

DEVELOPING A PROTOCOL FOR THE CONVERSION OF RANK-BASED TAXON NAMES TO PHYLOGENETICALLY DEFINED CLADE NAMES, AS EXEMPLIFIED BY TURTLES

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ABSTRACT—We present a rank-free phylogenetic nomenclature for 25 well-established ancient clades of living turtles. This is the first attempt to document fully the nomenclatural history of a clade with the intent of proposing a coherent nomenclatural system to replace the traditional rank-based nomenclature. Because of the imperative to retain connectivity to the literature for information retrieval, due consideration is given to balancing the desire to develop a consistent system against the desire to conserve traditional associations between names, taxa (i.e., clades), and characters. Novel issues and problems that emerged during this review include: the unclear name/clade association of traditional names; the creation of synonymy lists from which to choose a name; difficulties associated with selecting a single criterion for choosing among multiple ‘subjectively synonymous’ names; identifying authorship for a converted traditional name; and the potential loss of nomenclatural information due to ‘functional homonyms.’ This work may provide a useful road map to those intent on converting their traditional rank-based nomenclatures to explicitly phylogenetic nomenclatures under the precepts of the PhyloCode.

INTRODUCTION

THE GENERAL principles of phylogenetic nomenclature embodied in the draft PhyloCode (PhyloCode, 2003) were outlined more than a decade ago (de Queiroz, 1988; de Queiroz and Donoghue, 1988; de Queiroz and Gauthier, 1990), and their implications have inspired a lively debate among practitioners of this type of nomenclature (e.g., de Queiroz and Gauthier, 1992, 1994; Rowe and Gauthier, 1992; Bryant, 1994; de Queiroz, 1994; Schander and Tholleson, 1995; Chiappe, 1996; Holtz, 1996; Lee, 1996; Lee and Spencer, 1997; Sereno, 1998, 1999; Padian et al., 1999; Gauthier and de Queiroz, 2001; Bryant and Cantino, 2002). We apply those principles in proposing a comprehensive phylogenetic nomenclature for the 50 primary clades of turtles that we feel sure many zoologists will want to talk about. Our stated purpose is not to provide an overview or critique of the differences between both nomenclatural systems, but rather to propose a coherent, rank-free nomenclature to replace the current rank-based nomenclature governed (implicitly or explicitly) by the International Code of Zoological Nomenclature (ICZN, 1999).

Our proposed nomenclature is incomplete, thanks in no small part to the fact that knowledge of turtle phylogeny is still growing. However, there are at least three additional reasons for this shortcoming. First, and perhaps most importantly, there are unresolved questions about the conversion of Linnaean binomials—in which species names are unique but not constant due to changing generic assignments—into a nomenclatural system in which all genealogical entities of interest, be they species or clades (sensu PhyloCode, 2003, Glossary), have their own unchanging names (Cantino et al., 1999). A second problem is that there is no widely accepted protocol for associating a particular node-, stem-, or apomorphy-based clade with one among a realm of possible candidate names from the traditional taxonomic literature (e.g., Sereno, 1998, 1999). This is largely because the limits of the circumscription of many traditional rank-based taxa are often fuzzy, making it difficult to construct a coherent argument that any given taxon name governed (explicitly or implicitly) by the ICZN must objectively refer to a particular clade as well (Gauthier and de Queiroz, 2001; see below). Finally, any nomenclatural history necessitates a laborious review of an old and rare scientific literature that is often difficult to find. We consequently focus our efforts toward converting the names associated with the most widely studied, uncontroversial, long-recognized phylogenetic units,

which include extant species, and intentionally leave the conversion of currently ill-supported clades, or clades that contain fossils only, to subsequent reviewers.

Among extant vertebrates, turtles are an ideal clade to lead the transition from a rank-based nomenclatural system (ICZN, 1999) to a rank-free nomenclatural system that is based on phylogenetically defined clade names (PhyloCode, 2003). With fewer than 300 living species, turtles are manageable, yet diverse enough, with a long and complex history of ideas about phylogeny and nomenclature, to raise novel questions regarding the procedures of nomenclatural transition as proposed in the PhyloCode (2003).

Given the lack of transitional protocols, a primary goal of this paper is to identify difficulties that may be associated with the systematic conversion of names, explore promising solutions, and develop a protocol that allows the efficient mass conversion of names from one system to the other while maintaining optimal connection to their current meaning (i.e., their currently accepted circumscriptions). On this basis, we propose an internally consistent phylogenetic nomenclature for all well-accepted crown clades of extant turtles, and their stem counterparts, with the ultimate goal of nomenclatural precision, stability, and universality.

Among the plethora of namable clades, this contribution focuses on naming the crowns and panstems of the well-known clades of turtles (Gauthier and de Queiroz, 2001). Crown clades are clades delimited by living representatives (e.g., the clade that originates from the last common ancestor of all living turtles). In contrast, panstem clades are clades that include crowns, but are also specified by the next living representatives from outside of those crowns (e.g., the clade that contains living turtles plus all organisms more closely related to living turtles than to any other living organism). This emphasis on naming clades delimited by extant specifiers does not imply that fossils are somehow less deserving of our attention or that this article is not relevant to paleontologists. Quite to the contrary, we predict that this contribution will be of particular interest to paleontologists. This is because crown and panstem clades are precisely those clades about which neontologists and paleontologists so often want to communicate. At a time when morphological data from “stem groups” and age estimates of crown clades are arguably the most important contributions that paleontologists make to systematic biology, it is consequently of singular importance for all paleontologists to appreciate the differences among stem-, node-, and

apomorphy-based clade names in order to be able to communicate precisely their findings to their neontological colleagues using a nomenclatural system shared by both communities.

Abbreviations and notes.—Abbreviations used include: NCN for New Clade Name; CCN for Converted Clade Name; and ‘orig.’ to denote original taxonomic reference. We provide full citations for the names of specifier species (s. PhyloCode, 2003, Article 11.1) used in the main text. For the citations of all other species names listed in the Appendices, please refer to King and Burke (1989) or Iverson (1992). Throughout the text, double quotes are used when citing literally. In contrast, single quotes are used to highlight a particular word, not its meaning.

METHODS

A comprehensive literature search was undertaken to reconstruct the history of the systematics, taxonomy, and nomenclature of fossil and Recent turtles, with an emphasis on understanding the nomenclatural history of the major crown clades (i.e., clades delimited by extant species). A number of previously published reviews proved particularly useful starting points, such as Boulenger (1889), Siebenrock (1909), Hunt (1958), Kuhn (1961, 1967), Gaffney (1984), Bour and Dubois (1985, 1986), and King and Burke (1989). Special emphasis was placed on reading all primary literature, and not relying on secondary references, to avoid propagating incorrectly cited ideas about turtle taxa as governed by the ICZN (1999) and their associated circumscriptions and names. All books and articles used herein were searched for turtle-related ICZN-taxon names as well as their differentiating characters (= differentia) and proposed composition (= usages) with the aim of creating synonymy lists, that is, lists of names that apply to (arguably) comparable circumscriptions (non s. ICZN, 1999 and PhyloCode, 2003; see below). Following the current rules of the ICZN (1999), we consider only formal Latin names and ignore all literature using vernacular English, French, German, or Italian terms, such as ‘Chéloniens’ (Brongniart, 1800a, 1800b) or ‘Testuggini’ (Bonaparte, 1836b). This literature review is the basis against which we test ideas regarding current and past nomenclatural practices. It also serves as the foundation for the transitional protocols that we develop and the phylogenetic nomenclature of turtles that we propose.

As recommended by the PhyloCode (2003, Recommendation 6.1B), all clade names are distinguished from taxon names governed by the ICZN (1999), in this case by the use of italics (e.g., *Testudines* vs. *Testudines*). This approach may be considered problematic for genus and species names, because these are usually italicized following the recommendations of the ICZN (1999, B6). However, given that the PhyloCode (2003, Article 1) does not regulate species names and that isolated genus names are not used throughout the text, confusion is avoided for the moment. To further distinguish clade names from higher-ranked names as governed by the ICZN, we also italicize all grammatical derivatives of formal clade names (e.g., “all *cryptodiran* turtles possess a processus trochlearis oticum,” or “*kinosternoids* are *cryptodires*”). Throughout the text we use traditional binomials as ruled by the ICZN (1999), but include their original generic assignments in parentheses [i.e., *Chelonia* (orig. *Testudo*) *mydas*] when using them as internal specifiers in clade name definitions.

DISCUSSION

What is a taxon?—Significant miscommunications can quickly arise between followers of the ICZN and PhyloCode due to radically different definitions of ‘taxon.’ According to the ICZN (1999, Glossary), a taxon, herein referred to as an ICZN-taxon, is a category of classification (such as a family or genus) that is typified by a single species (type species). Names are assigned to

ICZN-taxa based on simple, rank-associated rules that are governed by the ICZN. For instance, it is hypothetically possible to unite all known turtles into a single family with the type species *Testudo graeca*. The correct name for this ICZN-taxon is ‘Testudinidae.’ However, it is also possible to unite terrestrial tortoises only into a family with the type species *Testudo graeca*, and the correct name for this ICZN-taxon remains ‘Testudinidae.’ According to the ICZN (1999, Article 23.3), both ICZN-taxa are ‘synonymous,’ because they have the same rank and contain the same type species, but they differ markedly in their assigned or circumscribed content or composition.

Following the PhyloCode (2003, Article 1), taxa, herein referred to as phylo-taxa, are species or clades. Names are tied to clades using phylogenetic definitions. To avoid nomenclatural confusion, the PhyloCode was drafted with the intention of governing this process. Continuing with the example above, a phylo-taxon ‘*Testudinidae*’ that contains all turtles cannot be considered ‘synonymous’ with a phylo-taxon ‘*Testudinidae*’ that contains only terrestrial tortoises, because these phylo-taxa differ in their actual composition as they derive from different most-recent common ancestors (PhyloCode, Article 14). Although it is our intention to propose a nomenclature of turtles following the rules of the PhyloCode (1999), we will distinguish both meanings of the word taxon throughout the text using prefixes (i.e., ICZN-taxon vs. phylo-taxon) to avoid confusion.

Information retrieval.—As many will agree, one of the major purposes of nomenclature is the efficient storage and retrieval of information, although there may be considerable disagreement about exactly what information is stored, and whether or not any of it is actually retrievable (e.g., de Queiroz and Gauthier, 1992; Mayr and Bock, 2002). A flow chart illustrates the differences between phylo-taxonomy and nomenclature as to be administered by the PhyloCode and ICZN-taxonomy and nomenclature as governed by the ICZN (Fig. 1). According to the methods advocated by the PhyloCode, authors attach names to clades by carefully circumscribing the clade to which the name is assigned by explicit reference to common ancestry. This system has three advantages. First, ideas regarding composition or apomorphies of a phylo-taxon can be precisely retrieved as originally conceived by the author by applying the appropriate name definition to a given phylogenetic hypothesis. Second, it is possible to assess the phylo-taxonomic status of all species unknown to the original author, thus alleviating the need to continually alter the meaning of names over time because of inevitable changes in our knowledge of biodiversity. Finally, although no information can be retrieved from the name itself, cognitive efficiency (= cognitive economy of Rosch, 1978) will be better served over time, because any given name will always refer to the same ancestor regardless of changing ideas about composition (= circumscription).

In traditional rank-based taxonomy, authors conceive increasingly inclusive classes of organisms that are united by defining characteristics (differentia), such as synapomorphies and/or symplesiomorphies. These classes of organisms are then assigned a categorical rank and a type species or specimen, thus becoming ICZN-taxa. Finally, each ICZN-taxon is given a diagnosis that circumscribes its composition by reference to its differentia, and, using the rules of the ICZN (1999), is assigned a certain name based on its rank and type species or specimen. Naturally, given that the ICZN (1999) does not govern taxonomic practice per se for the most part, this description of taxonomic practice should be understood as a simplification, not an authoritative account of traditional taxonomic practice.

The emphasis on rank allows any subsequent taxonomist to retrieve efficiently the rank of an ICZN-taxon and its relative placement within any ICZN-taxonomic system (at least for some levels in the taxonomic hierarchy). Names of the family group

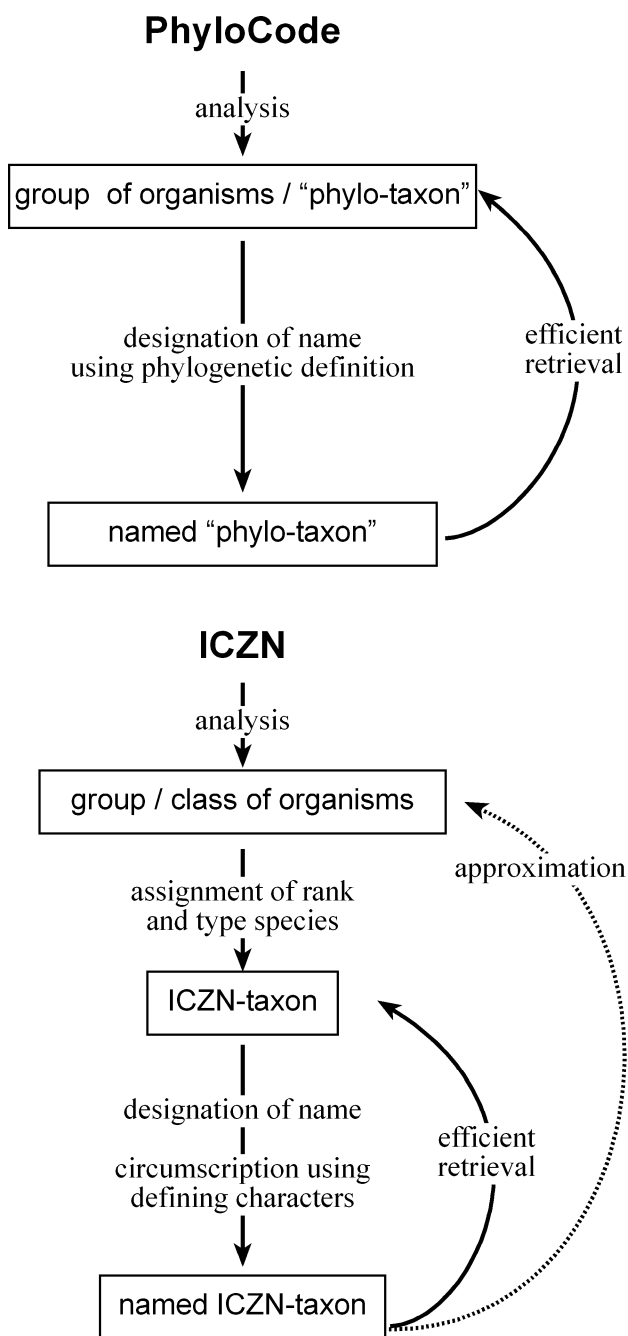


FIGURE 1—Flow chart illustrating differences between traditional taxonomy as governed by the ICZN and phylogenetic taxonomy as to be governed by the PhyloCode in the conception and naming of groups and the retrieval of information regarding groups from their names.

also efficiently refer to their type genus (ICZN, 1999, Articles 25–34); the type species, however, can only be retrieved after consulting the relevant literature (e.g., King and Burke, 1989, for turtles). Using the associated differentia, systematists are able to approximate the limits of the circumscription of an ICZN-taxon, but they will typically not be able to do so with precision. Furthermore, because names are not tied to groups of organisms, but rather to ranks and type species, any ICZN-taxon name can refer to a large number of different groups (as long as they include the

type), thus impeding cognitive efficiency. Because it is our intention to document the history of names associated with groups of turtles, most of the sections below are devoted to establishing methods that allow approximation of the groups to which traditional taxon names *might* refer.

Establishing synonymy.—One of the main objectives of this paper is to provide complete lists of all names that have been associated with any given set of species or apomorphies of turtles in order to document the history of name association and to guide the choice of crown clade names. We consider names that apply to the same group of organisms synonymous. This usage of the word synonymy contrasts that of the ICZN (1999, Article 23.3), where two names are considered synonymous only when they refer to ICZN-taxa of equal rank and with the same type species (see above). This usage also differs somewhat from that of the PhyloCode (2003, Article 14) where two names are considered synonymous only when they refer to the same phylo-taxa (i.e., clades), because not all historical groupings considered herein are necessarily clades.

Assessing the group of organisms to which a name refers is difficult in traditional taxonomy (see above). This is because the limits of the circumscription of an ICZN-taxon can only be approximated using the species and diagnostic characters listed by the author (Gauthier and de Queiroz, 2001). Only in very few cases, especially in pre-Darwinian times, did authors clarify how they conceptualized the circumscription of their ICZN-taxa, and how their proposed names were to be tied to those circumscriptions, thus leaving this decision to the inclinations of individual reviewers. All synonymies of circumscriptions of traditional taxon names, consequently, are based on approximations and must be considered subjective. For instance, Linnaeus (1758) made no explicit statement as to the nature of his genus *Testudo*. If it is circumscribed in terms of explicit composition, Linnaeus (1758) was referring to what later came to be known as *Cryptodira* Cope, 1868 (hide-necked turtles), because his species list does not include a single representative of *Pleurodira* Cope, 1865 (side-necked turtles). *Testudo*, consequently, could be considered the senior synonym of *Cryptodira*. However, if Linnaeus (1758) intended to apply a name to any set of species, so long as those species (or organisms) possessed the appropriate differentiating characteristics, we must conclude that pleurodires are included in *Testudo* because they display the relevant character differentia (viz., “corpus tetrapodum, caudatum, testa obtectum”—body four-legged, with a tail, covered by a shell). Last, but not least, because not a single fossil species is included in the *Systema Naturae*, it is not clear, if Linnaeus’ *Testudo* is to be restricted to the crown, or if it is to include any fossils from along the extinct *Testudo* stem. As such, how can *Testudo* Linnaeus, 1758 be objectively synonymized with any other ICZN-taxon name? Correspondingly, if it is unclear to what an author was referring, how can traditional name usage be inferred unambiguously?

