

MORPHOMETRICS OF GALAPAGOS TORTOISES: EVOLUTIONARY IMPLICATIONS

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The giant tortoises that inhabit a diversity of insular environments throughout the Galapagos Archipelago are among the largest of living terrestrial reptiles. In order to investigate the evolutionary relationships of Galapagos tortoises, morphological variation within living populations in the Galapagos and in museum collections is examined. Factor analysis and discriminant function analysis of morphometric data indicate considerable divergence of populations. Two major trends describing size and carapace shape appear to be related to environmental characteristics of the individual islands inhabited. Comparison of young tortoises from different islands reared under identical conditions suggests that morphological divergence is not environmentally controlled.

Carapace size correlates with a combination of altitudinal relief and dryness throughout the archipelago. The shape of the anterior margin of the carapace correlates with the area of the volcanoes or islands inhabited. Concurrent variation in these trends results in extreme divergence within the Galapagos. It is hypothesized that the elevation of the anterior carapace and related changes in neck and limb length simultaneously function to increase the vertical feeding range and individual success in aggressive encounters in dry habitats where inter- and intraspecific competition would be maximized during xeric climatic periods. Tortoises are poorly known in relation to other elements of the Galapagos biota.

During the historic visit of Charles Darwin to the Galapagos in 1834-35, he was informed by the Vice Governor of the archipelago that it was possible to tell from which island a tortoise came on the basis of its appearance (Darwin 1889). This so impressed Darwin that he began recording from which islands specimens came instead of labeling them as being from "Galapagos," as had many of his predecessors and as others would continue to do for many years. Although giant tortoises may have played an important role in prompting Darwin to compare island faunas, for the most part he chose to ignore tortoises in his writings except for a few notes on their natural history and habits. The diversity and divergence of tortoises in the Galapagos suggested by the Vice Governor was confirmed when additional material was studied by Günther (1875, 1877), Rothschild (1915), and Van Denburgh (1914).

Rothschild and Van Denburgh provided the last thorough reviews of taxonomic relationships of Galapagos tortoises, recognizing 13 species, with two other populations left unnamed because of inadequate material. Subsequent authors, such as Hendrickson (1966), Thornton (1971), MacFarland et al. (1974), and others have, without benefit of morphological or taxonomic review, tended to group all nominal taxa of tortoises from the Galapagos under *Geochelone elephantopus* (Harlan).

Van Denburgh (1914) diagnosed the taxa that he recognized on the basis of characteristics of the carapace and plastron, as well as a complex formulation of morphometric variables. Such characteristics are amenable to analysis using presently available statistical methods and current evolutionary theory. Thus it is now appropriate to ask if significant differences do occur within tortoises from the archipelago and what this variation can tell us about the evolutionary history of

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tortoises in insular ecosystems. The extent of speciation of tortoises in the Galapagos and the systematic relationships of the group are parts of a larger evolutionary study still in progress and will not be treated in this report. Instead, I shall review current morphological studies and examine the possible evolutionary implications of morphological and ecological variation.

To determine if significant interpopulational variation existed in samples available to Van Denburgh (1914), an oblique factor analysis was computed on the basis of 26 morphometric characteristics recorded from 139 tortoises collected by the 1905-06 expedition of the California Academy of Sciences. By using factor analysis to obtain an overview of morphometric variation, it is possible to view major trends and compare inter- and intra-populational similarities without *a priori* assumptions as to affinities or subjective selection of primary characteristics. Thus not until factor scores were computed for each specimen and the order of specimens determined on the major trends of variation (i.e. the vectors) was geographic origin of the samples taken into account. Oblique factor rotation was used in lieu of orthogonal rotation because the data set is entirely morphometric and even major trends are likely to show intercorrelations in such situations. A visual examination of the bivariate plot of factors 1 and 2 (Fig. 1) allows consideration of general

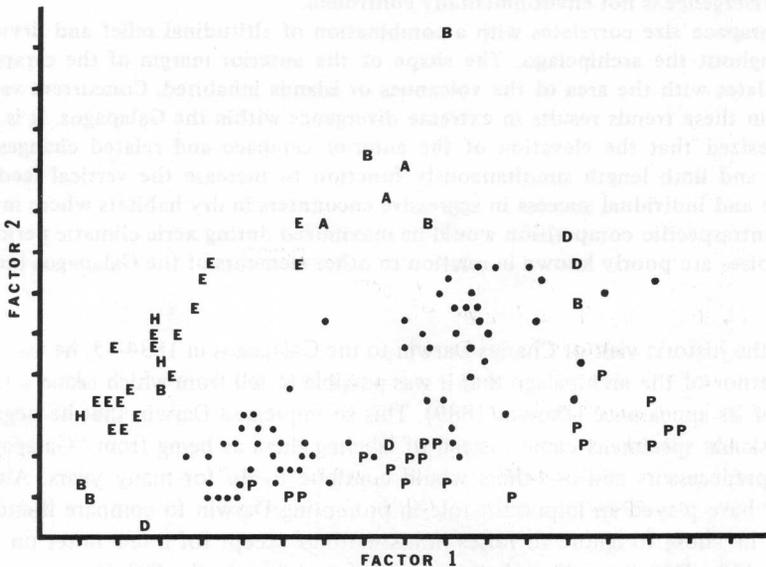


Fig. 1. Distribution of tortoises on the first and second principal components extracted from the data set described in the text. Symbols follow the taxonomic groupings of Van Denburgh (1914) except for the four southern volcanoes of Isabela. A=*Geochelone abingdoni*; B=*G. becki*; D=*G. darwini*; E=*G. epphipium*; and P=*G. porteri*. Dots represent tortoises of *G. vicina*, *guentheri*, and *microphyes*.

morphological relationships, and even from the conservative viewpoint of factor analysis, interpopulational variation can be noted, warranting further study.

