

## A large phylogeny of turtles (Testudines) using molecular data

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### Abstract

Turtles (Testudines) form a monophyletic group with a highly distinctive body plan. The taxonomy and phylogeny of turtles are still under discussion, at least for some clades. Whereas in most previous studies, only a few species or genera were considered, we here use an extensive compilation of DNA sequences from nuclear and mitochondrial genes for more than two thirds of the total number of turtle species to infer a large phylogeny for this taxon. Our results enable us to discuss previous hypotheses on species phylogeny or taxonomy. We are thus able to discriminate between competing hypotheses and to suggest taxonomical modifications. Finally, we pinpoint the remaining ambiguities for this phylogeny and the species for which new sequences should be obtained to improve phylogenetic resolution.

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### Introduction

Turtles form a monophyletic group with a highly specialized body plan. Their shell makes them easy to identify and there is no confusion with other vertebrates. On the other hand, debate over turtle phylogeny is vigorous. After Gaffney (1984), who used morphological data to provide the first important work on this topic, many authors focused on lower-ranking taxa and proposed various hypotheses for their relationships.

Despite this large volume of work, only during the course of the present study has a large phylogenetic analysis been published (Thomson and Shaffer, 2010). Such an extensive work, including species from all main clades, is useful for studying various problems, such as sex determining mechanisms (Janzen and Krenz, 2004), biogeography (Buhlman *et al.*, 2009) or for nomenclature (Joyce *et al.*, 2004). Until recently, the use of large datasets for phylogeny reconstruction was hampered by computational limitation. Circumventing this problem, the method of ‘supertrees’ (Sanderson *et al.*, 1998) provided a promising approach to obtain large phylogenies from several smaller ones. But some uncertainties remain about the methods and results obtained (Goloboff and Pol, 2002; Bininda-Emonds, 2004). New methods for inferring phylogenies allow the use of extensive datasets and produce outputs in a reasonable time (*e.g.* Goloboff, 1999; Guindon and Gascuel, 2003).

The DNA sequences available in GenBank are either mitochondrial (mtDNA) or nuclear (nuDNA). MtDNA has been and is still very popular in phylogenetic studies. Indeed, among other advantages compared to nuDNA, mitochondrial sequences lack introns and recombinations, making it relatively easy to align. MtDNA has been shown to evolve more rapidly than nuDNA in many eukaryotic animals, and especially in some turtle species (Caccone *et al.*, 2004). On the other hand, the microevolutionary rate of turtle mtDNA may be less rapid than first expected (Avise *et al.*, 1992). In any case, the fast evolutionary rate of mtDNA may cause higher levels of homoplasy and thus induce errors in phylogenetic reconstructions. However, the impact of high levels of homoplasy in phylogenetic constructions is still unclear. Some authors have even found, in some cases, a positive correlation between the level of homoplasy and the resolution of the phylogenies (Sanderson and Donoghue, 1996;

Kälersjö *et al.*, 1999). Engstrom *et al.* (2004) concluded that the use of mtDNA should still be considered, but authors should observe the following precautions: (i) to use ‘better data’, *i.e.* data from as large a number of species as possible and/or diversified molecular or morphological data, (ii) to use model-based approaches to calculate phylogenetic trees, such as maximum likelihood or Bayesian analyses.

Whenever authors have focused on higher clades of turtles, they have shown that, despite the fact that these clades are commonly recognized and supported, the phylogenetic relationships between some less inclusive clades typically ranked as super-families, families or sub-families are still debatable (Shaffer *et al.*, 1997; Fujita *et al.*, 2004; Krenz *et al.*, 2005). In some cases, previously erected taxa appear to be paraphyletic or polyphyletic. One good example is the Asian big-headed turtle *Platysternon megacephalum*, the sole member of a monotypic family, Platysternidae, which was thought to be closely related to snapping turtles (Chelydridae; Krenz *et al.*, 2005; Parham *et al.*, 2006). This hypothesis is now rejected by many authors, who consider *P.*

*megacephalum* a member of Testudinoidea (pond turtles and tortoises) based on phylogenetic results. However, its precise position is still uncertain (Parham *et al.*, 2006). Besides, the delimitation of some genera is still under discussion (*e.g.* *Emys*; Fritz *et al.*, 2011), both because of phylogenetic controversies and because of limitations inherent in rank-based nomenclature (Laurin, 2010). Genera for which monophyly has been questioned include *Elseya* from Chelidae (Seddon *et al.*, 1997; Georges *et al.*, 1998), *Trachemys* from Emydidae (Stephens and Wiens, 2003; Spinks and Shaffer, 2009), and *Kachuga* from Geoemydidae (Spinks *et al.*, 2004; Le *et al.*, 2007; Prasad *et al.*, 2007b).

To address these questions of taxonomy, we compiled all turtle mtDNA and best represented nuDNA sequences present in GenBank. Contrary to Thomson and Shaffer (2010), we used all information from mtDNA sequences that could be aligned without ambiguity. In order to limit species sampling effect and long-branch attraction that could perturb phylogeny reconstruction, we used all the available species, even those with few sequences. Then, we used maximum

Table 1. Number of species from each taxon included in this study compared to the total number of species in the considered taxon, and number of species for which we have the complete mitochondrial genome.

	Number of species		Complete mtDNA sequence	
	Studied	Total	Studied	Total
Pleurodira	38/79		1	0
Chelidae		25/52		0
Pelomedusoidea	13/27		1	0
Podocnemididae		5/8		0
Pelomedusidae		8/19		1
Cryptodira	192/238		29	
Chelydridae		2/2		2
Platysternidae		1/1		1
Chelonioidae	7/7		3	
Cheloniidae		6/6		3
Dermochelyidae		1/1		0
Kinosternoidea	5/26		0	
Dermatemydidae		1/1		0
Kinosternidae		4/25		0
Testudinoidea	150/171		19	
Geoemydidae		68/72		7
Emydidae		39/51		2
Testudinidae		43/48		10
Trionychia	27/31		4	
Carettochelyidae		1/1		0
Trionychidae		26/30		4

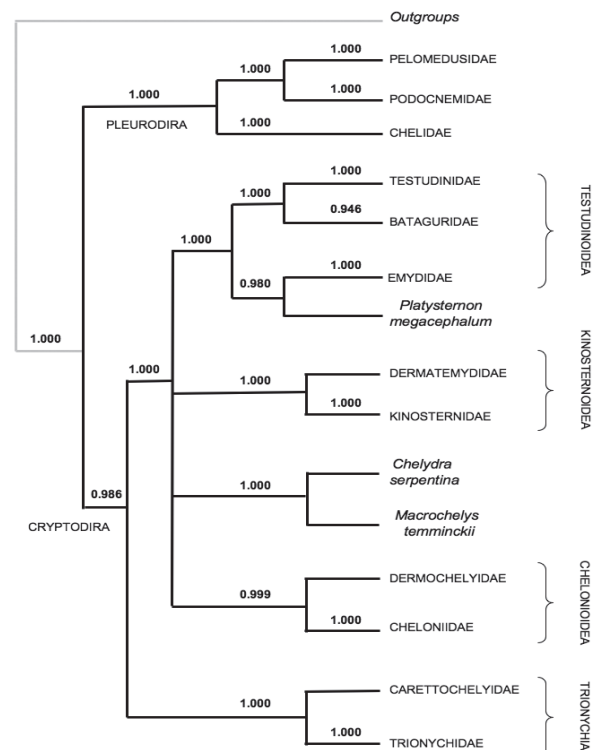


Fig. 1. Phylogenetic relationships between turtle major clades. Confidence values are indicated over each branch. Branches supports are in bold when exceeding 0.9.

likelihood to infer the phylogenetic tree and discuss current debates in turtle evolutionary relationships. The main objectives of this work were multiple: (i) of course, to propose a robust phylogeny for Testudines and help resolving some taxonomic ambiguities, (ii) to favour future work on character evolution for this group, (iii) to pinpoint the remaining ambiguities in the phylogeny to tag the species/groups that need to be sequenced more intensively.

**Material and methods**

*Taxonomic sampling and molecular data*

Species sampling was made according to the nomenclature described by Bisby *et al.* (2009). Authorities for each species are indicated in On-line supplementary table S1. We did not include taxa for which there was evidence for a hybrid origin, such as *Mauremys iver-soni*, *Mauremys pritchardi*, *Ocadia glyphistoma*, *Oca-dia philippeni* and *Sacalia pseudocellata* (Parham *et*

*al.*, 2001; Wink *et al.*, 2001; Spinks *et al.*, 2004; Stuart and Parham, 2007). To obtain a phylogeny as robust as possible, we included both mitochondrial (mtDNA) and nuclear (nuDNA) genes. We compiled all complete mi-tochondrial sequences available in October 2009 from GenBank (On-line supplementary table S2). We also compiled the sequences of five mitochondrial genes (12S, 16S, COI, NAD4, cytB) and four nuclear genes (R35, c-mos, RAG1 and RAG2). These particular genes were those for which the available number of sequen-ces was highest. We combined the different mtDNA and nuDNA sequences obtained for each species into a single matrix. Only regions of straightforward alignment were taken into account. The length of the final alignment was 20,000 nucleotides (available via: <http://purl.org/phylo/treebase/phyloWS/study/TB2:S12290>).

