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A nomenclature for fossil and living turtles using phylogenetically defined clade names

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Abstract

Over the last 25 years, researchers, mostly paleontologists, have developed a system of rank-free, phylogenetically defined names for the primary clades of turtles. As these names are not considered established by the PhyloCode, the newly created nomenclatural system that governs the naming of clades, we take the opportunity to convert the vast majority of previously defined clade names for extinct and extant turtles into this new nomenclatural framework. Some previously defined names are converted with minor adjustments. We also define a number of new clade names to close apparent nomenclatural gaps. In total, we establish 113 clade names, of which 79 had already received phylogenetic definitions and 34 are new.

Keywords: Phylogenetic nomenclature, PhyloCode, Phylonyms, Testudines, Testudinata

Introduction

Taxonomy is the science of delimiting groups of organisms. There are currently two main schemes for naming such groups (nomenclature), ranked nomenclature and phylogenetic nomenclature. Linnaean nomenclature grew over the course of nearly two centuries from the opus of Swedish taxonomist Carl von Linné (Carolus Linnaeus), who attempted to catalog and classify all known natural objects into a single system (e.g., Linnaeus 1758, 1766). This system, herein referred to as "rank-based nomenclature" remains theory-free regarding the evolutionary nature of species or groups of organisms (i.e., groupings can be mono-, para-, or polyphyletic) but provides strict nomenclatural rules that govern, among others, the use of ranks and indicative endings, the use of binomials for species, the availability of names, the principle of priority, and the use of the 26 letter Latin alphabet in the formation of names. A number of codes exist for different groups of organisms, of which the International Code of Zoological Nomenclature regulates the names of "animals" (ICZN 1999).

In a series of papers, de Queiroz and Gauthier (1990, 1992, 1994) summarized insufficiencies with rank-based nomenclature, in particular the use of ranks, which have no connection with evolutionary reality, yet play a vital role in its nomenclature. As an alternative, de Queiroz and Gauthier (1990, 1992, 1994) outlined a nomenclatural system, which they named phylogenetic nomenclature, that is solely focused on naming monophyletic groups (clades) by reference to specifiers in the context of phylogenetic hypotheses. A lively, subsequent debate focused on how a formalized system of phylogenetic nomenclature could be developed to replace rank-based nomenclature (e.g., Cantino et al. 1999; Lee 1999, 2001; Sereno 1999; Brochu and Sumrall 2001; Härlin 2001; Bryant and Cantino 2002; Pleijel and Härlin 2004; Laurin 2005). This discussion led to the formation of the International Society for Phylogenetic Nomenclature in

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2004 (Laurin and Cantino 2004), which supervised the formal compilation of a new set of nomenclatural rules, the International Code of Phylogenetic Nomenclature (Cantino and de Queiroz, 2020), also known as the PhyloCode, which governs the naming of clades (or monophyletic groups) while leaving the regulation of species names to the ICZN (1999).

The history of turtle clades being named closely traces the origin and development of phylogenetic nomenclature. Prior to the formalized introduction of this novel nomenclatural system, Gauthier et al. (1988) provided the first phylogenetic definition for turtles, by applying the common name Chelonia to its crown clade. Over the course of the subsequent decade, a number of names were assigned to select crown and total groups. In particular, Hutchison (1991) assigned the family name Kinosternidae to the crown group of mud turtles, Lee (1995) assigned the historically recognized subordinal names Pleurodira and Cryptodira to the crown groups of the two primary clades of turtles while coining the new names Pleurodiromorpha and Cryptodiromorpha for their total groups, respectively, whereas, Parham and Fastovsky (1997) assigned the family, subfamily, and tribe names Cheloniidae, Cheloniinae, and Carettini, to the total and crown clades of hard-shelled marine turtles and one of their primary subgroups, respectively.

As phylogenetic nomenclature was slowly gaining momentum at the beginning of the twenty-first century, Joyce et al. (2004) explored difficulties associated with converting a large number of traditionally used names to phylogenetically defined ones and provided an internally consistent nomenclature for the most important crown and total groups of turtles that evenly implemented the "crown group rule" (i.e., the application of the most commonly used name to crown groups) in combination with the "pan convention" (i.e., the creation of new names for total clade by combination with the crown group name with the prefix pan-). Although it is difficult to measure the impact of this study, its publication coincides with unprecedented stability in the application of names for the primary clades of turtles (mostly through an adjustment of the paleontological community) while serving as the basis for later studies that expanded upon the proposed nomenclature through the naming of further crown and total clades (Engstrom et al. 2004; Parham et al. 2006b; Lyson et al. 2012; Crawford et al. 2015; Joyce and Bourque 2016; Georgalis and Joyce 2017; Vlachos 2018; Vlachos and Rabi 2018) and the conversion of names pertaining to extinct clades (Joyce and Norell 2005; Danilov and Parham 2006; Joyce and Lyson 2010; Lyson and Joyce 2011; Joyce et al. 2013, 2016a, c; Sterli and de la Fuente 2013; Rabi et al. 2014; Cadena and Joyce 2015; Cadena and Parham 2015; Ferreira et al. 2015, 2018; Sterli 2015; Anquetin et al. 2017; Joyce 2017; Evers and Benson 2019). As an alternative to the system proposed by Joyce et al. (2004), Sereno and ElShafie (2013) suggested systematically tying common names to total clades, but this proposal did not gain traction.

The PhyloCode (Cantino and de Queiroz 2020, herein abbreviated as "PhyloCode 2020") was released earlier this year in concert with Phylonyms (de Queiroz et al. 2020, herein abbreviated as "Phylonyms 2020"), a special volume which includes definitions for about 300 clades of organisms, including seven clades of turtles (*Pan-Testudines*; *Testudinata*; *Testudines*; *Pan-Pleurodira*; *Pleurodira*; *Pan-Cryptodira*; *Cryptodira*; Joyce et al. 2020a-g) and serves as the starting publication for the new system. As a result, all other previously suggested clades names are not considered established ("available" in the terminology of the ICZN, 1999) under the PhyloCode (2020, Art. 7.1). As an internally consistent system of names has proven itself to be valuable to the community, we rectify this situation in the present work by converting the names of most previously defined clades into the new system while filling some of the remaining, major gaps. This work is intended to be a group effort by the community of turtle taxonomists who actively proposed or implemented phylogenetic definitions.

Methods and discussion

Choice of clades and names

The PhyloCode (2020) establishes continuity with the historic and current literature by explicitly mandating that clades be assigned preexisting names that represent a similar content (PhyloCode 2020, Art. 10.1-2). However, the PhyloCode (2020) leaves the selection of clades to be named to the taxonomic community. In this work, we focus on fixing name/clade associations that have been suggested for turtles over the course of the last two and a half decades, but are not considered established by the PhyloCode, as they were defined prior to publication of Phylonyms (PhyloCode 2020, Art. 7.1). For the subsequent discussion, we group these into five categories: crown clades, panclades, "total clades" of historically recognized monotypic "families," extinct clades, and clades more inclusive than the turtle crown (i.e., clades directly below the turtle crown but above *Reptilia* Laurenti, 1768 [Laurin and Reisz, 2020]).

Crowns are clades that originate from the common ancestor of extant taxa (PhyloCode 2020, Art. 2.2). Joyce et al. (2004) previously provided definitions for 10 crown clades that were historically ranked as "families", because these names were consistently used in the literature. In addition to these clades, we also fix the meaning of several well-supported "subfamilies" as well as one extant "tribe", as these too represent important phylogenetic

units, many of which have already received phylogenetic definitions (Parham and Fastovsky 1997; Joyce and Bourque 2016; Georgalis and Joyce 2017). The conversion of additional sub-familial names may be prudent in the future for other speciose clades, in particular *Geoemydidae*, but we suggest waiting until the basal phylogeny of these clades has been resolved with greater confidence. The assignment of the most commonly used names to the crown clades they approximate is explicitly recommended by the PhyloCode (PhyloCode 2020, Rec. 10.1B). As the usage of names has changed little in the last 20 years, the name/crown clade associations fixed herein generally overlap with those of previous authors, with exception of the name Geoemydidae Theobald, 1868, which is favored over Bataguridae Gray, 1870.

The PhyloCode considers species to be "extant" if they are alive on the date of publication of a particular definition. Exceptions can nevertheless be made for species that went extinct since 1500 CE (PhyloCode 2020, Art. 9.11). This can have a profound impact on the content of names. For example, *Meiolaniformes* is an ancient clade of stem turtles that persisted until the Late Pleistocene (Gaffney 1983, 1996), with some authors suggesting that the clade persisted into the Holocene (White et al. 2010; but see Sterli 2015; Rabi et al. 2019). There are no current or historical records of meiolaniform turtles, however, given the enormous impact that such a discovery would have on the definition of crown turtles, we explicitly exclude *Meiolaniformes* from the list of extant turtles, even if archeological finds were to reveal that this lineage of turtles survived past 1500 CE. In contrast, we specifically establish an exception for all species of the Mascarene tortoises, genus *Cylindraspis*, which are well documented to have been driven to extinction following the discovery of the Mascarene Islands in the sixteenth century (TTWG 2017).

Clades that include all taxa more closely related to a crown clade than with any other extant taxon are called total clades (PhyloCode 2020, Art. 2.2). The PhyloCode strongly suggests that total clades be named by adding the prefix "*Pan-*" to the name of the associated crown clade (PhyloCode 2020, Art. 10.3). If there are preexisting names that approximate a total clade, the PhyloCode allows using that name, but also suppressing it in favor of a panclade name (PhyloCode 2020, Art. 10.6). As there is little historic precedence in the turtle community for assigning unique names to total clades and as we wish to establish an internally consistent nomenclatural system, we here universally assign panclade names to panclades, either by converting preexisting panclade names or by forming new panclade names.

Among the many turtle lineages that emerged during the Cretaceous to Paleocene (Joyce et al. 2013; Pereira et al. 2017), four are unique in that they are represented by a single extant species: *Carettochelys insculpta*, *Dermatemys mawii*, *Dermochelys coriacea*, and *Platysternon megacephalum*. To provide a homogenous nomenclature, Joyce et al. (2004) conceptualized these four species as crown groups and created panclade names for their total groups by adding "*Pan-*" to their genus name (e.g., *Pan-Carettochelys*) and assigned the traditional family names associated with these species to less inclusive clades. Although this nomenclatural scheme has its merits, we here recognize a certain break with nomenclatural tradition and the awkwardness of the resulting terms. We, therefore, here provide maximum-clade definitions (formerly referred to as stem-based definitions) for the traditional family names associated with these four species. This has the added merit of returning these names to clades they historically approximated. We similarly use maximum-clade definitions for other clades with only one extant species or "genus" (e.g., *Pseudemydurinae* with *Pseudemydura umbrina*, *Erymnochelyinae* with *Erymnochelys madagascariensis*, *Hydromedusinae* with *Hydromedusa* spp.).

A significant portion of fossil turtle diversity forms clades that cannot be grouped into crown or total clades, as they lack extant representatives. There is a historic precedent of applying names to such clades, mostly family names. For instance, the name Adocidae was initially formed to unite a small assortment of turtles from the Late Cretaceous to Eocene of North America (Cope, 1869a), but now has grown to include all extinct taxa more closely related to the name-bearing *Adocus beatus* (Leidy, 1865) than any extant turtle, a circumscription that now includes Asian and North American turtles from the Late Jurassic to Paleogene (e.g., Syromyatnikova et al. 2013). We here consistently convert preexisting family names of extinct turtle groups to clades using maximum-clade definitions that exclude extant turtles, as this practice approximates the historically developed usage of these names. Such conversions predominate in the more recent literature (e.g., Lyson and Joyce 2011; Rabi et al. 2014; Cadena and Parham 2015). The notable exception is the name Meiolaniidae Boulenger, 1887, which had recently been assigned to the clade of horned turtles (Sterli 2015) within *Meiolaniformes* Sterli and de la Fuente, 2013 (the name with the maximum-clade definition). The definitions we use for various extinct turtle clades approximate maximum-clade definitions (PhyloCode 2020, Art. 9.6), but can be conceptualized as being opposite to maximum-crown-clade definitions, in that the internal specifier is extinct, while every extant taxon serves as an external specifier. To avoid the accidental inclusion of extant turtles, Joyce and Norell (2005) developed a definition that specifies that all extant organisms

are external specifiers (e.g., the most inclusive clade containing the fossil A, but no extant organism). This wording is impractical for registration in RegNum, as it demands creating the specifier "no extant organism". As an alternative, we here developed wording that clarifies that all extant organisms serve as external specifiers through insertion of the word "extinct" (i.e., the most inclusive *extinct* clade containing the fossil A). To avoid confusion with other maximum-inclusive clades, we suggest recognition of a novel definitional category (e.g., "maximum-extinct-clade definition") in future editions of the PhyloCode and RegNum.

Extinct clades are often nested with more inclusive extinct clades. In rank-based nomenclature, only a single name would be formed to unite these clades, but we here form two separate names using minimum-clade definitions (formerly referred to as node-based definitions) and maximum-clade definitions, as it is important to distinguish between hierarchically nested clades within entirely extinct clades, particularly if these include high taxonomic richness. For example, we apply the names *Baenoidea* and *Paracryptodira* to the minimally and maximally inclusive clades, respectively, formed by *Baenidae* and *Pleurosternidae* (Fig. 1a).

A number of clades exist that are intermediate between the crown and total clade of turtles. As turtles were historically conceptualized by the presence of their shell, we here follow Joyce et al. (2004) by applying the name *Testudinata* to the clade defined by the presence of a turtle shell. We furthermore follow Joyce (2017) by naming two additional clades, *Mesochelydia* and *Perichelydia*, which are intermediate between *Testudinata* and *Testudines* and help characterize important phases in turtle evolution. We also formalize the previously proposed clades names *Ankylopoda* Lyson et al., 2012 and *Archelosauria* Crawford et al., 2015, for the possible crown clades formed by turtles with lepidosaurs and archosaurs, respectively.

The PhyloCode does not allow provisionally naming clades for which there is no current support (PhyloCode 2020, Art. 7.2b). We, therefore, here do not follow Joyce et al. (2004) by converting the names *Chersemyda* Strauch, 1862 for the clade of kinosternoids and testudinoids, *Emychelydia* Joyce et al., 2004 for the clade of emydids and geoemydids, *Trionychoidea* Fitzinger, 1826 for the clade of trionychians and kinosternoids, or *Cryptoderinea* Vaillant, 1894 for the clade formed by *Platysternon megacephalum* as sister to testudinoids, as none of these currently enjoy any support (e.g., Crawford et al. 2015; Pereira et al. 2017).

The vast majority of names that we here establish as new clades names are panclade names formed through the addition of the prefix "*Pan-*" to the associated crown clade name. We, therefore, only provide an etymology section for the two names we newly create herein (see *Australochelida* and *Hesperochelida* below), even though this is not required by the PhyloCode (2020).

In total, we here establish according to the rules of the PhyloCode (2020) 113 clade names, of which 79 had already received phylogenetic definitions prior to publication of Phylonyms (2020). The remaining 34 definitions fill notable gaps.

Authorship of preexisting names

The PhyloCode (2020) wishes to maintain continuity with rank-based nomenclatural practices and, therefore, distinguishes between nominal authors and definitional authors. The nominal author is the author who first coined a particular name with a particular spelling in conformity with a rank-based code, regardless of its initial application (PhyloCode 2020, Art. 19.1). If a preexisting name is converted to a clade name, the original author remains the nominal author (PhyloCode 2020, Art. 19.1). However, as the PhyloCode does not acknowledge the rule of coordination of the ICZN (1999), the nominal author recognized by the PhyloCode may be different from the author recognized by the ICZN (1999). For instance, following the rules of the ICZN (1999), Batsch (1788) should be regarded as the author of the name Testudinoidea, as he was the first to create a family group name (*Testudines*) that included *Testudo graeca* (see Lapparent de Broin 2001 as an example of the adaptation of this rule). By contrast, the PhyloCode recognizes Batsch (1788) as the nominal author of *Testudines*, but Fitzinger (1826) as the nominal author of *Testudinoidea*, as these authors were the first to coin names with this particular spelling.

To be considered preexisting by the PhyloCode, historic zoological names must either have been made available under the rules of the ICZN (1999) (PhyloCode 2020, Art. 6.2a) or must have been "in use" (i.e., a rank-based name above the family group or a phylogenetically defined name, PhyloCode 2020, Art. 6.2b). This broadly covers all names proposed for turtles following the publication of the 10th edition of the Systema Naturae (Linnaeus 1758). As a minimum requirement for the recognition of clade names, we demand an explicit phylogenetic definition, which is consistent with Note 6.2.1 of the PhyloCode (2020), which clarified that (only) names that received phylogenetic definitions should be considered preexisting. However, as the meaning of pan-names is self-evident, we consider these to be preexisting, if they are associated with an explicitly defined crown name.

A number of preexisting names for panclades were formed by adding the prefix "*Pan*," to the non-capitalized name of the associated crown clade (e.g., *Panchelidae*

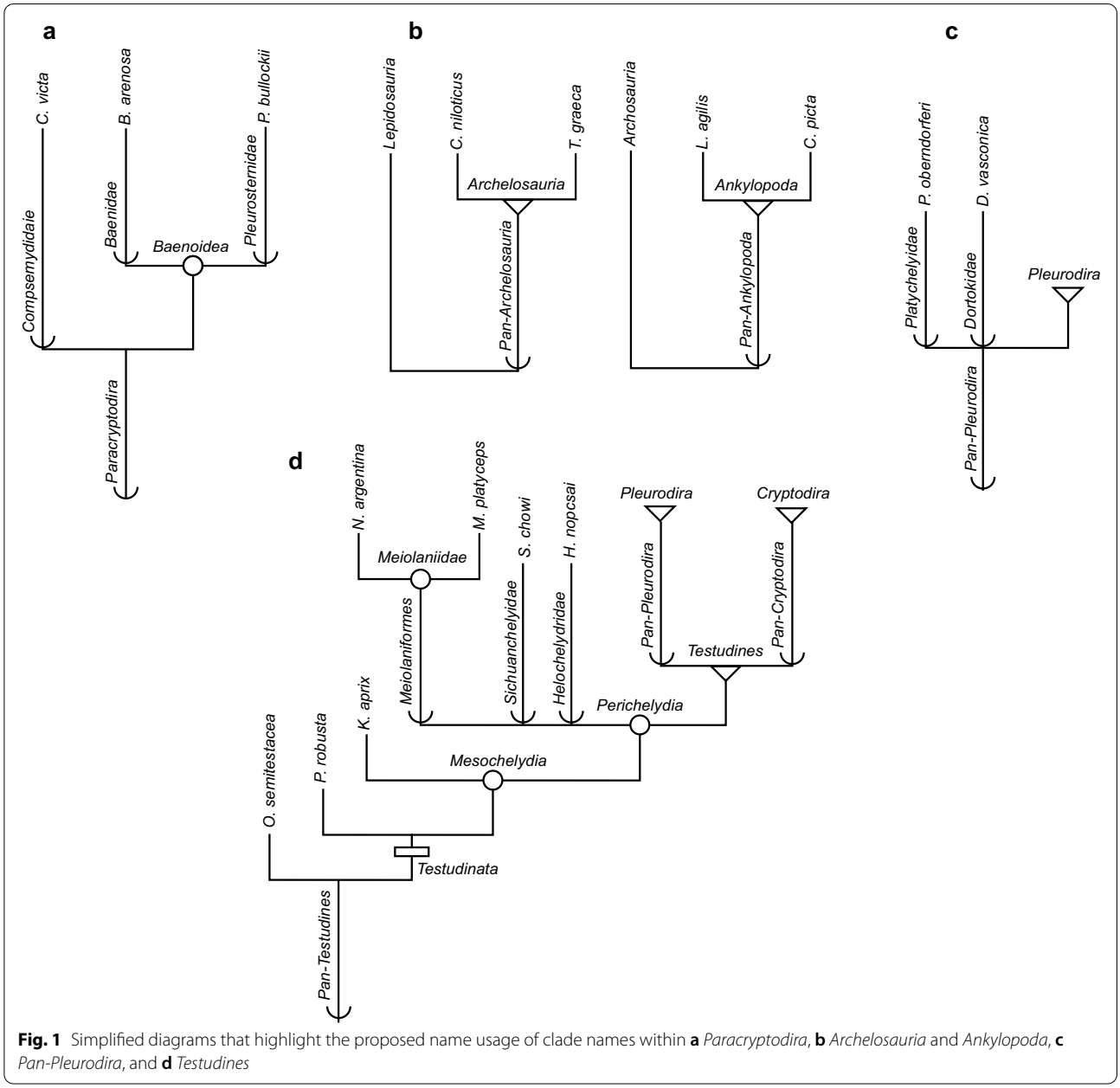

Fig. 1 Simplified diagrams that highlight the proposed name usage of clade names within **a** *Paracryptodira*, **b** *Archelosauria* and *Ankylopoda*, **c** *Pan-Pleurodira*, and **d** *Testudines*

Joyce et al., 2004). This differs in nuances from the newly established rules of the PhyloCode, which demand the formation of panclade names by placing the prefix "*Pan-*" in front of the capitalized name of the associated crown clade (e.g., *Pan-Chelidae*; PhyloCode 2020, Art. 13.3). Although we are unaware of appropriate rules, we here recognize the two as variant spellings of the same name. Authorship, therefore, transfers to the first to create a panclade name using the prefix "*Pan*," regardless of the use of a hyphen or the capitalization of the crown name.

The nominal authors herein recognized generally overlap with those identified by Joyce et al. (2004) and subsequent authors as they utilized the same criteria to establish nominal authorship. We adjusted the authorship of a small selection of traditional names, however, as we found earlier uses. If additional literature work reveals adjusting the authorship of other names, this has no implications for the establishment of the clades named herein (PhyloCode 2020, Art. 9.15.1).

Registration

To be considered established, all clade names must be formally recorded at the Registration Database for Phylogenetically Defined Names (RegNum; PhyloCode 2020, Art. 8.1) and the official registration number must accompany the definition (PhyloCode 2020, Art. 7.2e). All names are, therefore, here associated with their formal registration number.

