



A DIVERGENCE DATING ANALYSIS OF TURTLES USING FOSSIL CALIBRATIONS: AN EXAMPLE OF BEST PRACTICES

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ABSTRACT—Turtles have served as a model system for molecular divergence dating studies using fossil calibrations. However, because some parts of the fossil record of turtles are very well known, divergence age estimates from molecular phylogenies often do not differ greatly from those observed directly from the fossil record alone. Also, the phylogenetic position and age of turtle fossil calibrations used in previous studies have not been adequately justified. We provide the first explicitly justified minimum and soft maximum age constraints on 22 clades of turtles following best practice protocols. Using these data we undertook a Bayesian relaxed molecular clock analysis establishing a timescale for the evolution of crown Testudines that we exploit in attempting to address evolutionary questions that cannot be resolved with fossils alone. Some of these questions, such as whether the turtle crown originated in the Triassic or Jurassic, cannot be resolved by our analysis. However, our results generate novel age-of-origination estimates for clades within crown Testudines. Finally, we compare our fossil calibrations and posterior age estimates to those from other studies, revealing substantial differences in results and interpretation.

INTRODUCTION

THE STUDY of the timing of evolutionary history has become a synthetic science in recent years, as studies increasingly combine molecular and paleontological data (Donoghue and Benton, 2007). On the molecular side, much progress has been achieved through the development of increasingly complex and accurate models of molecular evolution, combined with better gene and taxon sampling. In parallel, paleontologists have focused their efforts on providing well-supported divergence estimates (i.e., fossil calibrations) for a representative sample of major lineages, and with communicating their results clearly to the molecular community (e.g., Brochu, 2004; Müller and Reisz, 2005; Smith et al., 2006; Donoghue and Benton, 2007; Anderson, 2012; Parham et al., 2012). Furthermore, it has been demonstrated that calibrations have a pejorative impact on the accurate estimation of evolutionary rates and dates (Ho and Phillips, 2009; Inoue et al., 2010; Clarke et al., 2011; Warnock et al., 2012; dos Reis et al., 2012).

Turtles are morphologically diverse, have an excellent fossil record, and display relatively low levels of extant diversity, therefore serving as an excellent model system in which to explore the efficacy of divergence dating studies using fossil calibrations. Near et al. (2005) presented a suite of turtle fossil calibrations for divergence time estimation, which they used to establish an *a posteriori* cross validation method for evaluating the accuracy of component calibrations within a set. These calibrations were used subsequently in other studies as a basis for the development of additional methods of assessing and implementing calibrations (Marshall, 2008; Pyron, 2010; Dornburg et al., 2011; Heath, 2012), the process of justifying fossil calibrations (Parham and Irmis, 2008), and the evolution of body size (Jaffe et al., 2011), sex determination (Valenzuela and Adams, 2011), and sexual dimorphism (Ceballos et al., 2012). Some of the calibrations from the Near et al. (2005) study

were used also in divergence dating studies of turtle lineages in particular, or tetrapods in general (e.g., Hugall et al., 2007; Shen et al., 2011; Spinks and Shaffer, 2009; Wong et al., 2010; Chiari et al., 2012).

It could be argued that turtles are a poor model for fossil calibration studies because their fossil record, particularly that of cryptodires, is so well understood that any such study runs the risk of producing circular results. For example, the calculated divergence estimates of Near et al. (2005) do not differ from the prior fossil calibrations in any material sense. This close relationship, between fossil dates and estimated ages, is a consequence in part of the dense fossil record of turtles, but also of the false-precision of the errorless fossil calibrations compiled and employed by Near et al. (2005), a reflection of common practice at the time (Hedges and Kumar, 2004). Since that study, advances in Bayesian statistical phylogenetics (Drummond et al., 2006; Yang, 2006; Yang and Rannala, 2006) allow calibrations to encompass a range of dates. This methodological approach is a more accurate reflection of the fossil record, since a fossil can only give a minimum estimate of origination and not a precise time of origin as a point estimate implies (Reisz and Müller, 2004; Benton and Donoghue, 2007). Even though the fossil record of turtles is relatively dense, well sampled, and well understood, it is still necessary to justify the temporal and phylogenetic position of calibrations (Parham et al., 2012). In particular, Parham and Irmis (2008) showed that it was impossible to reproduce the phylogenetic position and geologic age assigned to the fossil calibrations by Near et al. (2005). Since turtles have become a model system for analyzing the efficacy of competing approaches to the fossil calibration in divergence time estimation, it has become imperative that we establish a fully-justified suite of fossil calibrations for turtle phylogeny.

The purpose of our study is to provide explicitly justified and highly conservative minimum and maximum temporal

constraints on the age of 22 clades of turtles following the best practice protocols established in Parham et al. (2012). Our calibrations reflect the current knowledge of the fossil record of turtles and we expected them to eventually be replaced by other dates as new fossils are found and new insights into the phylogeny of turtles emerge. We then present the results of a Bayesian relaxed clock divergence time analysis from which we establish a timescale for the evolution of crown Testudines. Using this we attempt to address evolutionary questions that cannot be resolved with fossils alone, in particular the age of the turtle crown (Testudines) and soft-shelled turtles (Trionychidae), the diversification of side-necked turtles (Pleurodira), and the origin of marine turtles (Chelonioidae).

MATERIALS AND METHODS

Institutional abbreviations.—Institutional abbreviations use here include: BMNH=Natural History Museum, London, UK; CCMGE=Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia; FHSM=Sternberg Museum of Natural History, Fort Hays, Kansas, U.S.A.; FM=Fur Museum, Norderby, Denmark; FPDm=Fukui Prefecture Dinosaur Museum, Katsuyama, Fukui, Japan; IVPP=Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; MIMP=Museo Geológico José Royo y Gómez, paleontological collection INGEOMINAS (Instituto Colombiano de Geología y Minería), Bogotá, Colombia; MGB=Museo de Geología de Barcelona, Barcelona, Spain; MNHNFr=Museum National d'Histoire Naturelle, Paris, France; MNHNCu=Museo nacional de Historia Natural, La Habana, Cuba; MPA=Museo Municipal de Ciencias Naturales "Carlos Darwin," Punta Alta, Buenos Aires Province, Argentina; MPSC=Museu Paleontológico de Santana do Cariri, Ceará State, Brazil; NMK=National Museum of Kenya, Nairobi, Kenya; QM=Queensland Museum, Brisbane, Australia; ROM=Royal Ontario Museum, Toronto, Ontario, Canada; SDSM=South Dakota School of Mines, Rapid City, South Dakota, U.S.A.; SEPCP=Secretaría de Educación y Cultura, Colección Paleontológica, Saltillo, Coahuila, Mexico; SMF=Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; UCMP=University of California Museum of Paleontology, Berkeley, California, U.S.A.; USNM=United States National Museum of Natural History, Washington D.C., U.S.A.; YPM=Yale Peabody Museum of Natural History, New Haven, Connecticut, U.S.A.

We follow the phylogenetic nomenclature of turtles codified by Joyce et al. (2004). All taxonomic names therefore reflect clade names. Authorships are provided for all fossil taxa listed throughout this publication. Authorships for extant taxa are summarized in Rhodin et al. (2008).

Fossils do not provide a precise time of origination because a lineage may have existed for some time before its first representative, bearing indicative apomorphies, was fossilized. Nevertheless, until recently, fossil calibrations have been implemented as precise, errorless estimates of the timing of divergence events, taking no account of the imperfection of the fossil record (Reisz and Müller, 2004; Benton and Donoghue, 2007). Since the widespread adoption of Bayesian inference in divergence dating studies, a fossil calibration can be implemented as a minimum age constraint, more faithfully reflecting the nature of fossil stratigraphic data. Minimum constraints alone are not sufficient, however, since meaningful divergence time estimates also require a maximum constraint (Sanderson, 1997; Kishino et al., 2001; Thorne and Kishino, 2005; Yang and Rannala, 2006), which is not based on a single fossil, but could be based, for instance, on an informed but conservative assessment of preservation potential (Reisz and Müller, 2004; Donoghue and Benton, 2007). Existing software for Bayesian divergence time

estimation also allow the degree to which minimum and maximum constraints approximate divergence timing to be expressed in the form of a prior probability density (Yang and Rannala, 2006; Drummond et al. 2006; Donoghue and Benton, 2007; Ho and Phillips, 2009; Inoue et al., 2010). The justification for non-uniform calibration priors is elusive and difficult to reproduce (Parham et al., 2012), and so for this study we employ a uniform probability distribution between a hard minimum and soft maximum (as explained below) to express the equal likelihood of divergence time between these bounds.

Establishing minima.—In establishing minimum constraints we followed the "best practice" recommendations of Parham et al. (2012). First, all calibrations are based on a single fossil specimen or sets of explicitly referable specimens, that are housed in publicly accessible museum collections, that exhibit the characters that substantiate their phylogenetic placement, and that are figured in sufficient detail to display the relevant characters. As a result, many fossils that may have provided a minimum constraint that is a closer approximation of the true divergence date were dismissed *a priori* because they have yet to be deposited in publicly accessible collections, do not display relevant characters, or are not sufficiently well figured to allow for confirmation of their identity. All such specimens are nevertheless informative in establishing maxima (see below).

In addition to providing voucher specimens for fossil calibrations, Parham et al. (2012) recommend that the phylogenetic placement of all fossils used in calibrations be explicitly demonstrated and, if based on morphological data, reconciled with potentially conflicting topologies based on molecular data. One way to do this is by building a global character/taxon matrix that includes molecular and morphological data, but this is not currently feasible for turtles, as sampling of extant taxa remains poor in all available global morphological matrices (e.g., Gaffney et al., 2007; Joyce, 2007; Sterli et al., 2012). It was therefore necessary to assess the phylogenetic placement of fossils with reference to published subtrees. Unfortunately, the topologies of many subtrees differ substantially depending on whether morphological or molecular evidence is used and the placement of any given fossil will differ as a result (e.g., Geoemydidae: Hirayama, 1985 versus Spinks et al., 2004; Chelidae: Gaffney, 1977 versus Georges et al., 1998; Trionychidae: Meylan, 1987 versus Engstrom et al., 2004). We follow Danilov and Parham (2006, 2008) in bridging the conflict between molecular and morphological data by analyzing phylogenetically our morphological matrices using a conservative molecular backbone topological constraint. In all instances we cite the source of the morphological matrix and, where necessary, provide the character scores of a fossil taxon, as well as citing the relevant molecular phylogeny employed as the backbone constraint. In some instances there is no conflict between current molecular and morphological phylogenetic trees (e.g., Kinosternoidea: Hutchison and Bramble, 1981 versus Krenz et al., 2005) and the evolutionary history of diagnostic traits is therefore uncontroversial. Under these circumstances we used unambiguous characters to diagnose fragmentary remains.

To avoid biasing results in favor of a particular worldview, including our own, we consciously avoided using contentious fossils. For instance, the Late Triassic fossil *Proterochersis robusta* Fraas, 1913 has been argued traditionally to be the oldest known representatives of the pleurodire lineage (Fraas, 1913; Gaffney et al., 2007), but it has been interpreted more recently as a stem-turtle (e.g., Rougier et al., 1995; Danilov and Parham, 2006; Joyce, 2007; Sterli and de la Fuente, 2011; Anquetin, 2012). Similarly, it has been argued that platemid softshell turtles represent the oldest unambiguous crown trionychids (Joyce

TABLE 1—Summary of justified minimum and maximum calibration dates for 21 clades of extant turtles developed as part of this study and a comparison with those proposed by Near et al. (2005) for the same clades.

	Minimum	Maximum	Minimum of Near et al., 2005	Difference between minimum of this study and Near et al. (2005)	MCMC Tree mean	MCMC Tree 95% HPD lower	MCMC Tree 95% HPD upper
Node 1, Testudines	151.7 Ma	251.4 Ma	210 Ma	−26%	212.33	194.90	231.41
Node 2, Pleurodira	111.0 Ma	165.2 Ma	110 Ma	+1%	164.09	155.6	171.35
Node 3, Pelomedusoides	92.8 Ma	149.5 Ma	110 Ma	−16%	125.03	110.66	138.56
Node 4, Pelomedusidae	5.3 Ma	149.5 Ma	18 Ma	−71%	53.67	39.86	66.36
Node 5, Chelidae	65.2 Ma	149.5 Ma	71 Ma	−8%	116.01	99.35	133.19
Node 6, Chelodiniinae	11.6 Ma	149.5 Ma	15 Ma	−23%	94.62	76.31	113.52
Node 7, <i>C. fimbriatus</i> – <i>P. gibbus</i>	13.4 Ma	149.5 Ma	11.6 Ma	+16%	71.98	54.32	90.92
Node 8, Cryptodira	124.0 Ma	200.2 Ma	110 Ma	+13%	190.42	168.73	202.69
Node 9, Trionychia	124.0 Ma	177.6 Ma	NA	NA	162.83	145.66	178.57
Node 10, Trionychidae	17.3 Ma	149.5 Ma	110 Ma	−84%	104.96	85.80	125.62
Node 11, Durocryptodira	88.6 Ma	149.5 Ma	NA	NA	118.57	103.83	133.31
Node 12, Americhelydia	70.0 Ma	149.5 Ma	NA	NA	113.14	99.33	127.78
Node 13, Chelonioidea	48.4 Ma	149.5 Ma	110 Ma	−56%	66.18	50.22	82.94
Node 14, Chelydroidea	70.0 Ma	149.5 Ma	NA	NA	110.41	96.46	124.33
Node 15, Kinosternoidea	70.0 Ma	149.5 Ma	65 Ma	+8%	91.05	78.97	103.75
Node 16, Kinosternidae	52.8 Ma	149.5 Ma	50 Ma	+6%	55.67	52.80	60.99
Node 17, Testudinoidea	50.3 Ma	149.5 Ma	90 Ma	−44%	85.83	72.88	99.78
Node 18, Emydidae– <i>P. megacephalum</i>	32.0 Ma	100.5 Ma	NA	NA	82.43	68.58	96.53
Node 19, Emydidae	32.0 Ma	100.5 Ma	34 Ma	−6%	44.15	32.14	55.47
Node 20, <i>T. scripta</i> – <i>G. pseudogeographica</i>	3.0 Ma	34.0 Ma	5 Ma	−40%	14.51	9.25	20.28
Node 21, Testuguria	50.3 Ma	100.5 Ma	52 Ma	−3%	57.68	50.30	66.99
Node 22, <i>H. spinosa</i> – <i>M. reevesii</i>	5.3 Ma	65.8 Ma	50 Ma	−89%	41.16	30.37	51.84

and Lyson, 2010a), but a comparable analysis arrived at contradictory conclusions (Head et al., 2009). In all such instances we have taken the most conservative interpretation of dismissing taxa whose phylogenetic classification is still currently being debated.

