



Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles



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ABSTRACT

Despite their complex evolutionary history and the rich fossil record, the higher level phylogeny and historical biogeography of living turtles have not been investigated in a comprehensive and statistical framework. To tackle these issues, we assembled a large molecular dataset, maximizing both taxonomic and gene sampling. As different models provide alternative biogeographical scenarios, we have explicitly tested such hypotheses in order to reconstruct a robust biogeographical history of Testudines. We scanned publicly available databases for nucleotide sequences and composed a dataset comprising 13 loci for 294 living species of Testudines, which accounts for all living genera and 85% of their extant species diversity. Phylogenetic relationships and species divergence times were estimated using a thorough evaluation of fossil information as calibration priors. We then carried out the analysis of historical biogeography of Testudines in a fully statistical framework. Our study recovered the first large-scale phylogeny of turtles with well-supported relationships following the topology proposed by phylogenomic works. Our dating result consistently indicated that the origin of the main clades, Pleurodira and Cryptodira, occurred in the early Jurassic. The phylogenetic and historical biogeographical inferences permitted us to clarify how geological events affected the evolutionary dynamics of crown turtles. For instance, our analyses support the hypothesis that the breakup of Pangaea would have driven the divergence between the cryptodiran and pleurodiran lineages. The reticulated pattern in the ancestral distribution of the cryptodiran lineage suggests a complex biogeographic history for the clade, which was supposedly related to the complex paleogeographic history of Laurasia. On the other hand, the biogeographical history of Pleurodira indicated a tight correlation with the paleogeography of the Gondwanan landmasses.

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1. Introduction

Living and extinct species of Testudinata exhibit one of the most autapomorphic morphologies found in amniotes. The body of turtles is characteristically encased in a carapace (Zangerl, 1969), which significantly obscures their phylogenetic relationships to other lineages of terrestrial vertebrates. However, independently of the higher-level phylogenetic position of Testudinata within amniotes, this clade has been consistently recovered as monophyletic and is frequently divided into two subclades: Pleurodira, the side-necked freshwater turtles, which are geographically restricted to the Southern Hemisphere; and Cryptodira, the hidden-necked turtles that are globally distributed (Gaffney et al., 2006; Shaffer, 2009).

The studies of Shaffer et al. (1997), Seddon et al. (1997) and Georges et al. (1998) pioneered the use of DNA to establish phylogenetic relationships of turtles. Since then, several phylogenetic analyses based solely on molecular data were published (e.g., Krenz et al., 2005; Le et al., 2006; Barley et al., 2010; Lourenço et al., 2012), and few works were based on total evidence analyses (Shaffer et al., 1997; Sterli, 2010). In general, early studies were focused on issues within particular clades (e.g., relationships among Australian and South American chelids, relationships among podocnemidids). Later studies carried out more comprehensive analyses, including representatives of a larger number of clades. These studies contained, however, few representatives from each clade, having a total number of taxa ranging from 10 to 35 (e.g., Krenz et al., 2005; Parham et al., 2006; Barley et al., 2010; Lourenço et al., 2012; Crawford et al., 2015).

Previous studies based on molecular data questioned the results obtained from morphological analyses, including the monophyly of

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the long-necked chelids, the affinities of *Platysternon megacephalum* with chelydrids, and the sister-group relationships between trionychians and kinosternoids, among others. In fact, the general turtle tree has been changed by molecular data, and the new topology has become widely accepted. More exhaustive molecular sampling within the main clades has been recently published (e.g., Spinks et al., 2004; Le et al., 2006, 2014; Fritz and Bininda-Emonds, 2007; Naro-Maciel et al., 2008; Spinks et al., 2009; Iverson et al., 2013). The intense work on sampling the DNA of turtles, combined with the development of software and hardware capable of processing an increasing amount of data, allowed the compilation of all the available information in order to implement large-scale phylogenetic analyses of turtles (Thomson and Shaffer, 2010; Guillon et al., 2012; Rodrigues and Diniz-Filho, 2016).

However, no large-scale study so far was able to recover the interrelationships within Durocryptodira as proposed by Crawford et al. (2015) with statistically supported branches. For instance, Thomson and Shaffer (2010) recovered Chelydridae, Chelonioidae, and Kinosternoidea as a monophyletic group, sister to the Testudinoidea. Guillon et al. (2012) reported an unresolved polytomy including Chelydridae, Kinosternoidea, Chelonioidae and Testudinoidea, whereas Rodrigues and Diniz-Filho (2016), estimated unorthodox relationships within Cryptodira, suggesting the rearrangement of Durocryptodira lineages into (Kinosternidae (Emydidae (Platysternidae ((Chelonioidae (Chelydridae + Dermatemydidae)) (Testudinidae + Geoemydidae))))). Therefore, studies improving taxonomic and gene sampling were unable to corroborate genome-wide analysis with reduced number of terminals, making the higher-level phylogeny of turtles still inconsistent.

