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Invited Review Article

Trinidad and Tobago geogenomics: Exploring connections between geology and vicariance and dispersal biogeography — a review and synthesis

John C. Weber [a,*], Jeanette C. Arkle [b], Laurent de Verteuil [c], John C. Murphy [d], Nigel C. Noriega [e], David N. Reznick [f], Michael J. Jowers [g]

[a] *Department of Geology, Grand Valley State University, Allendale, MI 49401, USA*
[b] *Department of Geology, Augustana College, Rock Island, IL, USA*
[c] *Independent Consultant, 92 Camden Court, London, ON N5X 2K4, Canada*
[d] *Science and Education, 1400 S. Lake Shore Drive, Chicago Field Museum, Chicago, IL 60605, USA*
[e] *Sustainable Innovation Initiatives, Hamgel Field Station, Manuel Congo, Trinidad and Tobago*
[f] *Department of Biology, University of California-Riverside, Riverside, CA 92521, USA*
[g] *Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Campus de Móstoles, 28933 Madrid, Spain*

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ABSTRACT

In this paper we draw on the wealth of biological and geological knowledge derived from over a century of work on the rich fauna and complex geology of Trinidad and Tobago, and the surrounding region, through petroleum exploration, academic research, and other studies. We use molecular studies from the last 20 years that address phylogeography, phylogenetics, population genetics, morphology, and biogeography to link biological events to the geology, neotectonics, and geomorphology of this area of the southeast Caribbean and northern South America. We focus on studies that provide molecular timings of speciation, vicariance, and dispersal events to compare these to geological data. We first develop and review two relatively clear-cut biology-geology connections; we then review and speculate on other possible yet-unknown connections.

1. Introduction

Trinidad and Tobago display the highest biodiversity observed in the Caribbean islands. In the current study we explore the geological basis for some of this diversity and do so by applying the principles of geogenomics. Geogenomics is an emerging field that exploits connections between biology and geology to paint a holistic picture of how our living planet functions (Baker et al., 2014). Genetics can now provide geological-time-scale clocks that can precisely (± 5 ka) date the timing of key vicariance (isolation) and dispersal events that, in part, drive biotic evolution. Such biological events may, in turn, be driven by geological processes that can be studied using paleogeography which relies largely on the stratigraphic and fossil record of deep time to date surface landscape evolution. Biogeography is a key and allied field that existed long before genetic analyses were available.

Geogenomics *sensu stricto,* uses dates estimated from divergences in DNA sequences among isolated populations to estimate the age of the key geological events that may have shaped species distributions (Baker et al., 2014). Conversely, geological events can be used to calibrate key vicariance and dispersal events and hence help to calibrate genetic trees. Jowers et al. (2024a) referred to this "two-way street" type of geogenomics as a "geological-molecular" approach.

The Great American Biotic Interchange is a well-documented example of how geological processes, in this case, the development of the Isthmus of Panama by subduction, arc volcanism, obduction, collision, and accretion, affect biology (Fig. 1) (Stehli and Webb, 1985; Bacon et al., 2015). Precisely and accurately dating the timing of these geological events has been a major achievement in understanding the timing of faunal and floral dispersal between the two Americas (Montes et al., 2012a; Montes et al., 2012b; Montes et al., 2015). A similar but less well-documented story, dispersal across the Greater Antilles-Aves Ridge land bridge (GAARlandia), has been proposed to explain the distribution of mammals in Cuba and in the eastern Caribbean (Fig. 1) (MacPhee and Iturralde-Vinent, 1994). As new geological data come in, the GAARlandia hypothesis is being challenged (Ali and Hedges, 2021). This controversy is ripe for, and may ultimately be resolvable by, using a

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* Corresponding author.
E-mail address: weberj@gvsu.edu (J.C. Weber).

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geogenomics approach.

Recent advances have clarified disputes regarding the history of tectonic events surrounding Trinidad and Tobago (Fig. 1). Here, we aim to integrate genetic and recent geological information with the goal of developing zoogeographical hypotheses to describe select faunal elements of Trinidad and Tobago.

1.1. *Motivation for Trinidad and Tobago geogenomic case studies*

Located at about ten degrees north latitude, Trinidad sits in the tropics, where biodiversity is generally the highest of all ecological biozones on the planet. The combination of its latitude and its continental island status makes for a rich and diverse set of terrestrial organisms that can be used to study the timing and causes of Trinidad's vicariance and dispersal events (Figs. 2, 3). Tobago, roughly 25 km to the north, is on the other hand, an oceanic island (Figs. 2, 4). The largely South American flora and fauna on the two islands have been the focus of intensive study for well over a century.

One motivation for this work was the surprising result that emerged from two early efforts to apply genetic tools (electrophoresis and PCR based sequencing of individual genetic loci) to characterize the genetic diversity of guppy (*Poecilia reticulata*) populations in Trinidad (Carvalho et al., 1991; Alexander et al., 2006). Both studies revealed an unexpectedly large genetic divergence between guppies from the Oropuche River drainage in northeast Trinidad, which drains eastward into the Atlantic Ocean, and those from the Caroni River drainage in northwest Trinidad, which flows to the west into the Caroni swamp and Gulf of Paria (Figs. 2, 3). The difference is surprising and may be related to some combination of surface uplift, subsidence, and sea-level change. The authors of these guppy papers recognized that in the previous decade, Hans Boos (1984) had acknowledged a similar east-west divide in some species of reptiles. He proposed a "two arcs" hypothesis, suggesting that the colonization of Trinidad from the mainland had come from at least two distinct sources.

From a geologic perspective, as we began to study and understand the geomorphology of Trinidad and Tobago (e.g., Ritter and Weber, 2007; Arkle et al., 2017a, 2017b), we began to envision possible connections between Trinidad's evolving landscape and its evolving organisms. Northern Trinidad's landscape contains tectonically affected elements, including flights of uplifted marine terraces, buried and exposed alluvial fans, and both submerged and emergent shorelines. The distribution of these features, i.e., Trinidad's "megageomorphology", demonstrates that the surface of northeastern Trinidad is uplifting whereas that of northwestern Trinidad and eastern Venezuela is sinking (Weber, 2005; Ritter and Weber, 2007; Arkle et al., 2017a, 2017b, 2021) (Fig. 2). The active sinking in western Trinidad and eastern Venezuela occurs across the Gulf of Paria pull-apart basin but may ultimately be related to deep lithospheric tearing (Govers and Wortel, 2005; Levander et al., 2014; Arkle et al., 2021) (Fig. 2).

A second motivation for this review stemmed from recognizing that the east-to-west differences in northern Trinidad's "megageomorphology" discussed above could also be used to explain a vicariance event that isolated neighboring populations of *Phytotriades auratus* (Hylidae), which are high-elevation tree frogs, and their egg hosts, deep tanks in the cloud-forest giant bromeliads *G. erectiflora* in northwestern Trinidad and north-eastern (Paria Peninsula) Venezuela (Jowers et al., 2024a).

Trinidad and Tobago are of biogeographic interest in several other ways. These islands sit in the SE corner of the Caribbean Sea just off the coast of Venezuela and, as such, form a major stepping-stone archipelago between continental South America and the modern and emergent Lesser Antilles, as well as possibly also from the mainland to the Aves Ridge, a submerged and ancient island arc volcanic chain (Fig. 1). What role did these two stepping-stone islands play in the northward migration of South American continental life fauna and flora? What can geology, genetics, and distributions of extant organisms tell us about the timing and causes of migrations? Further, as the Caribbean plate pushed eastward through the gap between North and South America a marine continental borderland was progressively replaced by a coastal mountain belt that is generally referred to as the Southern Caribbean orogen. How did this geographic change affect biological evolution?

Other distributional anomalies exist that we explore here include

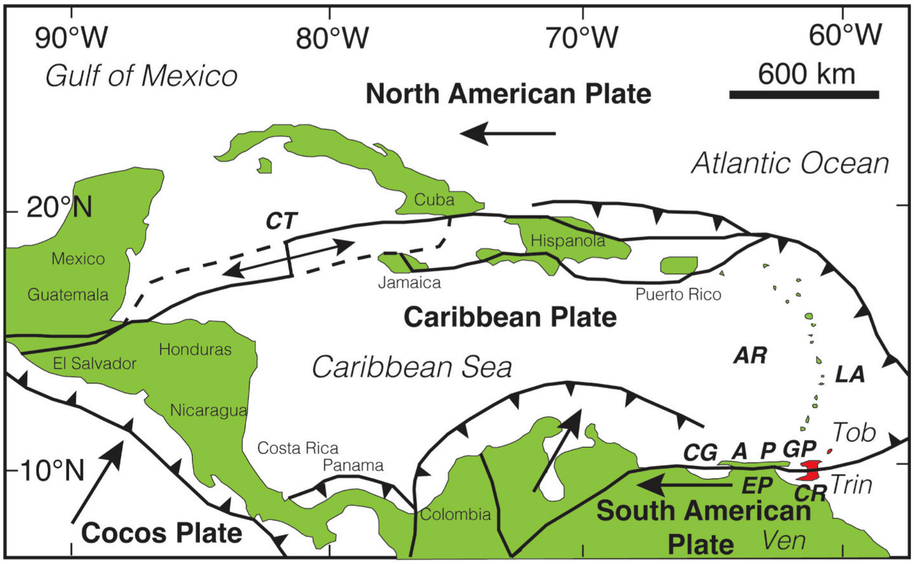


Fig. 1. Map showing the basic geography of the Caribbean plate (Ca), its plate boundaries, and surrounding plates: North American (NA), South American (SA), and Cocos (CO). Transform (sliding) boundaries are shown as thick lines; subduction zones and convergent boundaries are shown as solid lines with sawtooth patterns on upper (non-subducting) plate; significance of the short Cayman trough (CT) spreading center is discussed in the text. Large arrows show schematically how neighboring plates move relative to an arbitrarily fixed (stationary) Ca plate. AR - Aves Ridge submerged arc; LA - Lesser Antilles modern arc. The map highlights the location of the Trinidad-Tobago and eastern Venezuela study area which straddles the Ca-SA active transform (sliding) plate boundary: EP-El Pilar and CR-Central Range transform faults; GC-Gulf of Cariaco and GP-Gulf of Paria pull-apart basins. With strong geological and biological links to South America, Trinidad has been long considered to be a continental island, whereas Tobago's geology – largely a Mesozoic volcanic arc and forearc – demonstrates that it is an oceanic island which has traveled eastward and been accreted to South America.

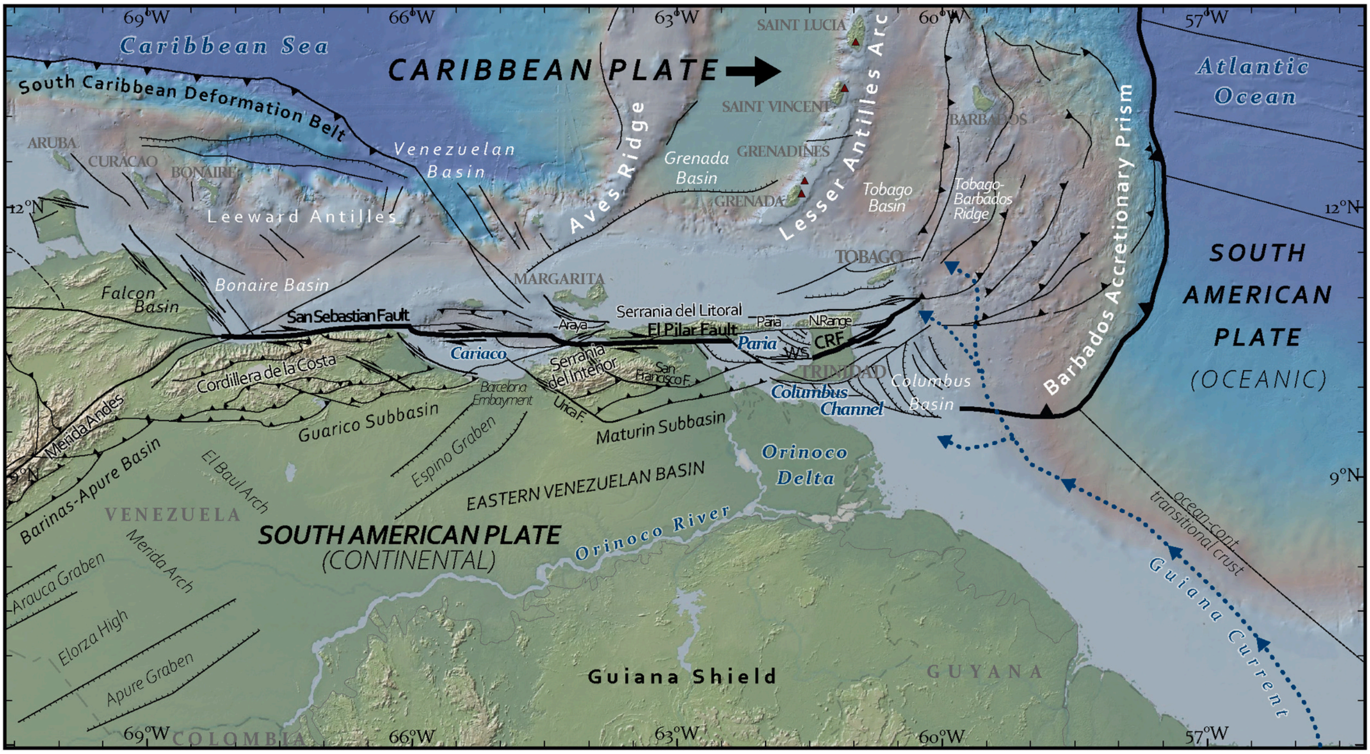


Fig. 2. Map showing southern Caribbean- northern South America tectonic elements and structures modified from Bouysse et al., 2021; Lugo and Audemard, 2021; Alvarez et al., 2021; Duerto and McClay, 2011 and using topo-bathymetry from Global Multi-Resolution Topography (GMRT) v.4.1.1 (Ryan et al., 2009) and ESRI Ocean Basemap. Ca-SA plate boundary dextral (right-handed) transform (sliding) faults (thick lines), the El Pilar (EPF) and Warm Springs (WS)-Central Range (CRF) faults step to the right and link up across normal faults (thin lines with tick marks on down-dropped sides) defining a zone of stretching (extension) and subsidence in the Gulf of Paria pull-apart basin. The Columbus Basin (CB) forms a second zone of extension that occurs due to offshore, shelf-edge collapse of the Orinoco delta southeast of Trinidad. Trinidad sits on and helps to define the South American continental shelf, whereas Tobago island forms an uplifted horst block surrounded by normal and strike-slip faults (thin lines). Zone of contraction, likely associated with current subsurface location of deep lithospheric STEP tear, and subsea subduction zone – due to Ca-SA plate convergence, both east of Trinidad, are shown using solid lines with sawtooth patterns. Modern eastward ~20 mm/yr Caribbean plate motion from GPS study of Weber et al. (2001a).

amphibians found in Venezuela and Tobago, but not Trinidad, which lies between the two. How could an amphibian leapfrog Trinidad, which lies between Tobago and the mainland, then colonize Tobago? Are such distributions due to Boos' (1984) "two arcs" mechanism, tectonics, or other factors? Can genetics and geology be used together to form a more coherent picture of how the region evolved and developed?

Furthermore, much high-caliber genetics work has been done in the southeastern Caribbean, but to date, this has only been done on a study-by-study basis. In this review we attempt to integrate those results into a more coherent regional picture that is connected to the geology and geomorphology when appropriate.

Trinidad's sedimentary geology and paleontology have been intensively studied since the discovery of oil in 1857–1866, early in the British colonial period (Persad, 2011; Carr-Brown, 2008). In addition, even before plate tectonics had been formalized, Wilson (1966a, 1966b) suggested that Trinidad straddles the Caribbean-South American transform (sliding or shearing) plate boundary as we know it today (e.g., Weber et al., 2001a) (Figs. 2, 3). Active transform tectonics not only shears and shifts landmasses laterally but also causes local sinking and rising due to the local extension and contraction that occurs where transform faults bend or end and connect across fault step-overs. The tectonically driven rising and sinking of land is one of several major factors that can drive the vicariance and dispersal of terrestrial organisms. Other important ones include paleogeographic changes due to sea level rise and fall, and isolation and speciation events that occur due to ecological competition or gradients (e.g. Haffer, 1997). Trinidad straddles the South American continental shelf and is separated from the mainland only by shallow seas. This defines it as a continental island that has been repeatedly joined to and separated from the mainland in response to sea level fluctuations, e.g., driven by glacial cycles during the Pleistocene.

2. Geology and paleogeography

2.1. Review of Trinidad's tectonics, geology, and landscape (geomorphology) as key paleogeographical issues

The geological history of Trinidad and the southeast Caribbean is rich and complex. Many aspects of this history have been extensively studied, but significant gaps in our knowledge and differences in interpretation still exist, even in the most recent syntheses (e.g., see Bartolini, 2021 and papers therein). These gaps and differences impact reconstructions of Trinidad's Neogene paleogeography. Differences center mainly around these three issues: 1) whether the Caribbean plate moved essentially parallel to the *E*-W-trending Caribbean-South American plate boundary throughout the entire Neogene, or whether it involved a component of convergence in the Early Neogene and then later (~10 Ma) turned to move parallel to the boundary, 2) which plate boundary faults were active at which time, and 3) the past positions of Tobago and the metamorphic Northern Range-Paria mountains relative to south Trinidad. Plate tectonic reconstructions vary significantly in these ways; this can be seen by comparing the reconstructions of Pindell et al. (1998), Erlich and Barrett (1990), Speed (1985), Meschede and Frisch (1998), and Escalona et al. (2021). In assessing the paleogeographic evolution of our study area through time, not all tectonic models, structural restorations, and facies assessments will be compatible:

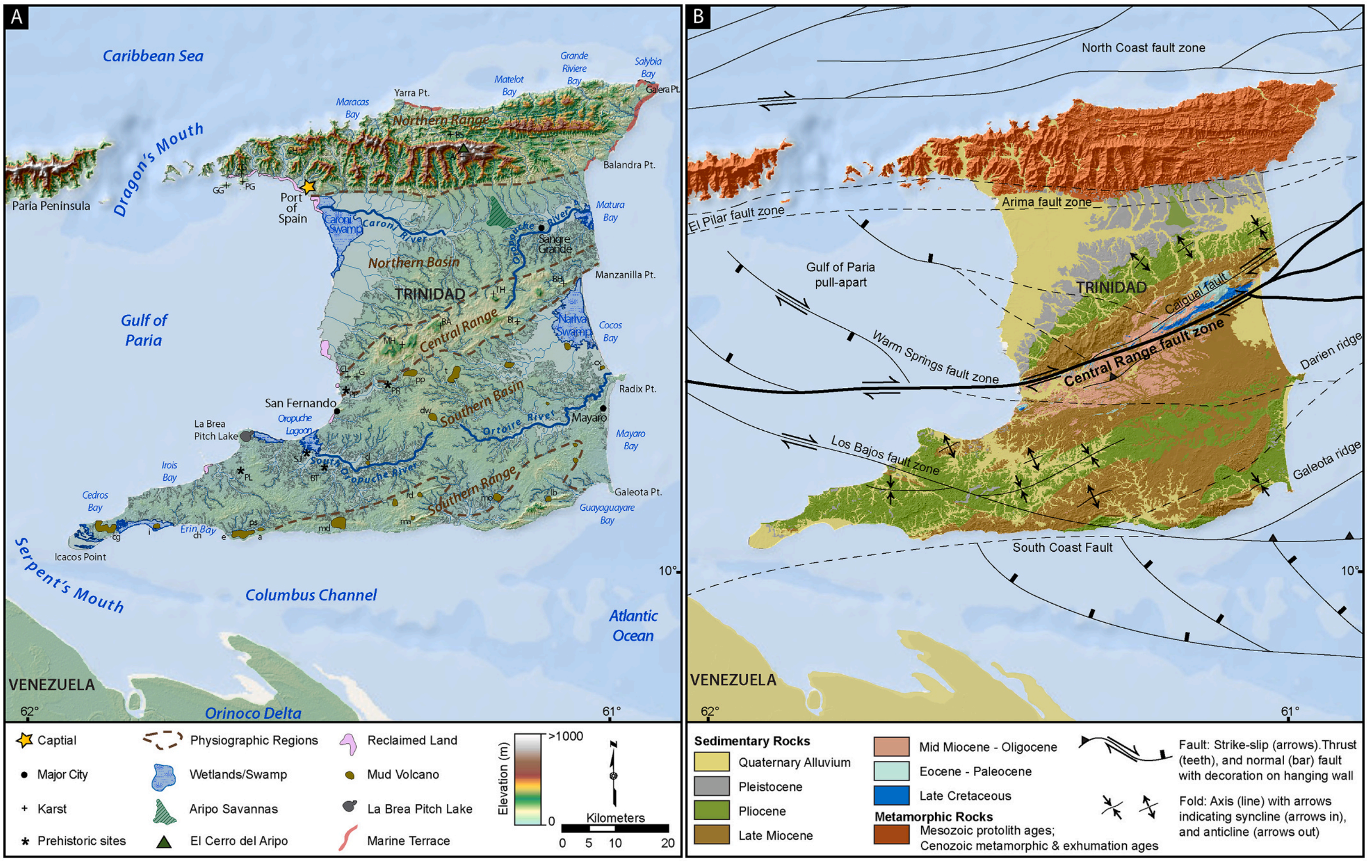


Fig. 3. a) Map showing the on-land topography and geology and offshore bathymetry in and around Trinidad. Modified from Arkle et al. (2017b).

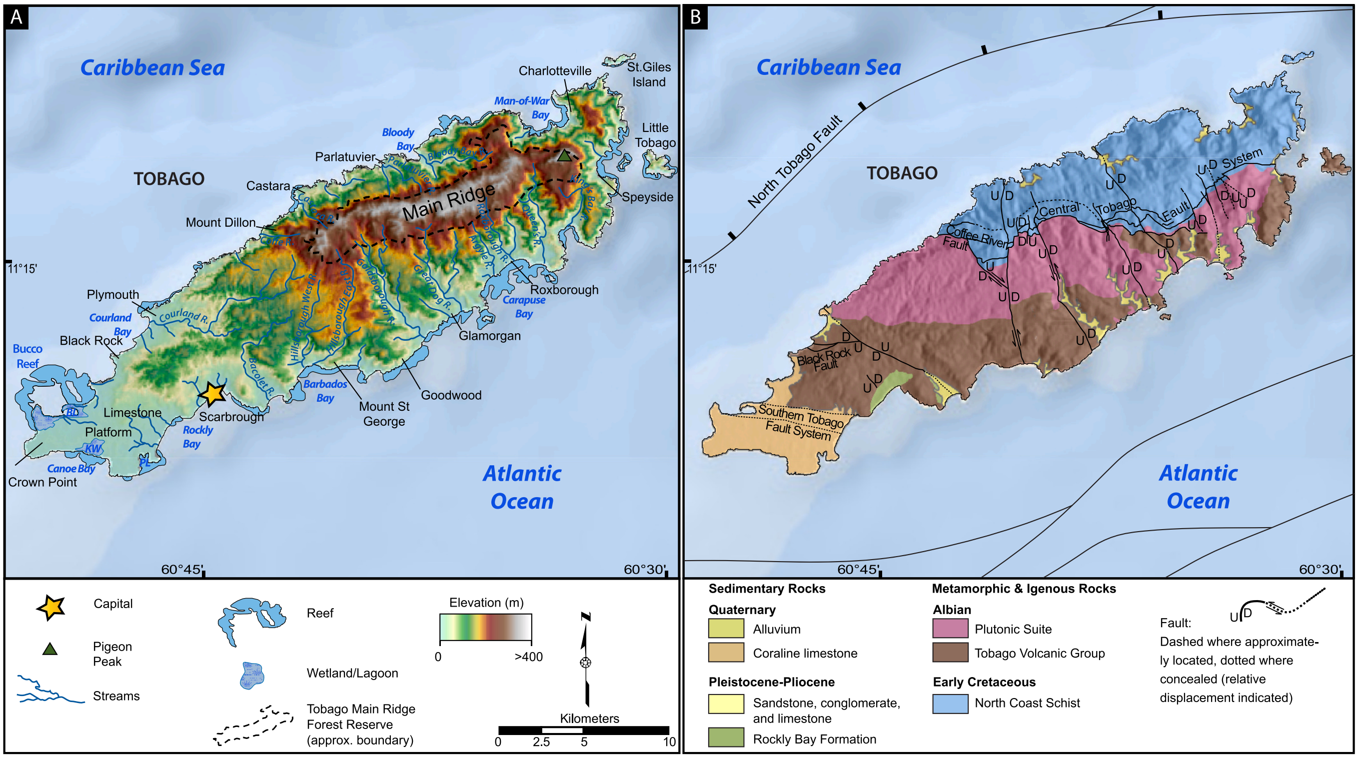


Fig. 4. a) Map showing the on-land topography and geology and offshore bathymetry in and around Tobago. Modified from Arkle et al. (2017b).

producing a single unified interpretation thus requires making choices. We next review and discuss some of the key issues related to this exercise and we outline the choices that we make below.