This situation contrasts to Phylogenetic Nomenclature as governed by the PhyloCode in which phylo-taxon names are explicitly defined in regard to their ancestry (de Queiroz and Gauthier, 1990). Based on any given tree topology, it then follows that any two phylo-taxon names can objectively be considered synonymous if their definitions point to the same most recent common ancestor (de Queiroz and Gauthier, 1992). For instance, according to Gauthier (1994, p. 138), *Anapsida* is defined as applying “to chelonians (turtles) and all other amniotes more closely related to them than they are to saurians,” whereas Laurin and Reisz (1995, p. 186) defined *Parareptilia* as “Testudines and all amniotes more closely related to them than to diapsids.” As both definitions objectively point to the same clade, these names are unambiguously synonymous within the context of current phylogenetic hypotheses. Because we are only able to approximate the limits of the

circumscriptions to which ICZN-taxon names refer, we term all synonymies based on ICZN names 'subjective synonymies,' and all synonymies based on phylogenetically defined names 'objective synonymies.' These two terms should not be confounded with identical ones used by the ICZN (see ICZN 1999, Glossary).

Providing subjective synonymy lists from the neontological literature is straightforward if ICZN-taxon names are equated to sets of species, as is often the case in the post-Hennigian literature. That is because most extant turtles can be divided into well-known sets of morphologically distinctive groups, allowing the composition of various ICZN-taxa to be compared objectively and without much difficulty. Nevertheless, two problems remain. First, eighteenth- and nineteenth-century zoologists were not yet aware of significant portions of extant turtle diversity, rendering it unclear if species unknown to a worker were to be referred to by an ICZN-taxon name coined by that worker. For these cases, we fixed the reference between a name and a set of species by applying their published differentia of an ICZN-taxon—or at least those characters now regarded as apomorphies—toward all living turtles, whether known to the original author or not, provided that they were not explicitly excluded from the group. For instance, Linnaeus (1758) did not include any representatives of *Pleurodira* into his single turtle genus *Testudo*, most likely because he was not familiar with these animals. However, we conclude that Linnaeus' (1758) '*Testudo*' refers to all extant turtles, because he did not intentionally exclude *Pleurodira* from that group, and because all extant turtles, including all pleurodires, possess all the apomorphies listed among his morphological differentia.

The second problem with assessing taxonomic composition from the early neontological literature reflects a preliminary (and now thought to be incorrect) placement of species originally known from very incomplete material. In these cases, we remove such mistaken attributions from the composition of the relevant ICZN-taxa, because we conclude that the author's 'true' intention is not reflected by their inclusion, because these turtles actually lack the relevant differentia. For instance, the morphologically derived turtle *Carettochelys insculpta* Ramsay, 1887 was initially known from incomplete specimens that did not reveal its currently accepted identity as a *cryptodiran* turtle related to soft-shelled turtles (*Trionychidae* Gray, 1825). Based on the few characters known and its geographic distribution, Boulenger (1889) classified this species as a *pleurodiran* turtle, thus making his '*Pleurodira*' a polyphyletic group in the context of any current turtle phylogeny. Given how poorly known *Carettochelys insculpta* was to Boulenger (1889), however, we do not believe that he was attempting to make a bold statement by proposing this systematic assignment. Consequently, we consider the composition of his '*Pleurodira*' to be equivalent to modern applications of that name. In our experience, this second problem is minor within the neontological turtle literature, affecting only the placement of *Carettochelys insculpta* (as described above) and *Manouria emys* (Schlegel and Müller, 1844), which was originally thought to be an Asian pond turtle (*Bataguridae* Gray, 1870), but now is thought to be a terrestrial tortoise (*Testudinidae* Gray, 1825).

When considering ICZN-taxa that include fossil species, producing even subjective synonymies proves more difficult because many ICZN-taxon names have been applied to a swarm of interrelated clades. For example, Rowe and Gauthier (1992) described how the ICZN-taxon name *Mammalia* has been applied to a broad range of clades originating anywhere from the Carboniferous to the late Jurassic, and differing only in the extent to which they include the phylogenetic stem of crown mammals. Among turtles, a similar swarm of clades is associated, for instance, with the turtle ICZN-taxon name *Dermochelyidae* (e.g., Gray, 1825; Seeley, 1880; Lydekker, 1889; Hirayama, 1994). What unifies these usages is the presumably honest intent of any given author to

include only fossil stem representatives that they deem anatomically 'mammalian' or 'dermochelyid' in some essential feature(s). That is to say, authors generally referred fossils to '*Dermochelyidae*' because their characters were thought to be sufficiently similar to those of extant *Dermochelys coriacea*. Because we are most interested in documenting the names associated with crown clades, we chose from a list of available stem-associated ICZN-taxon names that name which most nearly circumscribes the crown in its referred composition.

Although ICZN-taxa are often explicitly conceptualized as clades in more recent literature, the connection between a name and a clade is seldom unambiguous (e.g., Laurin, 2002). Typically, names are written next to nodes, thus implying a node-based understanding of the specified ICZN-taxon. Subsequent nomenclatural decisions often turn on characters, however, implying an apomorphy-based conceptualization. To enable a comparison of ICZN-taxon names used in the cladistic literature with names from the traditional neontological and paleontological literature, we decided to consider all names used in cladograms as referring to the node they label.

Using this method of establishing synonymy, several apomorphy-based ICZN-taxa can refer to different nodes at different times. That comes as no surprise to traditional taxonomists because the circumscription of an ICZN-taxon is allowed to vary. For instance, based on a series of apomorphies, Gaffney (1975a, 1975c) assigned the name *Eucryptodira* to the crown node composed of all *cryptodiran* turtles. Soon after, several fossil taxa were discovered that also exhibited the defining apomorphies of '*Eucryptodira*,' but were situated just basal to the *cryptodiran* crown. Gaffney (1984) accordingly included them in '*Eucryptodira*.' Gaffney (1975c, and proposed a new apomorphy-based name—*Polycryptodira*—for the collection of species previously called '*Eucryptodira*'. Since then, Gaffney (1996) referred to '*Polycryptodira*' a new fossil stem species that possessed all these apomorphies, thus leaving crown *Cryptodira*—one of the primary clades of turtles we presume most herpetologists want to talk about—without a name once again.

Character versus node versus stem: Who gets the name?.—With the advent of modern methods of phylogenetic inference and explicit phylogenetic hypotheses, a discussion quickly emerged about which among a series of internested clades should receive the most widely used name (sensu de Queiroz and Gauthier, 1992). Following the arguments presented in a series of articles (de Queiroz and Donoghue, 1988; de Queiroz and Gauthier, 1990, 1992, 1994; Rowe and Gauthier, 1992; Gauthier and de Queiroz, 2001), we assign all widely used names to crown clades. Although we urge the interested reader to refer to the publications listed above, we will briefly summarize two major arguments that favor this approach below.

First, the largest body of literature that utilizes ICZN-taxon names is neontological, not paleontological. If currently used names are converted and tied to the crown clades, then all statements made in the neontological literature remain accurate (or at least justifiable). Furthermore, neontologists will be able to continue to use the names that they are most familiar with; only paleontologists, a minority to which all three authors of this paper belong, will need to rethink parts of the nomenclature with which they are familiar (de Queiroz and Gauthier, 1992). In other words, we believe that most zoologists would prefer using the familiar names '*Testudines*,' '*Cryptodira*,' and '*Pleurodira*,' rather than the more obscure names '*Casichelydia*,' '*Polycryptodira*,' and '*Eupleurodira*.' All major crown clades deserve a name, and we prefer to christen them with the currently most widely used names for the sake of cognitive efficiency. Second, if commonly used names are tied to crown clades, unjustified phylogenetic inferences will be minimized (de Queiroz and Gauthier, 1992). As an

example, according to many textbooks on turtles, all members of the *Cryptodira* retract their necks along a vertical plane (albeit to a variable degree, e.g., Pritchard, 1979; Ernst and Barbour, 1989; Zug et al., 2001), an observation based on living cryptodiran turtles only. Given this information, it seems plausible to infer that *Kayentachelys aprix* from the Lower Jurassic of Arizona, the “oldest known Cryptodire” (Gaffney et al., 1987, p. 289), also retracted its neck vertically. That assertion is not justified, however, because *Kayentachelys aprix* is currently hypothesized to be situated far outside of crown *Cryptodira* and to have existed long before vertical neck retraction originated. One might reasonably infer the capacity for that style of neck retraction from structural correlates, but that requires a less secure inferential chain than one derived from direct observations of living species (Gauthier and de Queiroz, 2001).

To accommodate fossil species that are situated outside of crowns, we decided to create new, stem-based clade names. Every crown possesses a plethora of nameable stem clades (Gauthier and de Queiroz, 2001), however, making it once again necessary to choose one among many. We will here name only the most inclusive stems that do not overlap with the stems of any other living taxon. We term this type of stem—the ‘total group’ of Jefferies (1979)—a ‘panstem clade’ (pan = whole, entire) or simply ‘panstem.’ Following Gauthier and de Queiroz (2001), panstems will be formed by addition of the prefix ‘pan-’ to crown-name roots; hence ‘Testudinidae’ for crown tortoises and ‘Pantestudinidae’ for panstem tortoises. Cognitive efficiency is thereby increased in two ways. First, merely by adding the prefix ‘pan-’ to any crown name, any zoologists seeing such a construction would know instantly that the name refers to a panstem, and not to any other stem or node. Second, adding only ‘pan-’ to crown names will effectively reduce by half the number of different names with which anyone will have to contend. In some cases, this practice requires rejecting perfectly good ICZN-taxon names defined by previous authors. *Cryptodiromorpha* Lee, 1995 is one such example because ‘*Pan-cryptodira*’ would replace it under this convention, even though these names are plainly synonymous, with the former name having publication priority over the latter. Although some may disagree with this approach, we feel confident in overriding priority because the benefits to future generations of zoologists far outweigh the disadvantages created from disrupting the connection with the current literature (it is admittedly difficult to credit priority in the absence of a formal starting date for the PhyloCode). Fortunately, within turtles, this conflict exists only with three panstems, and the names proposed for them have not been used since they were proposed (see *Panpleurodira*, *Pan-cryptodira*, and *Pancheloniidae* below), thus making it possible to replace them without any true disruption of connection to the current literature.

As an example, we propose that the crown clade arising from the most recent common ancestor of all living terrestrial tortoises be referred to as ‘*Testudinidae*.’ All fossil species that are situated along the phylogenetic stem of *Testudinidae* should be included in the more inclusive clade called ‘*Pantestudinidae*.’ As informal equivalents, we refer all members of *Testudinidae* as ‘*testudinids*,’ and all members of *Pantestudinidae* as ‘*pantestudinids*.’ Finally, should the term prove useful, one might wish to refer to all representatives of the extinct and paraphyletic stem of *testudinids* as ‘stem-testudinids.’ However, the latter has no formal phylo-taxonomic status and ought not to be italicized like formal phylogenetic names (see below).

Choice of name and functional homonyms.—The formal clade names proposed here were selected from the list of subjective and objective synonyms discussed above. No single criterion of name choice, however, would ensure satisfying results every time, which is to “minimize disruption of current usage” (PhyloCode,

2003, Recommendation 10a). We therefore established a hierarchy of criteria.

Generally, our first criterion of choice was not priority, but current common usage (i.e., current common clade/name associations based on composition). This somewhat unconventional method was necessary because our literature searches indicated that almost no single phylo-taxon is currently addressed by its original name. For instance, under strict priority, Cryptopodi Latreille, 1825, not Testudinoidea Fitzinger, 1826, should be considered the correct name for the clade composed of all pond turtles and terrestrial tortoises. The resurrection of a multitude of largely unfamiliar names serves little purpose beyond strict adherence to priority, and at too steep a cost, if the overarching goal is to conserve the associations between names and phylo-taxa used in the current literature. However, whereas rules of priority provide a precise framework for choosing names, the term ‘common usage’ naturally invites ambiguity. We consider a name commonly used if a clear majority of systematists applied it during the last 25 years to the same phylo-taxon. Some systematists designated apomorphy/clade associations (e.g., Gaffney, 1975a, 1975c), so the pool of potential synonyms was reduced arbitrarily to phylo-taxa having that apomorphy. Finally, ‘common usage’ was sometimes rejected when it came into conflict with our desire to reserve widely used names for crown clades.

Only in rare circumstances did we ignore these rules, usually to favor a more recognizable name to avoid confusion among similarly spelled clade names. The introduction of cladistic methods resulted in the recognition of a plethora of new clades that may warrant their own names. All need not be given formal names—a cladogram or similar device often will serve—but if biologists want to talk about them, they ought to be able to name them (de Queiroz and Gauthier, 1992).

Fueled by the traditions growing from the rules and recommendations of the ICZN (1999), it is common practice to form new names by slightly altering well-established genus-group names by the addition of ever so slightly altered suffixes. Bour and Dubois (1985), for example, provide a framework for forming up to 13 new ICZN-taxon names within the family group alone. The resulting names often cannot be easily distinguished, thus becoming ‘functionally homonymous,’ owing to the limited ability of humans to easily distinguish among them by sound alone. Drastic examples among turtles, extracted from the primary literature, include the derivatives of *Testudo* Linnaeus, 1758 (*Testudo*, *Testudia*, *Testudinata*, *Testudines*, *Testudininei*, *Testudininae*, *Testudinina*, *Testudinini*, *Testudinidi*, *Testudinidae*, *Testudinoidea*, *Testudinoidea*, *Testudinoides*) or the derivatives of *Chelonia* Brongniart, 1800b and Cuvier, 1800 (*Chelonia*, *Cheloniana*, *Chelone*, *Chelonii*, *Chelonides*, *Chelona*, *Chelonea*, *Cheloniadae*, *Cheloniidae*, *Cheloninae*, *Cheloniae*, *Cheloniinae*, *Cheloniidae*, *Cheloniidea*, *Cheloniida*, *Chelonida*, *Chelonidi*, *Chelonina*, *Chelonini*, *Chelonioida*, *Chelonioidae*). If ease of name recognition is a desirable goal of nomenclature, we conclude that too many similarly spelled names should be avoided. In rare instances, we decide to overrule both common usage and priority and assign clades with significantly different names. Detailed explanations for all decisions are presented in the discussion sections following each named clade.

The vast majority of living turtles can comfortably be grouped into inclusive clades, but four exceptions exist: *Carettochelys insculpta*, *Dermochelys coriacea*, *Dermatemys mawii*, and *Platysternon megacephalum*. Strictly speaking, these four species, traditionally placed in their own monotypic Linnaean families, are just some among many living species of turtles and consequently should receive no special nomenclatural attention. However, with the possible exception of *Platysternon megacephalum*, these species have fine fossil records that connect them to other living

turtles via long stem-lineages that typically extend into the Cretaceous. We consequently feel it desirable to create stem-based clade names for these single species, but we could find no protocols for how to define panstems based on single species (lineage segments *sensu de* Queiroz, 1998, 1999). Among many possibilities, we decided to form new panstem names by combining current Linnaean generic names with the prefix 'pan' (to automate the process of naming panstems). When possible, we then referred the traditional family names to less inclusive clades whose composition closely resembles the current name application.

No clade inherently possesses a true name, and phylogenetic nomenclature as governed by the PhyloCode (2003) is a process of assigning somewhat arbitrary words to a non-arbitrary meaning. As such, none of the names that we reject are 'wrong,' nor is this system 'right.' Instead, names become more or less informative, depending on the number of people who use them to convey the same meaning. Due to the vast array of literature considered in this review, we are confident that we found all relevant subjective synonyms, and that our putative names-to-clade associations have a reasonable connection to traditional usage as inferred herein. In order to minimize ambiguity, all clade names are clearly defined and the logic invoked in our decision-making process is explained in each case. If future research indicates an oversight on our part, we gladly welcome the clarification. However, because all names were chosen based on our subjective sense of synonymy (see above), we trust that future researchers who disagree will help maintain stability by avoiding the temptation to rename them.

Authorship.—The purpose of citing references in scientific work is to introduce the reader to a wider literature, to acknowledge those who developed an innovative idea, and, most importantly for nomenclatural purposes, to refer the reader to a specific article that clarifies the meaning of a given name.

According to the rules of the PhyloCode (2003, Article 19.1), a phylo-taxon name is attributed to the author of its protologue, that is, the defining formula of that phylo-taxon name (PhyloCode, 2003, Glossary). This convention is sensible, as it allows the efficient retrieval of the definition of any given phylo-taxon name. The PhyloCode (2003, Article 20.1) also states that "[i]f the author of a converted name is cited, the author of the preexisting name on which it is based must also be cited." Unfortunately, no guidelines are provided by the PhyloCode (2003) as to which among a number of possible candidate authors should be cited.

Following the spirit of the PhyloCode (2003), up to three people may justifiably be associated within any given ICZN-taxon name: the author who first recognized a phylo-taxon (i.e., a natural or monophyletic group); the author who developed a connection between particular characters (apomorphies) and a particular name; and the author who first applied a name to a certain phylo-taxon. Ideally, all three of these authors are the same person, but that is rarely the case. For instance, the first to recognize that all pond turtles and terrestrial tortoises form a natural group was Latreille (1825), who called them 'Cryptopodi.' The most commonly used name for this group today, 'Testudinoidea,' was soon after coined by Fitzinger (1826), who applied this name to terrestrial tortoises only. It was not until Baur (1893) that Testudinoidea was actually referred to Latreille's (1825) group comprised of pond turtles and terrestrial tortoises. Which of these three authors, then, deserves the credit and should therefore be cited after 'Testudinoidea' when this name is formally converted to its current clade application using the PhyloCode?

The rules and recommendations of the ICZN (1999) add an additional level of complexity by providing rules that may favor yet another author. In particular, the ICZN (1999, Article 50) maintains that credit be given to the author who first established

an ICZN-taxon regardless of the current circumscription of the group to which the ICZN-taxon name refers. More importantly, the ICZN (1999, Articles 36.1, 43.1) dictates that the first author of a family or genus group name be given credit for all other family or genus group names that contain the same type genus or type species, respectively. For instance, following these ICZN rules, Bour and Dubois (1985) correctly identified Batsch (1788) as the author of the 'superfamily Testudinoidea' (the group of turtles discussed above that is currently circumscribed to contain all pond turtles and terrestrial tortoises), because Batsch (1788) was the first to coin a family level ICZN-taxon containing the type species *Testudo graeca*. In conclusion, depending on the rationale used, four different authors may reasonably be associated with the converted clade name 'Testudinoidea.' Batsch (1788, the author who first coined the family group ICZN-taxon that contains *Testudo graeca*); Latreille (1825, the author who recognize the clade comprised of pond turtles and tortoises); Fitzinger (1826, the author to coin the name Testudinoidea); and Baur (1893, the author to first applied the currently accepted circumscription to the ICZN-taxon Testudinoidea).