The geographic locality of each fossil is provided alongside the stratigraphic time interval to which the fossil-bearing horizon at this locality can be referred. To establish the minimum constraint on clade age we established minimum absolute age interpretations of the minimum stratigraphic age interpretation, sometimes through an explicit chain of lithostratigraphic and biostratigraphic correlation steps. All minimum constraints were considered hard minima because, by adopting a conservative approach to fossil selection, it means that there is no equivocation over the phylogenetic interpretation or minimum age (Benton and Donoghue, 2007; Donoghue and Benton, 2007; Benton et al., 2009; Parham et al., 2012). The minimum constraints established in this study (see Results: Calibration Constraints below for details) are summarized in Table 1 and Figure 1.

Establishing soft maxima.—Various rationales have been outlined for establishing maximum constraints on divergence time estimates, but the peculiarities of the fossil record of turtles required us to develop our own protocol. In our experience, turtles are either extremely common in the fossil record, or exceedingly rare, that we interpret as a reflection of climate and depositional environment. Furthermore, like most groups of fossils, turtles are most commonly found as fragments, particularly the shell. Although most turtle fossils can be identified with confidence to family, genus, or even species level (e.g., Hutchison and Archibald, 1986; Holroyd and Hutchison, 2002), paleontologists specialized in turtle systematics are few in number and so most fragment-based turtle faunal fossil assemblages remain undescribed. Thus, the fossil record of turtles typically consists of well-sampled and well-studied faunas that either include or exclude particular taxa.

To establish soft maximum constraints, we first summarized the biogeographical history of a clade and deduced conservatively the continent or continents from which it originated. We then identified the geological time period, epoch, or age from which the youngest well-sampled turtle faunas originate that lack

representatives of the clade. In contrast to the highly stringent criteria that we use for establishing minima, our conservative approach demanded that even weak evidence was considered informative. Any reasonable report regarding the presence of a taxon in a particular formation was therefore taken as possible evidence for the presence of the group, even if the fossil was not described, figured, or deposited in a museum. We derived our absolute age from the bottom of the identified stratigraphic interval, again with reference to the geological literature. The maximum constraints established in this study (see Results: Calibration Constraints below for details) are summarized in Table 1 and Figure 1.

Divergence dating analysis.—We utilized a classic molecular dataset that had been used previously to infer divergence times among turtles (e.g., Near et al., 2005; Marshall, 2008; Dornburg et al., 2011; Heath, 2012). This dataset includes 23 taxa representing all major lineages of extant Testudines, and is comprised of the mitochondrial gene cytochrome *b* (*cytB*), the nuclear gene recombinase activating gene 1 (*RAG1*), and the nuclear intron R35 (*RM35*). Sequences were downloaded from GenBank and each marker was aligned independently as follows: protein sequences were unambiguously aligned using ClustalW (Thompson et al., 1994) and intron sequences were aligned using BlastAlign (Belshaw and Katzourakis, 2005), with further refinement using the ‘-refine’ option in MUSCLE 3.8 (Edgar, 2004). Regions that could not be aligned unambiguously were removed and the final matrix contained 4613 characters.

Bayesian molecular clock analysis was performed using MCMCTREE (Yang and Rannala, 2006; Rannala and Yang, 2007; Inoue et al., 2010), part of the PAML 4 package (Yang, 2007). The molecular data was partitioned into seven partitions by gene and by codon. We used the HKY+ Γ model with five gamma rate categories, independent transition/transversion rate ratios (κ), independent base frequencies, and independent gamma shape parameters (α). Gamma priors (mean and standard deviation) were assigned to κ G (3, 1.22) and α G (1, 1). Molecular clock estimates were obtained using the independent rates model, with a gamma prior G (0.041, 0.041) for the overall substitution rate and G (0.2, 0.2) for the rate-drift parameter. Node ages were constrained using a uniform prior distribution

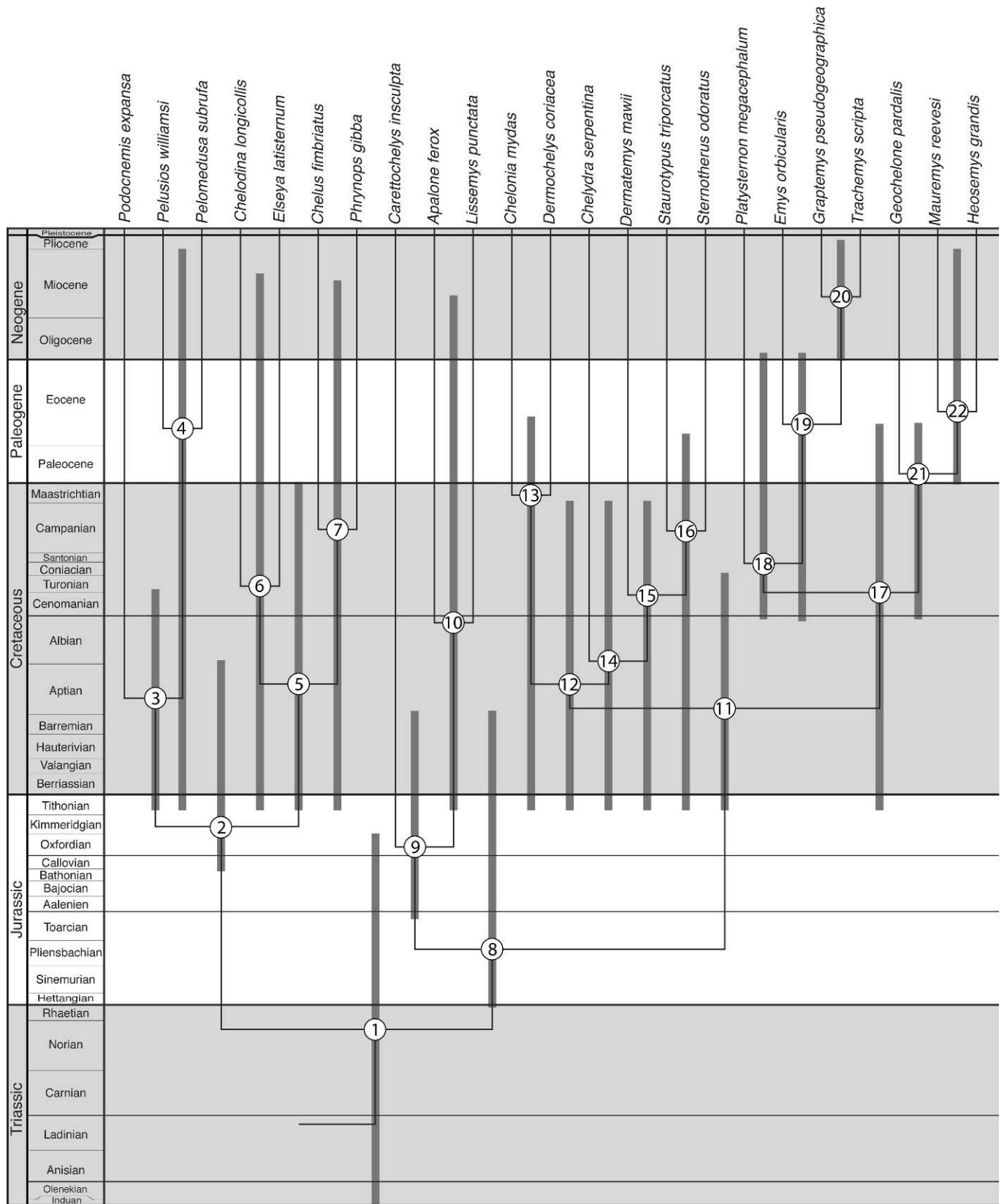


FIGURE 1—The phylogenetic hypothesis of turtle relationships and priors (gray bars) used in this study (see Table 1 for summary of minimum and maximum constraints). The priors were established using explicit best practice protocols. The numbers on the nodes are used throughout the text and in Table 1.

between the fossil-based minima and maxima. We implemented hard minimum and soft maximum constraints, allowing 2.5 percent of the probability distribution to exceed the maxima. Two independent runs were performed, each consisting of five million iterations, discarding the first 500,000 generations as burn-in and sampling every 100th generation, resulting in a total of 45,000 samples post burn-in. The analysis was also run without sequence data to examine the relationship between our specified priors and the effective calibration priors implemented in the analysis (Warnock et al., 2012). MCMC output was visualized (and 95% HPDs were calculated) using Tracer 1.5 (Drummond and Rambaut, 2007).

We did not explore the impact of topology on molecular clock estimates as part of this study (but see Dornburg et al., 2011). We therefore utilized the emerging consensus from molecular phylogenies of extant turtles (e.g., Fujita et al., 2004; Krenz et al., 2005; Barley et al., 2010) while assuming monophyly of Cryptodira and Pleurodira, which has been supported unambiguously by most recent morphological phylogenies (e.g., Hirayama et al., 2000; Gaffney et al., 2006; Joyce, 2007; Sterli et al., 2012; but see Krenz et al., 2005; Sterli, 2010). The resulting topology is illustrated in Figure 1.

RESULTS: CALIBRATION CONSTRAINTS

Testudines (Node 1).—Although many traditional and current phylogenies regard the Late Triassic turtle *Proterochersis robusta* as the oldest representative of crown Testudines (e.g., Gaffney, 1975; Gaffney and Meylan, 1988; Gaffney, 1996; Shaffer et al., 1997; Lapparent de Broin, 2000b; Hirayama et al., 2000; Gaffney et al., 2006), a growing number of more global phylogenies have come to question this conclusion (e.g., Rougier et al., 1995; Sukhanov, 2006; Joyce, 2007; Sterli, 2008, 2010; Sterli and de la Fuente, 2011; Anquetin, 2012). Regardless of whether this novel conclusion is correct, the competing hypotheses necessarily preclude us from using *Proterochersis robusta* as a basis for a minimum time constraint for the age of crown Testudines. Similar considerations also disqualify all currently known Lower and Middle Jurassic turtles, including *Kayentachelys aprix* Gaffney et al., 1987 (see Joyce and Sterli, 2012 for summary).

Following Joyce (2007), representatives of the three primary clades of turtles (total group Pleurodira, total group Cryptodira, and Paracryptodira) occur in the Late Jurassic. However, like Dryden (1988), Sterli and de la Fuente (2011), and Anquetin (2012) go beyond Joyce (2007) by also excluding all paracryptodires, xinjiangchelyids, eury sternids, and plesiochelyids from crown Testudines. Although these results may appear counterintuitive, it is imperative that our minimum constraint not be contingent on the outcome of this debate and so we therefore exclude these taxa from consideration as well. By contrast, the assessment that the holotype of *Caribemys oxfordiensis* de la Fuente and Iturralde-Vinent, 2001 (MNHNCu P-3209) from the Oxfordian Jugua Formation of Cuba is a total group pleurodire and thus placed inside crown Testudines has been universally accepted (e.g., de la Fuente and Iturralde-Vinent, 2001; Gaffney et al., 2006; Joyce, 2007; Sterli and de la Fuente, 2011; Anquetin, 2012) and is thus used for our minimum constraint on the age of crown Testudines (Fig. 2). Therefore, we place our minimum at the top of the Oxfordian (155.7 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 155.6 Ma.

Our constraint for the oldest possible age of the turtle crown must encompass *Proterochersis robusta*, even though its status as a crown turtle is highly questionable. The Lower to Middle Triassic has produced just one total group testudine, *Odon-tochelys semitestacea* Li et al., 2008, and we see no reason to doubt its placement as the oldest unambiguous stem-turtle (Anquetin, 2012). Rich Permian fossil sites worldwide have

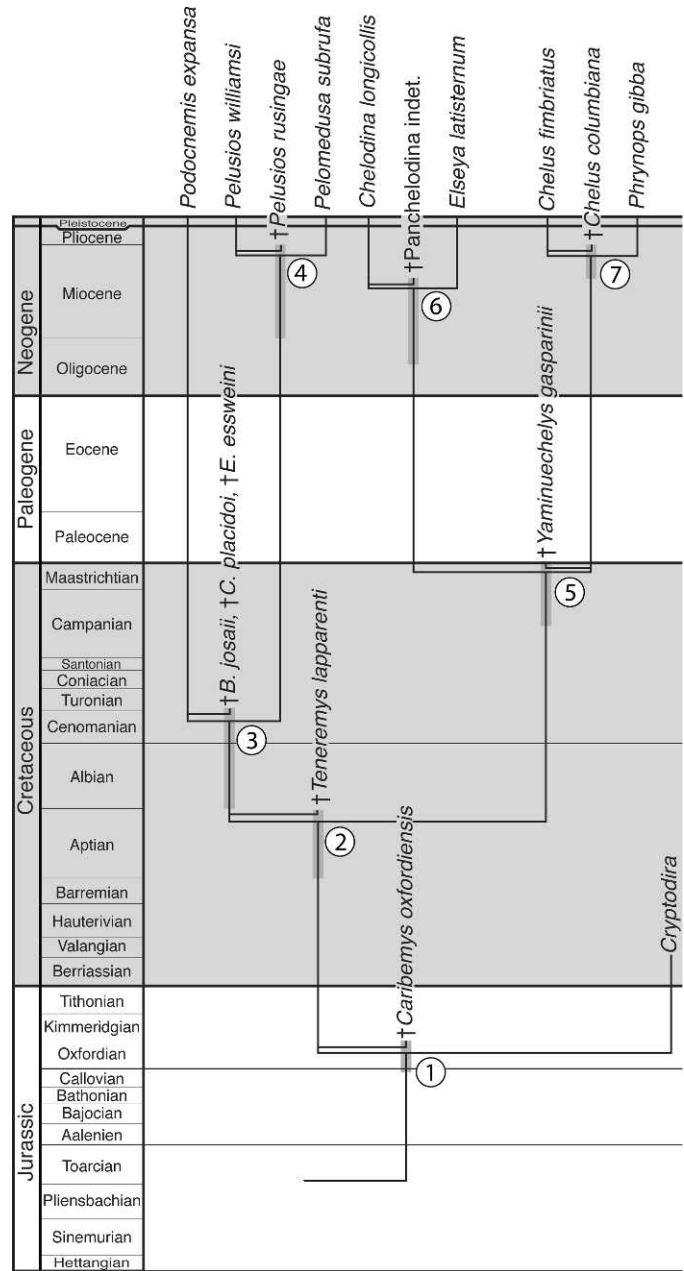


FIGURE 2—A phylogeny of turtles (node 1) and pleurodires (nodes 2–7) depicting the hypothesized phylogenetic position of fossils turtle used in this study within the molecular topology.

failed to yield anything that resembles a crown turtle, beyond the enigmatic *Eunotosaurus africanus* Seeley, 1892, which generally appears to serve the role of an early stem turtle well (Lyson et al., 2010). We therefore place our hard maximum at the base of the Triassic (251.0 ± 0.4 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 251.4 Ma.