A well resolved phylogeny is a requirement not only for understanding the evolutionary associations of turtles, but it is also necessary for conducting a meaningful historical biogeographical analysis of Testudines. In this sense, large scale biogeographical studies of turtles are scarce. Recently, Rodrigues et al. (2017) carried out ancestral area reconstruction of the main turtle lineages using the dataset of Rodrigues and Diniz-Filho (2016). However, no explicit test of biogeographic models was employed. For instance, the founder-event speciation or the speciation through long-distance dispersal models were not included in their analysis, although studies have demonstrated the importance of including such parameters in ancestor range reconstruction (Matzke, 2014).

Improved methodologies have recently been developed for a statistical historical biogeographic analysis, which has been implemented to estimate the ancestral ranges of diverse speciose clades, including amphibians (Pyrón, 2014; Frazão et al., 2015) and birds (hummingbirds, McGuire et al., 2014). Notably, the statistical approach provided by the likelihood framework allows a formal test between different models and their improvement by the inclusion of the founder-event speciation, represented by the +J parameter (Matzke, 2014). Because long-distance dispersal events cannot be ruled out in the evolutionary history of Testudines, e.g., the *Chelonioidis* lineage having dispersed from Africa to South America in the Eocene-Oligocene (de la Fuente et al., 2014), this parameter is crucial for a reliable inference of the ancestral areas of the clade. Until the study of Rodrigues et al. (2017), assumptions on the biogeographic history of turtles were based only on inferred ages from molecular dated phylogenies and on the revision of the fossil distribution. For instance, the Cryptodira-Pleurodira split, which was suggested had occurred in the Jurassic, is frequently linked to the breakup of Pangaea (Crawford et al., 2015; Joyce et al., 2016).

Statistical biogeographical analyses require ultrametric trees. Therefore, availability of a reliable time-dated phylogeny is needed for tackling this issue. Previously inferred phylogenies for Testudines, however, relied on a limited number of gene loci and/or terminal species. Consequently, in the present study, a full evaluation of

the phylogenetic and biogeographical history of Testudines is performed. To accomplish this goal, a time-dated molecular phylogeny was inferred using the largest gene and taxonomic sampling available to date, and we performed, for the first time, a formal statistical historical biogeographic analysis of this lineage.

2. Materials and methods

2.1. Sequences and alignment

We assembled a data set containing information for 13 gene loci from 294 species of Testudines, representing all extant genera. The crocodilian *Alligator sinensis* and the avian *Gallus gallus* were used as outgroups. Gene loci used in our analysis consisted of the mitochondrial ribosomal genes *12S rRNA* and *16S rRNA*, the mitochondrial coding regions *CYTB*, *COI*, *ND4*, and the nuclear genes *BDNF*, *BMP2*, *CMOS*, *HNFAL*, *NGFB*, *R35*, *RAG1* and *RAG2*. Accession numbers are available in Appendix S1. When multiple sequences were available for a given species, the longest sequence was used. All protein-coding sequences were aligned individually in SeaView (Gouy et al., 2010) using the MUSCLE algorithm (Edgar, 2004), whereas the ribosomal RNA genes were aligned in MAFFT (Katoh and Standley, 2013). Gblocks (Castresana, 2000; Talavera and Castresana, 2007) was used to exclude poorly aligned bases and divergent regions in the genes *12S rRNA* and *16S rRNA*. Individual genes were then concatenated into a single supermatrix in SeaView (Gouy et al., 2010) and the final supermatrix consisted of 12,354 bp. To identify rogue taxa for which phylogenetic information was significantly reduced or absent, an analysis using the program RogueNaRok (Aberer et al., 2012) was performed. The species terminal *Psammobates geometricus*, which presented a relative bipartition information criterion (RBIC) equal to 0.5, was removed from the analysis. The other sequences that showed values lower than 0.13 were retained.