Choice of definition

The choice of phylogenetic definition is essential to phylogenetic nomenclature, as a poorly constructed definition may jeopardize stability. As the phylogeny of turtles was not yet well resolved just 15 years ago, Joyce et al. (2004) formulated phylogenetic definitions that listed all currently recognized species of a traditionally recognized family as its internal specifiers, as a way to improve stability. In addition to being onerous, this type of definition has the clear downside of being difficult to implement rigorously, as not a single tree exists that samples every living species of turtle.

Although the PhyloCode allows creating phylogenetic definitions freely, it strongly encourages the use of set wordings to ease communication and avoid unintended consequences (PhyloCode, 2020, Rec. 9.4A). For instance, for a minimum-clade definition, the PhyloCode suggests using the wording "the clade originating in the most recent common ancestor of A and B" or "the smallest clade containing A and B" (PhyloCode, 2020: p23). Although the phylogeny of extant turtles is being resolved with ever greater confidence, we here follow these recommendations by evenly implementing maximum-clade definitions (PhyloCode 2020, Art. 9.9) for all crown clades we established herein. Following the rules of the PhyloCode, we use the name giving species of a clade as its internal specifier (PhyloCode 2020, Art. 11.10). *Testudo graeca*, the type species of the family Testudinidae in rank-based nomenclature, is, therefore, selected as the internal specifier of the clade *Testudinidae*. To restrict the number of specifiers we utilize, we select the internal specifiers of some clades as the external specifiers of others (see node-stem triplet of Sereno 1999). Along these lines, *Testudo graeca*, the internal specifier of *Testudinidae*, also serves as the external specifier of *Emydidae*. Although not required, we here list the original genus to which an internal specifier was originally referred. The authorships of all extant species follow TTWG (2017). All total clades are defined by reference to their crown clade (PhyloCode 2020, Art. 9.10).

Reference phylogeny and diagnostic apomorphies

To ensure that only clades are named for which there is evidence, the PhyloCode demands that each definition is either associated with reference to a phylogeny, ideally an explicit, reproducible analysis (PhyloCode 2020, Rec. 9.13a), or putative apomorphies that supports the monophyly of the clade being named (PhyloCode 2020, Art. 9.13).

The reference phylogeny for all crown clades in this study is that of Pereira et al. (2017) because this molecular analysis samples nearly every extant species of turtle. No single analysis that utilizes even a fraction of all known fossil turtles is available, however, so, for each extinct clade name, we select an analysis that focuses on the clade being named and, ideally, that includes the internal specifiers being used. As panclades differ from crown clades by the inclusion of their stem, we select phylogenies that highlight the known fossil content. However, whenever the currently hypothesized composition of a panclade equates that of a crown clade (i.e., when fossils are lacking that represent a stem lineage), we list the analysis of Pereira et al. (2017). Although not demanded by the PhyloCode, we additionally provide character evidence for most names with minimum-clade definitions. We do not provide lists of diagnostic characters for names with maximum-clade definitions, as these vary considerably depending on the phylogeny being used.

Composition

In order for a clade name to be considered established, its definition must include a statement regarding the currently hypothesized composition of the clade (PhyloCode 2020, Art. 9.14). This task has been simplified over the course of the last decade, as numerous publications are now available that summarize the extinct or extant content of most clades being named herein (e.g., TTWG 2017 for extant turtles). We, therefore, here only provide concise statements regarding the hypothesized composition for each clade and refer the reader to the relevant literature for further information.

Past synonymies

The PhyloCode only regards names as synonyms if they are correctly established under the code and refer to the same clade (PhyloCode 2020, Art. 14.1). To maintain continuity with the literature, the Companion to the PhyloCode (2020) nevertheless lists approximate (i.e., traditional taxon names that refer to a taxon with a similar composition to the clade being named) and unambiguous synonyms (i.e., phylogenetically defined names that objectively refer to the same clade). As listing approximate synonyms is not required by the PhyloCode and as the list of approximate synonyms is highly subjective (see Joyce et al. 2004 for extensive discussion), we here refer the reader to the lists of approximate (=subjective) synonyms compiled by Joyce et al. (2004) for most crown

clades named herein. Listing unambiguous synonyms is not mandated either, but we herein nevertheless list these under the heading "Not established phylogenetic definitions" following the format prescribed by the PhyloCode for established names (PhyloCode 2020, Art., 20.2), as the number is relatively small.

Future synonymies

We are confident that we are establishing names that will remain accepted (valid in the terminology of the ICZN 1999) for years to come. In the unlikely event that future research reveals two names to be heterodefinitional synonyms (PhyloCode 2020, Art. 14.1), priority will be given to the name associated with the lower registration number. For this reason, we name and number more inclusive clades prior to less inclusive clades.

Phylogenetic nomenclature

Pan-Archelosauria new clade name.
Registration Number—328.
Definition—The total clade of crown clade *Archelosauria* (see below) (Fig. 1b).
Reference Phylogeny—Crawford et al. (2015, Fig. 2).
Composition—Although the clade *Archelosauria* is retrieved from molecular data as a matter of routine (see *Archelosauria* below), even the most recent morphological analyses that densely sample fossils fail to retrieve this group (e.g., Bever et al. 2015; Schoch and Sues 2017; Li et al. 2018). It is, therefore, unclear which extinct taxa might populate the phylogenetic stem of a monophyletic *Archelosauria*.
Not established phylogenetic definitions—None.

Archelosauria Crawford et al., 2015, converted clade name.
Registration Number—439.
Definition—The smallest crown clade containing the archosaur *Crocodylus* (orig. *Lacerta*) *niloticus* (Laurenti, 1768) and the turtle *Testudo graeca* Linnaeus, 1758, but not the lepidosaur *Lacerta agilis* Linnaeus, 1758 (Fig. 1b).
Reference Phylogeny—Crawford et al. (2015, Fig. 2).
Composition—*Archelosauria* consists of *Pan-Testudines* (see below) and *Pan-Archosauria* Gauthier, 2020 (see Comments below).
Not established phylogenetic definitions—*Archelosauria* Crawford et al., 2015.
Diagnostic Apomorphies—Although there is strong molecular support for the monophyly of *Archelosauria* (e.g., Fong et al. 2012; Wang et al. 2013; Field et al. 2014; Crawford et al. 2015; Gemmell et al. 2020), unambiguous osteological apomorphies are currently lacking that uniquely diagnose the group (Rieppel 2000; Joyce 2015). Lyson and Bever (2020) note that a posterior ossification of the orbital cartilages of some stem turtles might be homologous with the archosaur laterosphenoid (Bhullar and Bever 2009; Bever et al. 2015).
Comments—The name *Archelosauria* was recently introduced by Crawford et al. (2015) for the clade that unites *Testudines* and *Archosauria* Cope, 1869b [Gauthier and Padian, 2020] exclusively. Previous authors had grouped crocodilians and turtles (e.g., Cataphracta Latreille, 1825; "Chélonochampsiens" Gervais, 1848), but excluded birds. Later usage of Cataphracta by Gray (1831a) added plesiosaurs and ichthyosaurs. *Archelosauria* is the first clade name that explicitly refers to turtles and all archosaurs.

Pan-Ankylopoda new clade name.
Registration Number—440.
Definition—The total clade of crown clade *Ankylopoda* (see below) (Fig. 1b).
Reference Phylogeny—Rieppel and Reisz (1999, Fig. 1).
Composition—The clade *Ankylopoda* was recovered in a number of phylogenetic analyses that are based on variants of the same character/taxon matrix (e.g., deBraga and Rieppel 1997; Rieppel and Reisz 1999; Li et al. 2008). However, although these matrices sample extinct taxa densely, none is recovered from the stem lineage of *Ankylopoda*.
Not established phylogenetic definitions—None.

Ankylopoda Lyson et al., 2012, converted clade name.
Registration Number—441.
Definition—The smallest crown clade containing the lepidosaur *Lacerta agilis* Linnaeus, 1758 and the turtle *Chrysemys* (orig. *Testudo*) *picta* (Schneider, 1783), but not the archosaur *Crocodylus* (orig. *Lacerta*) *niloticus* (Laurenti, 1768) (Fig. 1b).
Reference Phylogeny—Lyson et al. (2012, Fig. 2b).
Composition—*Ankylopoda* consists of *Pan-Testudines* (see below) and *Pan-Lepidosauria* Gauthier and de Queiroz, 2020 (see Comments below).
Not established phylogenetic definitions—*Ankylopoda* Lyson et al., 2012.
Diagnostic Apomorphies—Ankylopodans can be diagnosed by the fusion of the astragalus and calcaneum in postnatal ontogeny (Lyson et al. 2012).
Comments—A clade consisting of *Testudines* and *Lepidosauria* Haeckel, 1866 [de Queiroz and Gauthier, 2020] to the exclusion of *Archosauria* has been retrieved in a number of phylogenetic hypotheses (e.g., Rieppel and Reisz 1999; Rieppel 2000; Li et al. 2008), but was only named *Ankylopoda* relatively recently (Lyson et al. 2012). A similarly spelled name, Ancylopoda, also denotes a group of brachiopods (Gray 1848) and an extinct group of perissodactyl mammals (Cope 1899). However, neither

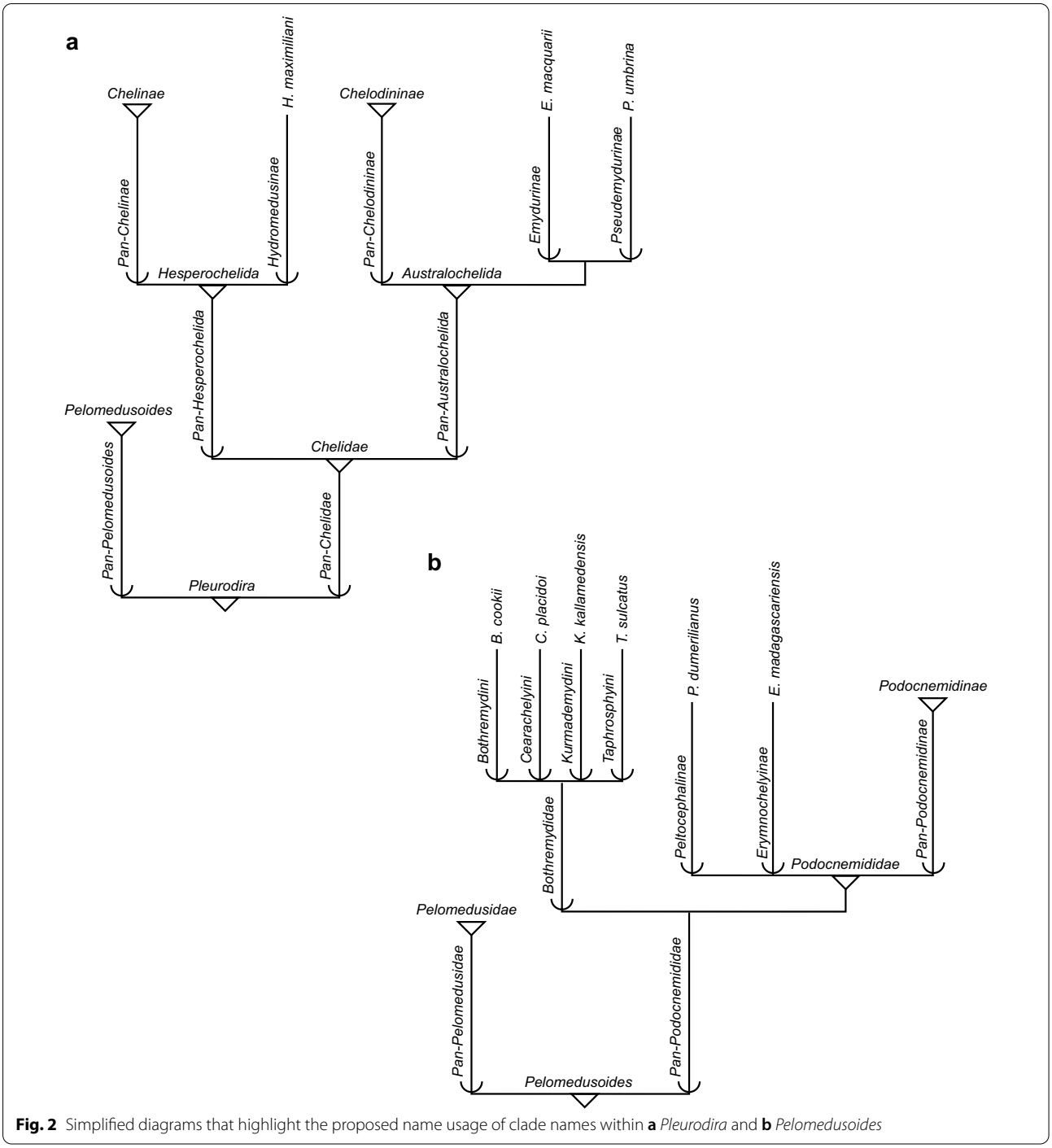

Fig. 2 Simplified diagrams that highlight the proposed name usage of clade names within **a** *Pleurodira* and **b** *Pelomedusoides*

the ICZN (1999) nor the PhyloCode (2020) recognize Ancylopoda as a homonym of Ankylopoda.

Pan-Testudines Joyce et al., 2004 [Joyce et al., 2020a].
Registration Number—272.
Definition—"The total clade of the crown clade *Testudines*" (Joyce et al. 2020a: 1041) (Fig. 1d).
Comment—See Joyce et al. (2020a) for further details.

Testudinata Klein, 1760 [Joyce et al., 2020b].
Registration Number—273.
Definition—"The clade for which a complete turtle shell, as inherited by *Testudo graeca* Linnaeus, 1758, is an apomorphy. A 'complete turtle shell' is herein defined

as a composite structure consisting of a carapace with interlocking costals, neurals, peripherals, and a nuchal, together with the plastron comprising interlocking epi-, hyo-, meso- (lost in *Testudo graeca*), hypo-, xiphiplastra and an entoplastron that are articulated with one another along a bridge" (Joyce et al. 2020b: 1044) (Fig. 1d).
Comment—See Joyce et al. (2020b) for further details.

Mesochelydia Joyce, 2017, converted clade name.
Registration Number—442.
Definition—The smallest clade containing *Condorchelys antiqua* Sterli, 2008, *Eileanchelys waldmani* Anquetin et al., 2009, *Heckerochelys romani* Sukhanov, 2006, *Kayentachelys aprix* Gaffney et al., 1987, and the extant turtle *Testudo graeca* Linnaeus, 1758 (Fig. 1d).
Reference Phylogeny—Zhou and Rabi (2015, Fig. 6).
Composition—*Mesochelydia* is currently hypothesized to include all Jurassic to Recent representatives of Testudinata, with the notable exception of the Early Jurassic *Australochelys africanus* (Joyce 2017).
Not established phylogenetic definitions—*Mesochelydia* Joyce, 2017.
Diagnostic Apomorphies—Fossil and extant mesochelydians can be diagnosed relative to more basal turtles by lacking lacrimals, lacrimal ducts, supratemporals, and supramarginals, and by possessing confluent external nares, a single vomer, an anatomically modern ear consisting of a formed cavum tympani, antrum postoticum, recessus scalae tympani, fenestra perilymphatica, and processus interfenestralis, a pair of basioccipital tubercles, eleven pairs of peripherals, a reduced posterior entoplastral process, and a pectoral girdle consisting of strap-like processes only connected by minor bony webs (Joyce 2017).
Comments—The name *Mesochelydia* was only recently introduced by Joyce (2017) as no other name had previously been suggested for this clade of turtles with notably more modern features that more basal representatives of *Testudinata* from the Triassic.

Perichelydia Joyce, 2017, converted clade name.
Registration Number—443.
Definition—The smallest clade containing the helochelydrid *Helochelydra nopcsai* Lapparent de Broin and Murelaga, 1999, the meiolaniform *Meiolania platyceps* Owen, 1886, the sichuanchelyid *Sichuanchelys chowi* Ye and Pi, 1997, and the extant turtle *Testudo graeca* Linnaeus, 1758 (Fig. 1d).
Reference Phylogeny—Joyce et al. (2016a, Fig. 8).
Composition—In addition to the groups included in its definition, *Meiolaniformes*, *Helochelydridae*, *Sichuanchelyidae*, and *Testudines* (see below), *Perichelydia* is currently hypothesized to include a small set of Mesozoic taxa with problematic relationships, in particular *Kallokibotion bajazidi* and *Spoochelys ormondea* from the Late Cretaceous of Europe and Australia, respectively (Joyce 2017).
Not established phylogenetic definitions—*Perichelydia* Joyce, 2017.
Diagnostic Apomorphies—Fossil and extant perichelydians can be diagnosed relative to more basal turtles by lacking an open interpterygoid vacuity and the presence of a clearly developed processus trochlearis oticum (Joyce 2017).
Comments—The name *Perichelydia* was only recently introduced by Joyce (2017) for this derived clade of turtles characterized by the presence of a developed otic trochlear system.

Helochelydridae Chkhikvadze, 1970, converted clade name.
Registration Number—444.
Definition—The largest extinct clade containing *Helochelydra nopcsai* Lapparent de Broin and Murelaga, 1999, but not the meiolaniform *Meiolania platyceps* Owen, 1886, the sichuanchelyid *Sichuanchelys chowi* Ye and Pi, 1997, or the paracryptodires *Pleurosternon* (orig. *Platemys*) *bullockii* (Owen, 1842) and *Baena arenosa* Leidy, 1870 (Fig. 1d).
Reference Phylogeny—Joyce et al. (2016a, Fig. 8).
Composition—*Helochelydridae* is currently hypothesized to include fossil material from the Late Jurassic to Late Cretaceous of Europe and North America (Joyce 2017). Notable examples include the North American *Naomichelys speciosa* and the European *Aragochersis lignitesta* and *Helochelydra nopcsai* (Hay 1908; Lapparent de Broin and Murelaga 1999; Joyce et al. 2011, 2014; Pérez-García et al. 2020a).
Not established phylogenetic definitions—*Helochelydridae* Chkhikvadze, 1970 [Joyce et al., 2016a].
Comments—A group of turtles with a similar composition as this clade was originally referred to as Helochelydrinae by Nopcsa (1928) and as Helochelydridae by Chkhikvadze (1970, 1973). Lapparent de Broin and Murelaga (1996) recognized this group as well, though to the exclusion of the then poorly understood *Helochelydra*, and created the alternative name Solemydidae. This name was regularly used in the literature in subsequent years. Joyce et al. (2016a) more recently clarified that the names of Nopcsa and Chkhikvadze are available and provided a phylogenetic definition for the clade for the first time. Chkhikvadze (1970) is the nominal author of this clade, as he was the first to use this spelling. As numerous characters (e.g., Evers et al. 2020), combined with biogeographic considerations, make it plausible that *Helochelydra nopcsai* is more closely related to *Pleurosternon* (orig.

Platemys) *bullockii* (Owen, 1842) or *Baena arenosa* Leidy 1870 than with any extant organism, we modify the original definition of Joyce et al. (2016a) to explicitly allow for the nesting of *Helochelydridae* within *Paracryptodira*.

Meiolaniformes Sterli and de la Fuente, 2013, converted clade name.
Registration Number—445.
Definition—The largest extinct clade containing *Meiolania platyceps* Owen, 1886 (Fig. 1d).
Reference Phylogeny—Joyce et al. (2016a, Fig. 8).
Composition—The composition of *Meiolaniformes* varies considerably depending on topology. At the least, the clade is thought to consist of fossil turtles from the Cenozoic of South America, in particular *Meiolaniidae* (see below) and *Peligrochelys walshae* (e.g., Joyce et al. 2016a). At its greatest, *Meiolaniformes* also includes fossil forms from the northern continents, such as *Mongolochelys efremovi* and *Kallokibotion bajazidi*, and turtles reaching back to the Early Cretaceous, such as *Chubutemys copelloi* and *Otwayemys cunicularius* (Sterli et al. 2015a, b).
Not established phylogenetic definitions—*Meiolaniformes* Sterli and de la Fuente, 2013.
Comments—The name *Meiolaniformes* was only recently coined by Sterli and de la Fuente (2013) for a group of fossil turtles more inclusive than classic, horned meiolaniids (see *Meiolaniidae* below). As this name is now well established in the literature, we here implement it as well. The definition of other, basal clades of turtles is chosen in such a way to allow them to nest within *Meiolaniformes*, in particular *Helochelydridae* and *Sichuanchelyidae* (see below). However, if future work concludes that *Meiolaniformes* is synonymous with other extinct clades established herein, such as *Paracryptodira*, we explicitly recommend that the definition of *Meiolaniformes* be amended by adding external specifiers so that it refers to a unique maximum-clade name for the lineage including *Meiolania platyceps* Owen, 1886.