Pleurodira (Node 2).—Given the uncertainty surrounding the age of the Santana Group turtles (see Pelomedusoides), the oldest uncontroversial crown pleurodire is the holotype of *Teneremys lapparenti* Broin, 1980 (MNHNF r GDF 820) from Gadoufaoua, Niger from the Early Cretaceous of Africa (Broin, 1980; Gaffney et al., 2006). This taxon was resolved well within crown Pleurodira by the global phylogenetic analysis of Gaffney et al. (2006; Fig. 2). The holotype specimen originates from layer GAD 5, at the top of the lower Tégama (Broin, 1980), and is therefore

Aptian (Taquet, 1976). We therefore base our minimum constraint on the top of the Aptian (112.0 ± 1.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 111.0 Ma, which coincides with the differently justified dates of Near et al. (2005) and Lourenço et al. (2012) using Santana fossils.

The pre-Aptian fossil record of total group pleurodires is very poor and it is thus difficult to rigorously assess the age of the crown. Late Jurassic localities worldwide have produced total group pleurodire material, none of which is attributable to the crown (e.g., Bräm, 1965; Cadena Rueda and Gaffney, 2005; Gaffney et al., 2006; Lapparent de Broin et al., 2007; Cadena et al., 2013). We therefore establish our soft maximum constraint conservatively at the base of the Late Jurassic (161.2 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 165.2 Ma.

Pelomedusoides (Node 3).—In comparison to the fossil record of chelids or pelomedusids, the fossil record of basal pelomedusoids is excellent (see Gaffney et al., 2006, 2011). To date, the Santana Group of Brazil has yielded many beautiful turtle specimens that represent at least three crown pelomedusoid species: the stem podocnemidids *Brasilemys josai* Lapparent de Broin, 2000b (MGB 37911), *Cearachelys placidoi* Gaffney et al., 2001 (MPSC uncat. + referred material), and *Euraxemys essweini* Gaffney et al., 2006 (SMF 4922) (see Gaffney et al., 2006 for a comprehensive summary and phylogenetic analysis; Fig. 2). *Caririemyx violeae* Oliveira and Kellner, 2007 is now considered to be a junior synonym of *E. essweini* (Romano et al., 2013). *Araripemys barretoii* cannot be used to date the minimum of the pelomedusoid crown, as some topologies show this taxon to be a stem pelomedusoid (see Gaffney et al., 2006).

As spectacular as the fossils are from the Santana Group, the stratigraphic sequence remains poorly dated to somewhere around the Early/Late Cretaceous (e.g., Maisey, 1990; Fara et al., 2005; Martill, 2007). The youngest possible age for the Santana Group is Cenomanian (Martill, 2007) and we therefore use the top of the Cenomanian for our minimum at 92.8 Ma (93.6 ± 0.8 Ma; Gradstein et al., 2004; Ogg et al., 2008).

As with all other crown pleurodiran taxa, our maximum is set at the base of the Cretaceous at 149.5 Ma (145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008).

Pelomedusidae (Node 4).—The fossil record of African pelomedusids is as poor as the fossil record of South American and Australian chelids. Although fossil turtles are presumably common elements among various Neogene hominid sites, this group has received a negligible amount of attention (for summary see Wood, 1973). In her review of the fossil turtles of Africa, Lapparent de Broin (2000a) listed a number of records that extend the presence of crown pelomedusids into the Paleocene, but this summary did not allow for detailed description of materials and we therefore agree with Gaffney et al. (2006) that her identifications cannot be reproduced at the moment. We agree with Near et al. (2005) that the holotype of *Pelusios rusingae* Williams, 1954 (NMK Ru F3617) is the oldest diagnosable pelomedusid (Fig. 2). Although this taxon has yet to be included in a phylogenetic analysis, its identity as belonging to the *Pelusios* lineage is uncontroversial, given that the holotype exhibits a fully formed anterior plastral hinge, a unique apomorphy of this taxon within Pleurodira (Williams, 1954).

The description of Williams (1954) is accompanied with very little locality data for the holotype of *Pelusios rusingae*, except that it originated from Rusinga Island, Kenya. Although most fossiliferous levels on this island are dated to be early Miocene, ashes are notably lacking from the upper portion of the section (Peppe et al., 2009). Until better geographic and geologic locality data has become available, we therefore conservatively date this node at the top of the Miocene at 5.3 Ma (5.332 Ma; Gradstein et al., 2004; Ogg et al., 2008).

As with all other pleurodires, we place the maximum for this clade at the base of the Cretaceous (145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma.

Chelidae (Node 5).—Phylogenetic analyses of morphological and molecular data concur that a clade comprised of *Chelus fimbriatus*, *Phrynops gibbus*, *Chelodina longicollis*, and *Elseya latisternum*, is synonymous with crown clade Chelidae (e.g., Gaffney, 1977; Georges et al., 1998; Bona and de la Fuente, 2005; Sterli et al., 2012). The holotype of *Yaminuechelys gasparinii* de la Fuente et al., 2001 (MPA 86-86-IC) makes for a problematic oldest demonstrable crown chelid (Near et al., 2005). The only phylogeny including this taxon resolves it as the sister taxon to *Hydromedusa* (Bona and de la Fuente, 2005), but the topology conflicts with those from molecular studies (e.g., Georges et al., 1998). However, if the topology of Georges et al. (1998) is forced upon the matrix of Bona and de la Fuente (2005), *Yaminuechelys* remains as the sister taxon to *Hydromedusa*. We thus agree that this taxon is the oldest demonstrable crown chelid (Fig. 2). It is unclear to us if the placement of the Aptian/Albian? taxon *Prochelidella cerrobarcinae* de la Fuente et al. 2011 within crown Chelidae (Sterli et al., 2012) is similarly unaffected by conflicting molecular and morphological hypotheses. Until more evidence is available, especially a species level phylogeny of chelid turtles, all older South American material otherwise referred to “Chelidae” (e.g., Lapparent de Broin and de la Fuente, 2001; Gaffney et al., 2006; de la Fuente et al., 2011) cannot be used for establishing a minimum time constraint for this clade.

The stratigraphy of the type locality of *Yaminuechelys gasparinii* remains poorly studied and de la Fuente et al. (2001) tentatively correlate this locality with strata of the upper Campanian to lower Maastrichtian Allen Formation. To remain as conservative as possible, we use the top of the Maastrichtian as our minimum date (65.5 ± 0.3 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 65.2 Ma.

Chelodiniinae (Node 6).—The fossil record of Australian chelids is extremely poor (e.g., Gaffney, 1981; Gaffney et al., 1989) and little is known about the evolution of this group. Identification of the oldest representative of Chelodiniinae (sensu Georges et al., 1998) is hampered further by the absence of a morphological phylogeny (e.g., Gaffney, 1977; Bona and de la Fuente, 2005) that recovers a monophyletic Chelodiniinae (i.e., the clade of Australian chelids). Thus, we identified the oldest fossil that can be assigned confidently to either the *Chelodina* or *Elseya* lineages.

Lapparent de Broin and Molnar (2001) described material attributable to *Chelodina* from the Eocene of Queensland. Unfortunately, although many non-discrete characters are available that allow this attribution (e.g., shell shape and shell ornamentation), Lapparent de Broin and Molnar (2001) concede that the material was too poorly preserved to reveal the necessary apomorphies for a positive referral to the *Chelodina* lineage. Although future material will likely confirm the assignment of this material to the *Chelodina* lineage, it is not yet sufficiently well established to serve as the basis of a minimum time constraint.

A number of Australian sites have produced diagnostic chelid fossils. Near et al. (2005) identified various fossil localities at Riversleigh Station as having produced the oldest remains of the *Chelodina* and *Elseya* lineages; we restrict ourselves to specimen QM F17418 from the Gag Site since this plastron can be diagnosed confidently as belonging to the *Chelodina* lineage (i.e., *Panchelodina* indet.) due to the presence of a large, fused gular that does not contribute to the anterior plastral lobe (see phylogenetic analysis of Gaffney et al., 1989; Fig. 2). Unfortunately, the chronostratigraphy of all Australian Tertiary terrestrial fossil sites is problematic. Some information indicates that

Riversleigh Station may be as old as late Oligocene, but other estimates are as young as 12 Ma (for summary see Gaffney et al., 1989). We utilize a conservative estimate for the middle Miocene as the top of the Serravalian age (11.6 Ma).

Although the fossil record of Australian chelids is extremely poor, chelid cervical material was recently reported from the Albian of Lightning Ridge (Smith, 2010) that most likely represents total group Chelidae or even total group Pleurodira. By contrast, no locality worldwide has produced a crown pleurodire in the Jurassic. We thus generously place our maximum at the base of the Cretaceous (145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008), thus 149.5 Ma.

Chelus fimbriatus—*Phrynops gibbus* (Node 7).—The Tertiary fossil record of South American chelids is only marginally better than that of Australia. Similarly, no morphology-based phylogenetic analysis has produced a topology that resembles any molecular phylogeny by placing *Chelus fimbriatus* and *Phrynops gibbus* closer to another, than either is to any extant Australian chelid (e.g., Gaffney, 1977; Bona and de la Fuente, 2005; Sterli et al., 2012). We have no recourse but to identify the oldest record that is diagnostic of either the *Chelus* or the *Phrynops* lineage. Given that the phylogenetic position of *Hydromedusa* remains uncertain (Georges et al., 1998), fossils from this lineage cannot be utilized for dating this node (e.g., de la Fuente and Bona, 2002).

We agree with Near et al. (2005) that various fossil *Chelus* presented by Wood (1976) were the oldest known representatives of either lineage at the time of their analysis (Fig. 2). More recently, Cadena et al. (2008) described older fragmentary material that was referred to *Chelus colombiana*. Specimen M1MP60505-79 consists of only a xiphiplastron, but the extremely deep anal notch and the shape of the pelvic suture are diagnostic of the *Chelus* stem lineage (Cadena et al., 2008). This specimen originated from the Laventan (Croft, 2007) Pubenza locality of the Barzalosa Formation, Colombia (Cadena et al., 2008) and is therefore early Miocene in age. We therefore establish our minimum time constraint at the top of the Laventan at 13.4 Ma (Madden et al., 1997).

The Late Cretaceous record of South American chelids is significantly better than the Tertiary record. A number of new taxa have been described in the last 20 years and some of these have been attributed to the *Chelus* or *Phrynops* lineages (e.g., Lapparent de Broin and de la Fuente, 2001). Even though some of these taxa are known from complete shells, most characters utilized are phenetic, and a phylogenetic analysis was not presented. Although the assessment of Lapparent de Broin and de la Fuente (2001) may be correct, it is not yet sufficient to substantiate a minimum time constraint.

For our soft maximum, we use the base of the Cretaceous (see Chelodiniinae for rationale; 145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma.

Cryptodira (Node 8).—Assessing the oldest representative of crown Cryptodira is difficult because the topology of morphological and molecular analyses differ and because few candidate taxa have been integrated into a global phylogeny. Near et al. (2005) suggested using *Sandownia harrisi* Meylan et al., 2000 from the Aptian of England, but the global analyses of Joyce (2007), Sterli and de la Fuente (2011), and Anquetin (2012) place doubt on the placement of *S. harrisi* within crown Cryptodira. Similar arguments could be made for the similarly aged *Santanachelys gaffneyi*, which Joyce (2007), Sterli and de la Fuente (2011), and Anquetin (2012) located outside of crown Cryptodira. Danilov and Parham (2006) and Tong et al. (2009b) concluded that the Late Jurassic adocusians *Yehguia tatsuensis* (Yeh, 1963) and *Basilochelys macrobios* Tong et al., 2009b should be considered the oldest known crown cryptodires,

respectively. Given the uncertainty associated with polarizing characters and assigning fossils at the base of Cryptodira, however, it is more conservative to calibrate this node with the oldest certain member of one of the more inclusive crown clades. Therefore, we suggest using the fragmentary stem trionychid remains that have been recovered from the Barremian Kitadani Formation of Japan (see Trionychia; Fig. 3) and place our minimum at the top of the Barremian (125.0 ± 1.0 Ma; Gradstein et al., 2004; Ogg et al., 2008), thus 124.0 Ma. Usage of adocusians leads to a slightly older minimum age of approximately 140 Ma (Lourenço et al., 2012).

For our soft maximum constraint we take special precaution and use the base of the Jurassic (199.6 ± 0.6 Ma; Gradstein et al., 2004; Ogg et al., 2008), thus 200.2 Ma.

Trionychia (Node 9).—Among turtles, total group (e.g., stem and crown) trionychids possess a unique surface sculpture that allows them to be positively identified even when only fragments are available (e.g., Holroyd and Hutchison, 2002). Traditionally, fragments were simply attributed to “Trionychidae” unless other characters are available, however, all fragments with such sculpturing should more correctly be classified as total group Trionychidae. Although the typical trionychid sculpture is found almost universally among total group trionychids, some trionychid taxa may lose this sculpture partially or completely and may therefore be incorrectly diagnosed (e.g., *Hutchemys* spp., Joyce et al., 2009). More significantly, the surface sculpture of a number of other turtle lineages converges upon that of total group trionychids (e.g., representatives of Adocusia). The identification of any partial shell fragment as a total group trionychid thus carries a certain amount of doubt. The recent discovery of the unique shell histology of total group trionychids consisting of layers of organized fibers that are integrated into the surficial portion of all metaplastically ossified shell bones (Scheyer et al., 2007) is thus highly significant. The presence of this diagnostic histology allows for the positive identification of highly fragmentary or worn material. Although less organized, the presence of fibrous layers was recently confirmed by Nakajima et al. (2009) to be present in the material (FPDM V-127) described by Hirayama (2002) and Hirayama et al. (2013) from the Barremian Kitadani Formation (Tetori Group; Fujita, 2003) of Japan (Fig. 3) and we therefore identify this material as Pantrionychidae indet. Our minimum constraint for crown Trionychia is therefore set at the top of the Barremian (125.0 ± 1.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 124.0 Ma. Unambiguous carettochelyid material from the “pre-Aptian” Sao Khua Formation of Thailand (Tong et al., 2009a) also supports a Barremian minimum age of this clade (Lourenço et al., 2012), though with less stratigraphic confidence.

