

Shell Morphology of North American Tortoises

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ABSTRACT.—Significant differences exist in adult carapace lengths among the four species of North American tortoises (*Gopherus* spp.). However, after measures of whole shell and scute dimensions are adjusted for these size differences, shape is more similar between the largest species, *G. flavomarginatus*, and the smallest species, *G. berlandieri*, than with either of the intermediate-sized species, *G. polyphemus* and *G. agassizii*. Recent data based on an analysis of mitochondrial DNA of North American tortoises provide a phylogeny of the four extant species. A phenogram based on a multivariate analysis of 31 scute and shell measurements of North American tortoises is not concordant with a phenogram based on genetic data, although relationships among three major populations of *G. agassizii* are the same. Morphometric data are also not concordant with a matrix based on measures of precipitation and temperature, but are significantly correlated with a matrix based on growth variables ($R^2 = 0.74$, $P = 0.029$). Other environmental parameters may affect shape of shells.

INTRODUCTION

Recently, the evolutionary relationships among North American gopher tortoises have been assessed based on mitochondrial DNA data (Lamb *et al.*, 1989). This work has supported the conclusions based on skeletal data that indicate that two species groups exist within the gopher tortoise complex (Auffenberg, 1976; Bramble, 1982). The differences in skeletal characters have been related to differences in ecology (Bramble, 1982). Some authors have recognized the genus *Xerobates* (*Scaptochelys* in Bramble, 1982) for *agassizii* and *berlandieri*, and *Gopherus* for *polyphemus* and *flavomarginatus* (Bramble, 1982; Lamb *et al.*, 1989). However, a recent analysis of this group recommends the retention of *Gopherus* for all four species (Crumly, 1993). Besides genetic and skeletal differences, shell morphology varies among species of North American tortoises (True, 1882; Bogert and Oliver, 1945; Woodbury and Hardy, 1948; Grant, 1960; Brame and Peerson, 1969; Auffenberg, 1976). Few of these morphological differences have been adequately tested, though, and many are based on ratios, which may not remove size from shape (Atchley *et al.*, 1976; Albrecht, 1978; Atchley and Anderson, 1978; Reist, 1985; Packard and Boardman, 1987; Jackson *et al.*, 1990; Jackson and Somers, 1991).

Genetic differences also exist within the geographic range of the desert tortoise *Gopherus agassizii* (Jennings, 1985; Rainboth *et al.*, 1989; Lamb *et al.*, 1989). The greatest genetic differences in *G. agassizii* populations occur E and W of the Colorado River. Tortoise populations inhabiting the extreme southern portion of the range exhibit smaller yet significant differences (Jennings, 1985; Lamb *et al.*, 1989). Groups formed within the range of *G. agassizii* based on genetic data roughly correspond to broad climatic and vegetational differences: Mojave desert scrub, Sonoran desert vegetation and Sinaloan thornscrub and deciduous woodland (Germano *et al.*, 1993).

Differences in morphometrics of closely related groups can be due to past selective

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pressures that led to the formation of the *Gopherus* group, but also can reflect current ecological differences among the various species. Comparison of morphology among groups can lead to testable hypotheses concerning performance that directly affect fitness (Arnold, 1983). Fritts (1983) has shown that quantitative differences in shell morphology of domed and saddleback Galapagos tortoises (*Geochelone elephantopus*) are related to differences in feeding and behavioral ecology.

This study quantifies differences in size and shape of the four species of North American tortoises. I compare differences in shell shape and size and scute morphology to a phenogram for North American tortoises based on mtDNA. Similar analyses were also performed on shell morphology of *Gopherus agassizii* from three distinct regions within its range.

MATERIALS AND METHODS

Data were gathered from museum and field specimens of 70 *Gopherus berlandieri*, 232 *G. agassizii*, 55 *G. polyphemus* and 69 *G. flavomarginatus*. I recorded 32 shell and scute measurements (Fig. 1; Appendix 1). Whole shells were measured to the nearest 1 mm with a pair of tree calipers or cloth tape. Scutes were measured to the nearest 0.1 mm with dial calipers. Measurements were not recorded for broken or misshapen characters. Most misshapen scutes occurred on the carapace, often as a result of additional vertebral or costal scutes. Sex identification was made using shell characteristics, or from internal palpation for wild *flavomarginatus* (G. Aguirre Leon, pers. comm.).

Shell morphology varies within the broad geographic range of *agassizii* (Bogert and Oliver, 1945; Brame and Peerson, 1969). Thus, I segregated *Gopherus agassizii* individuals into Mojave, Sonoran and Sinaloan populations for analyses.

Size differences were analyzed using carapace length (CL) as the measure of size. I compared mean and upper decile CLs among adults of each group, and mean and upper quartile CLs between sexes using ANOVA. Individuals were classified as adults based on the sizes at which secondary sex characteristics appear: *Gopherus berlandieri*, ≥ 105 mm CL (Auffenberg and Weaver, 1969); *G. agassizii*, ≥ 180 mm CL (Burge and Bradley, 1976; pers. observ.); *G. polyphemus*, ≥ 200 mm CL (Landers *et al.*, 1982); *G. flavomarginatus*, ≥ 250 mm CL (Legler and Webb, 1961). Upper decile values reduce the effect of sampling bias based on age structure (Case, 1976) and, therefore, may depict more accurately adult size. I used upper quartile values for comparisons between sexes.

Shell measurements covary significantly with body size (Appendix 2). To assess morphometric differences independent of size, I transformed data by using the residuals from regression analyses to remove as much of the effect of size as possible (Reist, 1985). Pooled within-group slopes for each variable on CL (Thorpe, 1976; Reist, 1985) were used along with the grand mean of CL to remove size effects.