Discriminant function analyses of the same data set result in increased separation of most populations and facilitate identification of the most divergent populations. Not all populations can be distinguished using these techniques, and some similarity can be noted between geographically distant populations. The question of how many species of tortoises occur in the Galapagos is an important one, but it must be dealt with in greater detail than possible at this time.

Van Denburgh recognized two major assemblages of tortoises, although there is no indication in his writings that he considered these as single evolutionary lines. "Saddle-backed" tortoises, heretofore referred to as saddles, named for their similarity in shape to ancient Spanish saddles,

have carapaces highly elevated anteriorly, proportionately longer necks and limbs, and usually are smaller in size (Fig. 2). Van Denburgh recorded taxa of this body form from Pinzón, Española, Volcán Wolf of Isabela, Fernandina and Pinta. It can now be shown that the extinct tortoises from Floreana (=Santa María) and Santa Fé also exhibited this body form. "Non-saddle-backed tortoises," herein called domes, have highly rounded carapaces, attain large body sizes, and in general possess a carapace similar in shape to tortoises living in other parts of the world (Fig. 3). Van Denburgh considered only the tortoises from Santa Cruz and Volcán Alcedo of Isabela to be consistently dome shaped. He considered tortoises from Santiago (=San Salvador), San Cristóbal and the volcanoes of Sierra Negra, Cerro Azul, and Volcán Darwin on Isabela to be intermediate between the two extremes. The single specimen collected on Isla Rábida was also considered intermediate, but this specimen was probably introduced by man from southern Isabela. It is doubtful that tortoises ever successfully colonized Isla Rábida (MacFarland and Reeder 1975).

Any attempt to systematically compare morphological variation in giant tortoises must consider ontogenetic and sexual variation, as well as populational and environmentally determined variation. To allow concurrent consideration of these aspects, the emphasis in this report will be on local populations rather than hypothesized taxonomic or island groupings. In general, the five large volcanoes of Isabela are treated as discrete entities in the comparison of ecological conditions. For present purposes, all individuals encountered in the same general vicinity (usually a radius of 2-3 km) are considered to comprise a local population or deme. Although museum specimens have been studied, analyses of size and shape relationships presented here are based on data that I recorded from living specimens in the Galapagos during 1976 and 1977, except where noted. Because some populations are represented by small samples and poorly known, it was not possible to include all samples in each analysis.

As noted by Van Denburgh (1914), populations appear to differ in size and shape. In order to distinguish components of evolutionary divergence, it is desirable to consider separately aspects of size and shape that vary. Thus, I have attempted to identify one morphometric variable that measures size and that is minimally influenced by variation in carapace shape. Such a variable would be one that correlates highly with most morphometric variables in both inter- and intra-populational correlation analyses. The rationale for selection of an independent estimator of size is presented by Kluge (1974).

Of 20 morphometric variables from the carapace and plastron of living tortoises, and 26 such variables from museum specimens, the curved width of the carapace (CW), a measurement also studied by Van Denburgh, was consistently highly correlated with most variables in both inter- and intra-populational correlation matrices. It is also significant that in principal component analyses CW is heavily emphasized on the first factor, which is hypothesized to measure size relationships.

Comparison of living populations of tortoises is facilitated by using CW as a measurement of size (Fig. 4). Because of the varying effects of man and introduced mammals on the natural population structure of individual tortoise populations (reproduction and survivorship), the range of size variation is more likely to depict previous populational differences than are populational means or variances. It can be noted that individuals from Española and Pinzón are relatively small in relation to most other populations, and that individuals from San Cristóbal and Pinta are intermediate in size, based on present samples. Size ranges evident in museum samples are similar, and it can be hypothesized that significant size differences do occur.

From the factor matrix of the principal component analyses, it can be determined that the second factor emphasizes three variables measuring vertical distortion of the anterior carapace: the height of the anterior carapace (FH), the height of the first marginal (H1M), and the height of the second marginal (H2M) were most strongly emphasized. Since this is an orthogonal vector, the trend it describes is independent of size considerations, and it can be considered to be a vector measuring the shape of the anterior carapace. By selecting the most heavily weighted of these variables (FH) as an indication of height, we can confine our preliminary comparisons