2.2. Phylogenetic analysis and dating

Because genomic segments evolve under different nucleotide substitution models, phylogenetic analysis was carried out partitioning the concatenated dataset (Lanfear et al., 2012; Kainer and Lanfear, 2015). We tested a total of 35 candidate partitions between genes. Coding genes were further partitioned into codon positions. Gene partitions were estimated using the likelihood-based heuristic search algorithm as implemented in PartitionFinder (Lanfear et al., 2012), which chose the best-fitting partitioning strategy consisting of 11 partitions. Maximum likelihood (ML) phylogenetic inference was performed in RAXML-HPC (8.1.24) (Stamatakis, 2014) as available on the XSEDE (Extreme Science and Engineering Discovery Environment) at CIPRES (Cyberinfrastructure for Phylogenetic Research, Miller et al., 2010). Each ML analysis used 200 searches for the optimal tree, with the optimal data partitioning schemes selected by PartitionFinder under the evolutionary model GTRGAMMA. Statistical supports for clades were assessed using 1000 nonparametric bootstrap replicates (BS).

Divergence time analysis was conducted under a Bayesian framework in PAML 4.8a's MCMCTree (Yang, 2007), using the relaxed molecular clock. We implemented a hard minimum and soft maximum constraints, allowing 2.5% of the probability density to exceed the maximum value. Due to computational limitations imposed by the large amount of species terminals, we used the approximate likelihood computation algorithm (Reis and Yang, 2011). Under this strategy, MCMCTree generated a Hessian matrix from the alignment, which was used to speed up the calculation of the likelihood of the data during the MCMC run. Priors for the *rgene* and *sigma2* parameters in MCMCTree were set as $G(2, 200)$

and G(1, 10), respectively. Markov chains were sampled every 1000th generation until 40,000 trees were collected, after a burn-in period of 10 million states. The analysis was performed twice to check for convergence of the chains. Effective sample sizes (ESS) of parameters were calculated in Tracer v. 1.5, and only runs with ESS > 200 were analyzed.

A total of 22 calibrations suggested by Joyce et al. (2013) were used as age priors for dating the ML phylogeny. We modified the prior on the minimum age of Cryptodira due to the discovery of an older fossil, namely, *Yehguia tatsuensis* (= *Sinaspideretes*, 145.5 Ma) (Tong et al., 2014). As in Joyce et al. (2013), all calibration prior constraints on node ages were uniformly distributed, which consists of a conservative approach for describing fossil uncertainty (Yang and Rannala, 2005). The minimum age of the root node was calibrated according to the oldest known turtle fossil *Odontochelys semitestacea* (=228 Ma) (Li et al., 2008), because it is the oldest unambiguous stem-turtle (Joyce et al., 2013). Due to the obscure relationships to other amniotes, the upper bound of the root was set according to the maximum age of crown Amniota (=332.9) as suggested by Benton et al. (2015). All nodes in which calibrations were applied are listed in the Table 1 and shown in the Fig. 1. The final tree was edited in the program Figtree v. 1.4.0, and the R packages Ape (Paradis et al., 2004), Phyloch v. 1.5-5 (Heibl, 2015) and Geiger (Harmon et al., 2007).

2.3. Inference of historical biogeography

We performed historical biogeography analyses using all DIVA, DEC and BAYAREA models implemented in the BioGeoBEARS R package (Matzke, 2013). We detected a significant likelihood improvement with the inclusion of the founder-event speciation (+J) through an ANOVA testing against all models ($p < 10^{-10}$). For DEC, we used the DEC* modification as suggested by Massana et al. (2015), which prohibits transitions into the null range. All marine turtle species were removed from this analysis due to their cosmopolitan distribution, reducing our dataset to 285 species. The maximum range size, which limits the number of areas by tips and nodes, was set to 2, based on the maximum occupation of the extant species. In agreement with Pyron (2014), we did not use constraints because they can incorrectly incorporate priors, and

either we did not remove ancestral areas available because removing them is different from merging them. As implemented by this author, we interpreted marginal landmasses based on the inferred times.