2.1.1. Review of Caribbean plate tectonics

An understanding of the Caribbean-South American (Ca-SA) plate tectonic framework (Fig. 1) is the foundation needed to recreate an accurate paleogeographic history for the SE Caribbean. The long history of attempts made to reconstruct the plate tectonic history of the Caribbean (Ca) and its surrounding plates, the North American (NA), South American (SA), Cocos (Co) and Nazca (Na) plates, has fortunately recently reached an unprecedented level of certainty. This certainty is due to clear imaging of the historic archive of subducted oceanic plates ("slabs") in the deep mantle beneath Ca and, in addition, due to the advent of a robust new technique for slab unfolding (van Benthem, 2013; Allen et al., 2019; Braszus et al., 2021; Chen et al., 2021; Chen et al., 2024).

Prior to this breakthrough, plate reconstructions were fraught with controversy and contention, mainly because the principal oceanic geological features that are classically used to determine plate motion – transform fault azimuths and isochrons along spreading ridges – are not present along most of the margins of the Caribbean plate (i.e., along the boundaries with neighboring plates). For example, the active transform fault was only recently identified in Trinidad, and it is an on-land, and continental, not oceanic transform (Weber et al., 2001a). We next briefly discuss two distinct generations of plate motion models as context for the development and construction of our paleogeographic reconstructions.

The Caribbean plate (Fig. 1) is a mosaic of several different types and ages of oceanic lithospheres and includes several different arc lithospheres as well. Being surprisingly unlike "normal" seafloor created at spreading ridges, most of the Caribbean plate's oceanic lithosphere does not contain magnetic stripes, i.e., isochrons (Bouysse, 1988). Most of this isochron-free lithosphere is also anomalously thick and is thus generally thought to have formed as an oceanic plateau (i.e., a large igneous province, or LIP) somewhere in the Pacific Ocean basin. Near consensus suggests that this LIP was then subsequently "rafted" across some kind of trench barrier into a gap between the Americas that developed during the break-up of the supercontinent Pangaea (e.g., Wilson, 1966a; Burke, 1988). Other attached lithospheric domains that make up today's Caribbean plate, most notably the Grenada Basin, are smaller and younger ocean sub-basins that formed behind active (Lesser Antilles) and ancient (Aves) volcanic arcs, at the modern and older, respectively, leading eastern edges of Ca (Bouysse, 1988; Allen et al., 2019).

Only the Cayman "trough", a short (∼100 km) spreading center in the northern Caribbean, preserves isochrons from which Ca plate motion (i.e., Ca-NA) rates (15–20 mm/yr) can be classically determined (Rosencrantz et al., 1988; Leroy et al., 2000; Van Avendonk et al., 2017) (Fig. 1). The oldest Cayman isochrons are Late Eocene in age. This limits how far back in time (45–50 Ma) we can track Ca motion using the traditional geological isochron-transform (rate-direction) technique. Spreading on the Cayman ridge feeds into N65°*E*-N85°E sliding on the large Swan Island, Motagua, Polochic, Oriente, Walton, and Septentrional transform faults from which the history of direction and rate of Eocene-Recent Ca-NA plate motion, and, or that of the Gonave microplate, can be determined (Rosencrantz and Mann, 1991; Leroy et al., 2000). All generation 1 Caribbean plate motion models use the Cayman data as an important, but somewhat limited, constraint. First-generation Ca-NA and Ca-SA plate motion and geometry studies then depart from one another on the issue of determining the relative distance that the Ca plate has traveled. Did it evolve largely in situ between the two American plates (Speed, 1985; James, 2009; Meschede and Frisch, 1998)? Or, has it traveled ≥1000 km from today's Pacific ocean basin into its current location in the gap between North and South America (Speed, 1985; Pindell et al., 1998)? Early on, key lines of evidence seemed to point most strongly to a far-traveled origin and long-distance transit.

First-generation Ca-SA plate motion models fall broadly into three groups based on the amount of prescribed boundary-normal convergence in the plate boundary zone (pbz): 1) collisional Ca-SA pbz (Speed, 1985), 2) transform pbz (Robertson and Burke, 1989; Burke, 1988), or a 3) hybrid with components of both convergent and transform motion (Pindell et al., 1998). Recent deep lithospheric imaging, modeling, and thermochronology suggests a fourth alternative model, the STEP (subduction-transform edge propagator) model (Govers and Wortel, 2005; Arkle et al., 2021; Alvarez et al., 2021). Accordingly, surface transform motion follows behind a migrating wave of surface contractile deformation as a deep, lithospheric STEP fault propagates eastward and progressively tears off the oceanic edge of rifted and stretched continental northern South America (Mann, 1999; Govers and Wortel, 2005; Clark et al., 2008; van Benthem, 2013). An understanding of Trinidad-Tobago neotectonics obtained using GPS (GNSS) and InSAR (Weber et al., 2001a, 2015, 2020; Higgins et al., 2021) provides key critical "time zero" (i.e., current) information regarding our understanding of the plate-scale tectonics of the Ca-SA pbz. Accordingly, today in Trinidad and Tobago, the pbz experiences little to no plate-boundary-normal relative plate convergence and experiences nearly pure transform tectonics.

Subsurface subducted slabs of oceanic material beneath the Caribbean plate's trench boundaries, i.e., those along the eastern and western edges of the Caribbean plate, in principle, provide a near complete archive of the history of Ca plate motion. New slab unfolding results led to a new generation (Generation 2) of Caribbean plate motion models by providing a leap forward in our understanding. They allow Ca motion to be tracked much further back in time (back to the Late Cretaceous) than was previously possible in Generation 1 models, and with a high degree of certainty (Allen et al., 2019; Braszus et al., 2021; Chen et al., 2024). This advance resolves ambiguities in interpreting the plate tectonics of the proto-Caribbean oceanic lithosphere that was present in the inter-American gap *before* the Caribbean plate entered. These new reconstructions demonstrate that there probably had never been an independent proto-Caribbean plate (which had been moved ad hoc in some earlier models). Rather, only oceanic lithosphere formed during Jurassic rifting attached to the NA and SA plates existed in the gap. We build our paleogeographic model and time slices using the GPS, InSAR, and high-resolution Generation 2 tomography and slab unfolding plate tectonic constraints as our plate tectonic foundation.

First clearly recognized by Speed (1985), there is now a substantial body of literature indicating that NNW-to-SSE thrusting of the Jurassic-Paleogene South American passive margin rocks and associated foreland basin loading is Paleogene-Neogene in age and gets younger from west to east in the Ca-SA plate boundary zone (e.g., Pindell and Kennan, 2009). This suite of tectonic process converted the paleogeography of the South American continental borderland from marine to terrestrial. This conversion is central to geogenomics and the study of extant terrestrial organisms. Ascribing a cause to this eastward propagating "wave" of contractile deformation and associated foreland basin loading and filling remains contentious. Was it due to an early (pre-15 Ma) phase of oblique plate-scale Ca-SA convergence as advocated by Speed (1985) and Pindell et al. (1998)? Or, was it due to a pre-STEP-related flexural down-warping and an advancing wave of associated contractile deformation that passed from west to east as the Caribbean plate and deep STEP tear propagated eastward (Govers and Wortel, 2005; Clark et al., 2008; van Benthem, 2013)? Based largely on the recent slab unfolding results discussed above (Braszus et al., 2021; Chen et al., 2021; Chen et al., 2024), and for the Oligocene to Recent time interval that we study, we ascribe to the pure transform kinematic model of Caribbean-South American plate motion, with no north-south relative plate convergence, but rather first contraction and loading, followed by deep STEP tearing.

2.1.2. Review of geology and geomorphology

Given our current understanding of the plate tectonics and the plate kinematic framework, geology and geomorphology next provided additional and more granular constraints on paleogeography. Below, we briefly discuss some of the key geological and geomorphic elements incorporated into our paleogeographic analysis and models. Fig. 2, an annotated regional digital elevation and bathymetry map, references the geography of the geological features discussed below.

Trinidad sits on the eastern margin of the Eastern Venezuela Petroleum System, a globally significant and prolific oil-producing region (see e.g., Erlich and Barrett, 1992). Due to the large number of high-quality petroleum exploration and production studies that have been done over the past century in Trinidad and Venezuela, a great deal is known about its Cretaceous-Neogene sedimentary geology (see e.g. the summary by Summa et al., 2003). For creating paleogeographic reconstructions, sedimentary features such as conglomerates, unconformities, facies and biofacies, and mapped sequence boundaries, together with the synthesized record of eustatic global sea-level, provide key constraints. Conglomerates allow the analyst to decipher the “where and when” of past surface uplift. Unconformities allow one to determine where and when periods of erosion took place. Facies refers to an assemblage of rocks with distinct and particular characteristics. Continental facies, for example, those containing coal beds, record the growth and accumulation of terrestrial plant material in coastal dry-land-edge settings. Additionally, the fossil record of benthic organisms, notably foraminifers but also other groups, permit determination of paleobathymetry, and other environmental features such as salinity and turbidity. For example, fossil pollen, algae, and organic palynofacies are particularly useful for delineating transitions from marine to non-marine conditions (Batten, 1996). Global sea-level curves and the mapping of sedimentary sequence boundaries allow reconstruction of the ancient shorelines. We extracted such critical geological information from Kugler's Treatise on the Geology of Trinidad (Kugler, 2001) together with his geological map of Trinidad (Kugler, 1959), from significant revisions to this map by Saunders et al. (1997) and de Verteuil et al. (2005), and from the published literature produced by the many research groups working in this region.

With a focus on its petroleum geology and its related sedimentary rocks, Trinidad and Tobago's igneous and metamorphic geology have, until recently, received significantly less attention than their sedimentary counterpart (Figs. 3, 4). Exceptions include the excellent mapping and geochronology analyses done by Professor Arthur Snoke and colleagues in Tobago (e.g., Frost and Snoke, 1988; Cerveny and Snoke, 1993; Snoke et al., 2001), which built on the early work of Maxwell (1948). Similarly, Trinidad's Northern Range's metamorphic geology received much less attention than that of the oil-rich rocks of central and south Trinidad, with notable exceptions that include early contributions from Barr (1963), Potter (1968, 1973), and Algar (1993). In this review, we rely heavily on the Northern Range metamorphic mapping and analyses of Weber and associates (Weber et al., 2001b; de Verteuil et al., 2005; Arkle et al., 2021; Genarro et al., 2022). These works provide hard, new constraints on both Northern Range tectonics and paleogeography. Yet limitations still exist. For example, thermochronology is a robust technique that has been successfully applied to determine the history of cooling and exhumation in Trinidad and Tobago's crystalline rocks (Cerveny and Snoke, 1993; Weber et al., 2001b; Arkle et al., 2014, 2021). But thermochronology gives information on rock exhumation, the difference between rock and surface uplift (England and Molnar, 1990), not on surface uplift, which is the desired quantity in paleogeography. Surface uplift must therefore be inferred using the thermochronology results in conjunction with additional geological constraints, such as the presence, age, sedimentology (provenance, paleocurrents), and clast composition of conglomerates.

Similarly, with such a huge spotlight on Trinidad's subsurface sedimentary and petroleum geology, until recently, the geomorphology of Trinidad and Tobago had received only minimal attention (Figs. 3, 4). Geomorphology informs paleogeography by constraining the modern time slice and by giving the modern sense (i.e., signs, + or -, up or down) of surface uplift and subsidence, and also the rates of surface processes. Geomorphic constraints are thus critical for informing our understand of extant faunal distributions. As an example, and reviewed in more detail below, understanding Trinidad's and Tobago's geomorphology provides the basic context for understanding the modern distribution and genetics in guppies (*Poecilia reticulata*), tree frogs (*Phytotriades auratus) (Hylidae)*, and their host bromeliads (*G. erectiflora*).

Ritter and Weber (2007) and Weber (2005), in an initial attempt to determine whether Trinidad's neotectonics have left a signal in the landscape, began to investigate, recognize, and interpret, patterns in Trinidad's mega-geomorphology. Trinidad has a submergent northwestern coastline and additional indications of sinking in the west, and an emergent northeastern coastline with exposed and elevated marine terraces that indicate recent surface uplift in the northeastern Northern Range (Fig. 3). Similarly in Tobago, Moonan et al. (2017) used subsurface industry data to begin mapping and interpreting Tobago's mega- and paleo-geomorphology (Fig. 4). Recent work by Arkle and colleagues (Arkle et al., 2017a, 2017b, 2021) has filled in many but not all knowledge gaps. Arkle et al. (2017a) used catchment-wide ^{10}Be to measure modern erosion rates in Trinidad's Northern Range. They observed slow erosion rates in the west and high rates in the east, which supported that western Trinidad sinks while eastern Trinidad rises. Arkle et al. (2021) then related this pattern to a deep lithospheric cause, the passing STEP. Finally, Arkle et al. (2017b) provides a comprehensive and fairly up-to-date summary of Trinidad and Tobago's geomorphology.

There are now several robust studies that have applied apatite and zircon helium (U—Th)/He (AHe and ZHe, respectively) and apatite and zircon fission-track (AFT and ZFT, respectively) thermochronometers to evaluate bedrock cooling and exhumation histories and rates in both Trinidad and Tobago (Cerveny and Snoke, 1993; Weber et al., 2001b; Arkle et al., 2014, 2021). Thermochronology exploits the principle that retention of radiogenic decay (daughter) products – fission tracks and helium – in minerals that move upward and experience a decrease in temperature as they “daylight” at Earth's surface are highly temperature sensitive. The retention of these daughters for each specific mineral species occurs through specific ranges of “blocking” temperatures. Additional details can be found in Dodson (1973), Green et al. (1986), Brandon et al. (1998), Farley (2000), Reiners (2005), and Flowers et al. (2009). Because exhumation is the difference between rock uplift and surface uplift, thermochronology alone cannot tell us what the paleotopography looked like, nor is it alone diagnostic of which process (e.g., erosion versus tectonic extension) caused the cooling, exhumation, and rock exposure. Thermochronology data must therefore be used together with additional geological constraints to infer the vertical (paleogeographic) component of topography.

2.2. Paleogeography methods and issues

Paleogeography is the disposition of land and water in times past, its topography and bathymetry, and its gross climate and oceanography. Paleogeography attempts to establish what Earth's surface looked like at specified times in the past and is largely determined by the geological history of an area. Analysts must integrate the dynamic interplay between tectonics and climate. While tectonic movement along plate boundaries and their subsidiary faults raises, lowers, and deforms Earth's crust, climate wears down elevated regions, sedimentary deposits build new land, and climate largely controls regional sea level fluctuations through time.

For this study, we developed a set of new semi-quantitative 2D paleogeographic maps using ESRI's ArcGIS Pro v. 3.3 software. Our paleogeographic maps consider a smaller region and a shorter and more recent time span than many previously published reconstructions do. Those generally more broadly cover the entire Caribbean basin and surroundings, and a Jurassic to present time interval (e.g. Pindell et al., 1998; Mann, 1999; Müller et al., 1999; Escalona et al., 2021a; Escalona et al., 2021; Watson and Escalona, 2021). Our narrower windows of time and space are needed for relating tectonics to geogenomics and to the extant biology; these narrow widows have the advantage of allowing us to use more precise plate kinematic constraints and more robust local geological datasets that those used in the region-wide reconstructions. For our new maps to be best appreciated in the context of biogeography and geogenomics, we introduce readers to key concepts and constraints, provide a general overview of our workflow, and provide citations to the published sources used to derive these maps. Notably, these maps are a snapshot of our current knowledge and can evolve as studies in this region continue.

The paleogeography of the Trinidad and Tobago region that we cover fits into a broader context of the tectonic evolution of South America, the Caribbean, and the Atlantic Ocean (Fig. 1). Until about 200 Ma ago, Pangea, a supercontinent comprising North and South America, Africa, Eurasia and other continents blocked passage of the Caribbean plate through an inter-American gap (e.g., Wilson, 1966a, 1966b). The break-up of Pangea, the opening of the north and south Atlantic, and the plate tectonic evolution of the Caribbean, occurred over time scales of tens to hundreds of millions of years, and together form the broadest geological context in which to set Trinidad and Tobago paleogeography. In addition, such deep-time tectonic events are important in the present context because many have left fundamental lithospheric-scale discontinuities that impact the younger paleogeography. Notably, Jurassic rifting between the Americas resulted in relatively thinned, transitional continental crust fringing the Guiana shield of South America (e.g., Speed, 1985; Alvarez et al., 2021), which continues to be a fundamental element in the style and kinematics of lithospheric-scale deformation in this region.

The elements that went into creating our paleogeographic restorations include data and interpretations from across a broad range of scales, from deep lithospheric tomography, to thin-section petrography, but mainly those from intermediate scales, including stratigraphic, geochemical, geophysical, and geochronological data. Results from computational modeling also influenced our mapping (e.g., Govers and Wortel, 2005). In compiling such maps, the decisions we made in choosing among geologic models, were based on our syntheses of published data, and are justified in the Paleogeographic Map Results section (Section 2.3 below). There, we provide a general overview of their development, introduce readers to key concepts and constraints, and provide citations to our sources.

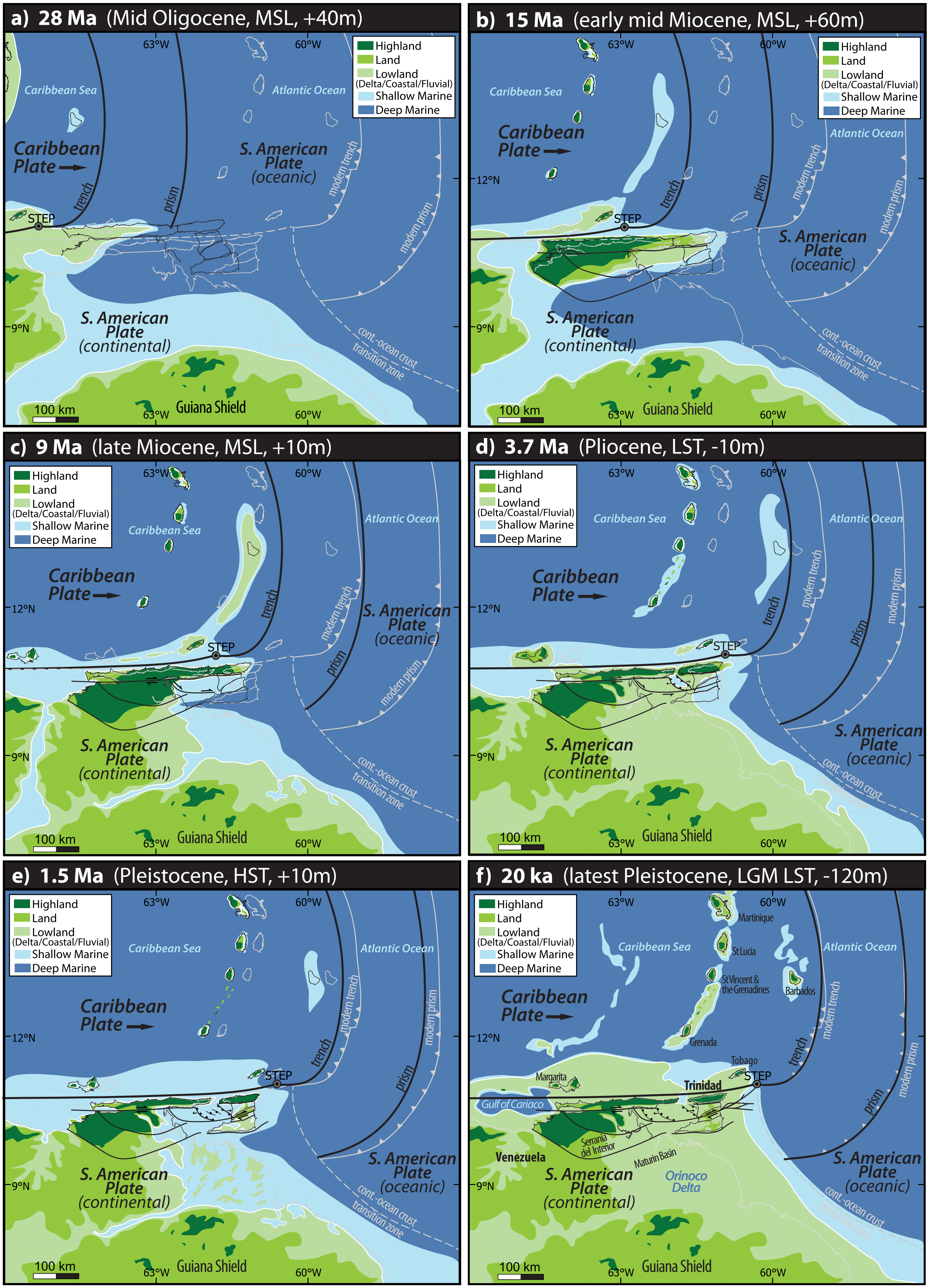
Each of our paleogeographic maps covers a specified and relatively limited interval of time. Our time slices span from the latest Oligocene to the Pleistocene. The Guiana shield was used as the stationary reference, given the relatively minor latitudinal and longitudinal movement of this Precambrian cratonic interior during the time periods mapped (e.g., Escalona and Mann, 2011). Following today's plate kinematics backward in time, we assumed pure *E*-directed transform Caribbean-South American plate movement at 20 km/m.yr. (e.g., Weber et al., 2001a, 2015, 2020) from the latest Oligocene-Recent relative to the Guiana shield, and also propagate STEP tearing (e.g., Govers and Wortel, 2005; Clark et al., 2008) along the rifted-oceanic subsurface edge of continental South America at this same rate.

The boundaries of rigid crustal blocks and deformable crustal zones were defined generally along major faults/fault zones or, where lacking, major structural transitions. Assumed rigid crustal blocks to the north and west of the CA-SA boundary (e.g., the Tobago and Araya blocks) were translated at the same rate and direction as that of the rigid Caribbean plate and block rotations were not accounted for due to the small map scale. South of the Caribbean plate, instead of translating rigid crustal blocks we deformed a broad zone in homogeneous simple shear by establishing and distorting a Cartesian grid (see Fig. 5). Major blocks and zone boundaries in Venezuela include the edges of the Maturin and Guarico sub-basins, the Serrania del Interior deformation front, and the Urica fault. In Trinidad the South Coast fault zone as defined by Weber et al. (2020) is taken as the southern edge of the deforming zone which extends north to the Tobago block.

Our method thus involved diachronous passage of: 1) a ~ 200 km wide zone of early dextral shear that produced the magnitude and timing of SSE-directed shortening and thin-skinned contractile tectonics observed in the foreland fold-thrust belt, followed by: 2) a narrower, 30–50 km wide, zone of dextral shearing, deep STEP tear fault passage, and exhumation. We propagated all elements at a rate of 20 km/my eastward relative to our Guiana shield reference frame. This method provides a paleogeographic solution that in a qualitative sense jointly best-fits the rock record (e.g., facies, conglomerates, benthic foraminifera paleobathymetry, etc.), structural geology, geochronology and thermochronology, and the plate kinematic constraints. Shortening percentages in the fold-thrust belt were determined from published balanced cross-sections, seismic sections, and tomography. For example, cross-section balancing in eastern Venezuela by Duerto and McClay (2011) suggests shortening of ~20 % across the fold-thrust belt. That of Lingrey (2007) in Trinidad gives ~35 % shortening, and that of Parra et al. (2011) in central Venezulea's Monagas belt gives values ranging from ~37–49 %. The distributed dextral shear we applied resulted in shortening of this approximate magnitude along a finite azimuth of 334° (N26W). Our broad and narrow zones of shearing also produced diachronous and regional E-W extension that initiates in the latest Miocene west of Trinidad and moves through to the present in the Gulf of Paria and in the offshore Columbus Basin. Some of the observed extension however could be related to STEP tearing and deep asthenospheric flow rather than the lithospheric shearing we apply.

Differential tectonic uplift and subsidence in the region makes it extremely difficult to locally and empirically determine the absolute magnitude of local sea-level fluctuations and the timing of when the islands were connected and disconnected to mainland South America. We decouple absolute sea level from vertical land motion by assuming a direct connection with global eustatic sea-level change such that the Caribbean Sea was ~120 m lower than present during the Late Pleistocene (20 ka) global last glacial maximum (LGM) (e.g. Muhs et al., 2011; Rohling et al., 2022). Ultimately land surfaces were placed in context of relative regional sea level using the determinations of the Rohling et al. (2022) Main Model, combined with paleobathymetry determined from lithofacies and biofacies. From the Oligocene to the late Miocene, absolute sea level was higher than present and the amplitude of eustatic sea level change between highstands and lowstands was <30 m (Rohling et al., 2022). Our first three maps use mean eustatic sea levels for this time interval (Fig. 5a-c), during which the Columbus Channel was deep and connections between emergent northern Trinidad with the mainland to the south were unlikely. During the Pliocene to Recent the amplitude of eustatic cycles increased to 40–120 m. During this time interval, sedimentation kept pace with subsidence in the Gulf of Paria and the Columbus Channel foredeep progressively filled as the Orinoco delta arrived into this area (Chen et al., 2016, 2017). During Plio-Pleistocene lowstands and as recently as the Holocene, Trinidad and much of the Gulf of Paria was thus likely repeatedly emergent and in subaerial communication with South America across the Columbus Channel. Tobago was also likely connected to the mainland multiple times during Pleistocene lowstands (e.g. Boomert, 2000).

