not favor one scheme over the other and a competing scheme for *Mauremys* has not been formally proposed in the scientific literature.

45. *Mauremys leprosa*: Fritz et al. (2006a) explicitly synonymized several subspecies of *leprosa* recently described by Schleich (1996) (*atlantica*, *erhardi*, *marokkensis*, *wernerkaestlei*, and *zizi*) plus *vanmeerhaeghei* Bour and Maran 1998, and only recognized *leprosa* and *saharica*.
46. *Mauremys reevesii*: Iverson et al. (1989) and Barth et al. (2003, 2004) refuted the validity of the terminal taxon *megalocephala* Fang 1934, but it has continued to be recognized by Chinese researchers (Guo et al., 1997; Zhao, 1997; Zhang et al., 1998), and Fritz and Havas (2006, 2007) listed it as a separate taxon with speculation about its relationships.
47. *Melanochelys trijuga edeniana*: The subspecies *wiroti* Reimann 1979 was recognized by Iverson (1992), but David (1994) suggested that it was synonymous with *edeniana*, and Fritz and Havas (2006, 2007) followed this arrangement.
48. *Pangshura* [formerly in *Kachuga*]: Das (2001) and Schleich and Kästle (2002) used the name *Pangshura* to refer to small-bodied *Kachuga*. A phylogeny based on DNA data (Spinks et al., 2004) showed that *Kachuga* was paraphyletic and so removed *flaviventer*, *smithii*, *sylhetensis*, *tecta*, and *tentoria* into the genus *Pangshura*. Praschag et al. (2007b) using mtDNA confirmed the well-supported monophyly of *Pangshura*.
49. *Pangshura tentoria flaviventer*: Schleich and Kästle (2002) elevated *flaviventer* to full species status based on sympatry with *circumdata*, but Praschag et al. (2007b) performed a phylogeographic analysis and retained *flaviventer* as a subspecies of *tentoria*.
50. *Siebenrockiella leytensis* [formerly in *Heosemys*]: Diesmos et al. (2005) placed *leytensis* into the genus *Siebenrockiella* based on strong genetic evidence for its sister relationship to *S. crassicollis*.
51. *Vijayachelys silvatica* [formerly in *Geoemyda*]: This species was originally named as a species of *Geoemyda*. However, a molecular study by Praschag et al. (2006) suggested a distant relationship with that genus and they recommended that it be placed in the new monotypic genus *Vijayachelys*.
52. The *Geochelone* complex: This generic complex includes the genera *Geochelone*, *Aldabrachelys*, *Astrochelys*, *Angonoka*, *Centrochelys*, *Chelonoidis*, *Dipsochelys*, and *Stigmochelys*. Lapparent de Broin (2000b), Gerlach (2001, 2004), Le et al. (2006), and Fritz and Bininda-Emonds (2007) recommended dividing the *Geochelone* complex into several genera, although their schemes differ somewhat. A general consensus on a generic-level revision for some members of the group is lacking while in other areas (e.g., *Astrochelys radiata*, *Chelonoidis*) there is agreement.
53. *Aldabrachelys* or *Dipsochelys*: Bour (1982) originally recommended that Aldabran tortoises (*dussumieri* or *gigantea*) be placed in the genus *Dipsochelys* instead of *Aldabrachelys*. However, *Aldabrachelys* is still widely used, including sometimes by Bour (Austin et al., 2003), though *Dipsochelys* is favored by others (Palkovacs et al., 2002, 2003; Gerlach, 2004). There is recent disagreement regarding the type specimen of *Testudo gigantea*, the type species of *Aldabrachelys*, that was presumed lost. Frazier (2006) designated a neotype for *T. gigantea*, an act that would seemingly validate the use of both *Aldabrachelys* and the terminal taxon *gigantea*. Around the same time, Bour (2006) rediscovered the original lost type specimen, which is actually an individual of the South American tortoise *Chelonoidis denticulata*. If this claim is correct, then the names *Aldabrachelys* or *gigantea* might not be applicable to Aldabran tortoises. Whether Frazier's neotype designation or Bour's specimen rediscovery prevails nomenclaturally remains a matter of ongoing debate, but since Bour (2006) was the most recently published authority we use the name *dussumieri* rather than *gigantea* in our list.