To root the phylogenetic tree, we used total mtDNA for four outgroup species (*Crocodylus porosus* for crocodiles, *Pycnonotus sinensis* for birds, *Lacerta vi-ridis* for squamates, and *Sphenodon punctatus* for Rhynchocephalia). Because nuDNA sequences were not always available for the same taxa, we hereafter

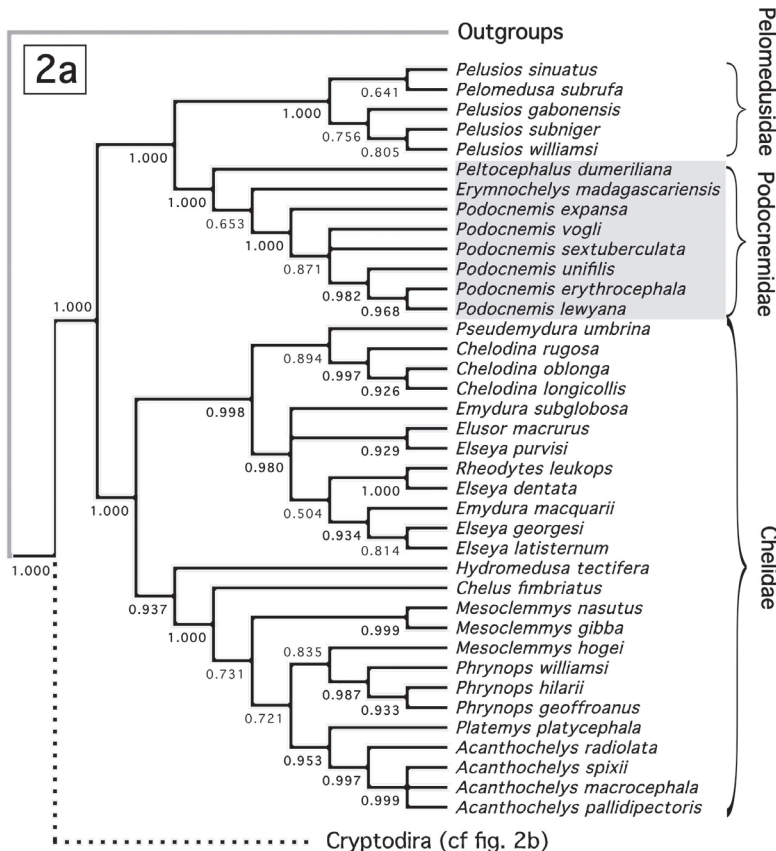


Fig. 2. Maximum likelihood phyloge-netic tree obtained using PhyML and the complete DNA dataset (-log(likelihood) = 286215.0). Fitted parameters of the GTR + I + G model are: freqA = 0.36109; freqC = 0.29917; freqG = 0.11484; freqT = 0.22491; A <-> C = 0.91133; A <-> G = 5.21616; A <-> T = 0.94284; C <-> G = 0.50873; C <-> T = 10.42092; G <-> T = 1.00000 ; Proportion of invariant sites = 0.233; Gamma shape parameter = 0.512. Confidence values are indicated under each branch. Branches with confidence value lower than 0.5 have been col-lapsed. Branch supports are in bold when exceeding 0.9.

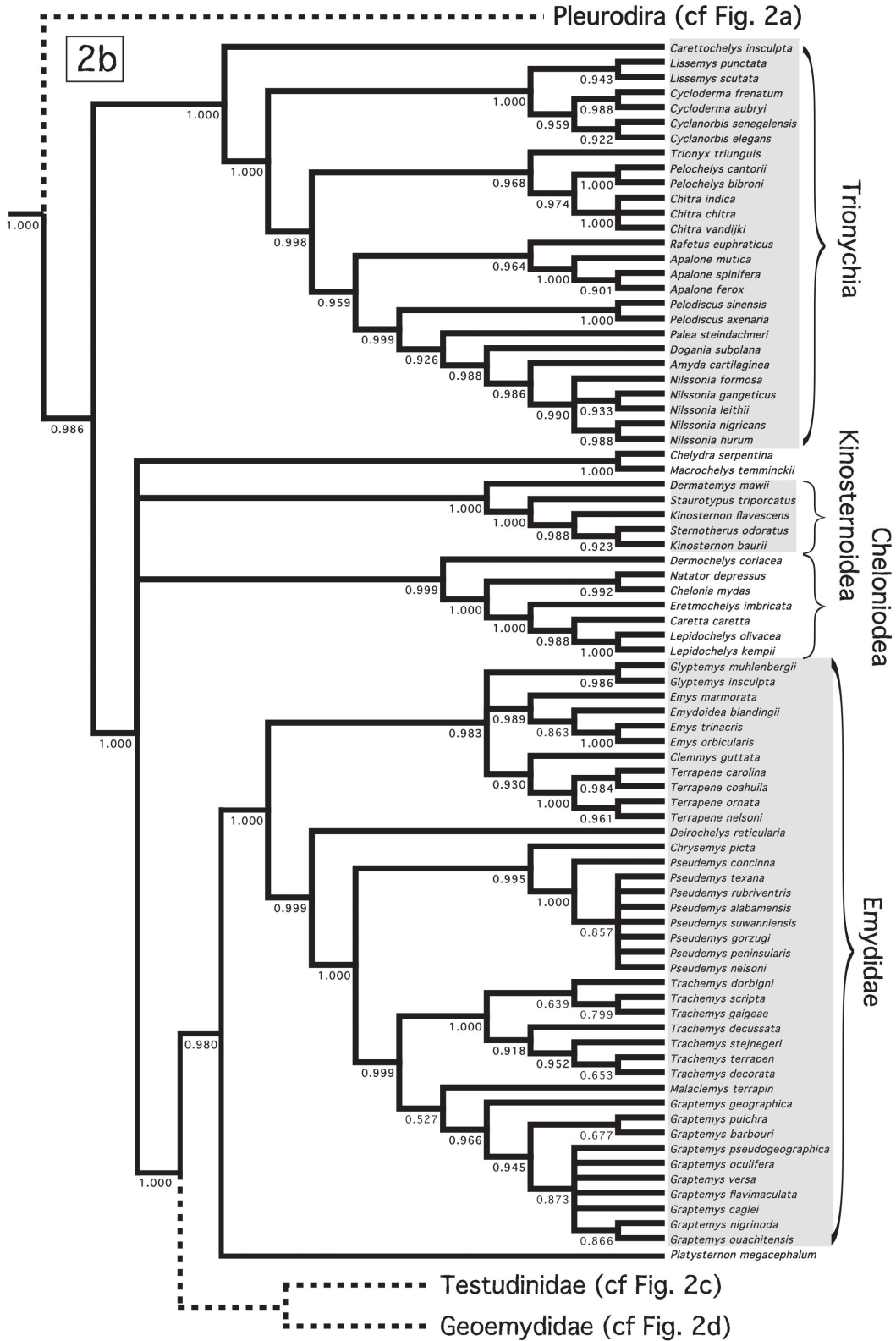


Fig. 2. (continued)

refer to outgroup species as ‘crocodiles’, ‘birds’, ‘squamates’ and ‘sphenodonts’ (references for all outgroup sequences are shown in Table S2). We root the tree either as sister-group of a clade that includes ‘birds’, ‘crocodiles’, ‘squamates’, and ‘sphenodonts’ (Reisz and Laurin, 1991; Laurin and Reisz, 1995; Lee 1997, 2001; Lyson *et al.*, 2010) or as sister-group of ‘birds’ and ‘crocodiles’ (Zardoya and Meyer 1998, 2001). It does not change the topology within the turtle clade.

*Phylogenetic analyses*

We used the maximum likelihood algorithm of PhyML (Guindon and Gascuel, 2003) to conduct the phylogenetic analysis, starting with a parsimony tree. Param-

eterization of PhyML was performed using jModel-Test 0.1 (Posada, 2008) to select a model of nucleotide substitution. To quantify branch support, we report confidence values (*cv*) as the result of an approximate likelihood-ratio test performed by PhyML (Anisimova and Gascuel, 2006). Nodes with *cv* < 0.5 have been considered as non-resolved and are polytomized.

**Results**

*Taxonomic sampling and phylogenetic analysis*

The complete mitochondrial genome was available in GenBank for 30 turtle species; partial or complete

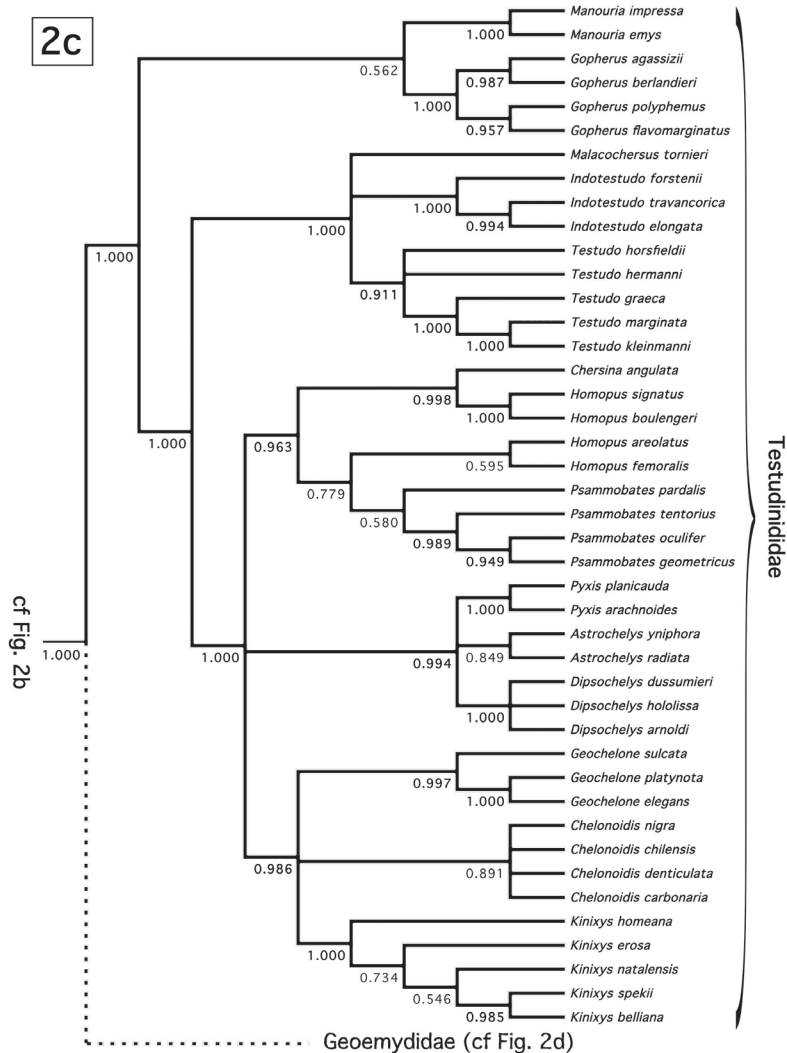


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mtDNA sequences were available for 226 species (Table S2). We obtained the sequence of at least one nuDNA gene for 179 species. From a total of 317 extant turtle species (The Reptile Database, 2011), 230 were represented in our phylogeny (Table 1). Amongst the 93 accepted genera, only *Claudius* and *Rhinemys* were not represented.

We ran jModelTest on a restricted alignment, in which only species with complete mtDNA were present. According to the Akaike information criterion, the model of nucleotide substitution selected by jModelTest was a general time reversible model (Lanave et al., 1984) allowing for a heterogeneous rate across sites with a 4-categories gamma distribution and for a

fitted proportion of sites to be invariable (GTR + I + G). It has been argued that using jModeltest to select the best model of evolution can lead to pitfalls because the program draws on a phenetic BIONJ tree (Marjanović and Laurin, 2007). However, we are rather confident in the model selected, because the second best model was associated with an Akaike weight inferior to  $10^{-12}$ . The numerical outputs of PhyML are presented in the legend to Fig. 2.

