Environmental and Ecological Factors Affecting the Presence of Giant Land Turtles in the Late Cenozoic

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Abstract:

Various species of turtles within Testudinidae (true tortoises) and the recently extinct Meiolaniidae of Australia grew to immense proportions throughout the late Cenozoic, including a significant number of taxa that have persisted into modern times. Although these giant land turtles mostly occur on islands today, there are cases of extinct giant land turtles on every non-Antarctic continent during the Cenozoic. This raises an interesting question: if giant turtles can occur on the continents, presumably in the presence of both predators capable of penetrating their defensive carapace and other herbivores competing for the same food sources, what other factors may be related to the evolution of gigantism in land turtles? This study tests the influence of two ecological factors, presence of durophagous (bone-crushing) predators and competing herbivores, and three environmental factors, mean annual temperature, aridity, and landmass type (insular versus continental) on occurrences of giant land turtles. The results of the Fisher exact tests collected demonstrate that the presence of competing herbivores and insularity have a significant effect on the occurrence of modern giant land turtles. Miocene giant land turtles appear to occur independently of all five factors, while Pliocene giants tend to occur in areas of higher average temperatures. Pleistocene forms were influenced by higher temperatures and a lack of herbivorous competition, an interesting combination of the significant factors of the preceding Pliocene and following Holocene Epochs.

Background:

Giantism, the phenomenon of size increase in a taxon of interest compared to other closely related species, and nanism, the phenomenon of size decrease in the same, are easily recognized in many cases of fossil and extant organisms, but the evolutionary mechanisms leading to giant or nanoid species are poorly understood (Gould and MacFadden, 2004). A variety of both ecological and environmental factors could be responsible for these phenomena, and it is entirely possible that the most important factors for one taxon's evolution of giantism or nanism are completely different from those most important in another taxon's case.

Giant land turtles play important roles in several modern island ecosystems as agents of seed dispersal and controlling local plant populations through grazing and trampling (Falcón *et al.*, 2019). There is significant evidence that extinct tortoises played similar roles in both continental and insular communities during much of the Cenozoic (Hansen *et al.*, 2010). The fact that Holocene giant land turtles are restricted to island communities has led ecologists to consider insular isolation from competition and predation as the driving factor of giantism in turtle lineages. However, the presence of giant land turtles in continental paleo-ecosystems shows that this is not always the case, which begs the question of what other environmental factors could be related universally to the rise of such species.

The traditionally suggested factors of a lack of predation and competition could certainly be valid, as both would remove evolutionary pressures on the turtles to remain at a small body size. Predation encourages the spending of energy for reproduction rather than growth, while competition for food sources reduces the total energy available to the organism to fulfill all its necessities and body functions. Possible non-human predators of adult giant land turtles would necessarily need to display adaptations for durophagy or bone-crushing in order to pierce the robust shells of their prey. Durophagy in extant terrestrial predators is limited to the subfamily Hyaeninae (bone-crushing hyaenas; Hartstone-Rose and Stynder, 2013), jaguars (*Panthera onca*; Miranda *et al.*, 2016), and wolverines (*Gulo gulo*) which do not overlap ranges with any turtle taxa, giant or otherwise, but further back in the Cenozoic other durophagous predators were present as well such as the diverse clades of borophagine dogs in North America (Tseng and Wang, 2010), entelodonts (so-called "terminator pigs" of the Eocene through the Miocene; Hunt, 2004), and temnocyonines ("bear-dogs"; Hunt, 2004).

Given that land turtles display extensive frugivory (Falcón *et al.*, 2019), their main competitors for food sources should also have significant fruit intake in their diets and be similarly ground-dwelling, as arboreal frugivores such as bats, birds, and monkeys could access fruits beyond the turtles' reach and so would be less prone to competing. According to Sridhara *et al.* (2016), several Asian members of Cervidae (deer), Suidae (pigs), Elephantidae, and Rhinocerotidae display high levels of frugivory, so other members of these groups on other continents are very likely to display these behaviors as well. Other frugivores include the cassowaries (*Casuarius* spp.; Bradford *et al.*, 2008) and musky rat-kangaroos (*Hypsiprymnodon* spp.; Dennis, 2002) of Australia, but cervids, suids, elephants, and rhinoceroses constitute the majority of relevant frugivores in most of the locations of interest in this study. Macraucheniids and astrapotheres from the Miocene of South America are posited to have had intermediate diets, suggesting at least a degree of frugivory (Vizcaino *et al.*, 2012). Although some extinct South American turtles would have had to contend with these two mammal groups, the four mammal families of cervids, suids, elephants, and rhinoceroses form much of the focus of the extinct giant land turtle ecology analyses as well.

Despite their plausibility when considering extant and recently extinct giant land turtles (Itescu *et al.*, 2014), these factors may have been superseded in the cases of extinct giant land turtles on the continents by high temperatures and aridity of the region. High temperatures have been associated with larger body size in both extant and extinct terrestrial reptiles (Makarieva *et al.*, 2005) and therefore could possibly play a role in the occurrence of giant land turtles, as is suggested in Esker *et al.* (2019). An arid climate might present an advantage to turtles' lower metabolisms (Cloudsley-Thompson, 1991) over more metabolically active mammalian predators and herbivores who would necessarily require a larger and more consistent intake of food, something that would be difficult to achieve in a dry region particularly lacking in plant and animal life. In addition, according to Cloudsley-Thompson (1991), reptiles such as turtles are especially suited to living in arid climates due to their ectothermic body temperature regulation and scaly integument which aids in the retention of water.

According to an article by Rick Routledge found in the *Encyclopedia of Biostatistics* (Armitage, 2005), the Fisher exact test is similar to the more well-known χ^2 test in that it assesses the significance of differing proportions among two groups using a two-by-two contingency table. However, the Fisher exact test is more effective than χ^2 when dealing with small sample sizes of frequency counts, making it the analysis of choice for this thesis.