The early fossil record of total group Trionychia is restricted to Asia (e.g., Rabi et al., 2010) and it therefore appears clear that this clade originated in Asia. Danilov and Parham (2008) suggest that *Yehguia tatsuensis* (Yeh, 1963) is on the stem of Trionychia (but see Cryptodira). To date, only a single pre-Cretaceous crown group trionychian has been reported worldwide: *Sinaspideretes wimani* (also see Trionychidae). Although the locality was originally dated as Jurassic, lack of detailed stratigraphic information (i.e., “locality along the Chengyu Railway, Sichuan”) makes an early Cretaceous age possible (Meylan and Gaffney, 1992). *Sinaspideretes wimani* was originally described as a “trionychid,” but most authors have since placed this taxon within total group Carettochelyidae based on surface sculpturing (e.g., Broin, 1987; Meylan and Gaffney, 1992; Brinkman et al., 2008). A more recent analysis of the type specimen convincingly demonstrated similarities of *S. wimani* with the *Yehguia tatsuensis* (Yeh, 1963) and its likely identity as a stem-trionychian (Tong and Ouyang, 2012). To remain as conservative as possible in establishing a maximum for our constraint, we accept *S.*

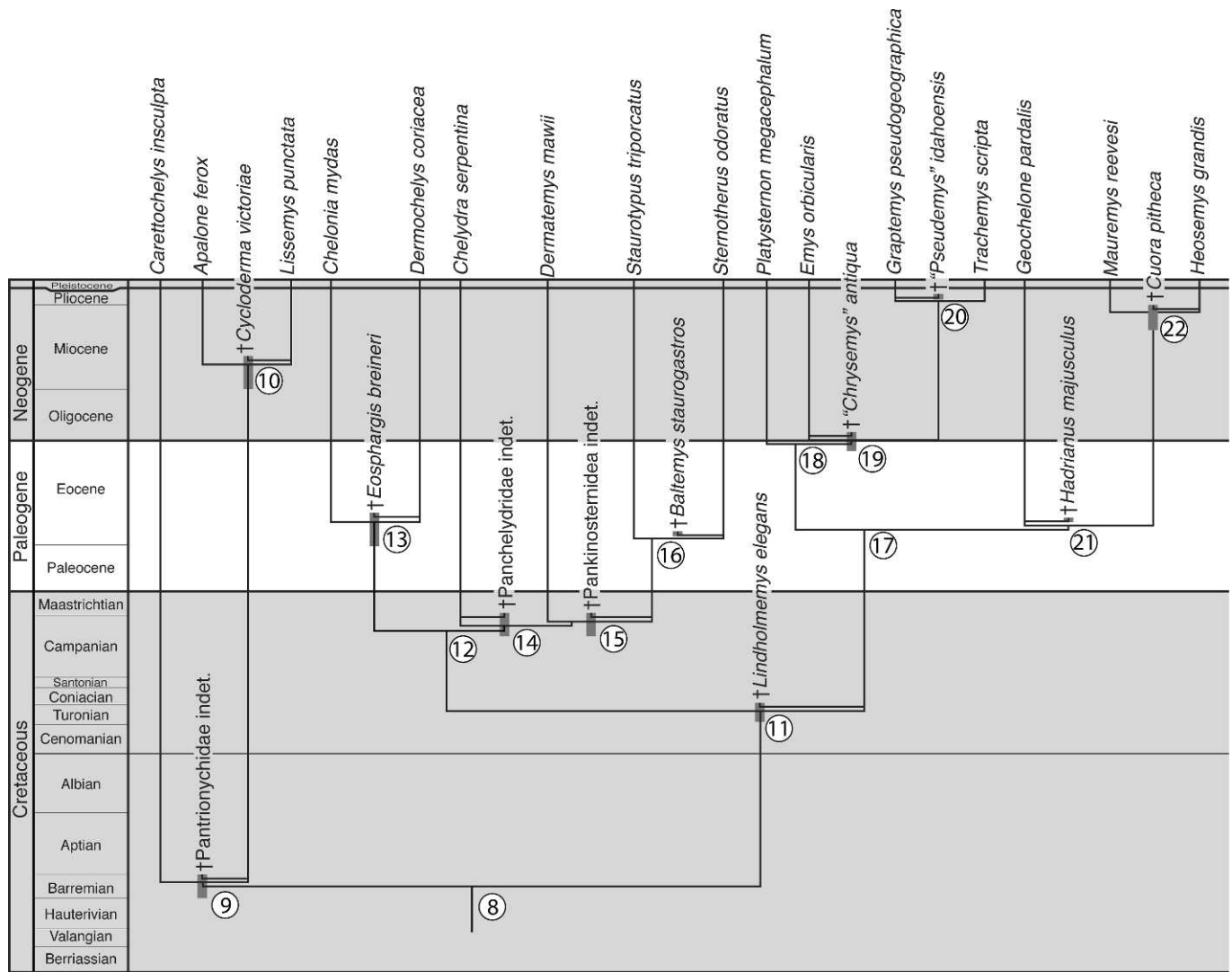


FIGURE 3—A phylogeny of cryptodires (nodes 8–11) depicting the hypothesized phylogenetic position of fossils within the molecular topology used in this study within the molecular topology.

wimani as a possible trionychian as well as its possible Jurassic age.

In contrast to other continents, Asia has rather extensive outcrops of Middle Jurassic continental deposits that have yielded a diverse vertebrate fauna. Yet, despite the preponderance of turtles in many such Middle Jurassic localities (for summary see Rabi et al., 2010), not a single fragment has been referred to total group Trionychia. Considering that we are forced to accept *S. wimani* as a potential Late Jurassic crown trionychian, we cautiously place the soft maximum constraint at the base of the Middle Jurassic (175.6 ± 2.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 177.6 Ma. Lourenço et al. (2012) discounted *S. wimani* and therefore arrived at the significantly younger, and likely more reasonable, maximum age of 131.5 Ma.

Trionychidae (Node 10).—Of all crown clades, the fossil record of Trionychidae is perhaps the most poorly understood. Fossils diagnostic of total group Trionychidae occur as far back as the Early Cretaceous of North America and Asia (for summary see Joyce and Lyson, 2010a) and more than 200 species of fossil trionychids have been named (Kuhn, 1964). Trionychids are usually classified using simplistic typological keys and, therefore, the phylogenetic position of the vast majority of fossils remains dubious. This includes the poorly characterized taxon “*Aspider-*

etes” *maortuensis* Yeh, 1965 (e.g., Danilov and Vitek, 2013), which has been used as an Early Cretaceous calibration in some studies (Near et al., 2005; Hugall et al., 2007; Marshall, 2008; Dornburg et al., 2011). Moreover, the stratigraphic provenance of this taxon is dubious and it may have actually been collected from Late Cretaceous strata (Brinkman et al., 2008).

Only a few studies have focused on the phylogenetic relationships of fossil trionychids, although interest has increased substantially in recent years (Gardner et al., 1995; Karl, 1999; Joyce et al., 2009; Head et al., 2009; Joyce and Lyson, 2010a, 2011; Vitek, 2011, 2012). All of these analyses are based on the morphology-based analysis of extant trionychids of Meylan (1987) with minor additions of characters and fossil taxa. However, the great level of homoplasy that is observed within Trionychidae (Meylan, 1987) makes it very difficult to achieve rigorous and reproducible results. The vast majority of analyses hypothesize that various Campanian to Paleogene trionychids of North American are crown trionychids (e.g., Gardner et al., 1995; Joyce et al., 2009; Joyce and Lyson, 2010a, 2011; Vitek, 2011, 2012), but minor changes to the matrix retrieve contrary results (e.g., Head et al., 2009). Although we think it to be highly reasonable that crown Trionychidae originated in the Late

Cretaceous, our protocols demand that we circumvent these studies until more rigorous results are available.

The oldest unambiguous crown-trionychid is the holotype of *Cycloderma victoriae* Andrews, 1914 from the early Miocene of Kenya (Andrews, 1914; BMNH 4105; Fig. 3). This fossil consists of an almost complete carapace and clearly preserves ‘split costiform processes’, a character that is uniquely encountered among crown Cyclanorbinae and, therefore, a diagnostic character of taxa deep within Trionychidae (Andrews, 1914; Meylan, 1987; Meylan et al., 1990). The early Miocene Karungu Beds of Kenya have been dated directly to 17.8 Ma \pm 0.5 Ma (Drake et al., 1988), providing a minimum age constraint of 17.3 Ma.

Given that even fragmentary shells are diagnostic of Trionychidae (see Trionychia), establishing a maximum date for the clade is somewhat easier than establishing a minimum date. Various poorly dated strata from the Early Cretaceous have been reported to contain fragmentary remains of “Trionychidae” (e.g., Hirayama et al., 2000; Sukhanov, 2000; Hirayama, 2002). Some of these fossils have since been revealed to be stem trionychids (Hirayama et al., 2013), and none of the rest is demonstrably from the crown (see Trionychia). An even older fossil trionychid was reported from the Late Jurassic of China (*Sinaspideretes wimani* Young and Chow, 1953), but recent reviews of this taxon reveals that it is not a trionychid and that the Late Jurassic date is dubious (Meylan and Gaffney, 1992; Tong and Ouyang, 2012). We therefore place our maximum for crown Trionychidae at the base of the Cretaceous (145.5 Ma \pm 4.0 Ma; Ogg et al., 2008) at 149.5 Ma.

Durocryptodira (Node 11).—Recent molecular phylogenies have support the monophyly of non-trionychian cryptodires (Fujita et al., 2004; Krenz et al., 2005; Parham et al., 2006; Barley et al., 2010), a clade named Durocryptodira by Danilov and Parham (2006) in reference to their hard shell. The oldest fossils that can be assigned to crown Chelydroidea or crown Chelonioida (or their total groups) are from the Campanian of North America (see sections for Chelydroidea and Americhelydia). Older fossils from Asia have been assigned to the stem of Testudinoidea, including fragmentary fossils from the Barremian (>125.0 Ma) of Japan (Hirayama, 2002) and the Albian/Cenomanian (>92.4 Ma) of Uzbekistan (Danilov, 1999). These records are not yet sufficiently substantiated to justify their use in establishing a minimum divergence time constraint. The next oldest stem testudinoid is *Lindholmemys elegans* Riabinin, 1935 from the Turonian Bissekty Formation of Uzbekistan (Feldmann et al., 2007).

Shaffer et al. (1997) were the first to include *L. elegans* in a phylogenetic analysis, but Danilov and Parham (2005) showed that the specimens used to code characters for the *Lindholmemys* in Shaffer et al. (1997) actually represent a chimera of different taxa. The skull has since been shown to belong to the adocid turtle *Adocus aksary* Nessov in Nessov and Krasovskaya, 1984 (Syromyatnikova and Danilov, 2009). However, Danilov and Parham (2005) did show that *L. elegans* (CCMGE 34/12175) could be placed on the testudinoid stem with confidence (Fig. 3). We therefore place our minimum time constraint at the top of the Turonian (~88.6 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 88.6 Ma.

Using the arguments outlined for Chelydroidea, Chelonioida, and Testudinoidea, we establish our soft maximum constraint for Durocryptodira at the base of the Cretaceous (145.5 \pm 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma.

Americhelydia (Node 12).—Recent molecular phylogenies strongly support a sister relationship between Chelydroidea and Chelonioida (Fujita et al., 2004; Krenz et al., 2005; Parham et al., 2006; Barley et al., 2010), but this important cryptodiran clade

remains unnamed to date. To fill this important nomenclatural gap, we herein suggest the name Americhelydia to refer to the clade that originated from the most recent common ancestor of *Chelonia mydas* (Linnaeus, 1758), *Chelydra serpentina* (Linnaeus, 1758), and *Kinosternon scorpioides* (Linnaeus, 1766). The name was chosen because the early fossil record of all subclades (Chelonioida, Chelydridae, Kinosternoidea) strongly hints at a North American origin of the clade (Parham and Hutchison, 2003).

No stem chelydroids have been identified to date, but specimens from the Late Cretaceous of North America have been identified as crown chelydroids and total group chelonioids (Fig. 3). In particular, the oldest chelydroids are stem kinosternids and stem chelydrids from the Cerro del Pueblo Formation (Campanian) of Mexico (see Chelydroidea). Assigning turtle fossils to total group Chelonioida, by contrast, is problematic because of the possibility that taxa traditionally assigned to that name may in fact belong to a separate, stem-cryptodiran marine radiation (see Chelonioida). The oldest total group chelonioids might be from the Late Cretaceous Niobrara Chalk Formation of the Western Interior, which ranges in age from the Coniacian to the Campanian. Some undescribed specimens from Coniacian (FHSM VP-13449) and Santonian (FHSM-17432) parts of the section might eventually be shown to be stem chelonioids, but pending description and analysis of those specimens we do not use them to establish a minimum age constraint for total group Chelonioida. The oldest definitive total group chelonioids, *Toxochelys* spp. and *Ctenochelys* spp., are known unambiguously from the Campanian portion of the Niobrara Chalk as well as the Campanian Mooreville Chalk Formation. This phylogenetic placement is supported by all recent phylogenetic analyses (Hirayama, 1994, 1998; Joyce, 2007; Anquetin, 2012). The most complete specimen assigned to either genus is ROM 28563 (referred to *Toxochelys latiremis* Cope, 1873 by Nicholls, 1988). It should be noted that the locality and stratigraphic position of ROM 28563 within the Niobrara Formation is in question (Everhart, personal commun.) and it may eventually be assignable to a level older than the Campanian age reported by Nicholls (1988). We conservatively retain the youngest possible age (Campanian) for this specimen. The oldest total group Chelonioida is therefore as old as the oldest total group Chelydridae and total group Kinosternoidea (see Kinosternoidea and Chelydroidea). We therefore use the top of the Campanian (70.6 \pm 0.6 Ma; Gradstein et al., 2004; Ogg et al., 2008), or 70.0 Ma, as our minimum for Americhelydia.

Using the arguments outlined for Kinosternidae, Kinosternoidea, Chelonioida, and Chelydroidea, we place our hard maximum for Americhelydia at the base of the Cretaceous (145.5 \pm 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma.

Chelonioida (Node 13).—Near et al. (2005) proposed that *Santanachelys gaffneyi* Hirayama, 1998 is the oldest known chelonioid, but global analyses that include *S. gaffneyi* as a separate terminal taxon (e.g., Joyce, 2007; Sterli and de la Fuente, 2011; Anquetin, 2012) universally place this taxon outside crown group Chelonioida and even outside of crown group Cryptodira. Prior to these analyses, *S. gaffneyi* was hypothesized to be a member of the Protostegidae (Hirayama, 1994, 1998), a relatively diverse and widespread radiation of Cretaceous marine turtles thought to belong to the total group of *Dermochelys coriacea*. It is not clear whether other protostegids (e.g., *Protostega gigas* Cope, 1871, *Archelon ischyros* Wieland, 1896) should also be placed with *S. gaffneyi* along the stem of Cryptodira. A comprehensive analysis that includes many fossil sea turtles along with other cryptodire groups is lacking and the status of protostegids and

most Cretaceous fossil sea turtles as chelonioids or even crown cryptodires therefore remains uncertain.