54. *Aldabrachelys* or *Dipsochelys* species: Gerlach and Canning (1998) recognized six species of tortoises in Aldabra, Madagascar, and the Seychelles (three of which were extinct: *abrupta*, *daudinii*, and *grandidieri*). The two species from Madagascar became extinct prior to modern times (*abrupta* Grandidier 1868 in ca. 1250 AD and *grandidieri* Vaillant 1885b in ca. 950 AD) so we do not include them in our list of modern taxa. Palkovacs et al. (2002, 2003) questioned the validity of multiple extant species based on their analysis of genetic data, recognizing only a single living taxon (*Dipsochelys dussumieri*). Gerlach and Bour (2003) reemphasized the validity of the extant species based on the observation that the hatchlings are diagnostic. Fritz and Havas (2006, 2007) recognized only one extant species of Indian Ocean giant tortoise which they referred to *Aldabrachelys gigantea*, but did not address the findings of Gerlach and Bour (2003) or Bour (2006). As we consider the issues surrounding the validity of these species as remaining unresolved, we list all these species as potentially valid.
55. *Aldabrachelys* or *Dipsochelys dussumieri*: Iverson (1992) listed this species as *Geochelone gigantea* Schweigger 1812. Many authors now use *dussumieri* for the Aldabra tortoise (see above), but others persist in using the older name *gigantea* (e.g., Fritz and Havas, 2006, 2007), and others have used the name *elephantina* Duméril and Bibron 1835 (David, 1994; Devaux, 2007).
56. *Astrochelys* or *Angonoka yniphora*: Le et al. (2006) named *Angonoka* for *yniphora* because of its uncertain phylogenetic position. Fritz and Bininda-Emonds (2007) recovered a weak sister relationship between *yniphora*

and *Astrochelys radiata* under some algorithms and recommended that *yniphora* be placed in *Astrochelys*.

57. *Chelonoidis petersi*: According to Cabrera (1998), citing morphologic and osteologic work by Fernández (1988), *Chelonoidis chilensis* should be divided into two species, *chilensis* and *petersi* Freiberg 1973, but he considered the taxon *donosobarrosi* Freiberg 1973 to be synonymous with *chilensis*. Fritz and Havas (2006, 2007) speculated that *petersi* may not be valid and synonymized it under *chilensis*, citing phenotypic plasticity in other tortoise species as a reason for not accepting the reported differences between *petersi* and *chilensis*.
58. *Chelonoidis nigra*: Most recent authors have considered the various taxa of Galapagos tortoises as subspecies of *nigra* (e.g., Pritchard, 1996; Caccone et al., 1999; Fritz and Havas, 2006, 2007), but Caccone et al. (2002) and Russello et al. (2005, 2007) treated them as distinct species. The nomenclatural and survival status of these taxa were discussed in detail by Pritchard (1996).
59. *Chelonoidis nigra chathamensis*: This taxon described from western Chatham Island (San Cristóbal) appears to have been extirpated from its original range, but a population of tortoises persists on eastern Chatham Island that was considered a possible separate subspecies by Pritchard (1996). Pending genetic analysis and resolution of this issue we continue to list *chathamensis* as the extant taxon from Chatham, whereas Fritz and Havas (2006, 2007) listed it as extinct, but made no mention of the extant population.
60. *Chelonoidis nigra duncanensis*: This taxon from Duncan Island (Pinzón) was historically usually referred to *ephippium* Günther 1875, but Pritchard (1996) demonstrated that *ephippium* was a synonym of *abingdonii* and therefore resurrected the old nomen nudum *duncanensis* Garman 1917.
61. The nominotypical subspecies *nigra* from Charles Island (Santa Maria or Floreana) is considered to be extinct and is therefore included separately on this list.
62. *Chelonoidis nigra phantastica*: This taxon was listed by Fritz and Havas (2006, 2007) as extant, but Pritchard (1996) considered it probably extinct.