Turtle phylogeny

Phylogenetic relationships between major clades of turtles are indicated in Fig. 1. The complete phyloge-

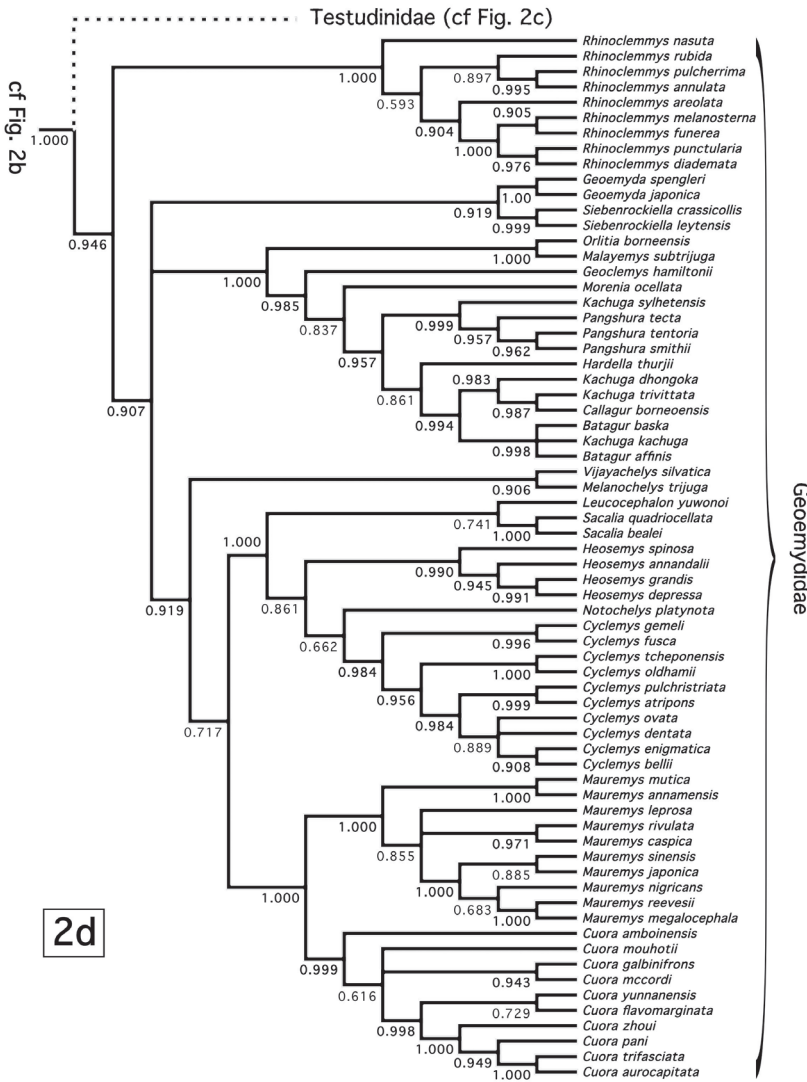


Fig. 2. (continued)

ny with all species is presented in Fig. 2. The distribution of confidence values (*cv*) at nodes is highly skewed in favour of high confidence values (Fig. 3).

Our phylogeny shows a clear separation between monophyletic Pleurodira (*cv* = 1) and Cryptodira (*cv* = 0.986). In Pleurodira (Fig. 2a), Chelididae forms a clade (*cv* = 1), which is the sister-group to the Pelomedusoidea, grouping all Pleurodira except Chelididae (*cv* = 1). The species included in Pelomedusoidea are separated into two monophyletic groups, corresponding to the Podocnemididae (*cv* = 1) and Pelomedusidae (*cv* = 1). We observe a clear separation of Chelididae into three clades, corresponding to Chelidinae (*cv* = 1), Chelodinae (*cv* = 0.998) and Hydromedusinae, although Hydromedusinae is represented in our study by only one species (Table S2). Chelodinae is the sister-group to all other Chelididae, and *Hydromedusa tectifera*, the only species of Hydromedusinae in our phylogeny, is sister to Chelidinae. Four pleurodiran genera are found to be polyphyletic (*Mesoclemmys*, *Elseya*, *Emydura*) or paraphyletic (*Pelusios*). *Mesoclemmys hoguei* is grouped with *Phrynops* (*cv* = 0.835), rather than with *M. nasutus* and *M. gibba*. *Elseya dentata* is grouped with *Rheodytes leukops* (*cv* = 1) and *Elseya purvisi* is grouped with *Elusor macrurus* (*cv* = 0.929) rather than with the other sampled species of *Elseya*. *Emydura macquarii* is grouped with *Elseya georgesi* and *Elseya latisternum* (*cv* = 0.934) rather than with *Emydura subglobosa*. *Pelusios sinuatus* is grouped *Pelomedusa subrufa* (*cv* = 0.641) rather than with the other sampled species of *Pelusios*.

Cryptodira is classically organized into five clades (Chelonioidea, Kinosternoidea, Testudinoidea, Trionychia and Chelydroidea, the latter taxon comprising Chelydridae and Platysternidae). Here, Trionychia (*cv* = 1) is sister to the group formed by all other Cryptodira (*cv* = 1). The only species from Carettochelyidae, *Carettochelys insculpta*, is separated from a group including all other Trionychia (*cv* = 1). The monophyly of Trionychinae (*cv* = 0.998) and Cyclanorbinae (*cv* = 1) is also well supported (Table S2, Fig. 2b). All species from the same genus are grouped together.

Trionychia is recovered as the sister group to all remaining clades of cryptodiran turtles which form a tetrapolytomy (Fig. 2b) including: (i) Chelonioidea (*cv* = 0.999), (ii) Chelydridae (*cv* = 1), (iii) Kinosternoidea (*cv* = 1), and (iv) a group formed by Geoemydidae, Testudinidae, Emydidae and *Platysternon megacephalum* (*cv* = 1).

In Chelonioidea, there is a clear separation between Cheloniidae (*cv* = 1) and Dermochelyidae (Ta-

ble S2, Fig. 2b), as between the two families included in Kinosternoidea, the monotypic Dermatemydidae (*Dermatemys mawii*) and Kinosternidae (*cv* = 1). However, *Kinosternon* appears paraphyletic, as *Kinosternon baurii* is closer to *Sternotherus odoratus* (*cv* = 0.923) than to *K. flavescens*. The fourth clade is composed of a group formed by Testudinidae and Geoemydidae (*cv* = 1), and a group formed by Emydidae and *Platysternon megacephalum* (*cv* = 0.980). According to the usual taxonomy, Testudinidae, Geoemydidae and Emydidae together form the clade Testudinoidea. This clade is then paraphyletic in our phylogeny due to the inclusion of *Platysternon megacephalon* as the sister-group to Emydidae (Fig. 2b).

Within the monophyletic Emydidae (*cv* = 1), Emydinae and Deirochelyinae are both monophyletic (*cv* = 0.983 and *cv* = 0.999, respectively; Table S2, Fig. 2b). All species from the same genus are grouped together except for *Emys*: *Emys orbicularis* and *Emys trinacris* are closer to *Emydoidea blandingii* (*cv* = 0.863) than to *Emys marmorata*.

Within the monophyletic Testudinidae (*cv* = 1), Gopherinae (*cv* = 0.562) and Testudininae (*cv* = 1) are monophyletic (Table S2, Fig. 2c). All species from the same genus are grouped together, except for *Homopus*. *Homopus areolatus* and *Homopus femoralis* are close to *Psammobates* (*cv* = 0.779), whereas *Homopus boulengeri* and *Homopus signatus* are grouped with *Chersina angulata* (*cv* = 0.998).

Within the monophyletic Geoemydidae (*cv* = 0.946), Batagurinae is monophyletic (*cv* = 0.985) and nested within Geoemydinae, which is thus paraphyletic (Table S2, Fig. 2d). All species from the same genus are grouped together except for *Batagur* and *Kachuga*. *Batagur affinis* and *Batagur baska* are recovered in a polytomy including *Kachuga kachuga* (*cv* = 0.998), whereas *Kachuga trivittata* is grouped with *Callagur borneoensis* (*cv* = 0.987) and *Kachuga sylhetensis* is grouped with *Pangshura* (*cv* = 0.999).

## Discussion

As a note of caution, it must be recalled that the present study makes a compilation of GenBank sequences, sequences that may not be devoid of errors. Problems may arise from taxonomic misidentification (Vilgalys, 2003; Stuart and Fritz, 2008; Fritz *et al.*, 2010), sequencing errors (Harris, 2003), and pseudogene amplification (Fritz *et al.*, 2010). We did not try to remove rogue taxa (Sanderson and Shaffer, 2002) from the



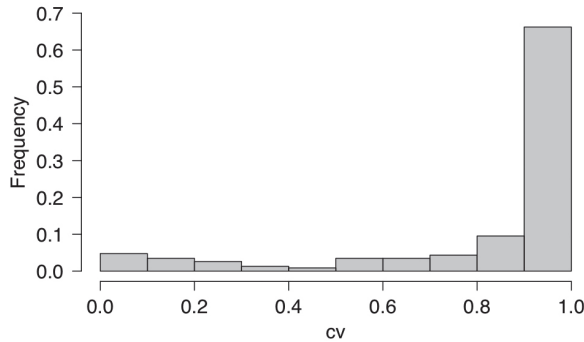


Fig. 3. Distribution of confidence values at nodes.

analysis, because the maximum likelihood method we employed for phylogenetic inference, and the resulting confidence values do not make use of bootstrapping (Guindon and Gascuel, 2003; Anisimova and Gascuel, 2006). Only highly supported branches ( $cv > 0.9$ ) will be discussed here.

Many studies assumed *a priori* the monophyly of Pleurodira and Cryptodira, and rooted the Testudines tree at the branch joining these two groups (Shaffer *et al.*, 1997; Fujita *et al.*, 2004; Thomson and Shaffer, 2010). Studies that used one or two outgroups (*Gallus* and/or *Alligator*) found ambiguous results concerning the monophyly of Pleurodira and Cryptodira, depending on the method used for phylogenetic inference (Cervelli *et al.*, 2003; Krenz *et al.*, 2005; Barley *et al.*, 2010). Sterli (2010) recently recovered a sister relationship between Pleurodira and Trionychia, based on morphological characters and 12S, 16S, cytb, RAG1 and R35 intron. This unorthodox result may be due to the inclusion of extinct species in the analysis of morphological characters, resulting in the basal position of Chelonioidea as sister to all other extant Testudines lineages. Using outgroups from four clades (Squamata, Rhynchocephalia, Aves and Crocodylidae), we find here good support for a basic divergence of Pleurodira and Cryptodira. The early appearance of Trionychia within Cryptodira is also better supported than in previous molecular studies with outgroups (Krenz *et al.*, 2005; Barley *et al.*, 2010).