Introduction:

Interrogation of the five factors described above, mean annual temperature, aridity, predation, competition, and landmass size, and their relation to giant land turtle occurrences must include a definition of a minimum parameter for a turtle taxon to be considered giant, a listing of all such taxa, knowledge of the formations or locations of occurrence for extinct and extant taxa respectively, collection of mean annual temperature and aridity index data for those areas at the time of occurrence, and finally a statistical analysis of all five factors using Fisher exact tests, in a similar manner to the one-way chi-squared tests presented in Lyson and Longrich (2010). The hypotheses being tested by the Fisher exact tests are that landmass size, mean annual temperature, aridity, presence of durophagous predators, or presence of competing terrestrial frugivores have a relation to occurrences of giant land turtles. Each factor also has a corresponding null hypothesis that there is no relation between said factor and occurrences of giant land turtles.

Methods:

This study began with an analysis of size distribution within Testudines to verify a suitable value of straight-line carapace length (CL) to use as the minimum threshold for considering turtle taxa as giants. The length of a turtle's carapace from front edge to rear edge is a useful indicator of the organism's general size, as most land turtles follow an extremely similar body plan with only minor variation. CL measurements are also frequently the only possible measurement available for extinct forms, as turtle shells tend to be more robust during fossilization than the rest of their skeleton. An extensive listing of late Cenozoic turtle taxa, most including CL measurements, was found in Rhodin *et al.* (2015). These were plotted on a histogram with CL bin sizes of 10 cm to determine the overall pattern of sizes within the clade Testudines.

Based on the analysis above, a value of 80 cm CL was chosen as the minimum size of giant land turtles. The Rhodin *et al.* (2015) taxa were then surveyed and assembled into a list of species that met this minimum threshold, along with some additional modern and recently extinct taxa with CLs greater than or equal to 80 cm from Hansen *et al.* (2010) that were not listed in the Rhodin *et al.* (2015) taxa. This list includes 23 extant or very recently extinct Holocene taxa and 21 extinct taxa from the Pleistocene or earlier. Any taxon with a listed formation or area of occurrence in Rhodin *et al.* (2015) was noted on the list of giant land turtle species. In cases where a taxon's locale or formation was not listed in Rhodin *et al.* (2015), the Paleobiology Database (PBDB) was utilized to determine this information by searching the species or genus name and interrogating the occurrences that appeared on the map for any that listed a formation. In all the cases of historical and extant taxa, the specific formation of occurrence was not available from the PBDB due to the fact that these species are found as non-fossilized remains in modern sediments, so the geographical name of the overall region inhabited by the giant land turtle was used instead (e.g. Galápagos for *Chelonoidis*, Aldabra for *Aldabrachelys*, etc.).

In total, there were 7 distinct locations (Aldabra, the Amazon Basin, Efate Island of Vanuatu, the Galápagos, Madagascar, the Mascarene Islands, and the Sahel Belt) of extant giant land turtles based on the above list. An additional 12 locations (Australia, Central America not including Mexico, Eastern Africa, Eastern Asia, the Eastern United States, India, Indonesia, Mediterranean Europe, Central Europe including the United Kingdom, Southeastern Asia, Southern Africa, and the Southwestern United States combined with Mexico) with non-giant turtle taxa present were selected from a map of global turtle distributions found in the Turtle Taxonomy Working Group's 2017 annotated checklist and atlas. These regions were selected by grouping as many adjacent instances of turtle taxa into one larger region while maintaining a roughly similar climate across the chosen region to minimize variation in temperatures and aridity across each region.

Each of the 18 total regions was then investigated individually using the PBDB to determine the ranges of present-day durophagous predator groups (hyaenas and jaguars) and frugivorous terrestrial herbivores (cervids, suids, elephantids, rhiocerotids, genus *Casuarius*, and species *Hypsiprymnodon moschatus*). If a region had at least one occurrence of Hyaenidae or *Panthera onca*, then the region was deemed to have durophagous predators present. The regions typified in this manner were the Sahel Belt, Southern Africa, Eastern Africa, the Amazon Basin, Central America, and Mexico (and thus by extension the Southwestern United States, although jaguars are only very rarely seen there). If a region had at least one occurrence of any of the six frugivore groups listed above, then said region was deemed to have competing herbivores present. The regions typified in this manner were the Amazon Basin, the Sahel Belt, Southern Africa, Australia, Central America, Eastern Africa, Eastern Asia, Eastern United States, India, Indonesia, Mediterranean Europe, Central Europe & the UK, Southeastern Asia, and the Southwestern United States including Mexico.

The climates of the 18 regions were then estimated based on a global map of aridity (FAO, 2015) and global mean annual temperature map (Matsuura & National Center for Atmospheric Research Staff, 2017). The latter source was verified using the Mitchell and Jones (2005) climatology dataset, which was interrogated for mean temperature values at various latitude-longitude pairs within each of the regions of interest. As the map and the dataset showed no disagreement in values, the map by Matsuura & National Center for Atmospheric Research Staff (2017) was deemed a suitable source for temperature estimates. In order to simplify the statistical analyses of the climatological variables, both temperature and aridity were divided into two categorical bins. Regions with temperatures greater than 20 degrees Celsius were deemed "hot" regions, while those in between 5 and 20 degrees Celsius were deemed "temperate". There was no need for a "cold" bin as no turtles occur in regions with mean annual temperatures lower than 5 degrees Celsius. Regions with an aridity index (AI) of greater than 0.5 (semi-humid to humid on the FAO 2015 map) were deemed "humid" regions, while those with an AI less than 0.5 (sub-arid to hyperarid) were deemed "arid".

Finally, the 18 regions were analyzed in terms of their landmass size and whether the organisms present on them are generally isolated from other nearby ecosystems. Regions that are islands consisting of volcanic (including coral atoll descendants of volcanic islands) or continental rock that are still isolated from nearby landmasses were deemed to be insular in nature from an ecological standpoint. These regions included the Galápagos, Aldabra, Efate, and Mascarene Islands as well as Madagascar, which has been isolated from other landmasses for the entirety of the Cenozoic (Storey *et al.*, 1995). All other regions were deemed to be continental in nature, including Indonesia which, despite being a series of continental rock-based islands, displayed extensive faunal exchange throughout the Cenozoic via land bridges formed at lower sea levels during glacial periods (Tougard, 2001).