After measurements were adjusted for size, I performed principal components analysis (PCA) using SAS program PRINCOMP (SAS Institute Inc., 1988) to quantify variation in shell and scute shape. If groups were apparent after PCA, then multivariate analysis of variance (MANOVA) was employed using the SAS GLM program (SAS Institute Inc., 1988) to determine the significance of differences in morphometrics among groups. Shape differences also were compared between sexes using 12 shell and scute characters. Significance of MANOVAs was determined using the greatest characteristic root (gcr) (Harris, 1985). If the overall MANOVA was significant, lower order discriminant functions were similarly tested. ANOVAs were used to determine which characters varied significantly across samples when treating characters independently, with overall significance tested using post hoc critical values (CV) (Harris, 1985);

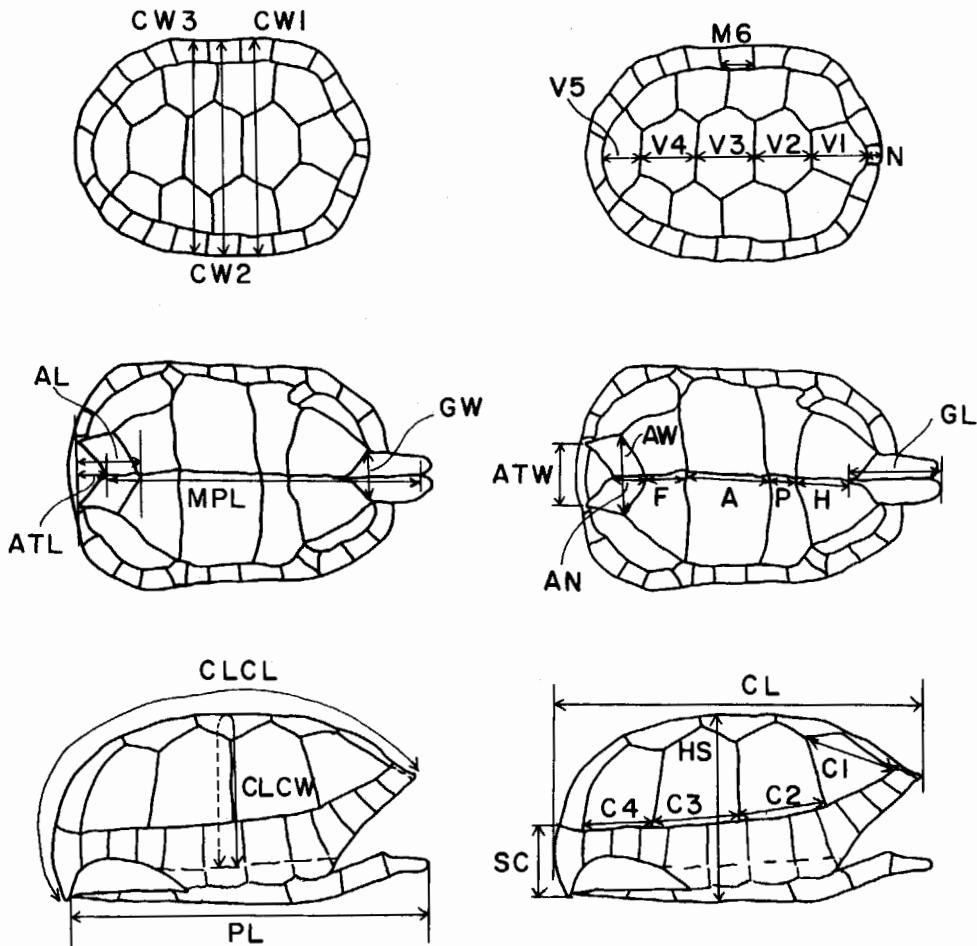


FIG. 1.—Thirty-two measurements were recorded on shells of North American tortoises. Nine measurements were taken from the shell and 23 were taken from scutes. Straight-line measurements of the shell were recorded using tree calipers and included CL, CW1, CW2, CW3, PL, MPL, and HS. Both CLCL and CLCW are curved-line measurements that were taken with a cloth tape. All scute measurements are straight-line measurements and were taken with dial calipers. Explanation of measurement abbreviations is given in Appendix 1

$$CV = \frac{df_{error}}{df_{effect}} \times \frac{\theta_{crit}}{1 - \theta_{crit}}$$

These post hoc critical values are more stringent than F values derived for independent ANOVAs. For those ANOVAs that were significant, comparisons among means were assessed using Scheffe's multiple comparison test. This method makes all pairwise comparisons and controls for Type I error while possibly inflating Type II error, making this a conservative test among means (Sokal and Rohlf, 1981; Harris, 1985).

I used the mean values for each size-adjusted variable to form a phenogram and a matrix

TABLE 1.—Mean and upper decile carapace lengths for all adults, and mean and upper quartile carapace lengths for male (M) and female (F) North American tortoises. Among groups, lengths without common letters are significantly different. Asterisks denote significant differences between sexes

Species	Sex	Carapace length						
		Mean (mm)	n	SD	Upper ¹ decile (mm)	n	SD	
<i>berlandieri</i>		155.3 a	74	27.4	202.9 a	7	8.43	
	M	166.5*	44	27.4	197.7*	11	9.81	
	F	138.8*	30	17.5	160.0*	8	8.28	
<i>agassizii</i>	Mojave	220.2 b	180	22.8	262.5 b	18	8.89	
		M	226.8*	96	25.3	258.8*	24	9.89
	F	212.9*	74	16.3	233.4*	19	9.87	
		M	232.3 c	82	23.4	270.5 b	8	10.4
	Sonoran	M	236.3	36	24.4	263.9	9	9.66
		F	232.2	38	23.0	258.1	10	12.6
Sinaloan		218.7 b,c	40	32.1	274.0 b,c	4	10.2	
	M	209.0*	24	33.7	251.5	6	24.0	
	F	230.4*	13	21.7	255.5	3	8.50	
<i>polyphemus</i>		246.1 c	65	26.3	292.1 c	7	11.7	
	M	248.8	29	24.2	281.6	7	6.65	
	F	242.4	31	27.7	279.3	8	16.9	
<i>flavomarginatus</i>		311.9 d	69	31.7	367.6 d	7	8.38	
	M	300.9*	15	24.7	318.5*	4	4.04	
	F	337.8*	19	32.2	369.6*	5	10.4	

¹ Upper quartile means for sexes

of morphological distances among North American tortoises in the same manner as Lamb *et al.* (1989) for genetic distance data. The phenogram was constructed by UPGMA clustering using the average linkage algorithm of the BMDP statistica! package (Dixon, 1981). I compared morphological distances to genetic distances given in Lamb *et al.* (1989, Table 3) using the Mantel test (Mantel, 1967; Sokal, 1979). For the genetic matrix, I used the average genetic distances among the three clones (a1–a3) of the Mojave *agassizii* from Lamb *et al.* (1989) to compare to the Mojave *agassizii* portion of the morphometric matrix.