The phylogeny of Cryptodira has been a matter of debate (Shaffer *et al.*, 1997; Fujita *et al.*, 2004; Krenz *et al.*, 2005; Chandler and Janzen, 2009; Thomson and Shaffer, 2010). We find a polytomy composed of four clades: (i) Chelonioidea ( $cv = 0.999$ ), (ii) Chelydridae ( $cv = 1$ ), (iii) Kinosternoidea ( $cv = 1$ ), and (iv) a group formed by Geoemydidae, Testudinidae, Emydidae and

*Platysternon megacephalum* ( $cv = 1$ ). Various studies have found different topologies, either grouping Chelonioidea with Kinosternoidea (Fujita *et al.*, 2004; using R35 intron), or grouping Chelonioidea with Geoemydidae, Testudinidae, Emydidae and *Platysternon megacephalum* (Parham *et al.*, 2006; using complete mtDNA). As the number of species from Kinosternoidea included in phylogenies is usually low (here only five out of 26 species), DNA sequencing of more species from this clade could help clarify these relationships. However, the reasons why certain deep nodes are difficult to resolve are probably twofold: (i) a relatively rapid radiation, and (ii) phylogenetic analyses using genes saturated with mutations. Recently, Barley *et al.* (2010) provided new sequence data for eight nuclear genes, and found good support for a sister relationship of Chelonioidea to a group formed by Chelydridae and Kinosternoidea. We find the same relationships ( $cv > 0.9$ ) after adding the sequences of Barley *et al.* (2010) to our alignment (results not shown).

The phylogenetic position of *Platysternon megacephalum* has long been enigmatic (Parham *et al.*, 2006). Indeed, the first analyses, based on morphological characters, have led authors to relate *P. megacephalum* with Chelydridae (*Chelydra serpentina* and *Macrochelys temminckii*). However, some molecular studies found that *P. megacephalum* was grouped with Testudinoidea (Cervelli *et al.*, 2003, based on U17 small nucleolar RNA; Krenz *et al.*, 2005, based on 12S, cytb and RAG1). In the phylogeny that Parham *et al.* (2006) obtained with complete mitochondrial genomes, *P. megacephalum* was included in Testudinoidea as the sister-species to Emydidae. We here find good support ( $cv = 0.980$ ) for the same hypothesis, as did Thomson and Shaffer (2010).

Within Pleurodira, a problematic taxon is *Elseya*, which appears polyphyletic, with the inclusion of *Rheodytes leukops* as sister to *Elseya dentata* ( $cv = 1$ ), and of *Elusor macrurus* as sister to *Elseya purvisi* ( $cv = 0.929$ ). The same position, albeit less supported, was already found for *Rheodytes leukops* by Seddon *et al.* (1997), based on 12S sequences. Thomson and Georges (2009) recently proposed the erection of a new genus, *Myuchelys*, including species previously named *Elseya latisternum* (type-species of the new genus), *Elseya georgesi*, *Elseya purvisi* and *Elseya novae-guineae*. More sequencing work would be useful to assess the monophyly of the resulting taxon, because it is not monophyletic in our phylogeny. Finally, *Emydura* is problematic, because *Emydura macquarii* is grouped



with *Elseya georgesi* and *Elseya latisternum* ( $cv = 0.934$ ), and not with *Emydura subglobosa*. However, it must be noted that *Emydura subglobosa* is here represented by only one sequence. The topology we find for Podocnemididae is in agreement with the one recently reported by Vargas-Ramirez *et al.* (2008), based on 12 genes (six mitochondrial and six nuclear).

Within Trionychia, our results are comparable with those of Engstrom *et al.* (2004), based on ND4, cytB and R35, except within *Nilssonina*. We find high support for a sister relationship between *Nilssonina hurum* and *Nilssonina nigricans* ( $cv = 0.988$ ), and between *Nilssonina gangeticus* and *Nilssonina leithii* ( $cv = 0.933$ ). This is in agreement with the results reported by Praschag *et al.* (2007a), based on cytB sequences. Within Kinosternoidea, Thomson and Shaffer (2010) found good support for a monophyletic *Kinosternon*. In contrast, we find a sister relationship between *Kinosternon baurii* and *Sternotherus odoratus* ( $cv = 0.923$ ). However, only one DNA sequence is available for *Kinosternon baurii*, so this result is only preliminary and warrants further investigation. The phylogeny we find within Chelonioidea is identical to that already described (Naro-Maciel *et al.*, 2008). Within Testudinidae, we find a sister relationship between *Kinixys belliana* and *Kinixys spekii* ( $cv = 0.985$ ), whereas Thomson and Shaffer (2010) found good support for a close relationship between *Kinixys belliana* and *Kinixys natalensis*. The reason for this difference is unclear because gene sampling for *Kinixys* was presumably very similar in both studies. There is also significant disagreement between our phylogeny of Testudininae and the one by Lourenço *et al.* (2012), who found *Indotestudo* and *Malacochersus* nested within *Testudo*. This may result from different species sampling because Lourenço *et al.* (2012) did not include *Testudo hermanni* and *Indotestudo travancorica* in their analysis. This is not the first time that *Homopus* is found to be polyphyletic. Thomson and Shaffer (2010) found the same relationships for *Homopus*, showing *Homopus signatus* and *Homopus boulengeri* grouped with *Chersina angulata* with good support, and *Homopus aerolatus* and *Homopus femoralis* grouped with *Psammobates* with lower support. We suggest that a taxonomic revision could be useful here.

A taxon that has been plagued by nomenclatural problems is Geoemydidae. Based on molecular phylogenies, Spinks *et al.* (2004) made three nomenclatural suggestions. They proposed (i) including all *Chinemys* and *Ocadia* species in *Mauremys*, (ii) re-including

*Chelopus annulata* and *Chelopus rubida* in the genus *Rhinoclemmys*, and (iii) classifying *K. tecta*, *K. tentoria* and *K. smithii* as members of a new genus, *Pangshura*. All these propositions are supported by our phylogeny and result in monophyletic genera. However, the taxonomic position of the remaining species of *Kachuga* (*K. dhongoka*, *K. kachuga*, *K. sylhetensis* and *K. trivittata*) is still problematic. As Le *et al.* (2007) and Praschag *et al.* (2007a) already recommended, we propose the inclusion of *Kachuga sylhetensis* in *Pangshura*, with which it is clearly grouped ( $cv = 0.999$ ), and the inclusion of *Callagur borneensis*, *Kachuga kachuga*, *Kachuga dhongoka*, and *Kachuga trivittata* in *Batagur*. Within Geoemydinae, the taxonomy within *Cuora* and *Cyclemys* has long been uncertain. Here we find *Cuora trifasciata* grouped with *Cuora aurocapitata* ( $cv = 1$ ) and *Cuora galbinifrons* grouped with *Cuora mccordi* ( $cv = 0.943$ ), in contrast with Honda *et al.* (2002), using 12S and 16S sequences, or Stuart and Parham (2004) and He *et al.* (2007), using COI and ND4. The phylogeny we obtain for *Cuora* is consistent with the one obtained by Spinks and Shaffer (2007), using COI and ND4 (but not what they obtained with nuclear DNA). Noticeably, we here used complete mtDNA for *Cuora aurocapitata*, *Cuora flavomarginata* and *Cuora mouhotii*. Uncertainty of specimen identification or hybridization between species, as is known to occur in *Cuora*, may also explain these discrepancies (Spinks and Shaffer, 2007). Within *Cyclemys*, we find close relationships between a group formed by *Cyclemys atripons* and *Cyclemys pulchriata*, and a group formed by *Cyclemys bellii*, *Cyclemys enigmatica*, *Cyclemys dentata* and *Cyclemys ovata*. This contrasts with the topologies found by Praschag *et al.* (2009) and Fritz *et al.* (2008), using cytB, c-mos, RAG2 and R35 intron. However, these studies obtained different topologies when analyzing separately mitochondrial and nuclear sequences, indicating that mitochondrial introgression may have occurred through hybridization. Finally, we suggest that the Batagurinae and Geoemydinae should be re-delimited, since Geoemydinae is currently not monophyletic (Table S2, Fig. 2d).

Within Emydidae, *Clemmys guttata* has been consistently recovered in two different positions: (i) as sister to *Terrapene* (Feldman and Parham, 2002, based on cytB and ND4; Stephens and Wiens, 2003, based on 16S, ND4 and cytB; Spinks and Shaffer, 2009, based on cytB, R35, RAG1 plus five more nuclear loci) or (ii) as sister to the *Emys* + *Emydoidea* clade (Stephens and Wiens, 2009, based on morphological

data, 16S, cytB, ND4, control region, and R35; Wiens et al., 2010, based on cytB, ND4, R35 plus five more nuclear loci). Our results support the first hypothesis ( $cv = 0.930$ ). However, the second hypothesis for *Clemmys guttata* was favored by data sets that were not totally included in ours, so we cannot reject it. Our results on Deirochelyinae are in good agreement with previous topologies (Stephens and Wiens, 2003, 2009; Wiens et al., 2010), but differ from those reported by Spinks et al. (2009), using seven nuclear loci including R35 and RAG1. We find *Trachemys* monophyletic ( $cv = 1$ ), grouped with *Graptemys* and *Malaclemmys terrapin* ( $cv = 0.999$ ), and *Pseudemys* grouped with *Chrysemys picta* ( $cv = 0.995$ ). Within *Graptemys* and *Pseudemys*, relationships are poorly resolved because mitochondrial DNA seems to exhibit low divergence between species (Wiens et al., 2010), and we have excluded fast evolving DNA regions from our 230-species alignment.

A parsimony analysis of the DNA matrix was also performed, and yielded a less resolved tree, with low bootstrap support for some clades that were well resolved in maximum likelihood analysis (results not shown). However, the monophyly of Pleurodira and Cryptodira is supported (bootstrap support = 0.81 and 0.76, respectively), as is the sister relationship of Trionychia (bootstrap support = 0.85) to a group formed by all other Cryptodira (bootstrap support = 0.87). When only bootstrap support > 0.7 is taken into account, the parsimony tree is fully compatible with the one obtained with maximum likelihood.

Our study has provided the largest phylogeny of turtles to date. By using both mtDNA and nuDNA data, we find that most genera are now monophyletic, with strong support, but we suggest some nomenclatural revisions and point at specific taxa that warrant further sequencing work. Polytomies still observed in our phylogeny ( $cv < 0.5$ ) are related with the species with the lowest number of sequences. On the 21 species with only one gene sequenced, one third is directly involved in a polytomy (this proportion is 0.11 when considering all species). New sequences from these seven species (*Cyclemys ovata*, *Emydura subglosa*, *Graptemys oculifera*, *Graptemys versa*, *Pseudemys alabamensis*, *Pseudemys gorzugi*, *Pseudemys suwan-niensis*) should be obtained in priority to better resolve the phylogeny. Because all but two turtle genera are represented in our phylogeny, our work provides a solid basis to help in further studies of the evolution of some characters in turtles or the ancient biogeographical distribution of turtles.