63. *Chelonoidis nigra porteri*: This taxon from Indefatigable Island (Santa Cruz) has often been referred to *nigrita* Duméril and Bibron 1835, but most recent authors, including Pritchard (1996) and Fritz and Havas (2006, 2007) have used *porteri*.
64. *Chelonoidis nigra vicina*: This widespread taxon from Albemarle Island (Isabela) was previously recognized as one of several valid taxa on that island, including *becki* Rothschild 1901, *microphyes* Günther 1875, *guentheri* Baur 1889, and *vandenburghi* De Sola 1930. Pritchard (1996) synonymized *microphyes*, *guentheri*, and *vandenburghi* under *vicina*, and recognized only *vicina* and *becki* from Albemarle.
65. *Cylindraspis indica*: Includes the recently described *borbonica* Bour 1978 in synonymy, based on genetic work by Austin and Arnold (2001).
66. *Cylindraspis vosmaeri*: Fritz and Havas (2006) credited Fitzinger 1826 with authorship of this name, but corrected it to Suckow 1798 in their 2007 checklist.
67. *Homopus*: A separate taxon of *Homopus* was referred to *H. bergeri* Lindholm 1906 by Branch (1989). However, that name was a junior synonym of *Psammobates tentorius verroxii* Smith 1839 (Branch, 1992; Boycott and Bourquin, 2000), and the new taxon was recently described as *H. solus* by Branch (2007).
68. *Indotestudo travancorica*: This taxon was previously considered a subspecies of *forstenii* (Hoogmoed and Crumly, 1984; Iverson, 1992), but was resurrected to species status by Pritchard (2000) based on morphology, a conclusion supported by mtDNA analysis by Iverson et al. (2001c).
69. *Kinixys belliana*: Fritz and Havas (2006, 2007) recognized only *belliana* and *nogueyi*, following Broadley (1993) uncritically, but others (Iverson, 1992; David, 1994; Iverson et al., 2001a) also recognized *domerguei* and *zombensis*. As the phylogeography of this broadly distributed species complex has not been analyzed, we list the four most widely recognized subspecies.
70. *Pyxis arachnoides*: The three recognized subspecies have recently been confirmed as genetically distinct lineages (Chiari et al., 2005).
71. *Stigmochelys* or *Psammobates pardalis*: Based on genetic analysis, Le et al. (2006) recommended that this taxon be included in an expanded genus *Psammobates*. Fritz and Bininda-Emonds (2007) argued for the retention of a monophyletic *Psammobates* exclusive of *pardalis*. Le at al. (2006) also found a high level of mitochondrial divergence between two specimens assigned to the two subspecies *pardalis* and *babcocki*. In conjunction with morphological distinctions between these two taxa (Loveridge and Williams, 1957; Broadley, 1989), the preliminary genetic data suggest that they may be different at the species level.
72. *Testudo* or *Agrionemys*: The species *horsfieldii* and *hermanni* have been alternatively placed in the genera *Testudo* or *Agrionemys* (Khosatzky and Mlynarski, 1966; Gmira 1993, 1995) and *hermanni* also recently in *Eurotestudo*. Lapparent de Broin (2000a,b) and Parham et al. (2006b) supported the placement of *horsfieldii* in the genus *Agrionemys*, but suggested that a new genus name was needed for *hermanni*. Later Lapparent de Broin et al. (2006) created the name *Eurotestudo* for *hermanni*, but Fritz and Bininda-Emonds (2007) demonstrated that older genus names (*Chersine* and *Medaestia*) are available for that species. Fritz and Bininda-Emonds (2007) recovered a weakly monophyletic clade that included *horsfieldii*, *hermanni*, and the three core species of *Testudo* (*graeca*, *kleinmanni*, and *marginata*). Based on this phylogeny they recommended that all of these species be placed in the genus *Testudo*. The genetic support for some nodes within this clade is not strong and the decision to lump or split is subjective (e.g., whether *Agrionemys* should be used for

horsfieldii is open to debate), therefore the taxonomy of this group may remain in flux for some time.