Meiolaniidae Boulenger, 1887, converted clade name.
Registration Number—446.
Definition—The smallest extinct clade containing *Meiolania platyceps* Owen, 1886 and *Niolamia argentina* Ameghino, 1899 (Fig. 1d).
Reference Phylogeny—Sterli et al. (2015b, Fig. 4).
Composition—*Meiolaniidae* is currently hypothesized to include a small set of horned turtles from the Cenozoic of South America and Australia (Sterli 2015). The best-known meiolaniids are *Niolamia argentina* from the Eocene of Argentina (Sterli and de la Fuente 2011) and *Meiolania platyceps* from the Pleistocene of Australia (Gaffney 1983, 1996).
Not established phylogenetic definitions—*Meiolaniidae* Boulenger, 1887 [Sterli, 2015].
Diagnostic Apomorphies—Meiolaniids can most easily be diagnosed relative to more basal meiolaniformes by a contact of the quadratojugal with the squamosal below the cavum tympani, presence of squamosal horns, absence of an antrum postoticum, presence of an intrapterygoid slit through which the palatine artery enters the skull, presence of a bony flooring for the canalis caroticus internus posterior to the bifurcation of the cerebral and palatine branches, formation of the foramen posterior canalis carotici interni by the pterygoid, and the presence of a tail club and tail rings (Sterli 2015).
Comments—The name *Meiolaniidae* has long been in use for the horned turtles of the Southern Hemisphere (e.g., Boulenger 1887; Gaffney 1983, 1996) and was phylogenetically defined by Sterli (2015). At present, this clade includes all known turtles with horns on their skull, but it is not defined by this character. It is, therefore, to be expected that more basal taxa are eventually found that are located outside of *Meiolaniidae*, but nevertheless posses

Sichuanchelyidae Tong et al., 2012a, converted clade name.
Registration Number—447.
Definition—The largest extinct clade containing *Sichuanchelys chowi* Ye and Pi, 1997, but not the meiolaniform *Meiolania platyceps* Owen, 1886, the helochelydrid *Helochelydra nopcsai* Lapparent de Broin and Murelaga, 1999, or the paracryptodires *Pleurosternon* (orig. *Platemys*) *bullockii* (Owen, 1842) and *Baena arenosa* Leidy, 1870 (Fig. 1d).
Reference Phylogeny—Joyce et al. (2016a, Fig. 8).
Composition—*Sichuanchelyidae* is currently hypothesized to include the Jurassic fossil turtles *Sichuanchelys chowi* and *Sichuanchelys palatodentata*, but also perhaps the Cretaceous turtle *Mongolochelys efremovi* (Joyce et al. 2016a) and the Paleocene turtle *Laurasichersis relicta* (Pérez-García 2020a).
Not established phylogenetic definitions—*Sichuanchelyidae* Tong et al., 2012a [Joyce et al., 2016a].
Comments—As initially conceived by Joyce et al. (2016a), the clade *Sichuanchelyidae* includes the enigmatic Late Jurassic *Sichuanchelys chowi* and Late Cretaceous *Mongolochelys efremovi*, but was recently expanded to also include the equally enigmatic *Laurasichersis relicta* from the Paleocene of France (Pérez-García 2020a). The family group name Mongolochelyidae was first used by Sukhanov (2000), but not made available, as he referred to another publication that was supposed to be in press, but never appeared. This was recently adjusted by Sukhanov and Pozdnyakov (in Danilov et al. 2017).

The name Sichuanchelyidae, by contrast, had already been made available by Tong et al. (2012a). Joyce et al. (2016a), therefore, gave priority to that name. An alternative system was recently proposed by Danilov et al. (2017) where the suborder Mongolochelydia unites the families Sichuanchelyidae and Mongolochelyidae, but we here nevertheless follow the system of Joyce et al. (2016a) as they provided an explicit phylogenetic definition. If future research routinely finds *Mongolochelys efremovi* outside of Sichuanchelyidae, it may be desirable to create a distinct clade name for its lineage.

Paracryptodira Gaffney, 1975, converted clade name.
Registration Number—448.
Definition—The largest extinct clade containing *Pleurosternon* (orig. *Platemys*) *bullockii* (Owen, 1842) and *Baena arenosa* Leidy, 1870 (Fig. 1a).
Reference Phylogeny—Joyce et al. (2016a, Fig. 8).
Composition—*Paracryptodira* is a diverse clade of extinct turtles restricted to the Late Jurassic to Paleogene of North America and Europe (Joyce and Lyson 2015; Joyce and Anquetin 2019). Although relationships are far from resolved, the two most speciose clades are Baenidae and Pleurosternidae (see below), but recent work suggests the presence of a speciose, more basal clade of paracryptodires, *Compsemydidae* (see below).
Not established phylogenetic definitions—*Paracryptodira* Gaffney, 1975 [Lyson and Joyce, 2011].
Comments—The name Paracryptodira was originally proposed by Gaffney (1975) for the clade of turtles diagnosed by the presence of a foramen posterius canalis carotici interni that is located midway along the suture of the basisphenoid with the pterygoid. As it remains unclear whether this character is a symplesiomorphy or a synapomorphy (e.g., Evans and Kemp 1975) or whether the assemblage of turtles with this characteristic form a monophyletic clade (e.g., Sterli et al. 2013), Lyson and Joyce (2011) suggested phylogenetically defining the name as applying to the most inclusive clade that includes the pleurosternid *Pleurosternon bullockii* and the baenid *Baena arenosa*, but no extant organism, as this is the assemblage of turtles most typically associated with the name. We fix this meaning herein. Our definition explicitly allows for the potential inclusion of fossil turtles with biogeographic ties that have historically been affiliated with paracryptodires, in particular *Kallokibotion bajazidi* and *Helochelydridae*.

Compsemydidae Pérez-García et al., 2015, converted clade name.
Registration Number—449.
Definition—The largest extinct clade containing *Compsemys victa* Leidy, 1856a, but not the baenid *Baena arenosa* Leidy, 1870 or the pleurosternid *Pleurosternon* (orig. *Platemys*) *bullockii* (Owen, 1842) (Fig. 1a).
Reference Phylogeny—Pérez-García et al. (2015, Fig. 6b).
Composition—*Compsemydidae* consists of at least two species of paracryptodires from the Late Cretaceous and Paleogene of Europe and North America (Pérez-García et al. 2015). Its possible presence in the Late Jurassic and Early Cretaceous of Euramerica has recently been proposed (Joyce and Rollot 2020).
Not established phylogenetic definitions—*Compsemydidae* Pérez-García et al., 2015 [Joyce and Rollot 2020].
Comments—The name Compsemydidae was coined to accommodate a newly recognized clade of turtles centered around the enigmatic big-headed turtle *Compsemys victa* (Pérez-García et al. 2015). We here follow Joyce and Rollot (2020) by defining this name as referring to a clade that may flexibly be situated anywhere within Paracryptodira, including within *Baenidae* and *Pleurosternidae*.

Baenoidea Williams, 1950, converted clade name.
Registration Number—450.
Definition—The smallest extinct clade containing *Pleurosternon* (orig. *Platemys*) *bullockii* (Owen, 1842) and *Baena arenosa* Leidy, 1870 (Fig. 1a).
Reference Phylogeny—Pérez-García et al. (2015, Fig. 6b).
Composition—*Baenoidea*, by definition, consists of the speciose clades *Baenidae* and *Pleurosternidae* (see below).
Not established phylogenetic definitions—*Baenoidea* Williams, 1950 [Lyson and Joyce, 2011].
Diagnostic Apomorphies—Baenoids can be diagnosed by possessing nasals with a midline contact, small prefrontals that lack a midline contact, a foramen posterius canalis carotici interni located halfway along the contact between the pterygoid and the basisphenoid, a dense surface texture that covers the shell, large mesoplastra, and a thickening of the plastron medial to the bridges (Joyce and Anquetin 2019).
Comments—As the name Paracryptodira is preoccupied for the most inclusive clade that contains *Pleurosternon bullockii* and *Baena arenosa*, Lyson and Joyce (2011) resurrected the name Baenoidea, which had historically been applied to the least inclusive clade that contains these fossil turtles (e.g., Williams 1950). As this usage now seems to be accepted (e.g., Pérez-García et al. 2015), we here permanently fix this name/clade association.

Pleurosternidae Cope, 1868b, converted clade name.
Registration Number—451.
Definition—The largest extinct clade containing *Pleurosternon* (orig. *Platemys*) *bullockii* (Owen, 1842), but not the baenid *Baena arenosa* Leidy, 1870 (Fig. 1a).

Reference Phylogeny—Pérez-García et al. (2015, Fig. 6b).
Composition—*Pleurosternidae* is currently hypothesized to consist of an assemblage of fossil turtles from the Late Jurassic of North America, which were for a short time referred to as Glyptopsidae Marsh, 1890 (see Lyson and Joyce 2011), and from the Late Jurassic to Early Cretaceous of Europe (Pérez-García et al. 2015). The clade serves as evidence of the former connection of Europe with North America during the Jurassic (Hirayama et al. 2000; Pérez-García and Ortega 2011; Joyce et al. 2016a).
Not established phylogenetic definitions—*Pleurosternidae* Cope, 1868b [Lyson and Joyce, 2011].
Comments—Although paracryptodires from the Late Jurassic of Europe were historically grouped under the name Pleurosternidae and those from North America under the name Glyptopsidae, we here follow the consensus that developed over the course of the last four decades that both should be grouped into a single clade named *Pleurosternidae* (e.g., Gaffney and Meylan 1988; Gaffney et al. 1991; Brinkman et al. 2000). This explicit name/clade association was first codified by Lyson and Joyce (2011).

Baenidae Cope, 1873a, converted clade name.
Registration Number—452.
Definition—The largest extinct clade containing *Baena arenosa* Leidy, 1870, but not the pleurosternid *Pleurosternon* (orig. *Platemys*) *bullockii* (Owen, 1842) (Fig. 1a).
Reference Phylogeny—Pérez-García et al. (2015, Fig. 6b).
Composition—*Baenidae* is a highly speciose clade of fossil turtles known from the Early Cretaceous to Paleogene of North America (Gaffney 1972; Joyce and Lyson 2015; Lively 2015).
Not established phylogenetic definitions—*Baenidae* Cope, 1873a [Lyson and Joyce, 2011].
Comments—The association of the name Baenidae with all turtles thought to be more closely related to *Baena arenosa* than *Pleurosternon bullockii* has a long tradition (Hay 1908; Gaffney 1972; Gaffney and Meylan 1988). We, therefore, fix this name/clade association, as was first proposed by Lyson and Joyce (2011).

Macrobaenidae Sukhanov, 1964, converted clade name.
Registration Number—453.
Definition—The largest extinct clade containing *Macrobaena mongolica* Tatarinov 1959, but not the thalassochelydian *Eurysternum wagleri* Meyer, 1839, the sinemydid *Sinemys lens* Wiman, 1930, the xinjiangchelyid *Xinjiangchelys junggarensis* Ye, 1986, the sandownid

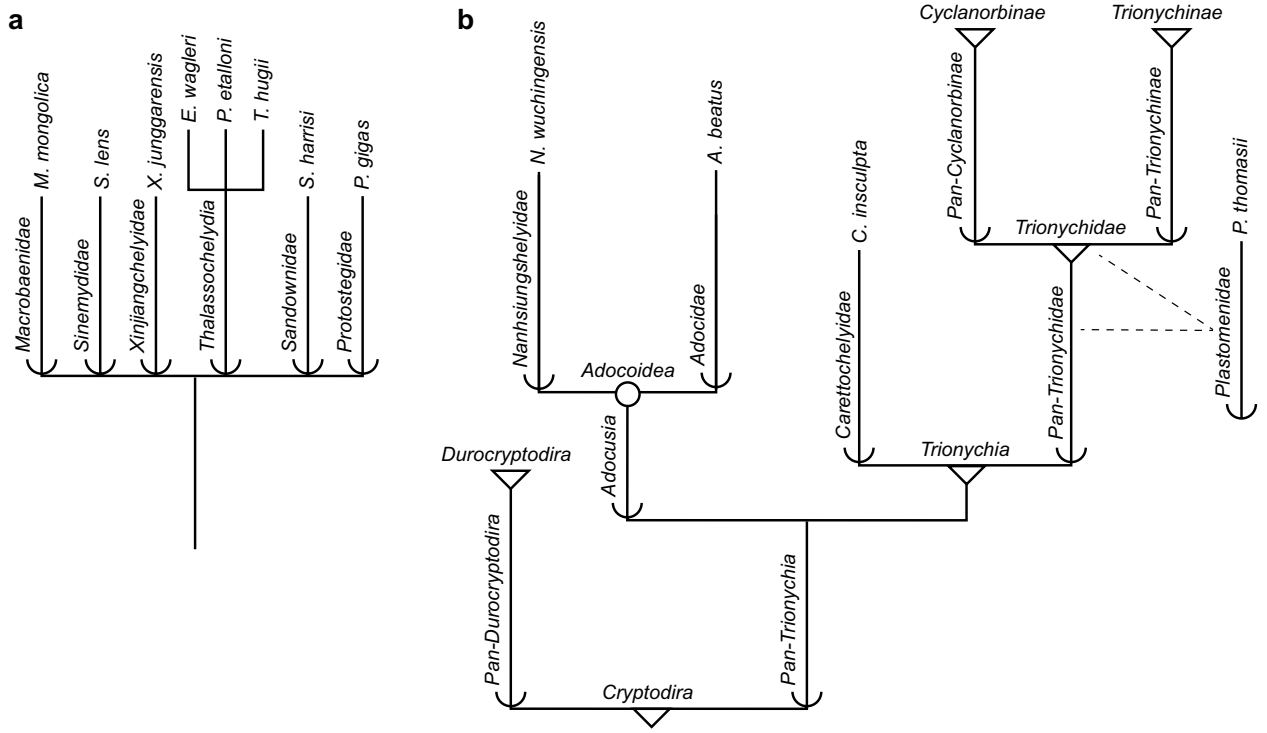

Fig. 3 Simplified diagrams that highlight the proposed name usage of clade names within **a** Mesozoic turtle clades with uncertain affiliations and **b** *Cryptodira*

Sandownia harrisi Meylan et al., 2000, or the protostegid *Protostega gigas* Cope, 1872b (Fig. 3a).
Reference Phylogeny—None (see Comments below).
Composition—Although a broad set of fossil turtles from the Cretaceous to Paleogene of the northern hemisphere have been attributed to *Macrobaenidae* over the course of the last decades (e.g., Rabi et al. 2014; Pérez-García et al. 2020b), *Macrobaena mongolica* has yet to be added to a single, well-sampled phylogenetic analysis. The content of this clade is, therefore, unknown beyond its internal specifier, *M. mongolica*.
Not established phylogenetic definitions—*Macrobaenidae* Sukhanov, 1964 [Rabi et al., 2014].
Diagnostic Apomorphies—Macrobaenids can be distinguished from other turtles by the combination of the following characters: presence of a carotid fenestra (sensu Rabi et al. 2013), formed cervical vertebrae with the formula 1((2((3((4))5))6))7}}8, a cruciform plastron with strap-like epiplastra, and the absence of extragulars (rephrased from Sukhanov 2000).
Comments—The names Macrobaenidae, Sinemydidae, and Xinjiangchelyidae were used historically to refer to poorly diagnosed assemblages of fossil turtles from the Jurassic to Paleogene of Laurasia (Sukhanov 2000; Parham and Hutchison 2003; Brinkman et al. 2010). Rabi et al. (2014) provided phylogenetic definitions for these three names. Although the exact content of these clades still remains unclear, in part because hypotheses regarding the relationships of pan-cryptodires are still evolving, we find these names to remain useful and, therefore, formally defined them herein following the suggestions of Rabi et al. (2014), but modified the definitions to include various Mesozoic marine turtles as additional external specifiers. As noted above, *Macrobaena mongolica* has yet to be included in a phylogenetic analysis. We, therefore, are here not able to provide a reference phylogeny. Instead, we here fulfill the requirements of the PhyloCode for the establishment of names by listing diagnostic synapomorphies.

Sinemydidae Yeh, 1963, converted clade name.
Registration Number—454.
Definition—The largest extinct clade containing *Sinemys lens* Wiman, 1930, but not the thalassochelydian *Eurysternum wagleri* Meyer, 1839, the macrobaenid *Macrobaena mongolica* Tatarinov, 1959, the xinjiangchelyid *Xinjiangchelys junggarensis* Ye, 1986, the sandownid *Sandownia harrisi* Meylan et al., 2000, or the protostegid *Protostega gigas* Cope, 1872b (Fig. 3a).
Reference Phylogeny—Zhou and Rabi (2015, Fig. 6).
Composition—The exact composition of *Sinemydidae* is not resolved. *Sinemydidae* at the very least encompasses a small set of species from the Late Jurassic to Early Cretaceous of China currently referred to *Sinemys* (Tong and Brinkman 2013) although other fossil forms from the Late Jurassic to Early Cretaceous of Asia might be referable to this lineage as well (e.g., Zhou and Rabi 2015).
Not established phylogenetic definitions—*Sinemydidae* Yeh, 1963 [Rabi et al., 2014].
Comments—See *Macrobaenidae* above.

Xinjiangchelyidae Nessov in Kaznyshkin et al., 1990, converted clade name.
Registration Number—455.
Definition—The largest extinct clade containing *Xinjiangchelys junggarensis* Ye, 1986, but not the thalassochelydian *Eurysternum wagleri* Meyer, 1839, the macrobaenid *Macrobaena mongolica* Tatarinov, 1959, the sinemydid *Sinemys lens* Wiman, 1930, the sandownid *Sandownia harrisi* Meylan et al., 2000, or the protostegid *Protostega gigas* Cope, 1872b (Fig. 3a).
Reference Phylogeny—Zhou and Rabi (2015, Fig. 6).
Composition—Although a rich assemblage of fossil turtles from the Middle Jurassic to Early Cretaceous of Asia and the Early Cretaceous of Europe are currently attributed to *Xinjiangchelyidae* (e.g., Hirayama et al. 2000; Rabi et al. 2010; Tong et al. 2012a, b; Pérez-García et al. 2017c), only few have been integrated into global phylogenetic analyses (e.g., Rabi et al. 2014; Joyce et al. 2016a; Evers and Benson 2019). The content of this clade, therefore, remains far from resolved.
Not established phylogenetic definitions—*Xinjiangchelyidae* Nessov in Kaznyshkin et al., 1990 [Rabi et al., 2014].
Comments—See *Macrobaenidae* above.

Thalassochelydia Anquetin et al., 2017, converted clade name.
Registration Number—456.
Definition—The largest extinct clade containing *Eurysternum wagleri* Meyer, 1839, *Plesiochelys* (orig. *Emys*) *etalloni* (Pictet and Humbert, 1857), or *Thalassemys hugii* Rütimeyer, 1873 (Fig. 3a).
Reference Phylogeny—None (see Comments below).
Composition—*Thalassochelydia* is currently hypothesized to consist of an exceptionally diverse assemblage of marine turtles from the Late Jurassic to Early Cretaceous of Europe and South America traditionally referred to the poorly defined, but speciose families Eurysternidae, Plesiochelyidae, and Thalassemydidae (Anquetin et al. 2017; Anquetin and André 2020). The clade is here purposefully defined to allow for the inclusion of other Mesozoic marine turtle clades, in particular *Sandownidae* and *Protostegidae* (see below).
Not established phylogenetic definitions—*Thalassochelydia* Anquetin et al., (2017).

Diagnostic Apomorphies—Thalassochelydians can be diagnosed by the presence of a long posteroventral process of the parietal that forms the posterior margin of the foramen nervi trigemini and that excludes the prootic from that foramen, a ventrally infolding ridge on the posterior surface of the processus articularis of the quadrate, a dorsally high and pointed coronoid process that forms a posteriorly facing notch, and three cervical scutes (Anquetin et al. 2017; Evers and Benson 2019).
Comments—Although currently available phylogenetic hypotheses sample few marine turtles from the Late Jurassic of Europe, we here follow Anquetin et al. (2017) by recognizing the clade *Thalassochelydia* based on apomorphic characters in combination with temporal and biogeographic considerations.
The phylogeny of Mesozoic marine turtles is still far from resolved and it, therefore, has been difficult to develop a stable nomenclatural system for the group (see Anquetin et al. 2017; Evers and Benson 2019). In contrast to Cadena and Parham (2015) and Anquetin et al. (2017), we here restrict the name *Protostegidae* to the more immediate clade associated with *Protostega gigas*, but expand the meaning of the name *Thalassochelydia* to potentially include *Sandownidae* and *Protostegidae*. The first adjustment helps fulfill the demands of the PhyloCode (2020, Art. 9.15) in regards to the conversion of preexisting names, as an extended nomenclatural tradition exists that only associates the immediate relatives of *Protostega gigas* with the name *Protostegidae* (e.g., Hay 1908; Kuhn 1964; Młynarski 1976). As some evidence is available, however, that *Protostega gigas* and *Sandownia harrisi* are perhaps nested near or within *Thalassochelydia* (e.g., Joyce 2007; Evers and Benson 2019; Evers and Joyce 2020), the second adjustment allows maintaining the association of these names with their traditional content and diagnostic characters, regardless of their disputed evolutionary relationships.

Sandownidae Tong and Meylan, 2013, converted clade name.
Registration Number—457.
Definition—The largest extinct clade containing *Sandownia harrisi* Meylan et al., 2000, but not the thalassochelydians *Eurysternum wagleri* Meyer, 1839, *Plesiochelys* (orig. *Emys*) *etalloni* (Pictet and Humbert, 1857), and *Thalassemys hugii* Rütimeyer, 1873, the macrobaenid *Macrobaena mongolica* Tatarinov, 1959, the sinemydid *Sinemys lens* Wiman, 1930, the protostegid *Protostega gigas* Cope, 1872b, or the xinjiangchelyid *Xinjiangchelys junggarensis* Ye, 1986 (Fig. 3a).
Reference Phylogeny—Cadena (2015b, Fig. 8).
Composition—At present, *Sandownidae* is hypothesized to consist of four Cretaceous to Paleocene marine turtles with a circum-Atlantic distribution (Cadena 2015b; Evers and Benson 2019).
Not established phylogenetic definitions—*Sandownidae* Tong and Meylan, 2013 [Evers and Benson, 2019].
Comments—The four currently recognized species of sandownid turtles have only been named over the course of the last two decades but the monophyly of the group was only suggested recently (Tong and Meylan 2013; Cadena 2015b) and the name Sandownidae only defined recently as well (Evers and Benson 2019). As numerous external specifiers are listed, the name is defined in such a way to closely retain the currently understood content of the clade, while allowing Sandowniidae to be nested within other clades, such as *Chelonioidea* or *Thalassochelydia*, but not *Protostegidae*. A similar clade was previously defined as Angolachelonia by Mateus et al. (2009) but also including the Late Jurassic *Solnhofia parsonsi* as an internal specifier. While *S. parsonsi* may very well belong to Sandownidae based on numerous shared apomorphies (Evers and Joyce 2020), the phylogeny of Mateus et al. (2009) is not reproducible (due to the absence of the dataset) and we, therefore, follow Tong and Meylan (2013) and Evers and Benson (2019) with our definition of Sandownidae.

