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Comparative biogeography of North American turtle faunas: Neogene regionalization

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Abstract

North America harbors substantial species diversity in non-marine turtles (includes tortoises and terrapins), much of which arose in the Neogene Period (Miocene and Pliocene epochs) within *Kinosternon*, *Emyinae*, *Trachemys*, *Pseudemys*, *Graptemys*, and *Gopherus*. This diversity is distributed among 16 biogeographical provinces, but natural, hierarchical relations among provinces are unresolved. We used three-item analysis to identify such relations among provinces for these clades, following a recent, relatively complete phylogenetic reconstruction. The final three-item analysis identified 53,353 taxon-area cladograms — free of paralogy and multiple areas on a single branch. The final intersection tree has a retention index of 73.6% and a completeness index of 75.4%, both indicating moderately strong congruence in patterns among turtle clades. All six turtle clades support some nodes on the intersection tree, which is divided into eastern and western forks. The crown group on the eastern fork includes four provinces almost entirely east of the Mississippi River drainage, whereas the western fork is split into wet tropics and aridlands sub-forks. The east-west transition zone spans the Mississippi River drainage and Great Plains. Our summary of divergence estimates and geological history suggests that although phylogenetic synchrony existed between select taxa, there was general asynchrony because provincial turtle faunas developed over an extended period (Neogene). Temperature-sensitive distributions of various taxa responded to climatic cycles by expanding during periods of warming, but contracting during periods of cooling. Grassland expansion and geomorphic change in the Neogene created provincial boundaries that, although sometimes crossed under favorable climates, more commonly acted as dispersal barriers. Despite asynchrony in faunal assembly, existence of shared patterns reveals natural relations among provinces, producing a regionalization for North American turtles, useful for understanding their evolution as well as the biogeography of North America.

Highlights

- Six speciose, Neogene-age clades of North American turtles exhibit moderately strong congruence in natural, hierarchical relations among all-turtle provinces, indicating the presence of regionalization.
- This congruence identifies distinct eastern and western regions within North America, with the western region subdivided into aridland and wet-tropics subregions.
- The present regionalization appears to reflect long-term faunal differentiation across a continent with persistent geographical boundaries and fluctuating climates.

Keywords: all-turtle provinces, bioregionalization, comparative biogeography, Miocene, North America, Pliocene, speciation, taxon-area cladogram, three-item analysis, turtle biogeography

Introduction

The practice of biogeographical regionalization, also known as bioregionalization, seeks to identify natural classifications (i.e., hierarchical organizations) that exist among biogeographic areas (Morrone 2015a, Ung 2018). These can be discovered through analysis of phylogenetic evidence present within clades used to define the areas being analyzed (Holt et al. 2013, Morrone 2018). For instance, cladistic methods in comparative biogeography analyze phylogenies and associated biotic areas to discover regional organization (Ebach and Parenti 2015, Morrone 2018). When similar inter-area relations occur across multiple, unrelated clades, this indicates a biogeographic pattern (Parenti and Ebach 2009, Ebach and Parenti 2015, Morrone 2020), suggesting there is faunal regionalization, thus providing opportunity to develop a putative explanation for its origin (e.g., Hoagstrom et al. 2014, Morrone 2014, Ung et al. 2016a, 2016b).

The goal of this study was to discover and explain regionalization in North American turtles. Ennen et al. (2017) developed the first quantitative biogeographic provinces for North American turtles. This included an analysis of how provinces grouped together according to their faunal similarity, but lacked a cladistic assessment of provincial relations necessary to determine regionalization. Thereafter, Thomson et al. (2021) produced an updated, relatively comprehensive, phylogeny for global turtles. Availability of this inclusive and rigorous phylogeny created potential to determine natural relations among North American turtle provinces because it facilitates a comparative, cladistic approach. As already noted, discovering natural relations among areas (i.e., provinces) is necessary for bioregionalization.

Our analysis focused on six major radiations of North American turtles (Table 1), which mainly diversified during the Neogene Period (Miocene and Pliocene epochs, 23.0-2.6 Ma; dated phylogeny in Thomson et al., 2021). Throughout the Neogene, representatives of these clades adapted to and dispersed among modernizing ecosystems (e.g., Stephens and Wiens 2003a, 2004, Martin et al. 2013, Bramble and Hutchison 2014). The Neogene is significant to North American biogeography because this is when modern landforms (Potter and Szatmari 2009, Snedden and Galloway 2019) and ecosystems (Strömberg et al. 2011, Pound et al. 2012, Herbert et al. 2016) developed. For turtles, the beginning of the Neogene was associated with reduced biodiversity due to ongoing climatic cooling (Hutchison 1982, Joyce and Bourque 2016, Vlachos 2018). However, climatic cooling also initiated sea-level lowering (Miller et al. 2020, which ultimately, exposed new coastal lands. This, combined with Paleogene extinction of many turtle lineages, allowed those turtles that survived into the Neogene to, thereafter, diversify into the modern turtle fauna (e.g., Weems and George 2013, Thomson et al. 2021).

Indeed, Neogene diversification was widespread among turtle clades and across North America. Despite being colder than much of the preceding Paleogene Period, the Neogene was warmer than the present, with temperatures peaking during the Middle Miocene Climatic Optimum (MMCO 17.0-15.0 Ma) at a level that has not been approached since (Zachos et al. 2001). The post-MMCO climate cooled and aridity increased, with aridity peaking in the Late Miocene (Chapin 2008, Eronen et al. 2012). Nevertheless, the Pliocene Epoch (5.3-2.6 Ma) was still warmer than the subsequent Quaternary Period, which includes the present

Table 1. Turtle clades used for analysis. Geographical taxa are monophyletic species or species groups, based on references provided. Appendix S1 provides raw data including provincial distributions and phylogenetic relations. Appendix S2 provides the data file used for analysis, with very widespread taxa and provinces with only one taxon removed.

Clade	Description	Geographical taxa: raw/ analyzed (n)	References
<i>Kinosternon</i>	Genus; aquatic and semi-aquatic	15/15	Iverson et al. 2013 Thomson et al. 2021
Emydinae	Subfamily; aquatic, semi-aquatic, and terrestrial	11/7	Martin et al., 2013 Thomson et al. 2021
<i>Trachemys</i>	Genus; aquatic	12/12	Fritz et al. 2012 Parham et al. 2013 Parham et al. 2015 Vargas-Ramírez et al. 2017 Thomson et al. 2021
<i>Pseudemys</i>	Genus; aquatic	07/7	Thomson et al. 2021
<i>Graptemys</i>	Genus; aquatic	09/9	Thomson et al. 2018 Thomson et al. 2021
<i>Gopherus</i>	Genus; terrestrial	06/6	Edwards et al., 2016 Thomson et al. 2021

day (Salzmann et al. 2011, Haywood et al. 2016). Accordingly, sea levels of the Pliocene were higher than in the Quaternary (Rovere et al. 2015, Klaus et al. 2017). The Quaternary climate diverged from the Neogene, with onset of glacial cycles (Ehlers et al. 2018) that dramatically affected continental hydrography (e.g., Blum and Hattier-Womack 2009, Bentley et al. 2016), ecosystem geography (e.g., Webb et al. 2004), and turtle distributions (e.g., Amato et al. 2008, Rödder et al. 2013). To avoid confounding Quaternary patterns with those of the Neogene, we focused on Neogene diversification to elucidate its significance to biogeographic relations among provinces of North American turtles.

Once our cladistic biogeographic analysis was completed, we employed the comprehensive phylogeny of Thomson et al. (2021) to assess whether biogeographical patterns were synchronous or established episodically, over time (Morrone 2020). This was necessary because a shared pattern does not prove synchronicity (Donoghue and Moore 2003, Naka and Brumfield 2018, Busschau et al. 2022). That is, the same biogeographical pattern can be repeated through time (e.g., Keck and Near 2010, Blanton et al. 2013). Further, a shared pattern does not identify mode of diversification (e.g., dispersal or vicariance, Parenti and Ebach 2009, Morrone 2015b). To address this, we reviewed speciation modes indicated by turtle taxonomists and incorporated their conclusions with temporal patterns and inter-provincial relations revealed here to compose an integrative biogeographic scenario (*sensu* Morrone 2020), which we propose could inform future taxonomic and biogeographical study.

Materials & Methods

Our primary goal was to determine a natural classification of all-turtle provinces of Ennen et al. (2017) using a cladistic approach, a process also known as bioregionalization (Ebach 2013, Ebach and Parenti 2015). Comparative cladistic approaches follow the assumption that phylogenetic relations among taxa reflect biogeographic relations among areas they inhabit (Ebach and Parenti 2015, Morrone 2020). Although various cladistic approaches are available (Ebach and Parenti 2015, Morrone 2020), we used three-item analysis for the following reasons. Three-item analysis is the only comparative cladistic method to rely on hierarchical hypotheses when determining area relations (Cao et al. 2007), allowing it to accurately extract natural hierarchies from phylogenetic data (Rineau et al. 2020) for biogeographical analysis. Other cladistic approaches may misconstrue hierarchical relations because they do not correctly resolve relations involving widespread species (i.e., species in multiple biotic areas, Williams and Ebach 2006, Parenti and Ebach 2009), whereas paralogy-free subtrees provide a logical means to resolve paralogy issues (Zaragüeta Bagils et al. 2012, Rineau et al. 2020). Three-item analysis also facilitates accurate calculation of the retention index (Rineau et al. 2020), an important measure for assessing the proportion

of available phylogenetic information retained in a cladogram (Zaragüeta Bagils et al. 2012). Further, three-item analysis treats missing and inapplicable data differentially and accurately, allowing for removal of missing data from analysis (Zaragüeta-Bagils and Bourdon 2007). Hence, results are explicitly based on data that provide meaningful information (Rineau et al. 2020).