In order to identify a minimum constraint for Chelonioidea, it is necessary to identify a non-protostegid fossil that can be placed within the crown group. The phylogenetic placement of the oldest (Campanian, >70 Ma) fossils traditionally placed on the cheloniid stem, *Toxochelys* and *Ctenochelys*, remains controversial as many authors assign one or both of these taxa to stem Chelonioidea (i.e., outside the crown; Kear and Lee, 2006; Joyce, 2007). Other Late Cretaceous marine turtles, *Nichollsemys baieri* Brinkman et al., 2006 and *Mexichelys coahuilaensis* (Brinkman et al., 2009), are placed close to *Toxochelys* and *Ctenochelys* in cladistic analyses of marine taxa (Brinkman et al., 2009; Parham and Pyenson, 2010) and therefore have the potential to be stem chelonioids.

Current global analyses (Joyce, 2007; Sterli and de la Fuente, 2011; Anquetin, 2012) do not include many Latest Cretaceous or Cenozoic sea turtles and so it is not known whether many of these taxa can be placed within the crown of Chelonioidea (either on the cheloniid or *D. coriacea* stems). This is especially true for putative stem cheloniids because they tend to exhibit only symplesiomorphies of Chelonioidea and are difficult to distinguish from stem chelonioids. For this reason we are reluctant to use any stem-cheloniid as the basis for our minimum constraint.

The other major branch of chelonioids, the *D. coriacea* lineage (Dermochelyidae), suffers similarly from a lack of phylogenetic analyses that integrate fossil species, although the highly specialized morphology of this lineage allows us to assign some taxa with confidence. *Mesodermochelys undulatus* Hirayama and Chitoku, 1996 from the Maastrichtian was placed on the stem of *D. coriacea* when it was described (Hirayama and Chitoku, 1996) and this placement has been confirmed by every subsequent phylogenetic analysis (Hirayama, 1998; Lehman and Tomlinson, 2004; Brinkman et al., 2006; Kear and Lee, 2006), including the global analysis of Joyce (2007) and Anquetin (2012). Reports of much earlier fossils attributed to the *M. undulatus* lineage (Hirayama and Chitoku, 1996; Hirayama, 1997; Hirayama and Hikida, 1998) appear to extend the antiquity of Chelonioidea to the Santonian (>85 Ma) but many of these reports are based on fragmentary specimens. Still, although it might be tempting to constrain the age of this node based on the type specimen of *M. undulatus*, new material referred to this taxon reportedly changes its phylogenetic position. Hirayama (2007) attributed an isolated skull to *M. undulatus* and mentioned that a new analysis now places this species as a protostegid. The referral of this new specimen and details of this new analysis are not yet published but the preliminary report is sufficient to cast doubt on the phylogenetic placement of *M. undulatus* and its use in establishing a minimum time constraint for Chelonioidea. The only other Cretaceous sea turtle placed on the stem of *D. coriacea* is *Corsochelys halinches* Zangerl, 1960 from the Campanian (>70 Ma) of the U.S.A. Like most other Cretaceous sea turtles, *C. halinches* still needs to be studied in the context of global phylogenetic analysis. Given the close association and confusion between taxa assigned to Protostegidae and the stem of *D. coriacea*, we consider the position of *C. halinches*, and fragmentary remains referred to it (Tong and Hirayama, 2004), as total group Cryptodira incertae sedis.

Several secure records of dermochelyids are known from the Paleogene. Among these include forms characterized by a “leatherback shell,” a carapace comprised a mosaic of ossicles replacing most of the typical carapacial bones. This mosaic is an unambiguous synapomorphy of the *D. coriacea* lineage. The earliest turtle with a mosaic, *Arabemys crassiscutata* Tong et al., 1999 is known from the late Paleocene–early Eocene Aruna

Formation of Saudi Arabia although the exact age is poorly constrained (Thomas et al., 1999). However, approximately coeval with *A. crassiscutata* are two species of *Eosphargis* from the early Eocene (Ypresian) of Europe. *Eosphargis* species lack the mosaic, but share the reduced costal ossification and highly modified skull seen in all definitive dermochelyids (see phylogenies of Hirayama, 1994 and Wood et al., 1996; Fig. 3). Both known species of *Eosphargis*, *E. gigas* (Owen, 1861) and *E. breineri* Nielsen, 1959, are known from the early Eocene, but we choose the holotype of *E. breineri* (FM uncat.) because it is the best-described specimen that we can assign to a specific geologic unit, i.e., the Ypresian Fur Formation of Denmark, Ypresian (Nielsen, 1959). Most specimens of *E. gigas* from the London Clay are more incomplete than the holotype of *E. breineri* whereas the best-known specimen referred to *E. gigas*, from Belgium (Quintart and Plisnier-Ladame, 1968), has not yet been assigned to a specific stratigraphic unit. We derive our minimum constraint from the top of the Ypresian (48.6 ± 0.2 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 48.4 Ma.

The maximum age for this node is difficult to ascertain because of the aforementioned uncertainty concerning the phylogenetic placement of Cretaceous taxa. No Cretaceous marine turtle can be resolved phylogenetically with any significant level of precision. At various times, Cretaceous species have been assigned to the stem of Cheloniidae, the stem of *D. coriacea*, or the incertae sedis clade Protostegidae. On the other hand, turtles from Late Jurassic marine deposits have not been referred to Chelonioidea in the last 100 years (e.g., Kuhn, 1964; Bräm, 1965; Mlynarski, 1976; Joyce, 2000, 2003; Lapparent de Broin, 2001). We therefore establish the maximum constraint on the Jurassic–Cretaceous boundary (145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma.

Chelydroidea (Node 14).—Many traditional classifications of turtles recognized a close phylogenetic relationship between Chelydridae and Kinosternoidea (e.g., Baur, 1893; Mlynarski, 1976), though typically to the exclusion of *Dermatemys mawii* (e.g., Gray, 1869, 1870; Vaillant, 1894; Williams, 1950; Romer, 1956), but this phylogenetic arrangement fell into disfavor given the prevalence of cranial characters that united Kinosternoidea with Trionychia (e.g., Meylan and Gaffney, 1989). As a result, most fossil turtles described over the course of the last 30 years were analyzed phylogenetically under the assumption that chelydrids and kinosternoids are not closely related and that the similarities they share must have been independently derived. However, recent molecular studies (e.g., Krenz et al., 2005; Barley et al., 2010) have suggested that chelydrids and kinosternoids are sister taxa, so that is the topology that we used to assess possible calibrations.

The monophyly suggested by the molecular results is supported by morphological synapomorphies. In addition to the near identical cervical column mentioned above, chelydrids and kinosternoids are also easily diagnosed by being the only turtles to possess “true” rib-like costiform processes (see Joyce, 2007 for discussion of this character). In kinosternoids, this process is a triangular spine that runs along the visceral side of the wedge-shaped first peripheral and that inserts into the second peripheral. In chelydrids, this process is rib like, runs along the visceral side of the first two rectangular peripherals and inserts into the third peripheral. Considering that all potential outgroups do not have such well-developed costiform processes and that this character complex forms a morphocline, it is apparent that the extant kinosternid condition is basal for the clade (Knauss et al., 2011) and cannot be used to diagnose fossil kinosternoids. In contrast, the chelydrid condition is unique among turtles allowing confident assignment of fossil turtles to the chelydrid lineage

(e.g., person. observation of *Emarginachelys cretacea* Whetstone, 1978 by WGJ, contra Meylan and Gaffney, 1989).

The oldest total group chelydrids known from partial skeletons are *Protochelydra zangerli* Erickson, 1973 from the Tiffanian NALMA (late Paleocene) of North Dakota, *Denverus middletoni* Hutchison and Holroyd, 2003 and *Tullochelys montana* Hutchison, 2013 from the Puercan NALMA (early Paleocene) of Colorado and Montana, respectively, and *Emarginachelys cretacea* from the Maastrichtian of Montana (Whetstone, 1978). Hutchison and Archibald (1986) and Holroyd and Hutchison (2002) reported on Maastrichtian fragments and Brinkman and Rodriguez de la Rosa (2006), Brinkman (2003, 2005), Hutchison et al. (1998, in press) reported on Campanian fragments. Brinkman (2003) discuss even older fragments from the Santonian Milk River Formation whereas Eaton et al. (1999) mention Turonian material from Utah. Unfortunately, although we think it is feasible that many of these fragments are total group chelydrids, the only figured fragment from the Mesozoic that have unambiguous synapomorphies is SEPCP 9/493 (Brinkman and Rodriguez de la Rosa, 2006, fig. 8), a peripheral fragment articulated with the rib-like costiform process of chelydrids. This fragment is therefore identified as Panchelydridae indet. As such, the oldest confirmed total group chelydrid (SEPCP 9/493) and the oldest confirmed total group kinosternoid (SEPCP 48/282, see Kinosternoidea) both originate from the Campanian Cerro del Pueblo Formation of Mexico and both remains therefore serve as the oldest known representatives of Chelydroidea (Fig. 3). We therefore derive our minimum constraint from the top of the Campanian (70.6 ± 0.6 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 70.0 Ma.

The North American fossil record is characterized by a paucity of fossils that fill the substantial gap between the widespread Late Jurassic (Tithonian) Morrison Formation and equally widespread Late Cretaceous (Campanian) sediments. A number of publications list fossil turtles from this time span, but only few formal descriptions exist. Eaton et al. (1999) reported the oldest total group chelydrid from the Turonian of Utah, but we are unaware of any reports of chelydrid from the Lower Cretaceous. As with a number of other North American clades, we set the maximum at the base of the Cretaceous (145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma, because not a single crown cryptodire has been reported from the Jurassic, despite 130 years of extensive collecting (e.g., Hay, 1908; Carrano and Velez-Juarbe, 2006).

Kinosternoidea (Node 15).—We agree with Near et al. (2005) that *Hoplochelys* spp. was the oldest known representative of crown Kinosternoidea in 2005. However, the lack of stratigraphic detail accompanying all specimens then published would have permitted only a minimum constraint at the end of the Puercan NALMA of New Mexico (Gilmore, 1919). Various Mesozoic fragments have been referred to *Hoplochelys* as well (e.g., Hell Creek Formation, Hutchison and Archibald, 1986; Cerro del Pueblo, Brinkman and Rodriguez de la Rosa, 2006), but we conclude that these specimens are too fragmentary to provide a rigorous assessment of their phylogenetic position. The oldest unambiguous representative of the *Dermatemys mawii* lineage is the complete shell of *Hoplochelys clark* Knauss et al., 2011 described from the late Maastrichtian Hell Creek Formation (Knauss et al., 2011). Older specimens from the Cenomanian–Turonian of Mongolia previously referred to *Hoplochelys* sp. are now identified as “macrobaenids” (Sukhanov et al., 2008).

More recently, Brinkman and Rodriguez de la Rosa (2006) reported specimens from the Campanian Cerro del Pueblo Formation that indicate a phylogenetic placement outside of Kinosternidae, but within Kinosternoidea (Fig. 3). Although no

complete specimen is available, we agree that the costal elements depicted by Brinkman and Rodriguez de la Rosa (2006, SEPCP 48/282, fig. 4C) display enough morphology to be diagnostic of total group Kinosternidae (i.e., Pankinosternidae indet.), in particular the presence of narrow hexagonal scutes, the diminutive size, and the high-domed cross-section (see phylogenies of Hutchison and Bramble, 1981 and Hutchison, 1991). We therefore place our minimum constraint at the top of the Campanian (70.6 ± 0.6 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 70.0 Ma. Following the arguments outlined for Kinosternidae, we place our maximum at the base of the Cretaceous (145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma.

Kinosternidae (Node 16).—We concur with Near et al. (2005) that *Baltemys* is the oldest known representative of Kinosternidae, but some minor adjustments are nevertheless necessary to fulfill all of our criteria. The only species currently placed in *Baltemys* is the type species *B. staurogastros* Hutchison, 1991. In the original description, a large number of fragments were referred to this taxon from the Wasatchian North American Land Mammal Age (NALMA) (early Eocene). In a later publication, Holroyd et al. (2001) provided a more precise assessment of the age distribution of this taxon as being Wasatchian 1–2 to Wasatchian 6 and cite specimens that document the minimum and maximum of this stratigraphic range. Although we have little reason to doubt the referral of any of Hutchison’s (1991) or Holroyd et al.’s (2001) hypodigm specimens to *B. staurogastros* or even *Baltemys* sp., only the holotype and one paratype specimens are figured (Hutchison, 1991; UCMP 127200) and thus allow for the reproduction of his character observations and confirmation of the phylogenetic placement of these two specimens. The holotype is the older of the two specimens and we consequently choose this specimen to establish our minimum constraint. The phylogenetic analysis of basal kinosternoids by Hutchison (1991) is the most comprehensive to date and amply demonstrates the placement of *B. staurogastros* within crown Kinosternidae (Fig. 3). The holotype originated from UCMP locality V81170, which is interpreted as being from the Wasatchian 6 (Lysititan) portion of the Willwood Formation (Hutchison, 1991). An Argon–Argon date from a Wasatchian 7 ash layer allows us to place the minimal at 52.8 Ma (Wing et al., 1991; Smith et al., 2003).

Kinosternids are extremely rare in the fossil record, in part because most are small bodied and fragile (for summary see Bourque, 2013). Among fossil kinosternoids in general, even heavy shelled taxa such as *Hoplochelys* spp. are only seldom found and typically only as fragmentary material (e.g., Holroyd et al., 2005; Knauss et al., 2011). Kinosternid-like material has been reported from the Paleocene of South Carolina (Hutchison and Weems, 1999), but specimens are too fragmentary to allow confident referral to the crown. Fragments were also reported from the Hell Creek Formation of Montana (Hutchison and Archibald, 1986) but were once again too incomplete to allow a phylogenetic assessment. Brinkman and Rodriguez de la Rosa (2006) recently presented ‘kinosternid’ material from the Campanian of Mexico that is demonstrably placed along the stem of total group Kinosternidae, but is nevertheless surprisingly derived in many of its features. Similar ‘kinosternid’ material from the Campanian of Utah (Hutchison et al., in press) is also likely placed outside the crown group. It nevertheless seems at least plausible that more extensive fieldwork in the Late Cretaceous of Mexico and Central America, the current paleobiogeographic center of the group, may result in the discovery of Mesozoic crown kinosternids.