Protostegidae Cope, 1873a, converted clade name.
Registration Number—458.
Definition—The largest extinct clade containing *Protostega gigas* Cope, 1872b, but not the thalassochelydians *Eurysternum wagleri* Meyer, 1839, *Plesiochelys* (orig. *Emys*) *etalloni* (Pictet and Humbert, 1857), and *Thalassemys hugii* Rütimeyer, 1873, the macrobaenid *Macrobaena mongolica* Tatarinov, 1959, the sandownid *Sandownia harrisi* Meylan et al., 2000, the sinemydid *Sinemys lens* Wiman, 1930, or the xinjiangchelyid *Xinjiangchelys junggarensis* Ye, 1986 (Fig. 3a).
Reference Phylogeny—Evers and Benson (2019, Fig. 12).
Composition—*Protostegidae*, as here defined, is currently believed to consist of a speciose clade of Early to Late Cretaceous marine turtles with a worldwide distribution (Kear and Lee 2006; Cadena and Parham 2015; Evers and Benson 2019). The content remains relatively constant, regardless of whether *Protostegidae* is nested just within (Hirayama 1994; Cadena and Parham 2015; Evers and Benson 2019) or just outside (Raselli 2018; Evers et al. 2019; Gentry et al. 2019) of *Chelonioidea*.
Not established phylogenetic definitions—*Protostegidae* Cope, 1873a [Cadena and Parham, 2015].
Comments—See Thalassochelydia above.

Testudines Batsch, 1788 [Joyce et al., 2020c].
Registration Number—274.

Definition—"The smallest crown clade containing the pleurodire *Chelus* (originally *Testudo*) *fimbriatus* (Schneider, 1783), the trionychian *Trionyx* (originally *Testudo*) *triunguis* (Forskål, 1775), the americhelydian *Chelonia* (originally *Testudo*) *mydas* (Linnaeus, 1758), and the testudinoid *Testudo graeca* Linnaeus, 1758" (Joyce et al. 2020c: 1049) (Fig. 1d).
Comment—See Joyce et al. (2020c) for further details.

Pan-Pleurodira Joyce et al., 2004 [Joyce et al., 2020d].
Registration Number—275.
Definition—"The total clade of the crown clade *Pleurodira*" (Joyce et al. 2020d: 1052) (Fig. 1c).
Comments—See Joyce et al. (2020d) for further details.

Platychelyidae Bräm, 1965, converted clade name.
Registration Number—459.
Definition—The largest extinct clade containing *Platychelys oberndorferi* Wagner, 1853 (Fig. 1c).
Reference Phylogeny—López-Conde et al. (2017, Fig. 3).
Composition—The clade *Platychelyidae* is currently hypothesized to include a small assortment of fossil turtles currently classified within the genera *Notoemys* and *Platychelys* from the Late Jurassic to Early Cretaceous of Europe, North America, and South America (López-Conde et al. 2017).
Not established phylogenetic definitions—*Platychelyidae* Bräm, 1965 [Cadena and Joyce, 2015].
Comments—Although the name Platychelyidae was originally coined for the Late Jurassic *Platychelys oberndorferi* only, it has consistently expanded in the last two decades to include fossil forms more closely related to *Platychelys oberndorferi* than any extant turtle (Cadena Rueda and Gaffney 2005; López-Conde et al. 2017). Fixing this name/clade association, as first proposed by Cadena and Joyce (2015), is, therefore, unproblematic.

Dortokidae Lapparent de Broin and Murelaga, 1996, converted clade name.
Registration Number—460.
Definition—The largest extinct clade containing *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996 (Fig. 1c).
Reference Phylogeny—Gaffney et al. (2006, Fig. 292).
Composition—*Dortokidae* is currently hypothesized to consist of three species from the Early Cretaceous to Paleogene of Europe (Pérez-García et al. 2017a).
Not established phylogenetic definitions—*Dortokidae* Lapparent de Broin and Murelaga, 1996 [Cadena and Joyce, 2015].
Comments—Dortokids are poorly understood fossil turtles from the Early Cretaceous to Paleogene of Europe that are thought to represent an independent lineage of stem pleurodires (Lapparent de Broin and Murelaga 1996; Gaffney et al. 2006; Pérez-García et al. 2017a). If future work reveals these turtles to be situated within one of the extant pleurodiran clades, the name will remain accepted, although its utility may be limited. However, if *Dortokidae* is revealed to be synonymous with any of the other extinct clades named here (e.g., Bothremydini), we explicitly stipulate that *Dortokidae* should not receive priority, even if it has a lower registration number.

Pleurodira Cope, 1865 [Joyce et al., 2020e].
Registration Number—276.
Definition—"The smallest crown clade containing the chelid *Chelus* (originally *Testudo*) *fimbriatus* (Schneider, 1783) the pelomedusid *Pelomedusa* (originally *Testudo*) subrufa (Bonnaterre, 1789) and the podocnemid *Podocnemis* (originally *Emys*) *expansa* (Schweigger, 1812)" (Joyce et al. 2020e: 1055) (Figs. 1c, 2a).
Comments—See Joyce et al. (2020e) for further details.

Pan-Chelidae Joyce et al., 2004, converted clade name.
Registration Number—461.
Definition—The total clade of crown clade *Chelidae* (see below) (Fig. 2a).
Reference Phylogeny—de la Fuente et al. (2017, Fig. 11b).
Composition—In addition to the crown group (TTWG 2017), *Pan-Chelidae* is currently hypothesized to include a series of fossil forms from the Cretaceous of Argentina and Australia (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—*Panchelidae* Joyce et al., 2004; *Cheloides* Gaffney et al., 2006 [Sereno and ElShafie, 2013].
Comments—The name Chelidae was traditionally applied by paleontologists to the total group of Chelidae, as all fossil forms with chelid characteristics that were attributed to the group. However, as the name Chelidae is now occupied for the crown group (see below), we here follow Joyce et al. (2004) by applying the name *Pan-Chelidae* (*Panchelidae* of Joyce et al. 2004) to the total group, a convention that is now well established in the paleontological community (e.g., Maniel and de la Fuente 2016).

Chelidae Lindholm, 1929, converted clade name.
Registration Number—462.
Definition—The largest crown clade containing *Chelus* (orig. *Testudo*) *fimbriata* (Schneider, 1783), but not the pelomedusid *Pelomedusa* (orig. *Testudo*) *subrufa* (Bonnaterre, 1789) or the podocnemidid *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812) (Fig. 2a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Chelidae* is currently hypothesized to consist of 58 extant species (TTWG 2017) and a small assortment of fossil species from the Late Cretaceous to

Holocene of South America and Australia (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—*Chelidae* Lindholm, 1929 [Joyce et al., 2004].
Diagnostic Apomorphies—Chelids can most readily be diagnosed from other turtles by the presence of a deep lower temporal emargination, loss of the quadratojugals, and presence of a biconvex fifth cervical (Maniel and de la Fuente 2016).
Comments—The clade *Chelidae* was first recognized in its current taxonomic composition by Baur (1888), Boulenger (1888), and Günther (1888), who utilized the name Chelydidae. The currently used spelling was introduced by Lindholm (1929) and he is, therefore, herein recognized as the nominal author. We here follow Joyce et al. (2004) by explicitly referring the name to the crown clade thereby capturing current usage implicit (e.g. TTWG 2017) and explicit (Maniel and de la Fuente 2016).
There is not much tradition for classifying chelid turtles. In the more recent literature, Gaffney (1977) recognized Pseudemydurinae (i.e., *Pseudemydura umbrina*) as opposed to Chelinae (e.g., all other chelids), but more recent molecular phylogenies reject this arrangement (e.g., Georges et al. 1998; Pereira et al. 2017; Holley et al. 2020). Georges et al. (1998) recognized three subfamilies instead, which they named Chelidinae (i.e., *Chelus fimbriata* + all short-necked South American chelids), Chelodininae (i.e., all Australasian chelids), and Hydromedusinae (i.e., *Hydromedusa* spp.). TTWG (2012) broadly followed Georges et al. (1998), but renamed Chelidinae as Chelinae to follow the etymological conventions of the ICZN (1999) in regards to the formation of family names. TTWG (2017) more recently further subdivided the group into Chelinae, Chelodininae, Hydromedusinae, and Pseudemydurinae. Ferreira et al. (2018), by contrast, suggested the names Chelini and Chelina for two subclades of chelids centered around *Chelus fimbriata*, but the names are inapplicable to all current molecular phylogenies. None of the above-mentioned nomenclatural schemes has been used broadly outside of these publications. We, therefore, conclude that no nomenclatural tradition exists that could be preserved.
Current trees based on molecular data suggest that extant chelids form a South American versus Australasian lineages and that these can further be subdivided into five primary lineages (e.g., Pereira et al. 2017; Holley et al. 2020). As these five primary lineages clearly extend into the Cretaceous, far deeper than those of any other "family" of turtles, we find it plausible that researchers, especially paleontologists, will want to communicate about them in the future and that distinct names are needed. We, therefore, follow TTWG (2017) in assigning the names *Chelinae* and *Chelodininae* to the most inclusive crown clades centered around *Chelus fimbriata* and *Chelodina longicollis*, respectively, and the names *Pan-Chelinae* and *Pan-Chelodininae* to their total clades. As the PhyloCode does not recognize monotypic taxa, such as *Pseudemydura umbrina*, to represent crown groups, we follow the protocol we implemented herein for other monotypic taxa and assign the name *Pseudemydurinae* to the "total clade" of *Pseudemydura umbrina*. Similarly, although the two extant species of *Hydromedusa* do form a crown, we nevertheless refer the name *Hydromesudinae* to the total clade, as referring it to the crown would create a redundancy with the genus. As this arrangement leaves a speciose clade of Australasian chelids unnamed (Pereira et al. 2017; Holley et al. 2020), we create the new names *Emydurinae* and *Pan-Emydurinae* to encompass this group.
The five clades discussed above form the two primary clades of chelids, which are currently restricted to South America versus Australasia. Instead of forming novel names by adding new endings to existing names, we here introduce two etymologically new names that allude to the biogeographic distribution of these two clades: *Australochelida* for the crown clade of Australasian chelids and *Hesperochelida* for the crown clade of South American chelids. Their respective total clades are *Pan-Australochelida* and *Pan-Hesperochelida*.

Pan-Hesperochelida, new clade name.
Registration Number—463.
Definition—The total clade of crown clade *Hesperochelida* (see below) (Fig. 2a).
Reference Phylogeny—Holley et al. (2020, Fig. 2).
Composition—No fossil taxon is currently hypothesized to populate the stem lineage of crown *Hesperochelida* (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Hesperochelida, new clade name.
Registration Number—464.
Definition—The largest crown clade containing *Chelus* (orig. *Testudo*) *fimbriata* (Schneider 1783) and *Hydromedusa maximiliani* (Mikan 1825), but not *Chelodina* (orig. *Testudo*) *longicollis* (Shaw 1794), *Emydura* (orig. *Chelys*) *macquarii* (Gray 1831c), or *Pseudemydura umbrina* Siebenrock 1901 (Fig. 2a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Etymology—A contraction of ἑσπέριος, Greek for western, and chelida, a variation of Chelidae that does not imply a rank.

Composition—*Hesperochelida*, by definition, consists of *Pan-Chelinae* and *Hydromedusinae* (see below).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Pan-Chelinae, new clade name.
Registration Number—465.
Definition—The total clade of crown clade *Chelinae* (see below) (Fig. 2a).
Reference Phylogeny—Holley et al. (2020, Fig. 2).
Composition—No fossil taxon is currently hypothesized to represent the stem lineage of crown *Chelinae* (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Chelinae Chkhikvadze, 1970, converted clade name.
Registration Number—466.
Definition—The largest crown clade containing *Chelus* (orig. *Testudo*) *fimbriata* (Schneider, 1783), but not *Chelodina* (orig. *Testudo*) *longicollis* (Shaw, 1794), *Emydura* (orig. *Chelys*) *macquarii* (Gray, 1831c), *Hydromedusa maximiliani* (Mikan, 1825), or *Pseudemydura umbrina* Siebenrock, 1901 (Fig. 2a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Chelinae* is currently hypothesized to consist of 20 extant species (TTWG 2017) and a small assortment of extinct taxa from the Neogene of South America (Maniel and de la Fuente 2016).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Hydromedusinae Georges et al., 1998, converted clade name.
Registration Number—467.
Definition—The largest clade containing *Hydromedusa maximiliani* (Mikan, 1825), but not *Chelus* (orig. *Testudo*) *fimbriata* (Schneider, 1783), *Chelodina* (orig. *Testudo*) *longicollis* (Shaw, 1794), *Emydura* (orig. *Chelys*) *macquarii* (Gray, 1831c), or *Pseudemydura umbrina* Siebenrock, 1901 (Fig. 2a).
Reference Phylogeny—Holley et al. (2020, Fig. 2).
Composition—In addition to the crown group *Hydromedusa*, which consists of two species (TTWG 2017), *Hydromedusinae* is currently hypothesized to include a small sample of extinct taxa from the Late Cretaceous and Paleogene of Argentina referred to *Yaminuechelys* and *Hydromedusa* (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Pan-Australochelida, new clade name.
Registration Number—468.
Definition—The total clade of crown clade *Australochelida* (see below) (Fig. 2a).
Reference Phylogeny—Holley et al. (2020, Fig. 2).
Composition—No fossil species are currently hypothesized to represent the stem lineage of *Australochelida* (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Australochelida, new clade name.
Registration Number—469.
Definition—The largest crown clade containing *Chelodina* (orig. *Testudo*) *longicollis* (Shaw, 1794), *Emydura* (orig. *Chelys*) *macquarii* (Gray, 1831c), and *Pseudemydura umbrina* Siebenrock, 1901, but not *Chelus* (orig. *Testudo*) *fimbriata* (Schneider, 1783) or *Hydromedusa maximiliani* (Mikan, 1825) (Fig. 2a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Etymology—A contraction of *australis*, Latin for southern, and chelida, a variation of Chelidae that does not imply a rank, formed in allusion to the southern continent Australia.
Composition—*Australochelida*, by definition, consists of *Pan-Chelodininae* and *Pseudemydurinae* (see below).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Pan-Chelodininae, new clade name.
Registration Number—470.
Definition—The total clade of crown clade *Chelodininae* (see below) (Fig. 2a).
Reference Phylogeny—Holley et al. (2020, Fig. 2).
Composition—In addition to crown *Chelodininae* (see below), *Pan-Chelodininae* is currently hypothesized to include a small assortment of extinct taxa from the Cenozoic of Australia (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Chelodininae Georges et al., 1998, converted clade name.
Registration Number—471.
Definition—The largest crown clade containing *Chelodina* (orig. *Testudo*) *longicollis* (Shaw, 1794), but not *Chelus* (orig. *Testudo*) *fimbriata* (Schneider, 1783), *Emydura* (orig. *Chelys*) *macquarii* (Gray, 1831c), *Hydromedusa maximiliani* (Mikan, 1825), or *Pseudemydura umbrina* Siebenrock, 1901 (Fig. 2a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—The Ausalasian *Chelodininae* is currently hypothesized to consist of 15 extant species either classified as *Chelodina*, or as *Chelodina*, *Macrochelodina*, and *Macrodiremys* (Maniel and de la Fuente 2016; TTWG

2017; Holley et al. 2020). Only a single fossil species, *Chelodina insculpta* from the Plio/Pleistocene of Australia, is currently believed to be situated within this clade (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Pan-Emydurinae, new clade name.
Registration Number—472.
Definition—The total clade of crown clade *Emydurinae* (see below) (Fig. 2a).
Reference Phylogeny—Holley et al. (2020, Fig. 2).
Composition—No fossils are currently known that might populate the stem lineage of *Emydurinae* (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Emydurinae, new clade name.
Registration Number—473.
Definition—The largest crown clade containing *Emydura* (orig. *Chelys*) *macquarii* (Gray, 1831c), but not *Chelodina* (orig. *Testudo*) *longicollis* (Shaw, 1794), *Chelus* (orig. *Testudo*) *fimbriata* (Schneider, 1783), *Hydromedusa maximiliani* (Mikan, 1825), or *Pseudemydura umbrina* Siebenrock, 1901 (Fig. 2a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Emydurinae* is currently hypothesized to consist of 20 extant species (TTWG 2017), but only a single fossil species, *Birlimar gaffneyi*, from the Miocene of Australia (Maniel and de la Fuente 2016; Holley et al. 2020).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Pseudemydurinae Gaffney, 1977, converted clade name.
Registration Number—474.
Definition—The largest clade containing *Pseudemydura umbrina* Siebenrock, 1901, but not *Chelodina* (orig. *Testudo*) *longicollis* (Shaw, 1794), *Chelus* (orig. *Testudo*) *fimbriata* (Schneider, 1783), *Emydura* (orig. *Chelys*) *macquarii* (Gray, 1831c), or *Hydromedusa maximiliani* (Mikan, 1825) (Fig. 2a).
Reference Phylogeny—Holley et al. (2020, Fig. 2).
Composition—*Pseudemydurinae* is currently hypothesized to consist of a single extant species, *Pseudemydura umbrina* (TTWG 2017), and unnamed fossil material from the Miocene of Australia (Gaffney et al., 1989).
Not established phylogenetic definitions—None.
Comments—See *Chelidae* above.

Pan-Pelomedusoides Joyce et al., 2004, converted clade name.
Registration Number—475.
Definition—The total clade of crown clade *Pelomedusoides* (see below) (Fig. 2a, b).
Reference Phylogeny—Ferreira et al. (2018, Fig. 1).
Composition—The hypothesized composition of *Pan-Pelomedusoides* typically overlaps with that of *Pelomedusoides* (e.g., Gaffney et al. 2006; Cadena 2015a), but a small number of Early Cretaceous fossils were recovered just outside the crown in a recent phylogeny (Ferreira et al. 2018).
Not established phylogenetic definitions—*Panpelomedusoides* Joyce et al., 2004; *Cheloides* Broin, 1988 [Sereno and ElShafie, 2013].
Comments—See *Pelomedusoides* below.

Pelomedusoides Broin, 1988, converted clade name.
Registration Number—476.
Definition—The largest crown clade containing *Pelomedusa* (orig. *Testudo*) *subrufa* (Bonnaterre, 1789) and *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812), but not the chelid *Chelus* (orig. *Testudo*) *fimbriata* (Schneider, 1783) (Fig. 2a, b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—Although *Pelomedusoides* is currently hypothesized to consist of just 27 extant species restricted to the southern hemisphere (TTWG 2017), the clade was extremely diverse and globally distributed throughout the Cretaceous and Paleogene (e.g., Gaffney et al. 2006; 2011; Cadena 2015a; Ferreira et al. 2018).
Not established phylogenetic definitions—*Pelomedusoides* Broin, 1988 [Joyce et al., 2004]; *Podocnemidoidea* Broin, 1988 [Sereno and ElShafie, 2013].
Diagnostic Apomorphies—*Pelomedusoides* can be diagnosed by a midline contact of the prefrontals, absence of nasals, splenials, and a parietal–squamosal contact, absence of a cervical scute, and presence of a biconvex second cervical vertebra (Gaffney et al. 2006).
Comments—Extant pelomedusoids clearly consists of two groups (TTWG 2017), pelomedusids ("African mud turtles;" *Pelomedusa* spp. and *Pelusios* spp.) and podocnemidids ("South American and Malagasy river turtles;" *Erymnochelys madagascariensis*, *Peltocephalus dumerilianus*, and *Podocnemis* spp.). Cope (1868a) referred the name Pelomedusidae to this grouping, but Boulenger (1888) and Günther (1888) soon after restricted usage of that name to the African mud turtles only. Pelomedusidae was used in both ways for much of the twentieth century, until Broin (1988) coined the name Pelomedusoides for the more inclusive group (including podocnemidids) and restricted Pelomedusidae to the less inclusive group. This usage now predominates in the literature (e.g., Gaffney et al. 2006, 2011; TTWG 2017). We, therefore, here follow Joyce et al. (2004) by referring these names to

the two appropriate crown groups and using names with pan- prefixes for their total groups.

Pan-Pelomedusidae Joyce et al., 2004, converted clade name.
Registration Number—477.
Definition—The total clade of crown clade *Pelomedusidae* (see below) (Fig. 2b).
Reference Phylogeny—Ferreira et al. (2018, Fig. 1).
Composition—The fossil record of African turtles is still poorly described and no fossils are, therefore, known that can unambiguously be referred to the stem lineage of *Pelomedusidae* (Cadena 2015a; Ferreira et al. 2018).
Not established phylogenetic definitions—*Panpelomedusidae* Joyce et al., 2004; *Pelomedusidae* Cope, 1868a [Sereno and ElShafie, 2013].
Comments—See *Pelomedusoides* above.

Pelomedusidae Cope, 1868a, converted clade name.
Registration Number—478.
Definition—The largest crown clade containing *Pelomedusa* (orig. *Testudo*) *subrufa* (Bonnaterre, 1789), but not the podocnemidid *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812) (Fig. 2b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—At present, *Pelomedusidae* is thought to include 27 extant species (TTWG 2017) and a small number of fossil species restricted to the Neogene (Joyce et al. 2013).
Not established phylogenetic definitions—*Pelomedusidae* Cope, 1868a [Joyce et al., 2004].
Diagnostic Apomorphies—Pelomedusids can be diagnosed relative to other pleurodires by the absence of a vomer, the formation of the occipital condyle by the exoccipitals only, lack of a palatine canal, and an incomplete neural series (Gaffney et al. 2006).
Comments—See *Pelomedusoides* above.

Pan-Podocnemididae Joyce et al., 2004, converted clade name.
Registration Number—479.
Definition—The total clade of crown clade *Podocnemididae* (see below) (Fig. 2b).
Reference Phylogeny—Ferreira et al. (2018, Fig. 1).
Composition—In addition to crown *Podocnemididae*, *Pan-Podocnemididae* is comprised of a rich assortment of extinct taxa from the Cretaceous to Cenozoic globally, including the particularly speciose clade *Bothremydidae* (Gaffney et al. 2006, 2011; Ferreira et al. 2018).
Not established phylogenetic definitions—*Panpodocnemidae* Joyce et al., 2004; *Podocnemidinura* Gaffney et al., 2006 [Sereno and ElShafie, 2013].
Comments—See *Podocnemididae* below.