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## On-line supplementary material

- S1. Authorities for species used in this study.  
 S2. GenBank accession numbers of the sequences used in this study.

Species	Authority
<b>Pleurodira</b>	
<b>Chelidae</b>	
Chelidinae	
<i>Acanthochelys macrocephala</i>	(Rodin, Mittermeier & McMorris, 1984)
<i>pallidipectoris</i>	(Freiberg, 1945)
<i>radiolata</i>	(Mikan, 1820)
<i>spixii</i>	(Duméril & Bibron, 1835)
<i>Chelus fimbriatus</i>	(Schneider, 1783)
<i>Mesoclemmys gibba</i>	(Schweigger, 1812)
<i>hogeii</i>	(Mertens, 1967)
<i>nasutus</i>	(Schweigger, 1812)
<i>Phrynops geoffroanus</i>	(Schweigger, 1812)
<i>hilarii</i>	(Duméril & Bibron, 1835)
<i>williamsi</i>	Rhodin & Mittermeier, 1983
<i>Platemys platycephala</i>	(Schneider, 1792)
Chelodinae	
<i>Chelodina longicollis</i>	(Shaw, 1794)
<i>oblonga</i>	Gray, 1841
<i>rugosa</i>	Ogilby, 1890
<i>Elseya dentata</i>	(Gray, 1863)
<i>georgesi</i>	Cann, 1997
<i>latisternum</i>	Gray, 1867
<i>purvisi</i>	Wells & Wellington, 1985
<i>Elusor macrurus</i>	Cann & Legler, 1994
<i>Emydura macquarii</i>	(Gray, 1831)
<i>subglobosa</i>	(Krefft, 1876)
<i>Pseudemydura umbrina</i>	Siebenrock, 1901
<i>Rheodytes leukops</i>	Legler & Cann, 1980
Hydromedusinae	
<i>Hydromedusa tectifera</i>	Cope, 1870
<b>Pelomedusidae</b>	
<i>Pelomedusa subrufa</i>	(Lacepède, 1788)
<i>Pelusios gabonensis</i>	(Duméril, 1856)
<i>sinuatus</i>	(Smith, 1838)
<i>subniger</i>	(Lacepède, 1788)
<i>williamsi</i>	Laurent, 1965
<b>Podocnemididae</b>	
<i>Erymnochelys madagascariensis</i>	(Grandidier, 1867)
<i>Peltocephalus dumeriliana</i>	(Schweigger, 1812)
<i>Podocnemis erythrocephala</i>	(Spix, 1824)
<i>expansa</i>	(Schweigger, 1812)
<i>lewyana</i>	Duméril, 1852
<i>sextuberculata</i>	Cornalia, 1849
<i>unifilis</i>	Troschel, 1848
<i>vogli</i>	Müller, 1935
<b>Cryptodira</b>	
<b>Chelydridae</b>	
<i>Chelydra serpentina</i>	(Linnaeus, 1758)
<i>Macrochelys temminckii</i>	(Troost, 1835)
<b>Platysternidae</b>	
<i>Platysternon megacephalum</i>	Gray, 1831
<b>Chelonioidea</b>	
<b>Cheloniidae</b>	
<i>Caretta caretta</i>	(Linnaeus, 1758)
<i>Chelonia mydas</i>	(Linnaeus, 1758)
<i>Eretmochelys imbricata</i>	(Linnaeus, 1766)
<i>Lepidochelys kempii</i>	(Garman, 1880)
<i>olivacea</i>	(Eschscholtz, 1829)
<i>Natator depressus</i>	(Garman, 1880)
<b>Dermochelyidae</b>	
<i>Dermochelys coriacea</i>	(Vandellius, 1761)
<b>Kinosternoidea</b>	
<b>Dermatemydidae</b>	
<i>Dermatemys mawii</i>	Gray, 1847
<b>Kinosternidae</b>	
<i>Kinosternon baurii</i>	Garman, 1891
<i>flavescens</i>	Agassiz, 1857
<i>Staurotypus triporcatus</i>	(Wiegmann, 1828)

<i>Sternotherus odoratus</i>	(Latreille, 1801)
<b>Testudinoidea</b>	
<b>Geoemydidae</b>	
<b>Batagurinae</b>	
<i>Batagur affinis</i>	(Cantor, 1847)
<i>baska</i>	(Gray, 1830)
<i>Callagur borneoensis</i>	(Schlegel & Müller, 1845)
<i>Geoclemys hamiltonii</i>	(Gray, 1831)
<i>Hardella thurjii</i>	(Gray, 1831)
<i>Kachuga dhongoka</i>	(Gray, 1832)
<i>kachuga</i>	(Gray, 1831)
<i>syhetensis</i>	(Jerdon, 1870)
<i>trivittata</i>	(Duméril & Bibron, 1835)
<i>Morenia ocellata</i>	(Duméril & Bibron, 1835)
<i>Pangshura smithii</i>	(Gray, 1863)
<i>tecta</i>	(Gray, 1830)
<i>tentoria</i>	(Gray, 1834)
<b>Geoemydinae</b>	
<i>Cuora amboinensis</i>	(Daudin, 1801)
<i>aurocapitata</i>	Luo & Zong, 1988
<i>flavomarginata</i>	(Gray, 1863)
<i>galbinifrons</i>	Bourret, 1939
<i>mccordi</i>	Ernst, 1988
<i>mouhotii</i>	(Gray, 1862)
<i>pani</i>	Song, 1984
<i>trifasciata</i>	(Bell, 1825)
<i>yunnanensis</i>	(Boulenger, 1906)
<i>zhoui</i>	Zhao, 1990
<i>Cyclemys atripons</i>	Iverson & McCord, 1997
<i>bellii</i>	Gray, 1863
<i>dentata</i>	(Gray, 1831)
<i>enigmatica</i>	Fritz, Guicking, Auer, Sommer, Wink & Hundsdörfer, 2009
<i>fusca</i>	Fritz, Guicking, Auer, Sommer, Wink & Hundsdörfer, 2009
<i>gemeli</i>	Fritz, Guicking, Auer, Sommer, Wink & Hundsdörfer, 2009
<i>oldhamii</i>	Gray, 1863
<i>ovata</i>	Gray, 1863
<i>pulchriatrata</i>	Fritz, Gaulke & Lehr, 1997
<i>tcheponensis</i>	(Bourret, 1939)
<i>Geoemyda japonica</i>	Fan, 1931
<i>spengleri</i>	(Gmelin, 1789)
<i>Heosemys annandalii</i>	(Boulenger, 1903)
<i>depressa</i>	(Anderson, 1875)
<i>grandis</i>	(Gray, 1860)
<i>spinosa</i>	(Gray, 1830)
<i>Leucocephalon yuwonoi</i>	(McCord, Iverson & Boeadi, 1995)
<i>Malayemys subtrijuga</i>	(Schlegel & Müller, 1845)
<i>Mauremys annamensis</i>	(Siebenrock, 1903)
<i>caspica</i>	(Gmelin, 1774)
<i>japonica</i>	(Temminck & Schlegel, 1835)
<i>leprosa</i>	(Schweigger, 1812)
<i>megaloccephala</i>	(Fang, 1934)
<i>mutica</i>	(Cantor, 1842)
<i>nigricans</i>	(Gray, 1834)
<i>reevesii</i>	(Gray, 1831)
<i>rivulata</i>	(Valenciennes, 1833)
<i>sinensis</i>	(Gray, 1834)
<i>Melanochelys trijuga</i>	(Schweigger, 1812)
<i>Notochelys platynota</i>	(Gray, 1834)
<i>Orlitia borneensis</i>	Gray, 1873
<i>Rhinoclemmys annulata</i>	(Gray, 1860)
<i>areolata</i>	(Duméril & Bibron, 1851)
<i>diademata</i>	(Mertens, 1954)
<i>funerea</i>	(Cope, 1876)
<i>melanosterna</i>	(Gray, 1861)
<i>nasuta</i>	(Boulenger, 1902)
<i>pulcherrima</i>	(Gray, 1856)
<i>punctularia</i>	(Daudin, 1801)
<i>rubida</i>	(Cope, 1870)
<i>Sacalia bealei</i>	(Gray, 1831)
<i>quadriocellata</i>	(Siebenrock, 1903)
<i>Siebenrockiella crassicolis</i>	(Gray, 1831)



<i>leytensis</i>	(Taylor, 1920)
<i>Vijayachelys silvatica</i>	(Henderson, 1912)
<b>Emyridae</b>	
Deirochelyinae	
<i>Chrysemys picta</i>	(Schneider, 1783)
<i>Deirochelys reticularia</i>	(Latreille, 1801)
<i>Graptemys barbouri</i>	Carr & Marchand, 1942
<i>caglei</i>	Haynes Mckown, 1974
<i>flavimaculata</i>	Cagle, 1954
<i>geographica</i>	(LeSueur, 1817)
<i>nigrinoda</i>	Cagle, 1854
<i>oculifera</i>	(Baur, 1890)
<i>ouachitensis</i>	Cagle, 1953
<i>pseudogeographica</i>	(Gray, 1831)
<i>pulchra</i>	Baur, 1893
<i>versa</i>	Stejneger, 1925
<i>Malaclemys terrapin</i>	(Schoepff, 1793)
<i>Pseudemys alabamensis</i>	Baur, 1893
<i>concinna</i>	(LeConte, 1830)
<i>gorzugi</i>	Ward, 1984
<i>nelsoni</i>	Carr, 1938
<i>peninsularis</i>	(Carr, 1938)
<i>rubriventris</i>	(Le Conte, 1830)
<i>suwanniensis</i>	(Carr, 1937)
<i>texana</i>	Baur, 1893
<i>Trachemys decorata</i>	(Barbour & Carr, 1940)
<i>decussata</i>	(Gray, 1831)
<i>dorbigni</i>	(Duméril & Bibron, 1835)
<i>gaigeae</i>	(Hartweg, 1939)
<i>scripta</i>	(Schoepff, 1792)
<i>stejnegeri</i>	(Schmidt, 1928)
<i>terrapin</i>	(Lacépède, 1788)
Emydinae	
<i>Clemmys guttata</i>	(Schneider, 1792)
<i>Emydoidea blandingii</i>	(Holbrook, 1838)
<i>Emys marmorata</i>	Baird & Girard, 1852
<i>orbicularis</i>	(Linnaeus, 1758)
<i>triacris</i>	Fritz, Fatizzo, Guicking, Tripepi, Pennisi, Lenk, Joger & Wink, 2005
<i>Glyptemys insculpta</i>	(LeConte, 1830)
<i>muhlenbergii</i>	(Schoepff, 1801)
<i>Terrapene carolina</i>	(Linnaeus, 1758)
<i>coahuila</i>	Schmidt & Owens, 1944
<i>nelsoni</i>	Stejneger, 1925
<i>ornata</i>	(Agassiz, 1857)
<b>Testudinidae</b>	
Gopherinae	
<i>Gopherus agassizii</i>	(Cooper, 1863)
<i>berlandieri</i>	(Agassiz, 1857)
<i>flavomarginatus</i>	Legler, 1959
<i>polyphemus</i>	(Daudin, 1801)
<i>Manouria emys</i>	(Schlegel & Müller, 1840)
<i>impressa</i>	(Günther, 1882)
Testudininae	
<i>Astrochelys radiata</i>	(Shaw, 1802)
<i>yniphora</i>	(Vaillant, 1885)
<i>Chelonoidis carbonaria</i>	(Spix, 1824)
<i>chilensis</i>	(Gray, 1870)
<i>denticulata</i>	(Linnaeus, 1766)
<i>nigra</i>	(Quoy & Gaimard, 1824)
<i>Chersina angulata</i>	(Schweigger, 1812)
<i>Dipsoschelys arnoldi</i>	Bour, 1982
<i>dussumieri</i>	Gray, 1831
<i>hololissa</i>	(Günther, 1877)
<i>Geochelone elegans</i>	(Schoepff, 1795)
<i>platynota</i>	(Blyth, 1863)
<i>sulcata</i>	(Miller, 1779)
<i>Homopus areolatus</i>	(Thunberg, 1787)
<i>boulengeri</i>	Duerden, 1906
<i>femorialis</i>	Boulenger, 1888
<i>signatus</i>	(Gmelin, 1789)
<i>Indotestudo elongata</i>	(Blyth, 1853)
<i>forstenii</i>	(Schlegel & Müller, 1845)