I also compared morphological distances to matrices composed of environmental parameters and growth measures. Environmental parameters included 20-yr means of monthly precipitation and temperatures from weather stations within the ranges of each species, estimates of geometric mean latitude and longitude of the range of each species, and mean predictability, constancy, and contingency of precipitation data (from Germano, 1989). Measures of predictability (P), constancy (C) and contingency (M) (Colwell, 1974) were made for each species' range. Predictability essentially measures variability with $P = 1$ indicating an absolutely predictable environment and $P = 0$ for a completely unpredictable environment. Constancy and contingency sum to the value of P. Constancy measures the evenness of rainfall among months and contingency measures the seasonality of rainfall within a year. These measures of climatic data accurately depict seasonality and variability of long-term data (Stearns, 1981). Growth measures were taken from an analysis of growth (Germano, 1989) using Richards' (1959) growth curves with jackknife confidence intervals

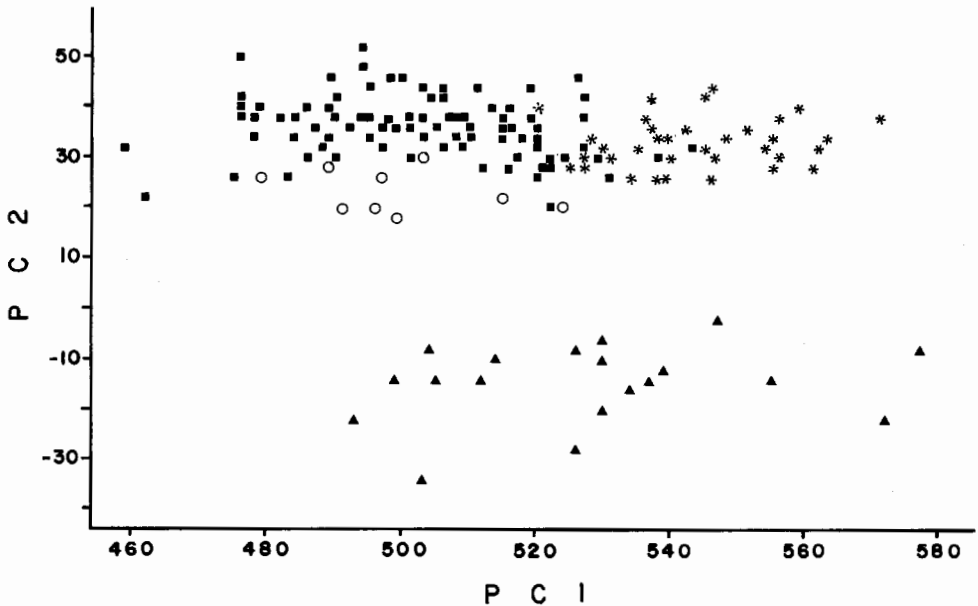


FIG. 2.—Morphometric space of North American tortoises based on the first two Principal Components (PC) of size-adjusted shell and scute measurements. Solid squares = *G. agassizii* ($n = 96$, 12 observations hidden); open circles = *G. polyphemus* ($n = 11$, 2 observations hidden); asterisks = *G. berlandieri* ($n = 40$, 5 observations hidden); solid triangles = *G. flavomarginatus* ($n = 19$)

(Bradley *et al.*, 1984). This analysis gives four growth parameters for each population: asymptotic size (upper decile CL), weighted mean growth rate, percentage of asymptotic size achieved at curve inflection, and time period in years to grow from 10 to 90% of asymptotic size. Also included were the mean and coefficient of variation of the width of annuli (mm) of the second costal scute and age at first reproduction (from Germano, 1989).

RESULTS

Adult CL varies significantly across samples (Table 1) with the largest species, *Gopherus flavomarginatus*, being almost twice as large as the smallest, *G. berlandieri*. *Gopherus agassizii* from the Mojave Desert are smaller than *G. polyphemus*, although *agassizii* from Sonoran and Sinaloa regions are similar in CL to *polyphemus* (Table 1). Significant differences in mean CL also exist between sexes for *berlandieri* and *flavomarginatus*, and for *agassizii* from the Mojave Desert and from Sinaloa habitats (Table 1). The small mean CL of male *agassizii* from Sinaloa habitats is due to several individuals <180 mm CL that were unquestionably males. Two preserved specimens of 156 mm and 168 mm CL showed distinct plastral indentations and were preserved with their penises everted. Male and female *agassizii* from Sinaloa habitats are not significantly different for comparisons of upper quartile CL (Table 1). Size dimorphism between sexes reversed pattern from the smallest species to the largest. In *berlandieri* and *agassizii* from the Mojave Desert, males are larger than females; in *flavomarginatus*, females are larger than males (Table 1).

PCA yielded eight principal components (PC) with eigenvalues ≥ 1 . The first two PCs separated tortoises into four groups, which were identifiable as the four species (Fig. 2).

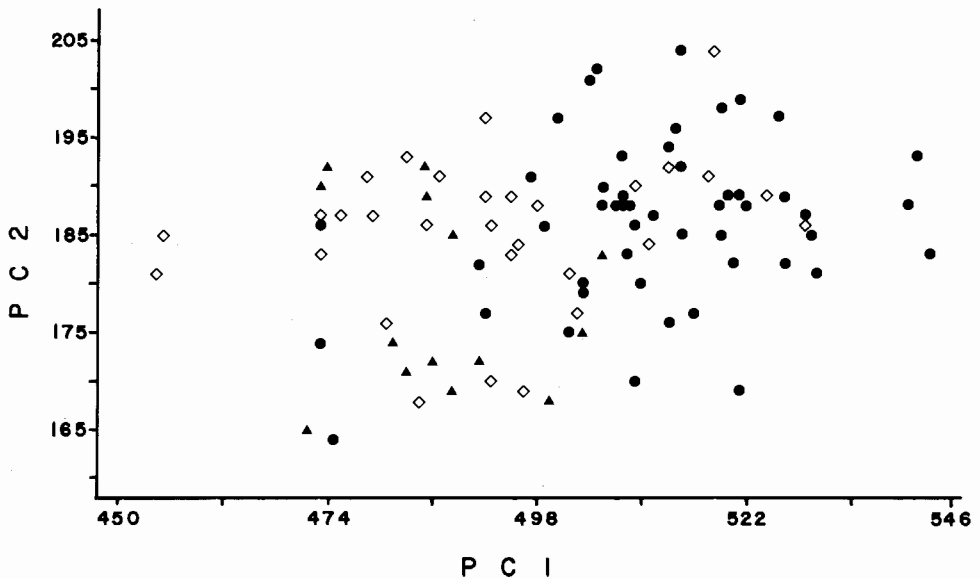


FIG. 3.—Morphometric spaces of populations of *G. agassizii* based on the first two Principal Components (PC) of size-adjusted shell and scute measurements. Solid circles = Mojave desert ($n = 50$, 2 observations hidden); open diamonds = Sonoran desert ($n = 30$); solid triangles = Sinaloan habitats ($n = 14$)

Sexes within these four groups created by PCA were not segregated. For *Gopherus agassizii*, PCA gave nine PCs with eigenvalues ≥ 1 . A plot formed by the first two PCs did not separate the three populations of *agassizii* (Fig. 3).