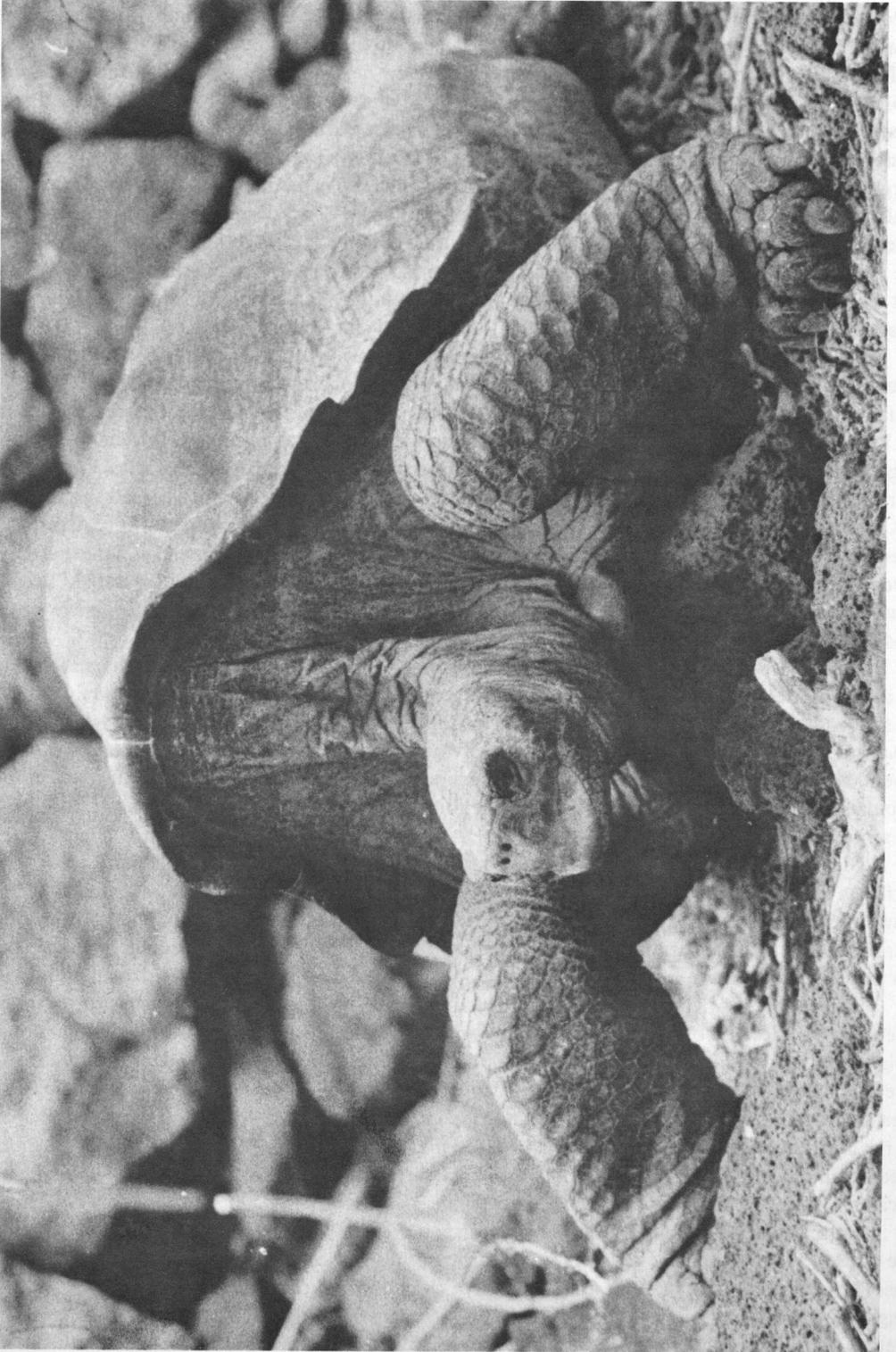


Fig. 2. Anterior view of an adult male from Pinta (CW = 931mm) showing a saddled shape of the carapace.



Fig. 3. Anterior view of a male from Volcán Alcedo, Isabela, showing a domed shape of the carapace.

to bivariate relationships of height (FH) and of size (CW) in investigating shape relationships.

It is apparent from Figs. 5-10, which depict shape relationships for individual populations, that adult males are consistently larger than females. With the possible exception of tortoises from Santiago, shape relationships are similar for both sexes within the population (i.e. populations can be represented as a continuous straight line). The shape relationships for the sexes from Santiago, in contrast, form two parallel lines, suggesting increased sexual dimorphism in this population. Comparison of the slopes (b) of the regression lines of Figs. 5-10 reflects populational differences in carapace shape. Specifically, populations from Pinzón, Española and San Cristóbal have larger slopes, indicating an increase in the height of the anterior carapace in relation to overall size. Of the populations considered here, the two judged to be of the saddle-backed type by Van Denburgh have the largest slopes (Española 0.479 and Pinzón 0.514). The population from San Cristóbal has a smaller slope (0.414), and other populations range from 0.209 to 0.313. This relationship provides a quantitative measure of carapace shape and allows comparison of populations. A high value for the slope indicates a high anterior carapace relative to size, whereas a low value reflects a low anterior carapace. Tortoises from Pinzón and Española have anterior carapaces nearly equal in height to those of much larger tortoises from other populations. Tortoises from San Cristóbal are intermediate in slope values as well as in overall size.

Gould (1971) pointed out that allometric changes in shape were the rule rather than the exception in groups with significant size variation. Such allometry presumably facilitates the maintenance of functional relationships (usually structural or physiological) of individual morphological components. Thus it might be expected that the size variates within a single population might reflect some of the same functional shifts seen in interpopulational comparisons. Frazzetta

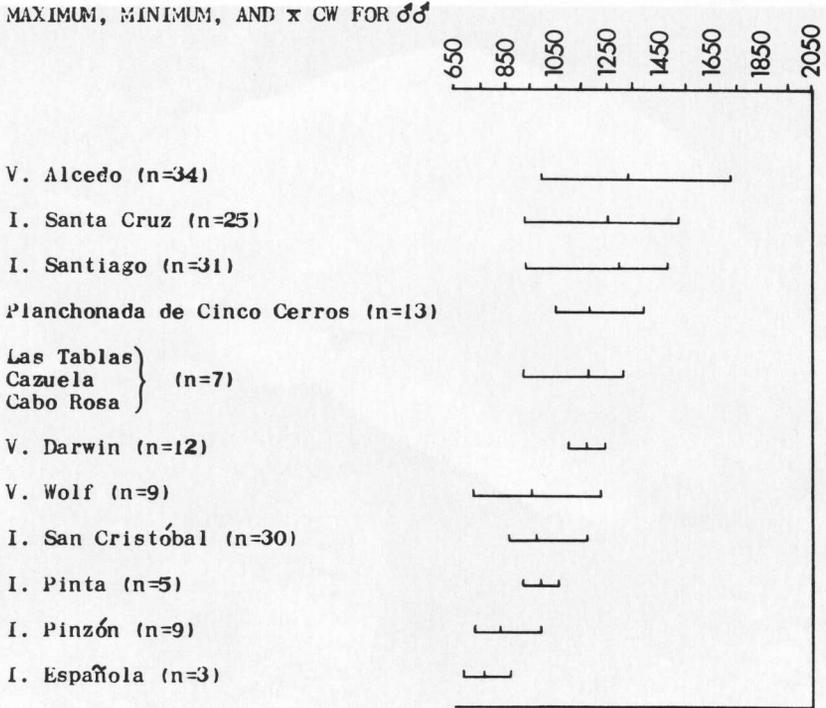


Fig. 4. Minimum, maximum, and mean curved widths of tortoises in living populations in Galapagos.