<i>travancorica</i>	(Boulenger, 1907)
<i>Kinixys belliana</i>	(Gray, 1831)
<i>erosa</i>	(Schweigger, 1812)
<i>homeana</i>	Bell, 1827
<i>natalensis</i>	Hewitt, 1935
<i>spekii</i>	Gray, 1863
<i>Malacochersus tornieri</i>	(Siebenrock, 1903)
<i>Psammobates geometricus</i>	(Linnaeus, 1758)
<i>oculifer</i>	(Kuhl, 1820)
<i>pardalis</i>	(Bell, 1828)
<i>tentorius</i>	(Bell, 1828)
<i>Pyxis arachnoides</i>	Bell, 1827
<i>planicauda</i>	(Grandidier, 1867)
<i>Testudo graeca</i>	Linnaeus, 1758
<i>hermanni</i>	Gmelin, 1789
<i>horsfieldii</i>	Gray, 1844
<i>kleinmanni</i>	Lortet, 1883
<i>marginata</i>	Schoepff, 1793
<b>Trionychia</b>	
<b>Carettochelyidae</b>	
<i>Carettochelys insculpta</i>	Ramsay, 1886
<b>Trionychidae</b>	
<b>Cyclanorbinae</b>	
<i>Cyclanorbis elegans</i>	(Gray, 1869)
<i>senegalensis</i>	(Duméril & Bibron, 1835)
<i>Cycloderma aubryi</i>	(Duméril, 1856)
<i>frenatum</i>	Peters, 1854
<i>Lissemys punctata</i>	(Lacepède, 1788)
<i>scutata</i>	(Peters, 1868)
<b>Trionychinae</b>	
<i>Amyda cartilaginea</i>	(Boddaert, 1770)
<i>Apalone ferox</i>	(Schneider, 1783)
<i>mutica</i>	(LeSueur, 1827)
<i>spinifera</i>	(LeSueur, 1827)
<i>Chitra chitra</i>	Nutaphand, 1986
<i>indica</i>	(Gray, 1831)
<i>vandijki</i>	Mccord & Pritchard, 2003
<i>Dogania subplana</i>	(Geoffroy Saint-Hilaire, 1809)
<i>Nilssonina formosa</i>	(Gray, 1869)
<i>gangeticus</i>	(Cuvier, 1825)
<i>hurum</i>	(Gray, 1831)
<i>leithii</i>	(Gray, 1872)
<i>nigricans</i>	(Anderson, 1875)
<i>Palea steindachneri</i>	(Siebenrock, 1906)
<i>Pelochelys bibroni</i>	(Owen, 1853)
<i>cantorii</i>	Gray, 1864
<i>Pelodiscus axenaria</i>	(Zhou, Zhang & Fang, 1991)
<i>sinensis</i>	(Wiegmann, 1834)
<i>Rafetus euphraticus</i>	(Daudin, 1801)
<i>Trionyx triunguis</i>	(Forsskål, 1775)

Table S1: Authorities for species used in this study.

Species	Complete genome	Mitochondrial genome						Nuclear genome			
		12S	16S	COI	ND4	cytB	R35	Cmos	RAG1	RAG2	
<b>OUTGROUPS</b>											
<b>Pleurodira</b>											
<b>Chelidae</b>											
Chelidinae											
<i>Acanthocheilus macrocephala</i>				EF535294.1	EF535282.1						
<i>pallidipectoris</i>	U40392.1	AF113634.1	AF113658.1	EF535295.1	EF535283.1						
<i>radiolata</i>		AY283249.1		EF535302.1	EF535290.1			AF109204.1			
<i>spixii</i>		AY283250.1		EF535300.1	EF535288.1						
<i>Chelus fimbriatus</i>	U81320.1	AF113632.1	AF113656.1	U81343.1	U81343.1			AY339640.1	AY109203.1	AY687918.1	
<i>Mesoclemmys gibba</i>	U40646.1	AF113636.1	AF113660.1	EF535304.1	U81348.1			AY742455.1	AF109206.1	AY687919.1	
<i>hogeii</i>		AY283252.1	AY283246.1								
<i>nasutus</i>	U40645.1	AF113637.1	AF113661.1					AY339637.1			
<i>Phrynops geoffroanus</i>	U40647.1	AY283254.1	AY283244.1					AF109205.1			
<i>hilarii</i>		AY283255.1	AY283245.1								
<i>williamsi</i>		AY283257.1	AY283248.1								
<i>Platemys platycephala</i>	U40648.1	AF113633.1	AF113657.1	EF535298.1	EF535286.1						
Chelodinae											
<i>Chelodina longicollis</i>	U40633.1	AF113629.1	AF113653.1		U81356.1			AY339636.1		AY687921.1	
<i>oblonga</i>	U40634.1	AF113630.1	AF113654.1					AF109202.1			
<i>rugosa</i>	U40635.1	AF113631.1	AF113655.1					AF039486.1			
<i>Eelseya dentata</i>	U40637.1	AF113626.1	AF113650.1					AF039485.1			
<i>georgesi</i>	AF095894.1	AF113628.1	AF113652.1								
<i>latisternum</i>	U40638.1	AF113625.1	AF113649.1		U81354.1			AY339643.1		AY687920.1	
<i>purvisi</i>	AF095893.1	AF113627.1	AF113651.1								
<i>Elusor macrurus</i>	U40639.1	AF113622.1	AF113646.1					AF109200.1			
<i>Emydura macquarii</i>	U40640.1	AF113623.1	AF113647.1								
<i>subglobosa</i>								AY339632.1			
<i>Pseudemydura umbrina</i>	U40650.1	AF113620.1	AF113644.1								
<i>Rheodytes leukops</i>	U40651.1	AF113621.1	AF113645.1					AF109201.1			
Hydromedusinae											
<i>Hydromedusa tectifera</i>	U62017.1	AF113638.1	AF113662.1					AF109207.1	AY988104.1		
<b>Pelomedusidae</b>											
<i>Pelomedusa subrufa</i>	AF039066.1							AY339639.1	AF109208.1	FJ230878.1	
<i>Pelusios gabonensis</i>										FJ230879.1	
<i>sinuatus</i>	U40644.1	AF113641.1	AF113665.1							AY988103.1	
<i>subniger</i>											
<i>williamsi</i>	U81324.1				U81347.1			AY339629.1		AY687923.1	
<b>Podocnemididae</b>											
<i>Erymnocheilus madagascariensis</i>	AM943824.1	AF113640.1	AF113664.1	FM165619.1	AM943834.1	AM943849.1			AY988099.1	AM943835.1	
<i>Peltocephalus dumeriliana</i>	U40643.1	AF113643.1	AF113667.1	FM165622.1	AM943833.1	AM943848.1			AY988101.1	AM943837.1	
<i>Podocnemis erythrocephala</i>	AM943822.1			FM165621.1	AM943832.1	AM943845.1				AM943841.1	
<i>expansa</i>	AM943820.1	AF113642.1	AF113666.1	FM165620.1	AM943830.1	AY742456.1		AF109209.1	AY687924.1	AM943839.1	
<i>lewynana</i>	AM943817.1		FM165625.1	FM165617.1	AM943827.1	AM943826.1				AM943825.1	
<i>sextuberculata</i>	AM943819.1			FM165616.1	AM943831.1	AM943844.1				AM943840.1	
<i>unifilis</i>	AM943818.1			FM165623.1	AM943829.1	AY339634.1				AM943842.1	
<i>vogli</i>	AM943821.1			FM165618.1	AM943828.1	AM943846.1				AM943838.1	
<b>Cryptodira</b>											
Chelydridae											
<i>Chehydra serpentina</i>	NC_011198.1							AY742461.1	FJ230855.1	FJ230857.1	
								AY742461.1	FJ230855.1	FJ230858.1	