Bothremydidae Baur, 1891a, converted clade name.
Registration Number—480.
Definition—The largest extinct clade containing *Bothremys cookii* Leidy, 1865 (Fig. 2b).
Reference Phylogeny—Ferreira et al. (2018, Fig. 1).
Composition—*Bothremydidae* is a diverse clade of fossil turtles that persisted from the Early Cretaceous to the Paleogene with a nearly worldwide distribution (e.g., Gaffney et al. 2006; Romano et al. 2014). The most important clades are *Bothremydini*, *Cearachelyini*, *Kurmademydini*, and *Taphrosphyini* (see below).
Not established phylogenetic definitions—*Bothremydidae* Baur, 1891a [Joyce et al., 2016c].
Comments—One of the more surprising realizations of the last 25 years has been that the stem lineage of *Podocnemididae* is populated by an extremely rich assemblage of turtles that includes a large, monophyletic clade with an almost global distribution. Gaffney et al. (2006) proposed a nomenclatural scheme that united the tribes Bothremydini, Cearachelyini, Kurmademydini, and Taphrosphyini in the family Bothremydidae. Joyce et al. (2016c) more recently proposed fixing the meaning of these names through the use of maximum-clade definitions, as this captured how these names were used and modified ever since they had been proposed by Gaffney et al. (2006). As there are no alternative nomenclatural schemes, we permanently fix all names as suggested by Joyce et al. (2016c).

Bothremydini Gaffney et al., 2006, converted clade name.
Registration Number—481.
Definition—The largest extinct clade containing *Bothremys cookii* Leidy, 1865, but not *Cearachelys placidoi* Gaffney et al., 2001a, *Kurmademys kallamedensis* Gaffney et al., 2001b, or *Taphrosphys* (orig. *Platemys*) *sulcatus* (Leidy, 1856b) (Fig. 2b).
Reference Phylogeny—Gaffney et al. (2006, Fig. 1).
Composition—*Bothremydini* is a diverse clade of fossil turtles that persisted from the Late Cretaceous to Paleogene with distribution across Africa, Arabia, Europe, and North America (e.g., Gaffney et al. 2006; Ferreira et al. 2018).
Not established phylogenetic definitions—*Bothremydini* Gaffney et al., 2006 [Joyce et al., 2016c].
Comments—See *Bothremydidae* above.

Cearachelyini Gaffney et al., 2006, converted clade name.
Registration Number—482.
Definition—The largest extinct clade containing *Cearachelys placidoi* Gaffney et al., 2001a, but not *Bothremys cookii* Leidy, 1865, *Kurmademys kallamedensis* Gaffney

et al., 2001b, or *Taphrosphys* (orig. *Platemys*) *sulcatus* (Leidy, 1856b) (Fig. 2b).
Reference Phylogeny—Gaffney et al. (2006, Fig. 1).
Composition—*Cearachelyini* is currently hypothesized to include only a small number of fossil turtles from the late Early Cretaceous to early Late Cretaceous of Africa and South America (Gaffney et al. 2006).
Not established phylogenetic definitions—*Cearachelyini* Gaffney et al., 2006 [Joyce et al., 2016c].
Comments—See *Bothremydidae* above.

Kurmademydini Gaffney et al., 2006, converted clade name.
Registration Number—483.
Definition—The largest extinct clade containing *Kurmademys kallamedensis* Gaffney et al., 2001b, but not *Bothremys cookii* Leidy, 1865, *Cearachelys placidoi* Gaffney et al., 2001a, or *Taphrosphys* (orig. *Platemys*) *sulcatus* (Leidy, 1856b) (Fig. 2b).
Reference Phylogeny—Gaffney et al. (2006, Fig. 1).
Composition—*Kurmademydini* is a small clade of turtles currently known only from the Late Cretaceous of India (Gaffney et al. 2006).
Not established phylogenetic definitions—*Kurmademydini* Gaffney et al., 2006 [Joyce et al., 2016c].
Comments—See *Bothremydidae* above.

Taphrosphyini Gaffney et al., 2006, converted clade name.
Registration Number—484.
Definition—The largest extinct clade containing *Taphrosphys* (orig. *Platemys*) *sulcatus* (Leidy, 1856b), but not *Bothremys cookii* Leidy, 1865, *Cearachelys placidoi* Gaffney et al., 2001a, or *Kurmademys kallamedensis* Gaffney et al., 2001b (Fig. 2b).
Reference Phylogeny—Gaffney et al. (2006, Fig. 1).
Composition—*Taphrosphyini* is hypothesized to be a diverse clade of turtles from the Late Cretaceous to Paleogene with a wide geographic distribution across Africa, Asia, Europe, and North America and South America (Gaffney et al. 2006; Pérez-García 2019).
Not established phylogenetic definitions—*Taphrosphyini* Gaffney et al., 2006 [Joyce et al., 2016c].
Comments—See *Bothremydidae* above.

Podocnemididae Cope, 1868b, converted clade name.
Registration Number—485.
Definition—The largest crown clade containing *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812), but not the pelomedusid *Pelomedusa* (orig. *Testudo*) *subrufa* (Bonnaterre, 1789) (Fig. 2b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—In addition to eight extant species (TTWG 2017), *Podocnemididae* is currently believed to include a rich assemblage of fossil forms from the Cenozoic of Africa, Europe, India, Madagascar, North and South America, and the West Indies (Gaffney et al. 2011; Pérez-García et al. 2017b).
Not established phylogenetic definitions—*Podocnemidae* Reinach, 1903 [Joyce et al., 2004].
Diagnostic Apomorphies—Podocnemidids can be differentiated from other pleurodires, among others, by the presence of expanded triturating surfaces with accessory ridges and a contribution from the palatine, widely spaced basioccipital tubercles, a cavum pterygoidei that is formed by basisphenoid, pterygoid, prootic, and quadrate and underlain by the pterygoid and basisphenoid, and saddle-shaped cervical vertebrae (Gaffney et al. 2011).
Comments—Over the course of the last century, the names Podocnemidae and Podocnemididae were either used to group all non-chelid pleurodires or South American and Malagasy river turtles and their fossil relatives only. Following the introduction of the term Pelomedusoides for the more inclusive group by Broin (1988), the less inclusive application of the name became more pervasive, although both Podocnemidae and Podocnemididae were still used in parallel. In contrast to Joyce et al. (2004) who referred *Podocnemidae* to the crown clade and *Pan-Podocnemidae* to the total clade, because *Podocnemidae* was more commonly used, we here refer *Podocnemididae* and *Pan-Podocnemididae* to these clades, because Podocnemididae pervades the more recent literature.

Podocnemidinae Zangerl, 1947, converted clade name.
Registration Number—486.
Definition—The largest clade containing *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812), but not *Erymnochelys* (orig. *Dumerilia*) *madagascariensis* (Grandidier, 1867) or *Peltocephalus* (orig. *Emys*) *dumerilianus* (Schweigger, 1812) (Fig. 2b).
Reference Phylogeny—Cadena et al. (2020, Fig. 5a).
Composition—In addition to fossil and recent species referable to *Podocnemis*, *Podocnemidinae* is currently hypothesized to include *Cerrejonemys wayuunaiki* from the Paleocene of Colombia (Cadena et al. 2010, 2020).
Not established phylogenetic definitions—None.
Comments—As currently understood, crown Podocnemididae includes a diverse assemblage of fossil turtles, which often are thought to group into clades without modern representatives (e.g., Gaffney et al. 2011; Ferreira et al. 2018). Previous taxonomies mostly focused on naming extinct clades, often with cacophonous results (e.g., Erymnochelydand, Peiropemydodda, or Stereogenyita of Gaffney et al. 2011). As we find it useful to communicate the placement of fossils by reference to their most recent relatives and as the three currently recognized

recent podocnemidid clades, currently classified as genera, are believed to have stem lineages that extend well into the Cretaceous (e.g., Vargas-Ramírez et al. 2008; Pereira et al. 2017), we here provide formalized names for the total clades associated with these three genera to aid communication in the future. As two of the three extant groups of podocnemidids form monotypic assemblages (e.g., *Erymnochelys madagascariensis* and *Peltocephalus dumerilianus*) and as species of the third are currently grouped into a single genus (i.e., *Podocnemis*), we assign subfamily names to all three, similar to the primary subclades of *Chelidae* (see *Chelidae* above).

Erymnochelyinae Broin, 1988, converted clade name.
Registration Number—487.
Definition—The largest clade containing *Erymnochelys* (orig. *Dumerilia*) *madagascariensis* (Grandidier, 1867), but not *Peltocephalus* (orig. *Emys*) *dumerilianus* (Schweigger, 1812) or *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812) (Fig. 2b).
Reference Phylogeny—Cadena et al. (2020, Fig. 5a).
Composition—The extant South America turtle *Peltocephalus dumerilianus* had long been considered to be the imminent sister to the Malagasy *Erymnochelys madagascariensis* in cladistic analyses (e.g., Gaffney et al. 2011), which either suggests enormous ghost lineages, despite the richness of the podocnemidid fossil record, or implausible biogeographic scenarios. The more recent analyses of Ferreira et al. (2018) and Cadena et al. (2020), however, suggests that a diverse assortment of extinct taxa from the Cenozoic of Africa, Europe, India, and South America are referable to the stem lineages of these extant species instead. Although many details are likely to emerge in the coming years, these hypotheses are much consistent with the fossil record and highlight the need for naming the clades *Erymnochelyinae* and *Peltocephalinae* to aid communication.
Not established phylogenetic definitions—None.
Comments—See *Podocnemidinae* above.

Peltocephalinae new clade name.
Registration Number—488.
Definition—The largest clade containing *Peltocephalus* (orig. *Emys*) *dumerilianus* (Schweigger, 1812), but not *Erymnochelys* (orig. *Dumerilia*) *madagascariensis* (Grandidier, 1867) or *Podocnemis* (orig. *Emys*) *expansa* (Schweigger, 1812) (Fig. 2b).
Reference Phylogeny—Cadena et al. (2020, Fig. 5a).
Composition—See *Erymnochelyinae* above.
Not established phylogenetic definitions—None.
Comments—See *Podocnemidinae* above.

Pan-Cryptodira Joyce et al., 2004 [Joyce et al., 2020f].
Registration Number—277.
Definition—"The total clade of crown clade *Cryptodira*" (Joyce et al. 2020f: 1058) (Figs. 1d, 3b).
Comments—See Joyce et al. (2020f) for further details.

Cryptodira Cope, 1868b [Joyce et al., 2020g].
Registration Number—278.
Definition—"The smallest crown clade containing the testudinoid *Testudo graeca* Linnaeus, 1758, the chelonioid *Chelonia* (originally *Testudo*) *mydas* (Linnaeus, 1758), the trionychian *Trionyx* (originally *Testudo*) *triunguis* (Forskål, 1775), the kinosternoid *Kinosternon* (originally *Testudo*) *scorpioides* (Linnaeus, 1766), and the chelydrid *Chelydra* (originally *Testudo*) *serpentina* (Linnaeus, 1758)" (Joyce et al., 2020g: 1061) (Figs. 1d, 3b).
Comments—See Joyce et al. (2020g) for further details.

Pan-Trionychia Joyce et al., 2004, converted clade name.
Registration Number—489.
Definition—The total clade of crown clade *Trionychia* (see below) (Fig. 3b).
Reference Phylogeny—Joyce et al. (2016a, Fig. 8).
Composition—Although relationships are still far from resolved, most recent phylogenies agree that *Pan-Trionychia* includes the clade *Adocusia* in addition to *Trionychia* (e.g., Danilov and Parham 2006; Zhou and Rabi 2015; Joyce et al. 2016a).
Not established phylogenetic definitions—*Pantrionychia* Joyce et al., 2004.
Comments—Fossils of the two primary clades of *Adocusia*, *Adocidae* and *Nanhsiungchelyidae*, were historically classified as dermatemydids (e.g., Hay 1908; Młynarski 1976), but more recent analyses conclude that they are sister to trionychians (e.g., Meylan and Gaffney 1989; Joyce 2007). The most compelling character evidence is perhaps the presence of opisthocoelous cervical vertebrae in both adocusians and trionychians (Williams 1950; Meylan and Gaffney 1989; Brinkman and Peng 1996), but also the entry of the internal carotid from the ventral side of the skull. For the choice of name, please see *Trionychia* below.

Adocusia Danilov and Parham, 2006, converted clade name.
Registration Number—490.
Definition—The largest extinct clade containing *Adocus* (orig. *Emys*) *beatus* (Leidy, 1865) and *Nanhsiungchelys wuchingensis* Yeh, 1966 (Fig. 3b).
Reference Phylogeny—Danilov and Syromyatnikova (2009, Fig. 3).
Composition—*Adocusia* is currently hypothesized to be a diverse clade of fossil turtles that persisted from the Late Jurassic to Paleogene of Asia and North America (Danilov and Syromyatnikova 2009; Danilov et al. 2013).

The two primary subclades are *Adocidae* and *Nanhsiungchelyidae* (see below).
Not established phylogenetic definitions—*Adocusia* Danilov and Parham, 2006.
Comments—Although adocids and nanhsiungchelyids were historically grouped with an eclectic assortment of other turtles into the wastebasket taxon Dermatemydidae (e.g., Hay 1908; Młynarski 1976), an exclusive sister group relationship was only realized more recently (Brinkman and Peng 1996). As there is no nomenclatural tradition for naming this clade, we herein follow Danilov and Parham (2006) by applying the name Adocusia to the most inclusive clade that includes adocids and nanhsiungchelyids, but no species of extant turtle.

Adocoidea Chkhikvadze, 1975, converted clade name.
Registration Number—491.
Definition—The smallest extinct clade containing *Adocus* (orig. *Emys*) *beatus* (Leidy, 1865) and *Nanhsiungchelys wuchingensis* Yeh, 1966 (Fig. 3b).
Reference Phylogeny—Danilov and Syromyatnikova (2009, Fig. 3).
Composition—*Adocoidea*, by definition, consists of the speciose clades *Adocidae* and *Nanhsiungchelyidae* (see below).
Not established phylogenetic definitions—None.
Diagnostic Apomorphies—Adocoids are currently best differentiated from other pan-trionychians by the presence of the neural formula $6>4<6<6<6<6$ (Joyce 2007; Danilov and Syromyatnikova 2009).
Comments—Although current phylogenetic hypotheses are not sampled sufficiently to rigorously highlight differences, the most inclusive and the least inclusive clades that contain *Adocus beatus* and *Nanhsiungchelys wuchingensis* are not the same and, therefore, demand two different names. As the name *Adocusia* is preoccupied for the more inclusive clade, we here designate the name *Adocoidea* for the less inclusive clade. This name is especially appropriate, as it has been consistently applied to the less inclusive clade since it was introduced by Danilov and Syromyatnikova (2009) for this clade and because the ending is similar to that of *Baenoidea*, which serves a similar purpose within the clade *Paracryptodira*. To our knowledge, no name has previously been defined phylogenetically for this clade.

Adocidae Cope, 1869a, converted clade name.
Registration Number—492.
Definition—The largest extinct clade containing *Adocus* (orig. *Emys*) *beatus* (Leidy, 1865), but not *Nanhsiungchelys wuchingensis* Yeh, 1966 (Fig. 3b).
Reference Phylogeny—Danilov and Syromyatnikova (2009, Fig. 3).
Composition—*Adocidae* is currently hypothesized to consist of a rich assemblage of turtles that inhabited aquatic environments from the Late Jurassic to Paleogene of Asia and the Late Cretaceous to Paleocene of North America (Danilov and Syromyatnikova 2009; Danilov et al. 2013).
Not established phylogenetic definitions—*Adocidae* Cope, 1869a [Joyce and Norell, 2005].
Comments—Fossil turtles were traditionally attributed to "Adocidae" or "Adocinae" if they were similar with *Adocus beatus* (e.g., Hay 1908; Młynarski 1976), but the name has more recently been applied to all turtles that are more closely related to *Adocus beatus* than *Nanhsiungchelys wuchingensis* (Danilov and Syromyatnikova 2009). We herein fix this name/clade association. We are unaware of any previously existing phylogenetic definitions for the name Adocidae or the clade named herein.

Nanhsiungchelyidae Yeh, 1966, converted clade name.
Registration Number—493.
Definition—The largest extinct clade containing *Nanhsiungchelys wuchingensis* Yeh, 1966, but not *Adocus* (orig. *Emys*) *beatus* (Leidy, 1865) (Fig. 3b).
Reference Phylogeny—Danilov and Syromyatnikova (2009, Fig. 3).
Composition—*Nanhsiungchelyidae* is currently hypothesized to consist of a morphologically heterogeneous assemblage of turtles that inhabited terrestrial environments throughout the late Cretaceous of Asia and North America (Danilov and Syromyatnikova 2009).
Not established phylogenetic definitions—*Nanhsiungchelyidae* Yeh, 1966 [Joyce and Norell, 2005].
Comments—The majority of nanhsiungchelyids were historically referred to the wastebasket taxon Dermatemydidae (Hay 1908; Młynarski 1976), but more recent analyses (Meylan and Gaffney 1989) revealed close relationships with the bizarre Late Cretaceous fossil turtle *Nanhsiungchelys wuchingensis* Yeh, 1966. Following the realization that adocids are the sister of nanhsiungchelyids (Brinkman and Peng 1996), Joyce and Norell (2005) defined the name Nanhsiungchelyidae as referring to the clade of all turtles more closely related to *Nanhsiungchelys wuchingensis* than *Adocus beatus* or any extant organism. We follow this name/clade association herein as well.

Trionychia Baur, 1891b, converted clade name.
Registration Number—494.
Definition—The largest crown clade containing *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) and *Carettochelys insculpta* Ramsay, 1887, but not the chelonioid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), the testudinoid *Testudo graeca* Linnaeus, 1758, the chelydrid

Chelydra (orig. *Testudo*) *serpentina* (Linnaeus, 1758), or the kinosternoid *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766) (Fig. 3b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Trionychia*, by definition, consists of the speciose clades *Pan-Trionychidae* and *Carettochelyidae* (see below).
Not established phylogenetic definitions—*Trionychia* Baur, 1891b [Joyce et al., 2004].
Diagnostic Apomorphies—Fossil and recent trionychians are diagnosed by a long list of osteological characteristics, including fused premaxillae, presence of an intermaxillary foramen, absence of a prefrontal/palatine contact, presence of a basisphenoid/palatine contact, absence of a well-defined external pterygoid process, and the absence of plastral scutes (Meylan 1987; Joyce 2007). The extant representatives of the clade can furthermore be diagnosed externally by the presence of a fleshy proboscis (Meylan 1987).
Comments—Soon after the discovery of the extant *Carettochelys insculpta* by Ramsay (1887), Baur (1891b) established that this species is the closest living relative of trionychids. Over the course of the following century, two names were commonly used to unite these lineages: Trionychia and Trionychoidea. However, as early cladistic work utilized the name Trionychoidea for a more inclusive clade consisting of carettochelyids, dermatemydids, kinosternids, and trionychids (Gaffney 1975), use of Trionychia became more prevalent for the less inclusive clade in the subsequent years. We, therefore, here fix this name/clade association, as already suggested by Joyce et al. (2004). Joyce et al. (2004) assigned nominal authorship of Trionychia to Hummel (1929), but we here note the earlier usage of this term by Baur (1891b).

Carettochelyidae Gill, 1889, converted clade name.
Registration Number—495.
Definition—The largest clade containing *Carettochelys insculpta* Ramsay, 1887, but not the trionychid *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) (Fig. 3b).
Reference Phylogeny—Joyce (2007, Fig. 18).
Composition—The clade *Carettochelyidae* is currently believed to have originated in Asia during the Early Cretaceous, to have expanded across the northern hemisphere, including India, during the Paleogene, and to then have moved southwards to Africa and Australia during the Neogene (Joyce 2014). At present, only a single species survives in Australia and the Island of New Guinea (TTWG 2017).
Not established phylogenetic definitions—*Pancarettochelys* Joyce et al., 2004.
Comments—In contrast to Joyce et al. (2004) and Joyce (2014), we here do not assign the name Pan-Carettochelys to the total clade of the extant *Carettochelys insculpta*, but rather the traditional family name *Carettochelyidae*. Our rationale is explained in detail above (see "Methods and discussion" above).

Pan-Trionychidae Joyce et al., 2004, converted clade name.
Registration Number—496.
Definition—The total clade of crown clade *Trionychidae* (see below) (Fig. 3b).
Reference Phylogeny—Brinkman et al. (2017, Fig. 5).
Composition—The phylogeny of pan-trionychid turtles has been difficult to resolve, as the earliest representatives of the group resemble extant trionychines by having a highly reduced shell (e.g., Li et al. 2015). All fossils included in explicit phylogenetic analyses were, therefore, retrieved within the crown (e.g., Joyce and Lyson 2010; Vitek 2012; Danilov et al. 2014) and the group lacked a well-supported stem lineage. New fossil material combined with new characters and methods recently suggested that the earliest known pan-trionychids from the late Early Cretaceous of Asia may represent the stem lineage of the group, which implies that the trionychine bauplan is plesiomorphic for the group (Brinkman et al. 2017; Vitek et al. 2018). All remaining fossils, however, are still attributable to crown *Trionychidae* (see below).
Not established phylogenetic definitions—*Pantrionychidae* Joyce et al. 2004.
Comments—See *Trionychidae* below.