The methodology for constructing the ecological and environmental datasets for the Miocene, Pliocene, and Pleistocene giant turtle taxa was performed very similarly to that of the extant taxa, with a few key modifications. The PBDB was used extensively to determine formations of occurrence for each of the 21 extinct giant taxa, as well as formations or regions where non-giant members of the Testudinidae and Meiolaniidae occurred. In several cases, particularly giant Pleistocene taxa, a definite formation was not listed, so the modern region name was used instead. A total of 3 giant-bearing formations and 8 non-giant-bearing formations were found in the Miocene Epoch, 8 giant-bearing formations and 10 non-giant-bearing formations in the Pliocene Epoch, and 7 giant-bearing formations and 9 non-giant-bearing formations in the Pleistocene Epoch.

The ecological database construction for the extinct taxa involved further use of the PBDB to determine occurrences of borophagine dogs, entelodonts, temnocyonines, and various durophagous genera within the family Hyaenidae (*Hyaena*, *Lycyaenops*, *Chasmaporthetes*, *Crocuta*, and *Pachycrocuta*) in each of the formations. Similarly, the PBDB provided information on frugivorous herbivore occurrences (families Cervidae, Suidae, Elephantidae, Rhinocerotidae, Macraucheniidae, and Astrapotheriidae) in the formations of interest. Of the Miocene formations, 2 of the 3 giant-bearing formations and 5 of the 8 non-giant-bearing formations had durophagous predators present, while the same two giant-bearing formations and 7 of the non-giant-bearing formations had herbivorous competition present. Of the Pliocene formations, 3 of the 8 giant-bearing formations and 7 of the 10 non-giant-bearing formations had durophagous predators present, while 7 of the giant-bearing and all the non-giant-bearing formations had herbivorous competition present. Of the Pleistocene formations, 1 of the 7 giant-bearing formations and 6 of the 9 non-giant-bearing formations had durophagous predators present, while 2 of the giant-bearing formations and 9 of the non-giant-bearing formations had herbivorous competition present.

Construction of the environmental datasets for the extinct taxa proved more time-consuming, as research into the paleoclimates and paleogeography of the late Cenozoic epochs was needed. Boucot *et al.* (2013) provided a highly detailed Miocene paleoclimate map with accurate paleogeography. The climates of regions on this map with Miocene land turtle taxa present were interrogated to determine the correct temperature and aridity bins in which they should be placed, e.g. Tropical climate indicated hot and humid, Arid indicated arid and either hot or temperate depending on the paleolatitude of the region, and Warm Temperate indicated temperate and humid. A similar map of Pliocene climate was found in Salzmann *et al.* (2011) detailing vegetation types and temperatures that were translated into the humid or arid bins and hot or temperate bins. Finally, the Pleistocene formation climates were estimated using Figure 1 from Behl (2011), which provided vegetation types and temperature estimates for the entire globe during the Last Glacial Maximum. Generally, areas of desert and dry steppe on the map were considered to be arid, while forests and grasslands were deemed humid. Tropical regions and equatorial deserts indicated hot temperatures, while non-equatorial deserts or steppes and areas listed as temperate or not tropical indicated a temperate climate.

Based on the papers above and the paleogeography feature of the PBDB, each of the Miocene, Pliocene, and Pleistocene formations were determined to be an overall hot or temperate climate, humid or arid climate, and insular or continental landmass. The Miocene giant-bearing formations included 0 hot and 3 temperate, 3 humid and 0 arid, and 0 insular and 3 continental formations, while the non-giant-bearing formations included 3 hot and 5 temperate, 7 humid and 1 arid, and 1 insular and 7 continental formations. The Pliocene giant-bearing formations included 7 hot and 1 temperate, 6 humid and 2 arid, and 1 insular and 7 continental formations, while the non-giant-bearing formations included 3 hot and 7 temperate, 10 humid and 0 arid, and 1 insular and 9 continental formations. The Pleistocene giant-bearing formations included 6 hot and 1 temperate, 4 humid and 3 arid, and 3 insular and 4 continental formations, while the non-giant-bearing formations included 0 hot and 9 temperate, 3 humid and 6 arid, and 0 insular and 9 continental formations.

The datasets of ecological and climatological factors assembled above were then entered into a spreadsheet in the Paleontological Statistics Software Package (Hammer, 2019) as five separate two-by-two tables. Each table was then selected and submitted to a univariate contingency table test, which gave p-values for both chi-squared and Fisher's exact tests. The Fisher exact test p-values were then compared to an alpha-value of 0.05 to determine significance. If the p-value was less than the alpha-value, the results were significant enough to reject the null hypothesis and indicated a likely relationship between the presence of giant land turtles and the factor being investigated in that given contingency table. If the p-value was greater than the alpha-value, the results were not significant enough to reject the null hypothesis, meaning there is no relationship between the presence of giant land turtles and that factor.

In the interest of providing a more nuanced analysis of the environmental and ecological factors, the above analyses were then run again in varied groupings. These included a combined analysis of all the land turtle-bearing formations investigated regardless of time period, an analysis of all the prehistoric or pre-Holocene formations (i.e. Pleistocene plus Pliocene plus Miocene), and analyses of the Neogene formations (i.e. Miocene plus Pliocene) compared with the Quaternary formations (i.e. Pleistocene plus Holocene). These analyses were performed in exactly the same manner as stated above, with the cell values for each of contingency tables being determined from the sums of the corresponding cells from the combined epoch-specific analyses.

Results:

Figure 1 is a diagram from Chiari *et al.* (2009) showing various measurements of parts of a turtle's shell. This is primarily included to emphasize that straight carapace length, shown here as the long vertical line labelled CL in the Dorsal Carapace View, is the straight-line measurement from the front edge (closest to the turtle's head) to the rear edge of the shell.