The six lineages of North American turtles analyzed here (Table 1) represented the only turtle clades that (1) existed by the Early Miocene, (2) diversified to become major clades in the Neogene (Miocene-Pliocene), and (3) became distributed broadly across North America. For each clade, we followed the maximum-clade-credibility chronogram of Thomson et al. (2021) to determine interspecific relations. Because we followed the phylogeny of Thomson et al. (2021), we also followed nomenclature presented in their tree (this was done for the convenience of the reader, not necessarily as an endorsement of any particular names). We inferred the positions of taxa that were missing from the Thomson et al. (2021) chronogram using recent studies (Table 1, Appendix S1). Within each clade, we recognized lineages that arose within the Neogene (based on divergence estimates in Thomson et al. 2021) as independent geographical taxa. We estimated the provincial distributions of geographical taxa as equivalent to the modern distributions of living descendants. If a Neogene geographical taxon diversified into two or more species in the Quaternary, this diversification was not included in analyses. In other words, we grouped all descendant species of Quaternary age into a single Neogene taxon, representing the Most Recent Common Ancestor (MRCA).

When applied comparatively among non-related clades, three-item analysis tests for shared distributional patterns among areas (*sensu* Parenti and Ebach 2009, Ung et al. 2016b). Three-area relations repeated across multiple clades are interpreted as biogeographical patterns suitable for general interpretation (Parenti and Ebach 2009, Ung et al. 2016a). For endemic areas, we used all-turtle provinces of Ennen et al. (2017). These are based on distributional patterns of continental turtles, terrapins, and tortoises (aquatic, semi-aquatic, terrestrial), excluding marine turtles. Of 16 initial provinces, we excluded Vizcaino-Magdalena and California Coast because each has only one extant turtle taxon from the clades used in this study (i.e., a shared pattern cannot occur in a province with only one taxon). Based on high faunal similarity and several shared species in this study, the Mexican Gulf Province of Ennen et al. (2017), as used here, is presumed to include the Central American Pacific Slopes, Mosquitia-Isthmus-Río Atrato-Magdalena, and Upper Usumacinta regions of Ennen et al. (2020). That is, the Mexican Gulf Province conceptually extended to the northwestern slopes of the Andes (Ennen et al., 2020). We included one separate, extra-continental region—Cis Andes, South America—in the analysis because it was colonized by turtles from multiple North American clades (Pereira et al. 2017). The Cis Andes

region as defined here includes all of South America east and south of the Andes.

Using the remaining 14 provinces and the external Cis Andes region, we converted cladograms of taxa for each clade into taxon-area cladograms (TACs), replacing terminal taxa with the provinces their living descendants inhabit (Zaragüeta Bagils et al. 2012). Following standard procedure (Parenti and Ebach 2009), we grouped sister taxa that shared the same provincial distributions as one geographical taxon because separate treatment of sister taxa that have identical provincial distributions provides no additional information (Appendix S1). For example, *Kinosternon acutum*, *K. creaseri*, and *K. herrerae* form a three-species clade confined to the Mexican Gulf Coast Province (Iverson et al. 2013, Thomson et al. 2021). Thus, in this study, we combined them into one geographical taxon.

We used LisBeth version 1.3 (Zaragüeta Bagils et al. 2012) to conduct a congruence analysis based on compatibility principles (Wilkinson 1994) where the TACs—free of paralogy and of multiple areas on a single terminal-branch (MASTs)—were combined to create optimal area cladograms for each turtle clade. LisBeth built a consensus tree (intersection tree) from the three-area statements that were derived from these TACs (e.g., Grand et al. 2014, Hoagstrom et al. 2014, Ung et al. 2016a). We estimated the validity of findings with the retention index (percentage of found three-area statements included in optimal area cladograms) and completeness index (percentage of found three-area statements deduced from the intersection tree and present in the paralogy- and MASTs-free TACs) (Zaragüeta Bagils et al. 2012). In each index, greater inclusion indicates greater biogeographical congruence.

We initially used complete phylogenies for analysis to avoid discarding any potentially useful information (Appendix S1). From a computational point of view, LisBeth (Zaragüeta Bagils et al. 2012) implements an exact-tree calculation to reconstruct the consensus tree (i.e., this is an exhaustive tree, not a heuristic). Thus, complexity of calculations increases exponentially with the number of terminals and depending upon the topology of the cladogram (Zaragüeta Bagils et al. 2012). Cases with many widespread taxa (i.e., taxa inhabiting numerous provinces) can introduce excessive complexity that overloads computational capacity (Ung et al. 2016b). However, because of diffuse distributions, these widespread taxa typically provide little useful information (Murphy et al. 2019). As an example, in our study, the complete cladistic analysis on the raw dataset (all taxa) resulted in decomposition into an excessive number (1522) of three-area statements (Table S1). Reconstruction of the consensus tree was stopped after 24 h of calculation on a virtual machine installed on a MacOS X Mojave with 16Go of RAM (Lisbeth runs on Microsoft Windows), with the result that only 0.11% of 176,685 terminals had been so far explored. Based on this, it was determined that the raw data set (all taxa) was too confounded for meaningful computation.

Thereafter, we used an investigative approach to remove only those widespread species that confounded the analysis. This was done to avoid excluding taxa that could provide meaningful information. For each clade, we ran separate biogeographical treatments to eliminate paralogy (i.e., paralogy-free subtree analysis) followed by the transparent method (Ebach et al. 2005, Parenti and Ebach 2009). This revealed that Emydinae was the only clade with excessive computational difficulties (Table S2). Specifically, Emydinae generated 294,208 TACs (Table S2). Once this was known, we used an iterative approach to determine which widespread taxa should be removed from Emydinae to facilitate analysis. We removed widespread taxa one at a time, beginning with the most widespread taxon. With each removal, we reran the paralogy-free subtree analysis and transparent method. From this, it was found that removal of *Terrapene carolina* (eight provinces), *T. mexicana* (six provinces), and *T. ornata* (six provinces) allowed computation to proceed (Table S2). All other taxa were included in a revised (i.e., pruned) Emydinae clade for use within the final, multi-clade three-item analysis (Appendix S2, *sensu* Murphy et al. 2019).

To interpret the branching pattern in the intersection tree, we determined which clades supported each node (i.e., synapomorphic taxa, Ung et al. 2016b) and then identified phylogenetic relations within those clades that informed branch arrangement on the intersection tree. For these phylogenetic relations, we reported divergence estimates in Thomson et al. (2021) to determine likely timing of reproductive isolation between provinces. Within this temporal context, we reviewed literature on turtle biogeography, river-drainage evolution, climatic trends, and ecosystem evolution to propose biogeographical scenarios of province relations, which could be useful hypotheses for future study.

Results

As described in the Materials and Methods, three of 60 initial geographical taxa were pruned from the Emydinae tree due to widespread distributions. Before removal, these species confounded the three-item analysis, producing 347,560 MAST- and paralogy-free TACs (Table S1). In addition, two other geographical taxa were removed because they only occurred in areas with a single geographical taxon. These were both colonists from continental North America to adjacent areas (1) *Emys orbicularis-E. trinacris* (Emydinae), which colonized Eurasia from North America (Spinks and Shaffer 2009); (2) a lineage of *Trachemys* that colonized the Antilles Archipelago from North America (Parham et al. 2013). With all of these taxa removed, 55 geographical taxa were included in the analysis (Table S1, Appendix S2). Three-item analysis of the pruned data produced 53,353 MAST- and paralogy-free TACs with an intersection tree retention index of 73.6% (156,860 of 213,160 TACs included), indicating moderately strong congruence within and among clades. The intersection tree completeness index is 75.4% (343 of 455 TACs included), demonstrating moderately strong congruence among trees. All clades

contributed to support of some nodes within the intersection tree. Nodes were variously supported by one to five clades (Fig 1).

The intersection tree (Fig 1) has two main forks separating eastern and western provinces. The boundary is the transition zone from woodland to grassland, which spans the Tallgrass Prairie and High Plains-Río Grande provinces on the west and Central Gulf Coast and Interior Highlands provinces on the east (Fig 2). The west fork of the intersection tree holds nine provinces and has relatively complex structure (Fig 1). The Pluvial Proglacial Province is the first branching area (Fig 1, node 1), supported by Emydinae (two taxa) and *Trachemys* (one taxon) (Table S3). Above this branch, node 2 is a split between a wet tropics subfork holding two provinces (Cis Andes, Mexican Gulf Coast) and a western aridlands subfork holding six provinces. Evolutionary relations within *Kinosternon* (three taxa), *Trachemys* (two taxa), and *Gopherus* (one taxon) support the relation of these two subforks (Table S4). Within the wet tropics, three sister relations (*Kinosternon angustipons-dunni* with *K. leucostomum*; *Kinosternon scorpioides* with

K. integrum; and *Trachemys callirostris*-*T. chichiriviche* with *T. emolli*-*T. grayi*-*T. venusta*) support a sister relation of the Cis Andes region with the Mexican Gulf Coast Province (Fig 1, node 8). Divergences within these groups are estimated as Middle-Late Miocene, Pliocene-Early Pleistocene, and Pliocene, respectively (Thomson et al. 2021).