Trionychidae Bell, 1828, converted clade name.
Registration Number—497.
Definition—The largest crown clade containing *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775), but not the carettochelyid *Carettochelys insculpta* Ramsay, 1887 (Fig. 3b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Trionychidae* is currently thought to include 32 extant species (TTWG 2017) and a rich, near-global fossil record that spans from Late Cretaceous to Holocene (Vitek and Joyce 2015; Georgalis and Joyce 2017; Brinkman et al. 2017).
Not established phylogenetic definitions—*Trionychidae* Bell, 1828 [Joyce et al., 2004].
Diagnostic Apomorphies—Extinct and extant trionychids are easily diagnosed by a long list of osteological and soft-tissue characters, the most apparent of which pertain to the shell: the complete absence of scutes, presence of a textured shell surface combined, presence of layers of interwoven fibers near the surface of the shell, absence of pygals, suprapygals, and peripherals, presence of a V-shaped entoplastron, and absence of central

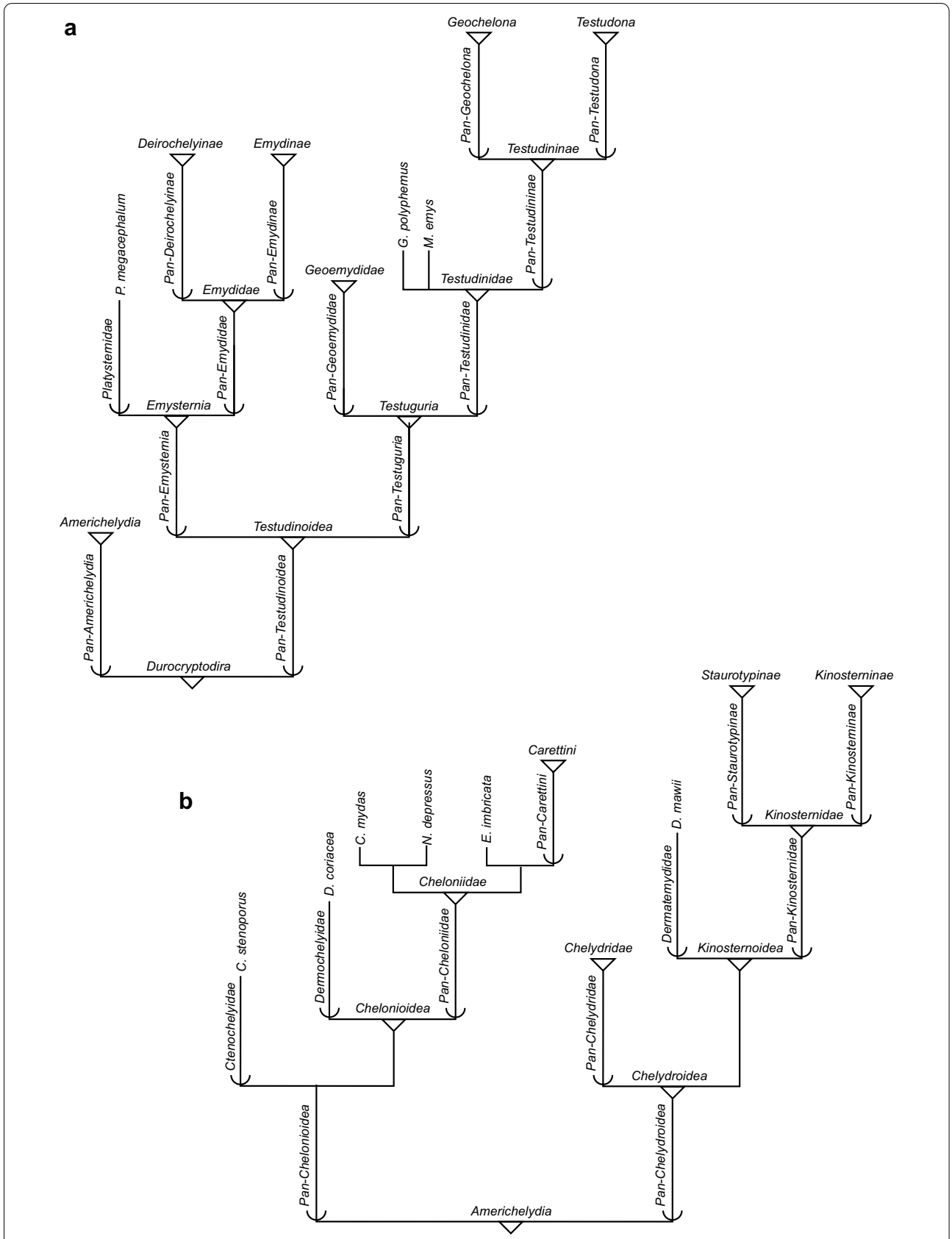

Fig. 4 Simplified diagrams that highlight the proposed name usage of clade names within **a** *Durocryptodira* and **b** *Americhelydia*

articulation between the cervical and dorsal vertebrae (Meylan 1987; Joyce 2007; Scheyer et al. 2007).
Comments—As turtle paleontologists traditionally did not distinguish between total clades and crown clades, and as the content of both was thought to be the same until recently (Brinkman et al. 2017), restriction of the name Trionychidae to the crown group, as has been done for nearly 200 years, and attribution of the name Pan-Trionychidae to the total clade, as first proposed by Joyce et al. (2004), is unproblematic. Joyce et al. (2004) incorrectly indicated that Gray (1825) is the nominal author of Trionychidae, but he actually coined the term Trionicidae. Nominal authorship, therefore, goes to Bell (1828).

Plastomenidae Hay, 1902, converted clade name.
Registration Number—498.
Definition—The largest extinct clade that contains *Plastomenus* (orig. *Trionyx*) *thomasii* (Cope, 1872a) (Fig. 3b).
Reference Phylogeny—Joyce et al. (2018, Fig. 4).
Composition—*Plastomenidae* is currently hypothesized to consist of a rich assemblage of fossil trionychids from the Late Cretaceous to Eocene of North America (Vitek and Joyce 2015; Joyce et al. 2016b, 2018).
Not established phylogenetic definitions—*Plastomeninae* Williams, 1950 [Joyce and Lyson, 2010]; *Plastomenidae* Hay, 1902 [Joyce and Lyson, 2011].
Comments—Although the exact content of this clade has been under debate for over a century (e.g., Hay 1908; Vitek and Joyce 2015), the name Plastomenidae (sometimes Plastomeninae) has consistently been applied to the group of turtles that includes all forms more closely related to the fossil *Plastomenus thomasii* than any extant trionychid turtles. We, therefore, fix this name/clade association. The phylogenetic definition implemented herein explicitly allows *Plastomenidae* to be nested anywhere within *Pan-Trionychidae*. Joyce and Lyson (2010) listed Hay (1905a) as the nominal author of Plastomenidae, but we here note an even earlier usage of this term in Hay (1902).

Pan-Cyclanorbinae Georgalis and Joyce, 2017, converted clade name.
Registration Number—499.
Definition—The total clade of crown clade *Cyclanorbinae* (see below) (Fig. 3b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—Fossil pan-cyclanorbines have historically been reported from the Neogene of Africa and India only and all are easily attributable to extant genera (Georgalis and Joyce 2017). The only currently available fossil that may reasonably represent the cyclanorbine stem lineage is *Nemegtemys conflata* from the Late Cretaceous of Mongolia (Danilov et al. 2014), but this taxon is only represented by highly fragmentary material. Some phylogenetic hypotheses interpret plastomenids (see above) to be pan-cyclanorbines as well (e.g., Joyce and Lyson 2010), but this conclusion is not supported by more recent analyses with better sampling (e.g., Brinkman et al. 2017; Joyce et al. 2018; Vitek et al. 2018).
Not established phylogenetic definitions—*Pan-Cyclanorbinae* Georgalis and Joyce, 2017.
Comments—See *Cyclanorbinae* below.

Cyclanorbinae Lydekker, 1889, converted clade name.
Registration Number—500.
Definition—The largest crown clade containing *Cyclanorbis* (orig. *Cryptopus*) *senegalensis* (Duméril and Bibron, 1835), but not the trionychine *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) (Fig. 3b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—At present, *Cyclanorbinae* is thought to consist of seven extant species (TTWG 2017) and a relatively rich fossil record from the Neogene of Afro-Arabia and India (Georgalis and Joyce 2017).
Not established phylogenetic definitions—*Cyclanorbinae* Lydekker, 1889 [Engstrom et al., 2004].
Diagnostic Apomorphies—Fossil and recent cyclanorbines can generally be diagnosed by the presence of a split comb of lateral nuchal processes, a preneural, enlarged eighth costals, hyo/hypoplastra that fuse soon after hatching, a posterior process of the hypoplastron that laterally embraces the anterior xiphiplastral processes, and well-developed epiplastral and entoplastral callosities (Meylan 1987; Georgalis and Joyce 2017).
Comments—As the fossil record of cyclanorbines is too poor to necessitate distinguishing between total and crown clades, restriction of the traditionally used name Cyclanorbinae to the crown group and attribution of the name Pan-Cyclanorbinae to the total clade, as first proposed by Engstrom et al. (2004) and Georgalis and Joyce (2017), respectively, is unproblematic. We, therefore, fix this name/clade association herein. Engstrom et al. (2004) assigned nominal authorship of Cyclanorbinae to Hummel (1929), but we here note much earlier usage of this term in Lydekker (1889).

Pan-Trionychinae Georgalis and Joyce, 2017, converted clade name.
Registration Number—501.
Definition—The total clade of crown clade *Trionychinae* (see below) (Fig. 3b).
Reference Phylogeny—Brinkman et al. (2017, Fig. 5).
Composition—See *Trionychinae* below.
Not established phylogenetic definitions—*Pan-Trionychinae* Georgalis and Joyce, 2017.
Comments—See *Trionychinae* below.

Trionychinae Lydekker, 1889, converted clade name.
Registration Number—502.
Definition—The largest crown clade containing *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775), but not the cyclanorbine *Cyclanorbis* (orig. *Cryptopus*) *senegalensis* (Duméril and Bibron, 1835) (Fig. 3b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Trionychinae* at the very least consists of 25 extant species of soft-shelled turtles (TTWG 2017). The fossil record has yielded a rich record of soft-shelled turtles with a trionychine morphotype from the Early Cretaceous to Holocene (Vitek and Joyce 2015; Georgalis and Joyce 2017; Vitek et al. 2018) and it is, therefore, to be expected that some fossil forms represent the stem lineage. Current phylogenies nevertheless consistently retrieve all included extinct taxa as crown trionychines (e.g., Vitek 2012; Danilov et al. 2014; Vitek et al. 2018).
Not established phylogenetic definitions—*Trionychinae* Lydekker, 1889 [Engstrom et al., 2004].
Diagnostic Apomorphies—The monophyly of *Trionychinae* is well-supported by molecular data (e.g., Pereira et al. 2017) and extant trionychines can readily be distinguished from their cyclanorbine cousins by a long list of characteristics, particularly to the shell (Meylan 1987). However, the recent realization that the trionychine morphotype (i.e., a shell with poorly formed carapacial and plastral callosities) may represent the basal condition for crown *Trionychidae*, indicates that most of these characteristics are likely plesiomorphic (Brinkman et al. 2017). Future work will, therefore, need to determine which morphological characters are indeed unique to this clade.
Comments—The attribution of the names *Trionychinae* and *Pan-Trionychinae* to the trionychine crown clade and total clade, as first suggested by Engstrom et al. (2004) and Georgalis and Joyce (2017), is unproblematic, as a poor understanding of the fossil record of the group has only recently necessitated distinguishing between the two. We, therefore, fix these name/clade associations herein.

Pan-Durocryptodira Joyce et al. (2016a), converted clade name.
Registration Number—503.
Definition—The total clade of crown clade *Durocryptodira* (see below) (Fig. 3b).
Reference Phylogeny—Joyce et al. (2016a, Fig. 8).
Composition—At present, *Pan-Durocryptodira* is only known to consist of *Durocryptodira* (e.g., Joyce et al. 2016a).
Not established phylogenetic definitions—None.
Comments—See *Durocryptodira* below.

Durocryptodira Danilov and Parham, 2006, converted clade name.
Registration Number—504.
Definition—The largest crown clade containing the testudinoid *Testudo graeca* Linnaeus, 1758, the kinosternoid *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766), the chelonioid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), and the chelydrid *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), but excluding the trionychians *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) and *Carettochelys insculpta* Ramsay, 1887 (Figs. 3b, 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Durocryptodira* is currently hypothesized to consist of the speciose clades *Pan-Testudinoidea* and *Pan-Americhelydia* (see below).
Not established phylogenetic definitions—*Durocryptodira* Danilov and Parham, 2006.
Diagnostic Apomorphies—Extant durocryptodires can be diagnosed by the entry of the internal carotid from the back of the skull (i.e., the foramen posterius canalis carotici interni is not positioned on the ventral skull surface, but within the cavum acustico-jugulare as an incised trough or just below the margin of the fenestra postotica, as in chelonioids), the absence of extragular scutes (Joyce 2016, b), and the presence of at least one biconvex cervical vertebra (Williams, 1950).
Comments—Although many groupings have been proposed for extant turtles over the course of the last two centuries, the group of turtles that includes all extant hard-shelled cryptodires was only recognized in the last decade through the use of molecular phylogenies (e.g., Krenz et al. 2005; Guillon et al. 2012; Crawford et al. 2015). We, therefore, here support the formal association of the newly formed name Durocryptodira for this clade, as first proposed by Danilov and Parham (2006).

Pan-Testudinoidea Joyce et al., 2004, converted clade name.
Registration Number—505.
Definition—The total clade of crown clade *Testudinoidea* (see below) (Fig. 4a).
Reference Phylogeny—Joyce (2007, Fig. 18).
Composition—An assortment of fossil turtles from the Cretaceous of Asia historically grouped into the paraphyletic assemblage "Lindholmemydidae" is usually thought to represent the stem lineage of *Testudinoidea* (e.g., Sukhanov 2000; Claude and Tong 2004; Danilov et al. 2017). However, as current global phylogenies only sample the group lightly (e.g., Joyce 2007; Cadena et al. 2013), this statement is still lacking rigorous phylogenetic support.
Not established phylogenetic definitions—*Pantestudinoidea* Joyce et al., 2004.

Comments—Although recent studies have concluded that some Late Cretaceous "lindholmemydid" may indeed represent the testudinoid crown (e.g., Danilov and Sukhanov 2013; Danilov et al. 2017), there is no historic precedent of referring Cretaceous stem testudinoids to *Testudinoidea*, as they were either referred to the wastebasket taxon Dermatemydidae (e.g., Williams 1950) or the paraphyletic Lindholmemydidae (e.g., Sukhanov 2000). We, therefore, find attribution of *Pan-Testudinoidea* to the total group of *Testudinoidea*, as first proposed by Joyce et al. (2004), to be unproblematic.

Testudinoidea Fitzinger, 1826, converted clade name.
Registration Number—506.
Definition—The largest crown clade containing the testudinid *Testudo graeca* Linnaeus, 1758, the emydid *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), and the geoemydid *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789), but not the chelonioid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), the chelydroid *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), or the trionychian *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Testudinoidea* is currently hypothesized to consist of *Pan-Emydidae*, *Pan-Geoemydidae*, *Pan-Testudinidae*, and *Platysternidae* (Parham et al. 2006a; Guillon et al. 2012; Crawford et al. 2015; Pereira et al. 2017).
Not established phylogenetic definitions—*Testudinoidea* Fitzinger, 1826 [Joyce et al., 2004].
Diagnostic Apomorphies—Fossil and recent testudinoids can be diagnosed osteologically by the apomorphic presence of three or fewer inframarginals (homoplastically developed in pleurodires and chelydroids), well-developed axillary and inguinal buttresses that contact the costals (homoplastically developed in baenids and pleurodires), laterally curved iliac blade, and a biconvex cervical VIII (homoplastically developed in pan-trionychians) (Gaffney and Meylan 1988; Danilov et al. 2017).
Comments—The name Testudinoidea has consistently been applied to the clade formed by emydids, geoemydids, and testudinids for the last decades. We, therefore, here fix this name/clade association without hesitation. Although the phylogenetic placement of *Platysternon megacephalum* within *Testudinoidea* appears to be increasingly well supported by molecular data (e.g., Parham et al. 2006a; Guillon et al. 2012; Crawford et al. 2015; Pereira et al. 2017), we here follow Joyce et al. (2004) by not utilizing this taxon as an internal specifier.

Pan-Testuguria Joyce et al., 2004, converted clade name.
Registration Number—507.
Definition—The total clade of crown clade *Testuguria* (see below) (Fig. 4a).
Reference Phylogeny—Vlachos (2018, Fig. 1).
Composition—Well-sampled phylogenies of basal testudinoids are still lacking, but preliminary analyses suggest that the Paleocene *Elkemys australis* (Yeh, 1974) and *Pseudochrysemys gobiensis* Sukhanov and Narmandakh, 1974 may be representatives of the testugurian stem lineage, but this result is not retrieved consistently (Tong et al., 2016, 2019).
Not established phylogenetic definitions—*Pantestuguria* Joyce et al., 2004.
Comments—See *Testuguria* below.

Testuguria Joyce et al., 2004, converted clade name.
Registration Number—508.
Definition—The largest crown clade containing the testudinid *Testudo graeca* Linnaeus, 1758 and the geoemydid *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789), but not the emydid *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758) or the platysternid *Platysternon megacephalum* Gray, 1831b (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Testuguria*, by definition, is comprised of the speciose clades *Pan-Geoemydidae* and *Pan-Testudinidae* (see below).
Not established phylogenetic definitions—*Testuguria* Joyce et al., 2004.
Diagnostic Apomorphies—*Testuguria* has only recently been identified using molecular data (e.g., Shaffer et al. 1997; Guillon et al. 2012; Crawford et al. 2015; Pereira et al. 2017) and is only retrieved in morphological analyses using backbone constraints (e.g., Tong et al. 2016, 2019; Vlachos 2018). We are, therefore, unaware of osteological characters that unite these morphologically disparate groups of testudinoids.
Comments—The conclusion that a monophyletic Testudinidae and Geoemydidae form a clade is still relatively novel. Shaffer et al. (1997) proposed using the name Testudinoidae for this clade which was followed by Claude and Tong (2004), but Joyce et al. (2004) suggested the creation of a new name instead, Testuguria, to avoid confusion with the near homonymous Testudinidae and Testudinoidea. This clade has since been consistently retrieved by molecular analyses (e.g., Krenz et al. 2005; Guillon et al. 2012; Crawford et al. 2015; Pereira et al. 2017) and the name Testuguria appears to have gained general acceptance (e.g., Claude 2006; Sasaki et al. 2006; Benson et al. 2011; Pereira et al. 2017; TTWG 2017). We, therefore, herein formally define the crown clade as *Testuguria* and the total clade as *Pan-Testuguria*.

Pan-Testudinidae Joyce et al., 2004, converted clade name.
Registration Number—509.

Definition—The total clade of crown clade *Testudinidae* (see below) (Fig. 4a).
Reference Phylogeny—Vlachos and Rabi (2018, Fig. 3b).
Composition—In addition to *Testudinidae*, *Pan-Testudinidae* is currently hypothesized to include a selection of Eocene fossils with a distribution across the northern hemisphere (Vlachos and Rabi 2018).
Not established phylogenetic definitions—*Pantestudinidae* Joyce et al., 2004, *Pan-Testudinidae* Vlachos and Rabi, 2018.
Comments—See *Testudinidae* below.

Testudinidae Gray, 1825, converted clade name.
Registration Number—510.
Definition—The largest crown clade containing *Testudo graeca* Linnaeus, 1758, but not the emydid *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), the geoemydid *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789), or the platysternid *Platysternon megacephalum* Gray, 1831b (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—An extremely rich fossil record that spans most of the Cenozoic documents the spread of testudinids from Asia across the globe (Lapparent de Broin 2000, 2001; Holroyd and Parham 2003; Joyce et al. 2016a; de la Fuente et al. 2018; Vlachos and Rabi 2018; Kehlmaier et al. 2019; Georgalis et al. in press). At present, 65 extant species are recognized with a near-global distribution (TTWG 2017).
Not established phylogenetic definitions—*Testudinidae* Gray, 1825 [Joyce et al., 2004].
Diagnostic Apomorphies—*Testudinidae* is characterized, among others, by a closure of incisura columella auris, wide fissure ethmoidalis, a narrow descending processes of the frontals that expands the crista cranii, a ridge on the ventral surface of the vomer, a wide and expanded coracoid, no webbing between the digits, phalangeal reduction, fused trochanters of the femur, and a coincidence between pleuromarginal sulci and costo-peripheral sutures (Vlachos and Rabi 2018).
Comments—The name 'Testudinidae' has persistently been applied to the clade of extant tortoises for more than a century. The attribution of *Testudinidae* to the crown clade and *Pan-Testudinidae* to the total clade, as first proposed by Joyce et al. (2004), is, therefore, unproblematic.

Pan-Testudininae, new clade name.
Registration Number—511.
Definition—The total clade of crown clade *Testudininae* (see below) (Fig. 4a).
Reference Phylogeny—Vlachos and Rabi (2018, Fig. 3b).
Composition—No fossils are currently hypothesized to populate the stem lineage of crown *Testudininae* (Vlachos and Rabi 2018).
Not established phylogenetic definitions—None.
Comments—See *Testudininae* below.

Testudininae Siebenrock, 1909, converted clade name.
Registration Number—512.
Definition—The largest crown clade containing *Testudo graeca* Linnaeus, 1758, but not *Manouria* (orig. *Testudo*) *emys* (Schlegel and Müller, 1840) and *Gopherus* (orig. *Testudo*) *polyphemus* (Daudin, 1801) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—Testudininae is currently thought to include 57 species of extant tortoises (TTWG 2017) and a particularly rich, nearly global fossil record that spans much of the Cenozoic (e.g., Vlachos and Rabi 2018).
Not established phylogenetic definitions—*Testudininae* Siebenrock, 1909 [Vlachos and Rabi, 2018].
Diagnostic Apomorphies—*Testudininae* is characterized by having no foramen caroticopharyngeale, a strongly interdigitated suture between the surangular and the dentary, a cervical scute longer than wide (lost subsequently within *Testudininae*), a long major trochanter of the humerus, and no contact between the radius and the distal carpals (Vlachos and Rabi 2018).
Comments—The name Testudininae was historically associated with all tortoises (e.g., Lindholm 1929; Williams 1950; Auffenberg 1964), but has been in use since Gaffney and Meylan (1988) to refer to the clade of tortoises that excludes *Gopherus* and *Manouria*. This name/clade association was formally fixed by Vlachos and Rabi (2018) who used a minimum-clade definition based on two internal specifiers (*Testudo graeca* and *Geochelone elegans*). We modify this definition following our practice of applying maximum-clade definitions to crown clades. In addition, here the nominal author of the Testudininae is changed from Batsch (1788) as in Vlachos and Rabi (2018) to Siebenrock (1909).