MANOVA results show significant differences among the species in morphometrics (Fig. 4, Table 2). Adults differ significantly on six of eight whole shell measures and nine of 23 scute measures. *Gopherus berlandieri* and *G. flavomarginatus* are the widest and tallest species. Sinaloan *agassizii* is narrowest and the most flat. *Gopherus berlandieri* also has the longest carapace measured from the anterior edge of the nuchal to the posterior edge of the supra-caudal (CLCL). This length comes from the elongation of the rear scutes of the carapace (Table 2) causing the shell to curve downward and turn anteriorly. There are no significant differences in overall plastron shape among species, but gulars are longest in *G. berlandieri* and shortest in Sonoran *agassizii*. Gulars are significantly widest in *flavomarginatus* and *polyphemus*. *Gopherus berlandieri* also have the widest anal scutes and the longest anal scute projections. *Gopherus polyphemus*, although distinct, is close morphologically to *G. agassizii*. *Gopherus flavomarginatus* is the most distinct morphologically, based on distance in morphological space (Figs. 2 and 4).

The three groups of *Gopherus agassizii* differ little among themselves in shape when compared to other tortoise species (Fig. 4). However, comparisons among *agassizii* independent of the other species show that individuals from the three regions are significantly different morphologically (Fig. 5, Table 2). *Gopherus agassizii* from the Mojave Desert are significantly wider than tortoises from Sonoran or Sinaloan habitats. Tortoises from Sinaloan habitats are the most narrow. Tortoises from the Mojave Desert are more domed than tortoises from Sinaloan habitats based on a significantly greater height of shell, greater

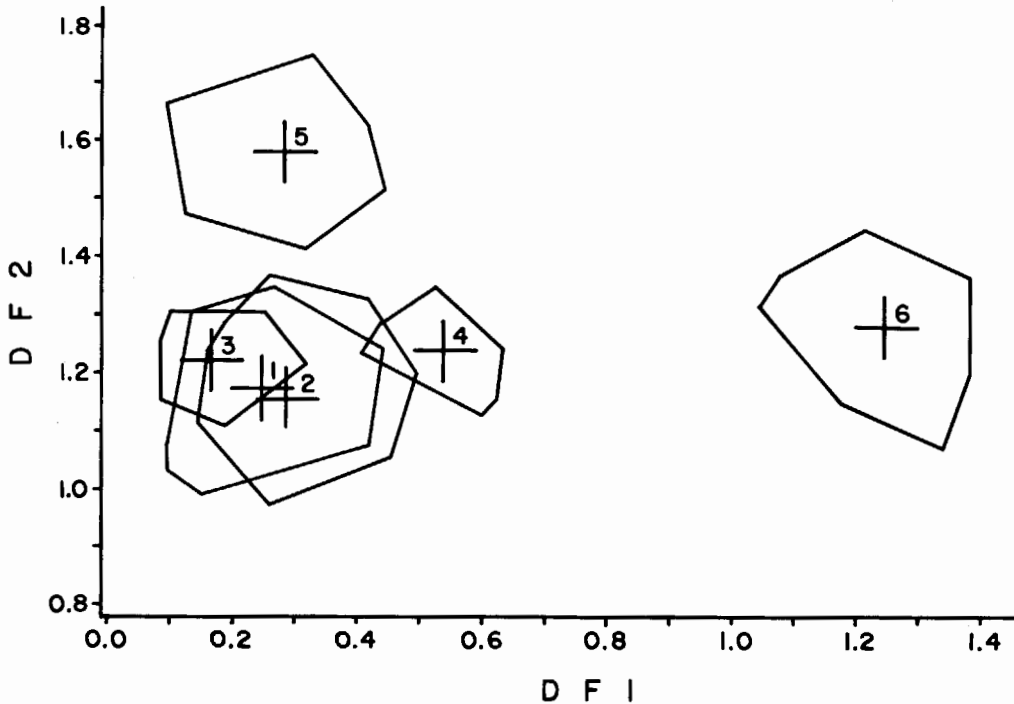


FIG. 4.—Morphometric areas encompassed by the six groups of North American tortoises based on the first two Discriminant Functions (DF) from MANOVA of size-adjusted shell and scute measurements. 1 = Mojave *G. agassizii*; 2 = Sonoran *G. agassizii*; 3 = Sinaloan *G. agassizii*; 4 = *G. polyphemus*; 5 = *G. berlandieri*; 6 = *G. flavomarginatus*. DF1 accounts for 69.3% of the variance and DF2 accounts for 14.2%

curved-line carapace length, and curved-line carapace width; tortoises from the Sonoran Desert are intermediate. In addition, *agassizii* from the Mojave Desert have significantly longer gulars than tortoises from the Sonoran Desert, but not longer than tortoises from Sinaloan habitats. *Gopherus agassizii* from the Sonoran Desert have a significantly shorter length of projection of their anal scutes than either tortoises from the Mojave Desert or Sinaloan habitats.

Sexes of five of the six groups are distinct morphologically (Table 3). The MANOVA value for *agassizii* from Sinaloan habitats is not significant between sexes based on the 12 measures used in this analysis. No single character is significant among the five significant MANOVA comparisons, although several are significant based on ANOVA tests (Table 3). For all groups, males have longer ATW and larger CLCL than females, and for all groups but *agassizii* from Sinaloan habitats, males have longer GL, based on ANOVA. Although male and female Bolson tortoises are not readily distinguishable morphologically (Morafka, 1982), males are larger than females for 10 of 12 characters tested by ANOVA (Table 3).

The morphological distance matrix (Table 4) is not concordant with the genetic distance matrix presented in Lamb *et al.* (1989; $R^2 = 0.07$, $P = 0.61$, 4 df, $t = 0.55$). The resultant phenogram also differs, although relationships among populations of *agassizii* are the same

TABLE 2.—Comparison of shell and scute measurements of adult North American tortoises among groups. Values given are least square means of 31 size-adjusted variables. For comparisons of characters, means without common letters are significantly different. F values from MANOVA (asterisks denote significant F, * $P < 0.05$, ** $P < 0.01$). *ber* = *G. berlandieri*; *poly* = *G. polyphemus*; *flavo* = *G. flavomarginatus*