Within the western aridlands subfork of the intersection tree, the Mojave Desert Province was the first branching area (Fig 1, node 3). Two turtle taxa occupy this Province (*Emys marmorata*-*E. pallida*; *Gopherus agassizii*) and both exhibit evolutionary relations with other western aridlands provinces (Table S3). The Mexican Pacific Coast Province occupies the second lowest branch within the western aridlands

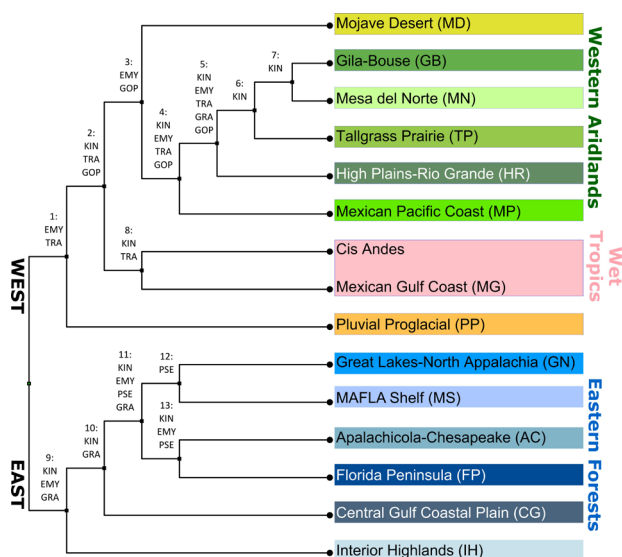


Figure 1. Intersection tree of Taxon Area Cladograms (TACs) showing relations among biogeographical provinces for six major clades of North American turtles that diversified in the Neogene. Three-item analysis produced 53,353 MAST- and paralogy-free TACs with an intersection tree retention index of 73.6% (156,860 of 213,160 TACs included), indicating moderately strong congruence within and among clades. The intersection tree completeness index is 75.4% (343 of 455 TACs included), again demonstrating moderately strong congruence among trees. Colored branches correspond to the map (Figure 2). Yellow-green palette represents western aridland provinces; Blue-gray palette represents eastern forest provinces. Nodes are numbered from top to bottom for reference in text. Turtle clades supporting each node are listed as three-letter abbreviations: KIN = *Kinosternon*, EMY = Emydinae, TRA = *Trachemys*, PSE = *Pseudemys*, GRA = *Graptemys*, GOP = *Gopherus*.

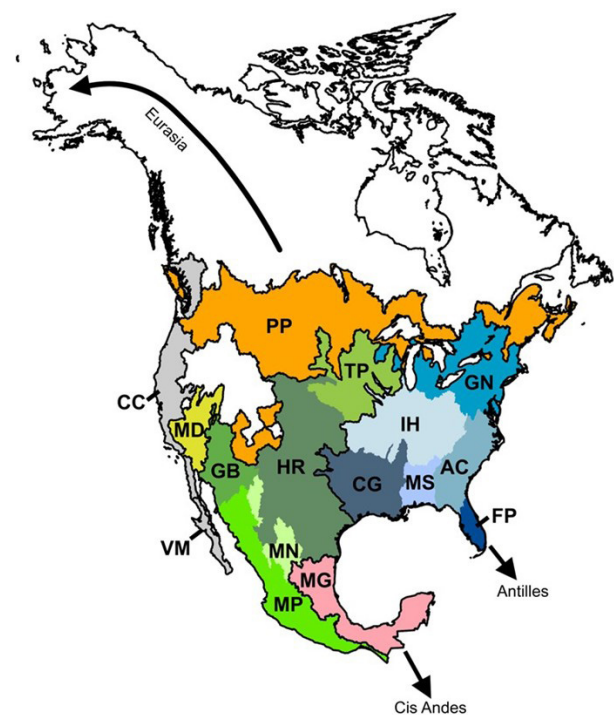


Figure 2. Map of all-turtle provinces for North America from Ennen et al. (2017), with revised names: VM = Vizcaino-Magdalena, CC = California Coast, MD = Mojave Desert, MG = Mexican Gulf Coast, GB = Gila-Bouse, MN = Mesa del Norte, MP = Mexican Pacific Coast, HR = High Plains-Río Grande, TP = Tallgrass Prairie, GN = Great Lakes-North Appalachia, PP = Pluvial Proglacial, FP = Florida Peninsula, AC = Apalachicola-Chesapeake, IH = Interior Highlands, CG = Central Gulf Coast, MS = MAFLA Shelf. Thickened, black boundaries among provinces highlight division of wet tropics, eastern forest, and western aridland branches and the color scheme corresponds to Figure 1. Yellow-green palette represents western aridland provinces; Blue-gray palette represents eastern forest provinces. Provinces in gray were excluded from analyses due to only one taxon present. Areas in white have no native turtles. Arrows indicate extra-continental areas colonized from North America by *Trachemys* (Antilles), multiple clades (Cis Andes), and *Emys* (Eurasia).

subfork (Fig 1, node 4). Representatives of *Kinosternon* (six taxa), Emydinae (one taxon), *Trachemys* (two taxa), and *Gopherus* (one taxon) exhibit evolutionary relations with other provinces on the western aridlands subfork (Table S3). Similarly, the High Plains-Río Grande Province is the third lowest Province on the western aridlands subfork (Fig 1, node 5) and representatives of *Kinosternon* (two taxa), Emydinae (one taxon), *Trachemys* (two taxa), *Graptemys* (one taxon), and *Gopherus* (one taxon) exhibit evolutionary relations with other western aridlands provinces (Table S3). In contrast, the Tallgrass Prairie Province (Fig 1, node 6) is supported only by a relation of the widespread *K. flavescens* with the Gila-Bouse and Mesa del Norte provinces (Table S3). This lone relation does not represent a pattern shared among multiple taxa. In contrast, the crown sister relation of the Gila-Bouse and Mesa del Norte provinces (Fig. 1, node 7) is supported by three separate relations within *Kinosternon*, each of varying age (Table S3), indicating this is a repeated pattern within the genus. Notably, across the western aridlands subfork of the intersection tree, provincial taxa varied in specific inter-provincial relations and in timings of divergence (Table S3).

The east fork of the intersection tree includes provinces of naturally forested ecoregions, extending east from the Central Gulf Coastal Plain and Interior Highlands provinces to the Atlantic Coast. The position of the Interior Highlands Province as first to branch from this fork (Fig 1, node 9) is supported by relations within *Kinosternon* (one taxon), Emydinae (two taxa), and *Graptemys* (three taxa) (Table S5). The next highest branch (Fig 1, node 10) separates the Central Gulf Coastal Plain from a crown group of four provinces. The position of the Central Gulf Coastal Plain as peripheral to this crown branch is supported by *Kinosternon* (one taxon) and *Graptemys* (five taxa) (Table S5). Estimated divergences of taxa supporting nodes 9 and 10 are variable (Early Miocene to Pleistocene, Table S5), indicating a sequential pattern of inter-province divergence.

A crown fork including four eastern forest provinces (Fig 1, node 11), arranged as sister-province pairs, is supported by *Kinosternon* (one taxon), Emydinae (three taxa), *Pseudemys* (two taxa), and *Graptemys* (one taxon) (Table S6). On this crown branch, the Great Lakes-North Appalachia Province is sister to the MAFLA Shelf Province (Fig 1, node 12). However, this sister relation is supported by a single phylogenetic relation (*Pseudemys alabamensis* – *Pseudemys rubriventris*) and thus does not represent a shared pattern. In contrast, the Apalachicola-Chesapeake and Florida Peninsula provinces are resolved as sisters within the crown of the branch (Fig 1, node 13), supported by *Kinosternon* (two taxa), Emydinae (one taxon), and *Pseudemys* (three taxa) (Table S7).

Discussion

East-West Subdivision of Intersection Tree

The east-west fork at the base of the intersection tree (Fig 1) represents major east-west divergences in *Kinosternon* (Oligocene to Early Miocene), *Gopherus*

(Late Oligocene-Early Miocene), and *Trachemys* (Middle-Late Miocene). The western lineages in each of these clades (Table 2) are confined to provinces on the west fork of the intersection tree. Further, except for the glaciated Tallgrass Prairie and Pluvial Proglacial provinces, all west-fork provinces include at least one taxon from one of these western lineages. There are at least three nonexclusive hypotheses for divergence of these western lineages from their eastern relatives.

- 1. Into-the-tropics hypothesis.** Periods of climatic cooling may have favored range expansion of temperate turtles into the tropics (Meseguer and

Table 2. Species lists for western and eastern lineages of *Kinosternon*, *Trachemys*, and *Gopherus* based on Thomson et al. (2021). Asterisks indicate descendants of eastern lineages that have distributions expanded into provinces of the west fork of the intersection tree.

Clade	Western Lineage	Eastern Lineage
<i>Kinosternon</i>	<i>K. angustipons</i>	<i>K. baurii</i>
	<i>K. dunni</i>	<i>K. subrubrum</i>
	<i>K. leucostomum</i>	<i>K. flavescens*</i>
	<i>K. herrerae</i>	<i>K. arizonense*</i>
	<i>K. acuta</i>	<i>K. durangoense*</i>
	<i>K. creaseri</i>	
	<i>K. alamosae</i>	
	<i>K. chimalhuaca</i>	
	<i>K. scorpoides</i>	
	<i>K. integrum</i>	
	<i>K. oaxacae</i>	
	<i>K. sonoriense</i>	
	<i>K. hirtipes</i>	
	<i>Trachemys</i>	<i>T. gaigeae</i>
<i>T. nebulosa</i>		<i>T. decussata</i>
<i>T. dorbigni</i>		<i>T. terrapen</i>
<i>T. medemi</i>		<i>T. decorata</i>
<i>T. ornata</i>		<i>T. stejnegeri</i>
<i>T. yaquia</i>		<i>T. adiutrix*</i>
<i>T. taylori</i>		<i>T. scripta elegans*</i>
<i>T. hartwegi</i>		
<i>T. callirostris</i>		
<i>T. chichiriviche</i>		
<i>Gopherus</i>	<i>T. emolli</i>	
	<i>T. grayi</i>	
	<i>T. venusta</i>	
	<i>G. berlandieri</i>	<i>G. flavomarginatus*</i>
	<i>G. agassizii</i>	<i>G. polyphemus</i>
	<i>G. morafkai</i>	
	<i>G. evgoodei</i>	

Condamine 2020). Evidence supports this hypothesis for east-west divergence in *Kinosternon*. Estimated divergence during the Oligocene-Miocene transition (Thomson et al. 2021) corresponds with cooling across the Northern Hemisphere during the Mi-1 glaciation (Zachos et al. 2001, Hyeong et al. 2014), which presumably favored southwestward range expansion of *Kinosternon*, although associated aridification of North America corresponded with range contractions and extinctions of kinosternids (Joyce and Bourque 2016), potentially separating eastern and western lineages. Concurrent sea-level fall (Miller et al. 2020) may have enabled range expansion for lineages colonizing southward (Thomson et al. 2021).