Pan-Testudona Parham et al., 2006b, converted clade name.
Registration Number—513.
Definition—The total clade of crown clade *Testudona* (see below) (Fig. 4a).
Reference Phylogeny—Vlachos and Rabi (2018, Fig. 3b).
Composition—No fossils are currently hypothesized to populate the stem lineage of crown *Testudona* (Vlachos and Rabi 2018).
Not established phylogenetic definitions—None.
Comments—See *Testudona* below.

Testudona Parham et al., 2006b, converted clade name.
Registration Number—514.

Definition—The largest crown clade containing *Testudo graeca* Linnaeus, 1758, but not *Geochelone* (orig. *Testudo*) *elegans* (Schoepff, 1795), *Gopherus* (orig. *Testudo*) *polyphemus* (Daudin, 1801), or *Manouria* (orig. *Testudo*) *emys* (Schlegel and Müller, 1840) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Testudona* is currently believed to include eight species of extant tortoises (TTWG 2017) and a rich fossil record across Africa, Europe, and Asia (Lapparent de Broin 2000, 2001; Vlachos and Rabi 2018; Georgalis et al. in press).
Not established phylogenetic definitions—*Testudona* Parham et al. 2006b.
Diagnostic Apomorphies—*Testudona* is characterized by an elongated prootic, a foramen jugulare posterius in the exoccipital/opisthotic suture, a coronoid that is excluded from foramen alveolare posterius, and a first pleural that touches but does not overlap the lateral sides of the nuchal (Vlachos and Rabi 2018).
Comments—Parham et al. (2006b) created *Testudona* for the clade of mostly Palearctic small tortoises that was well supported by molecular phylogenetics. The original definition was a minimum-clade definition based on four extant internal specifiers. We modify this definition following our practice of applying maximum-clade definitions to crown clades.

Pan-Geochelona, new clade name.
Registration Number—515.
Definition—The total clade of crown clade *Geochelona* (see below) (Fig. 4a).
Reference Phylogeny—Vlachos and Rabi (2018, Fig. 3b).
Composition—No fossils are currently hypothesized to populate the stem lineage of crown *Geochelona* (Vlachos and Rabi 2018).
Not established phylogenetic definitions—None.
Comments—See *Testudona* above.

Geochelona Vlachos and Rabi, 2018, converted clade name.
Registration Number—516.
Definition—The largest crown clade containing *Geochelone* (orig. *Testudo*) *elegans* (Schoepff, 1795), but not *Testudo graeca* Linnaeus, 1758, *Gopherus* (orig. *Testudo*) *polyphemus* (Daudin, 1801), or *Manouria* (orig. *Testudo*) *emys* (Schlegel and Müller, 1840) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—The clade *Geochelona* is currently believe to consists of 49 extant species of tortoises, including the Galapagos tortoise complex (TTWG 2017), and a rich Cenozoic fossil record (e.g., Lapparent de Broin 2000, 2001; Vlachos and Rabi 2018; Vlachos 2018; Georgalis et al. in press). *Cylindraspis* is the most basal branching clade of *Geochelona* (Kehlmaier et al. 2019). This recently extinct clade of Mascarene tortoises can delineate the crown following our explicit exception noted in "Methods and discussion" above.
Not established phylogenetic definitions—*Geochelona* Vlachos and Rabi, 2018.
Diagnostic Apomorphies—*Geochelona* is characterized by frontals longer than prefrontals, presence of a foramen nervi auriculotemporalis (subsequently lost in *Kinixys*), dentary with a medial tooth, an interdigitated suture between surangular and dentary, a long major trochanter of the humerus that extends beyond the head of the humerus, a radius completely separated by the distal carpals, and the contact of the sixth marginal with the third pleural scute (subsequently lost in *Kinixys*) (Vlachos and Rabi 2018).
Comments—Vlachos and Rabi (2018) created the name *Geochelona* for the *Geochelone* complex of Parham et al. (2006b). The original definition was a minimum-clade definition based on four extant internal specifiers. We modify this definition following our practice of applying maximum-clade definitions to crown clades.

Pan-Geoemydidae Vlachos, 2018, converted clade name.
Registration Number—517.
Definition—The total clade of crown clade *Geoemydidae* (see below) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—Although results are still preliminary, recent phylogenies suggest that numerous fossil testudinoids from the Eocene of the Northern Hemisphere traditionally classified as "geoemydids" may represent the stem lineage of *Geoemydidae* (Garbin et al. 2019).
Not established phylogenetic definitions—*Panbataguridae* Joyce et al., 2004; *Pan-Geoemydidae* Vlachos, 2018.
Comments—See *Geoemydidae* below.

Geoemydidae Theobald, 1868, converted clade name.
Registration Number—518.
Definition—The largest crown clade containing *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789), but not the testudinid *Testudo graeca* Linnaeus, 1758, the emydid *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), or the platysternid *Platysternon megacephalum* Gray, 1831b (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—At present, 62 extant species are recognized in many tropical to temperate regions across the globe, primarily Asia (TTWG 2017). Fossils are known from Asia (Claude et al. 2012; Garbin et al. 2019), Europe (Lapparent de Broin 2001), Africa (Lapparent de Broin 2000; Georgalis et al. in press), North America (Vlachos 2018), and South America (de la Fuente et al. 2018).

Not established phylogenetic definitions—*Bataguridae* Gray, 1870 [Joyce et al., 2004]; Geoemydidae, Theobald 1868 [Vlachos, 2018].
Diagnostic Apomorphies—Although there is strong molecular support for the monophyly of geoemydids (e.g., Pereira et al. 2017), osteological apomorphies are currently lacking that uniquely diagnose the group. Possible characters include the presence of a median keel in adults and presence of anterior and posterior musk duct foramina (Garbin et al. 2018).
Comments—McDowell (1964) was the first to realize that "pond turtles" comprise two different groups, which he named Emydinae and Batagurinae. The two groups were upgraded to the families Emydidae and Bataguridae by Gaffney and Meylan (1988). David (1994) soon after noted that the ICZN demands that Geoemydidae Theobald, 1868 be given priority over Bataguridae Gray, 1870, at least for the taxonomic concept of Gaffney and Meylan (1988). As the rules of priority as phrased by the ICZN (1999) are not relevant for clarifying authorship of clade names—neither Geoemydidae nor Bataguridae were originally coined for the group discovered by McDowell (1964) – Joyce et al. (2004) suggested retaining the name Bataguridae for McDowell's clade, as its use pervaded the literature. However, as usage of Geoemydidae has become near ubiquitous in the more recent literature (e.g., Claude et al. 2012; Lourenço et al. 2012; Crawford et al. 2015; TTWG 2017; Danilov et al. 2017; Garbin et al. 2018), we here conclude it prudent to fix this name/clade association instead, as recently proposed by Vlachos (2018).

Pan-Emysternia, new clade name.
Registration Number—519.
Definition—The total clade of crown clade *Emysternia* (see below) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—We are unaware of any fossil having been identified as a representative of the emysternian stem lineage, in part likely because this group has only been recognized recently using molecular data. The known content of *Pan-Emysternia,* therefore, overlaps fully with that of *Emysternia* (see below).
Not established phylogenetic definitions—None.
Comments—See *Emysternia* below.

Emysternia Crawford et al., 2015, converted clade name.
Registration Number—520.
Definition—The largest crown clade containing *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758) and *Platysternon megacephalum* Gray, 1831b, but not the testudinid *Testudo graeca* Linnaeus, 1758 or the geoemydid *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—The clade *Emysternia*, by definition, consists of *Platysternidae* and *Pan-Emydidae* (see below).
Not established phylogenetic definitions—*Emysternia* Crawford et al., 2015.
Diagnostic Apomorphies—Recent molecular phylogenies identify *Emysternia* with confidence (e.g., Guillon et al. 2012; Crawford et al. 2015; Pereira et al. 2017), but we are unaware of any morphological apomorphies that uniquely diagnose this clade.
Comments—Although previous authors had historically noted similarities of the big-headed turtle *Platysternon megacephalum* with testudinoids (e.g., Williams 1950), a sister group relationship with emydids was not proposed until quite recently using molecular data (Parham et al. 2006a). Our assignment of the newly created name Emysternia to this newly discovered clade, as suggested by Crawford et al. (2015), is, therefore, unproblematic. In addition, we here coin the name *Pan-Emysternia* for the total clade of *Emysternia.*

Pan-Emydidae Joyce et al., 2004, converted clade name.
Registration Number—521.
Definition—The total clade of crown clade *Emydidae* (see below) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—An eclectic set of fossil turtles from the Late Cretaceous and Paleogene of Asia and North America have been hypothesized to be stem emydids in recent analyses (e.g., Joyce et al. 2013; Danilov and Sukhanov 2013; Tong et al. 2016; Vlachos 2018), but as none of these analyses sample early testudinoids densely, a consensus is still lacking.
Not established phylogenetic definitions—*Panemydidae* Joyce et al., 2004.
Comments—See *Emydidae* below.

Emydidae Gray, 1825, converted clade name.
Registration Number—522.
Definition—The largest crown clade containing *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), but not the geoemydid *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789), the testudinid *Testudo graeca* Linnaeus, 1758, or the platysternid *Platysternon megacephalum* Gray, 1831b (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Emydidae*, by definition, consists of the clades *Pan-Emydinae* and *Pan-Deirochelyinae* (see below).
Not established phylogenetic definitions—*Emydidae* Gray, 1825 [Joyce et al., 2004].
Diagnostic Apomorphies—*Emydidae* can be diagnosed by the presence of wide rib head, a broad

costo-vertebral tunnel, paired marginals XII (also in the geoemydid *Mauremys*), and the expansion of vertebral V onto the pygal (modified from Vlachos 2018).
Comments—The term Emydidae, first coined by Gray (1825), not Bell (1825), had historically been used to unite all known hard-shelled cryptodires (e.g., Gray 1831b), but the successive removal of chelydrids (Swainson 1839), kinosternoids (Agassiz 1857), dermatemydids (Gray 1870), and geoemydids (McDowell 1964) resulted in a monophyletic groups of fossil and recent turtles centered in North America (TTWG 2017). As this usage has been near-universally accepted, we find the name clade association of Pan-Emydidae and Emydidae for the total and crown clade of North American pond turtles, as first proposed by Joyce et al. (2004), to be unproblematic.

Pan-Emydinae Vlachos, 2018, converted clade name.
Registration Number—523.
Definition—The total clade of crown clade *Emydinae* (see below) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—To date, no fossil turtle has been assigned to the stem lineage of *Emydinae*.
Not established phylogenetic definitions—None.
Comments—See *Emydinae* below.

Emydinae Cope, 1869b, converted clade name.
Registration Number—524.
Definition—The largest crown clade containing *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), but not the deirochelyine *Deirochelys* (orig. *Testudo*) *reticularia* (Latreille, 1801) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—In addition to 11 extant species distributed across North America and Europe (TTWG 2017), *Emydinae* is known from Neogene fossils found across North America and Eurasia (Fritz 1995; Vlachos 2018).
Not established phylogenetic definitions—None.
Diagnostic Apomorphies—*Emydinae* can be diagnosed by the exclusion of the palatine from the triturating surfaces, a posterior palatine foramen that is much larger than the foramen orbito-nasale, and the presence of anterior musk glands (Gaffney and Meylan 1988).
Comments—Using morphological characters, Gaffney and Meylan (1988) suggested that emydids consist of two subgroups to which they applied the names Emydinae and Deirochelyinae, a conclusion that has since been corroborated by molecular data (e.g., Stephens and Wiens 2003; Spinks et al. 2016; Pereira et al. 2017). As the recent literature consistently uses the terminology first introduced by Gaffney and Meylan (1988), we here refer the names Emydinae and Deirochelyinae to the crown clades and Pan-Emydinae and Pan-Deirochelyinae to the total clades. The pan-clade names were used by Vlachos (2018), so he is the nominal author of these names even though they were not formally defined.

Pan-Deirochelyinae Vlachos, 2018, converted clade name.
Registration Number—525.
Definition—The total clade of crown clade *Deirochelyinae* (see below) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—At present, no fossil turtle is thought to unambiguously represent the stem lineage of *Deirochelyinae* (Vlachos 2018). The known composition of *Pan-Deirochelyinae* is, therefore, the same as for *Deirochelyinae*.
Not established phylogenetic definitions—None.
Comments—See *Emydinae* above.

Deirochelyinae Gaffney and Meylan, 1988, converted clade name.
Registration Number—526.
Definition—The largest crown clade containing *Deirochelys* (orig. *Testudo*) *reticularia* (Latreille, 1801), but not the emydine *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Deirochelyinae* is currently thought to consist of 42 species of extant turtles distributed across the Americas and the Caribbean (TTWG 2017). The fossil record of the group is restricted to the Neogene of the same landmasses (Vlachos 2018; de la Fuente et al. 2018).
Not established phylogenetic definitions—None.
Diagnostic Apomorphies—*Deirochelyinae* can be diagnosed by the primitive placement of the humeropectoral sulcus posterior to the entoplastron, pronounced sexual size dimorphism with larger females, primitive absence of musk glands, jugal palatine contact, unossified epipubes, and a reduced to absent foramen caroticopharyngeale (Gaffney and Meylan 1988).
Comments—See *Emydinae* above.

Platysternidae Gray, 1869, converted clade name.
Registration Number—527.
Definition—The largest clade containing *Platysternon megacephalum* Gray, 1831b, but not the emydid *Emys* (orig. *Testudo*) *orbicularis* (Linnaeus, 1758), the geoemydid *Geoemyda* (orig. *Testudo*) *spengleri* (Gmelin, 1789), the testudinid *Testudo graeca* Linnaeus, 1758, the chelonioid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), the chelydrid *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), or the kinosternoid *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).

Composition—A number of fossil forms from the Cenozoic of Asia have been attributed to *Platysternidae* over the course of the last decades (e.g., Chkhikvadze 1989; Danilov et al. 2017), but the relevant fossils remain poorly figured. The Paleocene *Cardichelyon rogerwoodi* from North America has similarly been suggested more recently to be a platysternid as well (Hutchison 2013), but a more recent assessment suggests kinosternoid affinities instead (Joyce and Claude 2020).
Not established phylogenetic definitions—*Panplatysternon* Joyce et al., 2004.
Comments—Although the phylogenetic placement of *P. megacephalum* within *Testudinoidea* appears to be all but certain (e.g., Parham et al. 2006a; Guillon et al. 2012; Crawford et al. 2015; Pereira et al. 2017), we here phrase a more elaborate phylogenetic definition for the clade *Platysternidae* that utilizes representatives of all major clades of *Durocryptodira* as external specifiers. Our rationale for choosing the name *Platysternidae* over *Pan-Platysternon* for the total clade of *Platysternon megacephalum* is explained above (see "Methods and discussion" above).

Pan-Americhelydia, Joyce et al., 2016a, converted clade name.
Registration Number—528.
Definition—The total clade of crown clade *Americhelydia* (see below) (Fig. 4a).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—To date, no fossil turtle has been hypothesized to represent the stem lineage of *Pan-Americhelydia*. The hypothesized content of *Pan-Americhelydia*, therefore, currently equals that of *Americhelydia*.
Not established phylogenetic definitions—None.
Comments—See *Americhelydia* below.

Americhelydia Joyce et al., 2013, converted clade name.
Registration Number—529.
Definition—The largest crown clade containing the chelonioid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), the chelydrid *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), the dermatemydid *Dermatemys mawii* Gray, 1847, and the kinosternid *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766), but not the testudinoid *Testudo graeca* Linnaeus, 1758 and the trionychian *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) (Fig. 4a, b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Americhelydia* most likely consists of the subclades *Pan-Chelonioidea* and *Pan-Chelydroidea* (see below).
Not established phylogenetic definitions—*Americhelydia* Joyce et al., 2013.
Diagnostic Apomorphies—The evolution of characters remains unclear at the base of *Americhelydia*, because modern representatives are morphologically heterogeneous and because the clade is still poorly sampled at its base (e.g., Zhou and Rabi 2015; Joyce et al. 2016a; Lyson et al. 2017). Characters that are typical of americhelydians and that may reveal themselves to be apomorphic include presence of a narrow bridge, intergulars (sensu Joyce 2016, b; Joyce and Bourque 2016), and a reduced, cruciform plastron with strap-like epiplastra, an elongate, anchor-shaped entoplastron, and strap-like xiphiplastra.
Comments—The realization that chelonioids, chelydrids, kinosternids, and dermatemydids form a clade was only realized recently through the use of molecular data (e.g., Krenz et al. 2005; Guillon et al. 2012; Crawford et al. 2015; Pereira et al. 2017). As the oldest representatives of these lineages trace back to the Late Cretaceous of North America, Joyce et al. (2013) suggested naming this clade *Americhelydia*, a proposal that appears to have been accepted by the community (e.g., Crawford et al. 2015; Pereira et al. 2017; TTWG 2017). This is the only name available for this clade and we here, therefore, fix this name/clade association.

Pan-Chelonioidea Joyce et al., 2004, converted clade name.
Registration Number—530.
Definition—The total clade of crown clade *Chelonioidea* (see below) (Fig. 4b).
Reference Phylogeny—Cadena and Parham (2015, Fig. 11).
Composition—The phylogeny of fossil marine turtles is still poorly resolved so it remains unclear which Cretaceous lineages unambiguously populate the chelonioid crown group or stem lineage (see Cadena and Parham 2015, Zhou and Rabi 2015, and Evers and Benson 2019 for recent summaries of this issue). Because of this uncertainty, *Pan-Chelonioidea* is only certain to consist of *Chelonioidea* (see below). One of the main open questions is whether *Protostegidae* is a member of *Pan-Chelonioidea*. Other Cretaceous marine turtles, such as *Toxochelys latiremis* and ctenochelyids, are more confidently considered stem chelonioids (Hirayama 1994; Brinkman et al. 2006; Evers and Benson 2019; Gentry et al. 2019).
Not established phylogenetic definitions—*Panchelonioidea* Joyce et al., 2004.
Comments—See *Chelonioidea* below.

Ctenochelyidae Karl, 2012, converted clade name.
Registration Number—531.

Definition—The largest extinct clade containing *Ctenochelys* (orig. *Toxochelys*) *stenoporus* (Hay, 1905b), but not the cheloniid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), the dermochelyid *Dermochelys* (orig. *Testudo*) *coriacea* (Vandelli, 1761), the pan-chelonioid *Toxochelys latiremis* Cope, 1873b, or *Protostega gigas* Cope, 1872b (Fig. 4b).
Reference Phylogeny—Gentry et al. (2019, Fig. 4).
Composition—In addition to *Ctenochelys* spp., *Ctenochelyidae* is currently hypothesized to include a small assortment of fossil marine turtles from the Late Cretaceous of North America (Gentry 2018; Gentry et al. 2019).
Not established phylogenetic definitions—*Ctenochelyidae* Gentry, 2018
Diagnostic apomorphies—*Ctenochelyidae* can be diagnosed by the presence of a laterally serrated shell, extensive costal and plastral fontanelles, dorsally keeled neurals, and epineurals at various intervals along the neural series.
Comments—Gentry (2018) provided a minimum-clade definition for *Ctenochelyidae* based on *Ctenochelys stenoporus*, *Prionochelys matutina*, and *Peritiseus ornatus*. We modify this definition following our practice of applying maximum-clade definitions to extinct clades.

Chelonioidea Baur, 1893, converted clade name.
Registration Number—532.
Definition—The largest crown clade containing *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758) and *Dermochelys* (orig. *Testudo*) *coriacea* (Vandelli, 1761), but not the testudinoid *Testudo graeca* Linnaeus, 1758, the trionychian *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775), the chelydrid *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), or the kinosternoid *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Chelonioidea* is currently thought to include seven extant species with a worldwide distribution (TTWG 2017). The hypothesized fossil content for Chelonioidea is uncertain for the moment as it remains unclear what parts of the diverse Cretaceous marine turtle lineages are attributable to *Chelonioidea* (see Cadena and Parham 2015, and Evers and Benson 2019 for recent summaries of this issue). At the very least, *Chelonioidea* includes some Late Cretaceous taxa from North America and Cenozoic forms with a worldwide distribution (e.g., Wood et al. 1996; Parham and Pyenson 2010; Parham et al. 2014; Weems and Brown 2017; Gentry et al. 2019).
Not established phylogenetic definitions—*Chelonioidea* Baur, 1893 [Joyce et al., 2004].
Diagnostic Apomorphies—As the phylogenetic relationships of marine-adapted cryptodires remain poorly resolved (see Cadena and Parham 2015 for a recent summary), it is unclear which apomorphies uniquely diagnose chelonioids. The monophyly of the group, however, is consistently supported by molecular data (e.g., Shaffer et al. 1997; Crawford et al. 2015; Pereira et al. 2017).
Comments—Extant marine turtles (i.e., hard-shelled marine turtles and leatherback turtles) have historically been thought to form a natural group, although isolated opinions to the contrary were voiced in the late 19th and early twentieth centuries (e.g., Cope 1875; Dollo 1886; Hay 1908, 1922). Over the course of the nineteenth century, marine turtles were generally classified as a single family (see Joyce et al. 2004 for summary of names used), but the vast majority of authors has since favored their classification as two families within a superfamily (i.e., Cheloniidae, Dermochelyidae, and Chelonioidea, respectively). As first proposed by Joyce et al. (2004), we assign the name Cheloniidae to the crown clade of extant hard-shelled marine turtles and Chelonioidea to the crown clade of all extant marine turtles as this usage of the names still prevails in the recent neontological literature (e.g., TTWG 2017). Our rationale for assigning the name Dermochelyidae to the total clade of *Dermochelys coriacea*, not Pandermochelys as suggested by Joyce et al. (2004), is explained above (see "Methods and discussion" above).