Figure 1: Turtle Carapace Measurements

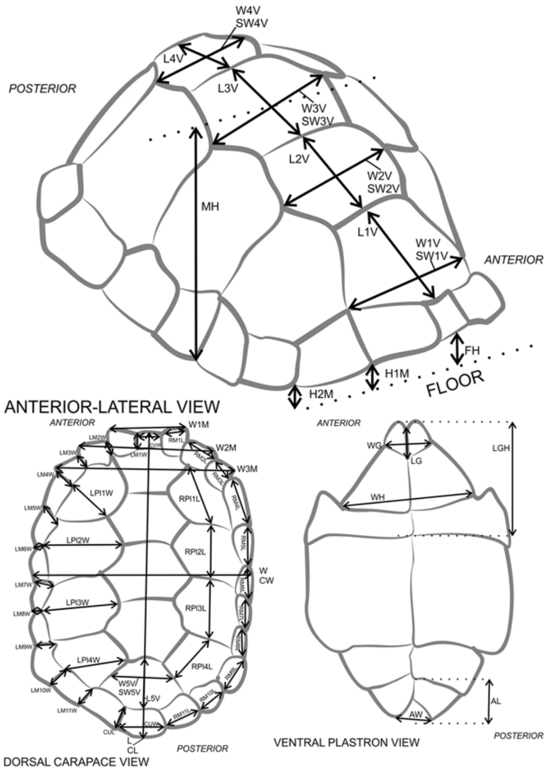


Figure 2 displays the results of the size distribution analysis of maximum CLs for the turtle taxa listed in Rhodin *et al.* (2015). There are two notable clusters of relatively high frequencies at 20 to 49 cm and at 90 to 109 cm, as well as a few outlying values in the 180 to 210 cm range. A local minimum in the dataset between the two clusters is apparent at the 80 cm bin, which suggests that a minimum CL of 80 cm for a turtle to be considered giant is a reasonable estimate of the size class division present within Testudines.

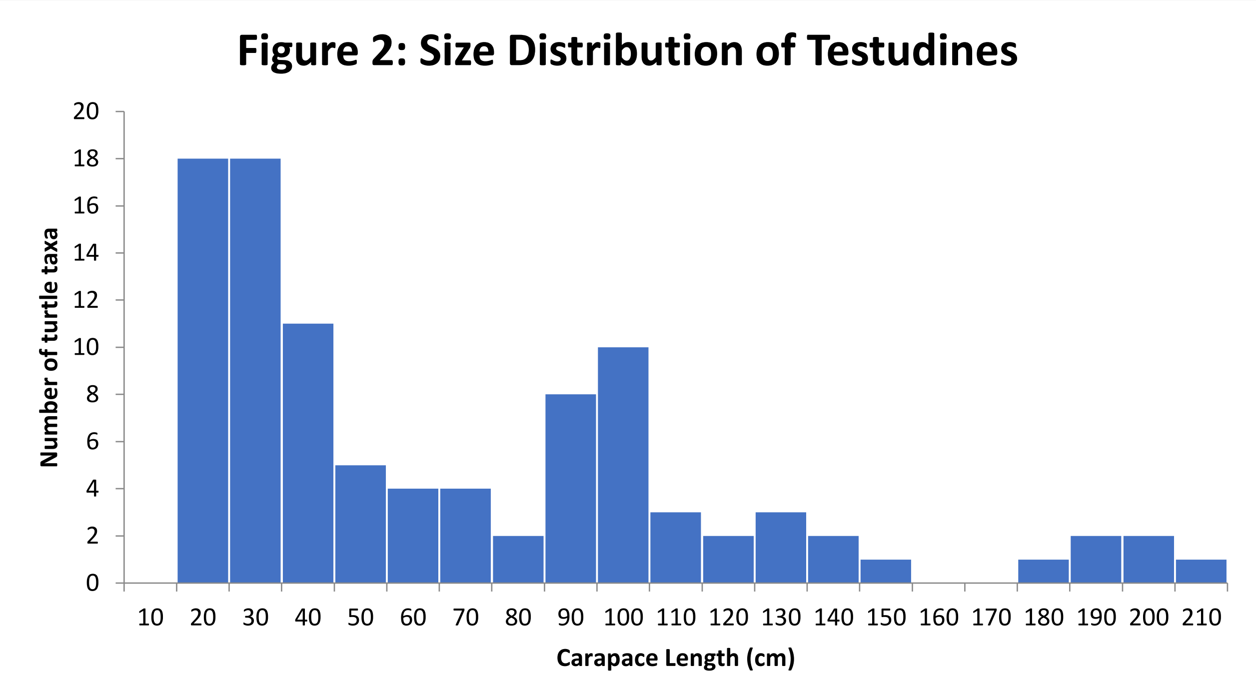


Figure 3 displays the list of all 23 extant or recently extinct giant turtle taxa and the 21 extinct taxa by epoch along with the regions where they occur according to the PBDB, Rhodin *et al.* (2015), and Hansen *et al.* (2010). This list, along with the data collected from the PBDB and all the sources referenced in the methodology, informed the construction of Figure 4, which displays the turtle-bearing locations and formations for each epoch. Figure 4 also establishes the climates and relevant ecologies of each location based on the five factors of interest. These include: whether the location is deemed an island or continent; mean annual temperature binned as temperate (5-20 degrees C) or hot (>20 degrees C); overall aridity binned as arid (AI < 0.5) or humid (AI > 0.5); the presence or absence of durophagous predators such as members of Hyaeninae, Temnocyoninae, Entelodontidae, and Borophaginae; and finally the presence or absence of competing frugivores such as members of Suidae, Cervidae, Elephantidae, and Rhinocerotidae in Eurasia, Africa, and the Americas as well as cassowaries (*Casuarius* spp.) and musky rat-kangaroos (*Hypsiprymnodon* spp.) in modern Australia and the macraucheniids and astrapotheres of Miocene South America.