73. *Testudo graeca*: This species complex has been the subject of massive taxonomic revisions at the species and subspecies level. These revisions have resulted in the naming and elevation of numerous taxa (e.g., Perälä, 2002a,b,c). Several studies (van der Kuyl et al., 2002, 2005; Harris et al., 2003; Carretero et al., 2005; Parham et al., 2006b,c; Fritz et al., 2007) have explicitly refuted the validity of many of these taxonomic acts. Fritz et al. (2007) proposed a taxonomic scheme that recognized five mitochondrial clades in the eastern part of the range of *T. graeca* as subspecies, but did not address the status of several North African subspecies. Since this is the most recent taxonomic suggestion, it is listed here. However, in their recent checklist, Fritz and Havas (2006, 2007) included not only the eleven taxa we list, but also *anamurensis* Weissinger 1987, *antakyensis* Perälä 1996, *floweri* Bodenheimer 1935, *nikolskii* Chkhikvadze and Tuniyev 1986, *pallasi* Chkhikvadze and Bakradze 2002, and *perses* Perälä 2002c. The relationships within this species complex remain uncertain and we expect its taxonomy to continue fluctuating.
74. *Testudo kleinmanni*: Baha el Din (2006), Siroky and Fritz (2007), and Attum et al. (2007) explicitly refuted the validity of *werneri* Perälä 2001 as a species distinct from *kleinmanni*.
75. *Testudo marginata*: Fritz et al. (2005b) explicitly refuted the validity of *weissingeri* Bour 1996 as a subspecies of *marginata*.
76. *Testudo hermanni*: Fritz et al. (2006b) explicitly refuted the validity of *hercegovinensis* Werner 1899 (previously resurrected by Perälä, 2002b) and recommended that *boettgeri* be considered a subspecies of *hermanni*.
77. *Testudo horsfieldii*: In a conference proceedings, Perälä (2002a) elevated two subspecies of *horsfieldii* (*kazachstanica* and *rustamovi*) to full species status. This was accepted by Lapparent de Broin et al. (2006), but warrants reconsideration, especially considering the evidence for unjustified taxonomic inflation in related tortoises in the same work (van der Kuyl et al., 2002, 2005; Fritz et al., 2005b, 2006b; Parham et al., 2006b,c).
78. *Carettochelys insculpta canni*: This subspecies from northern Australia described by Wells (2002a) was only weakly defined as different from the nominotypical subspecies from New Guinea. We list it tentatively pending further analysis, as did Fritz and Havas (2006), although they excluded it from their 2007 checklist.
79. *Apalone spinifera atra*: This taxon has usually been designated a subspecies of *spinifera* (usually with the original spelling *ater*), but others (e.g., Flores-Villela, 1993; David, 1994) have listed it as a full species, though usually without specific argumentation.
80. *Aspideretes* or *Nilssonia*: Engstrom et al. (2004) found *Aspideretes* to be paraphyletic with respect to *Nilssonia formosa* based on morphologic and genetic criteria. Praschag et al. (2007a) formally synonymized *Aspideretes* into an expanded concept of *Nilssonia* based on their analysis of mtDNA of all five included taxa.
81. *Aspideretes* or *Nilssonia nigricans*: Recent morphologic and genetic work on this species previously known only from a single captive population has demonstrated that it also occurs in the wild (Praschag and Gemel, 2002; Praschag et al., 2007a).
82. *Pelodiscus*: The genus has recently been recognized as including up to four separate species by some authorities (David, 1994; Zhao, 1997; Chen et al., 2005, 2006; Fritz and Havas, 2006, 2007). Relationships within the genus are far from resolved and also complicated by translocation and mixing of huge numbers of farm-raised individuals from many parts of the range.
83. *Rafetus swinhoei*: Includes the recently described *Pelochelys taihuensis* Zhang 1984 (Farkas, 1992) and *Rafetus leloii* Duc 2000 in synonymy (Farkas and Webb, 2003).