Subsequent, Middle Miocene warming and moistening corresponded with turtle range expansions (Hutchison 1982), but then was followed by Middle-Late Miocene cooling and aridification (Zachos et al. 2001, Chapin 2008, Eronen et al. 2012). This period of cooling corresponds with an apparent into-the-tropics invasion in *Trachemys*, which originated in temperate North America and colonized southward from there (Fritz et al. 2012). Aforementioned, Late Miocene aridification of central and western North America could have separated eastern and western lineages of this genus. In the same period, the MRCA of the *K. flavescens* group founded a population giving rise to *K. durangoense* at the northern edge of the tropics (Iverson 1979; Thomson et al. 2021), suggesting a shared history between western *Trachemys* and the *K. flavescens* group.

Divergence estimates in Thomson et al. (2021) imply the MRCA of *T. scripta elegans* and *T. adiutrix* dispersed from North to South America in the Late Pliocene-Early Pleistocene, yet another period of climatic cooling (Zachos et al. 2001). Notably, there do not seem to be examples of taxa from western lineages expanding northeastward, into eastern-forests provinces. This agrees with the asymmetric gradient of extinction and dispersal that is characteristic of turtles and is associated with the into-the-tropics hypothesis (Meseguer and Condamine 2020). However, an into-the-tropics pattern seems unlikely for *Gopherus* because estimated Early-Middle Miocene divergence (Thomson et al. 2021) corresponds with the warm MMCO.

2. Grassland expansion hypothesis. It is also possible that ecosystem changes account for east-west cladogenesis in turtle lineages. For *Gopherus*, Early-Middle Miocene timing of east-west divergence (Thomson et al. 2021) corresponds with a transition from wooded to open habitat in west-central North America (Kukla et al. 2022). During this period, rodents and lagomorphs declined in diversity, with extirpations eliminating woodland/shrubland taxa (Samuels and Hopkins 2017). Absence of living *Gopherus* from the Great Plains is consistent with a hypothesis that emergence of grasslands separated eastern and western lineages. As already mentioned, Middle-Late Miocene east-

west divergence in *Trachemys* (Thomson et al. 2021) corresponded with increased aridification in western North America (Chapin 2008, Eronen et al. 2012) when grassland came to dominate the northwestern Gulf Coast (Godfrey et al. 2018). On the other hand, ancestral *Kinosternon* appear to have been associated with grasslands (Bourque 2016) and *K. flavescens* remains widespread on the Great Plains and Tallgrass Prairie (Iverson 1979; Houseal et al. 1982), suggesting east-west divergence in this genus was not due to emergence of grasslands.

3. Geomorphic change hypothesis. River-drainage reorganization may also help explain east-west splits in *Kinosternon* and *Trachemys*. For *Kinosternon*, subdivision of the Oligocene Río Grande drainage into northern (Río Grande) and southern (Río Bravo/San Fernando) drainages (Snedden and Galloway 2019) may have been important. Fossil evidence suggests eastern *Kinosternon* originated in the Early Miocene Río Grande drainage, later expanding eastward (Bourque 2016). If so, then *Kinosternon* to the south, in the Early Miocene Río Bravo drainage, may have founded the western lineage. For *Trachemys*, if the progenitor of western lineage was widespread during the Middle Miocene Climatic Optimum (MMCO) (as suggested above), then stream transfers from the Middle Miocene Guadalupe River into the Late Miocene Río Grande (Snedden and Galloway 2019) could have shifted a population to the southwest. Several fishes were likely transferred to the Late Miocene Río Grande in this manner (Hoagstrom and Echelle 2022).

Terrestrial *Gopherus* seem less likely to have been affected by river-drainage reorganization, however, the Early Miocene was also a period of intense volcanism and massive landscape erosion across the region between the Gulf of México Coastal Plain and the Great Basin (Cather et al. 2012, Snedden and Galloway 2019). It is possible either emergence of volcanic mountains or ecological effects of landscape denudation (or both) contributed to east-west divergence within *Gopherus*. Isolation of western *Gopherus* in the Great Basin, with eastern *Gopherus* distributed along the Gulf Coast, is consistent with molecular evidence that eastern *G. polyphemus* and *G. flavomarginatus* diverged in the Late Miocene-Pliocene (Thomson et al. 2021). This possibility is congruent with biome reconstructions because during the Late Miocene, there was a forest-savanna corridor along the Gulf Coast (Pound et al. 2011), potentially occupied by a widespread MRCA of eastern *G. polyphemus*-*G. flavomarginatus*.

An additional pattern contributing to the east-west subdivision of the intersection tree is a paucity of *Pseudemys* and *Graptemys* within west-fork provinces. The geography (Spinks et al. 2013) and phylogeny (Thomson et al. 2021) of *Pseudemys* indicate westward colonization into the High Plains-Río Grande Province was during the Miocene-Pliocene transition, indicating that unlike the western lineages discussed above, presence of *Pseudemys* in a western border province

is attributable to more recent range expansion from the east. A similar history applies to *Graptemys* in the High Plains-Río Grande Province (Thomson et al. 2018, 2021). *Graptemys* species also occur in the Tallgrass Prairie and Pluvial Proglacial provinces, which is attributable to post-glacial colonization (discussed further below).

Taken together, evidence to explain the east-west subdivision of the intersection tree suggests that although common processes likely explain east-west splits within major turtle clades, divergence timings were asynchronous (apart from possible joint westward expansion in *Trachemys* and the *K. flavescens* group). The three above hypotheses are each potentially relevant to multiple clades, but the timings of when these processes influenced each lineage are varied. Asynchrony is attributable to the ancient age of turtle lineages, which set the stage for diversification to occur throughout the Neogene period, along with the fluctuating climate and dynamic geomorphology across the east-west transition zone.

East fork of intersection tree

Appalachian rejuvenation

Branching within the East Fork of the intersection tree is attributable to major Neogene events. During the Middle Miocene, some combination of uplift, drainage rearrangement, and increasing precipitation elevated relief along the Appalachian Divide and initiated drainage reorganization in the continental interior (Wagner et al. 2018, Snedden and Galloway 2019). These events potentially separated turtle populations of the Interior Highlands and Central Gulf Coastal Plain from provinces to the east (Fig. 2, node 10), like patterns in fishes (Hoagstrom et al. 2014, Hoagstrom and Echelle 2022). Accordingly, trans-Appalachian divergence estimates in turtles (Table S5) are Middle Miocene or younger, but different timings among lineages indicate multiple episodes of divergence across this boundary. Hence, although divergences likely occurred via allopatry (Lamb et al. 1994, Stephens and Wiens 2003b), it was evidently asynchronous.

In response to Appalachian rejuvenation, a Late Miocene-Early Pliocene Great Floridian River arose, extending southeast from the southern Appalachians, along the length of the Florida Peninsula (Warzeski et al. 1996, Missimer and Maliva 2017). This could explain the sister relation of the Apalachicola-Chesapeake and Florida Peninsula provinces because turtles therein would have had access to both provinces. Non-emydine taxa linking these provinces (Table S7, *Kinosternon* and *Pseudemys*) are distributed among the MAFLA Shelf, Apalachicola-Chesapeake, and Florida Peninsula provinces, suggesting close biogeographic relations, but histories of these taxa are difficult to discern due to poorly resolved phylogenetic relations (Walker et al. 1998, Iverson et al. 2013, Spinks et al. 2013). Late Miocene-Pliocene divergence of Antillean *Trachemys* (Thomson et al. 2021) suggests the MRCA of *Trachemys scripta scripta*-Antillean *Trachemys*

inhabited this river and, from its mouth, crossed the Straits of Florida to Cuba, perhaps upon discharged mats of floating vegetation (*sensu* Legler 1990). Late Miocene sea-level fall ~8.2 Ma (Miller et al. 2020) or the lack a major ocean current through the Florida Strait 11.5-9.5 Ma (Kirillova et al. 2019) could have facilitated flotsam delivery to Cuba. Relatively high salinity tolerance in *Trachemys* (Agha et al. 2018) may have also aided this crossing.

Great Lakes-North Appalachia and MAFLA Shelf relation

Only the sister relation of *Pseudemys rubriventris* and *P. alabamensis* supports a sister relation between the Great Lakes-North Appalachia and MAFLA Shelf provinces. Hence, this is not a general pattern (Parenti and Ebach 2009). Further, geography does not corroborate this relation because these provinces are disjunct (Fig 2). One explanation for sister pairing of *P. alabamensis* with *P. rubriventris* is incomplete lineage sorting, in which case more detailed studies with additional molecular markers or techniques could reveal different placement within the genus, as observed in preliminary analyses (Spinks et al. 2013). Alternatively, it is possible these two taxa descend from a common ancestor with a broader distribution, presently disjunct due to extinction of intervening populations. However, without a known aquatic connection between these provinces, this hypothesis seems to have less support.