Figure 3: List of Giant Land Turtles (GLTs) and Their Locations/Formations By Epoch

Extant (Holocene) Taxon	**Location/Formation**
Aldabrachelys abrupta	Madagascar
Aldabrachelys gigantea	Aldabra
Aldabrachelys grandidieri	Madagascar
Centrochelys sulcata	Sahel-belt of Central & Northern Africa
Chelonoidis abingdonii	Pinta Island, Galápagos
Chelonoidis becki	Isabela Island, Galápagos
Chelonoidis chatamensis	San Cristobal, Galápagos
Chelonoidis darwini	Santiago, Galápagos
Chelonoidis denticulata	Amazon Basin
Chelonoidis ephyppium	Pinzón Island, Galápagos
Chelonoidis guntheri	Isabela Island, Galápagos
Chelonoidis microphyes	Isabela Island, Galápagos
Chelonoidis nigra	Floreana Island, Galápagos
Chelonoidis phantastica	Fernandina Island, Galápagos
Chelonoidis porteri	Santa Cruz Island, Galápagos
Chelonoidis vandenburghi	Isabela Island, Galápagos
Chelonoidis vicina	Isabela Island, Galápagos
Cylindraspis indica	Réunion Island, Mascarene Islands
Cylindraspis inepta	Mauritius, Mascarene Islands
Cylindraspis triserrata	Mauritius, Mascarene Islands
Cylindraspis vosmaeri	Rodrigues, Mascarene Islands
Meiolania damelipi	Efate Island, Vanuatu
Stigmochelys pardalis	Southern Africa
Pleistocene Taxon	**Formation**
Centrochelys burchardi	Tenerife, Canary Islands
Centrochelys robusta	Malta
Chelonoidis cubensis	Cuba
Chelonoidis lutzae	Toropí Fm., Corrientes, Argentina
Chelonoidis sombrerensis	Sombrero Island, Anguilla
Meiolania platyceps	Wyandotte Fm., Queensland, Australia
Ninjemys oweni	Lord Howe Island, Australia
Pliocene Taxon	**Formation**
Aldabrachelys laetoliensis	Aldabra Limestone Fm.
Centrochelys marocana	C1 Fm., Morocco
Gopherus pertenuis	Blanco Fm., Texas
Hesperotestudo campester	Blanco Fm., Texas
Manouria punjabiensis	Tatrot Fm., Siwalik Grp.
Megalochelys atlas	Tatrot Fm., Siwalik Grp.
Megalochelys cautleyi	Tatrot Fm., Siwalik Grp.
Megalochelys margae	Kali Glagah Fm., Indonesia
Megalochelys sivalensis	Walanae Fm., Beru Mbr., Indonesia
Megalochelys sondaari	Laguna Fm., Philippines

Titanochelon gymnesica	Menorca, Balearic Islands
Miocene Taxon	**Formation**
Hesperotestudo crassiscutata	Bermont and Fort Thompson Fms., Florida
Meiolania brevicollis	Camfield Beds Fm., Australia
Titanochelon schafferi	Vatera Fm., Lesvos

Figure 4: Table of Locales/Formations and Corresponding Ecological & Environmental Data

Holocene Locations	**GLTs Present?**	**Temperature Bin**	**Aridity Bin**	**Durophagous Predators?**	**Competing Herbivores?**	**Insular/ Continental**
Aldabra	Yes	Hot	Humid	No	No	Insular
Amazon Basin	Yes	Hot	Humid	Yes	Yes	Continental
Efate Island	Yes	Hot	Humid	No	No	Insular
Galápagos	Yes	Hot	Humid	No	No	Insular
Madagascar	Yes	Hot	Humid	No	No	Insular
Mascarene Islands	Yes	Hot	Humid	No	No	Insular
Sahel Belt	Yes	Hot	Arid	Yes	Yes	Continental
Australia	No	Hot	Arid	No	Yes	Continental
Central America	No	Hot	Humid	No	Yes	Continental
Eastern Africa	No	Hot	Arid	Yes	Yes	Continental
Eastern Asia	No	Temperate	Humid	No	Yes	Continental
Eastern United States	No	Temperate	Humid	No	Yes	Continental
India	No	Hot	Humid	No	Yes	Continental
Indonesia	No	Hot	Humid	No	Yes	Continental
Mediterranean Europe	No	Temperate	Humid	No	Yes	Continental
Central Europe & UK	No	Temperate	Humid	No	Yes	Continental
Southeastern Asia	No	Hot	Humid	No	Yes	Continental
Southwestern United States & Mexico	No	Hot	Arid	Yes	Yes	Continental
Southern Africa	No	Hot	Arid	Yes	Yes	Continental
Pleistocene Formations	**GLTs Present?**	**Temperature Bin**	**Aridity Bin**	**Durophagous Predators?**	**Competing Herbivores?**	**Insular/ Continental**
Cuba	Yes	Hot	Humid	No	No	Continental
Lord Howe Island	Yes	Hot	Humid	No	No	Insular

Malta	Yes	Temperate	Arid	Yes	Yes	Continental
Sombrero Island	Yes	Hot	Humid	No	No	Insular
Tenerife	Yes	Hot	Arid	No	No	Insular
Toropí Fm.	Yes	Hot	Arid	No	Yes	Continental
Wyandotte Fm.	Yes	Hot	Humid	No	No	Continental
Canepatch Fm.	No	Temperate	Humid	No	Yes	Continental
Crete	No	Temperate	Arid	Yes	Yes	Continental
Guadix Fm.	No	Temperate	Arid	No	Yes	Continental
Kingsdown Fm.	No	Temperate	Arid	No	Yes	Continental
Olorgesailie Fm.	No	Temperate	Arid	Yes	Yes	Continental
Ryuku Grp.	No	Temperate	Humid	Yes	Yes	Continental
Sterkfontein Fm.	No	Temperate	Arid	Yes	Yes	Continental
Turlock Lake Fm.	No	Temperate	Arid	No	Yes	Continental
Yuanmou Fm.	No	Temperate	Humid	Yes	Yes	Continental