The paleotopography, including paleobathymetry, of uplifted rigid crustal blocks and that in our deforming zones was derived by integrating multiple datasets to capture a holistic picture of competing processes that build up and wear topography including: vertical slip (i.e., dip slip) on major faults; surface uplift, subsidence, exhumation, and erosion. Data that we integrate include mainly thermochronology, diagnostic sedimentary rock facies (e.g., conglomerates, coals, etc.) and biofacies, unconformities, geomorphology, and several additional data sources, as cited in the following section. Sedimentary basins require back-stripping, sediment decompaction, and (growth) fault restoration



(caption on next page)

Fig. 5. Original topographic map series showing the paleogeographic evolution of the Trinidad-Tobago and eastern Venezuela study area at approximately: 28 Ma (Oligocene); 15 Ma (early middle Miocene); 9 Ma (late Miocene); 3.7 Ma (Pliocene); 1.5 Ma (Pleistocene); and 20ka (latest Pleistocene, last glacial maximum). Sea levels indicated relative to modern. MSL = mean sea level; LST = lowstand sea level; HST = highstand sea level. See text for explanation of methods and constraints used.

to rigorously determine subsidence rates. The basin subsidence we determined and used on our maps, however, was estimated only semi-quantitatively. We categorize land surface elevation qualitatively in each time slice on a scale ranging from lowland, to land, to highland (mountains). The paleobathymetry that our maps depict was inferred predominantly from: biofacies (e.g. Kugler, 2001; Sanchez-Zambrano, 2010), sedimentary facies, qualitatively back-stripping sedimentary fill inferred from marine seismic reflection profiles and time-structure maps (e.g., Wenxiu and Escalona, 2011; Castillo and Mann, 2021), and lithostratigraphy datasets (e.g., Chen et al., 2018; Martinius et al., 2013). Our maps show two gross categories of depths: shallow (likely shelfal, <200 m) and deep marine (likely bathyal, >200 to +1000 m).

2.3. *Paleogeographic map results*

After considering the key and relevant aspects of both the geology (above) and the biology (below), the paleogeographic time slices that we choose to develop, and that we present below are: 1) Present (Figs. 2–4), 2) Latest Pleistocene last glacial maximum (LGM) (20 ka), 3) Early Pleistocene (1.5 Ma), 4) Early Pliocene (3.7 Ma), and 5) Late Miocene (9 Ma), 6) Early middle Miocene (15 Ma), and 7) Oligocene (28 Ma) (Fig. 5a-f).

A key component of these maps, which differs markedly from most past reconstructions, is that we interpret the protoliths of the Araya-Paria Peninsula and the Northern Range metamorphic rocks as being parautochthonous, having moved horizontally only about 100 km east and 30 km south from their original pre-deformational Mesozoic depositional sites. This contrasts with most of the previous restorations that derive these rocks 250 km to >400 km from the west (e.g. Escalona et al., 2021a, Escalona et al., 2021; Pindell and Kennan, 2007; also see additional references in Audemard, 2009). These previous reconstructions all assumed that large displacements were required the on the El Pilar fault system to the south of these ranges. Displacement along the El Pilar is however likely <100 km (e.g., Audemard, 2009). The reduced lateral offset between Paria Peninsula – Northern Range and the Eastern Venezuela Basin – Trinidad greatly simplifies biogeographic modeling between the Northern Range, eastern Venezuela, and southern Trinidad.

2.3.1. *Present*

Figs. 3 and 4 show the present-day topography and geology of Trinidad and Tobago. We take these configurations as partial starting points for our paleogeographic reconstructions. The modern picture of relative Caribbean-South American plate motion and its result in the deep lithosphere have increasingly become well-defined (e.g., Weber et al., 2001a, 2020; van Benthem, 2013; Allen et al., 2019; Braszus et al., 2021; Chen et al., 2021; Chen et al., 2024; Bezada et al., 2010; Levander et al., 2014). GPS, InSAR, and earlier GPS-to-triangulation analyses all consistently indicate eastward Ca plate motion relative to SA at 20 mm/yr (Weber et al., 2001a, 2015, 2020; Pérez et al., 2001; Higgins et al., 2021). A deep STEP tear is clearly imaged today beneath Trinidad (Clark et al., 2008). We assume and use today's rates of 20 km/my.yr. as constant and we propagate plate motion, bow wave contraction, and STEP tearing westward back in time into our earlier paleogeographic time slices.

Today, the Guiana Current is the principal ocean current that impacts Trinidad and Tobago's coastal ecology and morphology (Van Andel, 1967). The Guiana Current flows northward along South America and then bifurcates with a branch flowing to the west through the Columbus Channel along southern Trinidad, and a second branch flowing to the north along the coastlines of eastern Trinidad and SE Tobago (Van Andel, 1967) (Fig. 2). These currents carry vast quantities of nutrients, suspended sediment, and terrestrial plant detritus from the Orinoco and Amazon river deltas into the study region. This critically impacts coastal sedimentation and erosion, and, in large part, inhibits reef formation around much of Trinidad (Van Andel, 1967; Laydoo, 1991; Lapointe et al., 2010). Boos (1984) speculated on a “two source” biogeographic pattern in Trinidad that correlates with the splitting of the Guiana Current at Trinidad's southeastern coast. One branch of this current flows west into the Gulf of Paria; the other flows north along Trinidad's east coast and on to Tobago (e.g., Van Andel, 1967) (Fig. 2). Many cases exist in which oceanographic effects are well-known and well-documented to affect the distribution of terrestrial organisms. The water in the Guiana Current is loaded with sediment and debris from the Orinoco delta and might have also rafted organisms into Trinidad, possibly in two arcs. This configuration of the Guiana Current, however, has existed during the present inter-glacial highstand for only the last approximately 9 ka, and perhaps for short (~10 ka) periods during similar inter-glacials during the last 800 ka. For the majority of the late Pleistocene, during falling and lowstand glacial periods, the Gulf of Paria together with a broad swath of the continental shelf off eastern Trinidad would have been emergent coastal plain and wetlands. At such times the Guiana Current would flow primarily north off Trinidad's widened lowstand east coast, with Boos' western “arc” absent or greatly diminished. Then, rather than rafting by marine currents, the species discussed by Boos (1984) could have achieved a similar distribution by multi-generational dispersal along with their dynamic migrating habitats. Each mechanism predicts a distinctly different genetic pattern.

To the north of continental South America and Trinidad, Tobago is emergent as a structurally and topographically high-standing horst block within a series of regional horst and graben blocks on the stretched and extended southern edge of the Caribbean plate (Fig. 4) (Robertson and Burke, 1989; Snoke et al., 2001). Tobago's Mesozoic oceanic forearc and arc rocks form the easternmost subaerial exposure of a series of allochthonous terranes that were accreted between the Caribbean and South American plates. Today, Tobago rises to 572 m above mean sea level. The uplifted footwall of the Tobago horst block creates the Main Ridge mountains (Snoke et al., 2001). The offshore North Tobago fault dips steeply north (~55–80°), cuts the seafloor and so is demonstrably neotectonically active, and forms the northern boundary of the Tobago horst block. Recent earthquake activity along the sub-Tobago terrane boundary and coeval northward slip on a low angle (28°), north-dipping, normal fault between Trinidad and Tobago marks the reactivation and inversion of the Ca-SA oceanic/arc-continental suture (Weber et al., 2015).

2.3.2. *Quaternary: Late Pleistocene (20 ka) and Middle Pleistocene (1.5 Ma)*

Despite the modest horizontal rate of plate motion and a sustained near-equatorial position for much of the region's geologic history, significant changes in the nature and style of vertical tectonism, climatic shifts, and associated sea-level fluctuations have shaped the paleogeography of the SE Caribbean region throughout the Quaternary (e.g., Arkle et al., 2017b; Speed and Cheng, 2004, 2021). From the Pleistocene to the present, tectonism around the northeastern margin of continental South America underwent significant changes (Babb and Mann, 1999). However, it is still incompletely understood how this transform fault system has evolved through the Quaternary into its present configuration.

During this time, the Caribbean-South American plate boundary transform fault likely stepped southward, initially from along faults near the Serranía del Litoral and in Trinidad's North Coast marine area, across the Caroni Fault and perhaps the El Pilar Fault extension into Trinidad, finally to the Central Range Fault, where the majority of dextral shear, ~12–15 mm/yr, is presently accommodated (Weber et al., 2001a, 2020; Higgins et al., 2021). The Central Range Fault strikes ~N72°E through Trinidad and continues offshore to both the east and west. To the east, it connects through the Scorpion Fault offshore in the Angostura oil field, and then ultimately somehow still-to-be-determined to thrust faults and folds in the Barbados accretionary prism at the eastern leading edge of the Caribbean plate (e.g., Soto et al., 2007). To the west, it joins the Warm Springs Fault immediate offshore, then steps across a series of normal faults in the active Gulf of Paria pull-apart basin to merge ultimately with the El Pilar Fault in Venezuela (Van Andel and Sachs, 1964; Flinch et al., 1999; Higgins et al., 2021). Given this configuration, the southern half of Trinidad is currently on and moving with the South American plate, while land north of the Central Range fault, including northern Trinidad and Tobago, travels with the (relatively) east-moving Caribbean plate.

We assume that current plate motion rates (~20 mm/yr eastward) apply through the Quaternary, therefore the latitudinal position of Trinidad and Tobago have both remained in relatively close proximity to mainland South America. In eastern Venezuela, as seen today, the Serranía del Interior and the eastern Coastal Cordillera were topographically high, whereas the Maturin Basin likely remained topographically low due to earlier subsidence of this structural (loaded, foreland) basin (Duerto and McClay, 2011; Parra et al., 2011; Martinius et al., 2013). In southern Trinidad, we infer that Quaternary contractile tectonism is a result of the passing of the pre-STEP bow wave which is the cause of Quaternary thrusting and folding and positive topographic development in the Southern Range (e.g., Trinity Hills) (Hippolyte and Mann, 2021).

Both Trinidad and Tobago are positioned on a relatively shallow continental shelf (Figs. 2, 3, 4). Tobago and the northern SA mainland and north coast offshore were alternately emergent/exposed and likely connected multiple times (e.g., Fig. 5e, f). This is based on the shallow offshore structure (Robertson and Burke, 1989; Lugo and Audemard, 2021; Punnette et al., 2021) and high sedimentation during this time period in the north coast marine area (Punnette et al., 2021), determinations of localized surface uplift and erosion of the highlands (Arkle et al., 2017a, 2021) and estimates of magnitudes of sea level (Rohling et al., 2022). The overall slow rates and shallow magnitudes of Quaternary exhumation in the coastal Northern Range-Paria metamorphic belt (Arkle et al., 2021) are consistent with low rates of surface erosion measured over millennial-timescales (Arkle et al., 2017a), and are associated with subsidence (particularly in western Trinidad) into the Gulf of Paria pull-apart basin (Babb and Mann, 1999; Flinch et al., 1999).

The time slice shown in Fig. 5f, captures a scenario of maximum land exposed during the LGM (sea levels of −120 m bmsl) using the highest estimates of surface uplift and sedimentation. In this case, connections between SA, Trinidad, and Tobago may have been ubiquitous spatially, yet gradually imposed over ~100 ka, as global sea level fluctuations alone (not considering tectonism and sediment supply to the basin) are asymmetric on the fall toward full glaciation and relatively rapid on the rise to inter glacial ice melt (Rohling et al., 2022). Even during the LGM, an area west of Tobago remained inundated (Fig. 5f). This is because the Tobago Basin is under-filled and is an area of general deeper water. This may have biogeographic implications for migration from Tobago to Grenada. Note that during the LGM lowstand Grenada was, however, nor far from the exposed shelf off Venezuela and could perhaps have received migrations from there. During late Pleistocene lowstands Margarita was likely connected to the continent, but to the west the Gulf of Cariaco pull-apart remained inundated.

The Pleistocene sediment record north of Trinidad and west of Tobago, the North Coast Marine Area (NCMA), is well characterized by Punnette et al. (2021). It consists of mostly shallow (shelfal) marine muds with carbonate lime mudstone intervals, and two prominent clean sand units near the top of the section. The five carbonate horizons are thin (1–3 m) and occur down to the base of the 1800 m thick Pleistocene section, separated by intervals of clay. On seismic reflection profiles they are laterally continuous and are thus used as correlation markers among wells 10's of km apart. These limestone horizons represent highstand deposits of lime mud deposited on the NCMA shelf. Punnette et al. (2021) report middle to deep neritic (mid to outer shelf) paleobathymetry and environmental conditions for this entire ~2 Myr Pleistocene interval based on foraminiferal assemblages. At the very top of the interval, there is a thick, compositionally and texturally mature sand sheet in which cross-cutting fluvial meander channels can be seen in 3D reflection seismic images. This unit was deposited during the LGM, indicating subaerial emergence, and it is currently being transgressed by thin clays in about 150 m of water depth. There is a second ~70 m thick sand sheet about 150 m lower in the section which is similarly mature and continuous. Punnette et al. (2021) date this lower sand unit using nannofossils to the base of the *Emiliania huxleyi* zone and estimate that it was deposited during marine oxygen isotope stage 6, that is, during the penultimate glacial maximum lowstand. Other than these two very young sheet sands, there are no indications of continental shelf exposure during the Pleistocene on the shelf off the north coast of Trinidad.

Tobago's Pleistocene limestone platform includes the modern Buccoo Reef as well as the ~125 ka Pleistocene reef cover termed the Booby Point Formation and forms the southern lowlands of Tobago. This Quaternary fossil reef complex likely formed during the last several interglacials over the underlying oceanic arc and forearc bedrock of Tobago in the structural position of a structurally low, down-dropped half-graben (Wadge and Hudson, 1986; Snoke et al., 2001; Donovan and Jackson, 2010). Subsequent uplift and tilting have exposed the reef platform to heights of up to ~10 m amsl along the SSW coast and up to ~30 m amsl in NE Tobago (Donovan and Jackson, 2010).

Fig. 5f shows that in the late Pleistocene LGM (20 ka) a broad expanse of low-gradient continental shelf was exposed in what today lies offshore east of Trinidad. Soto et al. (2007) and others have noted and studied the presence of large abandoned and buried river paleo-channels just below the seafloor that are incised into the underlying Pliocene to Pleistocene strata. These must have developed during Pleistocene lowstand events and indicate that large, now-extinct river systems once flowed in this area. We hypothesize that the exposed Pleistocene shelf was drained by a river system that was able to physically connect NE Trinidad (Oropouche drainage system) to Suriname-Guyana and allowed for a Quaternary biological connection and dispersal of freshwater guppies and likely other fish species from the mainland into northeastern Trinidad.

2.3.3. Early Pliocene (3.7 Ma)

By the latest Miocene to Pliocene, the Caribbean-South American transform plate boundary began to step southward as the current phase of transform plate motion propagated through the region following the passing of the pre-STEP contractile deformation (Algar and Pindell, 1993; Pindell et al., 1998; Flinch et al., 1999; Weber et al., 2001a). Transform motion during this time was likely accommodated on the El Pilar fault south of the Paria Peninsula and then began to propagate eastward and shift southward possibly from along the El Pilar extension and Caroni Faults in Trinidad to the Central Range, Los Bajos, and South Coast fault zones in Trinidad (Fig. 2) (Flinch et al., 1999; Babb and Mann, 1999; Weber et al., 2020). Deformation, associated with the advance and passage of the deep STEP tear would have caused flexure loading and imbricate thrusting of the South American margin that progressed and migrated eastward (Fig. 5). This eastward progression may coincide with the eastward deceleration of exhumation observed in thermochronology data from the hinterland. Deceleration first occurred in the Paria Peninsula at ~7 Ma and then in the western Northern Range at ~5 Ma (Arkle et al., 2021). Synchronously, at ~4 Ma, exhumation accelerated in the eastern Northern Range (Arkle et al., 2021). It is likely that once STEP tearing occurred lithospheric strength was greatly reduced and flexural tectonic processes were replaced by isostatic and dynamic processes.

As a result of the shift from contractile to transform tectonics, the Tobago ophiolitic-arc terrane, which had previously overthrust the coastal metamorphic hinterland (Northern Range-Paria), became gravitationally unstable and began to slip northward (Weber et al., 2015). This gravitational collapse, following late Miocene convergence, led to shallow crustal extension in Trinidad's north coast marine area. Pliocene-Pleistocene crustal extension in Tobago, documented by fault kinematic data from the Rockley Bay Formation and Pleistocene reef cover, indicates ongoing N-S stretching along *E*-W normal faults since the Pliocene (Snoke et al., 2001; Ringerwole et al., 2011). Subsidence associated with these tectonic processes resulted in accommodation space for a thick accumulation of shallow marine sediments, primarily mudstones with intermittent clean sandstones (Cross et al., 2015). Four significant 30–70 m thick Pliocene sandstone units are present, which are reasonably continuous and represent shingled lowstand prograding shelf deposits redistributed by west-directed shallow marine currents. These sandstones form the gas reservoirs in Trinidad's North Coast Marine Area and in Dragon and other gas fields to the west in Venezuela. Pliocene eustatic amplitudes were moderate (30–70 m; Rohling et al., 2022) and given active Pliocene subsidence, marine disconnection of Tobago and its surrounding landmass from mainland South America was predominant. Brief (e.g., several ka) intervals of connection, however, might have been established during maximum lowstands. Barbados and the Lesser Antilles, however, would have certainly been isolated at this time (Fig. 5d).

Extension and subsidence of the Gulf of Paria pull-apart basin began in the early Pliocene, continued into the Pleistocene, and is active today (Fig. 5d) (e.g., Flinch et al., 1999; Babb and Mann, 1999; Jowers et al., 2024a). This caused major vicariance events in organisms living in the coastal ranges. At times a coastal plain with fringing mangroves (e.g., as recorded in Telemaque member of Manzanilla Fm. exposed along the present day Central Range flanks) extended south from the coastal range; at other times shallow marine embayments, as recorded in the Springvale Fm, extended up toward the southern range flank from the subsiding Gulf of Paria. The coastal ranges provided much of the clastic sediment deposited in this location. To the south of the Paria Peninsula, half-grabens developed along steeply dipping normal faults and accommodated a large influx of early Pliocene sediment (Flinch et al., 1999). As a direct or indirect (i.e., STEP-related) response to subsidence in the Gulf of Paria, the east-side-up tilting observed in the Northern Range is generally constrained to the Pliocene and Quaternary (Fig. 3; Weber, 2005; Ritter and Weber, 2007; Arkle et al., 2017a, 2021); this differential vertical motion resulted in both dispersal and vicariance events.

By about 5.8 Ma eustatic amplitude swings were 30–50 m and the difference in land area between highstand and lowstand conditions in lowland areas was significant, with shoreline retreat of 10s of km. By the early Pliocene, as shown in our 3.7 Ma map (Fig. 5d), eustatic fluctuations of 50–70 m were transitional to even higher-amplitude cycles in the Pleistocene.

The paleo-Orinoco delta reached Trinidad in the early Pliocene, and perhaps even as early as the latest Miocene (e.g., Chen et al., 2014, 2016, 2017; Osman et al., 2021). Southern Trinidad and the southern Gulf of Paria area were then dominated by low salinity, high turbidity deltaic sedimentation associated with the prograding Orinoco delta. During Pliocene highstands, tidally dominated coastlines were present in SW Trinidad, and are preserved for example in the Morne L'Enfer Fm, with SE Trinidad having been located further offshore in a shallow marine setting. During Pliocene lowstands dry land was exposed on the eastern shelf edge, at or just beyond the present-day east coast of Trinidad.

The Pliocene paleo-Orinoco flowed through the Meso-Cenozoic cover of continental SA along a generally eastward trend and carried a combination of sediments sourced from: 1) the topographically high Andes in the west, 2) the northern Cordillera metamorphic mountains along the north coast, and 3) the Paleozoic cover and Precambrain crystalline cratonic basement from the south (Wenxiu and Escalona, 2011; Escalona et al., 2021; Diaz de Gamero, 1996). It's arrival in Trinidad is marked by the Cruse and Morne L'Enfer Formations. These sand-mud sediment packages are found today as dry land exposure of Orinoco deltaic sediment that have subsequently to their deposition been uplifted to ~300 m and tilted to near vertical (e.g., in the Trinity Hills) (Chen et al., 2014, 2017; Osman et al., 2021). During the Pliocene and Pleistocene 12 km of Orinoco sediment accumulated in basinal areas around the shallow marginal self (Wenxiu and Escalona, 2011; Jaramillo et al., 2017). In the SE offshore the Columbus Basin is a continental-margin sedimentary prism that accumulated and prograded 500 km seaward and is laterally 200 km wide (Wood, 2000). High sedimentation rates of the Orinoco system caused not only deltaic shelf edge progradation and foredeep infill, but also east-facing gravity-driven detachment and extension (Chen et al., 2018; Wenxiu and Escalona, 2011; Escalona et al., 2021; Osman et al., 2021). The shifting loci of sediment depositional centers were driven by high sediment supply, tectonic subsidence producing accommodation space, and glacio-eustatic, climate-driven sea-level changes that repeated on ca. 100 ky and even higher frequency time scales (Chen et al., 2016, 2017, 2018; Osman et al., 2021). With such high sedimentation rates, particularly during relative sea-level falls, significant areas of Trinidad would have been exposed and connected to mainland South America, and then drowned and disconnected during sea level rises.

Throughout the late Pliocene and Pleistocene, transitions between highstand tidal deltas in south Trinidad and in the subsiding Gulf of Paria, and lowstand shelf-edge deltas east of present-day Trinidad, played out continuously for a total duration of ~3.5 million years. During this time the shelf edge east of Trinidad built out >100 km into the Columbus Basin (Chen et al., 2018), and at each lowstand a broad coastal plain would have extended almost to the shelf edge. The uplift of the Darian Ridge and Central and Southern Ranges during the late Pleistocene however complicates this picture. We also have limited data for the eastern extension of the Northern Basin, and how that might relate to lowland eastern migration routes from the Guianas to Tobago. These eustatic driven transgression/regression cycles did, however, result in multiple (>25; Chen et al., 2018; Rohling et al., 2022) radical transformations of the lowland landscape of the whole eastern Venezuelan and Trinidad area. In a single ~40 ka lowstand cycle event, full migration of tropical lowland forest and mangrove systems, together with their associated terrestrial ecosystems, occurred across the coastal plain to the geomorphic shelf edge (Figs. 5d-f).

2.3.4. *Late Miocene (9 Ma) and early Middle Miocene (15 Ma)*

The Caribbean plate was ~300 to 200 km west of its present position in the mid- to late Miocene, respectively (Fig. 5b, c). During this time, the Barbados Ridge likely represented an emergent area that contributed sediment to both the developing Tobago Basin and the Barbados accretionary prism (Aitken et al., 2011; Cedeño et al., 2021). By approximately 15 Ma, Tobago had emerged and included a landmass extending to the west and south based on offshore structure and sediment records (Robertson and Burke, 1989; Punnette and Mann, 2021; Punnette et al., 2021). Although connections between landmasses in the northern offshore during this period remain uncertain, it is possible that Tobago was connected to the Barbados Ridge and potentially to the southwest, via the offshore KK-Patao high to the Araya Peninsula. However, it is also plausible that a narrow marine channel separated the KK-Patao high from the coastal mountain ranges. Such scenarios suggest the existence of possible “stepping stone” islands between Tobago, Barbados, and by 9 Ma, perhaps Margarita Island, which may have been emergent and surrounded by a shallow shelf extending toward mainland South America.

During the early Miocene (~22 Ma), the northern Venezuelan orogeny intensified, as reflected in the mid-late- Miocene (~15–9 Ma) maps. The rocks exposed in the northern hinterland proto-ranges at this time were not yet metamorphic, however, but were the unmetamorphosed Paleogene and upper Cretaceous cover rocks above them (see e.g., Elling et al., 2021). Conglomerates and sediments derived from this cover were shed northward offshore and to the south as the Cunapo and Capiricual formations across a coastal plain and onto a shallow shelf that then deepened into the Eastern Venezuelan foredeep (e.g., Sanchez-Zambrano, 2010; Parra et al., 2011; Wenxiu and Escalona, 2011; Martinius et al., 2013; Castillo and Mann, 2021).

SSE-directed thin-skinned thrusting ahead of the advancing STEP produced foreland basin loading (Duerto and McClay, 2011; Martinius et al., 2013). This was followed, during the late Miocene and through the Pliocene, by STEP-tear-associated rapid vertical exhumation of crustal material north of the El Pilar-Trinidad transform fault system (Weber et al., 2001a; Cruz et al., 2007; Arkle et al., 2021). Arkle et al.'s (2021) thermal modeling of rocks from the metamorphic hinterland shows that the onset of rapid exhumation was first initiated in eastern Paria at ~13 Ma, then in the western Northern Range at ~9 Ma and finally in the eastern Northern Range at ~4 Ma. During this 13–9 Ma period of rapid exhumation, the eastern Paria Peninsula and western Northern Range were assumed, respectively, to have been positioned in front of the edge of the deep STEP tear (Fig. 5) by using the current plate motion rates (~20 mm/yr) as a proxy for the tear propagation rate.