West fork of intersection tree

Western aridlands subfork

The west fork of the intersection tree (Fig 1) includes nine provinces. The largest branch is the western aridlands subfork of six provinces. Taxa representing *Kinosternon*, Emydinae, *Trachemys*, *Graptemys*, and *Gopherus* all lend support to the unity and positioning of provinces on this subfork. Among the western aridlands provinces (besides the poorly resolved Tallgrass Prairie, discussed further below), numerous geographical taxa provide evidence of inter-provincial evolutionary relations. Almost all of these divergence events have been interpreted as Neogene range fragmentations (i.e., vicariance, Table S3). In one exceptional case, Iverson (1981) hypothesized that ancestral *K. hirtipes* traversed the Cochise Filter Barrier to reach the Sonoran Desert (Gila-Bouse Province), where it then diverged to become *K. sonoriense*.

As turtle distributions are sensitive to temperature and precipitation (e.g., Stephens and Wiens 2009, Ennen et al. 2016), it is commonly inferred that turtles of the western aridlands expanded distributions during warmer or wetter periods and fragmented when the climate cooled or dried (e.g., Milstead and Tinkle 1967, Spinks and Shaffer 2009). For coastal taxa, sea-level rises may also cause range fragmentation (e.g., Lamb et al. 1994; Berry et al. 1997; Martin et al. 2013). Notably, divergence timings vary substantially across the western aridlands region and, in each province, accumulation of turtle taxa evidently occurred

episodically, from Early Miocene to Early Pleistocene (Table S3).

Although excluded from analysis due to only one living geographical taxon, the California Coast Province may be justifiably considered sister to the Mojave Desert Province because *Emys marmorata*-*E. pallida* inhabits both (Spinks et al. 2014) and *Gopherus agassizii* did so in the Pleistocene (Vlachos 2018). The excluded Vizcaino-Magdalena Province supports only *Trachemys nebulosa*, a species also occurring in the Mexican Pacific Province (Legler and Vogt 2013, Parham et al. 2015), suggesting affiliation of these provinces.

Wet Tropics subfork

The separate wet tropics branch on the intersection tree indicates relatively independent histories of North American turtles in this region. Wet tropics *Kinosternon* include the *K. angustipons*-*K. dumni*-*K. leucostomum* group (Middle Miocene, Thomson et al. 2021) and the *K. acuta*-*K. creaseri*-*K. herrerae* group (Middle-Late Miocene, Thomson et al. 2021). In addition, *K. scorpiodes* evidently originated in the wet tropics (Pliocene-Early Pleistocene, Thomson et al. 2021) and then dispersed broadly during the Pleistocene (Iverson et al. 2013). The distribution of wet-tropics *Trachemys* (Fritz et al. 2012, Legler and Vogt 2013, Parham et al. 2015) is similar to *Kinosternon*, but divergence estimates (Thomson et al. 2021) indicate *Trachemys* originated later (Table S4). Once established on the Mexican Gulf Coast, wet tropics *Kinosternon* and *Trachemys* were positioned for range expansion into Central and South America, with at least three invasions for *Kinosternon* (Iverson et al. 2013) and two for *Trachemys* (Vargas-Ramírez et al. 2017).

A sister relation between the wet tropics and western aridlands subforks (Fig 1) is consistent with geographical proximity of these regions (Fig 2). Affiliation of these regions appears to result from three different patterns. First (Middle-Late Miocene), *Kinosternon flavescens* and *Gopherus berlandieri* each invaded the Mexican Gulf Coast Province (e.g., Reynoso and Montellano-Ballesteros 2004). Second (Pliocene-Pleistocene), the MRCA of *Trachemys scripta elegans*-*T. adiutrix* dispersed through the Mexican Gulf Coast, into South America (Fritz et al. 2012). Third (Pliocene-Early Pleistocene), there was separation of wet tropics and western aridlands lineages within *Kinosternon* (*K. scorpioides* from *K. integrum*) and *Trachemys* (*T. dorbigni*-*T. medemi* from *T. ornata*-*T. yaquia* – *T. hartwegi*-*T. taylori*). Thus, the relation between the western aridlands and wet tropics region appears complex, subsuming multiple of biogeographical events into one inter-region relation.

Quaternary effects on province placement

Grouping of the Pluvial Proglacial Province on the west fork (node 1) reflects three species that occur only marginally therein (*Clemmys guttata*, *Emys blandingii*, *Trachemys gaigeae*). Because these marginal distributions differ among taxa, the Pluvial Proglacial Province lacks definitive biogeographic relations with

other provinces. Most of the Pluvial Proglacial Province encompasses drainages that were either largely within the Last Glacial-Permafrost maximum or within the climatically harsh Great Basin (Ennen et al. 2017). The only turtle species widespread throughout the Pluvial Proglacial Province are cold-tolerant *Chelydra serpentina* and *Chrysemys picta* (Holman and Andrews 1994, Ennen et al. 2017), neither of which was part of this study.

Similarly, inclusion of the Tallgrass Prairie Province on the western aridlands subfork has limited support. This Province was within the Last Glacial-Permafrost maximum (French and Millar 2014) and the post-glacial ecosystem has been unstable, varying between forest and grassland (Baker et al. 2002, Nelson et al. 2006). Although unglaciated areas may have served as refugia for *Emys blandingii* (Sethuraman et al. 2014), *Glyptemys insculpta* is a post-glacial immigrant that likely followed glacial retreat from the southeast (Amato et al. 2008). *Kinosternon flavescens* and *T. ornata* appear to have colonized from the west, with eastward expansion of the Prairie Peninsula in the Holocene (Smith 1957, Houseal et al. 1982, Serb et al. 2001). *Graptemys ouachitensis* probably colonized this Province from the south via the Mississippi River (Brown et al. 2012).

Conclusions

This three-item analysis identifies natural sets of biogeographical provinces. At the continental scale, the most fundamental biogeographical pattern is subdivision between eastern and western provinces. These regions have divergent evolutionary legacies due to major evolutionary splits in *Kinosternon*, *Gopherus*, and *Trachemys*, along with the primarily eastern distributions in *Pseudemys* and *Graptemys*. Within the western provinces, the wet tropics subregion has a distinct evolutionary history from the western aridlands subregion, largely reflecting the evolution of separate lineages in western *Kinosternon* and *Trachemys*. Discovery of these shared patterns (and others described above) provides a regionalization for North American turtles, useful for understanding evolution of North American turtles and biogeography of North America.

Our summary of divergence estimates suggests that although there was some phylogenetic synchrony between select taxa, there was general asynchrony because provincial turtle faunas developed over time. Three factors likely help explain this pattern. First, long histories of each clade within North America allowed ample time for speciation (Stephens and Wiens 2003b, Rodrigues et al. 2017), consistent with phylogenetic evidence of sustained diversification over time (Thomson et al. 2021). Second, for a temperature-sensitive group like turtles (Ennen et al. 2016, Rodrigues et al. 2019), climatic fluctuations evidently caused periods of range expansion to alternate with periods of range contraction. Third, persistent landforms and biomes can influence species distributions through time and contribute to evolutionary divergence at any time (e.g., Keck and

Near 2010, Naka and Brumfield 2018). Reticulating expansion-contraction cycles in turtle distributions evidently interacted with persistent geological and ecological barriers to, asynchronously, produce geographically similar inter-provincial relations within and among turtle clades.

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Author Contributions

CH, VU and JE conceived the idea of the study. CH, JE and WM compiled phylogenetic, distributional, and geological evidence. VU developed and conducted the three-item analysis. SS conducted mapping. CH prepared the original manuscript. All authors contributed to revisions and gave final approval.

Data Availability Statement

Data used in this manuscript are available in the supplemental material.

Supplemental Material

The following materials are available as part of the online article at <https://escholarship.org/uc/fb>

Table S1. Summary of results from three item analyses with original data set and with iteratively pruned data sets

Table S2. Summary of biological treatments run individually by clade to eliminate paralogy

Table S3. Summary of turtle taxa supporting the positions of each branch of the West Fork of the intersection tree.

Table S4. Sister relations within turtle taxa that support a relation of western aridlands and wet tropics provinces in the intersection tree.

Table S5. Summary of turtle taxa supporting the positions of each branch of the East Fork of the intersection tree.

Table S6. Sister relations within turtle taxa that support a relation between the Great Lakes-North Appalachia, Mississippi-Alabama-Florida (MAFLA) shelf and Apalachicola-Chesapeake, Florida Peninsula sister pairs of provinces in the intersection tree.

Table S7. Sister relations within turtle taxa that support a sister relation between the Apalachicola-Chesapeake and Florida Peninsula provinces in the intersection tree.