When reviewing current taxonomies above the family group level, it became clear that most workers use a mosaic of criteria when choosing authors for ICZN-taxon names, because the ICZN (1999) does not provide any rules for these ranks. For instance, extending the recommendations of the ICZN (1999) to higher-ranked ICZN-taxa, Bour and Dubois (1985) gave Brongniart (1800a) credit for assigning all turtles to the ordinal name Chelonii, because he was the first to coin a name for turtles at the ordinal level (based on categorical ranks in the Linnaean tradition). However, they nevertheless credited Gaffney (1975a, 1975c) for naming the suborder Casichelydia, although Gaffney was not the first to name a turtle suborder that contained the cryptodiran type species *Testudo graeca* or *Chelonia mydas* (e.g., Mayer, 1849; Agassiz, 1857; Gray, 1870), nor the first to name an 'order group taxon' that contains the type *Testudo graeca*. Finally, Bour and Dubois (1985) credited Cope (1868) for the infraorder Pleurodira, even though he did not assign that name to the infraorder nor discover that clade. In conclusion, no single method is currently used when crediting an author with a name, admittedly because no criterion is mandated by the ICZN. This demonstrates primarily that there is no universal sense of authorship that one could follow when implementing the PhyloCode rule that authorship be granted the author of a converted name (PhyloCode, 2003, Article 20.1).

One of the major objectives of this paper is to document comprehensively the history of the discovery and naming of each clade. Ideally, all three non-rank-based authors (i.e., the author of the phylo-taxon, author of the name, and the author who first assigned a name to a phylo-taxon) should be listed after every name. However, because ICZN-taxon names cannot be objectively synonymized with the clades defined herein (see above), we conclude that the only author that can be determined objectively is the author of a name, however that name may have been conceived originally. We consequently cite only the actual author of the name directly after each phylo-taxon name but credit all other contributors to the meaning of those phylo-taxon names in the discussion section following the definition of each phylo-taxon name. Unfortunately, even though this procedure can be implemented objectively, we must conclude that this type of authorship is problematic, given that the author who coined a given ICZN-name typically has only the most tenuous connection to the clade being named.

Choice of crown and stem clades to be named.—With an estimated 289 turtle species alive today (see Appendices), a fully bifurcated tree could require at least 865 node- and stem-based names $\{n = [(number\ of\ terminals * 3) - 2]\}$. For instance, if fully

bifurcated, the approximately 25 species of *Kinosternidae* (American mud and musk turtles) form 24 crown clades, and each of these crown clades possesses potentially countless node and apomorphy-based clades, as well as stem clades relative to any other living *kinosternid*, or to any other turtle, or living being, not to mention any extinct species. However, like so many other groups of organisms, extant turtles form a number of easily recognizable, morphologically discrete clades resulting from long time-spans of separate evolution, the sequential accumulation of diagnostic characters, and the extinction of intermediate forms. Once discovered by naturalists, these groups have always received formal names—names that have become the *lingua franca* of turtle research—and we will continue to honor that tradition, not least because we too would like to communicate about these clades. Interestingly, although these groups are easily distinguishable from one another and are most certainly monophyletic, most of them have unresolved internal relationships.

One of the classic arguments against defining names phylogenetically is the risk that, over time, the composition associated with a name may change significantly due to changes in tree topology (see Benton, 2000, and references therein). Consider the following hypothetical example. According to some cladograms (e.g., Hirayama, 1985), it is possible to define a node-based version of crown ‘*Bataguridae*’ (Asian pond turtles) as the clade arising from the most recent common ancestor of *Batagur baska* and *Geoemyda spengleri* and correctly point to a group of turtles that has been recognized for almost 50 years (Fig. 2.1). However, if this definition is applied to the more recent hypotheses proposed by McCord et al. (2000), *Rhinoclemmys* is excluded from *Bataguridae*, thus changing the traditionally accepted composition associated with the name (Fig. 2.2).

If an idea about a particular composition (or characters) is important to the author of a phylo-taxon name, then that clade’s name should be defined explicitly with respect to those included species (or apomorphies). Similarly, if the author intends to exclude some species but include others, all species that are considered essential (internal specifiers of the PhyloCode, 2003, Article 11), or not permissible (external specifiers of the PhyloCode, 2003, Article 11), to the phylo-taxon name must be listed in the definition. For cases in which ideas about composition are paramount, space limitations may still make it difficult to list all included species in a phylogenetic definition, at least in highly speciose clades (e.g., *Eucaryota*). As an alternative, it is sufficient to list two or three exemplars, and then refer to the literature where the remaining species are listed (e.g., Gauthier and de Queiroz, 2001). This type of definition is especially useful for defining the names of node-based phylo-taxa with uncertain internal relationships; that is to say, name application would be fixed by composition regardless of ideas regarding ingroup relationships. As our understanding of the internal relationships of many turtle groups will doubtless change in the future, we consequently define all crown clades with respect to their total extant composition, and thus buffering them against that eventuality. Furthermore, as described above, we chose among the plethora of potentially nameable stem-groups only the most inclusive stem group that does not include the closest living turtle (or other amniote), and refer to them as ‘panstem clades,’ or simply as ‘panstems.’

CONCLUSIONS

Turtles provide an ideal test case to illustrate the transition from a rank-based nomenclatural system to a phylogenetic system based on defined clade names, while trying to maintain a clear connection to the traditional literature by applying widely used names to those clades that most closely approximate the original set of species (or characters) associated with those names. Most

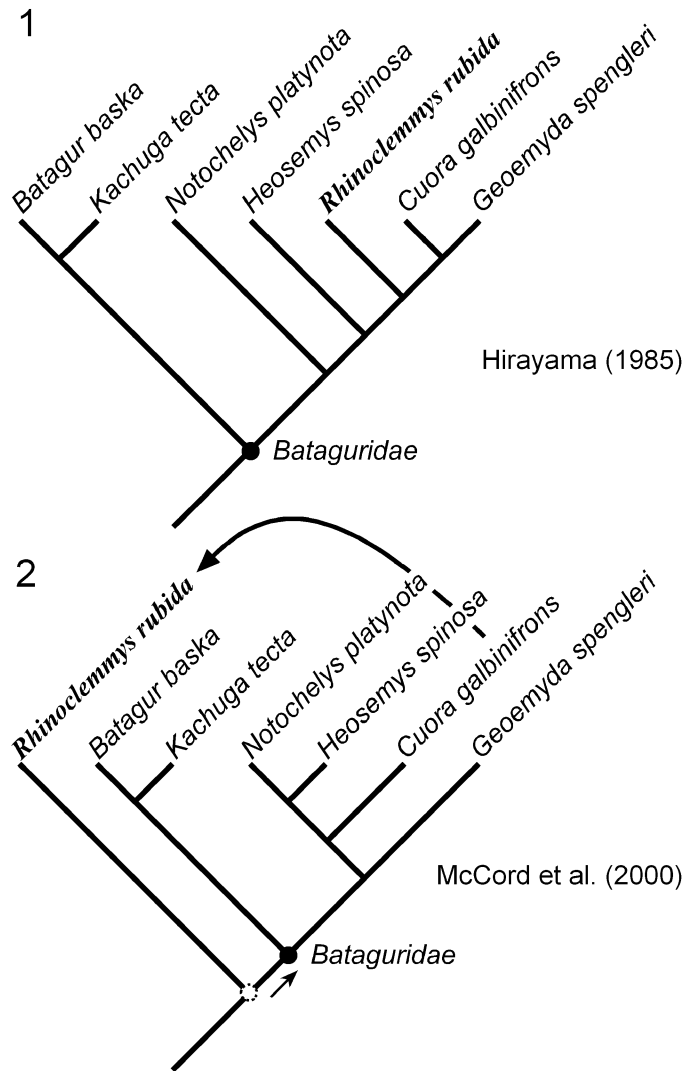


FIGURE 2—Undesirable modification of taxon composition due to changing phylogenetic hypotheses. According to the phylogenetic hypothesis proposed by Hirayama (1985), 1, it is possible to define the taxon ‘*Bataguridae*’ as the clade originating from the last common ancestor of *Batagur baska* and *Geoemyda spengleri* and successfully refer to all living taxa traditionally accorded to this name. If this definition is applied to the phylogenetic hypothesis furnished by McCord et al. (2000), 2, *Rhinoclemmys rubida* is removed from *Bataguridae*, thus altering the composition possibly intended by the original author. For clarity, taxon sampling is greatly reduced in both cladograms.

groups of turtles that closely correspond to currently well-supported clades were named at least once by the 1830s (Gaffney, 1984). Turtles thus provide a long and complex nomenclatural and taxonomic history, enabling us to discover diverse problems that might hinder a smooth transition between systems while at the same time illuminating several misconceptions regarding traditional nomenclatural practices.

A primary difficulty associated with a transition intent on conserving names used in traditional taxonomic literature is that it is seldom clear from most taxonomic works precisely which group of organisms a ICZN-taxon name was referring to (i.e., the limits of the circumscription of a ICZN-taxon are often vague), primarily because authors seldom explained exactly how they conceptualized their ICZN-taxa (Gauthier and de Queiroz, 2001). Did they intend a specific set of species? A specific set of characters?

Both? Are some species and/or characters of more importance to their ICZN-taxon concept than are others? Which species could be removed from their ICZN-taxon, and which added to it, without violating their concept? Consequently, it is often impossible to capture the 'true' or 'traditional' name application of any ICZN-taxon name (i.e., the intended name/phylo-taxon association). The 'meaning' of an ICZN-taxon name can nevertheless be approximated (consistent with the meaning in that the name/phylo-taxon associations vary among a range of internested ICZN-taxa), thus allowing the establishment of subjective synonyms. We address this problem by subjectively synonymizing traditional names with crown clades based on their currently hypothesized composition. Other methods might be equally desirable if the objectives are different. These lists of subjective synonymies provide startling evidence that debunks the idea that names have traditional meanings (=unambiguous applications). Instead, names were applied liberally in the past to various internested clades, as long as these clades include the type species or specimen.

When choosing a name for a clade from among a list of subjective synonyms, strict priority will typically favor unfamiliar names, making it necessary to use subjective criteria such as commonly used name/phylo-taxon association. Our taxonomy is consistent with current usage in the sense that we conserve connections between selected names and particular clades by reference to ideas about taxonomic composition or diagnostic characters as used in the last 25 years.

The rules of the PhyloCode (2003) demand citing an author with every converted clade name, but provides no guidelines as to how this author is to be determined. Up to three authors may justifiably be associated with a name: the author who coined a name in its current spelling; the author who discovered a phylo-taxon (clade); and the first author to apply any name to a clade. However, because it is not possible to objectively synonymize traditional ICZN-taxon names (see above), it also is not possible to objectively determine the author of a converted phylo-taxon. Sadly, the only author that can be readily determined is the author of a name in its current spelling. Moreover, this review indicates that these names were rarely coined for the phylo-taxon for which they are now used, thus rendering current rules regarding authorship counterintuitive. If due credit is to be given to the work of previous researchers, this underlines the necessity for comprehensive review of the history of the taxonomy and nomenclature of a group of organisms prior to converting nomenclatural systems.

This contribution may serve as a guide to those who wish to convert the nomenclature of other groups of organisms from traditional to phylogenetic systems.

PROPOSED PHYLOGENETIC TAXONOMY

*TESTUDINES*¹ Batsch, 1788 (CCN)

*PANTESTUDINES*² (NCN)

*TESTUDINATA*³ Klein, 1760 (CCN)

(¹crown node-, ²panstem-, and ³apomorphy-based versions of *Testudo* Linnaeus, 1758)

Definitions.—'*Testudines*' refers to the crown clade arising from the last common ancestor of *Chelonia* (orig. *Testudo*) *mydas* Linnaeus, 1758 and *Chelus* (orig. *Testudo*) *fimbriatus* Schneider, 1783, and all other valid species listed in Appendix 1. '*Pantestudines*' refers to the most inclusive clade containing *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), but not a single representative of *Aves* Linnaeus, 1758 (s. Gauthier and de Queiroz, 2001), *Crocodylia* Wermuth, 1953 (s. Benton and Clark, 1988), *Lepidosauria* Haeckel, 1866 (s. Gauthier et al., 1988a), or *Mammalia* Linnaeus, 1758 (s. Rowe, 1988). '*Testudinata*' refers to the clade arising from the first member of *Pantestudines* with a complete turtle shell that

is homologous with the shell present in *Chelonia* (orig. *Testudo*) *mydas* Linnaeus, 1758. According to Gaffney and Meylan (1988, p. 161), a "complete turtle shell" is composed of a "carapace formed from costal bones with fused ribs, neural bones with fused thoracic vertebrae, and marginal bones; plastron formed from interclavicle, clavicle, and three to five paired bones sutured together; carapace and plastron articulated at lateral margin and enclosing shoulder girdle and pelvic girdle."

Objective synonymies of Testudines.—*Chelonia* Gauthier et al., 1988a.

Objective synonymies of Pantestudines.—*Anapsida* Gauthier, 1994; *Parareptilia* Laurin and Reisz, 1995.

Subjective synonymies.—*Testudo* Linnaeus, 1758; *Testudinata* Klein, 1760; *Testudines* Batsch, 1788; *Chelonii* Latreille, 1800; *Chelonia* Ross and Macartney, 1802; *Cataphractae* Link, 1807; *Perostia* Rafinesque, 1814; *Chelonea* Fleming, 1822; *Fornicata* Haworth, 1825; *Chelynae* Wagler, 1828; *Sterichrotes* Ritgen, 1828; *Testudines* *hedraeoglossae* Wagler, 1830; *Chelonites* Giebel, 1847; *Tylopoda* Mayer, 1849; *Rhynchochelones* Dollo, 1886; *Chelonie* Hoffmann, 1890; *Cryptodira* Huene, 1956; *Casichelydia* Gaffney, 1975c.

Referred taxa of Testudines.—The turtle crown contains two primary crown clades, *Pleurodira* and *Cryptodira* (see below, Fig. 3), which combine for a known extant diversity of approximately 289 species (Appendices 2–10). The oldest representative of *Testudines* is currently thought to be *Proterochersis robusta*, a putative *panpleurodire* from the Late Triassic of Europe (Gaffney and Meylan, 1988), but a more recent reinterpretation of this taxon (Rougier et al., 1995) has placed it outside the crown. The next oldest candidate is *Kayentachelys aprix* (Gaffney et al., 1987) from the Early Jurassic of Arizona, but this taxon too may actually represent the phylogenetic stem of crown turtles (Dryden, 1988). Until this situation has been evaluated in detail, the age of *Testudines* remains controversial.

Referred taxa of Pantestudines.—The origin of turtles has been hotly debated for more than a century, and a consensus is still lacking. The precise composition of *Pantestudines* thus remains unclear. It is now generally agreed that turtles are not sister to a *mammalian* + *saurian* (s. Gauthier et al., 1988a) clade within *Amniota* (s. Gauthier, 1984), as was once thought (e.g., Gaffney, 1980). Some paleontologists placed turtles as sister to captorhinids (Gaffney and McKenna, 1979; Gaffney and Meylan, 1988; Gauthier et al., 1988b), but that relationship has been rejected in favor of hypotheses placing turtles as sister to *Sauria* within *Reptilia* (s. Gauthier et al., 1988a, 1988b; Gauthier, 1994), although the exact relationships are still in dispute [i.e., procolophonids (Reisz and Laurin, 1991; Laurin and Reisz, 1995) or pareiasaurs (Lee, 1995, 1997)]. Still other paleontologists take a more divergent view in which turtles are regarded as the sister to *Lepidosauria* (Rieppel and DeBraga, 1996; DeBraga and Rieppel, 1997; Rieppel and Reisz, 1999), and thus within the clade *Sauria* rather than among more basal *amniotes*.

Recent analyses of molecular data have allied turtles with nearly every major clade of living amniotes, depending on the DNA sequences studied, taxa included, and the methods of analysis. To name a few examples, turtles have been hypothesized to represent the sister of the *Haemathermia* (e.g., Gardiner, 1993), *Sauria* (e.g., Casper et al., 1996), *Lepidosauria* (e.g., Hedges, 1994; Zardoya and Meyer, 2000), *Archosauria* (e.g., Platz and Conlon, 1997; Kumazawa and Nishida, 1999), *Crocodylia* (McJilton and Reeder, 1999), *Sphenodon punctatus* (e.g., Fushitani et al., 1996), or even *Aves* (e.g., Pollock et al., 2000).