Prior to the Campanian, the North American fossil record is extremely poor (e.g., Cloverly Formation: Ostrom, 1970; Trinity Formation: Gaffney, 1972; Arundel Formation: Lipka et al.,

2006) making it impossible to assess whether kinosternids were present. However, the Late Jurassic Morrison Formation of North America is widely distributed, well exposed, and has been heavily prospected for vertebrate fossils. Large quantities of turtle material have been found to date in the Morrison Formation, and not a single specimen is referable to crown Cryptodira (Gaffney, 1979; Brinkman et al., 2000; Carrano and Velez-Juarbe, 2006). A similar argument can be made for other regions worldwide. We thus place our soft maximum constraint at the base of the Cretaceous (145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma.

Testudinoidea (Node 17).—The primary character that distinguishes all extant testudinoids relative to their outgroups is the reduction of the number of inframarginal scutes from four to two (the axillary and inguinal scutes). All known pre-Eocene testudinoids have more than two inframarginal scutes and, thus, may reasonably represent the stem of the crown clade. Given that no pre-Eocene testudinoid is therefore diagnostic of crown Testudinoidea, we use *Hadrianus majusculus* Hay, 1904 to establish a minimum constraint on age of this node (Fig. 3) and set our minimum at 50.3 Ma (for details see Testuguria).

Various Mesozoic Asiatic taxa have been referred to the testudinoid crown group (e.g., Chkhikvadze, 1983, 1987, 1990), implying multiple reductions of the inframarginal series. Considering that only a few of these Mesozoic forms have ever been integrated into a phylogenetic analysis, we must conclude that they are possibly part of the crown and so establish a soft maximum age constraint on the base of the Early Cretaceous (145.5 ± 4.0 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 149.5 Ma, prior to the first appearance of any fossils that resemble crown testudinoids.

Emydidae.—*Platysternon megacephalum (Node 18)*.—The fossil record of the *Platysternon megacephalum* stem lineage is very poorly known. Two fossil taxa have been described as belonging to this stem lineage, in particular *Planiplastron tatarinovi* Chkhikvadze, 1971 from the Oligocene of Kazakhstan and *Cardichelyon rogerwoodi* Hutchison, 2013 from the Paleogene of North America. However, although both studies list characters to support this hypothesis, the phylogenetic placement of both taxa remains dubious until they are better described and/or integrated into a global analysis. We therefore conservatively dated the Emydidae–*Platysternon megacephalum* node based on the oldest available emydid (Fig. 3) at 34 Ma (for details see Emydidae) and placed the maximum at the base of the Late Cretaceous at 100.5 Ma like all other testudinoid groups.

Emydidae (Node 19).—We agree with Near et al. (2005) and Lourenço et al. (2012) that “*Chrysemys*” *antiqua* (Clark, 1937) is the oldest known crown emydid, but some modifications are nevertheless necessary. “*Chrysemys*” *antiqua* was originally placed in *Trachemys*. More recently, Hutchison (1996) revised this taxon, confirmed its emydid nature, but concluded that an assignment to *Chrysemys* is more appropriate. Our insertion of “*Chrysemys*” *antiqua* into the matrix of Joyce and Bell (2004) using a molecular consensus backbone (Feldman and Parham, 2002; Spinks and Shaffer, 2009) once again confirms the emydid nature of this taxon and places it firmly within the deirochelyine lineage (Fig. 3). The same analysis places the coeval *Pseudograptemys inornata* just outside the crown (see Appendix 1 for details). The placement of “*Chrysemys*” *antiqua* within crown Emydidae is supported by the absence of an overlap of the humeropectoral sulcus with the entoplastron and the absence of anterior and posterior musk glands and musk ducts. The most parsimonious placement of “*C.*” *antiqua* is as sister to *Deirochelys reticularia*, but various alternative placements within crown Deirochelyinae are only one step longer. Any placement outside the *Chrysemys* node, however, is three steps longer. The

assignment of “*C.*” *antiqua* to *Chrysemys* should thus be viewed with caution.

In addition to providing a morphological summary of *Chrysemys antiqua*, Hutchison (1996) summarized its stratigraphic distribution within the White River Group as Chadronian to Whitneyan. Although the assignment of all referred material appears reasonable, SDSM 2754 is the only specimen that consists of a near complete carapace and plastron, allowing all characters to be seen that help determine its phylogenetic placement. This specimen originates from SDSM locality V271 within the Orellan (Oligocene) *Protoceras* channels of the White River Group of South Dakota. We therefore establish our minimum constraint on the top of the Orellan at 32.0 Ma (Prothero and Emry, 2004).

Various Asiatic Mesozoic taxa traditionally grouped under the term “Lindholmemydidae” are universally accepted to be the paraphyletic relatives of crown testudinoids (Shaffer et al., 1997; Sukhanov, 2000; Hirayama et al., 2000; Danilov and Parham, 2005; Joyce, 2007), but some of these taxa, in particular *Pseudochrysemys gobiensis*, have been affiliated with Emydidae (e.g., Chkhikvadze, 1983, 1987, 1990). Considering that the vast majority of “lindholmemydids” have yet to be analyzed in a phylogenetic context, we conservatively establish our soft maximum constraint for the age of crown Emydidae prior to the appearance of the first “lindholmemydids” at the base of the Early Cretaceous (99.6 ± 0.9 Ma; Gradstein et al., 2004; Ogg et al., 2008), thus 100.5 Ma. Lourenço et al. (2012) unfortunately did not elaborate how they arrived at the maximum age of 58.9 Ma for this clade.

Trachemys scripta–*Graptemys pseudogeographica (Node 20)*.—Establishing a meaningful minimum age constraint for this node is challenging. This difficulty is the result of the generally poor post-Eocene fossil record of aquatic North American turtles, the likely home range for this North American clade. Furthermore, most Miocene and Pliocene turtle remains are fragmentary and thus highly laborious to illustrate and describe. As a result, little attention has been given to aquatic turtles from this time period (Mlynarski, 1976).

Near et al. (2005) suggested calibrating this node with the late Miocene to early Pliocene taxon *Trachemys inflata* from Florida. Complete shells and skulls exist for this taxon, but we are unaware of any reference in which material of this taxon is sufficiently well described that the various taxonomic assessments for this taxon, especially the assignment to *Trachemys* (e.g., Weaver and Rose, 1967; Holman, 1977; Jackson, 1988) can be reproduced. A more detailed description and phylogenetic taxonomic analysis are required to justify use of *T. inflata* to establish a minimum age constraint. A major obstacle that must be addressed by future workers is that current molecular phylogenies indicate a close relationship of the rather autapomorphic molluscivore *Graptemys* spp. with the generalist *Trachemys* spp. (e.g., Spinks and Shaffer, 2009), but this topology is not well supported. Paleontologists have traditionally assumed that *Trachemys* spp. are most closely related to *Pseudemys* spp. and *Chrysemys picta* (e.g., Weaver and Rose, 1967; Holman, 1977; Jackson, 1988). Future phylogenetic studies of fossil “*Trachemys*” should consequently be certain to include extant *Graptemys*.

As an alternative to *Trachemys inflata* we suggest establishing a minimum age constraint for this node on the late Pliocene holotype (USNM 12059) of “*Pseudemys*” *idahoensis* (Gilmore, 1933) from the Pliocene Plesippus Quarry (=Horse Quarry of Ruez, 2009=Horse Quarry=USNM Horse Quarry=Smithsonian Institution Hill) of the Hagerman Fossil Beds. Unlike most other material described, this specimen is known from a nearly

complete skeleton that includes a complete shell, skull, and jaws. Gilmore (1933) described the holotype, noted similarities with *Graptemys* spp., but placed it in *Pseudemys*. Mlynarski (1976) noted similarities with *Graptemys* spp., but placed it in *Chrysemys*. Finally, Zug (1969) placed this taxon within *Trachemys* based on cranial similarities, an opinion supported by Jackson (1988). Unfortunately, none of these authors worked in an explicit phylogenetic framework, and so it remains uncertain if the characters they used represent symplesiomorphies or synapomorphies. We therefore scored *P. idahoensis* for the testudinoid matrix of Joyce and Bell (2004) and then ran the emydid portion of the matrix under a parsimony framework using a molecular backbone (Feldman and Parham, 2002; Spinks et al., 2004; Spinks and Shaffer, 2009; see Appendix 2 for details). The analysis indicates that *P. idahoensis* is most parsimoniously placed as sister to *Graptemys* and that this taxon therefore is a representative of stem *Graptemys* (Fig. 3). We establish our minimum constraint at 3.0 Ma based on an ⁴⁰Ar/³⁹Ar date of 3.7 ± 0.7 from near the type localities of this taxon (Hart and Brueseke, 1999).

The fossil record of emydid turtles is still relatively poorly understood and it is therefore difficult for us to establish a maximum date for the *Trachemys scripta*–*Graptemys pseudo-geographica* node. However, given that emydids are a North American clade, that the North American Paleogene fossil record is relatively well understood, and that no close relatives of *Graptemys* or *Trachemys* are apparent prior to the Miocene, we carefully establish our soft maximum constraint for this node on the base of the Oligocene (33.9 ± 0.1 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 34.0 Ma. The Oligocene taxon *Pseudograptemys inornata* (Loomis, 1904) bears resemblance with *Graptemys* spp. by name only (Hutchison, 1996; also see Emydidae).

Testuguria (Node 21).—Not much is known about the origin and early evolution of early testudinoids, although a number of Mesozoic forms have at times been affiliated with one of the three primary subclades of this taxon (Chkhikvadze, 1983, 1987, 1990). Holroyd and Parham (2003) allude to the existence of a Paleocene tortoise from Asia, but no specimen has of yet been formally described and figured. This situation changes drastically at the base of the Eocene, after numerous testudinoid lineages invaded both North America (Hutchison, 1998) and Europe (Lapparent de Broin, 2001), likely from an Asiatic center of origin. A number of early Eocene taxa have been assigned tentatively to Geoemydidae (e.g., European representatives of *Palaeochelys*, Hervet, 2004; North American representatives of *Echmatemys*, Hirayama, 1985), but given that these taxa have not been analyzed in a global phylogenetic context, these assignments must be considered tentative.

We agree with Near et al. (2005) that the oldest diagnosable representative of Testuguria is the early Eocene tortoise *Hadrianus majusculus*. The holotype of this taxon (YPM 2793) was found in the late nineteenth century in the Wasatchian badlands of New Mexico and has long been considered to be the oldest known tortoise (e.g., Hay, 1908). The phylogenetic placement of *Hadrianus majusculus* within or as sister to Testudinidae has never been questioned given the large number of testudinid apomorphies that this taxon possesses (Fig. 3). Unfortunately, the locality data associated with this fossil is extremely poor and so it is not currently possible to determine where within the Wasatchian San Jose Formation this fossil originated. Hutchison (1998) reported that *Hadrianus* spp. occur in North America from the Wasatchian 3 and Holroyd et al. (2001) conclude that *Hadrianus* spp. occurs in the Willwood Basin of Wyoming from the Wasatchian 5. Unfortunately,

Hutchison (1998) did not list any voucher specimens, and so it is not possible to verify the taxonomy underpinning his stratigraphic distribution data. The results of Holroyd et al. (2001) are more reproducible, because a voucher specimen was provided for the Wasatchian 5 date, but given that that specimen (UCMP 82346) was neither described, nor figured, we cannot readily verify its identity. Thus, we are left with the poorly dated holotype of *Hadrianus majusculus* and use the end of the Wasatchian as our minimum time calibration (50.39 ± 0.13 Ma; Smith et al., 2003; Robinson et al., 2004) at 50.3 Ma.

Although testudinid fossils are highly diagnostic, there are no characters currently recognized that allow fossil testugurians to be diagnosed with confidence among the rich Late Cretaceous testudinoid faunas of Asia. We therefore generously establish our soft maximum age constraint on the first appearance of diagnostic stem testudinoids, such as *Khodzhakulemys occidentalis* (Nessov in Nessov and Krasovskaya, 1984) from the Albian/Cenomanian Khodzhakul Formation of Uzbekistan (Danilov, 1999), or dubious fossils from the Barremian of Japan (Hirayama, 2002) at the base of the Late Cretaceous (99.6 ± 0.9 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 100.5 Ma.

Heosemys spinosa–*Mauremys reevesii* (Node 22).—Establishing a minimum date for the clade specified by *Heosemys spinosa* and *Mauremys reevesii* is extremely challenging. Like the post-Eocene fossil record of North American emydids, the Eurasian Tertiary fossil record of geoemydids is highly fragmentary, most material has not been described in any detail, and few fossils have ever been analyzed in an explicit phylogenetic context (e.g., Joyce and Lyson, 2010b).

Until quite recently, numerous fossil forms from the Paleogene of Europe were assigned to extant Asiatic taxa, such as *Ocadia* or *Mauremys* (e.g., Mlynarski, 1976), but more recent reviews of this material demonstrate that no close link exists between these taxa. The most comprehensive review is the extensive alpha taxonomic revision of European geoemydids undertaken by Hervet (2004), in which all Paleogene species from Europe were assigned to new genera. As such, *Ocadia crassa* (Owen and Bell, 1849) is now known as *Cuvierchelys crassa*. Hervet (2004) also performed an extensive phylogenetic analysis from which she concluded that all Paleogene taxa from Europe are placed outside of the extant taxon *Mauremys*. However, given that other living geoemydids were not included in the analysis, her results are difficult to interpret and it remains unclear where within Geoemydidae they should be placed. A reevaluation of this material in a global context is beyond the scope of this paper and so we are simply left to conclude that *Cuvierchelys crassa* should not be used to establish a minimum time constraint for this node, as was done by Near et al. (2005).