Appendix S1. Original data set for three-item analysis before removal of very widespread taxa and areas with only one taxon

Appendix S2. Pruned data set for three-item analysis after removal of very widespread taxa from Emydinae along with removal of areas with only one taxon

References

- Agha, M., Ennen, J.R., Bower, D.S., Nowakowski, A.J., Sweat, S.C., & Todd, B.D. (2018) Salinity tolerances and use of saline environments by freshwater turtles: implications of sea level rise. *Biological Reviews*, 93, 1634-1648. <https://doi.org/10.1111/brv.12410>
- Amato, M.L., Brooks, R.J., & Fu, J. (2008) A phylogeographic analysis of populations of the wood turtle (*Glyptemys insculpta*) throughout its range. *Molecular Ecology*, 17, 570-581. <https://doi.org/10.1111/j.1365-294X.2007.03580.x>
- Baker, R.G., Bettis III, E.A., Denniston, R.F., Gonzalez, L.A., Strickland, L.E., & Krieg, J.R. (2002) Holocene paleoenvironments in southeastern Minnesota—chasing the prairie-forest ecotone. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 177, 103-122. [https://doi.org/10.1016/S0031-0182\(01\)00354-6](https://doi.org/10.1016/S0031-0182(01)00354-6)
- Bentley Sr., S.J., Blum, M.D., Maloney, J., Pond, L., & Paulsell, R. (2016) The Mississippi River source-to-sink system: perspectives on tectonic, climatic, and anthropogenic influences, Miocene to Anthropocene. *Earth-Science Reviews*, 153, 139-174. <https://doi.org/10.1016/j.earscirev.2015.11.001>
- Berry, J.F., Seidel, M.E., & Iverson, J.B. (1997) A new species of mud turtle (genus *Kinosternon*) from Jalisco and Colima, Mexico with notes on its natural history. *Chelonian Conservation and Biology*, 2, 329-337. <http://dx.doi.org/10.11646/zootaxa.4885.4.3>
- Blanton, R.E., Page, L.M., & Hilber, S.A. (2013) Timing of clade divergence and discordant estimates of genetic and morphological diversity in the Slender Madtom, *Noturus exilis* (Ictaluridae). *Molecular Phylogenetics and Evolution*, 66, 679-693. <https://doi.org/10.1016/j.ympev.2012.10.022>
- Blum, M.D., & Hattier-Womack, J. (2009) Climate change, sea-level change, and fluvial sediment supply to deepwater depositional systems. External controls on deep water depositional systems: SEPM, Special Publication, 92, 15-39. <https://doi.org/10.2110/sepmsp.092.015>
- Bourque, J.R. (2016) New mud turtles (Kinosternidae, *Kinosternon*) from the middle-late Miocene of the United States. *Journal of Paleontology*, 89, 821-844. <https://doi.org/10.1017/jpa.2015.63>

- Bramble, D.N., & Hutchison, J.H. (2014) Morphology, taxonomy, and distribution of North American tortoises, an evolutionary perspective. In: *Biology and conservation of North American tortoises*. (ed. by D.C. Rostal, E.D. McCoy, and H.R. Mushinsky), pp. 1-12. Johns Hopkins University Press, Baltimore, MD.
- Brown, A.D., Temple-Miller, K., Roosenburg, W.M., & White, M.M. (2012) Mitochondrial DNA variation in the Ouachita map turtle. *Copeia*, 2012, 301-306. <https://doi.org/10.1643/CH-11-009>
- Busschau, T., Jordaan, A., Conradie, W., & Daniels, S.R. (2022) Pseudocongruent phylogeography reflects unique responses to environmental perturbations in a biodiversity hotspot. *Journal of Biogeography*, 49, 445-459. <https://doi.org/10.1111/jbi.14334>
- Cao, N., Zaragüeta Bagils, R., & Vignes-Lebbe, R. (2007) Hierarchical representation of hypotheses of homology. *Geodiversitas*, 29, 5-15. Available at <https://sciencepress.mnhn.fr/en/periodiques/geodiversitas/29/1/representation-hierarchique-des-hypotheses-d-homologie>
- Cather, S.M., Chapin, C.E., & Kelley, S.A. (2012) Diachronous episodes of Cenozoic erosion in southwestern North America and their relationship to surface uplift, paleoclimate, paleodrainage, and paleoaltimetry. *Geosphere*, 8, 1177-1206. <https://doi.org/10.1130/GES00801.1>
- Chapin, C.E. (2008) Interplay of oceanographic and paleoclimate events with tectonism during middle to late Miocene sedimentation across the southwestern USA. *Geosphere*, 4, 976-991. <https://doi.org/10.1130/GES00171.1>
- Donoghue, M.J., & Moore, B.R. (2003) Toward an integrative historical biogeography. *Integrative and Comparative Biology*, 43, 261-270. <https://doi.org/10.1093/icb/43.2.261>
- Ebach, M.C. (2013) The bioregionalisation revival. *Zootaxa*, 3635 (3), 269-274. <https://doi.org/10.11646/zootaxa.3635.3.6>
- Ebach, M.C., & Parenti, L.R. (2015) The dichotomy of the modern bioregionalization revival. *Journal of Biogeography*, 42, 1801-1808. <https://doi.org/10.1111/jbi.12558>
- Ebach, M.C., Humphries, C.J., Newman, R.A., Williams, D.M., & Walsh, S.A. (2005) Assumption 2: opaque to intuition? *Journal of Biogeography*, 32, 781-787. <https://doi.org/10.1111/j.1365-2699.2005.01283.x>
- Edwards, T., Tollis, M., Hsieh, P., Gutenkunst, R.N., Liu, Z., Kusumi, K., Culver, M., & Murphy, R.W. (2016) Assessing models of speciation under different biogeographic scenarios; an empirical study using multi-locus and RNA-seq analyses. *Ecology and Evolution*, 6, 379-396. <https://doi.org/10.1002/ece3.1865>
- Ehlers, J., Gibbard, P.L., & Hughes, P.D. (2018) Quaternary glaciations and chronology. In: *Past glacial environments, second edition* (ed. by J. Menzies and J.J.M. van der Meer), pp 77-101. Elsevier. <https://doi.org/10.1016/B978-0-08-100524-8.00003-8>
- Ennen, J.R., Agha, M., Matamoros, W.A., Hazzard, S.C., & Lovich, J.E. (2016) Using climate, energy, and spatial-based hypotheses to interpret macroecological patterns of North America chelonians. *Canadian Journal of Zoology*, 94, 453-461. <https://doi.org/10.1139/cjz-2016-0033>
- Ennen, J.R., Matamoros, W.A., Agha, M., Lovich, J.E., Sweat, S.C., & Hoagstrom, C.W. (2017) Hierarchical, quantitative biogeographic provinces for all North American turtles and their contribution to the biogeography of turtles and the continent. *Herpetological Monographs*, 31, 142-168. <https://doi.org/10.1655/HERPMONOGRAPHS-D-16-00013>
- Ennen, J.R., Agha, M., Sweat, S.C., Matamoros, W.A., Lovich, J.E., Rhodin, A.G., Iverson, J.B., & Hoagstrom, C.W. (2020) Turtle biogeography: Global regionalization and conservation priorities. *Biological Conservation*, 241, 108323. <https://doi.org/10.1016/j.biocon.2019.108323>
- Eronen, J.T., Fortelius, M., Micheels, A., Portmann, F.T., Puolamäki, K., & Janis, C.M. (2012) Neogene aridification of the Northern Hemisphere. *Geology*, 40, 823-826. <https://doi.org/10.1130/G33147.1>
- French, H.M., & Millar, S.W. (2014) Permafrost at the time of the Last Glacial Maximum (LGM) in North America. *Boreas*, 43, 667-677. <https://doi.org/10.1111/bor.12036>
- Fritz, U., Stuckas, H., Vargas-Ramírez, M., Hundsdörfer, A.K., Maran, J., & Päckert, M. (2012) Molecular phylogeny of Central and South American slider turtles: implications for biogeography and systematics (Testudines:

- Emydidae: *Trachemys*). *Journal of Zoological Systematics and Evolutionary Research*, 50, 125-136. <https://doi.org/10.1111/j.1439-0469.2011.00647.x>
- Godfrey, C., Fan, M., Jesmok, G., Upadhyay, D., & Tripathi, A. (2018) Petrography and stable isotope geochemistry of Oligocene-Miocene continental carbonates in south Texas: implications for paleoclimate and paleoenvironment near sea-level. *Sedimentary Geology*, 367, 69-83. <https://doi.org/10.1016/j.sedgeo.2018.02.006>
- Grand, A., Zaragüeta-Bagils, R., Vélez, L. M., & Ung, V. (2014) A cladistic re-analysis of the Gadiformes (Teleostei, Paracanthopterygii) using three-item analysis. *Zootaxa*, 3889, 525-552. <https://doi.org/10.11646/zootaxa.3889.4.3>
- Haywood, A.M., Dowsett, H.J., & Dolan, A.M. (2016) Integrating geological archives and climate models for the mid-Pliocene warm period. *Nature Communications*, 7, 1-14. <https://doi.org/10.1038/ncomms10646>
- Herbert, T.D., Lawrence, K.T., Tzanova, A., Peterson, L.C., Caballero-Gill, R., & Kelly, C.S. (2016) Late Miocene global cooling and the rise of modern ecosystems. *Nature Geoscience*, 9, 843-847. <https://doi.org/10.1038/ngeo2813>
- Hoagstrom, C.W., & Echelle, A.A. (2022) Biogeography of the *Macrhybopsis aestivalis* complex (Teleostei: Cyprinidae): emphasis on speciation and ancient heterospecific mitochondrial transfer. *Environmental Biology of Fishes*, 105, 261-287. <https://doi.org/10.1007/s10641-022-01220-0>
- Hoagstrom, C.W., Ung, V., & Taylor, K. (2014) Miocene rivers and taxon cycles clarify the comparative biogeography of North American highland fishes. *Journal of Biogeography*, 41, 644-658. <https://doi.org/10.1111/jbi.12244>
- Holman, J.A., & Andrews, K.D. (1994) North American Quaternary cold-tolerant turtles: distributional adaptation and constraints. *Boreas*, 23, 44-52. <https://doi.org/10.1111/j.1502-3885.1994.tb00585.x>
- Holt, B.G., Lessard, J.P., Borregaard, M.K., et al. (2013) An update of Wallace's zoogeographic regions of the world. *Science*, 339, 74-78. <https://doi.org/10.1126/science.1228282>
- Houseal, T.W., Bickham, J.W., & Springer, M.D. (1982) Geographic variation in the yellow mud turtle, *Kinosternon flavescens*. *Copeia*, 1982, 567-580. <https://doi.org/10.2307/1444657>
- Hutchison, J.H. (1982) Turtle, crocodylian, and chamosaur diversity changes in the Cenozoic of the north-central region of western United States. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 37, 149-164. [https://doi.org/10.1016/0031-0182\(82\)90037-2](https://doi.org/10.1016/0031-0182(82)90037-2)
- Hyeong, K., Lee, J., Seo, I., Lee, M.J., Yoo, C.M., & Khim, B.K. (2014) Southward shift of the Intertropical Convergence Zone due to Northern Hemisphere cooling at the Oligocene-Miocene boundary. *Geology*, 42, 667-670. <https://doi.org/10.1130/G35664.1>
- Iverson, J.B. (1979) A taxonomic reappraisal of the yellow mud turtle, *Kinosternon flavescens* (Testudines: Kinosternidae). *Copeia*, 1979, 212-225. <https://doi.org/10.2307/1443406>
- Iverson, J.B. (1981) Biosystematics of the *Kinosternon hirtipes* species group (Testudines: Kinosternidae). *Tulane Studies in Zoology and Botany*, 23, 1-74.
- Iverson, J.B., Le, M., & Ingram, C. (2013) Molecular phylogenetics of the mud and musk turtle family Kinosternidae. *Molecular Phylogenetics and Evolution*, 69, 929-939. <https://doi.org/10.1016/j.ympev.2013.06.011>
- Joyce, W.G., & Bourque, J.R. (2016) A review of the fossil record of turtles of the clade Pan-Kinosternoidea. *Bulletin of the Peabody Museum of Natural History*, 57, 57-96. <https://doi.org/10.3374/014.057.0104>
- Keck, B.P., & Near, T.J. (2010) A young clade repeating an old pattern: diversity in *Nothonotus* darters (Teleostei: Percidae) endemic to the Cumberland River. *Molecular Ecology*, 19, 5030-5042. <https://doi.org/10.1111/j.1365-294X.2010.04866.x>
- Kirillova, V., Osborne, A.H., Störling, T., & Frank, M. (2019) Miocene restriction of the Pacific-North Atlantic throughflow strengthened Atlantic overturning circulation. *Nature Communications*, 10, 1-7. <https://doi.org/10.1038/s41467-019-12034-7>
- Klaus, J.S., Meeder, J.F., McNeill, D.F., Woodhead, J.F., & Swart, P.K. (2017) Expanded Florida reef development during the mid-Pliocene warm period. *Global and Planetary Change*, 152, 27-37. <https://doi.org/10.1016/j.gloplacha.2017.02.001>