If turtles are regarded as the sister clade to all other reptiles, then *Pantestudines* contains such fossils as millerettids, pareiasaurs, and procolophonids. However, if turtles are considered nested within *Sauria*, then we should regard sauropterygians as

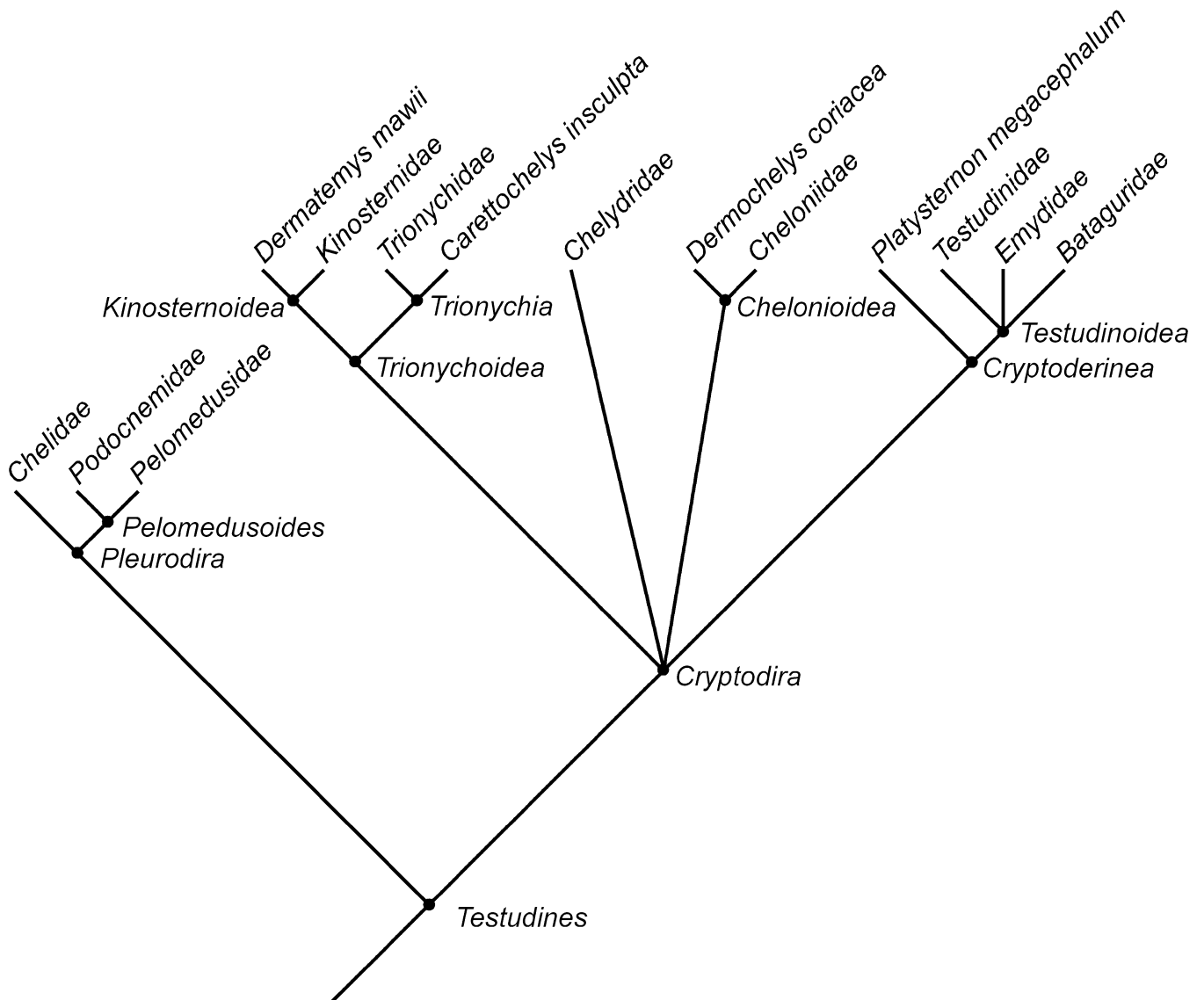


FIGURE 3—A phylogenetic hypothesis of turtles onto which most crown names defined herein have been applied.

stem turtles. Given any of the topologies discussed above, *Pan-testudines* contains *Testudines* and the turtle-shelled fossil taxa *Australochelys africanus*, *Proganochelys quenstedti*, and *Palaeochersis talampayensis* (Gaffney and Kitching, 1995; Rougier et al., 1995) and must have diverged no later than the Late Triassic.

Referred taxa of Testudinata.—In addition to crown clade *Testudines*, *Testudinata* is currently thought to at least include the Late Triassic/Early Jurassic taxa *Australochelys africanus*, *Proganochelys quenstedti*, and *Palaeochersis talampayensis* (Gaffney and Kitching, 1995; Rougier et al., 1995). All three of these taxa exhibit fully developed turtle shells. Gaffney and Meylan (1988). Due to the heavy ossification of the shell, *testudines* are commonly found in the fossil record (see Romer, 1956; Kuhn, 1964; Mlynarski, 1976; and Gaffney and Meylan, 1988 for extensive lists and discussion of fossil representatives).

Discussion.—Ever since Linnaeus (1758), turtles have been recognized as a natural group, and their monophyly has never been seriously questioned (Gaffney, 1984; Gaffney and Meylan, 1988; however, also see Deraniyagala, 1939). As Agassiz (1857, p. 252) noted, “even the uninitiated will recognize a turtle as a

turtle, as readily as they will know a bird to be a bird.” Despite this constancy, there has never been a consensus regarding the formal name of this clade. Of at least 17 proposed names, five are still in current use: *Testudinata* Klein, 1760, *Testudines* Batsch, 1788, *Chelonii* Latreille, 1800 (non Brongniart, 1800a), *Chelonia* Brongniart, 1800b and Cuvier, 1800, and *Casichelydia* Gaffney, 1975c. Because the ICZN (1999) does not regulate names above the family level, none of these names can claim validity. If all of these names were always applied to the same clade, then they could be considered synonymous and their multitude simply a nuisance readily resolved by invoking priority. Most of these names, however, have been applied to the crown as well as proximal parts of its stem (e.g., Gauthier et al., 1988a; Gaffney and Meylan, 1988; Lee, 1995). This situation demands clarification because different clades should not be designated with the same name in any taxonomic system.

Linnaeus (1758) originally classified all then-known turtles into the single genus ‘*Testudo*.’ This name remained in use for all turtles until Brongniart (1800b) and Cuvier (1800) removed living marine turtles from its composition. From then on, its meaning

(in terms of species composition) has been reduced stepwise until the last 25 years, in which '*Testudo*' has been restricted to a small clade of Old World terrestrial turtles composed of only six species (Appendix 8). As such, although '*Testudo*' clearly has priority over all other names that could apply to the 'turtle clade,' reinstating its original meaning makes little sense.

For most of the nineteenth century, '*Testudinata*' Klein, 1751 was one of the preferred names used when referring to turtles. However, with the advent of priority rules and the designation of a formal starting date, '*Testudinata*' was considered invalid by some (e.g., Hunt, 1958; Bour and Dubois, 1986) because it predates Linnaeus (1758). '*Testudinata*' was then ascribed to Oppel (1811) and, consequently, lost priority to other names. Unknown to most, Klein's (1751) work, including the formal name *Testudinata*, was translated from Latin into German by F. D. Behn and republished in 1760, just two years after Linnaeus (1758). We consequently consider *Testudinata* Klein, 1760 the oldest subjective synonym of *Testudo* Linnaeus, 1758, and arbitrarily assign the former name to the apomorphy-based version of that clade.

The first formal use of the word *Testudines* as a taxon name can be found in Batsch (1788). '*Testudines*' is also used in Linnaeus (1758), but as Bour and Dubois (1985) correctly noted, that should not be considered a formal name, because it only represents the correct grammatical declination (nominative plural) of Linnaeus's '*Testudo*' as required by Latin grammar. Therefore, the first formal use of *Testudines* Batsch, 1788 postdates the first formal use of *Testudinata* Klein, 1760 by more than a quarter century. Nevertheless, as the crown group demands a formal name, we arbitrarily assign *Testudines* to that clade. The primary reason for choosing *Testudines* over *Testudinata* as the crown clade designator is that the former name is more commonly used in the zoological literature (a basic search using the online services of Zoological Record retrieved 54 articles between 1978 and 2002 that use '*Testudinata*' in the abstract or title, in comparison to 610 hits for '*Testudines*'). '*Pantestudines*' is accordingly considered the most suitable name for the panstem including all crown turtles.

Potential synonyms of *Testudines*.—Some misconceptions exist regarding the name Chelonii. Bour and Dubois (1985) noted that Latreille (1800) coined the actual name Chelonii, but they assigned authorship to Brongniart (1800a) because he was the first to 'recognize' that turtles form the order 'Les Chéloniens' and not a genus (Linnaeus, 1758) or family (Batsch, 1788). Of course, ICZN rules do not apply above the family group, but even if they did 'Les Chéloniens' cannot qualify as a formal Latin or Greek name. Brongniart's (1800a) contribution, consequently, cannot be considered valid, and authorship must be awarded to Latreille (1800).

'Chelonia' is a no less popular name for turtles than is '*Testudines*,' especially in the herpetological literature (see e.g., Collins and Taggart, 2002, where 'Chelonia' was recently elevated to class level). The name Chelonia was first coined by Brongniart (1800b) and Cuvier (1800) to refer to all marine turtles. Two years later, Ross translated Cuvier's (1800) 'Lectures on Comparative Anatomy' into English, under the supervision of Macartney, and assigned the name Chelonia to all turtles. Even though 'Chelonia' in that sense is still commonly used today, it lacks priority, and applying that name to all turtles might cause confusion because a name of the same spelling is most commonly used for a clade (genus) comprised of marine turtles only.

Gaffney (1975a) was the first to realize that *Pleurodira* and *Cryptodira* form the crown of a more inclusive clade containing *Proganochelys*. Because *Proganochelys* fits the traditional character-based concept of 'turtle'—it has a complete plastron and carapace—Gaffney (1975a) assigned the more inclusive *Proganochelys* node the name *Testudines* Linnaeus, 1758 (as proposed

originally by Hunt, 1958) and proposed a new, apomorphy-based name, Casichelydia, which approximates the crown clade comprising extant *cryptodires* and *pleurodires*. This approach is fully legitimate as far as it acknowledges that different clades should have different names. However, according to our methods, Casichelydia is a junior synonym of *Testudines* Batsch, 1788 and thus must be disregarded due to priority.

PLEURODIRA Cope, 1865 (CCN)

PANPLEURODIRA (NCN)

(crown node- and panstem-based versions of Chelydidae Gray, 1831)

Definitions.—'*Pleurodira*' refers to the crown clade arising from the last common ancestor of *Chelus* (orig. *Testudo*) *fimbriatus* (Schneider, 1783), *Pelomedusa* (orig. *Testudo*) *subrufa* (Bonaterre, 1789), and *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812), and all other valid species listed in Appendix 1a, but none of the valid species listed in Appendix 1b. '*Panpleurodira*' refers to the panstem that includes crown *Pleurodira*.

Objective synonymies of Panpleurodira.—*Pleurodiromorpha* Lee, 1995.

Subjective synonymies.—Chelydidae Gray, 1831; Chelydidae Gray, 1831; Chelyda Strauch, 1862; Chelydes Gray, 1864; Pleurodera Cope, 1864; Pleurodira Cope, 1865; Pleuroderes Gray, 1870; Chelydina Vaillant, 1877; Pleuroderinea Vaillant, 1894; Pleurodeira Watson, 1917; Pelomedusoidea Lindholm, 1929; Pleurodirida Mlynarski, 1976; Eupleurodira Gaffney and Meylan, 1988.

Referred taxa.—*Pleurodira* contains three major crown clades: *Chelidae*, *Pelomedusidae*, and *Podocnemidae* (see below). In addition to its living members, this clade is also represented by an extensive fossil record (Mlynarski, 1976; Wood, 1985; Lapparent de Broin, 2000a). The oldest known *pleurodiran* turtles are *Araripemys barretoi* (Meylan, 1996), *Cearachelys placidoi* (Gaffney et al., 2001), and *Brasillemys josai* (Lapparent de Broin, 2000b) from the Early Cretaceous (Albian) of Brazil.

Despite the extensive fossil record of *pleurodiran* turtles, only three fossil taxa are currently hypothesized to be situated unambiguously along its phylogenetic stem: *Platychelys oberndorferi* from the Late Jurassic of Europe, *Caribemys oxfordiensis* from the Late Jurassic of Cuba, and *Notoemys laticentralis* from the Late Jurassic of Argentina (Broin, 1988; Gaffney and Meylan, 1988; Lapparent de Broin, 2000b; Fuente and Iturralde-Vinent, 2001).

Discussion.—A group that we would regard as *pleurodiran* was first recognized by Gray (1831), who united all then-known *pleurodires* into his family 'Chelydidae,' which he also referred to as 'Chelydidae.' In the following years, a paraphyletic assemblage of turtles was typically recognized that included all *pleurodires* with the exception of the unusual turtle *Chelus fimbriatus*, the type species of Gray's (1831) Chelydidae. As a replacement, this paraphyletic assemblage was typically referred to with a name derived from the currently unused genus name *Hydraspis* (e.g., Idraspidini/Hydraspidina Bonaparte, 1836b; Hydraspides Fitzinger, 1843; Hydraspidae Agassiz, 1857).

The name *Pleurodira* was first coined by Cope (1865), probably in reference to the informal French term 'Les pleurodères' of Duméril and Bibron (1834). Cope (1864) is frequently cited as the source of '*Pleurodira*,' but in that work Cope does not use '*Pleurodira*' per se, but rather the similarly spelled '*Pleurodera*.'

Even though the name '*Pleurodiromorpha*' was already coined for the panstem of *Pleurodira* (Lee, 1995), we created the new name '*Panpleurodira*' to maintain nomenclatural consistency with all other panstem names (see "Discussion"). Fortunately, this will disrupt connectivity with the literature only minimally because '*Pleurodiromorpha*' was used only once (Lee, 1995).

CHELIDAE Lindholm, 1929 (CCN)

PANCHELIDAE (NCN)

(crown node- and panstem-based versions of Chelydidae Baur, 1888a; Boulenger, 1888; Günther, 1888)

Definitions.—‘*Chelidae*’ refers to the crown clade arising from the last common ancestor of *Chelus* (orig. *Testudo*) *fimbriatus* (Schneider, 1783), *Chelodina* (orig. *Testudo*) *longicollis* (Shaw, 1794), and all other valid species listed in Appendix 2, but none of the other valid species listed in Appendix 1. ‘*Panchelidae*’ refers to the panstem that includes crown *Chelidae*.

Subjective synonymies.—Chelydidae Baur, 1888a, Boulenger, 1888, Günther, 1888; Chelyidae Lydekker, 1889; Chelyoidea Baur, 1893; Chelidae Lindholm, 1929.

Referred taxa.—With 52 living species (Appendix 2), *Chelidae* represents the great majority of living *Pleurodira*. Until recently, the fossil record of this group was considered extremely poor and restricted to the Tertiary (Mlynarski, 1976; Wood, 1985; Gaffney, 1991). Recent finds from South America, clearly diagnosable as close relatives of *Chelus fimbriatus*, *Hydromedusa*, and *Phrynops*, now firmly establish the presence of this crown clade in the Late Cretaceous (Fuente et al., 2001; Lapparent de Broin and Fuente, 2001). Even older specimens (see Fuente et al., 2001 and references therein) likely represent basal *panchelids*.

Discussion.—The first to practically recognize *Chelidae* as a group was Gray (1870), who united all known *chelids*—with the conspicuous exception of *Chelus fimbriatus*—to the family ‘Hydraspididae.’ This name was also used a little earlier by Cope (1868), but it is unclear to which taxon Cope’s group applied, because he did not list any included species or diagnostic characters. Soon after, Baur (1888a), Boulenger (1888), and Günther (1888) united all chelid turtles, including *Chelus fimbriatus*, under the name Chelydidae. While the currently used spelling, ‘Chelidae,’ seems to have been developed by Lindholm (1929), Gray (1831) is commonly cited by Linnaean taxonomists as the author of *Chelidae*, because he was the first to create a family group name with *Chelus fimbriatus* as the type species. Although this conclusion is correct according to the rules of the ICZN (1999), we ignore Gray’s (1831) contribution, primarily because he neither recognized the *chelid* clade, nor suggested the currently used name. Instead, Gray (1831) was the first to recognize that all pleurodiran turtles form a group, for which he suggested the similarly spelled name Chelydae (see *Pleurodira*).

PELOMEDUSOIDES Broin, 1988 (CCN)

PANPELOMEDUSOIDES New Name (NCN)

(crown node- and panstem-based versions of Pelomedusidae Günther, 1888; Boulenger, 1888)

Definitions.—‘*Pelomedusoides*’ refers to the crown clade arising from the last common ancestor of *Pelomedusa* (orig. *Testudo*) *subrufa* (Bonnaterre, 1789), *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812), and all other valid species listed in Appendices 3 and 4, but none of the other valid species listed in Appendix 1. ‘*Panpelomedusoides*’ refers to the panstem that includes crown *Pelomedusoides*.

Subjective synonymies.—Pelomedusidae Boulenger, 1888, Günther, 1888; Mesoplastralia Baur, 1888a; Pelomedusoides Broin, 1988.

Referred taxa.—*Pelomedusoides* contains two major crown clades, *Pelomedusidae* and *Podocnemidae* (see below). *Pelomedusoides* is represented by an extensive fossil record, most of which is currently grouped in Bothremydidae (Mlynarski, 1976; Meylan, 1996). The oldest representatives of *Pelomedusoides* are *Brasillemys josai* (Lapparent de Broin, 2000b) and *Cearachelys placidoi* (Gaffney et al., 2001) from the Early Cretaceous (Albian) of Brazil, both of which are currently diagnosed as basal members

of *Panpodocnemidae*. Despite the excellent fossil record of *Pelomedusoides*, only *Araripemys barretoii* and an additional unnamed taxon from the Early Cretaceous (Aptian) of Brazil are currently hypothesized to represent its phylogenetic stem (Meylan, 1996; Lapparent de Broin, 2000b; Gaffney et al., 2001).

Discussion.—*Pelomedusoides* was first recognized as a natural group by Boulenger (1888) and Günther (1888), who applied Cope’s (1868) name Pelomedusidae. This name application to taxa that we deem subjectively synonymous to Boulenger’s (1888) and Günther’s (1888) remained constant for 100 years, until Broin (1988) reassigned the name Pelomedusidae to a composition more comparable with Cope’s (1868), and coined ‘*Pelomedusoides*’ for Boulenger’s (1888) and Günther’s (1888) more inclusive group. Even though this revision only occurred within the last two decades, this usage clearly predominated during the last 25 years. We consequently follow this recent trend and chose the name ‘*Pelomedusoides*.’

PELOMEDUSIDAE Cope, 1868 (CCN)

PANPELOMEDUSIDAE (NCN)

(crown node- and panstem-based versions of Pelomedusidae Cope, 1868)

Definitions.—‘*Pelomedusidae*’ refers to the crown clade arising from the last common ancestor of *Pelomedusa* (orig. *Testudo*) *subrufa* (Bonnaterre, 1789), *Pelusios* (orig. *Testudo*) *subniger* (Bonnaterre, 1789), and all other valid species listed in Appendix 3, but none of the other valid species listed in Appendix 1. ‘*Panpelomedusidae*’ refers to the panstem that includes crown *Pelomedusidae*.