The selection of biogeographic areas followed zoogeographical regions found in the herpetological and biogeographical literature (Lomolino, 2010; Pyron, 2014; Vitt and Caldwell, 2009), namely: (1) Neotropical South America, including the entire South American region located south of the Panama/Colombia border; (2) Neotropical Central America, including Central America + Baja California Sur + parts of both the Pacific and Gulf coasts of Mexico; (3) West Indies, which includes the Caribbean Islands, Antilles + Bahamas + adjacent islands (4) Oriental (Or), including the Southeast Asian region from Myanmar to the Lesser Sunda islands, including Southeast China, Taiwan, the southern Ryukyu Islands + Philippines + Indo-Malaysian. All areas that were separated from Australasia by Weber's line (Lomolino, 2010); (5) Afrotropical, which consists of the Sub-Saharan Africa + Southern Arabian Peninsula; (6) Madagascar: Madagascar and adjacent islands (the Seychelles and the Comoros); (7) Western Palearctic: Europe (i.e., west of the Caspian Sea) + North Africa + Northern portion of the Arabian Peninsula + Southwestern Asia; (8) Eastern Palearctic: Asia - east of the Caspian Sea to northern China, including the major islands of Japan; (9) Australasia (Au): Australia + New Zealand and New Guinea, including islands until Weber's Line; (10) Nearctic: Temperate North America; (11) Indian subcontinent, including India, Pakistan, Bangladesh, Sri Lanka, Nepal, Bhutan (Supplementary Fig. 1).

We assigned the area of each species according to the distribution of Van Dijk et al. (2014). For species occupying the limits between North America and Neotropical Central America; between Eastern Palearctic and the Indian subcontinent, and between Eastern Palearctic and Oriental, we tested the distributions using the coordinate points downloaded from the 'rgbif' R package (Chamberlain et al., 2015). The coordinates were classified using the "SpeciesGeoCoder" R package (Töpel et al., 2016), with limits defined for WWF terrestrial ecoregions (worldwildlife.org/publications/terrestrial-ecoregions-of-the-world).

3. Results

3.1. Phylogenetic relationships, temporal and spatial diversification of Testudines

Our results recovered both Pleurodira and Cryptodira as significantly supported monophyletic groups (BS = 98 and 99, respectively) (Figure SM 2). The age of the Pleurodira/Cryptodira divergence was dated in the early Jurassic at approximately 199.5 Ma (178.8–225.4 Ma). Biogeographical analysis recovered South America and the Oriental region as the areas where the LCA of Testudines originated. In the paleogeographical context of the time it implies a Pangaeian distribution for the ancestors of the clades (Fig. 1). The probabilities of the most likely area recovered are available in supplementary Table 3. The analyses recovered a Gondwanan origin (Neotropics in BioGeoBEARS analysis) of Pleurodira and a Laurasian origin (the Oriental region in BioGeoBEARS analysis) for Cryptodira. Clades recognized as families by traditional taxonomy have been recovered as monophyletic and, in general, with high support values (above 98, except for Chelidae and Podocnemididae).

In all models, the divergence of all pleurodiran clades took place in regions that were part of Gondwana. Within Pleurodira, two clades were recovered, Chelidae (BS = 77) and Pelomedusoides (BS = 98), which were separated during the late Jurassic at 161.7 Ma (149.3–168.9 Ma). Chelidae was composed of two main

Table 1
List of calibration priors used.

Divergence	Age (Ma)	
	Min	Max
Root	228	–
Testudines	151.7	251.4
Pleurodira	111	165.2
Pelomedusoides	92.8	149.5
Pelomedusidae	5.3	149.5
Chelidae	65.2	149.5
Chelodiniinae	11.6	149.5
<i>Chelus</i> – <i>Phrynops/Mesoclemmys</i>	13.4	149.5
Cryptodira	145.5	200.2
Trionychia	124	177.6
Trionychidae	17.3	149.5
Durocryptodira	88.6	149.5
Americhelydia	70	149.5
Chelonioidae	48.4	149.5
Chelydroidea	70	149.5
Kinosternoidea	70	149.5
Kinosternidae	52.8	149.5
Testudinoidea	50.3	149.5
Emyidae–Platysternidae	32	100.5
Emyidae	32	100.5
<i>Trachemys</i> – <i>Graptemys</i>	3	34
Testuguria	50.3	100.5
<i>Heosemys</i> – <i>Mauremys</i>	5.3	65.8