By the mid-Miocene the emergent proto-coastal mountains in the western Trinidad area were connected to those of the Araya-Paria Peninsula (i.e., the Serranía del Litoral) and could facilitate west-to-east interchange of biota. Biotic movement to Trinidad's eastern Northern Range, however, was perhaps limited until that region became progressively emergent through the latest Miocene to Pliocene (Fig. 5b to d).

The growth of the topographically high Serranía del Litoral along northeastern South America and the fold-thrust belts of the Serranía del Interior caused load-induced (i.e., flexural) subsidence and the formation of a foredeep fringing the cratonic interior (i.e., the Guarico and Maturin sub-basins of the Eastern Venezuelan Basin; Parra et al., 2011; Wenxiu and Escalona, 2011; Martinius et al., 2013; Lugo and Audemard, 2021; Duerto and McClay, 2011). This foredeep separated the northern highlands from the Guiana Shield across a deep and broad marine basin, which was at times over >100 km wide (Fig. 5b; Hoorn et al., 2010a, 2010b; Jaramillo et al., 2017). Eustatic sea levels remained high between 23 and 14 Ma (40–60 m above present levels), with relatively minor fluctuations of only 10–20 m between highstands and lowstands, and cyclicities of 20,000 and 40,000 years dominating (Rohling et al., 2022). Tectonics, therefore, was dominant in determining the paleogeography. The development of an expansive structural foredeep in northern South America effectively isolated the emergent northern mountains from terrestrial biotic migration from the plains and uplands of the Guiana Shield to the south. Marine inundation in the region was also influenced by the presence of the Espino Graben, a deep basement low that underlies the Barcelona Embayment and trends SW below the Guarico sub-basin (Lugo and Audemard, 2021; Duerto and McClay, 2011; Hoorn et al., 2010a, 2010b; Wesseligh, 2008; Jaramillo et al., 2017). The Espino Graben terminates southward against the NW trending El Baúl Arch which separates the Guarico sub-basin from the Barinas Basin to the SW (Duerto and McClay, 2011; Fig. 2). This configuration fragmented the region, such that the western Coastal Cordillera and inboard Lara Nappes were separated from the proto-Serranía del Litoral and Serranía del Interior, by a shallow Barcelona Embayment and western littoral (Hoorn et al., 2010a, 2010b; Wesseligh, 2008; Jaramillo et al., 2017). The Barinas and Eastern Venezuela foredeeps separated the whole orogen from the Guiana Shield. Fig. 5b represents a maximum highstand during the Miocene Climatic Optimum; during lowstands prior to the infilling of the western Guarico sub-basin, the El Baúl Arch might potentially have provided a mountains-to-shield north-to-south migratory route.

By the late Miocene (Fig. 5c, 9 Ma) the Serranía del Litoral was a prominent topographic high and the western end of the Eastern Venezuelan basin (the Guarico sub-basin) filled and became emergent as a lowland (Parra et al., 2011; Martinius et al., 2013; Duerto and McClay, 2011). Connections between the western Coastal Cordillera and the mainland above the Espino Graben through the Barcelona Embayment region may have been disrupted by periodic marine flooding over a low gradient drainage, yet the sedimentological evidence for this remains speculative, perhaps occurring only during sea level highstands as mapped in Fig. 5c (Hoorn et al., 2010a, 2010b). Nonetheless, at some point during the late Miocene with the western infill of the Guarico sub-basin, there first developed what might be called a “long way around” route to populate proto-Trinidad with terrestrial species from the Guiana mainland.

The uplifted northern Cordillera hinterland also created a significant topographic barrier that inhibited drainages from the South American craton from flowing directly northward into the Caribbean Sea. As a result, the paleo-Orinoco River was progressively deflected eastward, ultimately establishing an eastward flow path into what became a shallow continental shelf in the proto-Trinidad region (Diaz de Gamero, 1996; Wenxiu and Escalona, 2011; Castillo and Mann, 2021). The WSW-ENE flowing proto-Orinoco along the margin of the Guiana Shield likely posed a physical barrier to dispersal of some organisms, e.g., similar to that recognized by A.R. Wallace in 1852 in the Amazon basin (Wallace, 1852).

SSE-directed mid- to late Miocene contractile tectonics in eastern Venezuela, due to the combined flexural downwarping and advancing “bow wave” ahead of the STEP fault, migrated progressively eastward to reach the Trinidad region (Fig. 5b,c). The presence of a mid-Miocene angular unconformity across much of southern Trinidad marks an intense but short-lived episode of erosion, which in the onshore Southern Basin occurred at ~12 Ma (Dyer and Cosgrove, 1992). This so called Middle Miocene unconformity has been interpreted to indicate subariel exposure (Payne, 1991; Pindell et al., 1998), but was more likely generated as a submarine tectonic unconformity in a deep water fold and thrust belt. The deep water of the Southern Basin foredeep would have been a significant barrier to terrestrial species dispersal and, with no marine opening to the north exiting the incipient Gulf of Paria, there was likely no strong westward directed arm of the Guiana current running through the proto-Columbus Channel as there is today (in Fig. 5c note the ~1000 m depths of the Columbus Channel).

Transform motion during the late Miocene was likely accommodated along the El Pilar fault south of the Paria Peninsula and then began to propagate eastward and shift southward with strike slip extension in the Gulf of Paria (Fig. 5c; Flinch et al., 1999; Babb and Mann, 1999; Weber et al., 2020). A thick stratal succession of Cunapo conglomerate accumulated in the Northern Basin immediately south of the Northern Range largely during the Middle Miocene (Kugler, 2001; Elling et al., 2021). This period of exposure and erosion of the coastal mountains likely also resulted in the removal of upper Cretaceous source rocks from the floor of today's Northern Basin and was related to contractile tectonics that preceded exhumation accompanying passage of the STEP fault.

2.3.5. Oligocene (28 Ma)

Subsequent to Jurassic rifting of North and South America, no landmass was present in the general Trinidad area (e.g., Russo and Speed, 1992, 1994; Castillo and Mann, 2021). From the Oligocene to the Miocene, the Tobago terrane, an allochthonous island arc and forearc terrane that formed in the eastern Pacific as part of the “Great Arc of the Caribbean”, was transported eastward along the leading edge of the Caribbean plate (Pindell et al., 1998; Speed and Smith-Horowitz, 1998; Snoke et al., 2001; Neill et al., 2014) and thrust over or wedged into the northern South American coastal metamorphic hinterland (Burke, 1988; Speed and Smith-Horowitz, 1998; Snoke et al., 2001). By the Oligocene, proto-Tobago was located west and north of the burgeoning western Cordillera de la Costa orogen. Thermochronology analyses (Snoke et al., 2001; Arkle et al., 2014) suggest that exhumation of Tobago's arc rocks began in the late Cretaceous. A proto-Tobago island may have been emergent as early as the Oligocene, and parts of the metamorphic basement surrounding it may have been connected by land to the coastal cordillera (e.g., see Fig. 5a). Evidence of Tobago's subaerial exposure is further supported by subsurface data from the north coast offshore (Lugo and Audemard, 2021; Punnette et al., 2021; Punnette and Mann, 2021), where ~10 km of Miocene-Pliocene clastic fill, derived from Tobago and the Northern Range, covers a now-submerged, previously subaerial paleo-topography.

Our Oligocene time slice captures the Caribbean plate's approach from the west with a "bow wave" migrating ahead of the Ca plate's leading edge and STEP system (Fig. 5a). This wave drove contractile deformation (i.e., thrusting and folding), imbricating Late Cretaceous to early Neogene passive strata into a SSE-verging thin skinned fold-and-thrust belt in Venezuela and Trinidad (Erlich and Barrett, 1990, 1992; Escalona and Mann, 2011; Giorgis et al., 2017). This eastward-migrating Caribbean-South American fold-thrust orogen includes the Lara Nappes, the Serranía del Interior and its extension into Trinidad., and associated pro- and retro-foreland basins (Speed and Smith-Horowitz, 1998; Giorgis et al., 2017). Latest Oligocene to early Miocene $^{40}Ar/^{39}Ar$ metamorphic mica ages demonstrate that the Cordillera de la Costa metamorphic hinterland (today's Northern and Paria Ranges) is an integral part of this orogen that was subsequently exhumed via STEP tectonics (see e.g., Genarro et al., 2022 and Arkle et al., 2021, and discussions and references therein).

Assuming a constant eastward relative plate motion rate of 20 mm/year, the Caribbean plate would have been positioned approximately 600 km west of its current location around 28 Ma in the middle Oligocene (Fig. 5a). From the Late Cretaceous to the Oligocene, the "Great Arc of the Caribbean", which is now extinct (e.g., the sunken Aves Ridge), was the active island arc (Aitken et al., 2011). As the slab hinge of the subducting Atlantic oceanic plate rolled back toward the east, the locus of active volcanism shifted and jumped to the Lesser Antilles arc by the late Oligocene (Aitken et al., 2011; Allen et al., 2019). The continued westward-directed subduction of the Atlantic oceanic plate from the late Oligocene through the mid-Miocene resulted in intrusion and uplift of the Lesser Antilles Arc and uplift of the Barbados Ridge, which pushed these topographic features toward shallow marine depths (Cedeño et al., 2021). This process also led to the separation of the Grenada and Tobago Basins (Aitken et al., 2011; Allen et al., 2019) (Figs. 5a-5c).

During and prior to the Oligocene there was no land in the Trinidad area. By the late Oligocene, thrusting responsible for the formation of the Serranía del Interior had commenced, but the range was not yet emergent (Fig. 5a; Duerto and McClay, 2011; Zavala et al., 2011; Parra et al., 2011). Low mountains or hills north of the developing Serranía began emerging. Whether these landmasses were connected to the west, across the Barcelona Embayment and Espino Graben, remains uncertain but possible. South of this young and subdued orogen, the Guiana Shield was emergent, although high sea levels (+40–50 m above present) and relatively small Milankovitch eustatic fluctuations (<20 m between maximum highstands and lowstands; Rohling et al., 2022) maintained a > 50 km wide interior seaway separating the shield from the emergent highlands of the northern Andes (Hoorn et al., 2010a, 2010b; Jaramillo et al., 2017). The retro-foreland basins within the interior of continental South America were infilled by clastic sediments from the Andes, as well as by marine sediments during transgressions (Bajolet et al., 2022). This developing Andes foredeep system, represented by the Llanos, Barinas, and Guarico Basins, effectively cut off the Guianas from the Andes and the emerging Serranías to the north and likely had a significant influence on biotic interchange (Fig. 5a).

3. Biology, phylogenetics, and genetic divergence results

In this section, we now turn from geology to biology and introduce the key Trinidad and Tobago taxa for which robust genetic data exist and for which we attempt to establish geological connections. A detailed discussion of our proposed connections (i.e., the geogenomics) then follows in the Discussion section (Section 4) below.

3.1. Fishes

3.1.1. Guppies, Poecilia reticulata and Poecilia (Acanthophacelus) obscura in South America and Trinidad and Tobago

Populations of the common guppy, *Poecilia reticulata,* in Trinidad, have been models for studies of evolutionary ecology and sexual selection for approximately 70 years. Following on Fajen and Breden's (1992) early mtDNA study, Alexander et al. (2006) present a nested clade analysis of mtDNA collected from guppies in locations across Trinidad, Venezuela, Guyana, and Suriname that revealed phylogenetic divergence between guppies in the east-flowing Oropuche drainage and west-flowing Caroni drainage of Trinidad, with guppies from west Trinidad and Venezuela nesting within one clade and east Trinidad guppies in another (Fig. 6). The affinities among these populations reveals the marked phylogenetic divergence between guppies in the east-flowing Oropuche drainage and west-flowing Caroni drainage of Trinidad. Guppies from the Caroni and north slope drainages nest with those from the Orinoco Basin, Cumana and Margarita Island. Those from the Oropuche drainage are instead more closely affiliated with samples from rivers that drain the Guyana highlands, southeast of the Orinoco basin (Fig. 6). Alexander et al. (2006) inferred from these results that Trinidad had been colonized by two different lineages of guppies derived from different rivers in South America. These results have been repeated and confirmed in the more recent, higher resolution phylogeny, based on >800 single nucleotide polymorphisms, constructed by Willing et al. (2010).

Oropuche guppies are so genetically distinct from Caroni guppies that some have advocated for designation as a separate species called *Poecilia obscura* (Schories et al., 2009) that was likely separated from *P. reticulata* before Trinidad's repeated periods of isolation from the mainland (Fajen and Breden, 1992; Meredith et al., 2010). However, Caroni and Oropuche populations readily interbreed if given the opportunity (Baillie, 2012; Willing et al., 2010). Tobago guppy populations appear to be nested in Trinidad's Caroni (*P. reticulata*) clade, and were thus likely ultimately derived from Venezuela, not from Guyana and Suriname (Baillie, 2012; Fajen and Breden, 1992).

3.1.2. The Killifish Rivulus hartii (Cyprinodontidae) from Trinidad, Tobago and the Paria Peninsula

The first molecular dating of a freshwater fish in Trinidad and Tobago employed cytochrome *b* mitochondrial DNA sequence dating in *Rivulus hartii* (Jowers et al., 2008). The low genetic divergence (0.5 %) between one northwestern Trinidad (Blue Basin, Diego Martin, Northern Range) haplotype (H1) and *Rivulus hartii* from north-western Venezuela (Paria Peninsula) and the high genetic divergence (~ 11 %) between these and the remaining other Trinidad and Tobago haplotypes (H2-H8; Trinidad: from additional Northern Range, Central Range, and Southern Range localities; Tobago: Main Range) suggested to the authors that that the islands may have been colonized by two lineages. Their dating of ~11 % divergence between the two Blue Basin-Paria haplotypes and all other haplotypes suggests that the lineages split circa 7 Ma. The authors argue that the low genetic differentiation between Blue Basin and Paria Peninsula *R. hartii* reflects recent dispersal from northern Venezuela to western Trinidad. These data are consistent with the bromeliad-tree frog scenario developed below.

3.2. Frogs and Toads

3.2.1. The Golden tree Frog Phytotriades auratus (Hylidae), western Trinidad and Paria Peninsula

The latest study to assess the genetic divergence of Trinidad and Northern Venezuela frog populations is that of Jowers et al. 2024a. The authors date a vicariant event through the mutualistic relationship of a

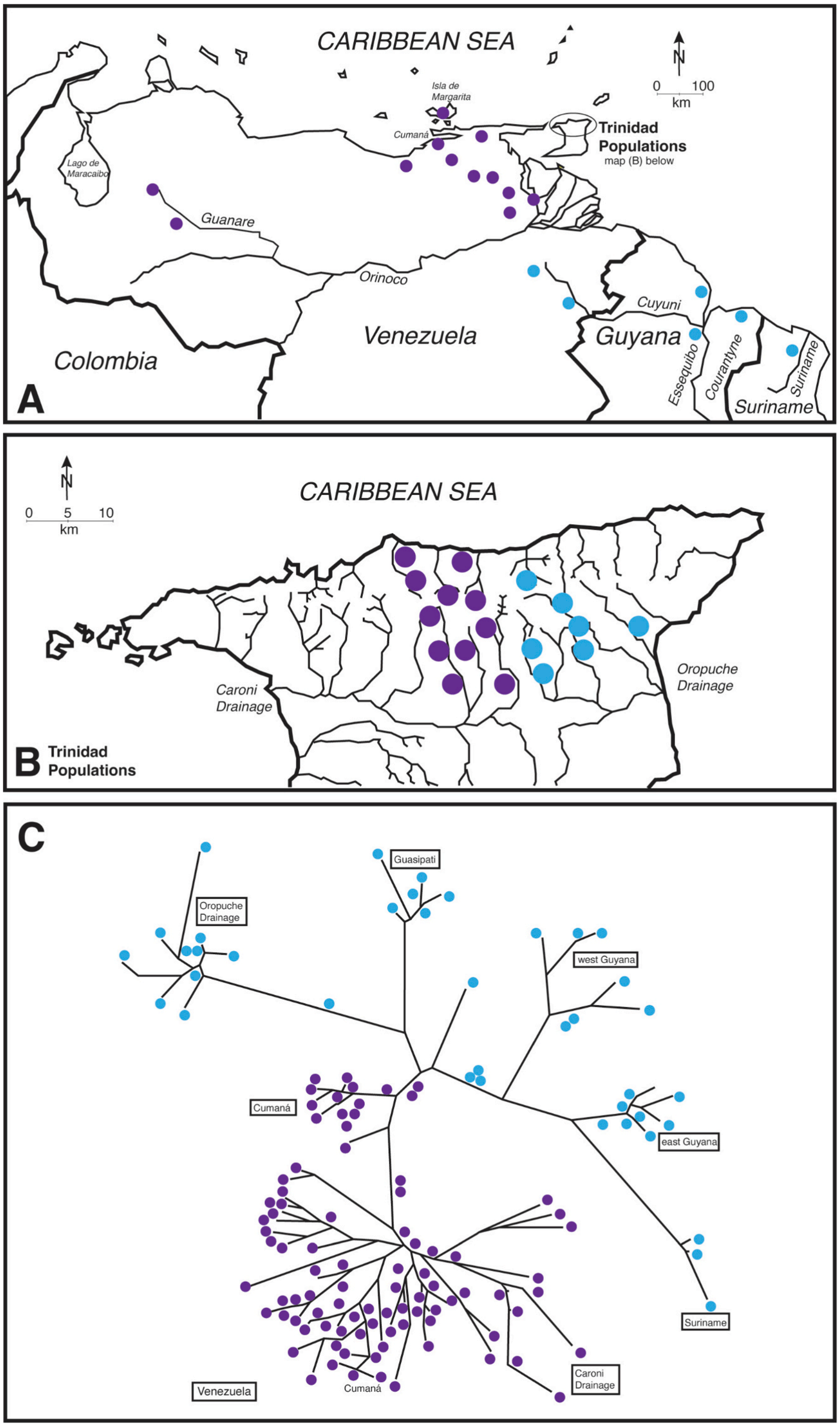


Fig. 6. Maps of Alexander et al.'s (2006) sampling sites in northeastern South America (A) and Trinidad (B), colour coded for the Caroni (purple) vs. Oropuche (blue) affinity groups. Note the genetic split between those in the Caroni (western) drainage basin on the sinking side of Trinidad island and those in the Oropouche (eastern) on the rising side of the island. C) Phylogenetic tree from Alexander et al. (2006). These results illustrate the clear split between Trinidad's eastern (Oropuche drainage) and western (Caroni drainage) populations placed in the context of samples from Venezuela, Guyana and Suriname. Here we can see the clear affinity between the Caroni drainage, sites in the Orinoco River system, Cumana, from northeast Venezuela, and Margarida Island. The Oropuche drainage instead has a closer affinity to the Cuyuni River, which originates in the Guyana highlands, in the vicinity of the town of Guasipati and rivers to the southeast in Guyana and Surname. It is this indication of the affinity of the Caroni and Oropuche guppies on Trinidad with very different regions of northeast South America that sustains our hypotheses for the different paths taken by guppies from what is now South America to the island of Trinidad. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hylid frog and its bromeliad host found in two isolated mountain ranges - one in Trinidad Northern Range and in the other on the Paria Peninsula (Venezuela) - as part of an island–continental split (Figs. 9, 10). Their calibration is based on the strict association of *P. auratus* with high-elevation cloud-forest giant bromeliads *G. erectiflora* as its habitat, as well as the dependency of tadpoles for feeding on its phytotelmata microalgae. This calibration is supported by ecological data suggesting a connective corridor between these mountain ranges in the past combined with geological evidence, including estimates of dates of the submergence of the connecting corridor. Because *Phytotriades auratus* is a cloud forest species that requires cool temperatures, high humidity, and bromeliad plants for laying eggs, it is unlikely this frog could disperse over water.

3.2.2. Collared Frogs, genus Mannophryne (Aromobatidae) in Venezuela, Trinidad and Tobago

Manzanilla et al. (2006, 2009) performed phylogenetic analyses of collared frogs (Anura: Aromobatidae: *Mannophryne*) using partial sequences of mitochondrial 16S rRNA and cytochrome oxidase I genes. They focused on *Mannophryne*, a genus exclusively found in Venezuela, Trinidad and Tobago. *Mannophryne* is never found far from a stream. It is unlikely to disperse over salt water (saltwater is lethal to most amphibians); nor, are they likely to disperse through dry, savannahs. Eggs are laid on the ground, guarded by one parent, and the parents of some species transport tadpoles to water.

Mazanilla et al. found that *Mannophryne* could be divided into three distinct clades – western Andes, central and eastern Serranía and Trinidad/Tobago - which likely diverged “relatively quickly” from each other. Their proposed sequences of divergence from common ancestors (three possible scenarios are proposed) occurred 27–18 Ma, largely in the Miocene. They appear to follow the eastward propagation and development of fold-thrust mountain belts that created appropriate habitat, separated by dry savannah, as the Caribbean corner STEP transform and contractile wave passed eastward across a swath of continental borderland that had previously been subsea and a marine shelf (Fig. 5a,b).

These initial data further supported the taxonomic legitimacy of *M. olmonae*, an endemic species on Tobago Island. Surprisingly, *M. olmonae* is more closely related to the continental (South American) species *M. riveroi* than to the Trinidad endemic *M. trinitatis*. This observation mirrors a common finding seen in other tropical frog clades, where molecular evidence suggests that species often found in geographical proximity are not closely related to neighboring species (Jowers et al., 2021a, 2021c).

The original timing constraints discussed above were supported, and a more targeted genetic analyses undertaken, in a subsequent investigation by Jowers et al. (2011). In that study mitochondrial DNA sequences were employed to explore the phylogenetic relationships and intraspecific genetic variations within *Mannophryne trinitatis*, specifically from Trinidad. Molecular clock estimates indicated that speciation of *M. trinitatis* and its sister species, *M. venezuelensis* have diverged from a common ancestor during the late Miocene (approximately 7.5 million years ago (95% HPD, 3.67–14.23).

Population analyses of *M. trinitatis* from ten Northern Range and four Central Range localities unveiled three distinct, well-resolved largely Pleistocene clades that do not seem to be purely geographic in nature. The largest clade encompassed haplotypes from Northern Range localities, while the other two clades consisted of haplotypes from a combination of both Central Range and Northern Range localities, with one single isolated haplotype from the Central Range. These findings implied that genetic diversity within *M. trinitatis* could be due to multiple admixture events triggered by climatic and sea level changes and/or tectonically-driven landscape changes during the Pleistocene (Fig. 5e, f). For example, the loci of fold-thrust deformation and the development of positive topography would have shifted to south Trinidad at this time; the sinking of the western Northern Range and the Northern Basin would have been ongoing. The Jowers et al. (2011) study sheds light on the granular and intricate evolutionary history of *Mannophryne* species, which seems particularly ripe for further geogenomic investigation.

3.2.3. The Glassfrog Hyalinobatrachium orientale (Centrolenidae) in Tobago and Paria Peninsula

Hyalinobatrachium imposes strict paleogeographic restrictions: it is never found far from a stream; it is unlikely to survive dispersal over salt water; nor are individuals likely to disperse through savanna-like habitats. On Tobago, individuals live on vegetation bordering streams. Eggs must be on leaves overhanging the water. The presence of *Hyalinobatrachium orientale* in both Tobago and northeastern Venezuela raises intriguing questions, particularly given its absence from Trinidad, which has often been proposed as the stepping-stone island for mainland fauna to reach Tobago. The possibility of an extended period of isolation on the “oceanic” island of Tobago has led to speculation that the *Hyalinobatrachium* population there might have undergone distinct evolutionary changes compared to its mainland counterpart (Jowers et al., 2015).

To shed light on this phenomenon, Jowers et al. (2015) used genetic data from 12S, and 16S rDNA gene fragments obtained from nine *Hyalinobatrachium orientale* specimens, encompassing both Tobago and mainland populations. The primary objectives were to elucidate their genetic relationships and taxonomy and unravel the tempo and mode of speciation. The study's findings indicate that *H. orientale* populations from Venezuela and Tobago share a common ancestor. The genetic divergence between these two populations from their common ancestor is estimated to have occurred at approximately 3.1 Ma (95% HPD, 0.8–7.8). However, the study acknowledges that the genetic divergence observed, while significant, does not merit recognizing the Tobago population as a distinct species.

Our discussion of Pliocene paleogeography (Subsection 2.3.3) speculates on the reasonable possibility of occasional short-lived land bridges between Tobago and the South American mainland during maximum lowstands at this time. The concomitant development of lowland tropical rainforest and drainage watersheds across these connections could have provided the narrow set of necessary conditions for the successful colonization of Tobago by *H. orientale*, accompanying its migrating ecosystem. Such a scenario provides an instance of geogenomics *sensu stricto*, whereby genomic data supply supporting evidence for a geological hypotheses.