Subjective synonymies.—Pelomedusidae Cope, 1868; Sternothaeridae Baur, 1888b.

Referred taxa.—Eighteen extant species of *Pelomedusidae* are currently recognized (Appendix 3). Although most fossils currently attributed to this clade exhibit few diagnostic characters, some specimens have been assigned to the genus *Pelusios* based on the unique shell closure mechanism in that clade. The fossil record of *Pelomedusidae* thus extends at least to the Miocene (Wood, 1985; Lapparent de Broin, 2000a). The only currently recognized *panpelomedusid* outside the crown is *Teneremys lapparenti* from the Aptian of Niger (Lapparent de Broin, 2000b).

Discussion.—The name *Pelomedusidae* was originally coined by Cope (1868) to refer to all turtles placed in the genera *Pelusios* and *Pelomedusa*, but soon after the name Pelomedusidae was referred to a more inclusive group equivalent to our *Pelomedusoides* (Günther, 1888; Baur, 1888a; Boulenger, 1889). This name/clade association remained stable for almost a century (Siebenrock, 1909; Lindholm, 1929; Williams, 1950; Kuhn, 1961; Mlynarski, 1976; Gaffney and Meylan, 1988) until Broin (1988) returned the name ‘*Pelomedusidae*’ to its original referents, *Pelusios* and *Pelomedusa* (see *Pelomedusoides*).

PODOCNEMIDAE Baur, 1893 (CCN)

PANPODOCNEMIDAE (NCN)

(crown node- and panstem-based versions of Podocnemididae Cope, 1868)

Definitions.—‘*Podocnemidae*’ refers to the crown clade arising from the last common ancestor of *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812), *Peltocephalus* (orig. *Emys*) *dumerilianus* (Schweigger, 1812), and all other valid species listed in Appendix 4, but none of the other valid species listed in Appendix 1. ‘*Panpodocnemidae*’ refers to the panstem that includes crown *Podocnemidae*.

Subjective synonymies.—Podocnemididae Cope, 1868; Peltocephalidae Gray, 1870; Podocnemidae Baur, 1893.

Referred taxa.—Eight living species of *Podocnemidae* are currently recognized (Appendix 4). Among fossil relatives of this

group, there has been a trend in the past to place all *panpodocnemid* turtles into the extant genus *Podocnemis*. Wood (1985), for example, reported fossil *Podocnemis* from the Late Cretaceous of South America, thus extending the presence of *Podocnemis*, and as such *Podocnemidae*, into the late Mesozoic. However, no characters are listed that would clearly diagnose these fossils as having been situated within crown *Podocnemidae*, much less *Podocnemis*. Nevertheless, the recent find of a mandible from the Upper Cretaceous (Maastrichtian) of Madagascar, appears to represent a close relative of the extant taxon *Erymnochelys madagascariensis* (Gaffney and Forster, 2003). If so, this would push the advent of *Podocnemidae* to the Mesozoic. Outside the crown, there is an extensive panpodocnemid fossil record that includes Bothremyidae and *Hamadachelys esculliei* (Meylan, 1996; Lapparent de Broin, 2000b). The oldest parts of this panstem—*Brasilemys josai* and *Cearachelys placidoi*—extend into the Early Cretaceous (Albian) of Brazil (Lapparent de Broin, 2000b; Gaffney et al., 2001).

Discussion.—*Podocnemidae* was recognized by Cope (1868) as a natural group, but he named it ‘Podocnemididae.’ The first record we found of the name *Podocnemidae* being applied to a taxon equivalent to the one defined herein is in Baur (1893).

CRYPTODIRA Cope, 1868 (CCN)

PANCRYPTODIRA (NCN)

(crown node- and panstem-based versions of
Cryptodira Cope, 1868)

Definitions.—‘*Cryptodira*’ refers to the crown clade arising from the last common ancestor of *Testudo graeca* Linnaeus, 1758, *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775), and all other valid species listed in Appendix 1b, but none of valid species listed in Appendix 1a. ‘*Pancriptodira*’ refers to the panstem that includes crown *Cryptodira*.

Objective synonymies of Pancriptodira.—*Cryptodiromorpha* Lee, 1995.

Subjective synonymies.—*Cryptodira* Cope, 1868; *Cryptodira* Nopcsa, 1923; *Eucryptodira* Gaffney, 1975c; *Cryptodirida* Mlynarski, 1976; *Polycryptodira* Gaffney and Meylan, 1988.

Referred taxa.—*Cryptodira* is a morphologically diverse clade of turtles that primitively inhabited fresh water aquatic habitats, but later invaded marine habitats at least once and terrestrial habitats at least four times (Joyce and Gauthier, 2004). Its fossil record is extensive (e.g., Hay, 1908; Mlynarski, 1976; Gaffney and Meylan, 1988). According to current hypotheses, the phylogenetic stem of *Cryptodira* contains a series of common fossil taxa, such as Baenidae, Meiolanidae, Pleurosternidae, Plesiochelydiidae, Sinemydidae, and Macrobaenidae (Gaffney, 1996; Gaffney et al., 1998; Parham and Hutchison, 2003). The oldest currently hypothesized *pancriptodire* is *Kayentachelys aprix* from the Early Jurassic of North America (Gaffney et al., 1987). The oldest reported *cryptodire* is a *pantestudinoid* from the Early Cretaceous (Berriasian) of Japan (Hirayama et al., 2000). Unfortunately, Hirayama et al. (2000) did not list diagnostic characters, so it is difficult to evaluate this claim.

Discussion.—‘*Cryptodira*’ was first used by Cope in 1868 in association with, as the name implies, a group of turtles that withdraws the head backwards, typically hiding the neck inside the shell during head retraction, in contrast to ‘*Pleurodira*,’ which bend their necks laterally. Unfortunately, the limits of Cope’s (1868) *Cryptodira* are not quite clear because he failed to describe specific defining characters or specify the composition of this taxon. Soon after, Cope (1871b, 1871c) made more explicit statements regarding his ‘*Cryptodira*,’ by excluding the allegedly ancestral taxon *Dermochelys coriacea*, making his taxon paraphyletic according to current estimates. Later authors excluded additional taxa from ‘*Cryptodira*,’ especially soft-shelled

turtles (e.g., Boulenger, 1889; Lydekker, 1889; Siebenrock, 1909), but eventually Nopcsa (1923) affirmatively united all of these taxa to establish the modern name application of *Cryptodira* as the clade of turtles that includes all living turtles with vertical neck retraction. The name ‘*Cryptodiromorpha*’ was coined previously for the panstem of *Cryptodira* (Lee, 1995). Nevertheless, we formed the new name ‘*Pancriptodira*’ for this clade to maintain nomenclatural consistency with other clade names (see “Discussion”).

CHELONIOIDEA Baur, 1893 (CCN)

PANCHELONIOIDEA (NCN)

(crown node- and panstem-based versions of *Chelonia*
Brongniart, 1800b; Cuvier, 1800)

Definitions.—‘*Chelonioidea*’ refers to the crown clade arising from the last common ancestor of *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), *Dermochelys* (orig. *Testudo*) *coriacea* (Vandellius, 1761), and all other valid species listed in Appendix 5, but none of the other valid species listed in Appendix 1. ‘*Panchelonioidea*’ refers to the panstem that includes crown *Chelonioidea*.

Subjective synonymies.—*Chelonia* Brongniart, 1800b, Cuvier, 1800; *Chelone* Brongniart, 1805; *Chelonii* Opper, 1811; *Chelonoptera* Rafinesque, 1814; *Chelonie* Schmid, 1819; *Edigitata* Haworth, 1825; *Carettoidea* Fitzinger, 1826; *Eretmochelones* Ritgen, 1828; *Oiacopoda* Wagler, 1828; *Pinnata* Bell, 1828; *Testudines* oiacopodes Wagler, 1830; *Cheloniadae* Gray, 1831; *Chelonae* Wiegmann and Ruthe, 1832; *Chelonidae* Bonaparte, 1831a; *Chelonidae* Bonaparte, 1832; *Chelonidi* Burmeister, 1835; *Thalassites* Holbrook, 1842; *Oiacopoda* Fitzinger, 1843; *Oiacopodes* Giebel, 1847; *Pterodactylia* Mayer, 1849; *Cheloniida* Strauch, 1862; *Chelonida* Vaillant, 1877; *Chelonioidae* Peters, 1882; *Chelonioidea* Baur, 1893; *Cheloniidea* Siebenrock, 1909; *Chelonioida* Lindholm, 1929; *Chelonoplastra* Chkhikvadze, 1970; *Euchelonioidea* Gaffney and Meylan, 1988.

Referred taxa.—Among living taxa, *Chelonioidea* contains *Dermochelys coriacea* and *Cheloniidae* (see below). Its oldest currently hypothesized representative, diagnosed by a series of characters from the cranium and postcranium, is *Santanachelys gaffneyi* from the Early Cretaceous (late Aptian to early Albian) of Brazil, currently placed (Hirayama, 1998) within *Pandermochelys* (see below). As no turtles are known from the phylogenetic stem of *Chelonioidea*, *Santanachelys gaffneyi* also represents the oldest *panchelonioid*.

Discussion.—The first authors to formally name natural groups within *Testudines* were Brongniart (1800b) and Cuvier (1800), who united all marine turtles known at that time into the genus *Chelonia* (‘*Testudines marinae*’ s. Meyer, 1795), and placed all remaining turtles into the revised (in terms of characters and composition) genus *Testudo*. Even though most subsequent authors recognized this group of marine turtles, its name varied considerably (see synonymy list). Much of this variation is the result of changing categorical ranks, ranging from the generic (Brongniart, 1800b), to the familial (Opper, 1811) and superfamilial levels (Baur, 1893), and up to the subordinal (Agassiz, 1857). The name most commonly attributed to all marine turtles today, *Chelonioidae*, was originally coined by Baur (1893) for the same taxon.

DERMOCHELYIDAE Lydekker, 1889 (CCN)

PANDERMOCHELYS (NCN)

(stem- and panstem-based versions of *Dermochelys coriacea*
Vandellius, 1761)

Definitions.—‘*Pandermochelys*’ refers to the panstem that includes *Dermochelys* (orig. *Testudo*) *coriacea* (Vandellius, 1761), but not *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758) or any of the other valid species listed in Appendix 1. ‘*Dermochelyidae*’ refers to the most inclusive clade containing *Dermochelys* (orig.

Testudo coriacea (Vandellius, 1761), but not the fossil taxon *Protostega gigas* Cope, 1871a, *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), or any other valid species listed in Appendix 1.

Subjective synonymies of Dermochelyidae.—Sphargidae Gray, 1825; Sphargidina Bonaparte, 1831a; Sphargidini Burmeister, 1835; Dermatochelyidae Fitzinger, 1843; Sphargididae Gray, 1869; Athecae Cope, 1871c; Dermatochelyidae Seeley, 1880; Dermochelyidae Baur, 1888a; Athecata Lydekker, 1889; Dermochelyidae Lydekker, 1889; Sphargida Strauch, 1890; Dermochelyidae Stejneger, 1907.

Referred taxa.—Despite an extensive fossil record that indicates significant past diversity (Wood et al., 1996), only one species of *Pandermochelys* remains alive today, *Dermochelys coriacea* (Vandellius, 1761). Prominent fossil taxa representing *Dermochelyidae* include *Eosphargis* and *Psephophorus* from the Eocene of Europe (Wood et al., 1996), whereas *Pandermochelys* may also include the Cretaceous marine turtles of the Protostegidae (Hirayama, 1994, 1998). The oldest undisputed *dermochelyids* are known from the Campanian of North America (Parham and Stidham, 1999) and Japan (Hirayama and Hikida, 1998).

Discussion.—Due to the unique morphology of *Dermochelys coriacea*, many early authors placed it in a monotypic genus (e.g., *Dermochelys* Blainville, 1816; *Sphargis* Merrem, 1820), and later in its own family (e.g., Sphargidae Gray, 1825), or even suborder (e.g., Athecae Cope, 1871c; Athecata Lydekker, 1889). Whereas earlier names were typically redundant in composition (each included only the single species *Dermochelys coriacea*), later names typically applied to more inclusive clades that contain one or more fossil taxa from the immediate stem of *Dermochelys coriacea*. In more recent literature (e.g., Hirayama, 1994, 1998; Hirayama and Hikida, 1998), ‘Dermochelyidae’ is typically applied to all marine turtles more closely related to *Dermochelys coriacea* than to *Protostega gigas* (the type genus and species of the Protostegidae). We felt it appropriate to capture this name/taxon association by tying this name to a stem-based taxon that is defined relative to the fossil species *Protostega gigas*. For the panstem of *Dermochelys coriacea*, we formed the new name ‘*Pandermochelys*.’ Should ‘*Dermochelyidae*’ and ‘*Pandermochelys*’ prove objectively synonymous, we specify that *Pandermochelys* be given priority in order to maintain nomenclatural consistency with other clade names (see “Discussion”).

CHELONIIDAE Bonaparte, 1832 (CCN)

PANCHELONIIDAE (NCN)

(crown node- and panstem-based versions of
Caretta Merrem, 1820)

Definitions.—‘*Cheloniidae*’ refers to the crown clade arising from the last common ancestor of *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), *Caretta* (orig. *Testudo*) *caretta* (Linnaeus, 1758), and all other valid species listed in Appendix 5, but none of the other valid species listed in Appendix 1. ‘*Pancheloniidae*’ refers to the panstem that includes crown *Cheloniidae*.

Objective synonymies of Cheloniidae.—*Cheloniinae* Parham and Fastovsky, 1997.

Objective synonymies of Pancheloniidae.—*Cheloniidae* Parham and Fastovsky, 1997.

Subjective synonymies.—*Caretta* Merrem, 1820; Cheloniadae Gray, 1825; Chelonina Bonaparte, 1831a; Chelonini Burmeister, 1835; Chelonidae Fitzinger, 1843; Cheloniidae Bonaparte, 1850; Cheloniina Bonaparte, 1850; Chelonioidae Agassiz, 1857; Pinnata Günther, 1888; Chelonidae Zittel, 1889; Cheloniida Strauch, 1890.

Referred taxa.—*Cheloniidae* is currently thought to include six species of hard-shelled marine turtles (Appendix 5) and a larger number of fossil taxa (Mlynarski, 1976). The oldest undisputed *cheloniid* is *Procolpochelys* from the middle Miocene of North

America (Zangerl and Turnbull, 1955; Weems, 1974). According to recent cladistic hypotheses (Hirayama, 1994, 1998; Hirayama and Chitoku, 1996; Lynch and Parham, 2003), *Pancheloniidae* is represented by such taxa as *Puppigerus* and *Euclastes*. The oldest hypothesized *pancheloniids* are the taxa *Toxochelys* and *Ctenochelys* from the Late Cretaceous of North America (Hirayama, 1998).

Discussion.—Merrem (1820) was the first to subdivide all living marine turtles into two subgroups, *Sphargis*, as represented by the single species *Dermochelys* (*Sphargis*) *coriacea*, and *Caretta* which contained all remaining hard-shelled taxa. Unfortunately, except for the genus *Sphargis*, which was later rejected in favor of *Dermochelys* Blainville, 1816, Merrem’s (1820) subdivision remained without much lasting influence and a series of additional names were coined in the following years (see synonymy list). Currently, the most prevalent name for all hard-shelled marine turtles, ‘Cheloniidae,’ was coined by Bonaparte (1832); however, he applied it to the more inclusive clade of living sea turtles along with *Dermochelys coriacea* (see *Chelonioidae*). The first application of the name Cheloniidae to living hard-shelled sea turtles can be found in Cope (1871b). Because most paleontologists combined all advanced *pancheloniids* into the taxon Cheloniidae, Parham and Fastovsky (1997) explicitly defined the name Cheloniidae phylogenetically as a stem-based taxon. We nevertheless reassign ‘*Cheloniidae*’ to the crown in order to retain nomenclatural consistency in which the most commonly used name is applied to the crown, a clade everyone wants to name, and in order to maximize justified inferences regarding widely used names (de Queiroz and Gauthier, 1992; Gauthier and de Queiroz, 2001).

TRIONYCHOIDEA Fitzinger, 1826 (CCN)

PANTRIONYCHOIDEA (NCN)

(crown node- and panstem-based versions of Trionychoidea
Gaffney, 1975a)

Definitions.—‘*Trionychoidea*’ refers to the crown clade arising from the last common ancestor of *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775), *Carettochelys insculpta* Ramsay, 1887, *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766), *Staurotypus* (orig. *Terrapene*) *triporcatius* (Wiegmann, 1828), *Dermatemys mawii* Gray, 1847, and all other valid species listed in Appendices 6 and 7, but none of the other valid species listed in Appendix 1. ‘*Pantrionychoidea*’ refers to the panstem that includes crown *Trionychoidea*.

Subjective synonymies.—Trionychoidea Gaffney, 1975a.

Referred taxa.—In addition to its principal crown groups, *Trionychia* and *Kinosternoidea* (see below), *Trionychoidea* is currently thought to include a series of basal turtles from the Early Cretaceous of uncertain phylogenetic relations, making it difficult to fix the ages of its basal divergences (see Gaffney and Meylan, 1988; Meylan and Gaffney, 1989; Meylan et al., 2000; and clade descriptions below). According to current trees, no turtle is hypothesized to be situated along the phylogenetic stem of *Trionychoidea*.

Discussion.—The name ‘Trionychoidea’ was originally coined by Fitzinger (1826) in reference to living soft-shelled turtles only. This name, however, was not commonly used until the end of the nineteenth century when soft-shelled turtles were considered ancestral to all other cryptodiran turtles, and thus awarded with a redundant name above the family level (Gray, 1870; Günther, 1888; Boulenger, 1889; Lydekker, 1889). In more recent years, ‘Trionychoidea’ has been used to refer to a much more inclusive clade that not only includes *Carettochelys insculpta* and *Trionychidae* as proposed by Ogilby (1907), but also all of *Kinosternoidea* (Gaffney, 1975a). Although ‘Trionychoidea’ is still applied to both clades today, there seems a clear preference for Gaffney’s (1975a) name/clade association.