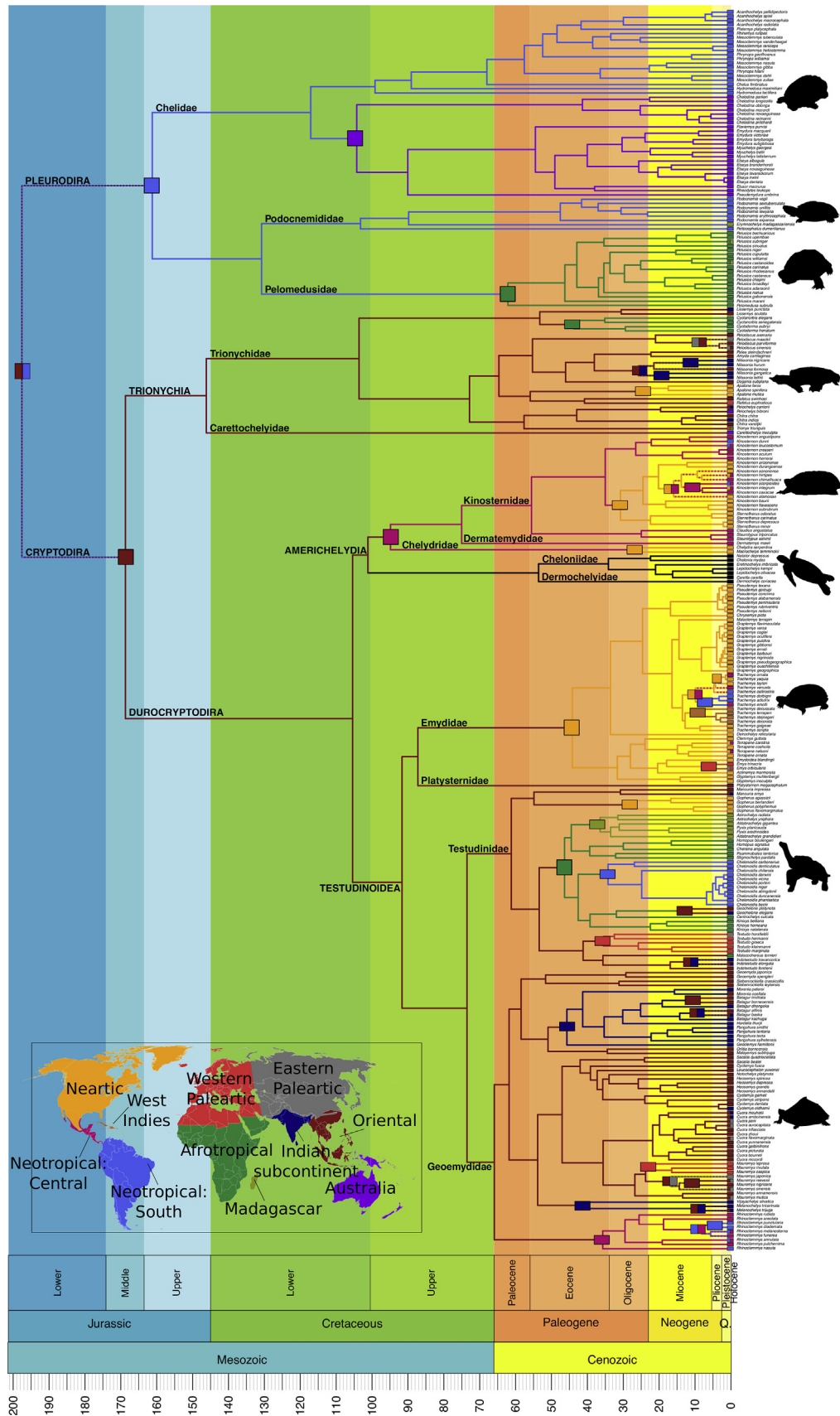


Fig. 1. Time-dated phylogeny of the Testudines with ancestral area reconstruction. Ancestral area reconstruction was based on DEC+J. Rectangle colors on nodes and terminals, as well as colors on branches, represent the inferred biogeographic areas. Global maps depicting the location of continental areas along the geological ages were indicated at the bottom. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

clades that split in the early Cretaceous at 117.4 Ma (99.4–135.3 Ma), one of the clades includes all the South American species (BS = 48), whereas all the Australasian species were clustered with BS = 80. *Hydromedusa* and *Chelus* were recovered as successive sister groups of the short-necked South American chelids (BS = 63). The origin of short-necked South American chelids was dated in the Paleocene at 57.1 Ma (47.1–68.7 Ma). *Hydromedusa tectifera* and *H. maximiliani* failed to be recovered as a monophyletic group in our analysis. Within the short-necked South American clade, neither *Mesoclemmys* nor *Phrynops* were recovered as monophyletic groups. The clade of the long-necked *Chelodina* (BS = 100) was recovered as the sister clade of the short-necked Australasian species (BS = 74). Both clades diverged during the early Cretaceous at 104.4 Ma (85.9–122.5 Ma). Pelomedusoides consists of two clades: the African Pelomedusidae (BS = 100) and South American Podocnemididae (BS = 57) that split during the early Cretaceous at 131.0 Ma (116.0–144.7 Ma). Within Pelomedusidae, the divergence between *Pelomedusa* and *Pelusios* was dated during the Paleocene at 62.3 Ma (59.9–77.1 Ma). Within Podocnemididae, *Podocnemis* and *Erymnochelys* (BS = 66) were recovered forming a monophyletic group, whose sister clade was *Peltocephalus*. *Erymnochelys* and *Podocnemis* split was dated around the late Cretaceous (mean: 90.0; HPD: 72.3–105.2 Ma).