- Kukla, T., Rugenstein, J.K.C., Ibarra, D.E., Winnick, M.J., Strömberg, C.A., & Chamberlain, C.P. (2022) Drier winters drove Cenozoic open habitat expansion in North America. *AGU Advances*, 3, e2021AV000566. <https://doi.org/10.1029/2021AV000566>
- Lamb, T., Lydeard, C., Walker, R.B., & Gibbons, J.W. (1994) Molecular systematics of map turtles (*Graptemys*): a comparison of mitochondrial restriction site versus sequence data. *Systematic Biology*, 43, 543-559. <https://doi.org/10.1093/sysbio/43.4.543>
- Legler, J.M. (1990) The genus *Pseudemys* in Mesoamerica: taxonomy, distribution, and origins. In: Life history and ecology of the slider turtle (ed. by J.W. Gibbons), pp 82-105. Smithsonian Institution Press, Washington, D.C.
- Legler, J., & Vogt, R.C. (2013) The turtles of Mexico: land and freshwater forms. University of California Press, Berkeley, CA.
- Martin, B.T., Bernstein, N.P., Birkhead, R.D., Koukl, J.F., Musmann, S.M., & Placyk Jr., J.S. (2013) Sequence-based molecular phylogenetics and phylogeography of the American box turtles (*Terrapene* spp.) with support from DNA barcoding. *Molecular Phylogenetics and Evolution*, 68, 119-134. <https://doi.org/10.1016/j.ympev.2013.03.006>
- Meseguer, A.S., & Condamine, F.L. (2020) Ancient tropical extinctions at high latitudes contributed to the latitudinal diversity gradient. *Evolution*, 74, 1966-1987. <https://doi.org/10.1111/evo.13967>
- Miller, K.G., Browning, J.V., Schmelz, W.J., Kopp, R.E., Mountain, G.S., & Wright, J.D. (2020) Cenozoic sea-level and cryospheric evolution from deep-sea geochemical and continental margin records. *Science Advances*, 6, eaaz1346. <https://doi.org/10.1126/sciadv.aaz1346>
- Milstead, W.W., & Tinkle, D.W. (1967) *Terrapene* of western Mexico, with comments on the species groups in the genus. *Copeia*, 1967, 180-187. <https://doi.org/10.2307/1442193>
- Missimer, T.M., & Maliva, R.G. (2017) Late Miocene fluvial sediment transport from the southern Appalachian Mountains to southern Florida: an example of an old mountain belt sediment production surge. *Sedimentology*, 64, 1846-1870. <https://doi.org/10.1111/sed.12377>
- Morrone, J.J. (2014) Cladistic biogeography of the Neotropical region: identifying the main events in the diversification of the terrestrial biota. *Cladistics*, 30, 202-214. <https://doi.org/10.1111/cla.12039>
- Morrone, J.J. (2015a) Biogeographical regionalisation of the world: a reappraisal. *Australian Systematic Botany*, 28, 81-90. <https://doi.org/10.1071/SB14042>
- Morrone, J.J. (2015b) Track analysis beyond panbiogeography. *Journal of Biogeography*, 42, 413-425. <https://doi.org/10.1111/jbi.12467>
- Morrone, J.J. (2018) The spectre of biogeographical regionalization. *Journal of Biogeography*, 45, 282-288. <https://doi.org/10.1111/jbi.13135>
- Morrone, J.J. (2020) Biotic assembly in evolutionary biogeography: a case for integrative pluralism. *Frontiers of Biogeography*, 12, e48819. <https://doi.org/10.21425/F5FBG48819>
- Murphy, D.J., Ebach M.C., Miller J.T., Laffan S.T., Cassis G., Ung V., Thornhill, A.H., Kerr, N., & Tursky M.L. (2019) Do phytogeographic patterns reveal biomes or biotic regions? *Cladistics* 35, 654-670. <https://doi.org/10.1111/cla.12381>
- Naka, L.N., & Brumfield, R.T. (2018) The dual role of Amazonian rivers in the generation and maintenance of avian diversity. *Science Advances*, 4, eaar8575. <https://doi.org/10.1126/sciadv.aar8575>
- Nelson, D.M., Hu, F.S., Grimm, E.C., Curry, B.B., & Slate, J.E. (2006) The influence of aridity and fire on Holocene prairie communities in the eastern Prairie Peninsula. *Ecology*, 87, 2523-2536. [https://doi.org/10.1890/0012-9658\(2006\)87\[2523:TIOAAF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2523:TIOAAF]2.0.CO;2)
- Parenti, L., & Ebach, M. (2009) Comparative biogeography: discovering and classifying biogeographical patterns of a dynamic Earth (Vol. 2). University of California Press, Berkeley, CA.
- Parham, J.F., Papenfuss, T.J., Buskirk, J.R., Parra-Olea, G., Chen, J.Y., & Simison, W.B. (2015) *Trachemys ornata* or not *ornata*: reassessment of a taxonomic revision for Mexican *Trachemys*. *Proceedings of the California Academy of Science*, 62, 359-367.
- Parham, J.F., Papenfuss, T.J., van Dijk, P.P., Wilson, B.S., Marte, C., Schettino, L.R., & Simison, W.B. (2013) Genetic introgression and hybridization in Antillean freshwater turtles (*Trachemys*) revealed by coalescent analyses of mitochondrial and cloned nuclear markers. *Molecular Phylogenetics and Evolution*,