TRIONYCHIA Hummel, 1929 (CCN)*PANTRIONYCHIA* (NCN)

(crown node- and panstem-based versions of Trionychoidea
Ogilby, 1907)

Definitions.—‘*Trionychia*’ refers to the crown clade arising from the last common ancestor of *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775), *Carettochelys insculpta* Ramsay, 1887, and all other valid species listed in Appendix 6, but none of the other valid species listed in Appendix 1. ‘*Pantrionychia*’ refers to the panstem that includes crown *Trionychidae*.

Subjective synonymies.—Trionychoidea Ogilby, 1907; Trionychidae Nopcsa, 1923; Trionychia Hummel, 1929; Trionychoidea Bour and Dubois, 1986.

Referred taxa.—Among extant taxa, *Trionychia* comprises the crown clade *Trionychidae* (see below) and *Carettochelys insculpta* Ramsay, 1887. A number of primitive cryptodires that were traditionally associated with *Dermatemys mawii*, such as *Adocus* spp., *Basilemys* spp., *Nanhsiungchelys* spp., *Peltochelys duches-telli*, and *Sandownia harrisi*, were more recently placed within *Pantrionychia*, but no consensus has emerged regarding their exact interrelations [see Meylan and Gaffney (1989) and Meylan et al. (2000) for character discussion]. Of the list of potential *pantrionychians*, the oldest is *Sandownia harrisi* from the Early Cretaceous (Aptian) of Europe. Significantly older fossils from the Early Cretaceous (Barremian) of Japan may be even older representatives of *Pantrionychia* (Hirayama, 2000; Hirayama et al., 2000), but no diagnostic characters were listed and no specimens were referred, making it difficult to assess this claim.

Discussion.—Even though Baur recognized *Trionychia* as a group in 1891, it was not formally associated with a formal name, Trionychoidea, until Ogilby (1907). Even though ‘Trionychoidea’ has been applied to this clade rather consistently, there is a recent trend toward applying Hummel’s (1929) newer name ‘Trionychia.’ We follow this trend to retain optimal connectivity with the recent literature.

CARETTOCHELYIDAE Gill, 1889 (CCN)*PANCARETTOCHELYS* (NCN)

(node- and panstem-based versions of
Carettochelys insculpta Ramsay, 1887)

Definitions.—‘*Carettochelyidae*’ refers to the clade arising from the last common ancestor of *Carettochelys insculpta* Ramsay, 1887 and *Anosteira ornata* Leidy, 1871, but none of the other valid species listed in Appendix 1. ‘*Pancarettochelys*’ refers to the most inclusive clade (panstem) containing *Carettochelys insculpta* Ramsay, 1887, but not *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) or any other valid species listed in Appendix 1.

Subjective synonymies.—*Carettochelyidae* Boulenger, 1887; *Carettochelyidae* Gill, 1889; *Carettochelyda* Strauch, 1890; *Carettochelydes* Baur, 1891; *Anosteirinae* Nopcsa, 1928; *Carettochelyoidea* Williams, 1950.

Referred taxa.—Despite the fact that the fossil record of this group is almost exclusively found in the Northern Hemisphere (Mlynarski, 1976), the only surviving member of *Pancarettochelys* is *Carettochelys insculpta* Ramsay, 1887 from New Guinea and Australia. The oldest representative of *Carettochelyidae* is *Kizylkumemys schultzi* from the middle Cretaceous (Albian and Cenomanian) of central Asia (Nessov, 1977; Meylan, 1988). Even older material, mentioned in Hirayama et al. (2000), likely represents the phylogenetic stem of *Carettochelyidae*.

Discussion.—Soon after the discovery of the remarkable turtle *Carettochelys insculpta* Ramsay, 1887, some authors thought it morphologically divergent enough to warrant placement in its own family (see synonymy list). Although the first names were originally intended to highlight the disparity of the only living

species, fossil stem representatives were included almost immediately (Lydekker, 1887). At present, the most commonly used name is ‘*Carettochelyidae*’ Gill, 1889, which is only second in priority to the similarly spelled name ‘*Carettochelydidae*’ Boulenger, 1887. Given that most stem taxa of *Carettochelys insculpta* are currently placed in ‘*Carettochelyidae*’ (Meylan, 1988), we decided to fix this name/taxon relationship by applying the name ‘*Carettochelyidae*’ to the clade of turtles that arises from the last common ancestor of *Carettochelys insculpta* and *Anosteira ornata*.

TRIONYCHIDAE Gray, 1825 (CCN)*PANTRIONYCHIDAE* (NCN)

(crown node- and panstem-based versions of
Trionyx Geoffroy-St.-Hilaire, 1809a, 1809b)

Definitions.—‘*Trionychidae*’ refers to the crown clade arising from the last common ancestor of *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775), *Cyclanorbis* (orig. *Cryptopus*) *senegalensis* (Duméril and Bibron, 1834), and all other valid species listed in Appendix 6, but none of the other valid species listed in Appendix 1. ‘*Pantrionychidae*’ refers to the panstem that includes crown *Trionychidae*.

Subjective synonymies.—*Trionyx* Geoffroy-St.-Hilaire, 1809a, 1809b; Trionychidae Gray, 1825; Trionychoidea Fitzinger, 1826; Trionycidae Bonaparte, 1831b; Chilotae Wiegmann and Ruthe, 1832; Trioncini Burmeister, 1835; Trionycidi Bonaparte, 1836b; Labiata Fitzinger, 1836; Trionycina Bonaparte, 1836a; Potamites Holbrook, 1842; Trionyches Fitzinger, 1843; Trionychida Strauch, 1862; Peltochelyidae Seeley, 1880; Diacostoidea Baur, 1887; Trionychida Baur, 1890; Ophioderinea Vaillant, 1894; Trionychinae Nopcsa, 1928; Trionychoplastra Chkhikvadze, 1970.

Referred taxa.—*Trionychidae* is currently thought to contain 23 species of living soft-shelled turtles (Appendix 6). Although the fossil record of *Pantrionychidae* extends deep into the Cretaceous (e.g., Romer, 1956; Mlynarski, 1976; Hirayama et al., 2000), only a few specimens have been included in cladistic analyses to determine if they are situated within the crown or along the panstem. *Aspideretoides allani*, *Aspideretoides foveatus*, *Aspideretoides splendidus*, and *Apalone latus* from the Late Cretaceous (middle Campanian) are hypothesized *trionychids* (Gardner et al., 1995), thus extending the age of the crown into the uppermost Cretaceous. Meylan (1987) reviewed the phylogenetic relationships of the living Trionychidae based on morphology.

Discussion.—The nomenclatural history of soft-shelled turtles is complex and, in many ways, resembles that of extant marine turtles (see *Chelonioidae*). Linnaeus (1758) was not aware of any trionychid turtles. But soon after the publication of *Systema Naturae*, a number of these turtles, covering the full range of extant diversity, were named by other authors and, based on their characters, placed within Linnaeus’s genus *Testudo*: *Amyda* (orig. *Testudo*) *cartilaginea* Boddaert, 1770; *Trionyx* (orig. *Testudo*) *triunguis* Forskål, 1775; *Apalone* (orig. *Testudo*) *ferox* Schneider, 1783; and *Lissemys* (orig. *Testudo*) *punctata* Bonnaterre, 1789. Soft-shelled turtles were later united with all other non-marine turtles into a paraphyletic genus *Testudo* (Brongniart, 1800b; Cuvier, 1800), and then with all freshwater aquatic turtles into a paraphyletic genus *Emys* (s. Duméril, 1806). The first to describe formally trionychid turtles as forming a natural group was Geoffroy-St.-Hilaire (1809a, 1809b), who united all then-known species into the genus *Trionyx*. A substantial list of additional names was coined for the same group during the following century, but most current authors use the term ‘Trionychidae,’ which was coined by Gray (1825), a name second in priority only to *Trionyx*.

KINOSTERNOIDEA (CCN)

PANKINOSTERNOIDEA (NCN)

(crown node- and panstem-based versions of Kinosternoidea
Gaffney and Meylan, 1988)

Definitions.—‘Kinosternoidea’ refers to the crown clade arising from the last common ancestor of *Dermatemys mawii* Gray, 1847, *Staurotypus* (orig. *Terrapene*) *triporcatus* (Wiegmann, 1828), *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766), and all other valid species listed in Appendix 7, but none of the other valid species listed in Appendix 1. ‘Pankinosternoidea’ refers to the panstem that includes crown *Kinosternoidea*.

Subjective synonymies.—Kinosternoidea Gaffney and Meylan, 1988.

Referred taxa.—Among living taxa, *Kinosternoidea* contains *Dermatemys mawii* Gray, 1847 and crown clade *Kinosternidae* (see below). Of the many Cretaceous turtle taxa traditionally assigned to ‘Dermatemydidae’ based on shared ancestral characters (Mlynarski, 1976), some may well be attributed to the phylogenetic stem of *Kinosternoidea*. For instance, according to Hutchison and Bramble (1981), the shell-based taxon *Agomphus* from the Late Cretaceous of North America may be such a misplaced taxon. Recent investigations (Meylan et al., 2000), however, placed this clade within an unresolved, more basal polytomy. New material and further cladistic analyses will test these hypotheses and will certainly add taxa to the list of basal *pankinosternoids*. Phylogenetic relationships within *Kinosternoidea* were reviewed by Hutchison and Bramble (1981), Gaffney and Meylan (1988), Meylan and Gaffney (1989), Hutchison (1991), and Meylan et al. (2000).

Discussion.—The sister group relationship between *Dermatemys mawii* and *Kinosternoidea* was only proposed within the last two decades, but currently enjoys strong support by morphological and molecular data (e.g., Gaffney and Meylan, 1988; Hutchison, 1991; Shaffer et al., 1997). The node encompassing this clade was initially labeled with the name Kinosternoidea by Gaffney and Meylan (1988). Their focus on apomorphies means that they were likely naming a more inclusive clade than specified here. Although this name has priority among all subjective synonyms (indeed, it is the only available name), we nevertheless decided to minutely alter its ending from the less familiar ‘-oidea’ to the more familiar ‘-idae’ to achieve nomenclatural consistency with other clade endings, thus avoiding the creation of functional homonyms (see “Discussion”). The fact that *Kinosternoidea* may be situated within *Trionychoidea* is irrelevant to us, because both names are not meant to reflect ranks.

DERMATEMYDIDAE Baur, 1888b (CCN)

PANDERMATEMYS (NCN)

(node- and panstem-based versions of *Dermatemys mawii* Gray,
1847)

Definitions.—‘*Dermatemydidae*’ refers to the clade arising from the last common ancestor of *Dermatemys mawii* Gray, 1847 and *Baptmys wyomingensis* Leidy, 1870, but none of the other valid species listed in Appendix 1. ‘*Pandermatemys*’ refers to the most inclusive clade (panstem) containing *Dermatemys mawii* Gray, 1847, but not *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766) or any of the other valid species listed in Appendix 1.

Subjective synonymies.—Dermatemydidae Gray, 1870; Dermatemydidae Baur, 1888b; Dermatemydinae Nopcsa, 1928; Dermatemydidae Alvarez del Toro, 1972.

Referred taxa.—A large number of fossil taxa—ranging back to the Cretaceous—were associated with *Dermatemys mawii* in the past (e.g., Romer, 1956; Kuhn, 1964; Mlynarski, 1976; Iversen and Mittermeier, 1980). However, these attributions were based on a series of plesiomorphic characters that these fossils

share with *Dermatemys mawii*. Preliminary cladistic analyses (e.g., Hutchison and Bramble, 1981; Gaffney and Meylan, 1988; Meylan and Gaffney, 1989) show that only *Baptmys* from the Eocene of North America is situated within *Pandermatemys*. As such, we use *Baptmys wyomingensis*, the type species of *Baptmys*, as the second internal specifier in our node-based taxon, *Dermatemydidae*.

Discussion.—In the past, only a few higher-level taxa were created to unite various fossil turtles with *Dermatemys mawii* (see synonymy list), but most recent investigations demonstrated all of these groupings to be polyphyletic (e.g., Hutchison and Bramble, 1981; Gaffney and Meylan, 1988; Meylan and Gaffney, 1989). We approximate the current name/taxon association of this recent body of literature by using *Dermatemys mawii* and *Baptmys wyomingensis* as internal specifiers for the definition of the clade name ‘*Dermatemydidae*.’

KINOSTERNIDAE Hay, 1892 (CCN)

PANKINOSTERNIDAE (NCN)

(crown node- and panstem-based versions of *Cinosternoidea*
Agassiz, 1857)

Definitions.—‘*Kinosternidae*’ refers to the crown clade arising from the last common ancestor of *Staurotypus* (orig. *Terrapene*) *triporcatus* (Wiegmann, 1828), *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766), and all other valid species listed in Appendix 7, but none of the other valid species listed in Appendix 1. ‘*Pankinosternidae*’ refers to the panstem that includes crown *Kinosternidae*.

Subjective synonymies.—*Cinosternoidea* Agassiz, 1857; *Emysauridae* Vaillant, 1894; *Cinosternidae* Siebenrock, 1907; *Kinosternidae* Lindholm, 1929.

Referred taxa.—*Kinosternidae* contains 25 living species (Appendix 7). Among fossil taxa, only *Hoplochelys* from the Paleocene (Hutchison and Bramble, 1981; Gaffney and Meylan, 1988) and *Agomphus* from the Late Cretaceous of North America (Meylan and Gaffney, 1989) can be placed along the phylogenetic stem of *Kinosternidae*. However, more recent investigations by Meylan et al. (2000) placed these taxa in a basal *kinosternoid* polytomy. The oldest putative representatives of *Pankinosternidae* are some undescribed remains from the Late Cretaceous (Campanian) of North America (Hutchison et al., 1998). A number of well-preserved Eocene fossils known from North America, such as *Xenochelys* and *Baltemys staurogastros*, can be securely placed within crown *Kinosternidae*.

Discussion.—Although naturalists were familiar with the full range of extant species diversity of *kinosternids* by the mid-nineteenth century, few authors recognized that they formed an exclusive natural group (e.g., Agassiz, 1857; Vaillant, 1894). Since the influential work of Siebenrock (1907), most authors have united these turtles into one group with two major subgroups, although there has been no consensus on whether this group should be regarded as a ‘family’ with two ‘subfamilies’ (e.g., Siebenrock, 1907, 1909; Lindholm, 1929; Zangerl, 1969; Mlynarski, 1976; Gaffney, 1984; Hutchison, 1991), or as two separate ‘families’ (e.g., Baur, 1893; Chkhikvadze, 1970; Bickham, 1981; Meylan and Gaffney, 1989; King and Burke, 1989). As such, no names are available that would truly continue any ‘current tradition.’ However, we decided to use ‘*Kinosternidae*’ in its more inclusive application because this seems to be favored by the majority of present-day herpetologists.

CHELYDRIDAE Swainson, 1839 (CCN)

PANCHELYDRIDAE (NCN)

(crown node- and panstem-based versions of *Chelonura*
Holbrook, 1842)

Definitions.—‘*Chelydridae*’ refers to the crown clade arising from the last common ancestor of *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758) and *Macrochelys* (orig. *Chelonura*)

temminckii (Troost, 1835), but none of the other valid species listed in Appendix 1. ‘*Panchelydridae*’ refers to the panstem that includes crown *Chelydridae*.

Subjective synonymies.—*Chelonura* Holbrook, 1842; *Chelydroidae* Agassiz, 1857; *Chelydraina* Gray, 1869; *Chelydridae* Cope, 1882; *Chelydrinae* Williams, 1950.

Referred taxa.—The taxonomic composition of *Chelydridae* is under current debate. By definition it contains its two internal specifiers, *Chelydra serpentina* and *Macrolemys temminckii*, but it remains unclear if extant *Platysternon megacephalum* Gray, 1831 is situated within (e.g., Gaffney, 1975b; Gaffney et al., 1991) or outside of *Chelydridae* (e.g., Whetstone, 1978a, 1978b; Haiduk and Bickham, 1982; Danilov, 1998; Fig. 4; also see discussion for *Cryptoderinea*). According to Eaton et al. (1999a, 1999b), the oldest *chelydrid* is known from the Eocene and the oldest *panchelydrid* from the Late Cretaceous (Turonian) of North America. No specimens were referred, however, making it difficult to assess this claim.

Discussion.—The close phylogenetic relationship between *Chelydra serpentina* and *Macrolemys temminckii* was never disputed. Originally, both species were placed in the same genus, *Chelonura* (Holbrook, 1842), but soon after, they were placed in two separate genera within the same family (Agassiz, 1857; Gray, 1869, 1870). The name ‘*Chelydridae*’ was originally developed by Swainson (1839) to refer to a polyphyletic group of ‘snapping turtles’ comprised of *Chelydra serpentina*, *Platysternon megacephalum*, and *Chelus fimbriatus*. The first application of ‘*Chelydridae*’ to *Chelydra serpentina* and *Macrolemys temminckii* only can be found in Cope (1882). This name usage has remained rather stable since, with the exception of the occasional inclusion of *Platysternon megacephalum* (e.g., Gaffney, 1975b, 1984). Because the placement of *Platysternon megacephalum* remains uncertain to date (see above), we purposefully define *Chelydridae* independent of the phylogenetic placement of *Platysternon megacephalum*.

Some authors (e.g., Bour and Dubois, 1985) consider Gray (1831) to be the correct author of the taxon or name ‘*Chelydridae*.’ This is not a valid argument, even under the rules of the ICZN (1999), because Gray (1831) was unaware of this grouping. Instead, Gray (1831) proposed the similarly spelled name ‘*Chelydidae*’ with the type species *Chelus* (orig. *Testudo*) *fimbriatus* (Schneider, 1783) to refer to *Pleurodira*.

CRYPTODERINEA Vaillant, 1894 (CCN)

PANCRYPTODERINEA (NCN)

(crown node- and panstem-based versions of *Cryptoderinea* Vaillant, 1894)

Definitions.—‘*Cryptoderinea*’ refers to the crown clade arising from the last common ancestor of *Platysternon megacephalum* Gray, 1831, *Testudo graeca* Linnaeus, 1758, *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), *Batagur* (orig. *Emys*) *baska* (Gray, 1831), and all other valid species listed in Appendices 8–10, but none of the other valid species listed in Appendix 1. ‘*Pancriptoderinea*’ refers to the panstem that includes crown *Cryptoderinea*.