The last common ancestor of Cryptodira was recovered as presenting an Eastern Laurasian distribution, corresponding to areas of the extant Oriental region. Trionychia was recovered as the sister group of Durocryptodira (BS = 100), with the age of the LCA in the middle Jurassic at 170.8 Ma (149.9–195.0 Ma). Statistical ancestral area reconstruction estimated an Australasian origin for Trionychia and a Laurasian origin (Asia + North America) for Durocryptodira. Trionychia is composed by Trionychidae and Caretochelyidae (BS = 99), which diverged during the Jurassic at 148.0 Ma (128.1–171.7 Ma). Trionychidae consisted of two clades, Cyclanorbininae (BS = 100) and Trionychinae (BS = 99). The LCA of trionychids has been recovered in the Oriental region, later dispersing to Africa (*Cycloderma* and *Cyclanorbis*); to the Australian region – New Guinea (*Pelochelys*); to the Nearctic (*Apalone*), and to the Indian subcontinent (*Chitra* and *Nilssonina*). Within Durocryptodira, Americhelydia (BS = 87) and Testudinoidea (BS = 100) split during the early Cretaceous at 106.5 Ma (94.3–121.2 Ma). The Americhelydia also split, during the early Cretaceous at 102.5 Ma (90.5–116.4 Ma), into Chelonioidea and Chelydroidea (Chelydriidae + Kinosternoidea, BS = 94). Biogeographic analysis recovered North America as the area where the LCA of chelydroids was distributed. On the other hand, the LCA of Testudinoidea was inferred to be distributed in North America + Asia (Oriental region). Testudinoidea consists of two main clades, Emysternina (Emydidae + Platysternidae, BS = 68) and Testuguria (Testudinidae + Geoemydidae, BS = 100). Their divergence is dated during the late Cretaceous at 92.1 Ma (79.8–1023.96 Ma). The split of Emydidae and Platysternidae was dated in the Coniacian at around 87.6 Ma (73.0–99.7 Ma), while the split between Geoemydidae and Testudinidae was dated during the late Cretaceous at 73.8 Ma (63.9–84.1 Ma).

4. Discussion

4.1. Temporal and spatial diversification of Testudines

This study is the first large-scale phylogeny of turtles with well-supported relationships, corroborating the phylogenomic topology proposed by Crawford et al. (2015). The divergence between the turtle and the archosaur lineages was dated in the Carboniferous/Permian 315.7 Ma (272.6–337.3 Ma). By then, all the continents were combined into Pangaea. The oldest records of stem Testudi-

nes come from the late Triassic from Europe, North America, South America and Southeast Asia (de Lapparent de Broin et al., 1982; Fraas, 1913; Jaekel, 1914; Jenkins et al., 1994; Joyce et al., 2009; Rougier et al., 1995; Sulej et al., 2012). The time between the oldest record of turtles and the calculated divergence with the archosaur lineage implies a ghost lineage of >100 My. This ghost lineage can be partially filled up with some probable stem testudinans like *Eunotosaurus africanus* from the late Permian (Lyson et al., 2010, 2016 and references therein), *Pappochelys rosinae* from the Ladinian (Schoch and Sues, 2015), and the indisputable *Odontochelys semitestacea* from the Carnian (Li et al., 2008). Our analyses also inferred an early vicariance event in crown Testudines (separation between Cryptodira and Pleurodira) between the late Triassic and the early Jurassic (with a mean in the early Jurassic), corroborating previous reports (Crawford et al., 2015; Joyce et al., 2016). The start of the Pangaeen spreading phase estimated in the middle Jurassic (Golonka, 2007) reinforces the hypothesis about the breaking up of Pangea as the process that triggered this vicariant event.