Using current molecular hypotheses (e.g., Spinks et al., 2004), it is possible to investigate whether known morphological characters diagnose clades recovered by molecular phylogenetic analyses, thereby reconciling the morphological and molecular hypotheses as suggested by Parham et al. (2012). To ensure that our minimum age constraint is based on a taxon that can be assigned with certainty to the *Mauremys reevesii*–*Heosemys spinosa* clade, we attempted to identify the oldest fossil of a subclade that can be identified unambiguously using morphological characters, by mapping the morphological characters of Joyce and Bell (2004) onto the phylogeny of Spinks et al. (2004). All fossil taxa that possess reversed neurals must be disregarded (e.g., *Mauremys thanhinensis* Claude et al., 2007), as this character also occurs outside the *Mauremys reevesii*–*Heosemys spinosa* clade (Joyce and Bell, 2004; Spinks et al., 2004). However, representatives of *Cuora* are diagnosed by a number of characters that are unique among geoemydids, most of which pertain to the well-

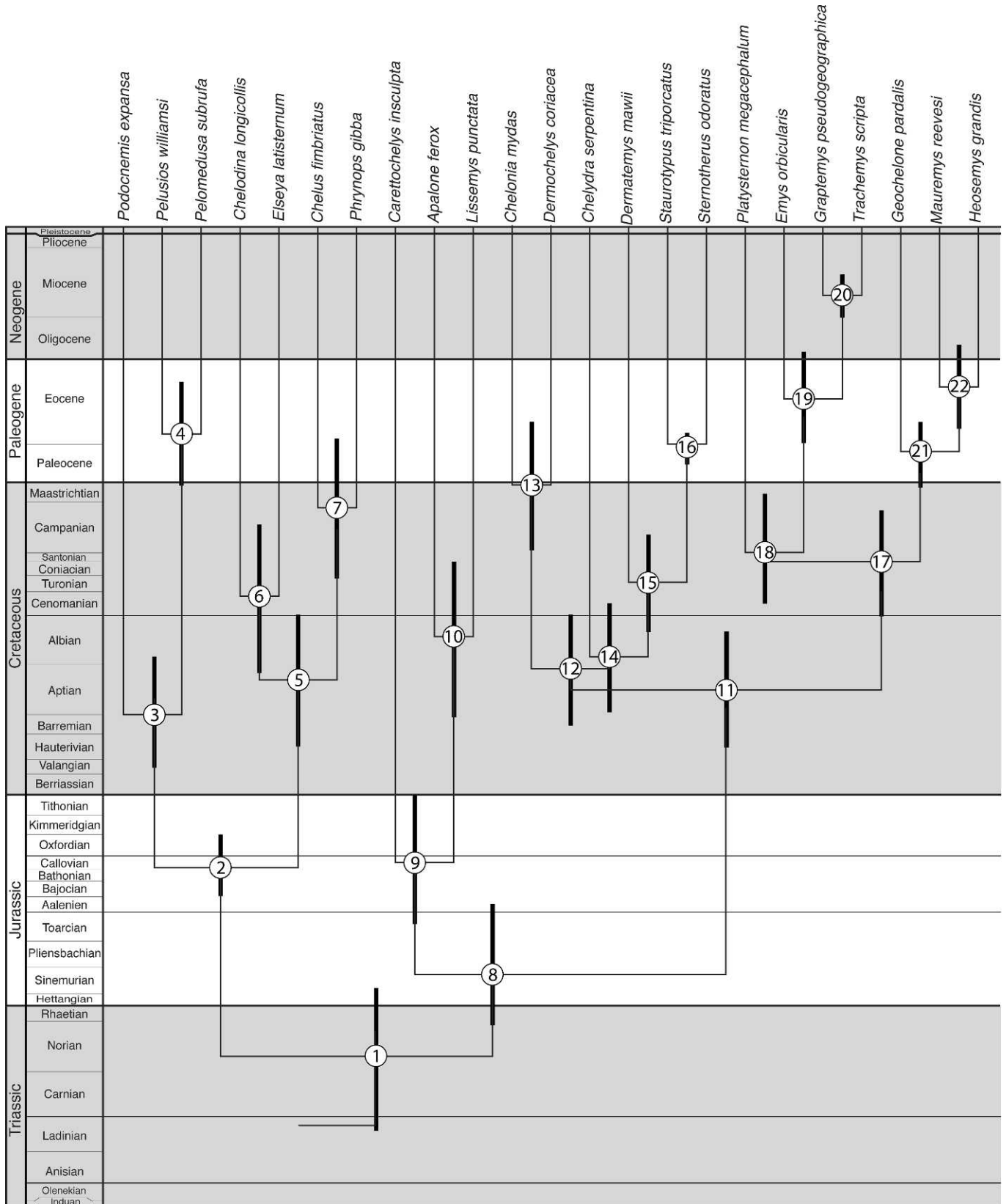


FIGURE 4—A timescale for the evolution of turtles. Black bars represent the 95 percent range and mean values of the posterior age estimates derived from the MCMC TREE analysis. See Table 1 for more detailed results.

developed box turtle hinge (Hirayama, 1985; Joyce and Bell, 2004). Our phylogenetic analysis of the holotype of the fossil taxon *Cuora pitheca* Yeh, 1981 (IVPP 6178) from the late Miocene of Shihuiba, Lufeng, Yunnan, China (Yeh, 1981) using the matrix of Joyce and Bell (2004) and the topology of Spinks et al. (2004) firmly affiliates *C. pitheca* with *Cuora* (see Appendix 3 for details of our analysis). The most parsimonious placement is as sister to *C. mouhotii*, but any other placement inside or as sister to *Cuora* is only one step longer. Although the exact placement of *Cuora pitheca* relative to extant *Cuora* spp. remains unclear, the placement of this fossil taxon within the *Mauremys reevesii*–*Heosemys spinosa* clade is robust (Fig. 3). We are confident that future work will result in much older minimum age constraints for this node and encourage global phylogenetic analysis of the relevant fossil taxa. In the interim, we derive our minimum age constraint from the top of the Miocene (5.332 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 5.3 Ma.

Although “reversed neurals” (see Joyce and Bell, 2004, characters 37, 38) are not diagnostic for the *Mauremys reevesii*–*Heosemys spinosa* clade, the occasional presence of this character is diagnostic for a more inclusive clade (*Mauremys*+*Heosemys*+*Melanochelys*) that is nested within Geoemydidae. As stated above, various Mesozoic fossils have been attributed with one or the other extant testudinoid crown group (e.g., Chkhikvadze, 1983, 1987, 1990), but to our knowledge none of them have reversed neurals. We therefore place our soft maximum age constraint from the base of the Tertiary (65.5.5 ± 0.3 Ma; Gradstein et al., 2004; Ogg et al., 2008) at 65.8 Ma.

RESULTS: THE IMPACT OF “BEST PRACTICES”

Using the protocols outlined by Parham et al. (2012), we developed explicitly justified minimum and maximum constraints for most major lineages of turtles. We only compare our calibrations to those of Near et al. (2005) because other studies either reused the calibrations of Near et al. (2005) or develop calibrations for other nodes. Our minimum calibrations do not overlap with those of Near et al. (2005) for a single node, although differences range from 16 percent older (node 7) to 89 percent younger (node 22) relative to the values of Near et al. (2005). Three primary causes can be identified that vary in their effects. First, we adjusted two minimum dates (nodes 8 and 15) based on recent fossil finds that reveal certain turtle clades are older than previously thought. This type of update will always produce older minimum ages and the increase in minimum age can be expected to be large in groups with a poor fossil record. Given that the fossil record of cryptodiran turtles is well known, our updates produced minimum ages that are just 8–13 percent older. In the future, we expect to see major increases in the minimum ages of pleurodire clades because their fossil record remains relatively less well-studied and understood.

We agree generally with Near et al.’s (2005) choice of fossils for nine clades, but our detailed review of the stratigraphic literature necessitated changes to the minimum absolute ages of these fossil, the second type of modification that we undertook. Three nodes (2, 7, 16) required slightly older ages (1%, 16%, and 6% older, respectively), four nodes (3, 5, 19, 21) required modestly younger ages (16%, 8%, 6%, and 3% younger, respectively), but two nodes (4, 6) demanded significantly younger ages (71% and 23% younger, respectively). Although it is easy to reject detailed stratigraphic work *a priori* as insignificant, it is apparent that the combined impact of our changes cannot be dismissed as negligible.

The final type of adjustment pertains to differing interpretations of the fossil record. We disagree with Near et al. (2005) in

the choice of fossil taxa used for calibrating six clades (nodes 6, 10, 13, 20, 17, 22). In all cases, these disagreements resulted in often drastically younger minimum dates (26%, 84%, 56%, 40%, 44%, and 89% younger, respectively) and their impact upon the analysis is obvious. In all six cases, this disagreement was caused by a lack of caution when interpreting the paleontological literature, as all of the fossils used had never been analyzed in a global phylogenetic context or at least justified using characters known to be non-homoplastic in a global context. We suggest that new fossils or new topologies only be used to overturn our minima when a solid basis is apparent that supports change.

RESULTS: MOLECULAR CLOCK ANALYSIS

The results of running the molecular clock analysis without sequence data (Fig. 5) showed that the effective calibration priors never precisely match the use-specified uniform calibrations, and for some nodes there is a large deviation between the specified and effective calibrations (e.g., nodes 11–16). This occurs because the calibration age priors for younger nodes are truncated in the construction of the joint time prior, to meet the condition that daughter nodes cannot be older than their parent nodes. This is a ubiquitous but rarely discussed phenomenon in molecular dating studies (Inoue et al., 2010; Heled and Drummond, 2012; Warnock et al., 2012; dos Reis et al., 2012). At the least, we can demonstrate that while our user-specified calibrations are not implemented faithfully, our temporal constraints are not violated.

The specified calibration priors and posterior estimates of divergence times obtained from the analysis using MCMCTREE are shown in the Figure 4 and presented in Table 1. All node ages were constrained using conservative minimum and maximum constraints. The posterior molecular clock estimates showed an average 65.3 percent reduction from the specified calibration priors. Our analysis constrains the interval for the origin of crown turtles (Testudines–node 1) from the Late Triassic to Early Jurassic with 95 percent HPDs (194.9–231.41 Ma). The estimated time of divergence of crown Pleurodira (node 2) is Middle to Late Jurassic (155.6–171.35 Ma), and within Pleurodira most of the major lineages appear to have diverged within the Early to Late Cretaceous, including Chelidae, Chelodinae, Pelomedusoides, *C. fimbriatus*–*P. gibbus*, and no later than the end of the Eocene (Pelomedusidae). The estimated time of divergence of crown Cryptodira (node 8) is the Late Triassic to the Middle Jurassic (168.73–202.69 Ma). We estimated the origin of Trionychia (node 9) to be in Late to Early Jurassic (145.66–178.57 Ma) and within Trionychia the origin of Trionychidae is estimated to have occurred within the Early to Late Cretaceous. The estimated time of divergence of Durocryptodira (node 11) is the Early Cretaceous (103.83–133.31 Ma). Our analysis places the diversification of a large number of major durocryptodiran lineages in the Early to Late Cretaceous, including Americhelelydia, Chelydroidea, Emydidae–*P. megacephalum*, Kinosternoidea, Testudinoidea, and Trionychidae, while the estimated divergence of crown Chelonioida spans the Late Cretaceous to the Eocene. More recent Tertiary estimates of durocryptodiran divergences include Emydidae, Kinosternidae, Testuguria, *H. spinosa*–*M. reevesii*, and *T. scripta*–*G. pseudogeographica*. In three cases (Cryptodira–node 8, Pleurodira–node 2, Trionychia–node 9) the upper posterior interval exceeds the specified soft maximum constraint. In contrast, the 95 percent posterior estimate for the divergence of Kinosternidae lies close to and encompasses the hard minimum age constraint.

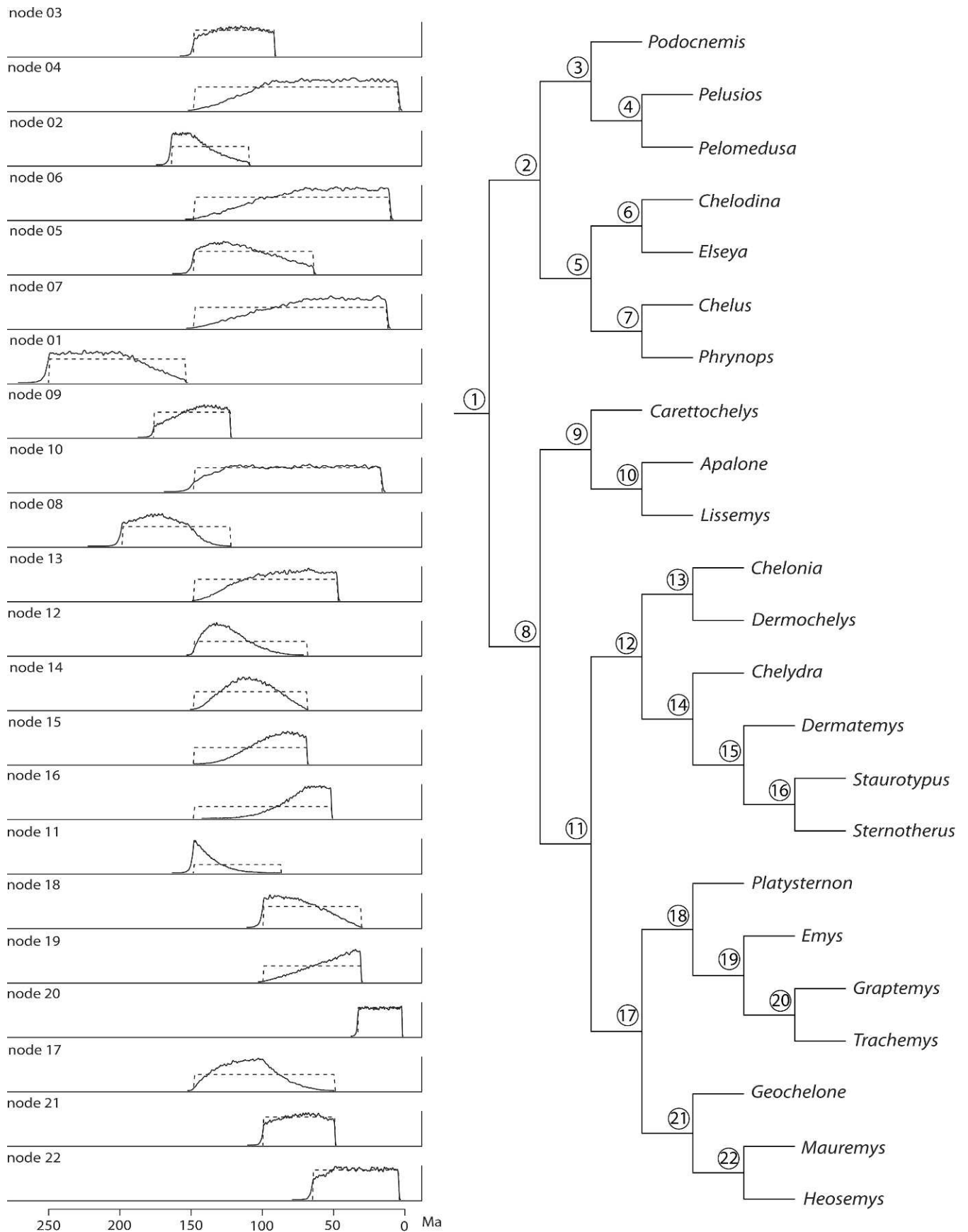


FIGURE 5—Plots contrasting the user-specified uniform calibration priors (dashed lines) with the effective marginal priors observed with the effective priors observed when the calibrations are combined in analysis using MCMCTREE (black lines). This diagram illustrates how the interaction between different calibrations in the joint prior can result in effective priors that deviate substantially from the initial user-specified distributions.