(1975:198) discussed a hypothetical example of size variation involving such relationships. This model predicts that individuals of two divergent taxa would be similar in shape at comparable sizes irrespective of age or life stage. On the basis of available data from Galapagos tortoises, such a model appears to be inappropriate. Shape differs between some populations throughout the entire range of adult sizes. In addition, individuals from populations with the largest body sizes differ less in shape from juveniles than do adults from populations with smaller body sizes. Instead of the giant differing from other life stages, extreme divergence in shell shape appears in populations not attaining large adult sizes. The possibility that the allometry of tortoises is adaptive in preserving an ecological function is considered later in this paper.

In the relationship between FH and CW, only two populations (Santiago and Planchonada de Cinco Cerros) appear to have curvilinear size relationships in adult samples. A logarithmic transformation (\log^{10}) of the frontal height was employed to investigate the possible curvilinearity of all populations. Table 1 compares correlation coefficients of transformed and untransformed values of FH with CW. Coefficients for populations hypothesized to be linear either decreased in value when transformed data were used or varied insignificantly, whereas those for Santiago and Planchonada de Cinco Cerros (PCC) appeared to increase. Using a *t*-test for comparison of correlation coefficients, it can be shown that the difference observed for SNT is insignificant whereas that for PCC is significant at $P < 0.05$ level. Thus it appears that only the tortoises from PCC on the eastern slopes of Cerro Azul show curvilinear relationships between FH and CW. In this population, larger individuals tend to have a disproportionately high frontal height, but since this exaggeration of FH occurs at a much larger size than in the populations from Pinzón, Española and San Cristóbal, a distinct carapace shape results. It is possible that pedomorphism has played an important role in the evolution of carapace shapes in Galapagos tortoises.

As a means of investigating the possibility of environmental effect on carapace size and

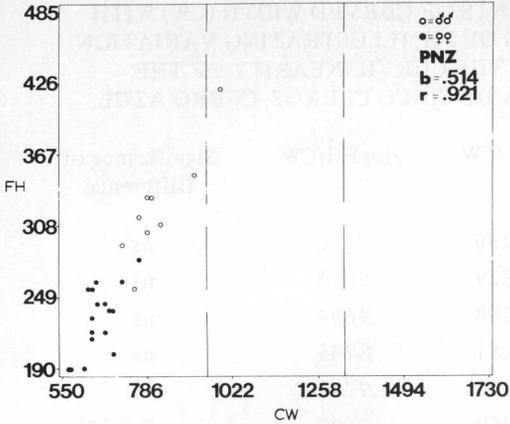


Fig. 5. Bivariate plot showing regression of FH on CW for tortoises from Isla Pinzón.

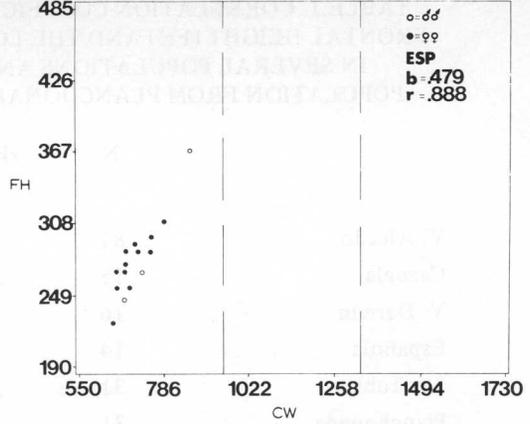


Fig. 6. Bivariate plot showing regression of FH on CW for tortoises from Isla Española.

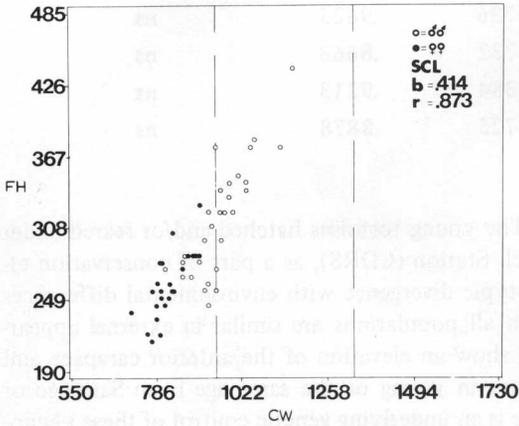


Fig. 7. Bivariate plot showing regression of FH on CW for tortoises from Isla San Cristóbal.

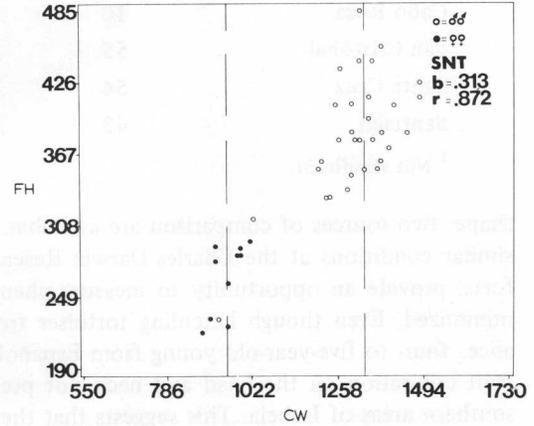


Fig. 8. Bivariate plot showing regression of FH on CW for tortoises from Isla Santiago.

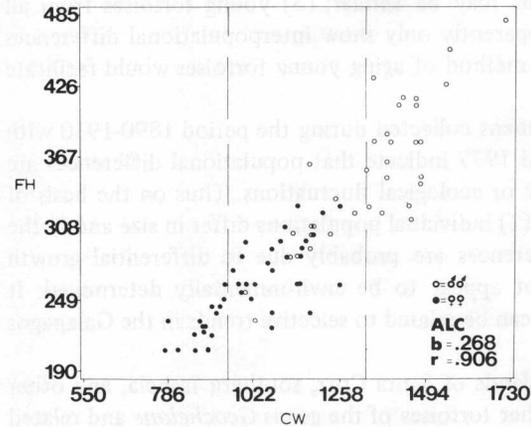


Fig. 9. Bivariate plot showing regression of FH on CW for tortoises from Volcán Alcedo, Isla Isabela.