4.2. Diversification of Pleurodira

Our results corroborate that the historical biogeography of Pleurodira is closely linked to the Gondwanan history, as suggested by Joyce et al. (2016). The origin of Pleurodira, as well as the ages of its two major subclades, the Chelidae and Pelomedusoides, was inferred in the late Jurassic, being associated with the Gondwana region. Based on the fossil record, studies have proposed that chelids originated and diversified in the southern part of Gondwana, while pelomedusoids did so in the north of Gondwana (de Lapparent de Broin, 1988; de Lapparent de Broin and de la Fuente, 1993; de la Fuente et al., 2014). This split could have also been driven by vicariance (de Lapparent de Broin, 2000) through terrestrial barriers like basaltic fields in Southeastern Brazil (Renne et al., 1992) and/or desertic areas in Southern Gondwana (Rees et al., 2000; Myers et al., 2011). Then, chelids split into the South American and Australasian clades in the early Cretaceous, long before the final breakup of Southern Gondwana which occurred between 50 and 35 Ma (Lawver et al., 2013; Woodburne and Case, 1996). This estimate is similar to the recovered age (100–64 Ma) for the separation between Australian and American Marsupialia (Meredith et al., 2009). This is consistent with the oldest records attributed to the Pan-Chelidae clade that have been registered in the Aptian-Albian from Argentina (de la Fuente et al., 2011) and in the Albian from Australia (Smith, 2010).

The divergence between short- and long-necked chelids in Australasia occurred in the Albian (early Cretaceous). Unfortunately, the fossil record from Australia during the late Cretaceous and Paleogene is almost nonexistent; consequently, these phases in chelid evolution have not yet been recovered. The estimated age of short-necked South American chelids in the Thanetian (Paleocene) is quite young when compared with some extinct chelids that have been proposed to be part of the lineage of short-necked chelids from South America, such as *Linderochelys rinconensis* (tentatively assigned to the *Phrynops* group sensu de Lapparent de Broin and de la Fuente, 1993 by de la Fuente, 2007) and *Palaeophrynops patagonicus* (tentatively assigned to the *Phrynops* group sensu de Lapparent de Broin and de la Fuente, 1993 by de Lapparent de Broin and de la Fuente, 2001). It is worth mentioning that none of these Cretaceous chelids have been included in a phylogenetic context.

The split of Pelomedusoides into the African Pelomedusidae and the South American Podocnemididae was estimated during the early Cretaceous. This is coincident with the rifting of South America and Africa, which started 137 Ma (Valanginian, early Cretaceous; Storey, 1995; Renne et al., 1992) and reached final separation at approximately 100 Ma (Albian, early Cretaceous;

Szatmari and Milani, 1999). According to the fossil record, some podocnemidids seem to have dispersed to Africa and Europe in the Eocene, to Africa and Asia in the Miocene-Pliocene and South-east Asia in the Pliocene-Pleistocene (Gaffney et al., 2011). The biogeographical process explaining how the only extant representative of podocnemidids outside of South America arrived in Madagascar has been an issue of debate (Joyce et al., 2016). Eastern Gondwana (including Madagascar) started to break apart from Africa approximately 167 My. Later, at 130 My, Madagascar + Seychelles + India separated from Australia + Antarctica (Chatterjee et al., 2013). Our timescale indicated that the separation of *Erymnochelys madagascariensis* from *Podocnemis* occurred much later (late Cretaceous), excluding the possibility of crossing through Antarctica to Madagascar, making the vicariance hypothesis unlikely. Our analyses did suggest a dispersal event from South America to Madagascar, but the lack of any living or extinct species closely related with *E. madagascariensis* obscures its biogeographic history. Unfortunately, there is no fossil record of *E. madagascariensis* or related taxa in Madagascar. *Pelusios subniger* and *P. castanoides* dispersed sometime during the Neogene to Madagascar from Africa.

4.3. Diversification of Cryptodira

Our results suggest that the Cryptodiran lineage underwent a more complex biogeographic history, which is likely associated with the complex paleogeographic history of Laurasia. According to our results, the earliest divergences of cryptodirans took place in Eastern Laurasian (Trionychia and Durocryptodira – Jurassic; Carettochelyidae and Trionychiidae – Jurassic-Cretaceous; Americhelydia and Testudinoidea – Cretaceous). This is in complete agreement with the fossil findings of stem cryptodiran turtles, which are restricted to Laurasia (Joyce et al., 2016). Our analyses also recovered a dispersal to the Australian region by the only extant species of Carettochelyidae, *Carettochelys insculpta*. The fossil record of pan-carettochelyids, however, entails a more complex biogeographic history for this clade. This lineage has been recorded in Laurasia (North America, Europe, and Asia) during the Cretaceous and Paleogene, and they subsequently dispersed to Africa and New Guinea (Joyce, 2014). Our results recovered an Asian ancestor of trionyichids, with later dispersals to Africa during the Eocene (the ancestor of *Cycloderma* and *Cyclanorbis*), to Australia during the Miocene (the ancestor of *Pelochelys*), and to North America (*Apalone*). Fossil findings also suggests additional dispersal events in this lineage, namely, to North America (at least during the late Cretaceous; Vitek and Joyce, 2015), to Australia (during the Eocene-Pliocene; White, 1998; Gaffney and Bartholmai, 1979), and to northern South America during the Miocene-early Pliocene (Head et al., 2006; Sanches-Villagra et al., 2004; Wood and Patterson, 1973).