84. *Acanthochelys macrocephala*: Includes the recently described *Phrynops chacoensis* Fritz and Pauler 1992 in synonymy (Fritz and Pauler, 1999).
85. *Chelodina*: This genus was split into three genera by Wells and Wellington (1985), using *Chelodina* for the narrower-headed shorter-necked species (*longicollis*, *novaeguineae*), and establishing *Macrochelodina* for the broader-headed longer-necked species (*oblonga*, *expansa*, *rugosa*, *siebenrocki*), and *Hesperochelodina* for *steindachneri*. Iverson et al. (2001b) refuted the availability of the name *Hesperochelodina*, but validated *Macrochelodina*. Georges et al. (2002) retained *Chelodina* for the entire genus, but identified three phylogenetic clades within the genus and recommended recognition of three subgenera (but did not name them). Fritz and Havas (2006, 2007) accepted two of these clades (*Chelodina* and *Macrochelodina*) as separate genera.
86. *Chelodina canni*: This taxon is the same as the previously described *rankini* Wells and Wellington 1985, but that name was declared invalid as a *nomen nudum* by Iverson et al. (2001b). Wells (2007a) recently disputed this interpretation and redescribed *rankini*, but *canni* McCord and Thomson 2002 retains nomenclatural precedence and *rankini* Wells 2007a is therefore a junior synonym of *canni*.
87. *Chelodina mccordi roteensis*: This recently named subspecies described in the hobbyist literature needs genetic confirmation of its distinctiveness, but we recognize it pending further analysis.
88. *Chelodina oblonga*: Thomson (2000) showed that the holotype of *oblonga* Gray 1841 is a specimen of what is currently regarded as *Chelodina rugosa* Ogilby 1890. An application is before the International Commission for Zoological Nomenclature (ICZN) to conserve current usage of the name *C. rugosa* Ogilby 1890 for the northern snake-necked turtle and to apply the earlier available name *Chelodina collei* Gray 1856a to the long-necked species of southwestern Australia, while retaining the nomenclatural availability of the name

oblonga for potential future designation of distinct populations of *rugosa* (Thomson, 2006). Though no decision has yet been rendered by the ICZN, Fritz and Havas (2006, 2007) used the name *colliei* for this southwestern population. Georges et al. (2002) found support that this taxon represents a third subgenus under *Chelodina*, but did not formally establish it under a generic-level name.

89. *Chelodina timorensis*: This species recently described in the hobbyist literature by McCord et al. (2007b) was also described a few months later as a new subspecies of *mccordi* (‘*timorlestensis*’) by Kuchling et al. (2007), but the McCord et al. description has chronologic precedence. Concerns surrounding the history and methodology of the description of *timorensis* by McCord et al. are discussed by Kuchling et al. (2007) and serve to emphasize our recommendations (made in our other chapter in this volume) to follow certain procedural guidelines for descriptions of new taxa (Turtle Taxonomy Working Group, 2007).
90. *Chelodina kuchlingi*: This species was described from a single specimen, leading to doubts about its validity (Georges and Thomson, 2006; Fritz and Havas, 2006, 2007), but it remains listed pending further exploration of its remote area of provenance.
91. *Chelodina rugosa*: The species *siebenrocki* Werner 1901 was considered valid by Rhodin and Mittermeier (1976) and Rhodin and Genorupa (2000), but synonymized under *rugosa* by Georges et al. (2002) based on weakly differentiated allozymes within the broader *rugosa* complex.
92. *Elseya*: This genus has been recognized as consisting of two separate lineages (Georges and Rose, 1996; Georges and Thomson, 2006). It was subsequently split into two genera, *Elseya* and *Wollumbinia*, by Wells (2007c), with *latisternum* designated genotype of *Wollumbinia*. Papers by Wells (2002a,b; 2007a,b,c) and Wells and Wellington (1985) have been self-published without any peer review and also highlight our recommendations to follow certain procedural guidelines for descriptions of new taxa (Turtle Taxonomy Working Group, 2007).
93. *Elseya branderhorsti*: This species was considered valid by Rhodin and Genorupa (2000), Thomson et al. (2006), and Georges and Thomson (2006).