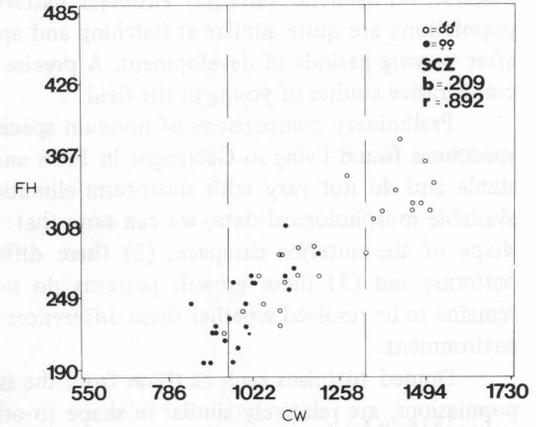


Fig. 10. Bivariate plot showing regression of FH on CW for tortoises from Isla Santa Cruz.

TABLE 1. CORRELATION COEFFICIENTS OF CURVED WIDTH (CW) WITH FRONTAL HEIGHT (FH) AND THE LOG OF FH, ILLUSTRATING VARIATION IN SEVERAL POPULATIONS AND THE CURVILINEARITY OF THE POPULATION FROM PLANCHONADA DE CINCO CERROS, CERRO AZUL

	N	$r_{FH/CW}$	$r_{\log FH/CW}$	Significance of Difference
V. Alcedo	81	.9236	.9250	ns ¹
Cazuela	15	.9829	.9675	ns
V. Darwin	16	.9808	.9694	ns
Española	14	.8881	.8745	ns
Las Tablas	31	.9821	.9779	ns
Planchonada de Cinco Cerros	31	.9460	.9690	$P < 0.05$
Pinzón	30	.9499	.9519	ns
Cabo Rosa	10	.9736	.9825	ns
San Cristóbal	55	.8732	.8663	ns
Santa Cruz	54	.9384	.9213	ns
Santiago	43	.8725	.8878	ns

¹ Not significant.

shape, two sources of comparison are available. The young tortoises hatched and/or reared under similar conditions at the Charles Darwin Research Station (CDRS), as a part of conservation efforts, provide an opportunity to measure phenotypic divergence with environmental differences minimized. Even though hatchling tortoises from all populations are similar in external appearance, four- to five-year-old young from Española show an elevation of the anterior carapace and light coloration on the head and neck not present in young of the same age from Santiago or southern areas of Isabela. This suggests that there is an underlying genetic control of these phenotypic differences, which will be examined in detail in a later paper. I have not included juveniles in the present analyses for three reasons: (1) except for a few populations, few data are available from young; (2) the present comparison of variation in adult populations is not intended to describe ontogenetic variation although patterns may be similar; (3) young tortoises from all populations are quite similar at hatching and apparently only show interpopulational differences after varying periods of development. A precise method of aging young tortoises would facilitate comparative studies of young in the field.

Preliminary comparisons of museum specimens collected during the period 1890-1910 with specimens found living in Galapagos in 1976 and 1977 indicate that populational differences are stable and do not vary with short-term climatic or ecological fluctuations. Thus on the basis of available morphological data, we can note that: (1) individual populations differ in size and in the shape of the anterior carapace; (2) these differences are probably due to differential growth patterns; and (3) these growth patterns do not appear to be environmentally determined. It remains to be resolved whether these differences can be related to selective trends in the Galapagos environment.

Domed tortoises such as those from the islands of Santa Cruz, southern Isabela, and other populations, are relatively similar in shape to other tortoises of the genus *Geochelone* and related genera in South America, Africa, Asia and North America. Nearly all are capable of retracting the head and neck within the carapace and protecting the anterior opening of the carapace by pulling up the forelimbs, which are covered with thick scales. Nearly all such tortoises passively protect

themselves from vertebrate predators in this manner. However, the elevation of the anterior carapace of saddles is found nowhere outside of the Galapagos and is unknown in the fossil record. Such a morphology presents a proportionately large opening of the anterior carapace which cannot be effectively covered by the forelimbs (Fig. 2). Since this deviation from a "typical" tortoise shape has evolved only in the Galapagos where there are no large native terrestrial predators, I suggest that predation pressure may have prevented such innovations in more complex ecosystems. This hypothesis is supported by the effect of predators introduced in the Galapagos by man. Dogs have been used to hunt tortoises since colonization of the islands by man and now, as feral populations, prey on tortoises on islands supporting both saddled and domed tortoises. The domed populations on Cerro Azul, Sierra Negra, and Santa Cruz have been reduced by a variety of factors, including predation by feral dogs and man, but they still persist in viable populations. In contrast, the saddled populations on the islands of Santa Fe and Floreana (=Santa María) became extinct soon after the arrival of man.

Darwin (1889) noted that in 1835, only four years after the island was colonized, the tortoises were sufficiently rare on Floreana to necessitate hunters traveling to other islands to secure tortoises for meat and oil. Tortoises were extinct on Santa Fe prior to 1905. It is probable that both populations were reduced by man, with feral dogs attacking and killing the remaining individuals. That at least adults of domed populations are more resistant to dog attacks is evidenced by their survival on Sierra Negra and Cerro Azul, both of which have large feral dog populations. Several specimens collected on Sierra Negra by the California Academy of Sciences' expedition in 1905-06 show severe scars from dog or pig attacks. Some individuals survived complete removal of scutes and underlying bone of all anterior marginals and had initiated regeneration of scales prior to being collected by the Academy expedition (pers. obs.).

Thus the saddle morphology appears to be unique to the Galapagos and to be an adaptation that is most likely to persist only in an environment devoid of large terrestrial predators. This, however, does not tell us why saddled tortoises evolved in the Galapagos, but rather suggests why they did not evolve or survive in continental faunas.