Size-adjusted character	F value	<i>agassizii</i>					
		<i>ber</i>	Mojave	Sonoran	Sinaloan	<i>poly</i>	<i>flavo</i>
CW1	22.47**	182.7 a	177.5 b	169.4 c	162.6	174.3 b,c	185.4 a
CW2	29.33**	186.9 a	179.5	172.4 b	165.4	172.6 b	188.6 a
CW3	33.44**	191.5 a	182.1	174.5 b	169.8 b,c	168.9 c	188.5 a
CLCL	30.44**	315.9	296.0 a	290.7 a,b	287.4 b	288.1 b	291.5 a,c
CLCW	72.62**	285.3	262.5 a	262.1 a	248.5 b	268.1 a	307.1 c
PL	NS ¹	239.5	233.3 a	228.1 b	229.8 a,b	231.9 a,b	229.8 a,b
MPL	NS	212.2	211.8	208.5	208.6	210.3	211.3
HS	37.15**	114.7	104.4 a,b	99.4 c	96.8 c	100.1 b,c	107.4 a
N	NS ¹	12.9 a	15.5	13.0 a	12.8 a	12.5 a	9.5
V1	NS ¹	49.2	45.9 a	44.8 a,b	46.4 a	44.2 a,c	43.6 b,c
V2	NS ¹	45.1 a,b	46.2 a	45.0 a,b	44.3 b	45.6 a,b	44.4 b
V3	NS	45.9	46.3	45.8	45.4	45.6	44.8
V4	17.86*	55.6	48.5 a	50.8 a,b	50.6 a,b	50.9 b	49.6 a,b
V5	25.91**	59.0	50.4 a	49.6 a	48.5 a,b	44.9 b	47.9 a,b
SC	NS ¹	38.4	34.8 a	31.6 b,c	30.7 b	33.6 a,c	35.8 a
C1	NS ¹	55.9	54.7 a	52.9 a	53.3 a	49.1 b	50.1 b
C2	NS ¹	50.6 a	48.6 b	48.4 b	48.4 a,b	48.9 a,b	45.9
C3	NS ¹	48.7 a,c	47.1 b	48.9 a,c	47.6 a,b	50.6 c	46.7 b
C4	46.35**	55.1	48.3 a	48.6 a	49.2 a,b	51.7 b	60.6
M6	NS ¹	32.4 a	30.5	31.3 a	32.1 a	31.3 a	26.2
GL	30.02**	50.6 a	42.3 b	36.9 c	39.2 b,c	40.0 b,c	47.4 a
GW	156.6**	37.8 a	36.6 a	37.8 a	35.4 a	47.5	58.6
H	80.78**	44.6	48.9 a	50.2 a	49.1 a	37.7	26.1
P	NS ¹	22.1 a	17.5 b	17.0 b	22.1 a	21.8 a	21.9 a
A	27.70**	64.3 a	63.6 a	64.8 a	60.0	69.7	53.8
F	NS ¹	33.4 a	29.2 b	28.2 b	29.5 b	33.6 a	33.2 a
AN	NS ¹	20.6 a	19.7 a	21.2 a	20.1 a	14.6	20.6 a
AL	NS ¹	39.0 a	36.4 b	34.5 b	36.1 b	32.2	40.3 a
AW	21.94**	75.1	65.1 a	65.0 a,b	64.9 a,b	61.7 b,c	61.7 a,c
ATL	37.61**	23.0	16.3 a	12.5	16.1 a	18.2 a	16.0 a
ATW	NS ¹	57.4	49.4 a	45.5 a,b	48.1 a,b	47.6 a,b	42.2 b
MANOVA	556.77**						

¹ F values were not significant based on MANOVA post-hoc critical values but were significant based on ANOVA

(Fig. 6). The matrix of shell morphology also is not concordant with a matrix based on environmental variables (Table 5; $R^2 = 0.05$, $P = 0.66$, 4 df, $t = -0.47$), but is concordant with a matrix based on measures of growth (Table 5; $R^2 = 0.74$, $P = 0.03$, 4 df, $t = 3.37$).

DISCUSSION

The size and shape of shells of North America tortoises differ, although these differences did not seem to be related to genetic differences or measures of regional climate. The earliest

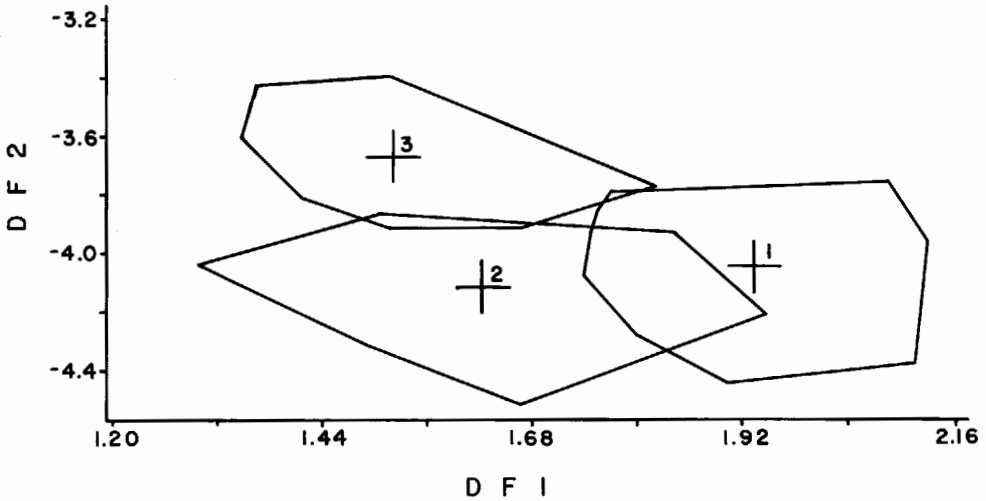


FIG. 5.—Morphometric areas encompassed by groups of *G. agassizii* based on the first two Discriminant Functions (DF) from MANOVA of size-adjusted shell and scute measurements. 1 = Mojave *G. agassizii*; 2 = Sonoran *G. agassizii*; 3 = Sinaloan *G. agassizii*. DF1 accounts for 67.8% of the variance and DF2 for 32.2%

comparison among North American tortoises, excluding the undiscovered *Gopherus flavomarginatus*, noted the dome shape of the carapace of *G. berlandieri* as a distinguishing characteristic from *G. agassizii* and *G. polyphemus* (True, 1882). The carapace of *G. agassizii* was found to be considerably depressed and nearly flat, whereas that of *G. berlandieri* was short and high, slightly marginate and revolute in front, and strongly incurvated behind (True, 1882). Besides the dome-shaped carapace of *G. berlandieri*, the shell of *G. agassizii* has been described as being longer than wide and wider than high, and that the shell shape of *G. polyphemus* and *G. agassizii* are more similar to each other than either is to that of *G. berlandieri* (Woodbury and Hardy, 1948). In a comparison of all four species, a discriminate function plot of shell morphometrics showed *flavomarginatus* more similar to *polyphemus* and *agassizii* than to *berlandieri* (Auffenberg, 1976), although this relationship among species is similar to differences in shell size.