Pan-Cheloniidae Joyce et al., 2004, converted clade name.
Registration Number—533.
Definition—The total clade of crown clade *Cheloniidae* (see below) (Fig. 4b).
Reference Phylogeny—Cadena and Parham (2015, Fig. 11).
Composition—In addition to *Cheloniidae*, *Pan-Cheloniidae* is currently thought to include a diverse assemblage of Cenozoic hard-shelled marine turtles with a global distribution (e.g., Parham and Pyenson 2010; Parham et al. 2014; Weems and Brown 2017). The only Cretaceous taxon certainly believed to be a member of this lineage is *Euclastes wielandi* (Brinkman et al. 2006; Parham et al. 2014; Gentry et al. 2019).
Not established phylogenetic definitions—*Cheloniidae* Cope, 1867 [Parham and Fastovsky, 1997]; *Pancheloniidae* Joyce et al., 2004.
Comments—See Cheloniidae below.

Cheloniidae Cope, 1867, converted clade name.
Registration Number—534.
Definition—The largest crown clade containing *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), but not the dermochelyid *Dermochelys* (orig. *Testudo*) *coriacea* (Vandelli, 1761) (Fig. 4b).

Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—At present, six extant species with a global distribution are referred to *Cheloniidae* (TTWG 2017) in addition to mostly fragmentary remains from the Neogene. The oldest certain members of this clade are from the latest Miocene or early Pliocene (Dodd and Morgan 1992; Zug 2001). Previous studies (e.g., Parham and Pyenson 2010) have suggested that more completely known middle Miocene taxa such as *Procolpochelys grandaeva* and *Syllomus aegyptiacus* (= *Trachyaspis lardyi*?) were in the crown clade, but this was not supported by a later study (Weems and Brown 2017).
Not established phylogenetic definitions—*Cheloniinae* Nopcsa, 1928 [Parham and Fastovsky, 1997]; *Cheloniidae* Cope, 1867 [Joyce et al., 2004].
Diagnostic Apomorphies—The characters that diagnose *Cheloniidae* are poorly understood because the most proximal fossils on the stem lineage are either known from fragmentary remains or else of uncertain phylogenetic position [e.g., *Syllomus aegyptiacus* (= *Trachyaspis lardyi*?)]. *Cheloniidae* are differentiated from most other members of *Pan-Cheloniidae* (where known) by having a surangular that extends onto the dentary, immovable articulations of the first and second digits, lacking a fossa between the femoral trochanters, and having a reduced metischial process, and a rib-free peripheral between sixth and seventh rib (lost in *Chelonia mydas*) (Parham and Pyenson 2010).
Comments—Parham and Fastovsky (1997) originally applied the name Cheloniinae to the crown group of extant hard-shelled marine turtles and Cheloniidae to their total group, but we follow Joyce et al. (2004) and the recommendations of the Phylocode in referring the most commonly used name, in this case the family name, to the crown. Joyce et al. (2004) referred the nominal authorship of Cheloniidae to Bonaparte (1832), but he actually coined the term Chelonidae. We, therefore, here assign nominal authorship to Cope (1867) instead.

Pan-Carettini, new clade name.
Registration Number—535.
Definition—The total clade of crown clade *Carettini* (see below) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—The Miocene taxon *Procolpochelys grandaeva* was placed on the stem lineage of crown *Carettini* by Zangerl and Turnbull (1955) and some later authors (e.g., Weems 1974; Parham and Fastovsky 1997; Parham and Pyenson 2010), but this has been questioned by recent analyses that include newly referred material of the closely related *Procolpochelys charlestonensis* (Weems and Brown 2017).
Not established phylogenetic definitions—None.
Comments—See *Carettini* below.

Carettini, Zangerl and Turnbull, 1955, converted clade name.
Registration Number—536.
Definition—The largest crown clade containing *Caretta* (orig. *Testudo*) *caretta* (Linnaeus, 1758), but not *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758) or *Eretmochelys* (orig. *Testudo*) *imbricata* (Linnaeus, 1766) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition.–*Carettini* includes three extant species and one fossil species (*Caretta patriciae* Zug 2001).
Not established phylogenetic definitions—*Carettini* Zangerl and Turnbull, 1955 [Parham and Fastovsky, 1997].
Comments—Zangerl and Turnbull (1955) divided extant cheloniids (as Cheloniinae) into two groups: Carettini (*Caretta* and *Lepidochelys*) and Chelonini [*Chelonia* (including *Natator depressus*) and *Eretmochelys*]. Parham and Fastovsky (1997) noted that Chelonini was paraphyletic, as both the morphological and molecular phylogenies placed *Eretmochelys imbricata* as more closely related to Carettini. Parham and Fastovsky (1997) did not provide an amended concept for Chelonini, but they did capture the name/clade association of Carettini with a phylogenetic definition. In doing so, they noted the many morphological synapomorphies of the clade as well as the tradition of usage, and explicitly excluded *Eretmochelys imbricata* from Carettini. Without comment, Naro-Maciel et al. (2008) expanded Carettini to include *Eretmochelys imbricata*. Parham and Pyenson (2010) discussed this matter and then reemphasized the restricted content of Carettini with an even more detailed, phylogenetic definition. TTWG (2012) noted the discrepancies in usage as well as the published phylogenetic definitions, but then further complicated matters by elevating the restricted concept of Carettini to the subfamily level (Carettinae) along with a paraphyletic Cheloniinae (includes *Eretmochelys*). Later, TTWG (2014) moved *Eretmochelys imbricata* from the Cheloniinae to the Carettinae, making both groups monophyletic while negating the redundant content between different concepts of Carettini and Carettinae. In this work we follow Parham and Fastovsky (1997) and Parham and Pyenson (2010) in capturing the original name/clade association of Zangerl and Turnbull (1955) for *Carettini*, and in refraining from naming any of the other groupings within *Cheloniidae*.

Dermochelyidae Lydekker, 1889, converted clade name.
Registration Number—537.
Definition—The largest clade containing *Dermochelys* (orig. *Testudo*) *coriacea* (Vandelli, 1761), but not the

cheloniid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758) (Fig. 4b).
Reference Phylogeny—Gentry et al. (2019, Fig. 4).
Composition—In addition to its extant representative, *Dermochelys coriacea*, *Dermochelyidae* is represented by a relatively continuous, though mostly fragmentary fossil record that is relatively rich from the Paleogene until Miocene (Wood et al. 1996). Potentially, the group extends back to the Late Cretaceous with *Allopleuron hoffmanni* (Rabi and Kear 2019; Gentry et al. 2019) and *Mesodermochelys undulatus* (e.g., Kear and Lee 2006) although the latter may represent a late protostegid instead (Sato et al. 2012). In contrast to earlier phylogenies (Hirayama 1994; Kear and Lee 2006), recent studies increasingly cast doubt on the dermochelyid affinities of the Cretaceous marine clade Protostegidae (Joyce 2007; Cadena and Parham 2015; Raselli 2018; Evers et al. 2019; Gentry et al. 2019).
Not established phylogenetic definitions—*Pandermochelys* Joyce et al., 2004.
Comments—See *Chelonioidea* above.

Pan-Chelydroidea, Joyce and Bourque, 2016, converted clade name.
Registration Number—538.
Definition—The total clade of crown clade *Chelydroidea* (see below) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—No fossil forms are currently known that represent the stem lineage of crown *Chelydroidea* (Lyson et al. 2017).
Not established phylogenetic definitions—None.
Comments—See *Chelydroidea* below.

Chelydroidea Baur, 1893, converted clade name.
Registration Number—539.
Definition—The largest crown clade containing the chelydrid *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), the dermatemydid *Dermatemys mawii* Gray, 1847, the kinosternid *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus 1766), but not the chelonioid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), the testudinoid *Testudo graeca* Linnaeus, 1758, or the trionychian *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Chelydroidea*, by definition, consists of the clades *Pan-Chelydridae* and *Pan-Kinosternoidea* (see below).
Not established phylogenetic definitions—None.
Diagnostic Apomorphies—Fossil and recent chelydroids can be diagnosed osteologically by the derived presence of well-developed costiform processes (often hidden in *Dermatemys mawii*), absence of pectoral scutes (possibly present in some fossil species), absence of a midline contact of the abdominal scutes (present in some kinosternoids), and contribution of the abdominal scute to the axillary notch (absent in dermatemydids; Lyson et al. 2017).
Comments—Although neontologists and paleontologists have long recognized shared similarities between chelydrids and kinosternoids (see Knauss et al. 2011 for summary), the monophyly of this clade, including the apomorphic *Dermatemys mawii*, was only fully appreciated recently through the use of molecular data (e.g., Parham et al. 2006a; Crawford et al. 2015; Pereira et al. 2017). The term Chelydroidea had originally been coined for this exact clade (e.g., Baur 1893), but was later restricted to include chelydrids only (e.g., Gaffney and Meylan 1988; TEWG 2014). We here follow Knauss et al. (2011) by reinstating the original name/clade association of Baur (1893), as this proposal seems to have gained momentum recently (e.g., Angielczyk et al. 2015; Crawford et al. 2015; Pereira et al. 2017; TTWG 2017). We similarly assign the name *Pan-Chelydroidea* to the total group, as had first been proposed by Joyce and Bourque (2016). It is interesting to note that neither name/clade association had previously been proposed formally using a phylogenetic definition. We, therefore, here do not recognize any non-established synonyms.

Pan-Chelydridae Joyce et al., 2004, converted clade name.
Registration Number—540.
Definition—The total clade of crown clade *Chelydridae* (see below) (Fig. 4b).
Reference Phylogeny—Lyson et al. (2017, Fig. 4).
Composition—In addition to crown *Chelydridae*, *Pan-Chelydridae* is currently hypothesized to include a rich assortment of fossil material from the Late Cretaceous (Campanian) to Pliocene of the northern hemisphere, including the *Chelydropsis* lineage, which persisted in Eurasia from the Eocene to Pliocene (Hutchison 2008; Joyce 2016, b; Lyson et al. 2017).
Not established phylogenetic definitions—*Panchelydridae* Joyce et al., 2004.
Comments—See *Chelydridae* below.

Chelydridae Swainson, 1839, converted clade name.
Registration Number—541.
Definition—The largest crown clade containing *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), but not the kinosternoid *Dermatemys mawii* Gray, 1847, the chelonioid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), the testudinoid *Testudo graeca* Linnaeus, 1758, or the trionychian *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) (Fig. 4b).

Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—In addition to five extant species (TTWG 2017), *Chelydridae* is currently hypothesized to include a small assortment of fossils from the Neogene of North and South America referable to *Chelydra* and *Macrochelys* (Joyce 2016, b; Cadena et al. 2017).
Not established phylogenetic definitions—*Chelydridae* Swainson, 1839 [Joyce et al., 2004].
Diagnostic Apomorphies—Fossil and recent chelydrids can be diagnosed osteologically by the apomorphic presence of squared vertebrals, development of rib-like costiform processes, restriction of the bridge to peripherals IV to VII (also found in some pan-kinosternoids), and the presence of extensive plastral fontanelles (Lyson et al. 2017).
Comments—Although the name Chelydridae has consistently been applied to the group of fossil and recent turtles believed to be closely related to the extant snapping turtle *Chelydra serpentina* over the course of the last century, authors have historically not differentiated between the corresponding total and crown clades. As there is no historical precedence, we follow Joyce et al. (2004) by referring *Chelydridae* to the crown clade and *Pan-Chelydridae* to the total clade.

Pan-Kinosternoidea Joyce et al., 2004, converted clade name.
Registration Number—542.
Definition—The total clade of crown clade *Kinosternoidea* (see below) (Fig. 4b).
Reference Phylogeny—Lyson et al. (2017, Fig. 4).
Composition—In addition to crown *Kinosternoidea*, *Pan-Kinosternoidea* is currently hypothesized to include a small assemblage of fossil species from the Late Cretaceous (Campanian) to Paleocene of North America, in particular the Campanian *Lutemys warreni*, the Maastrichtian *Emarginachelys cretacea*, and the late Maastrichtian to early Paleocene *Tullochelys montana* (Joyce and Bourque 2016; Lyson et al. 2017).
Not established phylogenetic definitions—*Pankinosternoidea* Joyce et al., 2004.
Comments—See *Kinosternoidea* below.

Kinosternoidea Hutchison and Weems, 1998, converted clade name.
Registration Number—543.
Definition—The largest crown clade containing *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766) and *Dermatemys mawii* Gray, 1847, but not the chelydrid *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758), the chelonioid *Chelonia* (orig. *Testudo*) *mydas* (Linnaeus, 1758), the testudinoid *Testudo graeca* Linnaeus, 1758, or the trionychian *Trionyx* (orig. *Testudo*) *triunguis* (Forskål, 1775) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Kinosternoidea*, by definition, consists of the clades *Dermatemydidae* and *Pan-Kinosternidae* (see below).
Not established phylogenetic definitions—*Kinosternoidea* Hutchison and Weems, 1998 [Joyce et al., 2004].
Diagnostic Apomorphies—Fossil and recent kinosternoids can be diagnosed by the apomorphic development of a highly domed shell, a thickened plastron (secondarily reduced in most extant members), a broad entoplastron, and a modified pelvis that exhibits a deep iliac notch and a strap-like ilium that is kinked at mid-length and possesses an incipient thelial process (Lyson et al. 2017).
Comments—The close phylogenetic relationships between the extant *Dermatemys mawii* and *Kinosternidae* has only been appreciated relatively recently (e.g., Hutchison and Bramble 1981; Meylan and Gaffney 1989) and there is, therefore, no extended nomenclature tradition of applying names to this clade. Gaffney and Meylan (1988) initially suggested the novel name Kinosternoidae for this clade, a modification of Cinosternoidae of Agassiz (1857). Joyce et al. (2004), by contrast, later suggested Kinosternoidea, a name that had first been introduced informally by Hutchison and Weems (1998) and Hutchison et al. (1998), perhaps to create nomenclatural consistency with other names ending with -oidea. We here fix the latter usage, as it appears to now have established itself robustly in the literature (e.g., TTWG 2007, 2012, 2014, 2017; Barley et al. 2010; Knauss et al. 2011; Crawford et al. 2015; Joyce and Bourque 2016; Lyson et al. 2017; Pereira et al. 2017).

Dermatemydidae Baur, 1888, converted clade name.
Registration Number—544.
Definition—The largest clade containing *Dermatemys mawii* Gray, 1847, but not the kinosternid *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766) or the chelydrid *Chelydra* (orig. *Testudo*) *serpentina* (Linnaeus, 1758) (Fig. 4b).
Reference Phylogeny—Lyson et al. (2017, Fig. 4).
Composition—In addition to the extant *Dermatemys mawii* (TTWG 2017), *Dermatemydidae* is thought to include an assemblage of fossil species from the Late Cretaceous (Maastrichtian) to Eocene of North America currently referred to the potentially paraphyletic genera *Hoplochelys* and *Baptemys* (Joyce and Bourque 2016). Fragmentary remains extend the known distribution of this lineage to as early as the late Campanian (Joyce and Bourque 2016).
Not established phylogenetic definitions—*Pandermatemys* Joyce et al., 2004.

Comments—The taxon Dermatemydidae historically served as a wastebasket for all shelled turtles that lack mesoplastra, but retain a full row of inframarginals, including adocusians, carettochelyids, stem testudinoids, paracryptodires, and various basal branching kinosternoids (e.g., Hay 1908; Młynarski 1976). Our rationale for here choosing the name *Dermatemydidae* over *Pan-Dermatemys* for the total clade of *Dermatemys mawii* is explained above (see "Methods and discussion").

Pan-Kinosternidae Joyce et al., 2004, converted clade name.
Registration Number—545.
Definition—The total clade of crown clade *Kinosternidae* (see below) (Fig. 4b).
Reference Phylogeny—Lyson et al. (2017, Fig. 4).
Composition—In addition to crown *Kinosternidae*, *Pan-Kinosternidae* is currently hypothesized to include the fossil *Yelmochelys rosarioae* from the late Campanian of Coahuila, Mexico (Brinkman et al. 2016). Figured remains of shell fragments from the Late Cretaceous (Campanian) of New Mexico (Sullivan et al. 2013) and Utah (Hutchison et al. 2013) likely represent the stem lineage as well (Joyce and Bourque 2016).
Not established phylogenetic definitions—*Pankinosternidae* Joyce et al., 2004.
Comments—See *Kinosternidae* below.

Kinosternidae Hay, 1892, converted clade name.
Registration Number—546.
Definition—The largest crown clade that contains *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus,, 1766), but not the dermatemydid *Dermatemys mawii* Gray, 1847 (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Kinosternidae*, by definition, consists of the clades *Pan-Kinosterninae* and *Pan-Staurotypinae* (see below).
Not established phylogenetic definitions—*Kinosternidae* Hay, 1892 [Joyce et al., 2004].
Diagnostic Apomorphies—Fossil and recent kinosternids can be diagnosed by the derived presence of short musk duct grooves, 10 pairs of peripherals, a short bridge restricted to peripherals IV–VII (also developed in some chelydrids), presence of only two inframarginal scutes (also present in testudinoids and some chelydrids), and the absence of abdominal scutes (Lyson et al. 2017). Extant kinosternids are notable for their unusually strong musky odor (Ernst and Barbour 1989).
Comments—There has been full agreement for the last 100 years that North American mud and musk turtles form a natural group, but there has been no consensus historically if they should be classified as two separate families (i.e., Kinosternidae and Staurotypidae) or as a single family with two separate subfamilies (i.e., Kinosternidae, Staurotypinae, and Kinosterninae) (see Joyce et al. 2004 for examples). As a trend was apparent in the more recent literature towards the use of a single family (e.g., Ernst and Barbour 1989; Hutchison 1991; Iverson 1998), Joyce et al. (2004) phylogenetically tied the name Kinosternidae to the more inclusive group. This usage still predominates in the current literature, although isolated proposals exist favoring usage of two family names (e.g., Iverson et al. 2013). We, therefore, here utilize the name Kinosternidae for the more inclusive clade and provide for the first time formal definitions of the names Staurotypinae and Kinosterninae for the two less inclusive clades.

Pan-Staurotypinae Joyce and Bourque, 2016, converted clade name.
Registration Number—547.
Definition—The total clade of crown clade *Staurotypinae* (see below) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—At present, no fossil forms are known that may represent the stem lineage of crown *Staurotypinae* (Joyce and Bourque 2016). The known content of *Pan-Staurotypinae,* therefore, currently equals that of *Staurotypinae*.
Not established phylogenetic definitions—None.
Comments—See *Kinosternidae* above.

Staurotypinae Siebenrock, 1907, converted clade name.
Registration Number—548.
Definition—The largest crown clade that contains *Staurotypus* (orig. *Terrapene*) *triporcatus* (Wiegmann, 1828), but not the kinosternine *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—At present, *Staurotypinae* is only known to include three extant species (TTWG 2017) and a single fossil species, *Staurotypus moschus*, from the early Miocene of Panama (Cadena et al. 2012; Joyce and Bourque 2016).
Not established phylogenetic definitions—None.
Diagnostic Apomorphies—Fossil and recent staurotypines can be diagnosed by the apomorphic development of elongate musk duct grooves that terminate at peripheral I, fused anals, and the overlap of the gular/humeral sulcus with the epi/hyoplastral suture (Lyson et al. 2017).
Comments—Joyce et al. (2004) assigned authorship of Staurotypinae to Lindholm (1929), but we here note

an earlier usage of this name by Siebenrock (1907). For additional comments, see *Kinosternidae* above.

Pan-Kinosterninae Joyce and Bourque, 2016, converted clade name.
Registration Number—549.
Definition—The total clade of crown clade *Kinosterninae* (see below) (Fig. 4b).
Reference Phylogeny—Lyson et al. (2017, Fig. 4).
Composition—In addition to crown *Kinosterninae*, *Pan-Kinosterninae* includes a small sample of fossil species from the Eocene and Oligocene of North America currently referred to the potentially paraphyletic genera *Baltemys* and *Xenochelys* (Hutchison, 1991; Joyce and Bourque 2016).
Not established phylogenetic definitions—None.
Comments—See *Kinosternidae* above.

Kinosterninae Lindholm, 1929, converted clade name.
Registration Number—550.
Definition—The largest crown clade that contains *Kinosternon* (orig. *Testudo*) *scorpioides* (Linnaeus, 1766), but not *Staurotypus* (orig. *Terrapene*) *triporcatus* (Wiegmann, 1828) (Fig. 4b).
Reference Phylogeny—Pereira et al. (2017, Fig. 1).
Composition—*Kinosterninae* is currently hypothesized to consist of 24 extant species (TTWG 2017) and a small assortment of fossil species from the Neogene of North and South America referable to *Kinosternon* and *Sternotherus* (Joyce and Bourque 2016).
Not established phylogenetic definitions—*Kinosterninae* Lindholm, 1929 [Joyce and Bourque, 2016].
Diagnostic Apomorphies—Fossil and extant kinosternines can be diagnosed by the presence of only six neurals (among kinosternoids also present in *Dermatemys mawii*), a distinctly elevated marginal X (among kinosternoids also present in *Claudius angustatus*), a distinct anal notch (among kinosternoids also present in *Dermatemys mawii*), absence of an entoplastron, and an anteriorly oriented epi/hyoplastral suture (Lyson et al. 2017).
Comments—See *Kinosternidae* above.

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Authors' contributions
WGJ and JFP conceived the idea of establishing turtle clade names under the PhyloCode and invited the remaining participants. All authors suggested and approved all names to be established. WGJ and JFP jointly wrote and the primary draft of the manuscript and created the figures. All remaining authors critically read the full text and suggested modifications. All authors approve of the final manuscript.

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