3.2.4. Pristimantis frogs (Ceuthomantinae) from Trinidad, Tobago and northern Venezuela (Paria Peninsula)

Pristimantis are terrestrial, leaf litter-dwelling forest species unlikely to disperse over marine environments or through savanna-like habitats. Individuals live on the ground but climb into vegetation, sit on understory plants, and call. In general, eggs are laid in terrestrial situations, are often guarded by one parent, and undergo direct development, hatching into miniature adults. The specific habits of three species in Trinidad and Tobago are not well known, but they likely have similar reproductive traits. As with *Hyalinobatrachium*, the dispersal of founding populations of *Pristimantis* to previously uncolonized areas, therefore, could have likely occured in conjunction with changes in climate and, or eustasy that facilitated migration and expansion of their habitat.

Only one study has assessed the genetic divergence of *Pristimantis* frogs in Trinidad and Tobago and compared island species divergence to that from the mainland in northern Venezuela. Jowers et al. (2021a) sequenced fractions of the mitochondrial genes 12S and 16S rDNA of the Trinidad and Tobago endemic *Pristimantis urichi* from both islands, as well as the Tobago endemics *P. charlottevillensis* and *P. turpinorum*. In addition, they sequenced geographically closely related species (*P. pariagnomus* and *P. nubisilva*) from the nearby Paria Peninsula in Northern Venezuela. The time tree analyses found that only the northern Tobago species *P. turpinorum* is closely related to mainland *Pristimantis*, with a genetic split dating to the Late Miocene, suggesting a vicariant event of mainland and island species (Fig. 5c). *Pristimantis urichi*, although identical between the two islands, remains highly divergent from the mainland species. Similar results were found for *P. charlottevillensis*. In addition, there was a high level of divergence between *P. urichi* and *P. charlottevillensis*. These findings suggest different island colonization events by different lineages.

The shared most common ancestor of *P. charlottevillensis* clade dates to 1 Ma (95% HPD, 0.24–2.5), showing a mean genetic divergence split to the shared most common ancestor of *P. gutturalis* from French Guiana at 5.3 Ma (95% HPD, 1.6–11). *Pristimantis urichi's* clade dates to 0.84 Ma (95% HPD, 0.17–2.14) and is highly divergent to all other *Pristimantis* species. *Pristimantis turpinorum* is basal to the sister clade composed of *P. pariagnomus* + *P. nubisilva*. This clade dates to 6.41 Ma (95% HPD, 1.8–14.7). The authors conclude that the genetic distances detected between *P. pariagnomus* and *P. nubisilva* with the Tobago endemic *P. turpinorum* require land connections between the Paria Peninsula and Tobago, probably as far back as the Late Miocene before sinking and segmentation across the Gulf of Paria. The time tree suggests that the presence of *P. turpinorum* in Tobago is likely the result of a vicariant event perhaps followed by a stepping-stone colonization event to Tobago (Fig. 5d, e, f).

3.2.5. *Elachistocleis frogs (Gastrophryninae) in Trinidad and Venezuela*

Elachistocleis are a terrestrial, leaf litter-dwelling savanna species unlikely to disperse over salt water, nor are they likely to disperse through forest habitats, but the degree to which forests are a barrier is unknown. In Trinidad and Tobago, individuals live on the ground and call from the ground or shallow water. Eggs are aquatic, and tadpoles do not receive parental care as far as is known.

Jowers et al. (2021c) used mtDNA and nuclear data together with morphological analyses of this extant group and found clear evidence for an Oligocene Andean origin for the genus with subsequent colonization in Trinidad by two different clades at 2.1 and 0.5 Ma, respectively, arriving from different mainland source regions (Venezuela and Guyana), most likely facilitated by sea-level drops during Pleistocene low stands (Fig. 5e, f). The time since the most recent common ancestor of *E. nigrogularis* from Venezuela and Trinidad dates to the Pleistocene (2.17 Ma, 95% HPD, 0.9–3.6) and is consistent with prolonged isolation between mainland and island populations. *E. surinamensis* shows a much more recent divergence between its Guyanese source and Trinidad conspecifics at approx. 0.5 Ma (95% HPD, 0.25-0.79). *Elachistocleis*, therefore, colonized Trinidad after its separation from Venezuela across the Gulf of Paria. Surprisingly, the Venezuelan individuals that showed close genetic affinities to *Elachistocleis nigrogularis* from Trinidad were from the geographically most distant localities for *Elachistocleis* in Venezuela.

3.2.6. *Beebe's toad Rhinella beebei (Bufonidae) from Trinidad and Venezuela*

Beebe's Toad is terrestrial with aquatic eggs. It is a savanna species that occurs in agricultural habitats, including orchards and plantations. Toads in the genus *Rhinella* tend to be saltwater tolerant. They lay aquatic eggs, and tadpoles are aquatic. As far as we know, they receive no parental care. Using 12S and 16S rDNA partial sequences, Murphy et al. (2017) calculated the genetic divergences between Trinidad's most recent common ancestor and its sister clade, in Venezuela and East Colombia, dates to 1.8 Ma. (95% HPD, 0.8–33 Ma). The molecular clock estimates indicated the time of the split from their most recent common ancestor for the Trinidad *R. beebei* and the mainland *R. humboldti* to have occurred about 9 Ma in the Miocene. Subsequent eastward speciation events may have followed the eastward migration of the Caribbean plate (relative to the mainland) and the development of its associated pre-STEP corner transform/contractile wave replacement of a marine continental borderland with high fold-thrust terrestrial topography.

3.3. *Reptiles*

3.3.1. *Coral Snakes (Elapidae) in Trinidad and Northern South America*

Coral snakes are fossorial (underground dwelling) and, as such, are poor colonizers of islands that are not close to the mainland. They lay eggs; some are forest-dwelling, while others are savanna species (e.g., *M. circinalis* is likely mostly a savanna species, while the larger *M. diutius* is mostly a forest dweller). Coral snakes tend to feed on other snakes and on elongated prey. Jowers et al. (2019) developed a phylogenetic framework utilizing an expanded molecular dataset for New World coral snakes. This dataset included newly acquired sequences for the only two sympatric species found on Trinidad; coral snakes are completely absent on Tobago. They included the two Trinidadian species in a larger-scale coalescent, phylogenetic reconstruction of the genus *Micrurus*. *Micrurus diutius* specimens from Guyana and Trinidad shared the same haplotypes, suggesting a vicariance event that occurred during the Late Pleistocene to Holocene period. Additionally, *M. lemniscatus*, a separate lineage resembling *diutius*-like snakes was identified in Guyana, thereby providing a voucher specimen and narrowing down the type locality for this species. This Pleistocene-Holocene Trinidad-Guyana connection that this study established may be yet another example of an eastern dispersion corridor that developed on the eastern shelf during low-stand events (Fig. 5f).

3.3.2. *The Black Headed-Snake Tantilla melanocephala (Colubridae) in Trinidad and Northern South America*

Tantilla melanocephala is a terrestrial semi-fossorial (semi-underground-dwelling) species that feeds on centipedes and spiders, lays eggs, and is known to prefer disturbed habitats, particularly coffee plantations. Jowers et al. (2020) sequenced mitochondrial and nuclear gene fragments from *T. melanocephala* from Guyana, Venezuela, Trinidad, and Tobago. Their phylogenetic and BEAST tree analyses recovered a strongly supported *T. melanocephala* Venezuela-Trinidad clade. The divergence between Guyana-French Guiana and Venezuela-Trinidad-Tobago dates to 1.8 Ma (95% HPD, 1.2–2.4 Ma). The divergence between the Tobago lineage and that of Trinidad plus Venezuela dates to 1.4 Ma (95% HPD, 0.91–2.03). A more recent TMRCA toward the end of the Pleistocene is recovered between Trinidad and Venezuela *T. melanocephala* (0.2 Ma, 95% HPD 0.014–0.48 Ma). Overall, their phylogenetic findings and time tree recovered close associations between Trinidad, Venezuela, and Guyana that date to the Pleistocene connections in the region (eg., Fig. 5f).

3.3.3. *The Three-Lined Snake Atractus trilineatus (Colubridae) in Trinidad, Tobago and Venezuela*

Atractus trilineatus is a terrestrial-fossorial species that feeds on soft-bodied invertebrates. They lay eggs in small clutches. They are probably forest-dwelling. Murphy et al. (2019a) examined the phylogenetic relationship and cladogenic events of *Atractus trilineatus* from eight localities in Trinidad, Tobago, and Guyana (but none from Venezuela) using several mitochondrial markers and one nuclear marker. They found that the populations from Trinidad and Tobago show close genetic affinity with the Guyanese mainland populations. Within *A. trilineatus*, the split between samples from Trinidad and Tobago dates to ~180,000 yr ago (95% HPD, 60–370 ka). The oldest split between Guyana and both Trinidad and Tobago *A. trilineatus* dates to ~1 Ma (95% HPD, 0.62–1.72 Ma). The most recent split between the mainland (Venezuela/Guyana) and Trinidad and Tobago dates to 410,000 yr ago (95% HPD, 180–690 ka).

3.3.4. *The Reduced Limb Lizards of the genus Bachia (Gymnophthalmidae) in Trinidad and Venezuela*

Bachia are leaf-litter-dwelling (cryptozoic) lizards (both species in Trinidad are forest-dwelling) that feed on small invertebrates. They lay eggs and have greatly reduced limbs. It is difficult to imagine these lizards moving significant distances. As such, enduring population migrations would need to accompany habitat migration over multiple generations, in line with landscape transformation due to climatic/eustatic perturbations. Murphy et al. (2019b) assessed for the first time the phylogenetic and systematic relationships of the reduced limbed lizards of the genus *Bachia* from a broadly distributed set of samples ranging from west of the Andes, across the mainland, through Trinidad and Tobago, and up into the Lesser Antilles using mitochondrial and one nuclear marker. They sampled populations from Trinidad and Tobago and Monos Island (NW Trinidad). The results supported changing the name of *Bachia heteropa trinitatis* to *B. trinitatis* which is found on Trinidad, Tobago and Monos Island, and the description of a new species formerly considered part of *Bachia flavescens* to *B. whitei* is presumed to be a Tobago endemic. The divergences dates were*: B. flavescens* + *B. whitei* -*B. trinitatis* 26.67 Ma (95% HPD, 11.0–48.2 Ma); *B. trinitatis* from Tobago-Monos Island 2.68 Ma (95% HPD, 0.27–8.06); *B. trinitatis* Trinidad-Monos Island plus Tobago dates to 6.98 Ma (1.37–17.54); and the South American *B. flavescens*-*B. whitei* 12.7 Ma (95% HPD, 2.88–28.18). The study was somewhat limited by calibration ranges that were too broad to point to any mode(s) or precise period(s) of colonization.

3.3.5. *The Neotropical Day Geckos of the genus Gonatodes (Sphaerodactylidae) in Trinidad and Tobago*

Gamble et al. (2008) found that the Trinidad gecko, *Gonatodes ceciliae*, and Tobago gecko *Gonatodes ocellatus* shared an ancestor 3.8 Ma. The authors relate the latter event to a cooling climate. Still, this late speciation event could be related to local Pliocene tectonics in the plate boundary and the related landscape response (see Subsection 2.3.3; Fig. 5d). Both Trinidad-Tobago geckos tend to be forest dwellers, found in deep shade of moist forests, particularly *G. ceciliae*. They overheat and die quickly in direct sun. *G. ocellatus* may be adapted to slightly more open habitats and higher temperatures than *G. ceciliae*.

3.3.6. *Hallowell's Ground Snake Atractus fuliginosus (Dipsididae) in Tobago and Eastern Venezuela*

The enigmatic presence of this rare and relatively poorly known fossorial (underground-dwelling) snake, *Atractus fuliginosus*, in Tobago, Western Venezuela and Colombia, but absent in Trinidad and Eastern Venezuela, raises interesting questions regarding its biogeography, mode, and timing of colonization on Tobago. Jowers et al. (2021 b) sequenced mitochondrial and nuclear loci from three specimens from Venezuela and one from Tobago. The low genetic divergence between island and mainland specimens was surprising, especially considering that today more than 1000 km separates them, and genetics suggest that the split occurred only 550,000 years ago (95% HPD, 270–960 ka) in the middle Pleistocene (e.g., Fig. 5e, f). Jowers et al. (2021b) assess possible scenarios to account for the species' low genetic differentiation and its presence in Tobago and absence in Trinidad. We concur that the most likely dispersal route could have been one of the dry land bridges that existed at times of high amplitude (>100 m) sea-level low stands that would have allowed for connections between mainland Venezuela and Tobago (e.g., Fig. 5f).

3.3.7. *Rutherford's Vine Snake Oxybelis rutherfordi (Colubridae) from Trinidad and Tobago*

Oxybelis rutherfordi is a forest and forest-edge snake that uses understory vegetation and small trees and bushes. It is mostly a diurnal ambush predator that feeds on lizards. Squamata that use bushes and small trees may be a likely species to be dispersed by flooding events and find their way to other islands or locations (Inger and Voris, 2001).

Using mitochondrial and nuclear markers Jadin et al. (2019) showed that *Oxybelis aeneus* from Trinidad and Tobago (Lineage 4 in their study, later named *Oxybelis rutherfordi* from Trinidad-Tobago) were monophyletic and with low genetic divergence between the populations on these two islands. Species of *Oxybelis* are extremely widespread, ranging from the SW USA through Mexico and Central America and into South America and the SE Caribbean (i.e., Trinidad and Tobago). Genetic splits from common ancestors have a tendency eastward and mirror the eastward rafting of the Caribbean plate through the inter-American gap. However, the time split from the Trinidad-Tobago (Lineage 4) to its sister clade of Lineage 3 from Panama (Isla of Coiba) occurred at a mean age of 3.02 Ma (95% HPD, 0.5–5.58 Ma), and to its sister clade of Lineage 2 from northern Central America at 4.23 Ma (95% HPD, 1.55–6.85) which are both much younger than even the proposed 13–15 Ma (Middle Miocene) closure of the Panama arc (Montes et al., 2015) in the wake of the entry of the Caribbean (e.g., see Fig. 1), so an east-to-west dispersal across northern mainland South America seems like a better fit to the data. Although the authors did not specify the exact timings of arrival to the islands or how, the low genetic divergence and a more basal ancestral clade of Trinidad suggests very recent colonization from Trinidad toward Tobago.

3.3.8. *Sipo snakes, Chironious cochrane and C. nigelnoriegai (Colubriadae) from Trinidad, Tobago and Northern Venezuela (Paria Peninsula)*

Chironius are slender snakes adapted to a diurnal and arboreal lifestyle. Using a multilocus sequence molecular data set using mitochondrial and nuclear DNA Jadin et al. (2024) inferred that the two *Chironius* species present on Trinidad were distantly related and both species differ in their colonization routes to Trinidad. More specifically, the sister-group relationship between *C. nigelnoriegai* from Trinidad and *C. flavopictus* from Ecuador may have resulted in a colonization event from the west. These two species appear to have diverged in the early Pliocene (4.2 Ma, 95% HPD, 1.7–7.3 Ma), an estimate congruent with most of Trinidad's isolation from the mainland (Murphy et al., 2023) and suggesting a vicariant speciation event (see, e.g. Fig. 5b, c). The other Trinidadian species, *Chironius cochranae* is composed of populations from Suriname, Guyana, Trinidad, and Venezuela (Paria Peninsula) and is sister to a clade of South American *C. foveatus*, *C. laurenti* and *C. multiventris* with a divergence between clades dating to 9.5 Ma (95% HPD, 6.6–12.4 Ma) (Fig. 5c). Trinidad and Paria populations similarity suggest ongoing gene flow.

3.3.9. *Hallowell's coffee snake Ninia atrata species complex (Colubridae) from Trinidad, Tobago and Northern Venezuela (Paria Peninsula)*

Ninia atrata is a small terrestrial snake that inhabits low and mid altitude elevations. It is believed to feed on insect larvae and termites and is a common snake. Jowers et al. (2024b) used a multilocus sequence molecular data set using mitochondrial and nuclear DNA from South American populations of *Ninia atrata* from South America, including Ecuador, Colombia, Trinidad, Tobago, and Venezuelan localities from near Caracas and the Paria Peninsula to examine its evolutionary history as well as to evaluate the possible existence of cryptic lineages.

The study confirms from a molecular perspective that the species from Trinidad and the Paria Peninsula are the same species, *Ninia franciscoi*. This clade is very recent, dating to 0.17 Ma (95% HPD, 0.31–0.07 Ma). The split between the Tobago and Trinidad lineages is estimated to have occurred 2.26 Ma (95% HPD, 1.84–2.74 Ma). The presence of species in Trinidad and Tobago suggests the existence of terrestrial corridors that connected the islands with the continent for at least brief periods during the Pliocene (ca. ~10 ka, see Subsection 2.3.3; Fig. 5d), corresponding with the drier climates and lower sea levels of the Pleistocene glaciation periods (Fig. 5f). A subsequent period of prolonged isolation in Trinidad and Tobago could explain why these *Ninia* populations are genetically distinct from those on the mainland. The data and morphological evidence points toward a different species in Tobago and further taxonomic work is ongoing.

The authors concluded that at the time of the split between the *N. atrata* lineages of Trinidad and Tobago, about 2.26 Ma, the island of Tobago was located north of Trinidad, about 50 km west of its current position (Jowers et al., 2015), moving along the edge of the South American plate to its current location to the northeast of Trinidad at a rate of 20 mm per year due to the movement of tectonic plates (Weber et al., 2001a, 2001b; Weber et al., 2015; Pindell and Kennan, 2007). Sea level rises during the interglacial periods of the Pleistocene may have restricted gene flow between the islands of Trinidad and Tobago (e.g., Fig. 5e), probably allowing the accumulation of some degree of genetic differentiation between these populations.

3.4. *Mammals*

3.4.1. *Marmosa robinsoni (Didelphidae) from Trinidad and Venezuela*

Robinson's mouse opossum, *Marmosa robinsoni*, is known to inhabit xeric shrublands, savannas, and deciduous forests spanning a geographical range from Panama through Colombia and Venezuela to the islands of Trinidad, Tobago, and Grenada. Gutiérrez et al.'s (2014) extensive geographic sampling unveils the species' phylogeographic structure. These authors utilized genetic data from the cytochrome-b gene and the X-linked intron O-linked *N*-acetylglucosamine transferase. Gutiérrez et al. (2014) revealed an interesting genetic pattern within isolated populations from the Península de Paraguaná in northwestern Venezuela. Despite their geographical proximity to mainland populations, these isolated populations were found to be more closely related to populations far to the west in Colombia and Panama. Conversely, populations in central and eastern Venezuela exhibited a close genetic affinity with those inhabiting the islands of Trinidad and Tobago with an estimated TMRCA dating to 0.35 Ma (95% HPD, 0.12–0.71 Ma).

4. Discussion

As outlined in the Introduction, in principle, genetic divergence – which can ultimately result in speciation events – can result from either: 1) vicariance, 2) dispersal, or 3) ecological “pressure”. Vicariance, or isolation, is generally chiefly driven by Earth processes (i.e. geology), such as sea-level rises and falls, land uplift or subsidence, etc. Dispersal may be driven by either geology or ecology, or combinations of the two. Ecological “pressures”, on the other hand, are largely biological and encompass a broad variety of factors including climate change, competition, opening and availability of new environments to colonize, for example by extinction events. Cause and effect are generally difficult to prove and those offered below are of course more suggestive than proven.

In this review, we nonetheless tried to build compelling geological cause and biological effect (i.e., geogenomics in its broad sense) cases for several groups of organisms, mostly amphibians and reptiles. Our proposed connections are discussed thematically below where we attempt to make some broad statements on the geogenomics (i.e., speciation events) of the organisms discussed in Section 3 above.

4.1. *Biogeographical connections between the Venezuelan Cordilleras, the Guiana Shield, and Trinidad*

The guppy genetic data presented above (Section 3.1.1) may have been anticipated by Boos' (1984) speculation that fauna colonized Trinidad in a “two-arc” pattern. The two arcs are possibly physically coincident with the two branches of inflow of the Guiana Current, or the divergent outflow of east- versus west-draining mainland waterways. In addition, genetics tells us that guppy populations in Trinidad's Caroni and Oropuche watersheds have separate origins on the South American mainland (Magurran, 2005) and have likely been separated for at least 200 kyr and perhaps as long as 1.2 Myr (Fajen and Breden, 1992; Alexander et al., 2006). Fig. 6 shows that the Caroni guppy sub-group or sub-species is present on today's western sinking side of the Northern Range. Whereas the Oropuche sub-group or sub-species is found on the uplifting eastern Northern Range. This correlation does not appear to be a simple coincidence and suggests that a STEP tectonic driver could be a reasonable cause for this surprising distribution pattern. The difference might for example be related to a “rolling” geomorphic divide, which is today coincident with the Guatapajro Anticline (Kugler, 1959).

The subsurface geology in the Gulf of Paria pull-apart basin shows that differential vertical motion across the Trinidad-Venezuela coastal mountain range began in the early Pliocene (Fig. 5d) (Flinch et al., 1999; Babb and Mann, 1999; Jowers et al., 2024a). Geology thus permits that a post-early-Pliocene vicariance event isolated taxa. We hypothesize a second possible “two arc” scenario based on generally established relationships between rivers and surface uplift that is consistent with both Trinidad's geomorphology and the guppy genetics. A key genetic constraint that must be met is that the two sub-populations have separate origins in South America and have been separated for 200 ka or more (Fajen and Breden, 1992; Alexander et al., 2006). On today's submergent eastern Trinidad continental shelf, Soto et al. (2007) and others mapped and noted the presence of large abandoned buried river paleo-channels that cut into underlying early Pleistocene (?) to Pliocene strata. These paleo-rivers must have flowed during Pleistocene lowstands. We hypothesize that these large now-drowned river systems that once flowed on the submerged offshore shelf grew in length via headward erosion toward the uplifting eastern side of the Northern Range (e.g., see Fig. 5f). In principle, this uplifting side of the range could have acted as a river/erosion “attractor”. Possible timing for large eastern shelf rivers that may have connected eastern Trinidad to the mainland and that honor both the geologic and genetic data include those that occurred during high amplitude lowstands during the odd-numbered marine isotope stages (MISs) 7, 9, 11, 13, 15, 17, 19 21, etc., which occurred regularly from 200 ka to 1.2 Ma during the major Pleistocene glaciations. Additional genetic data are needed to narrow this wide range of ages and to zero in on a more specific geological cause.

The two arc hypothesis is not exclusive to guppies and has been demonstrated in other vertebrates, although population structure data analyses have been more limiting than on guppies. A good example is the presence of two *Elachistocleis* frogs in Trinidad, with a TMRCA of the *E. nigrogularis* clade dating to 2.1 Ma, with genetic affinities to northern Venezuela and the TMRCA of the *E. surinamensis* clade to the Guianas dating to 0.5 Ma. This, we suggest may be due to a similar scenario to that proposed for the Oropuche guppies (*Poecilia reticulata*). Pleistocene low-stand connections by paleo-rivers flowing across Trinidad's eastern shelf eroded headward via attraction to the uplifting landscape in NE Trinidad (Fig. 5f). Their associated periodically wet and dry alluvial floodplains might have allowed *E. surinamensis* to disperse from Guyana into Trinidad. Studying the geography and genetics of this group of organisms at a more granular level may reveal additional insights. A very similar example to *Elachistocleis* species is the two New World Coral Snakes *Micrurus* from Trinidad. *Micrurus diutius* is distributed from the Guianas to Trinidad and *M. circinalis* is found in Trinidad and northern Venezuela. These two species show contrasting ancestral origins and likely contrasting colonization routes (Jowers et al., 2019). Similarly, two other snakes in Trinidad, the Sipo snakes, have colonized Trinidad from different routes at different times, *Chironious nigelnoriegai* from the west and *C. multiventris* from the Guianas.

4.2. *Biogeographical connections between Paria Peninsula and Tobago and excluding Trinidad*

The presence of the Glass Frog *Hyalobatrachium orientale* in Tobago and the Paria Peninsula and non-presence in Trinidad suggests that during at least some Pliocene lowstands, land-bridge formations likely connected the mainland with Tobago, creating a habitat corridor that facilitated the colonization of Tobago by *H. orientale* at a time when Tobago was proximal to the Paria Peninsula. The 95% HPD interval for this population separation event ranges to 7.8 Ma, in the late Miocene, suggesting a considerable window for such connections to occur. This colonization event likely occurred west of Trinidad, explaining its absence on the latter island (Jowers et al., 2015). The estimated divergence time (3.1 million years) post-dates the separation of northwestern Trinidad from the northeastern mainland during the early Pliocene (e.g., Fig. 5d). This divergence could imply that Trinidad's amphibian fauna was affected by extinction events, making it challenging to rule out the possibility of *H. orientale's* former presence on Trinidad, albeit currently unrecorded, but this hypothesis seems unlikely as this species has never been reported in the island despite vast herpetological surveys. Discrimination between possible causes for the distribution and evolution of this species awaits further coordinated biological and geological investigations.