There were several morphometric characters that I did not measure in this analysis that are sexually dimorphic. Male *berlandieri* have a greatly indented posterior portion of the plastron and noticeably recurved gulars. To a lesser degree these differences are seen in *Gopherus agassizii*, but they are less noticeable in *G. polyphemus* and almost nonexistent in *G. flavomarginatus*. I did compare 12 size-adjusted characters and found significant differences between sexes when all characters were combined. However, no one character gave a significant MANOVA critical value, although several characters were significant when tested by ANOVA. Overall size differences between the sexes showed a definite pattern. Males are significantly larger than females in the smaller species (*G. berlandieri*), equal in size to females in those intermediate in size (*G. agassizii* and *G. polyphemus*), and significantly smaller than females in the largest species (*G. flavomarginatus*). In a comparison of sizes between sexes of selected turtles of the world (Berry and Shine, 1980), males were listed as larger than females for all four species of *Gopherus*. This clearly is incorrect, and general theories of size dimorphism in turtles require more complete information. A more recent

TABLE 3.—Comparison of shell and scute measurements of male and female North American tortoises among groups. Values given are least square means of 12 size-adjusted variables. Means without common letters are significantly different. F values from MANOVA

Size-adjusted character	agassizii												flavomarginatus					
	berlandieri			Mojave			Sonoran			Sinaloa			polyphemus		F			
	F	Male	Female	F	Male	Female	F	Male	Female	F	Male	Female	F	Male	Female	F	Male	
CW1	NS	127.1	130.2	NS	175.0	173.9	NS	172.0	171.6	NS	153.0	155.2	NS	181.4	180.3	NS ¹	251.9	244.2
CW2	NS ¹	130.5	134.6	NS	176.5	175.9	NS	174.6	175.1	NS	156.2	157.0	NS	180.4	178.4	NS ¹	255.8	247.1
CW3	NS	134.5	135.9	NS	179.4	178.9	NS	178.2	176.1	NS	161.1	159.6	NS	176.6	174.7	NS ¹	258.6	249.5
CLCL	NS ¹	223.7	215.0	NS ¹	294.4	284.6	NS ¹	302.0	282.5	NS ¹	275.3	263.5	NS ¹	304.6	295.3	NS ¹	408.6	389.5
CLCW	NS ¹	198.6	204.1	NS	257.0	257.5	NS ¹	268.6	262.4	NS	235.7	231.4	NS	281.9	275.4	NS ¹	413.3	393.9
PL	NS	164.8	163.1	NS	229.1	227.9	NS ¹	232.9	228.2	NS	218.2	215.3	NS ¹	244.3	238.3	NS ¹	323.1	311.4
MPL	NS	144.1	145.8	NS	208.6	206.1	NS ¹	213.4	208.4	NS	198.4	195.2	NS ¹	220.4	216.6	NS ¹	297.9	282.8
HS	NS	82.3	80.8	NS	102.9	101.8	NS	101.1	99.6	NS	92.1	89.8	—	—	—	NS ¹	149.7	143.5
GL	NS ¹	35.0	31.5	NS ¹	43.8	38.1	NS ¹	39.5	35.6	NS	37.3	34.1	NS ¹	45.4	39.0	NS ¹	71.7	64.0
GW	NS ¹	24.9	27.3	NS ¹	35.0	36.7	NS	37.9	38.3	NS	33.8	32.7	NS	48.2	49.7	NS	72.6	72.1
ATL	NS	13.5	12.2	NS	16.3	15.0	NS	12.6	12.7	NS	14.5	14.5	NS	20.0	19.0	NS	28.9	28.1
ATW	NS ¹	38.7	33.7	NS ¹	50.5	45.2	NS ¹	49.3	43.0	NS ¹	46.7	40.1	NS ¹	54.7	45.4	NS ¹	78.7	57.1
MAN-OVA	62.12**			75.66**			44.64**			105.31			32.42*				361.57**	

¹ F values were not significant based on MANOVA post-hoc critical values, but were significant based on ANOVA (*P<0.05, **P<0.01)

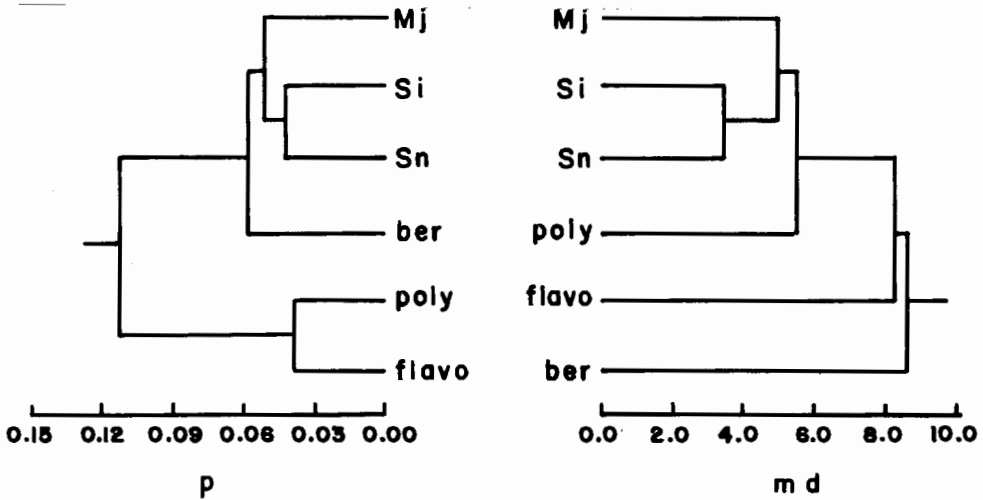


FIG. 6.—Phenograms based on genetic distances (p) (redrawn from Lamb *et al.* 1989, Fig. 3A) and morphometric distances (md). Symbols for populations are given in Table 4

listing of sizes of male and female *Gopherus* (Gibbons and Lovich, 1990) shows the same pattern of size reversal as I found. Exactly the opposite pattern of sexual size dimorphism (males smaller than females in the smaller species and males larger than females in the larger species) is found in kinosternine turtles (Berry and Shine, 1980; Iverson, 1991). The reversal of sexual size dimorphism in *Gopherus* is unexplained, but the larger tortoise species are more colonial than the smaller species.