Species	Complete genome	Mitochondrial genome					Nuclear genome					
		12S	16S	COI	ND4	cytB	R35	Cmos	RAG1	RAG2		
<i>Macrocheilus temminckii</i>	NC_009260.1						FJ234440.1	FJ230862.1	FJ234441.1	FJ230865.1		
<b>Platysernidae</b>												
<i>Platysternon megacephalum</i>	DQ016387.1						AY742462.1		AY687905.1			
<b>Chelonioidae</b>												
<b>Cheloniidae</b>												
<i>Caretta caretta</i>	AY770537.1	AY770545.1	AF385671.1	FJ009031.1	FJ009023.1	FJ009032.1	FJ009033.1	FJ009034.1	FJ009035.1	FJ009036.1	FJ009037.1	FJ009038.1
<i>Chelonia mydas</i>	NC_000886.1						AY339635.1	FJ039973.1	FJ039974.1	FJ039975.1	FJ039976.1	FJ039977.1
<i>Eremochelys imbricata</i>	NC_012398.1						FJ039991.1	FJ039992.1	FJ039993.1	FJ039994.1	FJ039995.1	FJ039996.1
<i>Lepidochelys kempii</i>	NC_011516.1						FJ039988.1	FJ039989.1	FJ039990.1	FJ039991.1	FJ039992.1	FJ039993.1
<i>Natator depressus</i>	FJ039955.1	FJ039956.1	AF385674.1	FJ039959.1	FJ039958.1	FJ039961.1	FJ039962.1					
<b>Dermochelyidae</b>												
<i>Dermochelys coriacea</i>	U81340.1	FJ039914.1	AF385678.1	FJ039909.1	FJ039918.1	FJ039919.1						
<b>Kinosternoidea</b>												
<b>Kinosternidae</b>												
<i>Dermatemys mawii</i>	U81341.1		U81364.1	AY339638.1			AY687910.1					
<b>Kinosternidae</b>												
<i>Kinosternon baurii</i>							AY339642.1					
<i>flavescens</i>			DQ256379.1				GU085686.1		GU085674.1			
<i>Sturotypus triporcatus</i>	AB090018.1	AB090046.1					U81349.1		AY339633.1			
<i>Sternotherus odoratus</i>							U81350.1		AY742463.1			AY687911.1
<b>Testudinoidea</b>												
<b>Geomydidae</b>												
<b>Batagurinae</b>												
<i>Batagur affinis</i>	AY434638.1		FN313570.1	AY434658.1			FN256245.1		FN256247.1			
<i>baska</i>	EU030185.1	EU030199.1	FN313567.1				EU030217.1		EU030234.1			
<i>Callagur borneensis</i>	AB090044.1	EU030200.1	AY434601.1	AY434659.1	EU030218.1	EU030235.1	EU030236.1	EU030237.1	EU030238.1	EU030239.1	EU030240.1	EU030241.1
<i>Geoclemys hamiltonii</i>	AY434632.1	EU030201.1	AY434673.1	AY434651.1	EU030219.1	EU030234.1	EU030235.1	EU030236.1	EU030237.1	EU030238.1	EU030239.1	EU030240.1
<i>Hardella thurii</i>	AB090025.1	EU030204.1	AY434603.1	AY434660.1	EU030222.1	EU030238.1	EU030239.1	EU030240.1	EU030241.1	EU030242.1	EU030243.1	EU030244.1
<i>Kachuga dhongoka</i>	EU030190.1	EU030205.1	AY434569.1	AY434649.1	EU030223.1	EU030239.1	EU030240.1	EU030241.1	EU030242.1	EU030243.1	EU030244.1	EU030245.1
<i>kachuga</i>	EU030191.1	EU030206.1	EU030215.1				EU030224.1					
<i>syhetensis</i>			AM495298.1									
<i>trivittata</i>	EU030192.1	EU030207.1	EU030216.1				EU030225.1		EU030240.1			
<i>Morenia ocellata</i>	AF043409.1	EU030209.1	AY434605.1	AY434662.1	EU030227.1	EU030242.1	EU030243.1	EU030244.1	EU030245.1	EU030246.1	EU030247.1	EU030248.1
<i>Pangshura (ex Kachuga) smithii</i>	EU030195.1	EU030211.1	AY434589.1				EU030229.1		EU030244.1			
<i>tecta</i>	AY434633.1	GQ398140.1	AY434583.1				EU030230.1		EU030245.1			
<i>tentoria</i>	AY434639.1	EU030213.1	AY434612.1				EU030231.1		EU030246.1			
<b>Geomydinae</b>												
<i>Cuora amboinensis</i>	AB090029.1	EU930738.1	AY357738.1	AY364609.1	EF011428.1	EU930759.1	EU930787.1					
<i>aurocapitata</i>	NC_009509.1				EF011430.1							
<i>flavomarginata</i>	NC_012054.1				DQ386659.1							
<i>galbiniifrons</i>	AF043395.1	EU930739.1	AY357748.1	AY364615.1	AJ564448.1	EU930760.1	EU930788.1					
<i>mccordi</i>			EF011471.1	EF011363.1	AY434568.1	EF011438.1						
<i>mouhotii</i>	NC_010973.1				EF011440.1							
<i>pani</i>	AB090031.1	AB090059.1	EF011476.1	EF011368.1	AY434574.1	EF011442.1						
<i>trifasciata</i>	AB090032.1	AB090060.1	EF011478.1	EF011370.1	AY434627.1	EF011445.1						
<i>yunnanensis</i>			AY590460.1	AY572868.1								
<i>zhoui</i>	AB090033.1	AB090061.1	EF011509.1	EF011401.1	AY434584.1	EF011463.1						
<i>Cyclemys atripons</i>	NC_010970.1				AM931623.1	AM931586.1	AM931605.1					
<i>bellii</i>			EF183501.1									
<i>dentata</i>	AF043402.1		AM931635.1		AM931696.1	AM931588.1	AM931608.1					
<i>enigmatica</i>			AM931646.1		AM931699.1	AM931591.1	AM931611.1					
<i>fusca</i>			AM931654.1		AM931701.1	AM931593.1	AM931613.1					

Species	Complete genome	Mitochondrial genome							Nuclear genome					
		12S	16S	COI	ND4	cytB	R35	Cmos	RAG1	RAG2				
<i>gemeli</i>								FM877770.1	FM877773.1	FM877766.1				FM877762.1
<i>oldhamii</i>								AM931675.1	AM931704.1	AM931598.1				AM931617.1
<i>ovata</i>								DQ444275.1						
<i>pulcherrima</i>								AM931693.1	AM931706.1	AM931601.1				AM931620.1
<i>icheponensis</i>								AY434577.1						
<i>Geoemyda japonica</i>								AY434602.1						
<i>spengleri</i>								AY434586.1	AY434655.1	EU030220.1	EU030236.1	EU030237.1	EU030254.1	EU030254.1
<i>Heosemys amandatii</i>								AY434598.1	AY434657.1					
<i>depressa</i>								AY434607.1		EU930762.1	EU930794.1			
<i>grandis</i>								AY434566.1						
<i>spinosa</i>								AY434578.1	AM931707.1	AM931602.1	AY687913.1			AM931621.1
<i>Leucocephalon yuwonoi</i>								AY434608.1	AM931708.1	AM931603.1				AM931622.1
<i>Malayemys subtrijuga</i>								AY434591.1	AY434656.1	EU030226.1	EU030241.1			EU030258.1
<i>Mauremys annamensis</i>								AY434564.1	DQ386655.1					
<i>caspica</i>								AY337338.2	AY339630.1	EU930763.1	EU930796.1			AM905437.1
<i>japonica</i>								AY337340.1	AY339630.1					
<i>leprosa</i>								AY337341.1	AY339630.1					
<i>megaloccephala</i>								AY434587.1		EU930764.1	EU930797.1			
<i>mutica</i>								AY434593.1						
<i>nigricans</i>									DQ386666.1		FJ770713.1			
<i>(ex Chinemys) reevesii</i>								AF348264.2	EF034111.1	AJ519500.1				
<i>rivulata</i>								AY337352.1	AY337344.1	AY434623.1				AY687914.1
<i>(ex Oecadia) sinensis</i>								AY434641.1	EU930744.1	EU930765.1	EU930798.1			AM905440.1
<i>Melanocheilus trijuga</i>								AF043391.1	AY337345.1	DQ386678.1				
<i>Notocheilus platynota</i>								AF043405.1	EU930746.1	AY434629.1	EU930767.1			
<i>Oritia borneensis</i>								AB090037.1	AB090065.1	AY434613.1	EU930800.1			
<i>Rhinoclemmys annulata</i>								AB090024.1	EU030210.1	AY434619.1	EU030243.1			EU030260.1
<i>areolata</i>								EU930726.1	EU930747.1	EU030228.1	EU030243.1			
<i>diademata</i>								EU930727.1	EU930748.1	EU930768.1	EU930801.1			
<i>funerea</i>								AY434640.1	EU930749.1	EU930769.1	EU930802.1			
<i>melanosterna</i>								EU930729.1	EU930750.1	EU930770.1	EU930803.1			
<i>nasuta</i>								DQ497267.1	DQ497290.1	EU930771.1	EU930804.1			
<i>pulcherrima</i>								DQ497268.1	DQ497291.1	DQ497359.1	EU030247.1			DQ497395.1
<i>punctularia</i>								EU930731.1	EU930752.1	DQ497360.1	EU030248.1			DQ497396.1
<i>rubida</i>								AY434637.1	EU930755.1	EU930773.1	EU930808.1			
<i>Sacalia bealae</i>								EU930735.1	EU930756.1	EU930776.1	EU930809.1			
<i>quadricellata</i>								AB090023.1	AB090051.1	EU930777.1	EU930810.1			
<i>Siebenrockiella crassicolis</i>								NC_011819.1		DQ386675.1	EU930811.1			
<i>leytensis</i>								AF043406.1	EU030214.1	AY954912.1	EU030249.1			EU030264.1
<i>Vijayachelys silvatica</i>										AY954911.1				
										AJ973611.1				
<b>Emydoidea</b>														
<b>Deirocheilyinae</b>														
<i>Chrysemys picta</i>														FJ770671.1
<i>Deirocheilus reticularia</i>								AF258865.1	AF258877.1	FJ770675.1	DQ497358.1			FJ770721.1
<i>Graptemys barbouri</i>								EU909370.1						DQ497394.1
<i>caglei</i>								EU909369.1						
<i>flavimaculata</i>								EU909371.1	GQ395734.1					FJ770728.1
<i>geographica</i>								EU909372.1	FJ770598.1					
<i>nigrinoda</i>								DQ646420.1						
<i>oculifera</i>								EU909374.1						
<i>ouachitensis</i>								EU909375.1	FJ770599.1					FJ770732.1
<i>pseudogeographica</i>								FJ770600.1						AY687916.1
<i>pulchra</i>								EU909377.1						
<i>versa</i>								DQ646422.1						