Pliocene Formations	**GLTs Present?**	**Temperature Bin**	**Aridity Bin**	**Durophagous Predators?**	**Competing Herbivores?**	**Insular/ Continental**
Aldabra Ls. Fm.	Yes	Hot	Humid	No	No	Insular
Blanco Fm.	Yes	Hot	Arid	Yes	Yes	Continental
C1 Fm.	Yes	Hot	Arid	Yes	Yes	Continental
Laguna Fm.	Yes	Hot	Humid	No	Yes	Continental
Menorca	Yes	Temperate	Humid	Yes	Yes	Continental
Kali Glagah Fm.	Yes	Hot	Humid	No	Yes	Continental
Tatrot Fm.	Yes	Hot	Humid	No	Yes	Continental
Walanae Fm.	Yes	Hot	Humid	No	Yes	Continental
Eastern China	No	Temperate	Humid	Yes	Yes	Continental
Goleta Fm.	No	Hot	Humid	Yes	Yes	Continental
Gonia Fm.	No	Temperate	Humid	Yes	Yes	Continental
Kuyal’nikian Fm.	No	Temperate	Humid	No	Yes	Continental
Mehrten Fm.	No	Temperate	Humid	Yes	Yes	Continental
Monte Hermeso Fm.	No	Temperate	Humid	No	Yes	Continental
Tamiami Fm.	No	Temperate	Humid	Yes	Yes	Continental
Thailand	No	Hot	Humid	No	Yes	Continental

Tomori Fm.	No	Temperate	Humid	No	Yes	Insular
Varswater Fm.	No	Hot	Humid	Yes	Yes	Continental
Miocene Formations	**GLTs Present?**	**Temperature Bin**	**Aridity Bin**	**Durophagous Predators?**	**Competing Herbivores?**	**Insular/ Continental**
Bermont & Ft. Thompson Fms.	Yes	Temperate	Humid	Yes	Yes	Continental
Camfield Beds Fm.	Yes	Temperate	Humid	No	No	Continental
Vatera Fm.	Yes	Temperate	Humid	Yes	Yes	Continental
Bannockburn Fm.	No	Temperate	Humid	No	No	Insular
Baode Fm.	No	Hot	Humid	Yes	Yes	Continental
Chitarwata Fm.	No	Hot	Humid	No	Yes	Continental
Collon Cura Fm.	No	Hot	Humid	No	Yes	Continental
Elisabeth Bay Fm.	No	Temperate	Humid	Yes	Yes	Continental
Ogalalla Fm.	No	Hot	Arid	Yes	Yes	Continental
Olesa-Les Fonts Fm.	No	Temperate	Humid	Yes	Yes	Continental
Temblor Fm.	No	Temperate	Humid	Yes	Yes	Continental

Figure 5 shows the output from the Paleontological Statistics (PAST) software by Hammer (2019) as a spreadsheet that was generated from the results in Figure 3. The p-values for both Fisher's exact and chi-squared tests are listed on the right of each of the four contingency tables. Based on these statistical results, insularity and the presence of competing herbivores appear to have a relationship to occurrences of modern giant land turtles, although temperature was also relatively close to crossing the threshold of significance. Pleistocene giant land turtles can be related to higher temperatures and a lack of competition from other herbivores, although insularity and lack of predation were also very close to being statistically significant. Of the Pliocene factors, only higher temperatures seem to correspond to giant land turtle occurrences. None of the factors exhibited statistically significant relationships to giant land turtle occurrences in the Miocene. The results of the combined analyses of all Late Cenozoic land turtle-bearing formations, the pre-Holocene formations, and the Neogene versus Quaternary formations are also included at the end of the table.

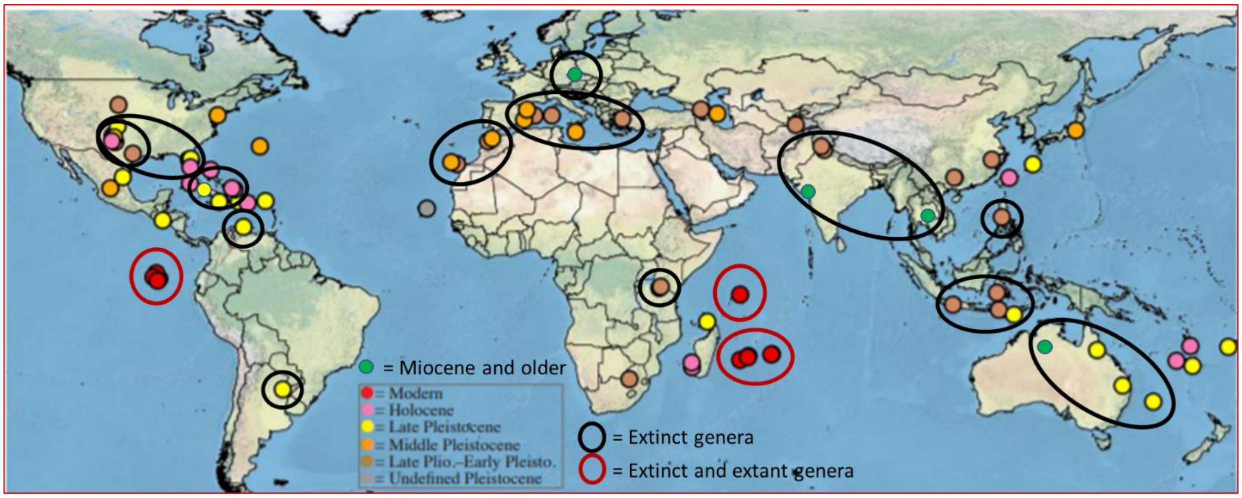
Figure 5: Summary of Statistical Analyses

Holocene Factors	Fisher p-value	Significance
Temperature	0.245	Not significant
Aridity	0.603	Not significant