In order to consider the adaptive nature of the saddled morphotype, it is necessary to scrutinize the individual islands and habitats where these tortoises occur. No island with a maximum elevation below 800 m has a native domed population, even though domed tortoises do occur below 800 m on other islands. In contrast, six of eight saddled populations occur on islands with a maximum elevation of less than 800 m (Table 2). If islands and major volcanoes are ranked by surface area, six of eight with the largest areas are inhabited by domed tortoises. The exceptions are Fernandina and San Cristóbal, both of which had native saddled tortoises. All six of the smallest tortoise islands have or have had in historical times saddled tortoises. Only three of the Galapagos islands that exceed 15 km² in area lack native tortoises, and all of these fail to exceed 400 m in maximum elevation. Apparently both island area and elevation are related to environmental conditions of humidity, temperature, and plant diversity, which affect tortoise distributions. And since the large islands usually have higher volcanoes than do the small islands, they also have larger areas that tend to be cooler and more mesic than any habitats on the small, low islands. These climatic differences are due to cloud capture and "garua" (fog drip or drizzle) produced by inversion layers and predominant winds from southeastern coordinates (Bowman 1961; Thornton 1971). The moisture-bearing clouds tend to build up against southeastern facing slopes at elevations of 300 to 800 m, increasing available moisture and moderating temperatures; at the same time, terrain above 800 m and below 300 m and northern exposures may be sunny and dry. These local climatic extremes, as well as volcanic activity, are possibly the most important factors maintaining the diversity of the archipelago's fauna and flora.

Since carapace size differences have been recognized within both saddled and domed populations, the possibility of correlation between carapace size and maximal altitude of the volcano inhabited was investigated. A preliminary analysis, based on the mean length of museum specimens,

TABLE 2. COMPARISON OF ENVIRONMENTAL CHARACTERISTICS WITH THE CARAPACE MORPHOLOGY OF POPULATIONS OCCUPYING ISLANDS WITHIN THE GALAPAGOS

	Area km ²	Altitude (in m)	Carapace Shape	Slope FH/CW
Sierra Negra	1590	1486	dome	—
Santa Cruz (SCZ)	985	864	"	.209
Fernandina	642	1494	saddle	—
Volcán Alcedo (ALC)	615	1113	dome	.268
Santiago (SNT)	584	907	dome	.313
San Cristóbal (SCL)	558	730	saddle	.414
Volcán Darwin (DAR)	530	1311	dome	—
Cerro Azul	530	1689	dome	.291
Volcán Wolf (WOL)	380	1707	saddle/dome	.305
Floreana	172	640	saddle	—
Española (ESP)	60	206	"	.479
Pinta	59	777	"	—
Santa Fe	24	259	"	—
Pinzón (PNZ)	18	458	"	.514

indicated a significant correlation of size with terrain elevation (Fig. 11). Subsequent analyses using curved widths of the carapace determined from living populations resulted in a significant correlation between carapace size and maximum terrain elevation for females ($r = .66$, $P < 0.05$) but not for males ($r = .47$, $P < 0.1$). Since the elevational effect was hypothesized to result from cooler and more mesic climates of higher zones, and since such effects are also dependent upon exposure to winds from southeastern coordinates, the location of major tortoise populations was included in the analysis. Dry, warm zones extend much higher on northern slopes than they do on southern slopes (Thornton 1971). Accordingly an elevational divisor was devised based on a simplistic model of exposure to the southeast. Populations occupying slopes in the southeastern quarter of an island or major volcano were assigned divisors of one, those in northeastern, southwestern or central areas two and those in the northwestern quarter three. The analysis was repeated using maximal elevations divided by the appropriate divisor and correlations for female and male samples were $r = .76$, $P < 0.01$ and $r = .68$, $P < 0.05$ respectively (Fig. 12).

A parallel situation can be seen in size variation within the tortoises related to *Geochelone chilensis* in Argentina (Freiberg 1973) where tortoises in dry, warm northern regions of the range are significantly smaller than those from southern extremes of the range where moister and more temperate conditions prevail. On the basis of a variety of evidences, it can be shown that saddled tortoises in the Galapagos occupy drier habitats with more extreme temperatures than do domed forms. This is true even of the three exceptional saddled populations from San Cristóbal, Fernandina, and Volcán Wolf; all are volcanoes that are drier than other large land masses in the Galapagos. In the case of Volcán Wolf, tortoises are restricted to the drier northern and western slopes by volcanic formations. At present only saddled tortoises remain on San Cristóbal, and these are confined to a low dry area occupying the half of the island to the northeast. Whether the extinct tortoises that occupied the higher and wetter regions on the rest of San Cristóbal were domed or saddled is not known. Fernandina, despite its large size and extremely high altitude, is quite

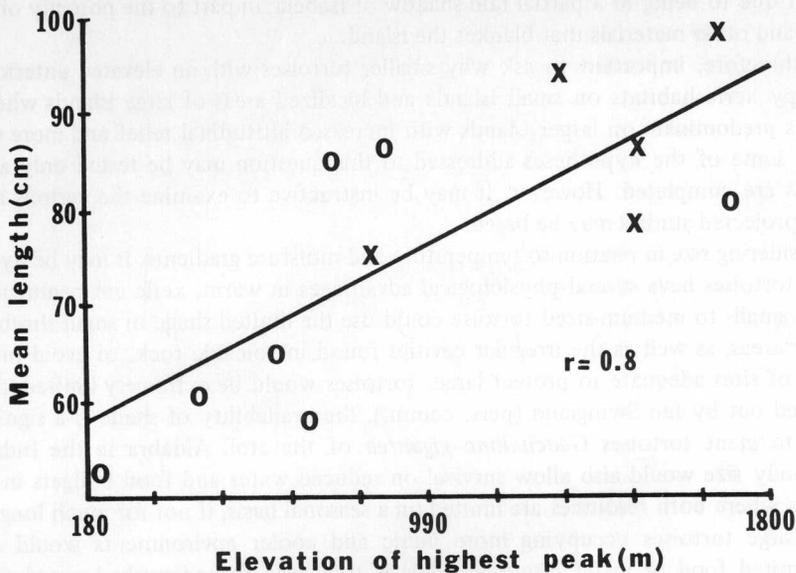


Fig. 11. Bivariate plot showing correlation of mean size (length of carapace) with the maximum elevation of volcanoes inhabited by 12 populations of tortoises represented in museum collections.