Other features that I did not quantify are the degree of anterior carapace revoluteness, the degree of marginal flaring of the carapace, or the angle of the anterior portion of the plastron. I measured straightline characters, not angles or deflections. The front portion of the carapace of *Gopherus berlandieri* is revolute; that of the other three species is relatively flat along the margins, including the nuchal (True, 1882; Grant, 1960; Auffenberg, 1976). In *G. berlandieri*, the nuchal is sometimes absent, or is considered small when present (True, 1882; Grant, 1960). However, I found that only eight of 81 adult *G. berlandieri* lacked a nuchal entirely, and that when the length of the nuchal is adjusted by CL, it is shortest in

TABLE 4.—Estimates of morphological distances of North American tortoises from UPGMA clustering based on means of 31 size-adjusted shell measurements. Mj, Sn, Si = Mojave, Sonoran, and Sinaloa *G. agassizii*, respectively. *ber* = *G. berlandieri*; *poly* = *G. polyphemus*; *flavo* = *G. flavomarginatus*

Group	Group					
	Mj	Sn	Si	<i>ber</i>	<i>poly</i>	<i>flavo</i>
Mj	0.00					
Sn	4.78	0.00				
Si	5.90	3.64	0.00			
<i>ber</i>	7.66	9.72	9.55	0.00		
<i>poly</i>	6.48	5.78	5.98	9.50	0.00	
<i>flavo</i>	8.81	8.97	8.95	10.09	8.51	0.00

TABLE 5.—Environmental and growth parameters for the four species of North American tortoises and for the three regions of the range of *Gopherus agassizii*. Data from Germano (1989). Species abbreviations are the same as in Table 2

Parameter	<i>agassizii</i>					
	<i>ber</i>	Mj	Sn	Si	<i>poly</i>	<i>flavo</i>
Environmental						
Annual precip. (mm)	674.6	136.2	249.4	545.0	1373.3	328.4
Winter precip. (mm)	136.2	56.0	51.4	55.2	239.4	21.3
Spring precip. (mm)	216.3	14.0	14.7	35.5	369.0	59.1
Summer precip. (mm)	233.3	32.5	138.8	378.8	508.2	205.5
Autumn precip. (mm)	128.9	36.4	47.2	76.1	224.4	42.5
Jan. vs. July precip. ^a	32.8	10.9	34.4	121.7	100.0	58.1
C.V. ^b annual precip.	0.297	0.561	0.339	0.245	0.178	0.389
Mean predictability	0.293	0.391	0.408	0.479	0.424	0.380
Mean constancy	0.131	0.272	0.204	0.226	0.275	0.153
Mean contingency	0.162	0.119	0.204	0.253	0.149	0.227
Mean July temp. (C)	29.3	30.2	32.2	31.1	27.4	26.2
Mean Jan. temp. (C)	11.6	7.7	9.9	16.3	13.5	9.5
Jan. vs. July temp. ^a	17.7	22.5	22.3	14.8	13.9	16.7
Geometric mean latitude ^c	26.23	34.89	32.07	27.32	29.38	26.44
Geometric mean longitude ^c	98.52	116.36	110.56	109.15	82.22	104.21
Growth						
Upper decile CL	202.9	262.5	270.5	274.0	292.1	367.6
Mean annuli width (mm)	1.54	1.82	1.57	1.41	1.68	3.01
C.V. ^b annuli width	0.555	0.555	0.445	0.415	0.561	0.601
Weighted mean growth rate	0.191	0.108	0.107	0.101	0.112	0.114
% Asymptote at inflection	26.3	36.7	35.6	39.7	39.5	41.6
Years from 10–90% asymptote	25.3	28.9	29.9	27.8	25.1	23.3
Age at first reprod. (yr)	13.3	14.9	15.7	13.8	14.4	13.9

^a Absolute difference in means

^b Coefficient of variation

^c Measured in degrees

G. flavomarginatus (Table 2). Although the revolute nature of the shell slightly decreases the relative length of the carapace of *G. berlandieri* along the midline, the overall reduction in proportionate measure compared to the other species does not substantially affect the use of CL as the standard for size. Another often-used standard for size is mass, but even for live animals, CL is a better standard than mass because mass can be greatly affected by the individual's level of hydration, nutritional state, female reproductive state, and amount of substrate ingested (*i.e.*, mineral-laden soil; *see* Esque and Peters, 1993).

Although I did not measure carapace flare along the marginals, I did find that *Gopherus berlandieri* and *G. agassizii* became wider towards the posterior portion of the carapace, *G. flavomarginatus* was nearly parallel, and *G. polyphemus* became narrower posteriorly. Aufenberg (1976) qualitatively assessed degree of shell flaring and found that flaring was best developed in *G. berlandieri* and *G. agassizii*, intermediate in *G. flavomarginatus*, and least developed in *G. polyphemus*. Also, the anterior portion of the plastron of *G. agassizii* is nearly flat compared to that of *G. polyphemus*, which is bent upward toward the carapace (True, 1882). Although I did not measure this character, I found that the shape of the plastron of

G. berlandieri is similar to that in *G. agassizii*, and the plastron of *G. flavomarginatus* is similar to that in *G. polyphemus*.

Besides differences in shell shape, skeletal differences exist between the *agassizii* (*Gopherus agassizii* and *G. berlandieri*) and the *polyphemus* (*G. polyphemus* and *G. flavomarginatus*) groups (Auffenberg, 1966, 1976; Bramble, 1982). *Gopherus polyphemus* and *G. flavomarginatus* have wider skulls, larger otoliths, shorter and thicker cervical vertebrae, and a wider manus with associated differences in carpal structure (Auffenberg, 1966, 1976; Bramble, 1982). These skeletal differences have been related to burrowing ability (Bramble, 1982). *Gopherus polyphemus* and *G. flavomarginatus* excavate long and extensive burrows (Auffenberg, 1969; Morafka, 1982), whereas *G. agassizii* and *G. berlandieri* generally excavate shallow burrows, although burrow length varies within the range of *G. agassizii* (Auffenberg, 1969; Woodbury and Hardy, 1948; Germano *et al.*, 1993). The extensive skeletal modifications for burrowing in *G. polyphemus* and *G. flavomarginatus* are useful in the friable and sandy soils in which these species occur (Bramble, 1982; Morafka, 1988), and the structurally more primitive manus of *G. agassizii* and *G. berlandieri* seems better suited to increased locomotion and digging in more resistant ground (Bramble, 1982).

Genetic data (Lamb *et al.*, 1989) support the conclusion that two species-groups exist within *Gopherus*, as originally determined based on skeletal differences (Auffenberg, 1976; Bramble, 1982). *Gopherus agassizii* and *G. berlandieri* have been placed in a separate genus by some authors (*Xerobates* in Bour and Dubois, 1984; Lamb *et al.*, 1989; *Scaptochelys* in Bramble, 1982). I have retained *Gopherus* for all four species, though, because they share numerous derived characters not found in other living species of tortoises, and *G. agassizii* and *G. berlandieri* are not sister taxa (Crumly, 1993). Based on the morphology of other tortoises of the world, it would be inconsistent to recognize *G. agassizii* and *G. berlandieri* as a separate genus (Crumly, 1993) or the separate populations of *agassizii* as separate species (Fig. 4).