Species	Complete genome	Mitochondrial genome						Nuclear genome						
		12S	16S	COI	ND4	cytB	R35	Cmos	RAG1	RAG2				
<i>Malaclemys terrapin</i>							DQ646423.1	FJ770602.1	FJ770602.1	EU169877.1			FJ770735.1	
<i>Pseudemys alabamensis</i>														
<i>concinna</i>							DQ646424.1	FJ770604.1	FJ770604.1	FJ770691.1			FJ770736.1	
<i>gorzugi</i>														
<i>nelsoni</i>														
<i>peninsularis</i>							EU909379.1	EU909384.1	EU909384.1	FJ770694.1			FJ770739.1	
<i>rubriventris</i>							EU909378.1	FJ770606.1	FJ770606.1	FJ770695.1			FJ770740.1	
<i>suwanniensis</i>							EU909380.1	EQ395708.1	EQ395708.1					
<i>texana</i>								EQ395711.1	EQ395711.1					
<i>Trachemys decorata</i>							DQ338475.1	EU909386.1	EU909386.1					
<i>decurcata</i>							DQ338515.1	EQ395712.1	EQ395712.1					
<i>dorbigni</i>							DQ338521.1							
<i>gaigeae</i>							DQ338513.1							
<i>scripta</i>	NC_011573.1						DQ338489.1							
<i>stejnegeri</i>							DQ338527.1	FJ770621.1	FJ770621.1	AY742458.1			AY687915.1	
<i>terrapeni</i>							DQ338523.1			FJ770709.1			FJ770754.1	
Emyridae														
<i>Clemmys guttata</i>							AF258858.1	AF258870.1	AF258870.1	DQ649461.1			FJ770719.1	
<i>Emydoidea blandingii</i>							AF258857.1	AF258869.1	AF258869.1	AY905211.2				
<i>Emys marmorata</i>		U81321.1					AF258855.1	AF258867.1	AF258867.1	AY339631.1			AY687917.1	
<i>orbicularis</i>		AB090021.1	AB090049.1	FJ402875.1			AF258856.1	AF258868.1	AF258868.1	EU277643.1				
<i>triacris</i>							AJ131416.1	FJ770678.1	FJ770678.1				FJ770723.1	
<i>Glyptemys insculpta</i>		DQ497265.1	DQ497288.1				AF258864.1	AF258876.1	AF258876.1	DQ661020.1			EU930786.1	DQ497393.1
<i>muhlenbergii</i>							AF258863.1	AF258875.1	AF258875.1	FJ770682.1			FJ770727.1	
<i>Terrapene carolina</i>		EU930737.1	EU930758.1				AF258859.1	AF258871.1	AF258871.1	FJ770703.1			EU930812.1	
<i>coahuila</i>							AF258860.1	AF258872.1	AF258872.1	FJ770699.1			FJ770742.1	
<i>nelsoni</i>							AF258861.1	AF258873.1	AF258873.1				FJ770745.1	
<i>ornata</i>							AF258862.1	AF258874.1	AF258874.1	DQ649464.1			FJ770749.1	
Testudinidae														
Gopherinae														
<i>Gopherus agassizii</i>		AY434630.1					AY673591.1	AY434652.1	AY434652.1	AY434646.1				
<i>berlandieri</i>							AY673482.1	AY678350.1	AY678350.1					
<i>flavomarginatus</i>							AY673473.1	AY678348.1	AY678348.1					
<i>polyphemus</i>		AF020879.1	AF020886.1				AY673485.1	DQ497307.1	DQ497307.1	DQ497340.1			EU930793.1	DQ497376.1
<i>Manouria emys</i>	DQ080040.1									AY434647.1			DQ497384.1	DQ497384.1
<i>imprensa</i>	NC_011815.1												DQ497350.1	DQ497386.1
Testudininae														
<i>Astrochelys radiata</i>		AF020883.1	AF020890.1				AY673595.1	DQ497304.1	DQ497304.1				DQ497337.1	DQ497373.1
<i>ypiphora</i>		AF020882.1	AF020889.1				AY673541.1	DQ497306.1	DQ497306.1				DQ497339.1	DQ497375.1
<i>Chelonoidis carbonaria</i>		AB090019.1	AF192926.1				AF351692.1	DQ497296.1	DQ497296.1	DQ497329.1			EU930790.1	DQ497365.1
<i>chilensis</i>			AF192924.1				AF351674.1	DQ497297.1	DQ497297.1	DQ497330.1			EU930791.1	DQ497366.1
<i>denticulata</i>		AF175336.1	AF192927.1				AF351693.1	DQ497298.1	DQ497298.1	DQ497331.1			EU930792.1	DQ497367.1
<i>nigra</i>		AY097636.1	AY097785.1				AY673457.1	DQ497300.1	DQ497300.1	DQ497333.1				DQ497369.1
<i>Chersina angulata</i>		DQ497248.1	DQ497269.1	EF120509.1			AY673443.1	DQ497292.1	DQ497292.1	DQ497325.1				DQ497361.1
<i>Dipsoschelys arnoldi</i>		AY081779.1	AY081780.1					DQ497293.1	DQ497293.1	DQ497326.1				DQ497362.1
<i>dussumieri</i>		DQ497249.1	DQ497270.1					DQ497294.1	DQ497294.1	DQ497327.1				DQ497363.1
<i>hololissa</i>		AY081783.1	AY081784.1					DQ497295.1	DQ497295.1	DQ497328.1				DQ497364.1
<i>Geocheilone elegans</i>		AY081785.1	AY081786.1				AY673465.1	DQ497299.1	DQ497299.1	DQ497332.1				DQ497368.1
<i>plahynota</i>		DQ497253.1	DQ497273.1				AY673554.1	DQ497303.1	DQ497303.1	DQ497336.1				DQ497372.1
<i>sulcata</i>		AF175334.1	AY081788.1				AY673478.1	DQ497305.1	DQ497305.1	DQ497338.1				DQ497374.1
<i>Homopus areolatus</i>							AY673587.1	AY678323.1	AY678323.1					
<i>boulengeri</i>		DQ497254.1	DQ497274.1				AY673433.1	DQ497308.1	DQ497308.1	DQ497341.1				DQ497377.1



Species	Mitochondrial genome							Nuclear genome				
	Complete genome	12S	16S	COI	ND4	cytB	R35	Cmos	RAG1	RAG2		
<i>femorialis</i>												
<i>signatus</i>		DQ497255.1	DQ497275.1		AY673435.1	AY678328.1						
<i>Indotestudo elongata</i>	DQ080043.1				AY673429.1	DQ497309.1		DQ497342.1		DQ497378.1		
<i>forstenii</i>	NC_007696.1							DQ497343.1	EU930795.1	DQ497379.1		
<i>travancorica</i>												
<i>Kinixys belliana</i>					AY673472.1	DQ497311.1		DO497344.1		DO497380.1		
<i>erosa</i>		DO497257.1	DO497277.1		AY673583.1	DQ497312.1		DO497345.1		DO497381.1		
<i>homeana</i>		DO497258.1	DO497278.1		AY673553.1	AY678414.1						
<i>natalensis</i>		DO497259.1	DO497279.1		AY673562.1	DQ497313.1		DO497346.1		DO497382.1		
<i>Malacocheilus tornieri</i>					AY673582.1	AY678397.1						
<i>spetii</i>					AY673581.1	AY678398.1						
<i>Malacocheilus geometricus</i>	DQ080042.1							DO497347.1		DO497383.1		
<i>Psammodromus ocellifer</i>					AY673580.1	AY678376						
<i>pardalis</i>	DQ080041.1				AY673576.1	AY678378.1						
<i>tenorius</i>		DQ497264.1	DQ497284.1		AY673571.1	DQ497318.1	AY742459.1	DO497334.1	AY687912.1	DO497370.1		
<i>Pyxis arachnoides</i>		AF020880.1	AF020887.1		AY673507.1	DQ497319.1		DO497351.1		DO497387.1		
<i>planicauda</i>		AF020881.1	AF020888.1		AY673547.1	DQ497320.1		DO497353.1		DO497389.1		
<i>Testudo graeca</i>	DQ080049.1							DO497354.1		DO497390.1		
<i>hermanni</i>		AF067503.1	EF016446.1	NC_007696.1	NC_007696.1	AY678389.1		AM491036.1		AM491038.1		
<i>horsfieldii</i>	DO080045.1		AM491034.1			AJ888362.1						
<i>kleinmanni</i>	DO080048.1							DO497355.1		DO497391.1		
<i>marginata</i>	DQ080047.1							DO497356.1		DO497392.1		
								AM491035.1		AM491037.1		
<b>Trionychia</b>												
<i>Carettocheilus insculpta</i>		U81334.1			AY673526.1	AY259546.1	AY259571.1		AY687904.1			
<b>Carettocheilidae</b>												
<b>Trionychiidae</b>												
Cyclanorbinae												
<i>Cyclanorbis elegans</i>					AY259615.1	AY259570.1	AY259595.1					
<i>senegalensis</i>					AY259614.1	AY259569.1	AY259594.1		AY687903.1			
<i>Cycloderma aubryi</i>					AY259611.1	AY259566.1	AY259591.1					
<i>frenatum</i>					AY259610.1	AY259565.1	AY259590.1					
<i>Lissemys punctata</i>	NC_012414.1						AY259593.1		AY687902.1			
<i>scutata</i>					AY259612.1	AY259567.1	AY259592.1					
Trionychinae												
<i>Amyda cartilaginea</i>			AF285230.1		AY259600.1	AY259550.1	AY259575.1					
<i>Apalone ferox</i>					AY259605.1	AY259555.1	AY259580.1	DQ785894.1	DQ785893.1			
<i>mutica</i>					AY259606.1	AY259556.1	AY259581.1	DQ529206.1	DQ529173.1			
<i>spinifera</i>		U81319.1			AY259607.1	AY259557.1	AY259582.1	DQ529193.1	AY687901.1			
<i>Chitra chitra</i>					AF414366.1	AY259562.1	AY259587.1					
<i>indica</i>					AF494491.1	AY259561.1	AY259586.1					
<i>vandijki</i>						AY259563.1	AY259588.1					
<i>Dogania subplana</i>	NC_002780.1						AY259576.1					
<i>Nilssonia formosa</i>					AY259597.1	AY259547.1	AY259572.1					
<i>gangeicus</i>			GQ398145.1		AY259599.1	AY259549.1	AY259574.1					
<i>hurum</i>					AY259598.1	AY259548.1	AY259573.1					
<i>leithii</i>					AM495226.1	AM495227.1						
<i>nigricans</i>					AM495227.1	AM495227.1						
<i>Palea steindachneri</i>		AY743419.2	AY743418.1		AY259602.1	AY259552.1	AY259577.1					
<i>Peltocheilus bibroni</i>					AF414361.1	AY259559.1	AY259584.1					
<i>cantorii</i>					AF414360.1	AY259560.1	AY259585.1					
<i>Pelodiscus</i> (ex <i>Trionyx</i> )		AY743421.2	AY583695.1									
<i>axenaria</i>	NC_006132.1					AY583693.1						
<i>sinensis</i>							AY259578.1	FJ230869.1	FJ230871.1	AF369089.1		

Species	Mitochondrial genome					Nuclear genome				
	Complete genome	12S	16S	COI	ND4	cytB	R35	Cmos	RAG1	RAG2
<i>Rafetus euphraticus</i>					AY259604.1	AY259554.1	AY259579.1			
<i>Tritonix iriunguis</i>	AB477345.1						AY259589.1			

*Supplementary Table S2*: GenBank accession numbers of the sequences used in this study.