Subjective synonymies.—*Cryptoderinea* Vaillant, 1894; *Testudinidae* Williams, 1950.

Referred taxa and discussion.—Among living turtles, *Cryptoderinea*, by definition, only contains *Platysternon megacephalum* and the crown taxon *Testudinoidea* (see below), with the assumption that *Platysternon megacephalum* alone is sister to *Testudinoidea*. If *Platysternon megacephalum* comes to be situated within *Testudinoidea*, we stipulate that *Cryptoderinea* be considered an objective junior synonym of *Testudinoidea*, even though *Cryptoderinea* has page priority in this article (Fig. 4). The first to recognize this group was Vaillant (1894), who united these

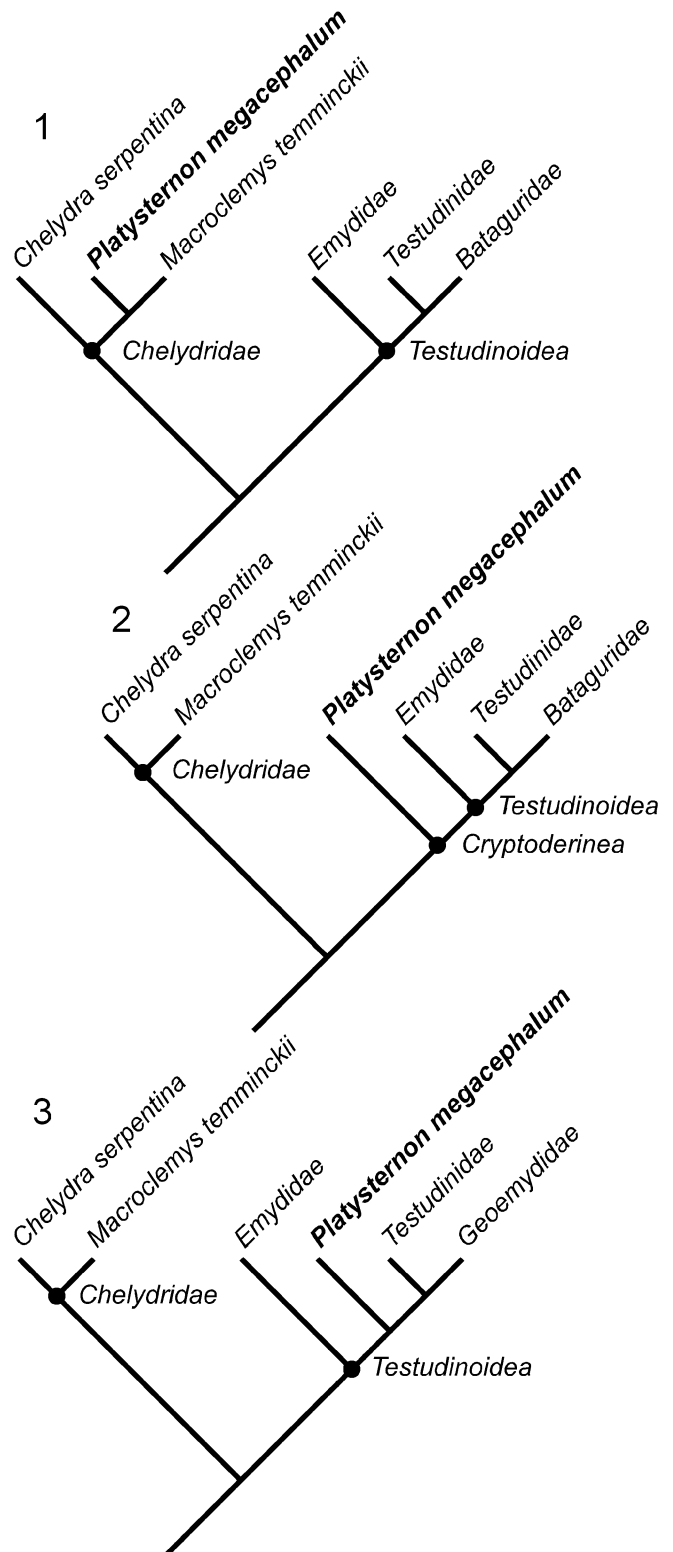


FIGURE 4—Application of the names *Chelydridae*, *Testudinoidea*, and *Cryptoderinea*, depending on the hypothesized phylogenetic position of *Platysternon megacephalum*.

turtles based on the unique arrangement of the articular surfaces on their cervical vertebrae. Williams (1950) reached the same conclusion in his comprehensive review of turtle cervical vertebrae.

PANPLATYSTERNON (NCN)

(panstem-based version of *Platysternon megacephalum* Gray, 1831)

Definition.—‘*Panplatysternon*’ refer to the most inclusive clade containing *Platysternon megacephalum* Gray, 1831, but not *Testudo graeca* Linnaeus, 1758 or any of the other valid species listed in Appendix 1.

Subjective synonymies.—Platysternidae Gray, 1869; Platysternoidea Baur, 1893; Platysterninae Nopcsa, 1928.

Referred taxa.—*Panplatysternon* is currently thought to contain only one living species, *Platysternon megacephalum* Gray, 1831. The oldest (and almost sole) representatives of *Panplatysternon* are a few highly fragmentary fossil specimens from the Oligocene (Chkhikvadze, 1971) and Paleocene (Nessov and Chkhikvadze, 1987) of Kazakhstan.

Discussion.—Due to the almost complete absence of fossils from its phylogenetic stem, all ‘higher’ taxonomic names proposed in the past (see synonymy list) are essentially redundant with *Platysternon megacephalum* in terms of known composition. With only a few exceptions, most current authors use the name ‘Platysternidae’ for a more inclusive taxon. As with the family names of the other monotypic extant turtle taxa, it may be desirable to refer the name ‘Platysternidae’ to a clade that contains only part of the phylogenetic stem of *Platysternon megacephalum*. However, given that all fossils currently associated with this species are known only from fragmentary remains that have never been included in a numerical phylogenetic analysis, we think that it would be premature to refer the name ‘Platysternidae’ to any clade.

TESTUDINOIDEA Fitzinger, 1826 (CCN)

PANTESTUDINOIDEA (NCN)

(crown node- and panstem-based versions of Cryptopodi Latreille, 1825)

Definitions.—‘*Testudinoidea*’ refers to the crown clade arising from the last common ancestor of *Testudo graeca* Linnaeus, 1758, *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), *Batagur* (orig. *Emys*) *baska* (Gray, 1831), and all other valid species listed in Appendices 8–10, but none of the other valid species listed in Appendix 1. ‘*Pantestudinoidea*’ refers to the panstem that includes crown *Testudinoidea*.

Subjective synonymies.—Cryptopodi Latreille, 1825; Podocheilonia Ritgen, 1828; Testudinidae Boulenger, 1889; Lydekker, 1889; Testudinoidea Baur, 1893; Neochelyidae Zangerl, 1969.

Referred taxa.—*Testudinoidea* contains three major crown clades, *Testudinidae*, *Emydidae*, and *Bataguridae* (see below). A number of fossil taxa from the Cretaceous of Asia, such as *Lindholmemyx* and *Mongolemys* spp., have been placed within ‘*Testudinoidea*’ primarily because of the development of an ossified bridge connecting the plastron with the carapace (Sukhanov, 2000; Danilov and Sukhanov, 2001), but in our nomenclature these should be regarded as *pantestudinoids*. Even older material was reported from the Early Cretaceous of Japan (Hirayama, 2000), but no diagnostic characters were listed, making it difficult to assess this claim.

Discussion.—Even though Latreille (1825) and Ritgen (1828) recognized the close similarity between terrestrial tortoises and pond turtles, most authors in the early nineteenth century isolated tortoises in their own group and lumped pond turtles with other freshwater aquatic turtles (e.g., Brongniart, 1805; Bell, 1825; Fitzinger, 1826; Wagler, 1830). During the twentieth century, most

authors recognized *Testudinoidea* as a natural group, but no consensus existed on whether it should be called ‘Testudinidae’ or ‘Testudinoidea.’ We follow the more common name application by using ‘Testudinoidea’ for the more inclusive clade and by assigning ‘Testudinidae’ to the less inclusive clade of terrestrial tortoises only (see *Testudinidae*).

There is an additional concern associated with the ambiguous phylogenetic position of *Platysternon megacephalum* Gray, 1831. Some authors have placed that taxon in Testudinoidea (e.g., Williams, 1950; Romer, 1956), while others have excluded it (Chkhikvadze, 1970; Gaffney, 1984). According to our definition, *Platysternon megacephalum* will only be included if it is phylogenetically placed within *Testudinoidea*. For the alternative case, in which *Platysternon megacephalum* represents the immediate living sister of *Testudinoidea*, we provide a phylogenetically defined name (see *Cryptoderinea*).

TESTUDINIDAE Gray, 1825 (CCN)

PANTESTUDINIDAE (NCN)

(crown node- and panstem-based versions of *Testudo* Brongniart, 1805)

Definitions.—‘*Testudinidae*’ refers to the crown clade arising from the last common ancestor of *Testudo graeca* Linnaeus, 1758, *Manouria* (orig. *Testudo*) *emys* (Schlegel and Müller, 1844), and all other valid species listed in Appendix 8, but none of the other valid species listed in Appendix 1, 9, or 10. ‘*Pantestudinidae*’ refers to the panstem that includes crown *Testudinidae*.

Subjective synonymies.—*Testudo* Brongniart, 1805; Testudia Rafinesque, 1814; Tortudines Schmid, 1819; Testudinidae Gray, 1825; Testudinoidea Fitzinger, 1826; Tylopoda Wagler, 1828; *Testudines* tylopodes Wagler, 1830; Chersinae Wiegmann and Ruthe, 1832; Testudinini Burmeister, 1835; Testudinina Bonaparte, 1836a; Tylopoda Fitzinger, 1843; Chersites Holbrook, 1842; *Testudines* Fitzinger, 1843; Tylopodes Giebel, 1847; Baenodactyli Mayer, 1849; Chersidae Leunis, 1883; Testudininae Siebenrock, 1909; Testudininei, Bour, and Dubois, 1986.

Referred taxa.—*Testudinidae* is represented by 43 extant species (Appendix 8). Due to the heavy ossification of some forms, and the tendency of others to live in burrows, this clade has an excellent fossil record (e.g., Auffenberg, 1974; Mlynarski, 1976). *Hadrianus* from the early Eocene of North America (Hutchison, 1980), and an undescribed species from the Paleocene of Asia (personal observations, JFP and WGJ; under study by V. B. Sukhanov), are currently classified as the oldest known members of ‘*Testudinidae*.’ A phylogenetic analysis is, however, necessary to assess if these taxa are situated within or outside of crown clade *Testudinidae*. The oldest affirmative representatives of *Testudinidae* include *Stylymys* or *Gopherus* from the Eocene of North America (Mlynarski, 1976; Hutchison, 1996). Phylogenetic relationships within *Testudinidae* based on morphology were discussed by Crumly (1982, 1985, 1994).

Discussion.—Terrestrial tortoises (‘*Testudines* terrestres’ s. Meyer, 1795) were among the first to be formally recognized as their own natural group by Brongniart (1805), who united them into the single genus *Testudo*, closely followed by Gray (1825), who elevated this group to the family *Testudinidae*. Even though this group of turtles was subsequently renamed a number of times (see subjective synonymy list), Gray’s (1825) family level name remained popular and is still the most widely accepted name used today.

BATAGURIDAE Gray, 1870 (CCN)

PANBATAGURIDAE (NCN)

(crown node- and panstem-based versions of *Batagurinae* McDowell, 1964)

Definitions.—‘*Bataguridae*’ refers to the crown clade arising from the last common ancestor of *Batagur* (orig. *Emys*) *baska*

(Gray, 1831), *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789), and all other valid species listed in Appendix 9, but none of the other valid species listed in Appendix 1, 8 or 10. ‘*Panbataguridae*’ refers to the panstem that includes crown *Bataguridae*.

Subjective synonymies.—Batagurinae McDowell, 1964; Bataguridae Gaffney and Meylan, 1988; Geoemydidae David, 1994.

Referred taxa.—With 62 extant species (Appendix 9), *Bataguridae* comprises a significant portion of the diversity of extant turtles. Unfortunately, due to the demands of the food and pet trade, many *batagurids* are now endangered and the survival of many species seems questionable (van Dijk et al., 2000 and references therein).

A number of primitive fossil turtles have been attributed (Mlynarski, 1976) to the clade *Panbataguridae* but the phylogenetic relationships of most of these taxa relative to the extant forms remain unclear. *Echmatemys* spp., from the Eocene of North America, was affirmatively attributed to the stem of *Bataguridae* by Hirayama (1985), but this assessment may be somewhat skewed because *Echmatemys* was determined to be situated along the stem a priori to resolve phylogenetic relationships among *Bataguridae*. Phylogenetic relationships within *Bataguridae* were discussed by Hirayama (1985), McCord et al. (2000), and Yasukawa et al. (2001).

Discussion.—The first to suggest *Bataguridae* as a natural group was McDowell (1964), who split all pond turtles then known into two subgroups that he named ‘Emydinae’ and ‘Batagurinae.’ The name ‘Batagurinae’ was used for a number of years when referring to this clade (e.g., Mlynarski, 1976; Hirayama, 1985), but it was eventually ‘elevated’ to familial status (e.g., ‘Bataguridae’ of Gaffney and Meylan, 1988). More recently, it has been suggested that the term ‘Geoemydidae’ should be used when referring to this group (David, 1994). This argument, underpinned by strict application of the ICZN (1999), is based on Theobald’s (1868) erection of the family name ‘Geoemydidae’ prior to Gray’s (1870) publication of ‘Bataguridae.’ From our standpoint, both names are equally undesirable, because Theobald (1868) only referred to the subclade composed of Asian leaf and box turtles, while Gray (1870) only referred to the subclade containing large Asian river turtles. Although acceptance for ‘Geoemydidae’ is currently growing, we nevertheless use ‘Bataguridae’ because the vast majority of literature from the last 25 years favors this name. Connectivity with the literature is thus maintained.

EMYDIDAE Bell, 1825 (CCN)

PANEMYDIDAE (NCN)

(crown node- and panstem-based versions of Emydinae
McDowell, 1964)

Definitions.—‘*Emydidae*’ refers to the crown clade arising from the last common ancestor of *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), *Chrysemys* (orig. *Testudo*) *picta* (Schneider, 1783), and all other valid species listed in Appendix 10, but none of the species listed in Appendices 1, 8, and 9. ‘*Panemydidae*’ refers to the panstem that includes crown *Emydidae*.

Subjective synonymies.—Emydinae McDowell, 1964; Emydidae Chkhikvadze, 1970.

Referred taxa.—*Emydidae* is currently thought to include 46 species of living turtles (Appendix 10), all of which live in the western hemisphere, with the exception of *Emys orbicularis* in Europe and western Asia. A number of fossil turtles have been associated (Mlynarski, 1976) with the group we call ‘*Panemydidae*.’ To this date, however, none have been integrated into a cladistic analysis and consequently cannot be referred with any confidence to *Emydidae*. Phylogenetic relationships within *Emydidae* were discussed by Gaffney and Meylan (1988), Bickham et al. (1996), and Feldman and Parham (2002).

Discussion.—The name ‘Emydidae’ was initially coined by Bell (1825), probably in reference to the French term ‘*emydes*,’ to refer to all freshwater aquatic turtles, including all members of *Kinosternoidea*, *Chelydridae*, and *Pleurodira*. In the ensuing years, the referred composition of Emydidae slowly diminished through the successive removal of taxa (Gray, 1831, 1855, 1869, 1870), until it contained only the species herpetologists have come to think of as the ‘pond turtles’ (e.g., Zittel, 1889). This name/taxon association remained stable for nearly 100 years until Chkhikvadze (1970) applied Emydidae to McDowell’s (1964) less inclusive group predominantly composed of North American pond turtles. This usage predominates today and we therefore adopt it too.

SUPPLEMENTARY TAXON NAMES

The following section contains a number of taxon names for groups of taxa that, while not currently useful owing to poor support and conflicting data, may eventually prove to be useful pending future phylogenetic analyses.

TESTUGURIA (NCN)

PANTESTUGURIA (NCN)

(crown node- and panstem-based versions of Testudinidae Bour and Dubois, 1986)

Definitions.—‘*Testuguria*’ refers to the crown clade arising from the last common ancestor of *Testudo graeca* Linnaeus, 1758, *Batagur* (orig. *Emys*) *baska* (Gray, 1831), and all other valid species listed in Appendices 8 and 9, but none of the other valid species listed in Appendix 1 or 10. ‘*Pantestuguria*’ refers to the panstem that includes crown *Testuguria*.

Subjective synonymies.—Testudinidae Bour and Dubois, 1986.

Comments.—Historically, pond turtles were thought to form a natural group and were classified as such. McDowell (1964) noted, however, that terrestrial tortoises seemed to have been derived from a “batagurid ancestor,” an idea later supported by Hirayama (1985). Given the preliminary nature of Hirayama’s (1985) contribution, and the poor taxon sampling characterizing more recent molecular work (e.g., Shaffer et al., 1997), we conclude that the interrelationships among the three major clades of *Testudinoidea* are currently still unclear. If *Testudinidae* and *Bataguridae* indeed form a monophylum, we propose the name *Testuguria* for that clade; if, however, *Bataguridae* and *Emydidae* form a monophylum, we suggest using the name *Emychelydia* for that clade (see below).

EMYCHELYDIA (NCN)

PANEMYCHELYDIA (NCN)

(crown node- and panstem-based versions of Emydoidae
Agassiz, 1857)

Definitions.—‘*Emychelydia*’ refers to the crown clade arising from the last common ancestor of *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), *Batagur* (orig. *Emys*) *baska* (Gray, 1831), and all other valid species listed in Appendices 9 and 10, but none of the other valid species listed in Appendix 1 or 8. ‘*Panemychelydia*’ refers to the panstem that includes crown *Emychelydia*.

Subjective synonymies.—Emydoidae Agassiz, 1857; Emydidae Zittel, 1889; Emydinae Siebenrock, 1909.