Our results inferred a dispersal event of Americhelydia from the Oriental region to Central America, which is in agreement with an earlier proposal by Crawford et al. (2015). The analysis recovered Central America as the area where the last common ancestor of this lineage was distributed probably because many extant taxa included in the chelydroid clade are found in Central and North America. Northern Central America has been connected to North America (also evidenced by the affinities of the faunas); however, both areas were connected with South America only with the formation of the Panama Isthmus, which began as a semi-emergent island chain in the late Oligocene and remained so until the complete rise of the Panama Isthmus sensu stricto approximately 2.8 Ma (Coates et al., 2003, 2004, 1992; Coates and Obando, 1996; Duque-Caro, 1990; Elmer et al., 2013; Farris et al., 2011; Montes et al., 2012; ODea et al., 2016). The fossil record of pan-kinosternids shows that this clade has been restricted to North

and Central America during the late Cretaceous to the Pliocene (Joyce and Bourque, 2016). The fossil record of Pan-chelydrids is limited to North America during the Cretaceous, with a later dispersion to Europe and Asia in the Paleocene, where they become extinct in the Pliocene (Joyce, 2016). The dispersal of chelydroids (pan-kinosternids and pan-chelydrids) to South America should have occurred through drifting during the appearance of the Panama Isthmus or shortly after (de la Fuente et al., 2014).

On the other hand, the last common ancestor of Testudinoidea remained in Asia (Oriental region), following previous hypotheses (Hirayama et al., 2000; Parham et al., 2006). The biogeographic history of the clade Testudinoidea, particularly of the clade Testudinidae, is far more complex than that of the chelydroids. Testudinidae is the most diverse and widely distributed clade of turtles, present in almost all continents (particularly speciose in Asia and North America) (Parham et al., 2006). All the first divergences in Testudinoidea occurred during the late Cretaceous: Emysternia–Testuguria, Emydidae–Platysternidae and Geoemydidae–Testudinidae. As with the chelydroids, three species of emydids later dispersed to South America. The divergence between Geoemydidae and Testudinidae occurred during the Campanian (late Cretaceous). Geoemydidae is mainly an Asian clade, with the most basal clade (*Rhinoclemmys* group) present in North America and a later (at least in the late Oligocene) dispersal to the circum-Mediterranean area (*Mauremys*), while Emydidae is mainly a North American group, with some recent dispersals to South America (some species of *Trachemys*) and to the circum-Mediterranean area (*Emys*). The lineage leading to the testudinids dispersed to Africa near the Selandian (Paleocene). From Africa, they dispersed, mainly during the Eocene, to South America (*Chelonoidis* complex), to the circum-Mediterranean area (*Testudo*) and to Madagascar (*Pyxis*, *Astrochelys*, *Aldabrachelys*, and *Dipsochelys*), and during the Oligocene-Miocene, they dispersed twice to Asia (*Geochelone* and *Indotestudo*).

5. Conclusions

In this study, we provided an assessment of the evolutionary history of extant turtles (Testudines) and an evaluation of the biogeographic events that influenced their distribution. Our analyses indicated that the initial diversification of Testudines was tightly associated with the final breakup of the supercontinent Pangaea during the Jurassic period. The origin and diversification of the major clades of Pleurodira were associated with the paleogeographic history of the Gondwanan landmasses. On the contrary, ancestral distributions of Cryptodira lineages was characteristically marked by a reticulated pattern, which is consistent with the complex geological dynamics of the Laurasian landmasses. Current statistical biogeographical analyses do not incorporate information on fossil occurrence and distribution, which may cause an underrepresentation of clades and areas. Future studies combining information from phylogeny and biogeography from both extant and extinct taxa will help further clarifying the macroevolutionary patterns of turtles. We expect, however, that the results and the hypotheses raised from this work will be useful to provide a foundation for future evolutionary and geographical analyses of Testudinata.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ympev.2017.05.008>.

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