The late Miocene divergence found by Jowers et al. (2011) between the TMRCA of *Mannophryne olmonae* from Tobago and the Paria Peninsula (*M. venezuelensis*) and Trinidad (*M. trinitatis*) sister clade, similarly suggests an ancient presence in Tobago, and possibly indicates a connection between Venezuela and Tobago as suggested for *H. orientale* (Fig. 5c).

The other example with molecular dating with populations present in Tobago and Northern Venezuela and absence in Trinidad derives from Hallowell's Ground Snake *Atractus fuliginosus*. Here, however, the timings differ to those estimated from *H. orientale*, and suggest 550 ka despite the >1000 km distance between populations (Jowers et al., 2021b). We concur that the most likely dispersal route would have been one on the dry land bridges that existed at times of Pleistocene high amplitude (>100 m) sea-level lowstands that would have allowed for connections between mainland Venezuela and Tobago (e.g., Fig. 5f). For additional examples and for a broad and synthetic overview on distribution patterns of snakes in Trinidad and Tobago we refer the reader to Murphy et al. (2023).

Although unlike the above where we comment upon examples at the population level, the frogs of the genus *Pristimantis* show similar patterns of distributions between species. Examples are the Tobago endemic frog *Pristimantis charlotevillensis* and closest known phylogenetic relationship to French Guiana dating to 5.3 Ma, and the Tobago endemic *Pristimantis turpinorum* with closest phylogenetic relationships to *Pristimantis pariagnomus* and *P. nubisilva*, both endemic from the Paria Peninsula, with aa divergence of the TMRCA of 6.4 Ma. These dates suggest that late Miocene land connections between the Paria Peninsula and Tobago might explain the genetic divergence between species following vicariance isolation. The time tree suggests that the presence of *P. turpinorum* in Tobago is likely the result of a vicariant event roughly at the time of the isolation of northern Trinidad from northern Venezuela circa 4–5 Ma, perhaps followed by a stepping-stone colonization event to Tobago (e.g., during a Pleistocene lowstand) with extinctions of intermediate populations in Trinidad thereafter (Jowers et al., 2021a) (Fig. 5d, e, f).

4.3. Pliocene and Miocene vicariance events and STEP tectonics

The high genetic divergence of the Killifish *Rivulus hartii* from northeastern Venezuela (Paria Peninsula; ~11 %) and those in Trinidad and Tobago, suggests circa 7 million years of genetic split. This date would have predated the opening of the northern Gulf of Paria and the symmetric sinking event that later (~4 Ma) isolated the organisms in eastern Paria from those on the western Northern Range. According to our paleogeography, the Paria Peninsula and Northern Range mountains would have been a continuous mountain range 7 million years ago, enabling a free exchange of *R. hartii* among neighboring streams draining the mountain slopes (Fig. 5c) (Jowers et al., 2008). The mystery to be solved is defining the origin of the second, more widespread lineage in Trinidad and Tobago. This question remains open and is ripe for further geogenomics (i.e., genetics and paleogeographic) evaluation. Another remaining puzzle is to understand why the genetics of Killfish and guppies, both freshwater aquatic species, give results that are incongruent.

Estimate dates of TMRCA between the collared frog *Mannophyne*

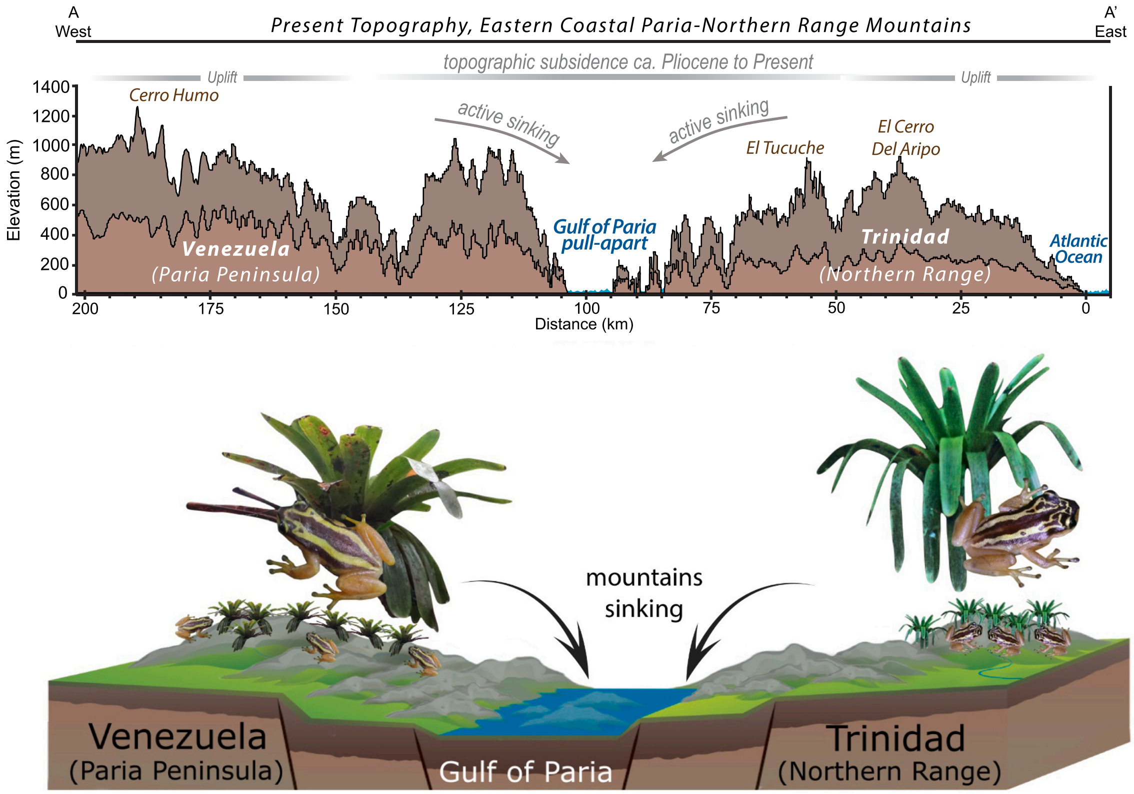


Fig. 7. Schematic diagrams showing modern day topographic swath profile and mean and maximum elevations across the Northern Range-Paria coastal mountain range and the proposed evolution of this range across the Gulf of Paria pull-apart basin and its effect on the biology, i.e., on golden tree frog (*Phytotriades auratus*) subpopulations as determined genetically and host bromeliads (*Glomeropitcairnia erectiflora*). Modified from Jowers et al. (2024a).

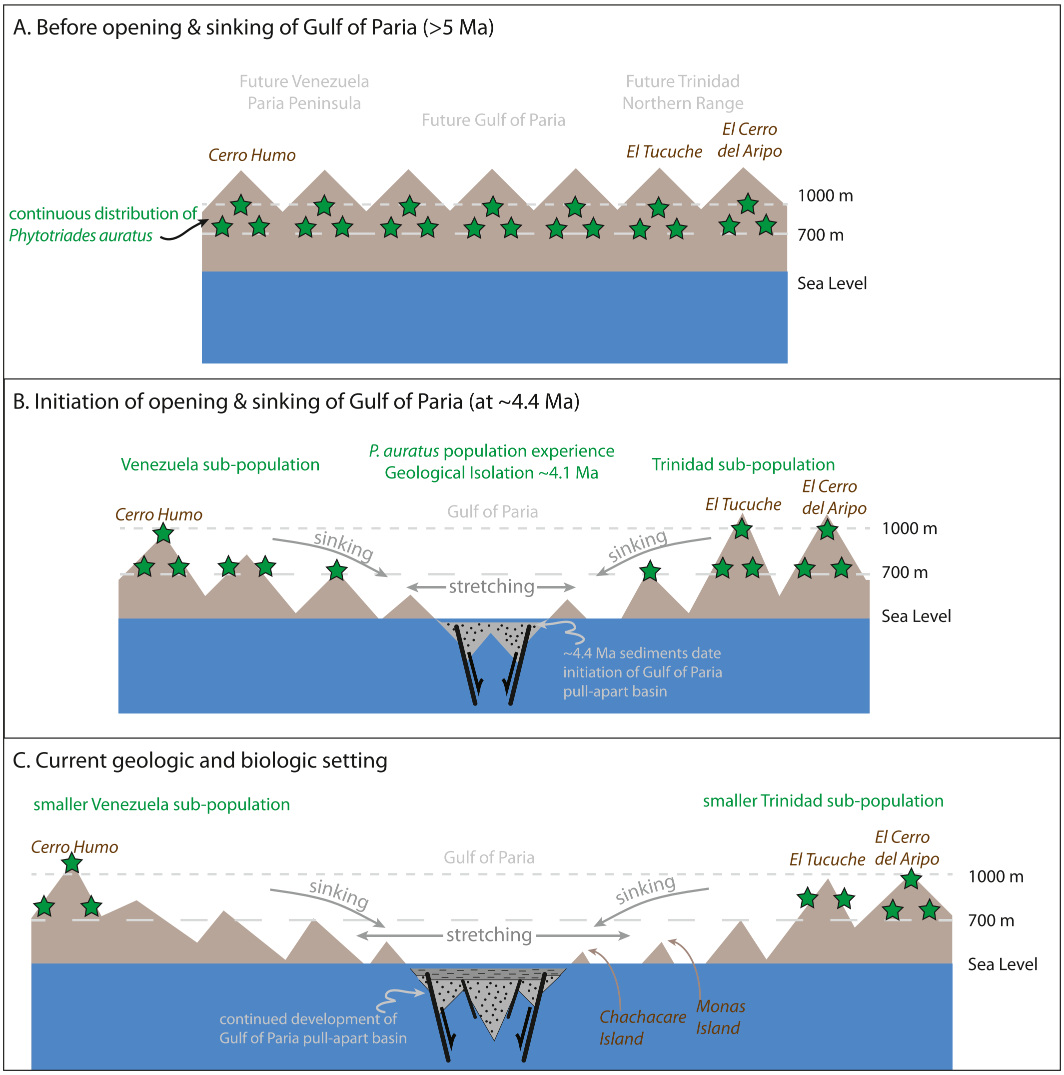


Fig. 8. Schematic time-series showing proposed evolution of the Northern Range-Paria coastal mountain range across the Gulf of Paria pull-apart basin and its effect on the biology, i.e., on golden tree frog (*Phytotriades auratus*) sub-populations as determined genetically and host bromeliads (*Glomeropitcairnia erectiflora*). Modified from Jowers et al. (2024a).

trinitatis and its sister species *M. venezuelensis* to around 7.5 Ma concur with the above example of *Rivulus hartii*. The observed divergence points to vicariance as the primary mechanism of speciation (Jowers et al., 2008). But as stated above, the separation and isolation of northwestern Trinidad from northeastern Venezuela did not occur until ~4 Ma (Jowers et al., 2024a) so we again suggest that divergence could have occurred as a bow wave of fold-thrust-related dry land and high topography passed eastward through the continental borderland in the late Miocene (see, e.g., Fig. 5c, d).

The mutualistic relationship of the hylid Golden Tree frog of Trinidad *Phytotriades auratus* and physiological adaptation to its host giant bromeliad *Glomeropitcairnia erectiflora,* and the strict association of that plant to cloud forest above 700 m in altitude, suggests that both populations can were isolated when submergence of the range was below 700 m (Figs. 7, 8). This timing is linked to ~4 Ma Gulf of Paria pull-apart tectonics (Jowers et al., 2024a). Other species not restrained to high altitude localities (ie., *Mannophyne*) should have been able to cross through this lowered mountain range much later and should be corroborated by even younger vicariance dates <4 Ma.

The reduced Limb Lizards *Bachia trinitatis* from Tobago-Monos Island recovered a divergence of 2.68 Ma, while *B. trinitatis* Trinidad-Monos Island plus Tobago dates to circa 7 Ma (95% HPD, 1.37–17.54 Ma), with Guyana *B. flavescens*-*B. whitei* dating at 12.7 Ma. These genetic results suggest limited dispersal opportunities for these leaf litter species between the Trinidad-Tobago clades, followed by multiple vicariance events between South America and Trinidad and Tobago from late Miocene (circa 5 Ma) through the Pliocene and into the Pleistocene (Fig. 5d, e, f) (Murphy et al., 2019b). Similarly, Gamble et al. (2008) estimates of divergence between the Trinidad gecko, *Gonatodes ceciliae*, and Tobago gecko *Gonatodes ocellatus* shared ancestor dating to 3.8 Ma suggest a connection between the islands during the Pliocene. The two Sipo snakes present in Trinidad (*Chironius nigelnoriegai* and *C. cochranae*) have also diverged in around the late and Middle Miocene (4.2 and 9.5 Ma) from their most recent common ancestors in western and eastern localities respectively suggesting vicariant speciation (Jadin et al., 2024).

4.4. Pleistocene eustatic sea level changes and STEP tectonics

Arrival of species to insular localities after flooding of the Paria Gulf indicates some sort of available topographically and environmentally suitable corridors or alternatively, and less likely, marine dispersal. As already discussed, an example of such a colonization to Trinidad is that of the two *Elachistocleis* frogs (at 2.1 and 0.5 Ma) suggesting likely

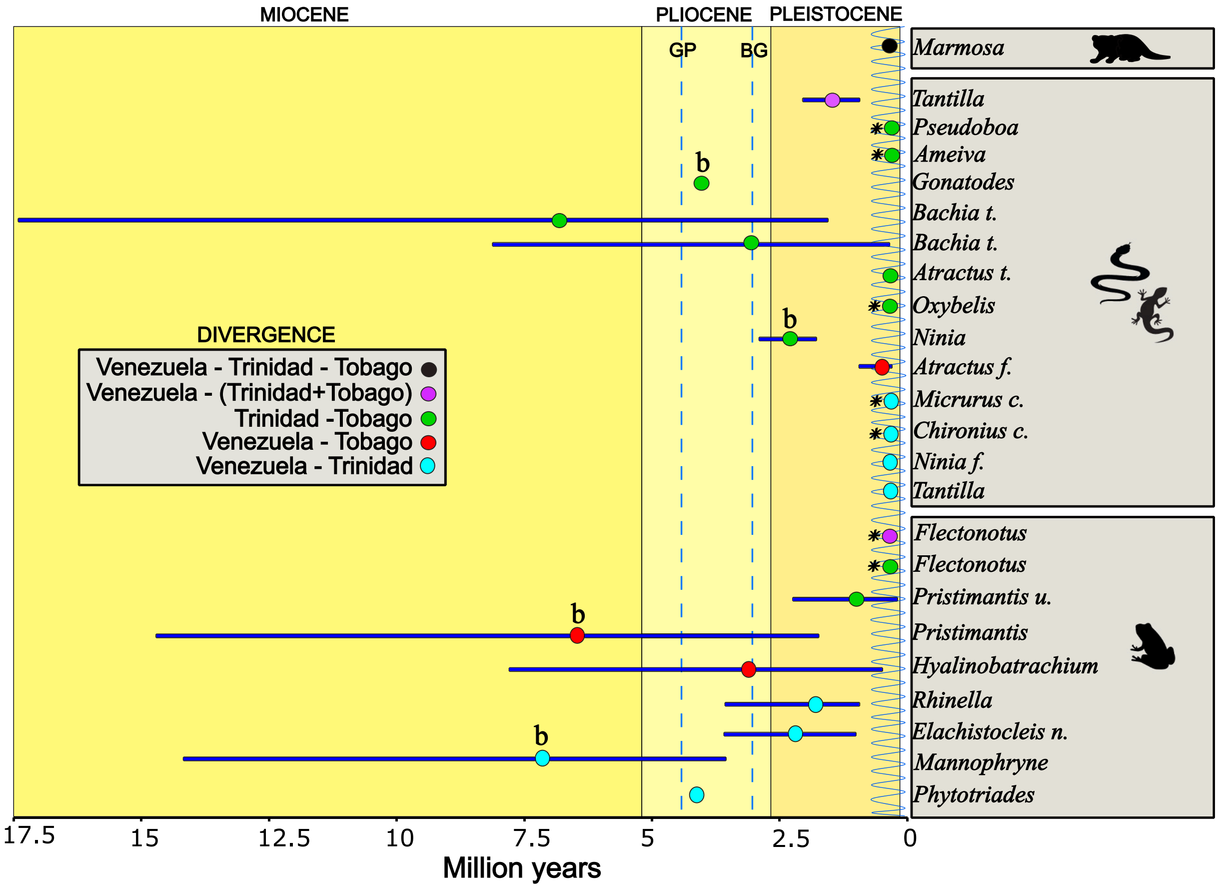


Fig. 9. Summary diagram showing terrestrial taxa reported in the text with dating of divergence between pairs of source and extant regions (see legend). The blue line represents 95 % High Posterior Density intervals (HPD). The nodes represent mean values of timing of divergence between pairs of regions. HPDs are not shown where those intervals fall close to the means. Taxa with initials are used to clarify species within the same genus; *Elachistocleis n.* (=*nigrogularis*), *Pristimantis u.* (=*urichi*), *Chironius c.* (=*cochranae*), *Atractus f.* (=*fuliginosus*), *Atractus t.* (=*trilineatus*), *Bachia t.* (=*trinitatis*). Species with asterisks (*) have no reported genetic dating but with dating inferred approximately by the reported divergences. The reported timing of *Bachia trinitatis* is that in between Monos Island, a now-sunken, former Trinidad Northern Range mountain top, and Tobago (Pliocene); the second *Bachia* dating corresponds to the divergence between that in Trinidad and on Monos Island and Tobago (Miocene). All divergences are intraspecific except when marked with a "b" which demarks divergence between species. The blue sinusoidal curve diagramatically represents Pleistocene sea-level changes which frequently dropped to −50 m below sea level and on three occasions to −120 m below sea level and resulted in multiple dry land connections between Venezuela, Trinidad, and Tobago. GP – vertical dashed line gives approximate inception age of opening in the Gulf of Paria pull-apart basin (Jowers et al., 2024a). BG – vertical dashed line gives approximate inception age of opening in the Boca Grande sub-basin (data extracted from Alvarez et al., 2021) beneath the modern Dragon's Mouth channel (see Fig. 3) in the Gulf of Paria. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

colonization following eustatic sea level drops that might have allowed for the establishment of suitable conditions for the frogs to disperse. Beebe's toad *Rhinella beebei* in Trinidad is another example of an ancient divergence from the mainland Venezuela and Eastern Colombia, dating to 1.8 million years ago (Murphy et al., 2017). A similar date was recovered for the divergence between *Ninia franciscoi* from Trinidad and *N. atrata* from Tobago, dating to 2.2 Ma (Jowers et al., 2024b). Other ongoing unpublished studies on several taxa (i.e. *Pseudoboa neuwiedii, Ameiva atrigularis*, *Micrurus circinalis*) similarly suggests low level of genetic divergence in the region (Fig. 9).

Similar timings are recovered from the monophyletic clade of the Black Headed-Snake *Tantilla melanocephala* from Venezuela, Trinidad, and Tobago, which exhibits a 1.8 Ma divergence from its southern Guyana populations, and a 1.4 Ma divergence between the sister clade composed of Trinidad, Venezuela, and Tobago populations. The timing between Trinidad and Venezuela dates to 200 ka. These Pleistocene dates point to timely connections during lowstand dry periods connecting Venezuela to western Trinidad and Guyana to eastern Trinidad (e.g., Fig. 5f). This dating is in agreement with the clade composed of Coffee snakes from the Paria Peninsula and Trinidad, *Ninia franciscoi*, with a 170 ka divergence (Jowers et al., 2024b).

Phylogenetic work on the Three-Lined Snake *Atractus trilineatus* shows a split between the TMRCA of samples from Trinidad and Tobago dating to ~180 ka, while the Guyana and both Trinidad and Tobago *A. trilineatus* dates are older (~1 Ma). The most recent split between the mainland (Venezuela/Guyana) and Trinidad and Tobago dates to 410 ka. Murphy et al. (2019a) further argue for dispersal during Pleistocene lowstand event(s) (e.g., Fig. 5f) but, based on such recent dates, overwater dispersal events could not be ruled out, especially for the colonization of Tobago. The genetic similarity observed among presently disjunct populations from Venezuela and Trinidad of Robinson's mouse opossum, *Marmosa robinsoni*, is believed to be a consequence of recent Pleistocene fragmentation dating to 340 ka for the clade composed of specimens from the islands and Venezuela following a more extensive Pleistocene dispersal on coastal plains exposed during the last glacial maximum and older lowstand events (Gutiérrez et al., 2014).

The Smooth-Skinned Ditch Frog *Leptodactylus validus* in Trinidad and Tobago similarly shows molecular dating between the islands to be rather recent. Carmargo et al. (2009) found a mainland origin for *L. validus* that colonized Trinidad at 1.4 Ma, with subsequent and independent colonization of Tobago and the Lesser Antilles (at 0.4 Ma) from Trinidad. These results indicated a historical vicariant event between populations in Trinidad and Tobago from those in the Lesser Antilles.

Interestingly, the low levels of genetic divergence between Trinidad coral snakes to the Guianas (*Micrurus diutius*) and northern Venezuela populations (*M. circinalis*) suggests a vicariance event that occurred during the late Pleistocene to Holocene period. This Pleistocene-Holocene Trinidad-Guyana connection and the Trinidad-Venezuela (*M. circinalis*, MJJ unpublished) connection that this study established may be yet another example of an eastern dispersion corridor that developed on the eastern shelf during lowstand events (Fig. 5f) (Jowers et al., 2019). Comparably low genetic species divergence between *Elachistocleis surinamensis* from Guyana, French Guiana, and Trinidad also suggests Pleistocene colonization events along today's eastern shelf region through eustatic sea-level falls. Reconstruction of Pleistocene habitat and vegetation suggests that northern Venezuela and Trinidad were dry forests bordered by savannah to the south during that period. Similarly, Guyana and coastal Venezuela were covered by dry forests, surrounded by savanna (Melo França et al., 2015) throughout. *E. nigrogularis* and *E. surinamensis* in Trinidad today are found in similar habitats, such as tropical evergreen forest, marsh forests, and savannas, including anthropogenic savannas.

Many species show similar patterns of low genetic differentiation between the Paria Peninsula and Trinidad and Tobago. Evidence of this are the multiple endemics found either sharing populations in Trinidad and Tobago and in the Paria Peninsula and Trinidad (Rivas et al., 2021). An example is the frog *Pristimantis urichi*, endemic to both islands and with low genetic differentiation between populations. Jowers et al. (2021a) suggested recent connectivity between the islands, possibly through Pleistocene lowstand land-bridges and/or human introductions.

Another example that could indicate recent colonization via Holocene connections and/or human introductions is the Threadsnake *Epictia tenella* (Leptotyphlopidae) in Trinidad and northern South America. Murphy et al. (2016) compared Trinidad and mainland (Guyana) populations and found minimal genetic diversification between island and mainland specimens. Because *Epictia tenella* is a fossorial (underground-dwelling) snake that rarely comes to the surface it is unlikely to be an efficient colonizer, and this species could not conceivably move nor swim any great distance (< a few 100 m), during a single lifetime; it inhabits forests as well as more open habitats. Despite other hypotheses for its arrival in Trinidad (e.g., over-water rafting via flood-stage floating Orinoco and Amazon delta vegetation mats via the Guiana/North Equatorial current, human-mediated dispersal, and avian-mediated dispersal), low divergence and widespread geographic distribution seem to require very recent (i.e., Holocene) dispersal, but recent colonization via a land bridge cannot be ruled out entirely. A similar distribution is found in the until recently supposed endemic frog, *Letpdactylus nesiotus*, to the Icacos Peninsula of Trinidad (Ponssa et al., 2010), which was recently found in Guyana, Suriname and French Guiana with very low genetic differentiation between the island and the mainland populations (99 % identical based on the 16S rDNA gene fragment) (Jairam and Fouquet, 2018).

The Dwarf Marsupial frog *Flectonotus fitzgeraldi* from Trinidad, Tobago and the Paria Peninsula recovered very low genetic differentiation, reflecting low genetic variability (Smith et al., 2021). But, whereas the data showed highly similar genetic divergence between populations, the Trinidad and Tobago animals were more closely related to one another than they were to those from Venezuela. The lack of shared haplotypes suggests some degree of genetic isolation among all three localities but remains low, suggesting recent gene flow between populations. Further genomic studies of this group should focus on establishing the timing of speciation events, branching from last common ancestors, and the paleogeography of origin and dispersion.

Although Murphy et al. (2019a) did not conduct a time tree, their phylogenetic work on the Haw's dark ground snake *Erythrolamprus melanotus* from Trinidad and Tobago recovered the populations in a clade with very low genetic differentiation. Thus, the data would suggest recent gene flow. Similarly, the clade composed of the two Trinidad and Paria Peninsula individuals of *Chironius cochranae* reflects recent gene flow, and suggests a very recent colonization (Jadin et al., 2024). Rutherford's Vine Snake *Oxybelis rutherfordi* shows again a similar pattern of low genetic divergence between the two islands (Jadin et al., 2019, 2020) with a likely colonization from Trinidad toward Tobago.