Comments.—Agassiz (1857) originally coined the name ‘Emydoidae’ for the group comprising all pond turtles, a group later renamed with the more familiar ‘Emydidae’ by Zittel (1889). This name/taxon association remained consistent, until Chkhikvadze (1970) assigned ‘Emydidae’ to McDowell’s (1964) ‘Emydinae,’ a less inclusive group restricted to North American pond turtles and *Emys orbicularis*. In the event that all Asian and American pond turtles turn out to be more closely related to another than

either is to any *testudinid*, resurrecting Agassiz's (1857) name for this taxon may be useful. However, given how closely the name 'Emydoidae' resembles the clade name 'Emydidae' (see above) and the genus/subgenus name 'Emydoidea,' we decided to create a significantly different name, 'Emychelydia,' to prevent confusion in the future.

CHERSEMYDA Strauch, 1862 (CCN)

PANCHERSEMYDA (NCN)

(crown node- and panstem-based versions of *Chersemyda* Strauch, 1862)

Definitions.—'Chersemyda' refers to the crown clade arising from the last common ancestor of *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766), *Staurotypus* (orig. *Terrapene*) *triporcatus* (Wiegmann, 1828), *Dermatemys* *mawii* Gray, 1847, *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), *Batagur* (orig. *Emys*) *baska* (Gray, 1831), *Testudo* *graeca* Linnaeus, 1758, and *Platysternon* *megacephalum* Gray, 1831, but none of the other valid species listed in Appendix 1.

Subjective synonymies.—*Chersemyda* Strauch, 1862; *Testudinida* Dollo, 1884; *Cryptodira* Siebenrock, 1909; *Testudinoidea* Lindholm, 1929.

Comments.—The name *Chersemyda* was introduced by Strauch (1862) to refer to all *cryptodiran* turtles except for *chelonoids* and *trionychoids*. The same grouping was also recognized by Dollo (1884), Siebenrock (1909), and Lindholm (1929), all of whom referred to it with different names (see subjective synonymy list). To our knowledge, no data currently support this grouping. Nevertheless, we consider *Chersemyda* the correct name should that grouping ever resurface.

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APPENDICES

To reduce the space requirements for this list, all species are enumerated using their modern genus assignments only. The genus assignments used here are based on the most recent phylogenetic analyses. Most of the species authors can be found in Iverson (1992). References for taxonomic changes since Iverson (1992) are given at the end of each Appendix.

Appendix 1.—Type species of 14 exclusive turtle clades (formerly “families”). A, *Chelus fimbriatus* (Schneider, 1783); *Pelomedusa subrufa* (Bonnaterre, 1789); *Podocnemis expansa* (Schweigger, 1812). B, *Batagur baska* (Gray, 1831); *Carettochelys insculpta* Ramsay, 1887; *Chelonia mydas* (Linnaeus, 1758); *Chelydra serpentina* (Linnaeus, 1758); *Dermatemys mawii* Gray, 1847; *Dermochelys coriacea* (Vandellius, 1761); *Emys orbicularis* (Linnaeus, 1758); *Kinosternon scorpioides* (Linnaeus, 1766); *Staurotypus triporcatus* (Wiegmann, 1828); *Testudo graeca* Linnaeus, 1758; *Trionyx triunguis* (Forskål, 1775).

Appendix 2.—Living species of Chelidae (n = 52). *Acanthochelys macrocephala* (Rhodin, Mittermeier, and McMorris, 1984); *A. pallidipectoris* (Freiberg, 1945); *A. radiolata* (Mikan, 1820); *A. spixii* (Duméril and Bibron, 1835); *Batrachemys dahli* (Zangerl and Medem, 1958); *B. heliostema* (McCord, Joseph-Ouni, and Lamar, 2001); *B. nasuta* (Schweigger, 1812); *B. raniceps* (Gray, 1855); *B. tuberculata* (Luederwaldt, 1926); *B. zuliae* (Pritchard and Trebbau, 1984); *Chelodina burrungandjii* Thomson, Kennet, and Georges, 2000; *C. canni* McCord and Thomson, 2002; *C. expansa* Gray, 1857; *C. kuchlingi* Cann, 1997; *C. longicollis* (Shaw, 1794); *C. mccordi* Rhodin, 1994; *C. novaeguineae* Boulenger, 1888; *C. oblonga* Gray, 1841; *C. parkeri* Rhodin and Mittermeier, 1976; *C. pritchardi* Rhodin, 1994; *C. reimanni* Philippen and Grossman, 1990; *C. rugosa* Ogilby, 1890; *C. steindachneri* Siebenrock, 1914; *Chelus fimbriatus* (Schneider, 1783); *Elseya belli* (Gray, 1844); *E. dentata* (Gray, 1863); *E. georgesi* Cann, 1997; *E. irwini* Cann, 1997; *E. latisternum* Gray, 1867; *E. novaeguineae* (Meyer, 1874); *E. purvisi* Wells and Wellington, 1985; *Elusor macrurus* Cann and Legler, 1994; *Emydura australis* (Gray, 1841); *E. krefftii* (Gray, 1871); *E. macquarrii* (Gray, 1831); *E. subglobosa* (Krefft, 1876); *E. tanybaraga* Cann, 1997; *E. victoriae* (Gray, 1842); *E. worrelli* (Wells and Wellington, 1985); *Hydromedusa maximiliani* (Mikan, 1820); *H. tectifera* Cope, 1870; *Mesoclemmys gibba* (Schweigger, 1812); *Phrynops geoffroanus* (Schweigger, 1812); *P. hilarii* (Duméril and Bibron, 1835); *P. hoguei* Mertens, 1967; *P. rufipes* (Spix, 1824); *P. tuberosus* (Peters, 1870); *P. vanderhaegei* Bour, 1973; *P. williamsi* Rhodin and Mittermeier, 1983; *Platemys platycephala* (Schneider,

1792); *Rheodytes leukops* Legler and Cann, 1980; *Pseudemysdura umbri-*
na Siebenrock, 1901.

This list is updated from Iverson (1992) by the following references: Cann (1998), McCord and Thomson (2002), McCord et al. (2000), and Georges et al. (2002). We do not recognize the taxonomic revision of *Phrynopis* by McCord et al. (2000) because the phylogeny of the group is poorly resolved.

Appendix 3.—Living species of Pelomedusidae (n = 18). *Pelomedusa subrufa* (Bonnaterre, 1789); *Pelusios adansonii* (Schweigger, 1812); *P. bechuanicus* FitzSimons, 1932; *P. broadleyi* Bour, 1986; *P. carinatus* Laurent, 1956; *P. castaneus* (Schweigger, 1812); *P. castanoides* Hewitt, 1931; *P. chapini* Laurent, 1965; *P. gabonensis* (Duméril, 1856); *P. marani* Bour, 2000; *P. nanus* Laurent, 1956; *P. niger* (Duméril and Bibron, 1835); *P. rhodesianus* Hewitt, 1927; *P. seychellensis* Siebenrock, 1906; *P. sinuatus* (Smith, 1838); *P. subniger* (Bonnaterre, 1789); *P. upembae* Broadley, 1981; *P. williamsi* Laurent, 1965.

This list is updated from Iverson (1992) by reference to Bour (2000).

Appendix 4.—Living species of Podocnemidae (n = 8). *Erymnochelys madagascariensis* (Grandidier, 1867); *Podocnemis erythrocephala* (Spix, 1824); *P. expansa* (Schweigger, 1812); *P. lewyana* Duméril, 1852; *P. sextuberculata* Cornalia, 1849; *P. unifilis* Troschel, 1848; *P. vogli* Müller, 1935; *Peltocephalus dumerilianus* (Schweigger, 1812).

Appendix 5.—Living species of Cheloniidae (n = 6). *Chelonia mydas* (Linnaeus, 1758); *Caretta caretta* (Linnaeus, 1758); *Eretmochelys imbricata* (Linnaeus, 1758); *Lepidochelys kempii* (Garman, 1880); *L. olivacea* (Eschscholtz, 1829); *Natator depressus* (Garman, 1880).

Appendix 6.—Living species of Trionychidae (n = 23). *Amyda cartilaginea* (Boddaert, 1770); *Apalone ferox* (Schneider, 1783); *A. mutica* (LeSueur, 1827); *A. spinifera* (LeSueur, 1827); *Aspideretes gangeticus* (Cuvier, 1825); *A. hurum* (Gray, 1831); *A. leithii* (Gray, 1872); *A. nigricans* (Anderson, 1875); *Chitra indica* (Gray, 1831); *Cyclanorbis elegans* (Gray, 1869); *C. senegalensis* (Duméril and Bibron, 1835); *Cycloderma aubryi* (Duméril, 1856); *C. frenatum* Peters, 1854; *Dogania subplana* (Geoffroy-St.-Hilaire, 1809a); *Lissemys punctata* (Bonnaterre, 1789); *L. scutata* (Peters, 1868); *Nilssonina formosa* Gray, 1869; *Palea steindachneri* (Siebenrock, 1906); *Pelochelys bibroni* (Owen, 1853); *Pelodiscus sinensis* (Wiegmann, 1835); *Rafetus euphraticus* (Daudin, 1801); *R. swinhoi* (Gray, 1873); *Trionyx triunguis* (Forskål, 1775).

Appendix 7.—Living species of Kinosternidae (n = 25). *Claudius angustatus* Cope, 1865; *Kinosternon acutum* Gray, 1831; *K. alamosae* Berry and Legler, 1980; *K. angustipons* Legler, 1965; *K. arizonense* Gilmore, 1922; *K. baurii* (Garman, 1891); *K. chimalhuaca* Berry, Seidel, and Iverson, 1997; *K. creaseri* Hartweg, 1934; *K. dunni* Schmidt, 1947; *K. durangoense* Iverson, 1992; *K. flavescens* (Agassiz, 1857); *K. herrerae* Stejneger, 1925; *K. hirtipes* (Wagler, 1830); *K. integrum* Le Conte, 1854; *K. leucostomum* (Duméril and Bibron, 1851); *K. oaxaca* Berry and Iverson, 1980; *K. scorpioides* (Linnaeus, 1766); *K. sonoriense* Le Conte, 1854; *K. subrubrum* (Bonnaterre, 1789); *Staurotyphlus salvinii* Gray, 1864; *S. triporcatus* (Wiegmann, 1828); *Sternotherus carinatus* (Gray, 1855); *S. depressus* Tinkle and Webb, 1955; *S. minor* (Agassiz, 1857); *S. odoratus* (Latreille, 1801).

This list is updated from Iverson (1992) by reference to Berry et al. (1997) and Serb et al. (2001).

Appendix 8.—Living species of Testudinidae (n = 43). *Chersina angulata* (Schweigger, 1812); *Dipsochelys dussumieri* (Gray, 1831); *Geochelone carbonaria* (Spix, 1824); *G. chilensis* (Gray, 1870); *G. denticulata* (Linnaeus, 1766); *G. elegans* (Schoepf, 1795); *G. nigra* (Quoy and Gaimard, 1824); *G. pardalis* (Bell, 1828); *G. platynota* (Blyth, 1863); *G. radiata* (Shaw, 1802); *G. sulcata* (Miller, 1779); *G. yniphora* (Vaillant, 1885); *Gopherus agassizii* (Cooper, 1863); *G. berlandieri* (Agassiz, 1857); *G. flavomarginatus* Legler, 1959; *G. polyphemus* (Daudin, 1802); *Homopus areolatus* (Thunberg, 1787); *H. boulengeri* Duerden, 1906; *H. femoralis* Boulenger, 1888; *H. signatus* (Schoepf, 1801); *Indotestudo elongata* (Blyth, 1853); *I. forstenii* (Schlegel and Müller, 1844); *I. travancorica* (Boulenger, 1907); *Kinixys belliana* Gray, 1831; *K. erosa* (Schweigger, 1812); *K. homeana* Bell, 1827; *K. lobatsiana* Power, 1927;

K. natalensis Hewitt, 1935; *K. spekii* Gray, 1863; *Malacochersus tornieri* (Siebenrock, 1903); *Manouria emys* (Schlegel and Müller, 1844); *M. impressa* (Günther, 1882); *Psammobates geometricus* (Linnaeus, 1758); *P. oculiferus* (Kuhl, 1820); *P. tentorius* (Bell, 1828); *Pyxis arachnoides* Bell, 1827; *P. planicauda* (Grandidier, 1867); *Testudo graeca* Linnaeus, 1758; *T. hermanni* Gmelin, 1789; *T. horsfieldii* Gray, 1844; *T. kleinmanni* Lortet, 1883; *T. marginata* Schoepf, 1792; *T. werneri* Perälä, 2001.

This list is updated from Iverson (1992) by reference to Broadley (1993), Iverson et al. (2001), Palkovacs et al. (2002), and Perälä (2001).

Appendix 9.—Living species of Bataguridae (n = 62). *Batagur baska* (Gray, 1831); *Callagur borneoensis* (Schlegel and Müller, 1844); *Cuora amboinensis* (Daudin, 1802); *C. aurocapitata* Luo and Zong, 1988; *C. bourreti* Obst and Reimann, 1994; *C. flavomarginata* Gray, 1863; *C. galbinifrons* Bourret, 1939; *Cuora mouhotii* (Gray, 1862); *C. pani* Song, 1984; *C. picturata* Lehr, Fritz, and Obst 1998; *C. trifasciata* (Bell, 1825); *C. yunnanensis* (Boulenger, 1906); *C. zhoui* Zhao, 1990; *Cyclemys dentata* (Gray, 1831); *C. oldhamii* Gray, 1863; *C. pulchristriata* Fritz, Gaulke, and Lehr, 1997; *C. tcheponensis* (Bourret, 1939); *Geoclemys hamiltonii* (Gray, 1831); *Geoemyda japonica* Fan, 1931; *G. silvatica* Henderson, 1912; *G. spengleri* (Gmelin, 1789); *Hardella thurjii* (Gray, 1831); *Heosemys depressa* (Anderson, 1875); *H. grandis* (Gray, 1860); *H. leytensis* Taylor, 1920; *H. spinosa* (Gray, 1831); *Hieremys annandalii* (Boulenger, 1903); *Kachuga dhongoka* (Gray, 1834); *K. kachuga* (Gray, 1831); *K. trivittata* (Duméril and Bibron, 1835); *Malayemys subtrijuga* (Schlegel and Müller, 1844); *Mauremys annamensis* (Siebenrock, 1903); *M. caspica* (Gmelin, 1774); *M. japonica* (Temminck and Schegel, 1835); *M. leprosa* (Schweigger, 1812); *M. mutica* (Cantor, 1842); *M. nigricans* (Gray, 1834); *M. reevesii* (Gray, 1831); *M. sinensis* (Gray, 1834); *Melanochelys tricarinata* (Blyth, 1856); *M. trijuga* (Schweigger, 1812); *Morenia ocellata* (Duméril and Bibron, 1835); *M. petersi* (Anderson, 1879); *Leucocephalon yuwonoi* (McCord, Iverson, and Boeadi, 1995); *Notochelys platynota* (Gray, 1834); *Orlitia borneensis* (Gray, 1873); *Pangshura smithii* (Gray, 1863); *P. sylhetensis* Jerdon, 1870; *P. tecta* (Gray, 1831); *P. tentoria* (Gray, 1834); *Rhinoclemmys annulata* (Gray, 1860); *R. areolata* (Duméril and Bibron, 1851); *R. diademata* (Mertens, 1954); *R. funerea* (Cope, 1876); *R. melanosterna* (Gray, 1861); *R. nasuta* (Boulenger, 1902); *R. pulcherrima* (Gray, 1855); *R. punctularia* (Daudin, 1801); *R. rubida* (Cope, 1870); *Sacalia bealei* (Gray, 1831); *S. quadriocellata* Siebenrock, 1903; *Siebenrockiella crassicolis* (Gray, 1831).

This list is updated from Iverson (1992) by reference to Yasukawa et al. (1992), Fritz et al. (1997), Parham et al. (2001), Stuart and Parham (in press), and Spinks et al. (in press).

Appendix 10.—Living species of Emydidae (n = 46). *Chrysemys picta* (Schneider, 1783); *Clemmys guttata* (Schneider, 1792); *Deirochelys reticularia* (Latreille, 1801); *Emys blandingii* (Holbrook, 1838); *E. marmorata* Baird and Girard, 1852; *E. orbicularis* (Linnaeus, 1758); *Glyptemys insculpta* (Le Conte, 1830); *G. muhlenbergii* (Schoepf, 1801); *Graptemys barbouri* Carr and Marchand, 1942; *G. caglei* Haynes and McKown, 1974; *G. ernsti* Lovich and McCoy, 1992; *G. flavimaculata* Cagle, 1954; *G. gibbonsi* Lovich and McCoy, 1992; *G. geographica* (LeSueur, 1817); *G. nigrinoda* Cagle, 1954; *G. oculifera* (Baur, 1890); *G. ouachitensis* Cagle, 1953; *G. pseudogeographica* (Gray, 1831); *G. pulchra* Baur, 1893; *G. versa* Stejneger, 1925; *Malaclemys terrapin* (Schoepf, 1793); *Pseudemys alabamensis* Baur, 1893; *P. concinna* (Le Conte, 1830); *P. floridana* (Le Conte, 1830); *P. nelsoni* Carr, 1938; *P. rubriventris* (Le Conte, 1830); *P. texana* Baur, 1893; *Terrapene carolina* (Linnaeus, 1758); *T. coahuila* Schmidt and Owens, 1944; *T. nelsoni* Stejneger, 1925; *T. ornata* (Agassiz, 1857); *Trachemys adiutrix* (Vanzolini, 1995); *T. callirostris* (Gray, 1855); *T. decorata* (Barbour and Carr, 1940); *T. decussata* (Gray, 1831); *T. dorbigni* (Duméril and Bibron, 1835); *T. emolli* (Legler, 1990); *T. gaigeae* (Hartweg, 1939); *T. nebulosa* (Van Denburgh, 1895); *T. ornata* (Gray, 1831); *T. scripta* (Schoepf, 1792); *T. stejnegeri* (Schmidt, 1928); *T. terrapen* (Bonnaterre, 1789); *T. taylori* (Legler, 1960); *T. venusta* (Gray, 1855); *T. yaquia* (Legler and Webb, 1970).

This list is updated from Iverson (1992) by reference to Ernst et al. (1994), Feldman and Parham (2001), Parham and Feldman (2002), and Seidel (2002).