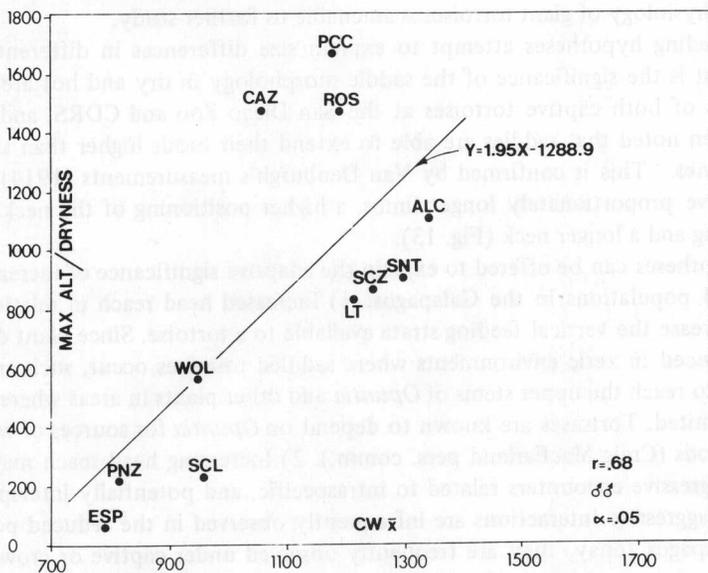


Fig. 12. The relationship of mean size of males with maximum altitude of volcanoes inhabited modified for exposure to moist southeastern winds. See text for explanation of altitude/dryness index (ordinate).

xeric, in part due to being in a partial rain shadow of Isabela, in part to the porosity of the recent volcanic ash and other materials that blanket the island.

It is, therefore, important to ask why smaller tortoises with an elevated anterior carapace should occupy xeric habitats on small islands and localized areas of large islands whereas larger domed forms predominate on larger islands with increased altitudinal relief and more mesic habitats. Clearly some of the hypotheses addressed to this question may be tested only after future investigations are completed. However, it may be instructive to examine the various alternatives upon which projected studies may be based.

In considering size in relation to temperature and moisture gradients, it may be hypothesized that smaller tortoises have several physiological advantages in warm, xeric environments. For instance: 1) A small- to medium-sized tortoise could use the limited shade of small shrubs and trees found in dry areas, as well as the irregular cavities found in volcanic rock, to avoid intense heat. The number of sites adequate to protect larger tortoises would be extremely limited in dry areas, and as pointed out by Ian Swingland (pers. comm.), the availability of shade is a significant limiting factor to giant tortoises *Geochelone gigantea* of the atoll Aldabra in the Indian Ocean. 2) Smaller body size would also allow survival on reduced water and food budgets in extremely xeric habitats where both resources are limited on a seasonal basis, if not for much longer periods. Conversely, large tortoises occupying more mesic and cooler environments would seldom be subject to limited food or water resources. This is true even in undisturbed populations in the Galapagos because the availability of nest sites is probably a major population-limiting factor, which normally maintains population levels below the carrying capacities of food or water supplies. At the same time, a large body size might function to prevent excessive heat loss during intermittent fogs and cool periods associated with higher elevations. The importance of these factors in the physiology of giant tortoises is amenable to further study.

The preceding hypotheses attempt to explain size differences in different island environments, but what is the significance of the saddle morphology in dry and hot areas? On the basis of observations of both captive tortoises at the San Diego Zoo and CDRS, and tortoises in the field, it has been noted that saddles are able to extend their heads higher than similarly sized or even larger domes. This is confirmed by Van Denburgh's measurements (1914), which indicate that saddles have proportionately longer limbs, a higher positioning of the neck on the anterior carapace opening and a longer neck (Fig. 13).

Two hypotheses can be offered to explain the adaptive significance of increased reach of the head in saddled populations in the Galapagos: 1) Increased head reach in relation to size could function to increase the vertical feeding strata available to a tortoise. Since plant density and palatability are reduced in xeric environments where saddled tortoises occur, such an increase could enable animals to reach the upper stems of *Opuntia* and other plants in areas where food and water resources are limited. Tortoises are known to depend on *Opuntia* for sources of water during prolonged dry periods (Craig MacFarland pers. comm.). 2) Increasing head reach may also confer an advantage in aggressive encounters related to intraspecific, and potentially interspecific, competition. Although aggressive interactions are infrequently observed in the reduced population densities in the Galapagos today, they are frequently observed under captive or crowded conditions. During these encounters, the tortoises extend their heads and necks as high as possible, and with limbs fully extended, they ultimately resort to lifting one forelimb, thereby gaining added height (Fig. 13). Extended to their maximum height, the tortoises may threaten each other with a "gaping" display of the mouth. Occasionally the highest tortoise will strike or bite the head of the other tortoise. The victor, or dominant individual, is nearly always the one that extends its head the highest. The loser, or subordinate, will acknowledge defeat by retracting its head into the carapace, simultaneously emitting a loud hiss, and turn or crawl away. Such encounters have been observed during feeding, drinking, and mating activities and occasionally when two tortoises move toward the same area for undetermined motives. These behaviors resemble ritualistic dominance



Fig. 13. Aggressive interaction of tortoises of divergent carapace shapes at the Charles Darwin Research Station. Male domed tortoise of unknown origin (CW=1198 mm) on right and male saddle-backed tortoise from Española (CW=860 mm) on left. Note height of head in relation to size.

interactions, well known in other animals, which function during intraspecific competition. The degree of intraspecific competition in undisturbed populations of tortoises in the Galapagos is unknown, but it is expected to be greater in xeric areas where food, water, and shade may be limited.