5. Conclusions

Geogenomics provides an exciting new tool to explore and refine our understanding of the interplay between geology and biology. This possibility is revealed in our southeastern Caribbean study area through a relatively complex narrative of how geological events have shaped the evolutionary trajectories of a diverse set of rapidly evolving organisms. Ultimately both data sets must resolve into coherent stori of how the Earth and its organisms evolve and change. Combing both geological and biological (genetic) chronometers should make for the most robust stories.

The findings presented in this review highlight the intricate interplay between geological processes and biological diversification in the southeastern Caribbean, focusing on the mechanisms of genetic divergence and speciation. The concepts of vicariance, dispersal, and ecological pressures are key to understanding how geological events, such as tectonic movements and sea-level changes, have influenced the distribution and evolution of various organisms in Trinidad, Tobago, and the surrounding regions. Our conclusions include:

1) The genetic data from guppy populations in Trinidad suggest a colonization pattern from two geographic sources, likely driven by pull-apart tectonics and sea-level change. The separate Caroni and Oropuche guppy populations align with Pleistocene vicariance and dispersal events that affected these two groups sometime between 200 ka and 1.2 Ma. Similar pull-apart tectonic processes also affected the Golden Tree frog *Phytotriades auratus* hylid frog and its host giant bromeliad *Glomeropitcairnia erectiflora* of Trinidad and eastern Venezuela earlier in the Pliocene. 2) The presence of species such as the Glass Frog and Hallowell's Ground Snake in Tobago but absent in Trinidad indicates historical mainland to island land bridges during periods of low sea levels, allowing for migration and colonization. This pattern is corroborated by molecular dating, suggesting that vicariance and colonization events were influenced by geological changes over millions of years. 3) The divergence of species like *Rivulus hartii* and *Mannophryne trinitatis* reflects ancient geological connections between the Paria Peninsula and Trinidad, disrupted by more recent STEP and pull-apart tectonic activity. 4) Numerous species exhibited genetic divergences dating back to Pleistocene lowstand events, pointing to recurring opportunities for dispersal between landmasses as sea levels fluctuated. This connection emphasizes the importance of environmental changes in facilitating or restricting species movement and again, highlights opportunities for geologic insights. 5) Despite significant historical divergences, low levels of genetic differentiation among certain species between Trinidad and Tobago suggest ongoing gene flow and possible recent colonization events, likely influenced by both natural geological processes and human activities.

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CRediT authorship contribution statement

John C. Weber: Writing – review & editing, Writing – original draft, Project administration, Methodology, Formal analysis, Conceptualization. **Jeanette C. Arkle:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Laurent de Verteuil:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **John C. Murphy:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis. **Nigel C. Noriega:** Writing – review & editing, Writing – original draft, Investigation. **David N. Reznick:** Writing – review & editing, Writing – original draft, Investigation. **Michael J. Jowers:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

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Data availability

Data will be made available on request.

References

Aitken, T., Mann, P., Escalona, A., Christeson, G.L., 2011. Evolution of the Grenada and Tobago basins and implications for arc migration. Mar. Pet. Geol. 28, 235–258.

Alexander, H.J., Taylor, J.S., Sze-Tsun, Wu, S., Breden, F., 2006. Parallel Evolution and Vicariance in the Guppy (*Poecilia Reticulata*) over Multiple Spatial and Temporal Scales. Evolution 60, 2352. https://doi.org/10.1554/06-288.1.

Algar, S.T., 1993. Structural, Stratigraphic, and Thermo-Chronological Evolution of Trinidad. Ph.D. thesis,. Dartmouth College.

Algar, S., Pindell, L., 1993. Structure and deformation history of the Northern Range of Trinidad and adjacent areas. Tectonics 12, 814–829.

Ali, J.R., Hedges, S.B., 2021. Colonizing the Caribbean: New geological data and an updated land-vertebrate colonization record challenge the GAARlandia land-bridge hypothesis. J. Biogeogr. 48, 2699–2707. https://doi.org/10.1111/jbi.14234.

Allen, R.W., Collier, J.S., Stewart, A.G., Henstock, T., Goes, A., Rietbrock, A., The VoiLA Team, 2019. The role of arc migration in the development of the Lesser Antilles: A new tectonic model for the Cenozoic evolution of the eastern Caribbean. Geology 47, 891–895. https://doi.org/10.1130/G46708.1.

Alvarez, T.G., Mann, P., Wood, L.J., 2021. Tectonic evolution of sedimentary basins around the arcuate southeastern margin of the Caribbean plate. In: Bartolini, C. (Ed.), South America–Caribbean–Central Atlantic Plate Boundary: Tectonic Evolution, Basin Architecture and Petroleum Systems, vol. 123. AAPG Memoir, pp. 183–238.

Arkle, J., Weber, J., Enklemann, E., Owen, L., 2014. Exhumation in the Southeastern Caribbean Plate Corner, (Poster), Thermochron-2014 Conference. Chamonix, France.

Arkle, J., Owen, L., Weber, J., Caffee, M., Hammer, S., 2017a. Transient Quaternary erosion and tectonic inversion of the Northern Range, Trinidad. Geomorphology 295, 337–353. https://doi.org/10.1016/j.geomorph.2017.07.013.

Arkle, J.C., Owen, L.A., Weber, J.C., 2017b. Geomorphology and Quaternary Landscape Evolution of Trinidad and Tobago. In: Allen, C.D. (Ed.), Landscapes and Landforms of the Lesser Antilles Volume, Geomorphological Landscapes of the World. Springer Publications, pp. 267–291.

Arkle, J., Weber, J., Enkelmann, E., Owen, L., Govers, R., Denison, C., O'Sullivan, P., Donelick, R., 2021. Exhumation of the coastal metamorphic belt above the subduction-to-transform transition in the Southeast Caribbean plate corner. Tectonics 40, e2020TC006414. https://doi.org/10.1029/2020TC006414.

Audemard, F.A., 2009. Key issues on the post-Mesozoic Southern Caribbean Plate boundary, *in* James, K.H., Lorente, M.A., Pindell, J.L., (Eds.) *the origin and evolution of the Caribbean Plate*. Geol. Soc. Lond. Spec. Publ. 328, 569–586.

Babb, S., Mann, P., 1999. Structural and Sedimentary Development of a Neogene Transpressional Plate Boundary between the Caribbean and South America Plates in Trinidad and the Gulf of Paria. In: Hsü, K. (Ed.), Sedimentary Basins of the World, 4. Elsevier, pp. 495–557.

Bacon, C., Silvestro, D., Jaramillo, C., Smith, B.T., Chakrabarty, P., Antonelli, A., 2015. Biological evidence supports an early and complex emergence of the Isthmus of Panama. PNAS 112, 6110–6115. https://doi.org/10.1073/pnas.1423853112.

Baillie, L., 2012. Genetic Population Structure of the Trinidadian Guppy (*Poecilia reticulata)* across Trinidad and Tobago. M.S. Thesis,. Dalhousie University, p. 154.

Bajolet, F., Chardon, D., Rouby, D., Dal'Asta, M., Loparev, A., Couëffe, R., Roig, J.-Y., 2022. The sediment routing systems of northern South America since 250 Ma. Earth Sci. Rev. 232, 104139.

Baker, P., Fritz, S., Dick, C., Eckert, A., Horton, B., Manzoni, S., Ribas, C., Garzione, C., Battisi, D., 2014. The emerging field of *geogenomics*: Constraining geological problems with genetic data. Earth Sci. Rev. 135, 38–47.

Barr, K.W., 1963. The Geology of the Toco District, Trinidad. W. I. Overseas Geological Surveys. Her Majesty's Stationary Office, London.

Bartolini, C., 2021. (Ed.,), South America–Caribbean–Central Atlantic plate boundary: Tectonic evolution, basin architecture, and petroleum systems. Am. Assoc. Petr. Geol. Mem. 123, 782.

Batten, D.J., 1996. 26A Palynofacies and paleoenvironmental interpretation. In: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Applications, vol. 3. AASP Foundation, pp. 913–918.

Bezada, M.J., Levander, A., Schmandt, B., 2010. Subduction in the southern Caribbean: Images from finite-frequency P wave tomography. J. Geophys. Res. 115, B12333. https://doi.org/10.1029/2010JB007682.

Boomert, A., 2000. Gateway to the mainland: Trinidad and Tobago (chapter 10). In: Kergran, W.F., Hoffman, C., Rodríguez-Ramos, R. (Eds.), The Oxford Handbook of Caribbean Archeology, pp. 141–154.

Boos, H., 1984. A consideration of the terrestrial reptile fauna on some offshore islands north west of Trinidad, living World. J. Trinidad and Tobago Field Naturalists' Club. 19–26.

Bouysse, P., 1988. Opening of the Grenada back-arc basin and evolution of the Caribbean plate during the Mesozoic and early Paleogene. Tectonophysics 149, 121–143.

Bouysse, P., García Reyes, A., de Lépinay, M.B., Ellouz-Zimmermann, N., Pubellier, M., Sautter, B., 2021. Structural Map of the Caribbean, Commission for the Geological Maps of the World (CGMW-CGMW), 1st edition, 1:4,000,000.

Brandon, M., Roden-Tice, M., Garver, J., 1998. Late Cenozoic exhumation of the Cascadia accretionary wedge in the Olympic Mountains, Northwest Washington State. Geol. Soc. Am. Bull. 110, 985–1009.

Braszus, B., Goes, S., Allen, R., Rietbrock, A., Collier, J., Harmon, N., Henstock, T., Hicks, S., Rychert, C., Maunder, B., van Hunen, J., Bie, L., Blundy, J., Cooper, G., Davy, R., Kendall, J., Macpherson, C., Wilkinson, J., Wilson, M., 2021. Subduction history of the Caribbean from upper-mantle seismic imaging and plate reconstruction. Nature 12, 4211. https://doi.org/10.1038/s41467-021-24413-0.

Burke, K., 1988. Tectonic evolution of the Caribbean. Annu. Rev. Earth Planet. Sci. 16, 201–230.

Camargo, A., Heyer, W.R., de Sá, R.O., 2009. Phylogeography of the frog Leptodactylus validus (Amphibia: Anura): patterns and timing of colonization events in the Lesser Antilles. Mol. Phylogenet. Evol. 53 (2), 571–579.

Carr-Brown, B., 2008. The Contribution of Trinidad Micropaleontology to Global E&P, Trinidad and Tobago: The Black Gold Book: Commemorating a Century of Oil and Gas Production. First Publishing, London, pp. 178–190. https://firstforum.org/publishing/specialistpublishing/trinidad-tobago-the-black-gold-book/.

Carvalho, G., Shaw, P., Magurran, A., Seghers, B., 1991. Marked genetic divergence revealed by the allozymes among populations of the guppy *Poecilia reticulata* (Poeciliidae), in Trinidad. Biol. J. Linn. Soc. 42, 389–405.

Castillo, K., Mann, P., 2021. Structure, stratigraphy, and hydrocarbon potential of the easternmost part of the Eastern Venezuelan foreland basin. In: Bartolini, C. (Ed.), South America–Caribbean–Central Atlantic Plate Boundary: Tectonic Evolution, Basin Architecture, and Petroleum Systems, vol. 123. AAPG Memoir, pp. 591–620.

Cedeño, A., Ahmed, M., Escalona, A., Abrahamson, P., 2021. Tectono-stratigraphic evolution of the western Barbados Accretionary Prism and the Tobago Basin: Implications for petroleum systems. In: Bartolini, C. (Ed.), South America–Caribbean–Central Atlantic Plate Boundary: Tectonic Evolution, Basin Architecture, and Petroleum Systems, vol. 123. AAPG Memoir, pp. 649–676.

Cerveny, P., Snoke, A., 1993. Thermochronological data from Tobago, west Indies: Constraints on the cooling and accretion history of the Mesozoic oceanic-arc rocks in the southern Caribbean. Tectonics 12, 433–440.

Chen, S., Steel, R., Dixon, J., Osman, A., 2014. Facies and architecture of a tide-dominated segment of the late Pliocene Orinoco Delta (Morne L'Enfer Formation) SW Trinidad. Mar. Pet. Geol. 57, 208–232.

Chen, S., Steel, R., Olariu, C., 2016. Upper-slope to shelf-edge delta architecture, Miocene Cruse Formation, Orinoco shelf margin, Trinidad. J. Sediment. Res. 86, 87–106. https://doi.org/10.2110/jsr.2016.7.

Chen, S., Steel, R., Olariu, C., Li, S., 2017. Growth of the paleo-Orinoco shelf-margin prism: Process regimes, delta evolution, and sediment budget beyond the shelf edge. Geol. Soc. Am. Bull. 130, 35–61. https://doi.org/10.1130/B31553.1.

Chen, S., Steel, R., Olariu, C., Li, S., 2018. Growth of the paleo-Orinoco shelf-margin prism: Process regimes, delta evolution, and sediment budget beyond the shelf edge. Bulletin 130 (1–2), 35–63.

Chen, Y.-W., Coli, L., Bird, D., Wu, J., Zhu, H., 2021. Caribbean plate titled and actively dragged eastwards by low-viscosity asthenospheric flow. Nature 12, 1603. https://doi.org/10.1038/s41467-021-21723-1.

Chen, Y.-W., Wu, J., Goes, S., 2024. Lesser Antilles slab reconstruction reveals lateral slab dragging under the Caribbean since 50 Ma. EPSL 627, 118561.

Clark, S.A., Sobiesiak, M., Zelt, C.A., Magnani, M.B., Miller, M.S., Bezada, M.J., Levander, A., 2008. Identification and tectonic implications of a tear in the south American plate at the southern end of the Lesser Antilles. Geochem. Geophys. Geosyst. 9, Q11004. https://doi.org/10.1029/2008GC002084.

Cross, N.E., Williams, Z.K., Jamankulov, A., Bostic, C.E., Gayadeen, V.C., Torrealba, H.J., Drayton, E.S., 2015. The dynamic behavior of shallow marine reservoirs: Insights from the Pliocene of offshore North Trinidad. AAPG Bull. 99, 555–583.

Cruz, L., Fayon, A., Teyssier, C., Weber, J., 2007, Exhumation and deformation processes in transpressional orogens: the Venezuelan Paria Peninsula, SE Caribbean-South American plate boundary, and the Southern Alps, New Zealand, GSA Special Paper 434, Exhumation Associated With Continental Strike-Slip Fault Systems, 149-165. (4.768, 22, 13).

de Verteuil, L., Weber, J.C., Ramlal, B., Gonzalez Alfonso, J.A., 2005. Geological Map of Trinidad. Republic of Trinidad and Tobago: Latinum Geological Consultants Limited.

Diaz de Gamero, M., 1996. The changing course of the Orinoco River during the Neogene: a review. Palaeogeogr. Palaeoclimatol. Palaeoecol. 123, 385–402.

Dodson, M.H., 1973. Closure temperature in cooling geochronological and petrological systems. Contrib. Mineral. Petrol. 40, 259–274. https://doi.org/10.1007/BF00373790.

Donovan, S., Jackson, T., 2010. Classic localities explained 6: Tobago. Geol. Today 26, 233–239.

Duerto, L., McClay, K., 2011. Role of the shale tectonics on the evolution of the Eastern Venezuelam Cenozoic thrust and fold belt. Mar. Pet. Geol. 28, 81–108.

Dyer, B.L., Cosgrove, P., 1992. Penal/Barrackpore field – West Indies, South Trinidad basin, Trinidad. In: Beaumont, E.A., Foster, N.H. (Eds.), Structural Traps VII. American Association of Petroleum Geologists, Tulsa, OK, pp. 139–157.

Elling, R., Philip Farfan, P., Weber, J., 2021. Cunapo Conglomerate, Northern Basin Floor and North Flank of the Central Range, Trinidad: Neogene Syn-Contractile or Syn-Transpressional Tectonic Marker Unit – Field and Petrographic Study. In: Bartolini, C. (Ed.), American Association of Petroleum Geology Memoir 123: Eastern Caribbean-Northeast South American Boundary–Tectonic Evolution, Basin Architecture, and Petroleum Systems.

England, P., Molnar, P., 1990. Surface uplift, uplift of rocks, and exhumation of rocks. Geology 18, 1173–1177.

Erlich, R., Barrett, S., 1990. Cenozoic plate tectonic history of the northern Venezuela-Trinidad area. Tectonics 9, 161–184.

Erlich, R., Barrett, S., 1992. Petroleum Geology of the eastern Venezuela Foreland Basin, American Association of Petroleum Geologists Memoir 55. Foreland Basins Fold Belt. 341–362.

Escalona, A., Mann, P., 2011. Tectonics, basin subsidence mechanisms, and paleogeography of the Caribbean-south American plate boundary zone. Mar. Pet. Geol. 28, 8–39.

Escalona, A., Ahmad, S.S., Watson, L., 2021. Late Cretaceous–Pliocene paleogeography of the circum-Caribbean region based on quantitative plate reconstruction and georeferenced databases. In: Bartolini, C. (Ed.), South America–Caribbean–Central Atlantic Plate Boundary: Tectonic Evolution, Basin Architecture, and Petroleum Systems: Am. Assoc. Petr. Geol. Mem, vol. 123, pp. 513–538.

Escalona, A., Norton, I., Lawver, L., Gaghan, L., 2021a. Quantitative plate tectonic reconstructions of the Caribbean region from Jurassic to present. In: Bartolini, C. (Ed.), South America–Caribbean–Central Atlantic plate boundary: Tectonic Evolution, Basin Architecture, and Petroleum Systems: Am. Assoc. Petr. Geol. Mem, 123, pp. 239–264.

Fajen, A., Breden, F., 1992. Mitochondrial DNA sequence variation among natural populations of the Trinidad guppy *Poecilia reticulata*. Evolution 46, 1457–1465. https://doi.org/10.1111/j.1558-5646.1992.tb01136.x.

Farley, K., 2000. Helium diffusion from apatite: General behavior as illustrated by Durango floroapatite. J. Geophys. Res. 105, 2903–2914.

Flinch, J., Rambaran, V., Ali, W., De Lisa, V., Hernández, G., Rodrigues, K., Sams, R., 1999. Structure of the Gulf of Paria Pull-apart Basin (Eastern Venezuela-Trinidad). In: Hsü, K. (Ed.), Sedimentary Basins of the World, vol. 4. Elsevier, pp. 477–494.

Flowers, R., Ketcham, R., Schuster, D., Farley, K., 2009. Apatite (U-Th)/he thermochronology using a radiation damage accumulation and annealing model. Geochim. Cosmochim. Acta 73, 2347–2365.

Frost, C., Snoke, A., 1988. Tobago, West Indies, a fragment of a Mesozoic island arc: petrochemical evidence. J. Geol. Soc. Lond. 146, 953–964.

Gamble, T., Simons, A.M., Colli, G.R., Vitt, L.J., 2008. Tertiary climate change and the diversification of the Amazonian gecko genus Gonatodes (Sphaerodactylidae, Squamata). Mol. Phylogenet. Evol. 46, 269–277.

Genarro, I., Weber, J., Brovarone, A., Chu, X., Arkle, J., 2022. Geothermometric constraints on the thermal architecture, metamorphism, and exhumation of the Northern Range, Trinidad. J. Metamorph. Geol. 41, 327–349. https://doi.org/10.1111/jmg.12697.

Giorgis, S., Weber, J., Sanguinito, S., Beno, C., Metcalf, J., 2017. Thermochronology constraints on Miocene exhumation in the Central Range Mountains, Trinidad. Geol. Soc. Am. Bull. 129, 171–178. https://doi.org/10.1130/B31363.1.

Govers, R., Wortel, M.J.R., 2005. Lithosphere tearing at STEP faults; response to edges of subduction zones. EPSL 236, 505–523. https://doi.org/10.1016/j.epsl.2005.03.022.

Green, P.F., Duddy, I.R., Gleadow, A.J.W., Tingate, P.R., Laslett, G.M., 1986. Thermal annealing of fission-tracks in apatite: 1. A quantitative description. Chem. Geol. Isot. Geosci. Sect. 59, 237–253. https://doi.org/10.1016/0168-9622(86)90074-6.

Gutiérrez, E.E., Anderson, R.P., Voss, R.S., Ochoa-G, J., Aguilera, M., Jansa, S.A., 2014. Phylogeography of *Marmosa robinsoni*: insights into the biogeography of dry forests in northern South America. J. Mammal. 95, 1175–1188.

Haffer, J., 1997. Alternative models of vertebrate speciation in Amazonia: an overview. Biodivers. Conserv. 6, 451–476.

Higgins, M., LaFemina, P., Weber, J., Geirsson, H., Ryan, G., 2021. Strain partitioning and interseismic fault behavior along the Caribbean-South American transform plate boundary. Tectonics. https://doi.org/10.1029/2021TC006740.

Hippolyte, J.-C., Mann, P., 2021. Neogene paleostress and structural evolution of Trinidad: Rotation, strain partitioning, and strike-slip reactivation of an obliquely colliding thrust belt. In: Bartolini, C. (Ed.), South America–Caribbean–Central Atlantic Plate Boundary: Tectonic Evolution, Basin Architecture, and Petroleum Systems: Tectonic Evolution, Basin Architecture, and Petroleum Systems: AAPG Memoir, vol. 123, pp. 317–346.

Hoorn, C., Wesselingh, F.P., Hovikoski, J., Guerrero, J., 2010a. The development of the amazonian mega-wetland (Miocene; Brazil, Colombia, Peru, Bolivia). Amazo. Landsc. Spec. Evolut.: A Look Into The Past 123, 142.

Hoorn, C., Wesselingh, F.P., Ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Antonelli, A., 2010b. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science 330 (6006), 927–931.

Inger, R.F., Voris, H.K., 2001. The biogeographical relations of the frogs and snakes of Sundaland. J. Biogeogr. 28, 863–891.

Jadin, R., Blair, C., Jowers, M., Carmona, A., Murphy, J., 2019. Hiding in the lianas of the tree of life: molecular phylogenetics and species delimitation reveal considerable cryptic diversity of New World Vine Snakes. Mol. Phylogenet. Evol. 134, 61–65.

Jadin, R.C., Blair, C., Orlofske, S.A., Jowers, M.J., Rivas, G.A., Vitt, L.J., Ray, J.M., Smith, E.N., Murphy, J.C., 2020. Not withering on the evolutionary vine: systematic revision of the Brown Vine Snake (Reptilia: Squamata: Oxybelis) from its northern distribution. Org. Divers. Evol. 20, 723–746.

Jadin, R.C., Jowers, M.J., Blair, C., Ludwig, R.K., Salgado-Irazabal, X., Murphy, J.C., 2024. Rectifying a century of misidentifications: a taxonomic re-evaluation of sipo snakes (Colubridae: Chironius) on Trinidad. Syst. Biodivers. 22, 2338064. https://doi.org/10.1080/14772000.2024.2338064.

Jairam, R., Fouquet, A., 2018. First records of *Leptodactylus nesiotus* (Anura: Leptodactylidae) for Guyana, Suriname and French Guiana. Herpetol. Notes. 11, 997–999.

James, K., 2009. *In situ* origin of the Caribbean: discussion of data. In: James, K., Lorente, M., Pindell, J. (Eds.), The Origin and Evolution of the Caribbean Plate. Geol. Soc, 328. Special Publications, London, pp. 77–125. https://doi.org/10.1144/SP328.3 0305-8719/09.

Jaramillo, C., Romero, I., D'Apolito, C., Bayona, G., Duarte, E., Louwye, S., Wesselingh, F.P., 2017. Miocene flooding events of western Amazonia. Sci. Adv. 3 (5), e1601693.

Jowers, M.J., Cohen, B.L., Downie, J.R., 2008. The Cyprinodont fish Rivulus (Aplocheiloidei: Rivulidae) in Trinidad and Tobago: molecular evidence for marine dispersal, genetic isolation and local differentiation. J. Zool. Syst. Evol. Res. 46, 48–55.

Jowers, M.J., Martínez-Solano, I., Cohen, B.L., Manzanilla, J., Downie, R.J., 2011. Genetic differentiation in the Trinidad endemic *Mannophryne trinitatis* (Anura: Aromobatidae): Miocene vicariance, in situ diversification and lack of geographical structuring across the island. Journal of. J. Zool. Syst. Evol. Res. 49, 133–140.

Jowers, M.J., Lehtinen, R.M., Downie, R.J., Georgiadis, A.P., Murphy, J.C., 2015. Molecular phylogenetics of the glass frog *Hyalinobatrachium orientale* (Anura: Centrolenidae): evidence for Pliocene connections between mainland Venezuela and the island of Tobago. Mitochondrial DNA 26, 613–618.

Jowers, M.J., Garcia Mudarra, J.L., Charles, S.P., Murphy, J.C., 2019. Phylogeography of West Indies Coral snakes (Micrurus): Island colonisation and banding patterns. Zool. Scr. 48, 263–276.

Jowers, M., Rivas, G., Jadin, R., Braswell, A., Auguste, R., Borzée, A., Murphy, J., 2020. Unearthing the species diversity of a cryptozoic snake, *Tantilla melanocephala*, in its northern distribution with emphasis to the colonization of the Lesser Antilles. Amphib. Reptile Conserv. 14, 206–217.