The matrix based on shell morphology is not concordant with matrices based on phylogeny or precipitation and temperature variables. The shell morphology matrix does, however, significantly correlate with a matrix based on growth data, which is not surprising given the probable commonality of selective pressures affecting growth and shell morphology. Understanding the differences in morphology among closely related species can yield insight into their ecology. Shape is important in the ability of organisms to thermoregulate (Gould, 1966). Therefore, size and shape differences in North American tortoises may affect thermoregulatory ability, but more data are required on the thermoregulatory properties of shells of North American tortoises to determine if shell shape and size have been selected to meet various environmental pressures. The question remains open as to the selective advantage, if any, of size differences among adults for these four closely related species. However, it is apparent that morphometrics do not simply reflect genetic relatedness.

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APPENDIX 1

Acronyms and characters measured on tortoise shells

Acronym	Character	Acronym	Character
CL	Carapace length	C1	Costal 1 length
CW1	Carapace width 1	C2	Costal 2 length
CW2	Carapace width 2	C3	Costal 3 length
CW3	Carapace width 3	C4	Costal 4 length
CLCL	Curved-lined carapace length	M6	Sixth left marginal width
CLCW	Curved-lined carapace width	GL	Gular length
PL	Plastron length	GW	Gular width
MPL	Minimum plastron length	H	Humeral seam length
HS	Height of shell (greatest)	P	Pectoral seam length
N	Nuchal length	A	Abdominal seam length
V1	Vertebral 1 length	F	Femoral seam length
V2	Vertebral 2 length	AN	Anal seam length
V3	Vertebral 3 length	AL	Anal length
V4	Vertebral 4 length	AW	Anal width
V5	Vertebral 5 length	ATL	Anal tip length
SC	Supracaudal length	ATW	Anal tip width

APPENDIX 2

Correlations (sample sizes) of shell measurements with carapace length for North American tortoises including pooled within-group slopes used to scale measurements across groups

Character	Group						Slope
	<i>G. berlandieri</i>	<i>G. agassizii</i>			<i>G. polyphemus</i>	<i>G. flavo-marginatus</i>	
		Mojave	Sonoran	Sinaloan			
CW1	0.96 (83)	0.98 (128)	0.98 (58)	0.99 (36)	0.99 (76)	0.99 (95)	0.75
CW2	0.97 (91)	0.99 (161)	0.99 (78)	0.98 (42)	0.99 (89)	0.99 (96)	0.75
CW3	0.97 (82)	0.99 (129)	0.95 (54)	0.99 (36)	0.99 (76)	0.99 (96)	0.77
CLCL	0.99 (90)	0.99 (150)	0.99 (79)	0.99 (42)	0.99 (87)	0.99 (95)	1.31
CLCW	0.97 (90)	0.99 (152)	0.99 (77)	0.99 (42)	0.99 (88)	0.99 (94)	1.16
PL	0.96 (92)	0.99 (141)	0.99 (72)	0.99 (42)	0.99 (89)	0.99 (57)	1.03
MPL	0.97 (92)	0.99 (123)	0.99 (74)	0.99 (42)	0.99 (89)	0.99 (57)	0.93
HS	0.91 (73)	0.94 (138)	0.97 (68)	0.98 (29)	0.99 (45)	0.99 (52)	0.45
N	0.40 (80)	0.88 (130)	0.74 (57)	0.78 (40)	0.88 (77)	0.89 (93)	0.08
V1	0.94 (80)	0.99 (136)	0.96 (59)	0.97 (40)	0.98 (76)	0.99 (94)	0.20
V2	0.93 (81)	0.98 (136)	0.97 (58)	0.97 (42)	0.99 (76)	0.99 (91)	0.19
V3	0.93 (81)	0.96 (133)	0.97 (60)	0.97 (41)	0.98 (77)	0.99 (87)	0.19
V4	0.95 (80)	0.97 (133)	0.94 (59)	0.97 (39)	0.98 (77)	0.99 (76)	0.24
V5	0.94 (82)	0.97 (136)	0.94 (60)	0.95 (40)	0.97 (78)	0.98 (77)	0.26
SC	0.90 (82)	0.98 (130)	0.94 (59)	0.96 (43)	0.99 (78)	0.97 (93)	0.17
C1	0.95 (83)	0.99 (135)	0.96 (63)	0.98 (42)	0.99 (78)	0.98 (91)	0.23
C2	0.96 (83)	0.98 (159)	0.97 (81)	0.96 (43)	0.98 (78)	0.98 (93)	0.21
C3	0.96 (82)	0.99 (137)	0.98 (63)	0.98 (41)	0.99 (78)	0.99 (92)	0.21
C4	0.95 (82)	0.99 (137)	0.96 (63)	0.97 (41)	0.99 (78)	0.98 (89)	0.24
M6	0.92 (83)	0.98 (138)	0.95 (63)	0.90 (42)	0.97 (78)	0.94 (96)	0.14
GL	0.95 (90)	0.90 (149)	0.91 (71)	0.94 (41)	0.94 (85)	0.98 (57)	0.23
GW	0.89 (89)	0.94 (149)	0.91 (69)	0.90 (41)	0.97 (85)	0.96 (57)	0.17
H	0.85 (82)	0.98 (131)	0.91 (58)	0.96 (42)	0.96 (78)	0.98 (57)	0.21
P	0.55 (83)	0.83 (131)	0.77 (58)	0.78 (42)	0.85 (78)	0.94 (57)	0.12
A	0.89 (82)	0.98 (126)	0.96 (58)	0.95 (42)	0.98 (77)	0.97 (57)	0.29
F	0.87 (81)	0.96 (124)	0.91 (58)	0.92 (42)	0.96 (77)	0.97 (57)	0.15
AN	0.70 (81)	0.95 (122)	0.90 (57)	0.88 (40)	0.87 (78)	0.96 (56)	0.10
AL	0.93 (89)	0.97 (141)	0.94 (71)	0.96 (42)	0.97 (85)	0.98 (58)	0.18
AW	0.95 (88)	0.97 (138)	0.95 (65)	0.97 (42)	0.98 (85)	0.98 (57)	0.32
ATL	0.77 (86)	0.72 (110)	0.57 (49)	0.87 (40)	0.80 (82)	0.91 (57)	0.14
ATW	0.92 (85)	0.93 (110)	0.83 (48)	0.91 (42)	0.91 (81)	0.93 (57)	0.28