Insularity	0.002	Significant
Durophagous predators	1.00	Not significant
Competing herbivores	0.002	Significant
Pleistocene Factors	**Fisher p-value**	**Significance**
Temperature	0.001	Significant
Aridity	0.615	Not significant
Insularity	0.063	Not significant
Durophagous predators	0.060	Not significant
Competing herbivores	0.005	Significant
Pliocene Factors	**Fisher p-value**	**Significance**
Temperature	0.025	Significant
Aridity	0.183	Not significant
Insularity	1.00	Not significant
Durophagous predators	0.342	Not significant
Competing herbivores	0.444	Not significant
Miocene Factors	**Fisher p-value**	**Significance**
Temperature	0.491	Not significant
Aridity	1.00	Not significant
Insularity	1.00	Not significant
Durophagous predators	1.00	Not significant
Competing herbivores	0.491	Not significant
All Formations Factors	**Fisher p-value**	**Significance**
Temperature	0.002	Significant
Aridity	0.778	Not significant
Insularity	0.002	Significant
Durophagous predators	0.207	Not significant
Competing herbivores	1.58 x 10^{-5}	Significant
Pre-Holocene Fms. Factors	**Fisher p-value**	**Significance**
Temperature	0.005	Significant
Aridity	1.00	Not significant
Insularity	0.199	Not significant
Durophagous predators	0.130	Not significant
Competing herbivores	0.004	Significant
Neogene Period Factors	**Fisher p-value**	**Significance**
Temperature	0.264	Not significant
Aridity	0.539	Not significant
Insularity	1.00	Not significant
Durophagous predators	0.466	Not significant
Competing herbivores	0.539	Not significant
Quaternary Period Factors	**Fisher p-value**	**Significance**
Temperature	0.001	Significant
Aridity	0.311	Not significant
Insularity	1.26 x 10^{-4}	Significant
Durophagous predators	0.461	Not significant
Competing herbivores	5.45 x 10^{-6}	Significant

Figure 6 displays a version of the map from Rhodin *et al.* (2015) with additional green dots for cases of extinct giant turtles from the Miocene and earlier. Some dots of other colors were added as well based on data from Rhodin *et al.* (2015) and Hansen *et al.* (2010), namely a yellow dot at the center of Cuba indicating the Late Pleistocene taxon *Chelonoidis cubensis*. The red and black circles indicate areas where giantism has occurred, both in modern and extinct turtles.

Figure 6: Cases of Cenozoic Turtle Taxa, with Emphasis on Giantism



Discussion:

Regarding errors and uncertainties, there are several possible sources that should be considered. First, any use of fossil data in analyses such as those conducted in this thesis is dependent on the assumption that the current fossil record is an approximately accurate representation of the true distributions and numbers of extinct organisms. This is not necessarily the case so there is inherently a significant and yet unquantifiable uncertainty in all paleontological science. Misidentification of taxa could introduce uncertainty into the initial listing of giant land turtle taxa, the locations of both giant and normal-sized turtles, and the possible ranges of durophagous predators and competing frugivores, especially in the pre-Holocene epochs. Poor preservation potential of specimens would similarly introduce uncertainty into any step that required definitive knowledge of a specific taxon's range or carapace length. However, both of these uncertainties are exceedingly difficult to quantify in any meaningful manner, given their ambiguous and qualitative nature, and would likely have very little impact on the final results of the statistical analyses unless extensive sections of a taxon's range are extremely underrepresented in the fossil or, in this case, extant ecological record. Additionally, the sources used for the Holocene values of the environmental variables, temperature and aridity, have some degree of experimental error in the measurement of said values. While this uncertainty could be propagated through the analyses of this paper, the fact that both the temperature and aridity values were each binned into two wide categories means that the generally small errors in those values will likely not have an effect on the final counts of regions that fall into each bin, and therefore should not affect the final results of the statistical analyses. Furthermore, a similar analysis cannot feasibly be performed for the environmental binning of pre-Holocene formations, as the sources used vary from epoch to epoch and sometimes base their climate estimates on different proxies. One last source of possible uncertainty is the very act of binning the continuous environmental variables into hot versus temperate and humid versus arid. This simplification may very well be masking more complex patterns in the data, especially amongst the prehistoric taxa. However, this study is a conservative first approach to analyzing the influence of several possible factors on giant land turtle evolution, rather than an in-depth analysis of a single factor such as temperature which would be better suited to determining the extent of such patterns.

Temperature, aridity, and the presence of bone-crushing predators do not show any relation to occurrences of extant giant land turtles and are thus unlikely to have played a major role in the evolution of the 23 giant species present within the last few thousand years. Competition from other ground-dwelling frugivores, however, appears to influence the occurrences of modern giant land turtles, as there are always possible competitors present in every region that lacks extant giant turtles compared to only 2 out of the 7 locations with giant turtles having possible competition. There is also a strong skew for insularity among modern giant land turtles which interestingly appears to be exactly equivalent to the herbivorous competition presence and absence data – the five insular locations with giant land turtles also lack competing herbivores while all 12 regions lacking giant land turtles are both continental and have competing herbivores present. These results are interesting as they support the traditional lack of competition hypotheses about modern giant land turtles, while predation, at least by large-bodied animals with bone-crushing dentition, appears to be unrelated to preventing large body size in land turtles. This may be because turtles tend to be preyed on as eggs and juveniles by a wide variety of typically small generalist organisms such as birds, rodents, and snakes, rather than the adults being a staple of larger carnivores' diets. However, predation of young giant turtles is likely similar to predation of young and even adult small turtles, rather than a possibly differential factor between giants and non-giants.