Jowers, M., Sánchez-Ramírez, S., Greener, M., Harper, L., Auguste, R., Marshall, T., Thomson, R., Byrne, I., Loughrey, C., Graham, L., McGhee, W., Murphy, J., Rivas, G., Beyts, C., Downie, J., 2021a. Ecology, conservation status, and phylogenetic placement of endemic *Pristimantis* frogs (Anura: Craugastoridae) in Trinidad and Tobago and genetic affinities to Northern Venezuela. Popul. Ecol. 2021, 1–14.

Jowers, M., Schargel, W., Muñoz-Mérida, A., Sánchez-Ramírez, S., Weber, J., Faria, J., Harris, D., Murphy, J., 2021b. The enigmatic biogeography of Tobago's marooned relics: the case study of a fossorial snake (Squamata, *Dipsadidae*). J. Zool. Syst. Evol. Res. 59, 1–8.

Jowers, M., Othman, S., Borzée, A., Rivas, G., Sánchez-Ramírez, Auguste R., Downie, J., Read, M., Murphy, J., 2021c. Unravelling unique island colonization events in Elachistocleis frogs: Phylogeography, cryptic divergence, and taxonomical implications. Organisms Diversity and Evolution Org. Divers. Evol. 21, 189–206.

Jowers, M.J., Muñoz-Pajares, J., Weber, J., Arcke, J., Arenas-Castro, S., Ho, S., Rivas, G., Murphy, J., Borzée, A., Pyron, R., Perez-Losada, M., De Freitas, M., Downie, R., Moreno-Rueda, G., Forcina, G., Sánchez-Ramírez, S., 2024a. Testing molecular date estimates using an ecological and vicariant case study in treefrogs: the Geological-Ecological Molecular Calibration. J. Biogr. 51, 2136–2151. https://doi.org/10.1111/jbi.14971.

Jowers, M.J., Ortigoza Dempster, O.C., Sierra-Angarita, T., Hurtado, J.P., Borzée, A., Murphy, J.C., Rivas, G., Ingrasci, M., Smith, E.N., 2024b. Biogeography and hidden cryptic diversity in the South American snake species complex *Ninia atrata* (Dipsadinae). under review.

Kugler, H.G., 1959. Treatise on the Geology of Trinidad, Part 2: Geological Map of Trinidad; Geological Sections through Trinidad: Port of Spain, Petroleum Association of Trinidad, scale 1:100,000. 1 sheet.

Kugler, H.G., 2001. Treatise on the Geology of Trinidad, Part 4: The Paleocene to Holocene Formations of Trinidad. Museum of Natural History, Basel, p. 309.

Lapointe, B., Langton, R., Bedford, B., Potts, A., Day, O., Hu, C., 2010. Land-based nutrient enrichment of the Buccoo Reef complex and fringing reefs of Tobago, West Indies. Mar. Pollut. Bull. 60, 334–343.

Laydoo, R.S., 1991. A Guide to the Coral Reefs of Tobago. Institute of Marine Affairs and the Asa Wright Nature Centre. Republic of Trinidad & Tobago.

Leroy, S., Mauffret, A., Patriat, P., Mercier de Lépinay, B., 2000. An alternative interpretation of the Cayman trough evolution from reidentification of magnetic anomalies. Geophys. J. Int. 141, 539–557.

Levander, A., Bezada, M.J., Niu, F., Humphreys, E.D., Palomeras, I., Thurner, S.M., Masy, J., Schmitz, M., Gallart, J., Carbonell, R., Miller, M.S., 2014. Subduction-driven recycling of continental margin lithosphere. Nature 515, 253–256. https://doi.org/10.1038/nature13878.

Lingrey, S., 2007. Plate tectonic setting and Cenozoic deformation of Trinidad: Foldbelt Restoration in a Region of significant Strike-Slip, 163-178. In: Lacombe, O., Roure, F., Lavé, J., Vergés, J. (Eds.), Thrust Belts and Foreland Basins. Frontiers in Earth Sciences. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-69426-7_9.

Lugo, J., Audemard, F.E., 2021. Cretaceous to Neogene arc-continent collision, orogenic float development, and implications on the petroleum systems of northern Venezuela. In: Bartolini, C. (Ed.), South America–Caribbean–Central Atlantic Plate Boundary: Tectonic Evolution, Basin Architecture, and Petroleum Systems, vol. 123. AAPG Memoir, pp. 1–84.

MacPhee, R.D.E., Iturralde-Vinent, M.A., 1994. First Tertiary land mammal from Greater Antilles: an early Miocene sloth (Xenarthra, Megalonychidae) from Cuba. Am. Mus. Novit. 3094, 1–13.

Magurran, A., 2005. Evolutionary Ecology: The Trinidadian Guppy. Oxford University Press, p. 193.

Mann, P., 1999. Caribbean sedimentary basins: Classification and tectonic setting from Jurassic to present. In: Mann, P. (Ed.), Caribbean Basins, 4. Elsevier Sedimentary Basins of the World, pp. 3–31.

Manzanilla, J., Jowers, M.J., La Marca, E., Garcia-París, M., 2006. Taxonomic reassessment of *Mannophryne trinitatis* (Anura: Dendrobatidae) with the description of a new species from Venezuela. Herpetol. J. 17, 31–42.

Manzanilla, J., La Marca, E., García-París, M.A., 2009. Phylogenetic patterns of diversification in a clade of Neotropical frogs (Anura: Aromobatidae: Mannophryne). Biol. J. Linn. Soc. 97, 185–199.

Martinius, Allard W., Hegner, Jan, Kaas, Inge, Bejarano, Celia, Mathieu, Xavier, Mjøs, Rune, 2013. Geologic reservoir characterization and evaluation of the Petrocedeño Field, early Miocene Oficina Formation, Orinoco Heavy Oil Belt, Venezuela. In: Hein, F.J., Leckie, D., Larter, S., Suter, J.R. (Eds.), Heavy- oil and oil-sand petroleum systems in Alberta and beyond: AAPG Studies in Geology, 64, pp. 103–131.

Maxwell, J.C., 1948. Geology of Tobago, British West Indies. Geol. Soc. Am. Bull. 59, 801–854.

Melo França, L., Asevedo, L., Trindade Dantas, M.A., Bocchiglieri, A., Santos Avilla, L., Pereira Lopes, R., Lopes da Silva, J.L., 2015. Review of feeding ecology data of late Pleistocene mammalian herbivores from South America and discussions on niche differentiation. Earth Sci. Rev. 140, 158–165.

Meredith, R., Pires, M., Reznick, D., Springer, M., 2010. Molecular phylogenetic relationships and the evolution of the placenta in Poecilia (Micropoecilia) (Poeciliidae: Cyprinodontiformes). Mol. Phylogenet. Evol. 55, 631–639.

Meschede, M., Frisch, W., 1998. A plate-tectonic model for the Mesozoic and early Cenozoic history of the Caribbean plate. Tectonophysics 296, 269–291.

Montes, C., Cardona, A., McFadden, R., Morón, S., Silva, C., Restrepo-Moreno, S., Ramírez, D., Hoyos, N., Wilson, J., Farris, D., Bayona, G., Jaramillo, C., Valencia, V., Bryan, J., Flores, J., 2012a. Evidence for middle Eocene and younger land emergence in Central Panama: Implications for Isthmus closure. Geol. Soc. Am. Bull. 124, 780–799. https://doi.org/10.1130/B30528.1.

Montes, C., Bayona, G., Cardona, A., Buchs, D., Silva, A., Morón, S., Hoyos, N., Ramírez, D., Jaramillo, C., Valencia, V., 2012b. Arc-continent collision and orocline formation: closing of the central American seaway. J. Geophys. Res. 117, B04105.

Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J., Valencia, V., Ayala, C., Pérez-Angel, L., Rodriguez-Parra, I., Ramirez, V., Niño, H., 2015. Middle Miocene closure of the central American seaway. Science 348 (6231), 226–229.

Moonan, X., Weber, J., Arkle, J., Giorgis, S., Hippolyte, J.-C., Ringerwole, N., 2017. Tobago: Exploring Connections between the Onshore and Offshore Geology & Paleo- and Neo-Tectonics.

Muhs, D., Simmons, K., Schumann, R., Halley, R., 2011. Sea-level history of the past two interglacial periods: new evidence from U-series dating of reef corals from South Florida. Quat. Sci. Rev. 30, 570–590.

Müller, R.D., Royer, J.-Y., Cande, S.C., Roest, W.R., 1999. New constraints on cretaceous/Tertiary plate tectonic evolution of the Caribbean. In: Hsü, K. (Ed.), Sedimentary Basins of the World, vol. 4. Elsevier, pp. 495–557.

Murphy, J.C., Rutherford, M., Jowers, M.J., 2016. The threadsnake tangle: lack of genetic divergence in *Epictia tenella* (Squamata, Leptotyphlopidae): evidence for introductions or recent rafting to the West Indies. Stud. Neotropical Fauna Environ. 51, 197–205.

Murphy, J.C., Angarita, S.T., Downie, J.R., Jowers, M.J., 2017. Toads, tall mountains and taxonomy: the Rhinella granulosa group (Amphibia: Anura: Bufonidae) on both sides of the Andes. Salamandra 53, 267–278.

Murphy, J.C., Salvi, D., Braswell, A., Jowers, M., 2019a. Phylogenetic Position and Biogeography of the Three-Lined Snake *Atractus trilineatus* (Squamata, Dipsadidae) in the Eastern Caribbean. Herpetologica 75, 247–253.

Murphy, J.C., Salvi, S., Santos, J., Braswell, A., Charles, S., Borzée, A., Jowers, M., 2019b. The reduced limbed lizards of the genus Bachia (Reptilia, Squamata, Gymnophthalmidae); biogeography, cryptic diversity and morphological convergence in the eastern Caribbean. Organ. Diver. & Evolut. Org Divers. Evol. 19, 321–340.

Murphy, J.C., Weber, J.C., Jowers, M.J., Jadin, R.C., 2023. Two Islands, two Origins. Islands and Snak.: Diversi. Conservat. 2, 81.

Neill, I., Kerr, A., Chamberlin, K., Schmitt, A., Urbani, F., Hastie, A., Pindell, J., Barry, T., Milar, I., 2014. Vestiges of the proto-Caribbean seaway: Origin of the San Souci Volcanic Group, Trinidad. Tectonophysics 626, 170–185.

Osman, A., Moonan, X., Ramsook, R., Steel, R.J., 2021. A review of the tectonic evolution and sedimentary fill of the Southern Basin, Trinidad, Middle cretaceous to Pleistocene. In: Bartolini, C. (Ed.), South America–Caribbean– Central Atlantic plate boundary: Tectonic evolution, basin architecture, and petroleum systems: Am. Assoc. Petroleum Geologists, Bull. Mem, pp. 621–648.

Parra, M., Sánchez, G., Montilla, Oswaldo M., Guzmán, J., Namson, J., Jácome, M., 2011. The Monagas Fold–Thrust Belt of Eastern Venezuela. Part I: Structural and thermal modeling. Mar. Pet. Geol. 28, 40–69. https://doi.org/10.1016/j.marpetgeo.2010.01.001.

Payne, N., 1991. An Evaluation of Post-Middle Miocene Geological Sequences, Offshore Trinidad, Transactions of the 2nd Geological Conference of the Geological Society of Trinidad and Tobago. Port-of-Spain, Trinidad.

Pérez, O., Bilham, R., Bendick, R., Velandia, J., Moncayo, C., Hoyer, M., Kozuch, M., 2001. Velocity field across the southern Caribbean plate boundary and estimates of Caribbean/south American plate motion using GPS geodesy 1994-2000. Geophys. Res. Lett. 28 (15), 2987–2990. https://doi.org/10.1029/2001GL013183.

Persad, K.M., 2011. The Petroleum Geology and Geochemistry of Trinidad and Tobago. Treatise of Petroleum, Trinidad and Tobago, Atlas One, First Edition, The Southern Energy Research Centre, p. 585.

Pindell, J.L., Kennan, L., 2007. Cenozoic kinematics and dynamics of oblique collision between two convergent plate margins: the Caribbean–South America collision in Eastern Venezuela, Trinidad and Barbados. In: Transactions of GCSSEPM 27th Annual Bob F. Perkins Research Conference, pp. 458–553.

Pindell, J., Kennan, L., 2009. Tectonic evolution of the Gulf of Mexico, Caribbean and northern South America in the mantle reference frame: an update. In Geol. Soc. Spec. Publ. 328, 1–55. https://doi.org/10.1144/SP328.1.

Pindell, J.L., Higgs, R., Dewey, J.F., 1998. Cenozoic palinspastic reconstruction, paleogeographic evolution, and hydrocarbon setting of the northern margin of South America. In: Pindell, J.L., Drake, C.L. (Eds.), Paleogeographic Evolution and Non-glacial Eustasy, Northern South America: SEPM (Society for Sedimentary Geology), vol. 58. Special Publication, pp. 45–86.

Ponssa, M.L., Jowers, M.J., De Sa, R., 2010. Osteology, natural history notes, and phylogenetic relationships of the poorly known Caribbean frog Leptodactylus nesiotus (Anura, Leptodactylidae). Zootaxa 2646, 1–25.

Potter, H.C., 1968. A preliminary account of the stratigraphy and structure of the eastern part of the Northern Range, Trinidad. In: Transactions of the Fourth Caribbean Geological Conference, Trinidad, pp. 15–20.

Potter, H.C., 1973. The overturned anticline of the Northern Range of Trinidad near Port of Spain. J. Geol. Soc. Lond. 129, 133–137. https://doi.org/10.1144/gsjgs.129.2.0133.

Punnette, S., Mann, P., 2021. Subsurface structure of the Hinge Line fault zone and its control on the distribution of gas fields of the North Coast marine area of offshore northern Trinidad. In: Bartolini, C. (Ed.), South America–Caribbean– Central Atlantic Plate Boundary: Tectonic Evolution, Basin Architecture, and Petroleum Systems, vol. 123. AAPG Memoir, pp. 357–386.

Punnette, S., Wood, L., Mann, P., 2021. Pleistocene to Holocene sedimentary evolution of the North Coast Marine Area, offshore Trinidad. In: Bartolini, C. (Ed.), South America–Caribbean–Central Atlantic Plate Boundary: Tectonic Evolution, Basin Architecture, and Petroleum Systems, vol. 123. AAPG Memoir, pp. 563–590.

Reiners, P.W., 2005. Zircon (U–Th)/he thermochronometry. Rev. Mineral. Geochem. 58, 151–179. https://doi.org/10.2138/rmg.2005.58.6.

Ringerwole, N., Weber, J., Hippolyte, J.-C., Giorgis, S., Johnson, M., 2011. Fault slip and paleomagnetic analysis of the tectonics of Tobago, West Indies [abstr.]. Geol. Soc. of Am., Annu. Meet. Abstr. Progr. 43, 622 (260-15).

Ritter, J., Weber, J., 2007. Geomorphology and Quaternary Geology of the Northern Range, Trinidad and Paria Peninsula, Venezuela: Recording Quaternary subsidence and uplift associated with a pull-apart basin. In: Proceedings, Geological Society of Trinidad and Tobago, Fourth Geological Conference.

Rivas, G.A., Lasso-Alcalá, O.M., Rodríguez-Olarte, D., De Freitas, M., Murphy, J.C., Pizzigalli, C., Weber, J.C., de Verteuil, L., Jowers, M.J., 2021. Biogeographical patterns of amphibians and reptiles in the northernmost coastal montane complex of South America. PLoS One 16 (3), e0246829. https://doi.org/10.1371/journal.pone.0246829.

Robertson, P., Burke, K., 1989. Evolution of southern Caribbean plate boundary, vicinity of Trinidad and Tobago. AAPG Bull.-Am. Assoc. Petr. Geol. 73, 490–509. https://doi.org/10.1306/44b49fdd-170a-11d7-8645000102c1865d.

Rohling, E.J., Foster, G.L., Gernon, T.M., Grant, K.M., Heslop, D., Hibbert, F.D., Roberts, A.P., Yu, J., 2022. Comparison and synthesis of sea-level and deep-sea temperature variations over the past 40 million years. Rev. Geophys. 60, e2022RG000775. https://doi.org/10.1029/2022RG000775.

Rosencrantz, E., Mann, P., 1991. SeaMARC II mapping of transform faults in the Cayman trough, Caribbean Sea. Geology 19, 690–693.

Rosencrantz, E., Ross, M., Sclater, J., 1988. Age and spreading history of the Cayman trough as determined from depth, heat flow, and magnetic anomalies. J. Geophys. Res. 93 (B3), 2141–2157.

Russo, R.M., Speed, R.C., 1992. Oblique collision and tectonic wedging of the south American continent and Caribbean terranes. Geology 20, 447–450. https://doi.org/10.1130/0091-7613(1992)020<0447:OCATWO>2.3.CO;2.

Russo, R.M., Speed, R.C., 1994. Spectral analysis of gravity anomalies and the architecture of tectonic wedging, NE Venezuela and Trinidad. Tectonics 13, 613–622. https://doi.org/10.1029/94TC00052.

Ryan, W.B.F., Carbotte, S.M., Coplan, J., O'Hara, S., Melkonian, A., Arko, R., Weissel, R. A., Ferrini, V., Goodwillie, A., Nitsche, F., Bonczkowski, J., Zemsky, R., 2009. Global Multi-Resolution Topography (GMRT) synthesis data set. Geochem. Geophys. Geosyst. 10, Q03014. https://doi.org/10.1029/2008GC002332.

Sanchez-Zambrano, D.A., 2010. Neogene History of the Carapita Formation, Eastern Venezuela Basin. Unpublished M.Sc. Thesis. The State University of New Jersey, Rutgers, p. 163.

Saunders, J.B., Roberts, C., Ali, W.M., Eggerston, B., 1997. Geological Map, Trinidad and Tobago. Ministry of Energy and Energy Resources, Trinidad and Tobago.

Schories, S., Meyer, M., Schartl, M., 2009. Description of *Poecilia (Acanthophacelus)* obscura n. sp., (Teleostei: Poeciliidae), a new guppy species from western Trinidad, with remarks on P. Wingei and the status of the "Endler's guppy". Zootaxa 2266, 35–50.

Smith, J., Jowers, M.J., Auguste, R., Hoskisson, P., Beyts, C., Muir, G., Greener, M., Thornham, D., Byrne, I., Lehtinen, R., Eyre, M., Rutherford, M., Murphy, J., De Freitas, M., Rivas, G., Downie, J., 2021. The distribution and conservation status of the Dwarf Marsupial Frog (*Flectonotus ftzgeraldi*, Anura, Hemiphractidae) in Trinidad, Tobago, and Venezuela. Amphib. Reptile Conserv. 15, 36–56 (e273).

Snoke, A.W., Rowe, D.W., Yule, D., Wadge, G., 2001. Geologic map of Tobago, West Indies, with explanatory notes. Geological Society of America Map and Chart Series MCH087.

Soto, M.D., Mann, P., Escalona, A., Wood, L., 2007. Late Holocene strike-slip offset of a subsurface channel interpreted from three- dimensional seismic data, eastern offshore Trinidad. Geology 35, 859–862. https://doi.org/10.1130/G23738A.

Speed, R.C., 1985. Cenozoic Collision of the Lesser Antilles Arc and Continental South America and the Origin of the El Pilar Fault. Tectonics 4, 41–69. https://doi.org/10.1029/TC004i001p00041.

Speed, R.C., Cheng, H., 2004. Evolution of marine terraces and sea level in the last interglacial, Cave Hill, Barbados. Geol. Soc. Am. Bull. 116 (1–2), 219–232.

Speed, R.C., Cheng, H., 2021. Marine terrace evolution of windward Barbados. In: Speed, R.C., Cheng, H., with Speed, C, Sedlock, R., Andreas, L. (Eds.), Emergence and Evolution of Barbados: Geological Society of America Special Paper, 549, pp. 1–20. https://doi.org/10.1130/2021.2549(01).

Speed, R.C., Smith-Horowitz, P.L., 1998. The Tobago Terrane. Int. Geol. Rev. 40, 805–830.

Stehli, F., Webb, D. (Eds.), 1985. The Great Biotic Interchange, Plenum, New York, p. 532.

Summa, L.L., Goodman, E.D., Richardson, M., Norton, I.O., Green, A.R., 2003. Hydrocarbon systems of Northeastern Venezuela: plate through molecular scale-analysis of the genesis and evolution of the Eastern Venezuela Basin. Mar. Pet. Geol. 20, 323–349.

Van Andel, T., 1967. The Orinoco delta. J. Sediment. Petrol. 17, 297–310.

Van Andel, T., Sachs, P., 1964. Sedimentation in the Gulf of Paria during the Holocene transgression: a subsurface acoustic reflection study. J. Mar. Res. 22, 30–50.

Van Avendonk, H.J.A., Hayman, N.W., Harding, J.L., Grevemeyer, I., Peirce, C., Dannowski, A., 2017. Seismic structure and segmentation of the axial valley of the Mid-Cayman Spreading Center. Geochem. Geophys. Geosyst. 18, 2149–2161. https://doi.org/10.1002/2017GC006873.

van Benthem, S., Govers, R., Spakman, W., Wortel, R., 2013. Tectonic evolution and mantle structure of the Caribbean. J. Geophys. Res. Solid Earth 118, 3019–3036.

Wadge, G., Hudson, D., 1986. The Neotectonics of Tobago, Geological Society of Trinidad and Tobago, 1st Geological Conference. Port-of-Spain, Trinidad.

Wallace, A.W., 1852. On the monkeys of the Amazon. Proc. Zool. Soc. London 20, 107–100.

Watson, L., Escalona, A., 2021. Creating spatial-based paleogeography from plate reconstructions: a methodology. In: Bartolini, C. (Ed.), American Association of Petroleum Geology Memoir 123: Eastern Caribbean-Northeast South American Boundary–Tectonic Evolution, Basin Architecture, and Petroleum Systems.

Weber, J.C., 2005. Neotectonics in the Trinidad and Tobago, West Indies Segment of the Caribbean–South American Plate Boundary. Geological Institute of Hungary, 204 (Occasional Papers), pp. 21–29.

Weber, J.C., Dixon, T.H., DeMets, C., Ambeh, W.B., Jansma, P., Mattioli, G., 2001a. GPS estimate of relative motion between the Caribbean and South American plates, and geologic implications for Trinidad and Venezuela. Geology 29, 75–78. https://doi.org/10.1130/0091-7613(2001)029<0075:GEORMB>2.0.CO;2.

Weber, J.C., Ferrill, D.A., Roden-Tice, M.K., 2001b. Calcite and quartz microstructural geothermometry of low-grade metasedimentary rocks, Northern Range, Trinidad. J. Struct. Geol. 23, 93–112. https://doi.org/10.1016/S0191-8141(00)00066-3.

Weber, J.C., Geirsson, H., Latchman, J.L., Shaw, K., La Femina, P., Wdowinski, S., Higgins, M., Churches, C., Norabuena, E., 2015. Tectonic inversion in the Caribbean-south American plate boundary: GPS geodesy, seismology, and tectonics of the Mw 6.7 22 April 1997 Tobago earthquake. Tectonics 34, 1181–1194. https://doi.org/10.1002/2014TC003665.

Weber, J.C., Geirsson, H., La Femina, P., Robertson, R., Churches, C., Shaw, K., 2020. Fault Creep and Strain Partitioning in Trinidad-Tobago: Geodetic Measurements, Models, and Origin of Creep. Tectonics 39, e2019TC005530. https://doi.org/10.1029/2019TC005530.

Wenxiu, Y., Escalona, A., 2011. Tectonostratigraphic evolution of the Guyana Basin. AAPG Bull. 95 (8), 1339–1368.

Wesseligh, F.P., 2008. Molluscan radiations and landscape evolution in Miocene Amazonia, Turun Yliopiston Julkaisuja Annales Univeritates Turkuensis, Sarja - Ser. AII OSA - Tom. Biolog. - Geogr. – Geol. 232, 40.

Willing, E.M., Bentzen, P., Van Oosterhout, C., Hoffmann, M., Cable, J., Breden, F., Weigel, D., Dreyer, C., 2010. Genome-wide single nucleotide polymorphisms reveal populationhistory and adaptive divergence in wild guppies. Mol. Ecol. 19 (5), 968–984. https://doi.org/10.1111/j.1365-294X.2010.04528.x.

Wilson, J.T., 1966a. Are the structures of the Caribbean and Scotia arc regions analogous to ice rafting? Earth Planet. Sci. Lett. 1 (5), 335–338.

Wilson, J.T., 1966b. Did the Atlantic close and then re-open? Nature 211 (5050), 676–681.

Wood, L., 2000. Chronostratigraphy and tectonostratigraphy of the Columbus Basin, eastern offshore Trinidad. Am. Assoc. Pet. Geol. Bull. 84 (12), 1905–1928.

Zavala, C., Marcano, J., Carvajal, J., Delgado, M., 2011. Genetic indices in hyperpycnal systems: a case study in the late Oligocene–early Miocene Merecure Formation, Maturin Subbasin, Venezuela. In: Slatt, R.M., Zavala, C. (Eds.), Sediment transfer from shelf to deep water— Revisiting the Delivery System, 61. AAPG Studies in Geology, pp. 53–73.