Both hypotheses attempt to relate the saddle morphology to increased fitness in intraspecific competition and subsistence in extreme xeric environments. No quantitative measurements of food abundance in the Galapagos are available; however, tortoises in xeric habitats on Pinzón, San Cristóbal and Volcán Wolf were rarely observed feeding during the dry periods of 1976, and the areas inhabited were largely devoid of living forbs and preferred food plants. In contrast, during the same period, tortoises in mesic habitats on other islands were often observed feeding, and the plants available as food plants did not appear reduced in relation to tortoise browsing.

The advantage of an increased feeding range and the ability to protect resources during intraspecific competition would be accentuated even more during extreme dry periods that span more than one year. Colinvaux (1972) and Colinvaux and Schofield (1976) have provided evidence that the Galapagos region was much drier during the late Pleistocene than during the Holocene. On the basis of Colinvaux's interpretation of sediments, the 15,000-year dry period was due to reduced rainfall in the wet season, with little change in present garua patterns. Since seasonal rains provide nearly all of the available moisture to lowland areas, small islands with minimal altitudinal relief would have been much more severely affected by this dry period than higher areas on large islands with the potential for cooler temperatures and significant moisture derived from garua and fog. While the exact mechanism accounting for the drying during Pleistocene times is open to dispute, the effect on some tortoise populations is more certain.

If tortoises inhabited lowland areas during drier periods when food and water resources were limited, two results could be expected: 1) animals might migrate to higher elevations where more mesic conditions persisted; or 2) on islands without sufficient altitudinal relief, there should have been a marked increase in intraspecific competition among the inhabitants for food, water and resting places.

An important factor influencing the survival of tortoises and any resultant evolutionary response during dry climatic periods would be the degree of ecological amplitude on the volcanoes inhabited by tortoises. Although the degree of evolutionary change would be related to both the amount of genetic variation in the original population and the intensity of selective pressures, we can estimate only the latter, using physical parameters of the volcanoes inhabited. Using the slopes (b), listed in Table 2, as a measure of the extent of morphological change and the areas (in km^2) of the individual volcanoes as measures of ecological amplitude, a negative correlation ($r = -.73$, $P < 0.05$) is evident. Islands and volcanoes with small areas show an increased tendency toward a saddle morphology and vice versa.

Upon examining all populations of tortoises for tendencies toward increasing the vertical reach of the head, several differences in carapace morphology were noted that may represent independent adaptations to similar selective pressures. (For examples of various populations, see the photos published by Van Denburgh [1914]). Inasmuch as the ability to extend the head vertically is governed by several aspects of carapace morphology, simple measurements of the height of the anterior carapace (FH) do not provide adequate insight into factors limiting head movement. For instance, tortoises from Santa Cruz tend to have the lowest anterior carapace. This is in part due to the extremely large convex anterior marginals, which slope ventrally toward their anterior margins. This results in a horizontal shelf that limits the elevation of the basal portion of the neck. Alternatively, tortoises from various populations on Volcán Alcedo, Cerro Azul, and Sierra Negra, Isabela have anterior marginals that are horizontal, or slope only slightly, which effectively raises the anterior margin of the carapace.

Individuals from Planchonada de Cinco Cerros, Isabela and Pinzón are quite distinct in appearance, but both tend to have anterior marginals that are reduced in size and less convex on

their anterior edges. This results in a shorter shelf above the basal neck, which possibly affects the angle at which the basal neck can be elevated. Tortoises from Española and Santiago have respectively large, recurved or dorsally flared anterior marginals. Both marginal types appear to reduce restriction of neck elevation. Such a diversity of anterior marginal types may provide evidence of similar selective trends during dry periods within a variety of insular populations.

An evaluation of evolutionary relationships of living and extinct populations of giant tortoises in the Galapagos is underway. Following analyses of morphological, ecological, and reproductive data, an estimate of the number of species within the archipelago will be possible. However, evidence is accumulating to suggest that tortoises, within the Galapagos Archipelago, have evolved in several directions. Clearly, our knowledge of giant tortoises presently lags far behind that of other elements of the Galapagos biota, but future studies promise to contribute significantly to an understanding of the evolutionary history of the Galapagos.

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RESUMEN

Las tortugas gigantes del Archipiélago del Colón son unas de las más grandes de los reptiles terrestres. Estos animales tienen varias formas morfológicas y ocurren en una variedad de ambientes en Galápagos. Análisis estadísticos como *factor analysis* y *discriminant function* indican que unas poblaciones insulares parecen distintas especies por su morfología. Hay dos fuentes mayores de variación: el tamaño y la forma del carapacho anterior. Las dos tendencias tienen relaciones con la ecología de las poblaciones y características ambientales. Estudios comparativos de tortugas criadas en condiciones iguales en la Estación Darwin indican que las diferencias morfológicas tienen bases genéticas y que probablemente no sean efectos ambientales.

El tamaño del carapacho de una población tiene relaciones adaptativas con la altura máxima del volcán en que viven y características de la humedad (lluvia y garúa). La forma del carapacho varía con la área del volcán o isla habitada y la humedad del ambiente. La variación de las dos tendencias resulta en la divergencia conocida en las tortugas de Galápagos.

Asumo una hipótesis que en zonas secas las características de un cuello largo, piernas largas y un carapacho alto anteriormente permitan a las tortugas alcanzar más alto con la cabeza. Con esta altura comen sobre una zona vertical más amplia y defienden recursos limitados (agua, comida y sombra) de otras individuales. La conducta de tortugas de Galapagos incluye una pelea con cabezas verticales; él que alcanza más alto domina al otro. Se encuentran estas adaptaciones extremas en las ambientes más secas del archipiélago donde la competición entre individuales es lo más grande.

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