Pleistocene giant land turtles appear to have been influenced by higher temperatures and a lack of competition, since all but 1 of the 7 giant-bearing formations were hot compared to all 9 non-giant-bearing formations being temperate, and 5 of the 7 giant-bearing formations lacked competing herbivore groups compared to none of the non-giant-bearing formations. Aridity displays roughly equivalent distributions between the giant- and non-giant-bearing formations, meaning it is almost certainly unrelated to giant land turtle occurrences. Insularity and durophagous predators, on the other hand, both have very low Fisher p-values (0.063 and 0.060 respectively) that do not quite reach the necessary level of significance. This suggests there may be a weak relationship between these two factors and Pleistocene giant land turtle occurrences which could be investigated with a more detailed analysis in future. These results suggest that unlike modern forms, Pleistocene giant land turtle populations were much more successful in hotter regions far away from the advancing glaciers but remained prominent in equatorial continental faunas, rather than being largely limited to insular communities. However, Pleistocene giant land turtles appear to share the Holocene taxa's reliance on a lack of competing herbivores in order to flourish, suggesting that as the four main ground-dwelling herbivore groups of interest (cervids, suids, elephants, and rhinoceroses) radiated into a wider diversity and global extent of species, they began to provide greater competition for resources with land turtles and thus limit their sizes in areas where the two lived side by side.

Pliocene giant land turtles displayed a significant relationship only with higher temperatures, as 7 of the 8 giant-bearing formations were hot and 7 of the 10 non-giant-bearing formations were temperate. The remainder of the factors displayed p-values much higher than the α-value of 0.05, and thus appear to be entirely unrelated to the evolution of giant land turtles in the Pliocene. This suggests that Pliocene giant land turtles were not limited by competition with other herbivores as in the later Pleistocene and Holocene Epochs, perhaps even being the dominant forms inhabiting the large-bodied ground-dwelling generalist niche. The Pliocene world was somewhat warmer overall than during the Pleistocene and Holocene, but giant land turtles were limited to hotter, generally equatorial regions as they would also later be in the Pleistocene.

Miocene giant land turtles displayed no significant relationships with any of the five factors of interest due to extremely high Fisher p-values (0.491 to 1.00) and nearly identical distributions of formations between arid and humid, durophagous predators present and absent, and insular and continental factors. Given the much warmer overall climate of the Miocene Epoch, these results suggest that the temperatures were high enough even in temperate regions to support giant-sized turtles, while competing herbivores may not have truly begun invading the ecological niche dominated by Miocene giant land turtles as they did in later epochs. However, the sample sizes for the Miocene formations are very small (3 giant-bearing and 8 non-giant-bearing), so these results are less well-supported than those for the Pliocene, Pleistocene, and Holocene Epochs. A more detailed analysis of one of the five factors interrogated here or perhaps an entirely different factor could help elucidate the controls on Miocene giant land turtle evolution.

The broadly grouped analyses showed very similar results to the epoch-specific analyses. Grouping all the studied formations together resulted in insularity, temperature, and herbivorous competition showing statistically significant effects on the distribution of formations. This is, in effect, a combination of the Holocene, Pleistocene, and Pliocene significant factors, and thus confirms the presence of a meaningful relationship between giant land turtle occurrences and these three factors. Durophagous predation and aridity remained insignificant, which also agreed with the results of the individual epoch analyses. Excluding the Holocene data from the combined analysis changed the distribution of insular and continental land turtles enough to render it insignificant to the pre-Holocene giant land turtle occurrences.

Upon breaking up the large combined analysis into the Neogene and Quaternary Period formations, the significant factors appeared to trend towards the extremes of each period; i.e. the Neogene formations displayed no significant relationships with the five factors in much the same manner as the more narrow Miocene analysis did, while the Quaternary as a whole showed significant relationships with higher temperatures, insular environments, and a lack of competing herbivores in a combination of the significant factors of the individual Pleistocene and Holocene Epoch analyses.

Conclusion:

The results of these analyses suggest several interesting possibilities for the evolution of giant land turtles during the late Cenozoic. There is a progression of limiting factors from the Miocene to the Holocene, as in the Miocene giant size in turtles appears to be independent of temperature, aridity, insularity, durophagous predators, and competing herbivores, while in the following Pliocene giant land turtles show a preference for hotter climates. Pleistocene forms display a similar preference for hotter climates but also begin to be limited by the spread of large-bodied mammalian herbivores who compete for the fruits and other low vegetation that constitute much of land turtles' diets. Finally, Holocene giant land turtles are largely ousted from the continents by fierce competition from herbivorous mammals and either take refuge or evolve anew on oceanic islands that are too isolated and small for large-bodied mammals to reach.

The combined analyses served to reinforce the results of the individual epoch analyses, showing an overall preference for giant land turtles occurring in hotter, insular locations away from competing herbivores throughout the Late Cenozoic. Similarly, grouping the epochs more broadly by period again showed relatively uniform distributions of giant land turtles unimpacted by any of the five factors during the Neogene Period, which then transitioned into a more skewed distribution during the Quaternary Period controlled by a need for higher temperatures and ecological isolation from increasing competition by mammalian generalist herbivores.

Of the five factors analyzed, aridity and the presence of durophagous predators were insignificant to the occurrences of giant land turtles in all four epochs. This suggests either that large-bodied, bone-crushing predators rarely preyed on giant land turtles even when the two inhabited the same areas, or that this predation was evenly distributed between giant and small forms. The latter is more likely given the roughly similar distributions of predator presence in giant- and non-giant-bearing formations for all epochs. Interestingly, some of the epochs showed a general preference of humid climates across both giant and non-giant turtles (0 out of 3 giant- and 1 out of 8 non-giant-bearing formations deemed arid in the Miocene, 2 out of 8 giant- and 0 out of 10 non-giant-bearing formations deemed arid in the Pliocene), so further study of rainfall and vegetation cover in relation to the presence of giant land turtles may reveal a more subtle relationship that was overlooked by the broad analyses used here.

Further research could be conducted with more specific and detailed analyses to determine the intricacies of how and why each factor relates or does not relate to giant land turtle occurrences, with special focus on Pliocene and Pleistocene temperatures, Pleistocene and Holocene herbivore distributions, and Holocene island isolation. Additionally, similar analyses could be applied to other well-known cases of nanism and giantism, such as nanoid proboscideans found on various islands throughout the Cenozoic or *Homo floresiensis* from the isle of Flores. In short, this thesis could have far-reaching implications and expand our understanding of the evolution of nanism and giantism in both insular and continental environments.

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