94. *Elseya jukesi*: The name *jukesi* Wells 2002b was a *nomen nudum* since no type specimen was designated, but the species was recently redescribed by Wells (2007b).
95. *Elseya schultzei*: This species was listed by Thomson et al. (2006) and Georges and Thomson (2006), but neither morphologic nor genetic data have been analyzed from the type population and its status remains unclear.
96. *Elseya stirlingi*: The previously named taxon *stirlingi* Wells and Wellington 1985 was declared invalid as a *nomen nudum* by Iverson et al. (2001b) (though spelled erroneously as *sterlingi*), but was recently redescribed as a valid species by Wells (2007b).
97. *Elseya* or *Wollumbinia bellii*: The taxon *dorriani* Wells 2002b is a *nomen nudum* without a type designation, but was recently considered a valid subspecies of *bellii* by Wells (2007c).
98. *Emydura macquarii*: The taxonomy of *E. macquarii* was previously reviewed by Georges and Adams (1996). Later, Cann et al. (2003) and McCord et al. (2003) described two new subspecies, but taxa previously described by Cann in 1998 (*binjing*, *dharra*, *dharuk*, and *gunabarra)*, plus *signata* Ahl 1932 were not specifically evaluated by those authors. However, these taxa were all recognized as subspecies of *macquarii* by Fritz and Havas (2006, 2007), and since phylogeographic variation in the *macquarii* species complex has not yet been fully resolved with adequate genetic work, we tentatively list all these subspecies as valid, pending further analysis.
99. *Emydura subglobosa worrelli*: Originally described as *Tropicochelymys worrelli*, this taxon was synonymized under *Emydura victoriae* Gray 1842 by Iverson (1992) and the nomenclatural validity of the species name confirmed by Iverson et al. (2001b). Cann (1998) considered it a distinct species, but Georges and Thomson (2006), partially based on electrophoretic work by Georges and Rose (1996), concluded that it was best referred to as a subspecies of *subglobosa* Krefft 1876. Fritz and Havas (2006, 2007) also listed it as a subspecies of *subglobosa*, but Georges et al. (2006) referred to it as a species, though without providing data or argument.
100. *Phrynops*: Wermuth and Mertens (1977) divided this genus into three subgenera: *Phrynops*, *Batrachemys*, and *Mesoclemmys*. Cabrera (1998) and Georges et al. (1998) elevated these subgenera to generic level. McCord et al. (2001) further divided the remaining monophyletic *Phrynops* into a total of four genera (*Bufocephala*, *Phrynops*, *Ranacephala*, and *Rhinemys*). Joyce et al. (2004) did not accept the taxonomic acts of McCord et al. (2001). Bour and Zaher (2005) synonymized *Bufocephala* and *Ranacephala* with *Mesoclemmys*, but recognized *Rhinemys* as distinct.
101. *Mesoclemmys heliostemma*: Rueda-Almonacid et al. (2007) questioned the validity of this taxon which is completely sympatric with *raniceps*, suggesting that it may simply represent a juvenile color morph of that taxon, and recommended genetic analysis.
102. *Pelomedusa subrufa*: Gasperetti et al. (1993) recommended that the two previously recognized subspecies (*nigra* Gray 1863b and *olivacea* Schweigger 1812) be abandoned.
103. *Pelusios seychellensis*: The taxonomic status of this species is unclear. Gerlach and Canning (2001) concluded that it is extinct.
104. Podocnemididae or Podocnemidae: Cope (1868) used the name Podocnemididae to refer to this clade. Baur (1893b) later referred to this group as Podocnemidae.

Joyce et al. (2004) phylogenetically defined Baur's name (Podocnemidae) to refer to this clade.

105. *Podocnemis unifilis*: This long-recognized species was briefly referred to as *P. cayennensis* Schweigger 1812 by David (1994), but that name was previously often used for what is now recognized as *P. erythrocephala* (Mittermeier and Wilson, 1974), and most authors have continued to use *unifilis*.

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