DISCUSSION

The temporal evolution of turtles.—Although our strict protocols forced us to establish extremely broad prior distributions, sometimes spanning more than 100 Ma (e.g., Chelodinae, Pelomedusidae, Trionychidae), our methods provide a truly independent test of evolutionary rates within Testudines. Even though large error bars remain for each clade (Fig. 4, Table 1), we are able to learn something new about the origin of various groups of turtles and to reflect upon the available fossil record.

The age of the crown Testudines.—The age of the turtle crown has become a controversial subject over the course of the last decade. For nearly 100 years, paleontologists regularly identified the Late Triassic turtle *Proterochersis robusta* as a basal pleurodire (Fraas, 1913; Gaffney, 1975; Gaffney et al., 2007), thus predicting a split of the turtle crown in the middle Triassic. A series of more recent papers, however, more rigorously tested the phylogenetic relationships of *P. robusta* by scoring it as a separate terminal taxon (rather than as part of a pleurodiran chimera) and concluded that it is situated along the stem of Testudines (e.g., Rougier et al., 1995; Sukhanov, 2006; Joyce, 2007; Sterli and de la Fuente, 2011; Anquetin, 2012). The age of the turtle crown therefore appears to be at least Middle Jurassic in age based on fossils (Danilov and Parham, 2006; Anquetin et al., 2009; Scheyer and Anquetin, 2008). This controversy was not advanced by the study of Near et al. (2005) who presumed *P. robusta* to be a stem pleurodire and were forced, therefore, to conclude a Triassic minimum age for the crown as well. This error was copied by Marshall (2008) and Jaffe et al. (2011) but was avoided by Dornburg et al. (2011), Lourenço et al. (2012), and Chiari et al. (2012).

Our analysis also avoids circularity and controversy by eliminating *P. robusta* from the discussion and by allowing the signal to emerge from the molecular evidence. The 95 percent range of HPDs of our analysis broadly predicts a divergence age of crown group Testudines (the Cryptodira–Pleurodira split) anywhere within the Late Triassic to Early Jurassic, which is relatively consistent with the Early to Middle Jurassic dates of Lourenço et al. (2012). Dornburg et al. (2012), by contrast, arrived at a broad Permian to Early Jurassic divergence estimate whereas Chiari et al. (2012) calculated a Late Jurassic split. Sterli et al. (2012) finally arrived at an early Late Jurassic age for crown group Testudines. A pre-Middle Jurassic divergence date for the turtle crown is not that surprising because numerous derived eucryptodires are already present in the Middle Jurassic of Asia (e.g., Danilov and Parham, 2006) and because the Early to Middle Jurassic fossil record is extremely poor. However, a pre-Jurassic divergence of turtles is also consistent with both competing hypotheses. The age of the turtle crown will therefore have to be further resolved using fossils, morphological arguments, and increased molecular sampling.

The diversification of Pleurodira.—The fossil record of the extant pleurodire lineages is poorly understood relative to that of the extant cryptodire lineages primarily because the terrestrial record of the Gondwanan continents they inhabit is sparse and poorly studied. Consequently, molecular divergence dating has the potential to teach us a lot about the timescale of pleurodire evolution.

Our analysis indicates that the principal divergence of crown Pleurodira occurred in the late Middle Jurassic to early Late Jurassic, which is only slightly younger than the age calculated by Near et al. (2005). Dornburg et al. (2011) obtained very broad results ranging from the Early Triassic to the Late Jurassic, Lourenço et al. (2012) reported Late Jurassic to Early Cretaceous dates, and Sterli et al. (2012) arrived at an Early Cretaceous interval. Interestingly, our results are partially outside the limits we set as the maximum, indicating that we may not have been conservative enough with our maximum age estimate. Although

only few fossils exist that could test this hypothesis, an early divergence of Pleurodira is consistent with Gaffney and Jenkins' (2010) otherwise unsubstantiated claim that the Late Jurassic taxon *Notochelys laticentralis* represents an early panpelomedusoid.

Near et al. (2005), Vargas-Ramirez et al. (2008), and Dornburg et al. (2011) estimate the principal diversification of crown Pelomedusoides within the middle of the Early Cretaceous and these predictions are confirmed by our results. These dates are not unexpected, however, given that Early Cretaceous fossils were used to calibrate this node and, thus, do not provide novel insight. For the less inclusive clade Pelomedusidae, we were forced to postulate extremely broad priors ranging from the Late Jurassic to the Pliocene, but our results mostly indicate a Paleogene age for crown Pelomedusidae, similar to Near et al. (2005) and Dornburg et al. (2011). This result is significantly more precise than our calibration priors, thereby revealing a novel insight from molecular divergence dating. Moreover, these results casts doubt on fragmentary “pelomedusid” fossil turtles reported from the Cretaceous of Africa (e.g., Lapparent de Broin, 2000a). These fossils are perhaps best viewed as stem-pelomedusids or even stem-pelomedusoides for the moment.

Our divergence estimation for Chelidae differ systematically from those of Near et al. (2005) and Dornburg et al. (2011) by revealing a late Early Cretaceous divergence and mostly Late Cretaceous divergences for the two primary subclades included in this study, instead of a mostly Tertiary radiation. Assuming that South American and Australian chelids are monophyletic relative to one another, our results imply that the clade split near the transition from the Early to Late Cretaceous, likely due to vicariance caused by the final breakup of Gondwana. Under this scenario, both groups diversified on their respective continents, and subsequent faunal bridges between South American and Australia were not utilized for dispersal.

The diversification of Trionychia.—The fossil record of trionychians is peculiar because it consists only of anatomically modern trionychids and carettochelyids, and lacks clear transitional taxa (see Hirayama et al., 2013 for a possible exception). Although our calibration priors allowed trionychians to have diverged within the Early Cretaceous, our analyses clearly push their origin to the Middle to Late Jurassic in accordance with the results of Near et al. (2005). The analysis of Dornburg et al. (2011) predicted broadly a divergence ranging the entire Triassic and Jurassic, which is highly inconsistent with the fossil record and perhaps a result of their unconventional topology created by rooting problems (Sterli, 2010), whereas Lourenço et al. (2012) obtained a divergence date in the Early Cretaceous, which is more consistent with the lack of crown Trionychian in the Jurassic. Sterli et al. (2012) finally arrived as a Paleogene divergence estimate, but this is the result of not sampling the rich record of fragmentary Mesozoic trionychians. Most basal eucryptodires originate from Asia and most authors have presumed that trionychians must have originated on that continent as well. However, given that the Middle and Late Jurassic fossil record of Asia is much more densely sampled than that of other continents (for most recent summary see Rabi et al., 2010), it is surprising that diagnosable trionychians are still missing, although they should be readily recognizable based on a series of characters. Future work along the southern and eastern perimeter of the Asian continent will perhaps produce new relevant fossils. After all, the oldest representatives of both trionychian lineages originate from this region (Tong et al., 2009a; Hirayama et al., 2013) and much fieldwork remains to be undertaken.

It remains unclear which characters diagnose crown Trionychidae and we therefore established extremely conservative priors for this group. Nevertheless, our analysis reveals that Trionychidae likely originated in the middle Cretaceous (i.e., between the

Aptian and Santonian). These results are broadly consistent with Near et al. (2005) and Dornburg et al. (2011). The phylogenetic identity of all “trionychids” originating from this time interval therefore remains unclear. Our results are consistent with *Sinaspideretes wimani* not being a trionychid (Meylan and Gaffney, 1992) as well as with an Early Cretaceous trionychid stem lineage (Hirayama et al., 2013).

The diversification of Durocryptodira.—Our analyses predict a late Early Cretaceous age for Durocryptodira and the subsequent origin of all major durocryptodiran lineages traditionally classified as families during the Late Cretaceous. The only exceptions are Testuguria and Kinosternidae, which likely diversified in the Paleogene. These results differ systematically from those of Near et al. (2005), who mostly predicted many more Tertiary origins, but are overall consistent with the results of Dornburg et al. (2011) and Lourenço et al. (2012).

The Late Cretaceous fossil record of testudinoids is comparatively rich (e.g., Sukhanov, 2000) but few taxa have been integrated into global phylogenies and those taxa that have been integrated into global phylogenies have often proven to be problematic (e.g., Joyce, 2007). Our analyses indicate that the platysternid, emydids, and testugurian stem lineages were fully differentiated no later than the Maastrichtian, similar to the results of Near et al. (2005), Dornburg et al. (2011), and Lourenço et al. (2012). It therefore appears plausible that many Late Cretaceous “lindholmemydids” are representatives of the testudinoid crown, not its stem lineage (also see Claude and Tong, 2012). A global phylogenetic analysis of these fossils is long overdue.

Our results have direct bearing on the discussion regarding the origin of modern marine turtles. All Cretaceous and Tertiary cryptodiran turtles found in marine sediments were traditionally classified as part of Cheloniodea (e.g., Lydekker, 1889; Romer, 1956; Mlynarski, 1976; Carroll, 1988) although some Cretaceous fossils were interpreted as an independent family, Prostegidae. This classificatory scheme was generally confirmed by the first cladistic analyses of the group (e.g., Hirayama, 1994, 1998) with Prostegidae interpreted as being situated within crown Cheloniodea along the phylogenetic stem of *Dermochelys coriacea*. More recent global phylogenetic analyses have questioned this placement of Prostegidae by placing the early prostegid *Santanachelys gaffneyi* far from chelonoids, along the phylogenetic stem of Cryptodira (e.g., Joyce, 2007). Our analysis indicates that crown Cheloniodea diverged somewhere between the late Late Cretaceous and the Paleogene. Near et al. (2005) and Dornburg et al. (2011) obtained a similar result, but only after removing *S. gaffneyi* from their analysis. Thus, it appears highly implausible for the Aptian–Albian prostegid *S. gaffneyi* to be a crown chelonoid.

CONCLUSIONS

Fossil calibration studies have the potential to significantly help unravel the temporal evolution of life beyond what is already known from the fossil record. Whereas most agree that well-constructed calibration studies should utilize as much fossil evidence as possible, studies that sample the fossil record well run the risk of producing circular results by simply reiterating the primary input data from the fossils. One way to avoid circularity is to focus efforts on unraveling the temporal history of organisms that have a poor fossil record, but this approach in return may be difficult due to a lack of appropriate fossils that could be used to calibrate those studies. The best compromise may therefore be found by focusing attention onto groups that generally have an excellent fossil record, but that exhibit significant, localized gaps that can be illuminated by way of rigorous fossil calibration studies.

Although turtles generally have an excellent fossil record, not all lineages are equally well documented and significant questions therefore remain regarding their temporal evolution. We here attempted to avoid circularity by focusing our efforts on resolving these very gaps while utilizing the rich record of other groups to establish extremely conservative calibrations. Although we were not able to further illuminate the age of the turtle crown, our analysis nevertheless produced intriguing results regarding the age of crown Pelomedusidae, Trionychidae, and Cheloniodea. We hope that our rigorous approach to establishing priors will spawn more research on fossil turtles and inspire those wishing to find fossil calibrations for other groups.

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APPENDIX 1

Phylogenetic analysis of *Pseudograptemys inornata* (Loomis, 1904) and “*Chrysemys antiqua*” (Clark, 1937).

For this analysis, we scored “*Chrysemys antiqua*” and *Pseudograptemys inornata* for the character/taxon matrix of Joyce

and Bell (2004) based on the illustrations and descriptions of Hutchison (1996). The scoring of *Pseudograptemys inornata* is:
<????? ????? ????? ????? ????? ????? ????? 00000 00000 00000 34000 0&11?00 00??? ?????>.

The scoring of “*Chrysemys antiqua*” is:
<????? ????? ????? ????? ????? ????? ????? 00000 00000 00000 34000 22200 10??? ?????>.

A heuristic search was performed with 1000 replicates using PAUP*, v. 4.0b10 (Swofford, 2002) using the same molecular backbone as for the analysis of “*Pseudemys idahoensis*”. All characters were run unweighted and unordered, minimum branches were set to collapse, and all geoemydids were designated as the outgroup.

The analysis resulted in a single most parsimonious tree with 205 steps. Deirochelyinae was resolved as follows: [*Pseudograptemys inornata* [*Chrysemys picta* [[“*Chrysemys antiqua*”, *Deirochelys reticularia*], [*Trachemys scripta*, *Pseudemys texana*], [*Malaclemys terrapin*, *Graptemys barbouri*]]]]].

APPENDIX 2

Phylogenetic analysis of “*Pseudemys idahoensis*” (Gilmore, 1933).

For this analysis, we scored the holotype of “*Pseudemys idahoensis*” for the character/taxon matrix of Joyce and Bell (2004) based on personal observations by WGJ of the holotype specimen (USNM 12059). Our scoring of the 70 characters is as follows:

<000?? ????00 00010 10?00 000?? 10?00 00001 00000 00000 00000 34000 22200 10??? ?????>.

The backbone constraint for the parsimony analysis is the consensus among recent molecular phylogenies (Feldman and Parham, 2002; Spinks et al., 2004; Spinks and Shaffer, 2009). In particular: [*Clemmys guttata*, *Terrapene ornate* [*Emys blandingii*, *Emys orbicularis*]], [*Chrysemys picta* [*Deirochelys reticularia* [*Graptemys barbouri*, *Malaclemys terrapin*, *Trachemys scripta*, *Pseudemys texana*]]]]. A heuristic search was performed with 1000 replicates using PAUP*, v. 4.0b10 (Swofford, 2002). All characters were run unweighted and unordered and minimum branches were set to collapse. All geoemydids were designated as the outgroup.

The analysis resulted in a single tree with 207 steps. Deirochelyines were resolved as follows: [*Chrysemys picta* [*Deirochelys reticularia* [*Trachemys scripta*, *Pseudemys texana*], [*Malaclemys terrapin* [“*Pseudemys idahoensis*”, *Graptemys barbouri*]]]]].

APPENDIX 3

Phylogenetic analysis of *Cuora pitheca* Yeh, 1981.

For this analysis, we scored the holotype of *Cuora pitheca* for the character/taxon matrix of Joyce and Bell (2004) based on the description provided by Yeh (1981). Our scoring of the 70 characters is as follows:

<????? ????? ????? ????? ????? ????? ????? 01100 00000 000?1 ?????1 10??? ?????>.

The backbone constraint for the parsimony analysis was taken from the molecular phylogeny of Spinks et al. (2004). A heuristic search was performed with 1000 replicates using PAUP*, v. 4.0b10 (Swofford, 2002). All characters were run unweighted and unordered and minimum branches were set to collapse. All emydid turtles were designated as the outgroup. The analysis resulted in a single tree with 205 steps that places *C. pitheca* as sister to *C. mouhoutii*.