- 67, 176-187. <https://doi.org/10.1016/j.ympev.2013.01.004>
- Pereira, A.G., Sterli, J., Moreira, F.R.R., & Schrago, C.G. (2017) Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. *Molecular Phylogenetics and Evolution*, 113, 59-66. <https://doi.org/10.1016/j.ympev.2017.05.008>
- Potter, P.E., & Szatmari, P. (2009) Global Miocene tectonics and the modern world. *Earth-Science Reviews*, 96, 279-295. <https://doi.org/10.1016/j.earscirev.2009.07.003>
- Pound, M.J., Haywood, A.M., Salzmann, U., & Riding, J.B. (2012) Global vegetation dynamics and latitudinal temperature gradients during the Mid to Late Miocene (15.97–5.33 Ma). *Earth-Science Reviews*, 112, 1-22. <https://doi.org/10.1016/j.earscirev.2012.02.005>
- Pound, M.J., Haywood, A.M., Salzmann, U., Riding, J.B., Lunt, D.J., & Hunter, S.J. (2011) A Tortonian (late Miocene, 11.61–7.25 Ma) global vegetation reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 300, 29-45. <https://doi.org/10.1016/j.palaeo.2010.11.029>
- Reynoso, V.H., & Montellano-Ballesteros, M. (2004) A new giant turtle of the genus *Gopherus* (Chelonia: Testudinidae) from the Pleistocene of Tamaulipas, México, and a review of the phylogeny and biogeography of gopher tortoises. *Journal of Vertebrate Paleontology*, 24, 822-837. [https://doi.org/10.1671/0272-4634\(2004\)024\[0822:ANGTOT\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2004)024[0822:ANGTOT]2.0.CO;2)
- Rineau, V., Masse, J.P., & Villier, L. (2020) A new cladistic insight on comparative anatomy and phylogeny of rudists (Bivalvia, Hippuritida). *Journal of Systematic Palaeontology*, 18, 1243-1297. <https://doi.org/10.1080/14772019.2020.1759705>
- Rödger, D., Lawing, A.M., Flecks, M., et al. (2013) Evaluating the significance of paleophylogeographic species distribution models in reconstructing Quaternary range-shifts of Nearctic chelonians. *PLoS One*, 8, e72855. <https://doi.org/10.1371/journal.pone.0072855>
- Rodrigues, J.F.M., Olalla-Tárraga, M.Á., Iverson, J.B., Akre, T.S.B., & Diniz-Filho, J.A.F. (2017) Time and environment explain the current richness distribution of non-marine turtles worldwide. *Ecography*, 40, 1402-1411. <https://doi.org/10.1111/ecog.02649>
- Rodrigues, J.F.M., Sobral, F.L., Iverson, J.B., & Diniz-Filho, J.A.F. (2019) Phylogenetic and spatial analyses suggest minimum temperature as an environmental filter for turtle communities. *Journal of Biogeography*, 46, 671-679. <https://doi.org/10.1111/jbi.13527>
- Rovere, A., Hearty, P.J., Austermann, J., Mitrovica, J.X., Gale, J., Moucha, R., Forte, A.M., & Raymo, M.E. (2015) Mid-Pliocene shorelines of the US Atlantic Coastal Plain—an improved elevation database with comparison to Earth model predictions. *Earth-Science Reviews*, 145, 117-131. <https://doi.org/10.1016/j.earscirev.2015.02.007>
- Salzmann, U., Williams, M., Haywood, A.M., Johnson, A.L., Kender, S., & Zalasiewicz, J. (2011) Climate and environment of a Pliocene warm world. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 309, 1-8. <https://doi.org/10.1016/j.palaeo.2011.05.044>
- Samuels, J.X., & Hopkins, S.S. (2017) The impacts of Cenozoic climate and habitat changes on small mammal diversity of North America. *Global and Planetary Change*, 149, 36-52. <https://doi.org/10.1016/j.gloplacha.2016.12.014>
- Serb, J.M., Phillips, C.A., & Iverson, J.B. (2001) Molecular phylogeny and biogeography of *Kinosternon flavescens* based on complete mitochondrial control region sequences. *Molecular Phylogenetics and Evolution*, 18, 149-162. <https://doi.org/10.1006/mpev.2000.0858>
- Sethuraman, A., McGaugh, S.E., Becker, M.L. et al. (2014) Population genetics of Blanding's turtle (*Emys blandingii*) in the midwestern United States. *Conservation Genetics*, 15, 61-73. <https://doi.org/10.1007/s10592-013-0521-8>
- Smith, P.W. (1957) An analysis of post-Wisconsin biogeography of the Prairie Peninsula region based on distributional phenomena among terrestrial vertebrate populations. *Ecology*, 38, 205-218. <https://doi.org/10.2307/1931679>
- Snedden, J.W., & Galloway, W.E. (2019) *The Gulf of Mexico sedimentary basin: depositional evolution and petroleum applications*. Cambridge University Press, Cambridge, UK.
- Spinks, P.Q., & Shaffer, H.B. (2009) Conflicting mitochondrial and nuclear phylogenies for the widely disjunct *Emys* (Testudines: Emydidae) species complex, and what they tell us about biogeography and hybridization. *Systematic*

- Biology, 58, 1-20. <https://doi.org/10.1093/sysbio/syp005>
- Spinks, P.Q., Thomson, R.C., Pauly, G.B., Newman, C.E., Mount, G., & Shaffer, H.B. (2013) Misleading phylogenetic inferences based on single-exemplar sampling in the turtle genus *Pseudemys*. *Molecular Phylogenetics and Evolution*, 68, 269-281. <https://doi.org/10.1016/j.ympev.2013.03.031>
- Spinks, P.Q., Thomson, R.C., Gidiş, M., & Shaffer, H.B. (2014) Multilocus phylogeny of the New-World mud turtles (Kinosternidae) supports the traditional classification of the group. *Molecular Phylogenetics and Evolution*, 76, 254-260. <https://doi.org/10.1016/j.ympev.2014.03.025>
- Stephens, P.R., & Wiens, J.J. (2003a) Ecological diversification and phylogeny of emydid turtles. *Biological Journal of the Linnean Society*, 79, 577-610. <https://doi.org/10.1046/j.1095-8312.2003.00211.x>
- Stephens, P.R., & Wiens, J.J. (2003b) Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *American Naturalist*, 161(1), 112-128. <https://doi.org/10.1086/345091>
- Stephens, P.R., & Wiens, J.J. (2004) Convergence, divergence, and homogenization in the ecological structure of emydid turtle communities: the effects of phylogeny and dispersal. *American Naturalist*, 79, 577-610. <https://doi.org/10.1086/422342>
- Stephens, P.R., & Wiens, J.J. (2009) Bridging the gap between community ecology and historical biogeography: niche conservatism and community structure in emydid turtles. *Molecular Ecology*, 18, 4664-4679. <https://doi.org/10.1111/j.1365-294X.2009.04378.x>
- Strömberg, C.A.E. (2011) Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences*, 39, 517-544. <https://doi.org/10.1146/annurev-earth-040809-152402>
- Thomson, R.C., Spinks, P.Q., & Shaffer, H.B. (2018) Molecular phylogeny and divergence of the map turtles (Emydidae: *Graptemys*). *Molecular Phylogenetics and Evolution*, 121, 61-70. <https://doi.org/10.1016/j.ympev.2017.11.012>
- Thomson, R.C., Spinks, P.Q., & Shaffer, H.B. (2021) A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. *Proceedings of the National Academy of Sciences USA*, 118, e2012215118. <https://doi.org/10.1073/pnas.2012215118>
- Ung, V. (2018) The need for standard protocols in bioregionalisation: Comments on "The spectre of biogeographical regionalization" by Morrone (2018). *Zootaxa*, 4532, 296-300. <https://doi.org/10.11646/zootaxa.4532.2.10>
- Ung, V., Michaux, B., & Leschen, R.A.B. (2016a) A comprehensive vicariant model for Southwest Pacific biotas. *Australian Systematic Botany*, 29, 424-439. <https://doi.org/10.1071/SB16032>
- Ung, V., Zaragüeta-Bagils, R., & Williams, D.M. (2016b) Comparative biogeography of Southeast Asia and the West Pacific region. *Biological Journal of the Linnean Society*, 117, 372-385. <https://doi.org/10.1111/bij.12670>
- Vargas-Ramírez, M., del Valle, C., Ceballos, C.P., & Fritz, U. (2017) *Trachemys medemi* n. sp. from northwestern Colombia turns the biogeography of South American slider turtles upside down. *Journal of Zoological Systematics and Evolutionary Research*, 55, 326-339. <https://doi.org/10.1111/jzs.12179>
- Vlachos, E. (2018) A review of the fossil record of North American turtles of the clade Pan-Testudinoidea. *Bulletin of the Peabody Museum of Natural History*, 59, 3-94. <https://doi.org/10.3374/014.059.0101>
- Wagner, L.S., Fischer, K.M., Hawman, R., Hopper, E., & Howell, D. (2018) The relative roles of inheritance and long-term passive margin lithospheric evolution on the modern structure and tectonic activity in the southeastern United States. *Geosphere*, 14, 1385-1410. <https://doi.org/10.1130/GES01593.1>
- Walker, D., Moler, P.E., Buhlmann, K.A., & Avise, J.C. (1998) Phylogeographic patterns in *Kinosternon subrubrum* and *K. baurii* based on mitochondrial DNA restriction analyses. *Herpetologica*, 54, 174-184.
- Warzeski, E.R., Cunningham, K.J., Ginsburg, R.N., Anderson, J.B., & Ding, Z.D. (1996) A Neogene mixed siliciclastic and carbonate foundation for the Quaternary carbonate shelf, Florida Keys. *Journal of Sedimentary Research*, 66, 788-800. <https://doi.org/10.1306/D426840A-2B26-11D7-8648000102C1865D>

- Webb III, T., Shuman, B., & Williams, J.W. (2004) Climatically forced vegetation dynamics in eastern North America during the late Quaternary Period. *Developments in Quaternary Sciences*, 1, 459-478. [https://doi.org/10.1016/S1571-0866\(03\)01021-2](https://doi.org/10.1016/S1571-0866(03)01021-2)
- Weems, R.E., & George, R.A. (2013) Amphibians and nonmarine turtles from the Miocene Calvert Formation of Delaware, Maryland, and Virginia (USA). *Journal of Paleontology*, 87, 570-588. <https://doi.org/10.1666/12-071>
- Wilkinson, M. (1994) Three-taxon statements: when is a parsimony analysis also a clique analysis? *Cladistics*, 10, 221-223. <https://doi.org/10.1111/j.1096-0031.1994.tb00174.x>
- Williams, D. M., & Ebach, M. C. (2006). The data matrix. *Geodiversitas*, 28, 409-420.
- Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292, 686-693. <https://doi.org/10.1126/science.1059412>
- Zaragüeta-Bagils, R., & Bourdon, E. (2007) Three-item analysis: hierarchical representation and treatment of missing and inapplicable data. *Comptes Rendus Palevol*, 6, 527-534. <https://doi.org/10.1016/j.crpv.2007.09.013>
- Zaragüeta-Bagils, R., Ung, V., Grand, A., Vignes-Lebbe, R., Cao, N., & Ducasse, J. (2012) LisBeth: new cladistics for phylogenetics and biogeography. *Comptes Rendus Palevol*, 11, 563-566. <https://doi.org/10.1016/j.crpv.2012.07.002>

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